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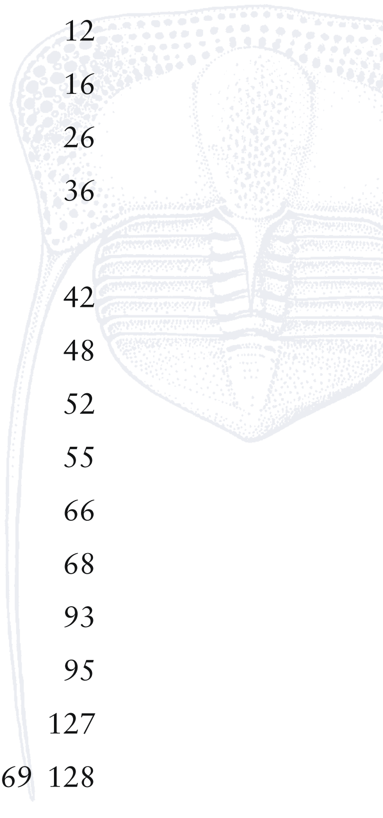
The Palaeontology Newsletter



Contents

From our correspondents

Reminder: The deadline for copy for Issue no 54 is 3rd October 2003

On the Web: **http://www.palass.org/**

Association Business

Nominations for Council

At the AGM in May 2004, the following vacancies will occur on Council:

President, Vice-President, Treasurer, Newsletter Editor

Nominations are now invited for these posts. Please note that each candidate must be proposed by at least two members of the Association and that any individual may not propose more than two candidates. Nomination must be accompanied by the candidate's written agreement to stand for election and a single sentence describing their interests.

All potential Council Members are asked to consider that:

'Each Council Member needs to be aware that, since the Palaeontological Association is a Registered Charity, in the eyes of the law he/she becomes a Trustee of that Charity. Under the terms of the Charities Act 1992, legal responsibility for the proper management of the Palaeontological Association lies with each Member of Council'.

The closing date for nominations is **Friday 26th September 2003**. They should be sent to the Secretary: Dr Howard A. Armstrong, Department of Earth Sciences, University of Durham, Durham DH1 3LE e-mail <**secretary@palass.org**>.

Council Members 2003-2004

President

Prof. D.E.G. Briggs, Department of Geology and Geophysics, Yale University, P.O. Box 208109, New Haven, CT 06520-8109, USA.

Vice-Presidents

Prof. D.A.T. Harper, Geologisk Museum, Københavns Universitet, Øster Voldgade 5-7, DK-1350 København K, Denmark.

Dr M.A. Purnell, Department of Geology, University of Leicester, University Road, Leicester LE1 7RH.

Treasurer

Prof. J. Hancock, Bleke House, Shaftesbury, East Dorset SP7 8QA.

Secretary

Dr H.A. Armstrong, Department of Geological Sciences, University of Durham, South Road, Durham DH1 3LE.

Newsletter Editor

Dr P.C.J. Donoghue, Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ.

Newsletter Reporter

Dr G. Budd, University of Uppsala, Department of Earth Sciences, Norbyvagen 22, Uppsala Se-752 36, Sweden.

Internet Officer

Dr J. Hilton, National Museums of Scotland, Chambers Street, Edinburgh EH1 1JF.

Publicity Officer

Dr P.L. Manning, The Yorkshire Museum, Museum Gardens, York YO1 7FR.

Editors

Dr P. Ahlberg, University of Uppsala, Department of Earth Sciences, Norbyvagen 22, Uppsala Se-752 36, Sweden.

Dr Lyall I. Anderson, Curator of Invertebrate Palaeontology, Dept. of Geology and Zoology, National Museums of Scotland, Edinburgh EH1 1JF, Scotland, UK.

Prof. E.N.K. Clarkson, Department of Geology & Geophysics, University of Edinburgh, West Mains Road, Edinburgh EH9 3JW.

Prof. Stephen K. Donovan, Department of Palaeontology, Nationaal Natuurhistorisch Museum, Postbus 9517, 2300 RA Leiden, The Netherlands.

Dr S.E. Evans, Department of Anatomy & Developmental Biology, University College London, Gower Street, London WC1E 6BT.

Dr E. Harper, Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ.

Dr P.D. Polly, School of Biological Sciences, Queen Mary College, University of London, London E1 4NS.

Dr C.H. Wellman, Centre for Palynology, University of Sheffield, Dainton Building, Brook Hill, Sheffield S3 7HF.

Ordinary Members

Dr M. Cusack, Division of Earth Sciences, University of Glasgow, Lilybank Gardens, Glasgow G12 8QQ.

Dr T. Servais, Univ des Sci et Tech de Lille, U.F.R. des Sciences de la Terre - SN5, UPRES A 8014, 59655 Villeneuve D'Ascq CEDEX, France.

SALARIED OFFICERS OF THE ASSOCIATION

Executive Officer

Dr T.J. Palmer, Institute of Geography & Earth Sciences, University of Wales Aberystwyth, Aberystwyth, Ceredigion SY23 3BD

Editor-in-Chief

Prof. D.J. Batten, Institute of Geography & Earth Sciences, University of Wales Aberystwyth, Aberystwyth, Ceredigion SY23 3BD

AGM 2003

The 46th Annual General Meeting of the Association was held on Wednesday 7th May 2003. Dr Smith extended a vote of thanks to the retiring members of Council, Dr Clack, Dr Gabbott, Dr Johnson, Dr Milsom, Dr Orr and Dr Sansom. Dr Purnell extended a vote of thanks to Dr Smith who was retiring as secretary and had completed ten years of service to Council.

New members of Council for the coming year are Dr Ahlberg (Editor) and Dr Anderson (Editor); Dr Purnell becomes a Vice President.

The following awards and prizes were announced:

Sylvester-Bradley Awards were made to: Broughton, Harrington, Hernandez Castillo, Gladwell, Joomun, Lane, Tetlie and Zuykov. This totalled £6,856. It was noted that the awards represented a wide range of international science from graduate students to established and recently retired academics.

Council are now investigating the possibility of reorganising the Association year so the AGM can be held during the Annual Christmas meeting.

Awards and Prizes

Sylvester-Bradley Award

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

Council will also consider awards in excess of £1,000. Typically these would aid pilot projects with an aim of supporting future applications to national research funding bodies.

Electronic submission of applications, through the website, is preferred and will comprise a CV, an account of research aims and objectives (5,000 characters maximum), and a breakdown of the proposed expenditure. Each application should be accompanied by the names of a personal and a scientific referee. Successful candidates must produce a report for *Palaeontology Newsletter* and are asked to consider the Association's meetings and publications as media for conveying the research results. **The deadline is 28th November 2003**.

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**. The award comprises a cash prize plus a framed scroll, and is usually presented at the Annual meeting.

Hodson Fund

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

Annual listing of PhD titles

The now annual list of palaeontology and palaeo-related PhD titles will be published in the next (Winter) issue of the *Newsletter*. If you are intending to offer a PhD project to begin October 2004, we would be grateful if you could submit these to the Newsletter <**newsletter@palass.org**> by the copy deadline, which is 3rd October 2003. Your email should include the project title, supervisors, and enquiry contact details including an email address for one of the supervisors. The listing will also be made available via the Association website. Remember that *Palaeontology Newsletter* gets sent to undergraduate winners of the Palaeontological Association Prize, which is for the best performance in palaeontology by an undergraduate student in their penultimate year of study. These students are, by definition, the very best palaeontologists in-the-making, so don't miss your opportunity to reach out to them!

Electronic access to *Palaeontology*

The password for accessing *Palaeontology* through Ingenta will change on 1st August 2003. Please note the instructions that follow. The password is the 13-letter word followed by two digits that appears following your name on the address label of the envelope that this newsletter was delivered in (or it can be obtained by sending an e-mail named 'password' to <**palass@palass.org**>).

1. Go to the Easylink URL <**http://www.ingenta.com/journals/browse/bpl/pala/**>
   (please note: **bpl** is lower-case L, not number 1)
2. Enter the username and password in the boxes at the bottom left of the screen:
   Username: palamember
   Password: *************##
3. Click the 'Enter' button below these boxes, then select the article you want from the contents lists.
4. Click 'Full Text' then click 'Download PDF'.

Please note that this service is a privilege to members and is only for personal use, so the username and password must not be disseminated to any other people. For details of free online access for subscribing institutions, please see the Blackwell website: <**http://www.blackwellpublishing.com/cservices/journal_online.asp**>

Sylvester-Bradley Award Recipients 2003

Julie Broughton
Department of Geological Sciences, University of California at Santa Barbara, USA
Palaeoclimate & palaeoecology of the Early Miocene Mohawk Valley Flora, northern Sierra Nevada (£936)

Genaro Hernandez Castillo
Edmonton, Alberta, Canada
Taxonomic reevaluation and systematics of primitive conifers from Euroamerica (£1,000)

David Gladwell
Department of Geology, University of Leicester, UK
Systematics of fossil starfish of Upper Silurian (Ludlow Series) age (£915)

Guy Harrington
Smithsonian Institution, Washington DC, USA
Spatial-Temporal characterization of subtropical vegetation change in the initial Eocene thermal maximum (£910)

Sarah Joomun
Department of Earth Sciences, University of Bristol, UK
Feeding biomechanics and trophic structure of Late Jurassic fishes (£645)

Phil Lane
Department of Earth Sciences & Geography, University of Keele, UK
The Silurian carbonate mound trilobite faunas of New South Wales (£1,000)

Odd Tetlie
Department of Earth Sciences, University of Bristol, UK
The genital appendage of Jaekelopterus rhenaniae *and implications for pterygotid phylogeny* (£450)

Michael Zuykov
Department of Palaeontology, St Petersburg State University, Russia
Brachiopods of the Family Porambonitidae from the Middle Ordovician of the East Baltic (£1,000)

See reports from previous years' Sylvester-Bradley Award recipients on page 68.

The deadline for the next round of Sylvester-Bradley Awards is 28th November (see page 4).

2004 changes in procedure for invoicing and payment by non-institutional members

We are making some changes that I hope will make the annual renewal cycle run more efficiently for all concerned.

Currently all members are asked to pay their annual Membership Dues using the coloured Membership Form which is distributed with the Autumn / Fall Newsletter. This works fine in many cases, but some members regard the extra sheets that are distributed with Newsletters as a pestilence, and discard them without further scrutiny. In future we will handle certain subscription renewals in a different way, in the hope that this will make it easier for members and myself. The procedure will henceforth be different for members in different parts of the world. We hope to have the new secure Credit Card payment system running by the end of this year, but Credit Card authorisations can still be made by mailing payment details to me in the usual way. Payments are due by 1st January. The late payment charge kicks in after January.

UK Members. Since most UK members look closely at the Newsletter, we will continue to send out Renewal Reminders (with the Personal Use disclaimer for signing) as previously, with the Autumn Newsletter. Please return the form with payment, in the usual way. The most economical way to pay is by cheque; card payments will attract an extra £1 levy to offset the charge made by the card company to the Association. You can fill in your bank details on the back of the form in order to set up a Standing Order; we will note the details and send the form on to your bank. We strongly encourage UK members to use this payment method, but in future we shall add a question to determine when Student Members expect to finish their courses. *N.B. The Republic of Ireland has not been part of the UK for nearly a century.*

Members in the geographic continent of Europe, including Eire and all of Russia. We will in future send a separate mailing to you in November, billing you in Euros. We shall also add a Pound Sterling figure for the few individuals who like to pay using a cheque drawn on a UK bank account. You may pay by Bank Draft in Sterling or Euros if you wish, but we would much prefer you to give authorisation for us to deduct your card, and we will not charge you extra for this. The amount deducted will be the Sterling equivalent of the Euro price on the day on which I process the payment.

In future we would like to keep your card details and use them again in the following November for the next year's subscription (and you will not receive a further invoice in such a case, until your card expires). We will of course give you the option of declining to use this scheme, in which case you will be billed again the following year as usual.

Members in the United States of America (but not Canada). We will in future send a separate mailing to you in November, billing you in US dollars. We shall also add a Pound Sterling figure for the few individuals who like to pay using a cheque drawn on a UK bank account. You may pay using a check drawn in US dollars as long as it is drawn on a bank in the USA. You may also give us an authorisation to deduct your Credit Card, and we will not charge you extra for this. The amount deducted will be the Sterling equivalent of the Dollar price on the day on which I process the payment.

In future we would like to keep your card details and use them again in the following November for the next year's subscription, as many of you have asked us to do (and you will not receive a further invoice in such a case, until your card expires). We will of course give you the option of declining to use this scheme, in which case you will be billed again the following year as usual.

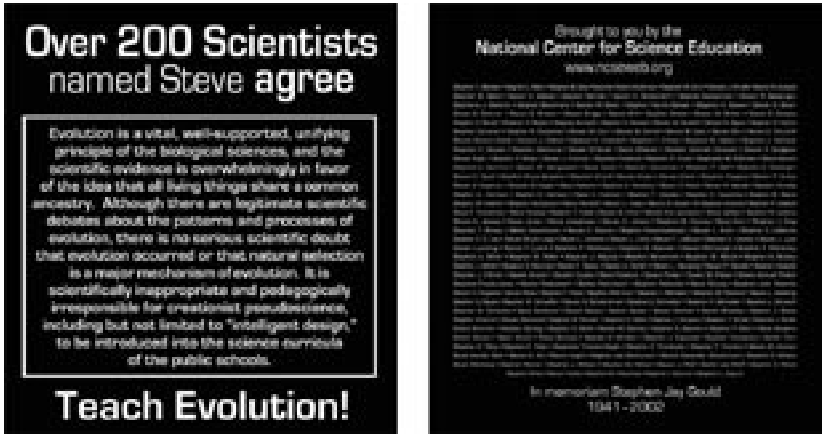
Members outside Europe (except the United States). We will in future send a separate mailing to you in November, billing you in US dollars. We shall also add a Pound Sterling figure for the few individuals who like to pay using a cheque drawn on a UK bank account. You may pay using a check drawn in US dollars as long as it is drawn on a bank in the USA, but we should prefer you to give us an authorisation to deduct your Credit Card, and we will not charge you extra for this. The amount deducted will be the Sterling equivalent of the Dollar price on the day on which I process the payment.

In future we would like to keep your card details and use them again in the following November for the next year's subscription, as many of you have asked us to do (and you will not receive a further invoice in such a case, until your card expires). We will of course give you the option of declining to use this scheme, in which case you will be billed again the following year as usual.

Tim Palmer
Executive Officer, Palaeontological Association

Calling all Steves

The *National Center for Science Education in America* has concocted an excellent retort to those creationist lists of 'scientists who doubt evolution'. After receiving too many emails asking if they could produce a list of those scientists who do accept evolutionary theory, they flinched, and decided to honour the late Stephen Jay Gould by producing one consisting entirely of scientists named Steve, and derivatives thereof (Stephan, Stephany, Etienne, etc). For more information, to buy the T-shirt (see below), and to sign up, visit <**http://www.ncseweb.org/**>.



NCSEA's T-shirt supporting the creationist-list parody.

Association Diary

2003	August	18-22	**Systematic Advances in the study of Human evolution** (PA-SA joint symposium) Organiser: Una Strand Vidarsdottir (Durham, UK) Location: 4th Systematics Association Biennial Meeting, Trinity College Dublin, Ireland. Contact: <**una.vidarsdottir@durham.ac.uk**>
	September	1	**Hodson Fund** closing date for nominations <**secretary@palass.org**>
		1	**Mary Anning Award** closing date for nominations <**secretary@palass.org**>
	October	3	**Copy deadline** for Newsletter 54
	October	3	**Deadline** for submission of PhD titles for the annual digest to be advertised in the Winter issue of the *Newsletter*.
	November	5-6	Review Seminar: **British Dinosaurs** Organisers: David Martill (Portsmouth, UK) & Martin Munt (Dinosaur Isle Location: Dinosaur Isle (Sandown) & Quay Arts Centre (Newport), Isle of Wight, UK. Contact: <**martin.munt@iow.gov.uk**> tel: +44(0)1983 404344
		26	**Sylvester-Bradley Awards** deadline for applications <**www.palass.org**>
	December	14-17	**2003 Annual Meeting** Organiser: Mark Purnell (Leicester, UK) Location: University of Leicester, UK. Contact: <**leicester2003@palass.org**>
		15	**2003 Annual Address** by Prof Mike Benton (Bristol, UK) *'Palaeontology and the future of life on Earth'.* Organiser: Mark Purnell (Leicester, UK) Location: University of Leicester, UK. Contact: <**map2@le.ac.uk**>

2004	February	10	**Copy deadline** for Newsletter 55
		11	**Lyell Meeting 2004**: Dinosaur Palaeobiology Organisers: Mike Benton (Bristol, UK) & Paul Barrett (NHM, UK) Location: The Geological Society, Burlington House, Piccadilly, London, UK. Contact: <**mike.benton@bristol.ac.uk**> <**p.barrett@nhm.ac.uk**>
	June		**Progressive Palaeontology 2004** Organiser: Location: Department of Earth Sciences, University of Cardiff, UK. Contact:
		25	**Copy deadline** for Newsletter 56
	August		**Stem groups and the establishment of vertebrate bodyplans** (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**>
	October	8	**Copy deadline** for Newsletter 57
	December	17-20	**2004 Annual Meeting** Organisers: Thomas Servais (Lille, France) Location: University of Lille, France. Contact: <**lille2004@palass.org**>
2005	Spring		**Lyell Meeting 2005: Applied Phylogeny** Organisers: Haydon Bailey & John Gregory Location: The Geological Society, Burlington House, Piccadilly, London, UK. Contact: <**haydonbailey@btconnect.com**>
	December	18-21	**2005 Annual Meeting** Organiser: Derek Siveter (Oxford, UK) Location: University of Oxford, UK. Contact: <**oxford2005@palass.org**>

ASSOCIATION MEETINGS

Annual Meeting of The Palaeontological Association
Department of Geology, University of Leicester *14 – 17 December 2003*

Announcement, Call for Abstracts and Registration

The 47th Annual Meeting of The Palaeontological Association will take place in the Department of Geology, University of Leicester. For the first time, registration, abstract submission and payment (by credit card) is by online forms at <**www.palass.org**> (if you wish to submit an abstract please prepare it, in MS Word or rtf file format, before using the forms; as part of the online submission process you will be asked to attach your abstract to a form). The **deadline for registration and abstract submission is 7th September 2003**. Registration (not abstract submission) may be possible after this date, but will incur a late payment charge.

Presentations on any aspect of palaeontology and evolutionary studies are welcome. Presentation options are 15 minute talk, 10 minute talk or poster. You will be asked to express a preference when you submit your abstract. Talks will be limited to one per speaker; poster sessions will be an integral part of the meeting. Overhead projector, slide projector, media projector and computer facilities will be available. For PowerPoint presentations, we will require a file on CD or zip-disk at least one day in advance. Guidelines for abstract content and formatting, and an MS Word template, are available at: <**http://www.palass.org/forms/AnnualAbsGuide.html**>.

Outline Programme

Sunday, 14th December:	afternoon seminar, Stem Groups – *Fossils, Origins and the Evolution of Body Plans* (see list of speakers below)
Monday, 15th December:	scientific sessions, followed by: Annual Address, “Palaeontology and the future of life on Earth”, by Mike Benton *(see page 13)* Annual Dinner, Beaumont Hall
Tuesday 16th December:	scientific sessions
Wednesday 17th December:	Field Excursion: The Precambrian Biota of Charnwood Forest

Further details of social events, the scientific programme and the field excursion will be available from the Association’s website at <**http://www.palass.org/**> as they become available.

Venue, Accommodation and Travel

Leicester is centrally located in England and is easily accessible by road or rail, with good links to international airports. For maps and details of routes to Leicester go to <**http://www.le.ac.uk/maps/maps.html**>. For overseas participants, Birmingham and East Midlands airports are within an hour of Leicester. There are direct trains from Stansted Airport (many budget flights from European countries fly into Stansted), and London (a little over one hour from St Pancras Station).

Technical sessions will take place on the main University Campus, in Bennett Building lecture theatres adjacent to the Department of Geology. Posters will be displayed in the large foyer areas outside the lecture theatres. Tea, coffee and lunch will also be served here.

Accommodation will be in Beaumont Hall, situated in landscaped grounds in Oadby, 3.5 km from the University Campus. Buses will be provided to transport participants to and from the University Campus at the beginning and end of each day; a scheduled bus service runs throughout the day.

Seminar: Stem Groups – Fossils, Origins and the Evolution of Body Plans

Sunday December 14 December 2003 (Part of the Annual Meeting, University of Leicester, UK)

This afternoon of thematic talks and discussion will explore what is perhaps palaeontology’s most important contribution to current evolutionary research: the nature of stem groups and their role in understanding the origins of major extant clades. It will address questions such as: What are stem groups? Why are they important? What have they got to do with Palaeontology?

The seminar will highlight the importance of stem groups in understanding the origins of extant phyla: without them we cannot hope to reconstruct the sequence and timing of character acquisition during the assembly of body plans, or have clear systematic criteria for recognising the true origins of clades. Only palaeontology can provide these crucial data, yet the value of stem groups is not appreciated by many active palaeontologists, and misconceptions about the definition of stem groups and their significance are commonplace.

Speakers and Provisional titles:

- Graham Budd, Uppsala University, *The search for stem groups in the Cambrian, and the origin of the phyla*;
- Mike Coates, University of Chicago, *Assembling a tetrapod body plan: definition, slippage & stems*;
- Else Marie Friis, NRM, Stockholm, *Stem groups and angiosperm origins*;
- Paul Kenrick, NHM, London, *Land plant origins: body-building from scratch*;
- Philip Donoghue, University of Bristol, *Stem groups, the fossil record and molecular dates for the origins of major clades*;
- David Unwin, Humbolt Museum, Berlin, *The origin of birds, feathers and flight: have stem groups solved the problem?*

Attendance at the seminar is free to conference participants, but only if booked in advance. Please do not turn up on the day without informing the organisers.

The Palaeontological Association runs a travel grant programme to assist overseas palaeontologists presenting talks or posters at the Annual Meeting. For the Leicester meeting, grants of up to £100 are available to registered full-time students whose presentations are accepted and who are travelling from outside the UK. Payment of these awards is given as a disbursement at the meeting, not as an advance payment. Students interested in applying for a Palass travel grant should contact the Executive Officer of the Palaeontological Association, Dr Tim Palmer, by e-mail to <**palass@palass.org**>.

Deadline for registration and abstract submission: 7th September 2003

Local secretary: Mark Purnell
Department of Geology, University of Leicester
University Road
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+44 (0)116 252 3645 (tel)
+44 (0)116 252 3918 (fax)
<**Leicester2003@palass.org**>

2003 Annual Address to the Palaeontological Association
University of Leicester *15 December 2003*

Professor Mike Benton

Department of Earth Sciences, University of Bristol, UK

'Palaeontology and the future of life on Earth'

Abstract

Palaeontology is the study of the life of the past. People are naturally concerned about what will happen to life in the future. Questions about how life diversifies, and how extinction events happen are so big that the best source of comparative information comes from study of the fossil record. Many topics are debated in quantitative palaeobiology at present: how does life diversify?; is the fossil record good enough to tell us much about the history of life?; why do molecular methods often give different results from morphological?; what kind of catastrophe are humans causing right now?

Lyell Meeting 2004: Dinosaur Palaeobiology
London *11 February 2004*

A Lyell Meeting to explore the latest in scientific understanding of the dominant animals of the Mesozoic. How did they become so large? How did dinosaurs move? How diverse were they? What did they eat? Were they warm-blooded or not? Were the images in *Walking with Dinosaurs* realistic or not? How was their evolution affected by Mesozoic palaeogeography?

This is a call for contributions on these, and related topics. Send proposals to the organizers, Professor Michael J. Benton (University of Bristol <mike.benton@bristol.ac.uk>) or Dr Paul Barrett (Natural History Museum, London <p.barrett@nhm.ac.uk>).

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**>) and John Gregory (Kronos Consulting, 33 Royston Road, St Albans, Hertfordshire AL1 5NF <**john@jgregory.demon.co.uk**>)

>>*Future* Meetings of Other Bodies

GSA Annual Meeting
Washington Convention & Trade Centre, Seattle, USA *2 – 5 September 2003*

Symposia sponsored by the Paleontological Society:

P2 His view of life: reflections on the scientific legacy of Stephen J. Gould (Warren D. Allmon, Patricia Kelley, Robert M. Ross);

T85 Signs of life: the role of palaeobiology in the history of evolutionary theory and our attempts to understand the changing nature of the biosphere (Roger D.K. Thomas, Gary D. Rosenberg);

T86 Fossil decapod crustacean palaeobiogeography, systematics, and evolution over the past 20 years: in honour of Ross and Marion Berglund (Elizabeth Nesbitt, Torrey G. Nyborg);

T87 Palaeo-Plant Ecophysiology (Dana L. Royer, Christopher J. Williams);

T88 The hunt for Precambrian life: an integrated approach (David J. Bottjer, J. William Schopf);

T89 Evolutionary and ecological links between terrestrial and marine ecosystems in the Phanerozoic (Wolfgang Kiessling, Allister Rees);

T90 Terrestrial palaeobiology of South America, Cretaceous through Neogene (Peter Wilf, Robyn J. Burnham, Maria A. Gandolfo, Kirk R. Johnson);

T91 Understanding Late Devonian biotic, climatic, and oceanographic events: toward an integrated approach (Jared R. Morrow, Paul B. Wignall, D. Jeffrey Over);

T92 Advances in the fossil record of insects and other terrestrial arthropods (Cary Easterday, Conrad Labandeira);

T93 Micropalaeontological proxies of ocean gateway palaeoceanography (Stephen A. Nathan, R. Mark Leckie);

T94 Bridging the gap: ostracodes in the Earth Sciences (Gene Hunt, Lisa E. Park).

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

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

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

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

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

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

For information please contact: Dr Andrew C. Kerr, Department of Earth Sciences, Cardiff University, Main Building, Park Place, Cardiff, Wales, UK CF10 3YE (tel +44 (0) 29 2087 4578; fax +44 (0) 29 2087 4326; e-mail <**kerra@cf.ac.uk**>). The meeting website is <**http://www.earth.cf.ac.uk/news/kerr_meeting.htm**>.

Bivalves – Open Meeting
Gonville & Caius College, Cambridge University, UK *15 – 16 September 2003*

This is planned as an open meeting to present papers covering a wide variety of bivalve-related topics both biological and palaeontological. A dinner will be held on the 15th to celebrate the lifetime's contribution to malacology made by Professor Brian Morton. If you are interested in attending please contact Liz Harper <**emh21@cam.ac.uk**>.

51st Symposium of Vertebrate Palaeontology and Comparative Anatomy
Oxford University Museum of Natural History, UK *17 – 19 September 2003*

For further details visit the Symposium website at <**http://www.svpca.org/2003/**>.

The Rhynie Hot Spring System: Geology, Biota and Mineralisation

Aberdeen, Scotland *17 – 20 September 2003*

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

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

8th International Symposium on Fossil Algae

Granada, Spain *18 – 20 September 2003*

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

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

18–20 September: Sessions, Granada.

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

The Pre-Symposium Field Excursion will focus on Cretaceous and modern Charales and Cretaceous dasycladaleans. Leaders: Bruno Granier and Carles Martin-Closas. The Post-Symposium Field Excursion will be devoted to Miocene microbial carbonates and Halimeda bioherms, and Pliocene coralline red algae. Leaders: Julio Aguirre, Juan C. Braga, Jose M. Martin and Robert Riding.

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

Evolution and Development UK 2003

King's Buildings, University of Edinburgh, Scotland *22 September 2003*

Six of the seven speakers have so far been confirmed:

Anthony Graham (King's, London): *Vertebrate head development and evolution*.

Wallace Arthur (Sunderland): *Effect of development on the direction of evolution*.

Wim Damen (Cologne): *Spider segmentation*.

Ralf Sommer (Tubingen): *Nematode evolution*.

Arial Chipman (Cambridge): *Arthropod segmentation evolution*.

Francois Mazet (Reading): *Ciona and the evolution of sense organs*.

The meeting will cost £10 registration. All enquiries to <**habib.maroon@kcl.ac.uk**> or <**mark.blaxter@ed.ac.uk**>.

2003 European Palaeontological Association (EPA) Workshop on Exceptional Preservation

Fundación Conjunto Paleontológico de Teruel, Spain *24 – 27 September 2003*

Keynote presentations will be given by invited speakers; all interested people are welcome to present posters (poster discussion is included in the programme). The programme of events is as follows:

24.09: i) Meeting at the Museo Nacional de Ciencias Naturales, Madrid (CSIC), with an opportunity to examine the collections of exceptionally preserved fossils held by the Museum.
Lunch.
Travel to Teruel;
ii) Meeting at the Palacio de Exposiciones, Teruel.
Visit to Dinopolis.

25.09: Keynote presentations, poster sessions, opening ceremony, EPA General Assembly.

26.09: Keynote presentations, poster sessions, closing ceremony.

27.09: Excursion to Teruel continental Miocene sites with exceptionally preserved fossils.

All interested people are kindly requested to contact the General Secretary, Luis Alcalá (Fundación Conjunto Paleontológico de Teruel, Avda. Sagunto s/n (Edificio Dinópolis), E-44002 Teruel (Spain); tel 34 978 61 76 30; fax 34 978 61 76 38; e-mail <**alcala@dinopolis.com**>; Web <**http://www.dinopolis.com/**>. Accommodation can be booked via Viajes Tivoli (tel 34 976 20 03 68; fax 34 976 20 14 04; e-mail <**congresos.citerea@mapfre.com**>).

AASP 2003

Niagara Peninsula, Canada *5 – 8 October 2003*

This is a joint meeting of the American Association of Stratigraphic Palynologists, the Canadian Association of Palynologists, and the North American Micropaleontological Section of SEPM, and will include the following symposia: Micropalaeontology and Palynology of the Atlantic and Gulf Coastal Plains of North America; Land-Sea Correlation in the Quaternary / Cenozoic; Great Lakes Palynology, Palaeoecology & Archaeology; Origins and Evolution of Microfossils: links between evolutionary history and palaeoenvironmental changes; Micropalaeontological Applications in Geoarchaeological Studies; Pragmatic Palynology; Micropalaeontological and Palynological Applications in Ecology and Palaeoecology.

For further details contact Francine McCarthy <**francine@craton.geol.brocku.ca**> or Kevin Gostlin <**gostlin@geology.utoronto.ca**>, or visit the conference website at <**http://www.geology.utoronto.ca/aasp2003/**>

63rd Annual Meeting of the Society of Vertebrate Paleontology

Radison Riverfront Hotel, St. Paul, Minnesota, USA *15 – 18 October 2003*

This year's meeting includes the following symposia: High-latitude Mesozoic and Cenozoic vertebrates: Evolution, palaeoclimate and palaeogeography (Case and Jaelyn Eberle); Biomineralization: Patterns, processes, and analysis of modern and fossil vertebrate skeletal tissues (Mark B. Goodwin and Sandra J. Carlson); Evolutionary transitions among vertebrates: A symposium in honour of Robert L. Carroll (Jason S. Anderson and Hans-Dieter Sues); Preparators Symposium.

There are also two field trips associated with the meeting: Minnesota's north shore – The Iron Range, World-class stromatolites, a failed rift, and wolves (12–14 October); Vertebrate palaeontology of the High Plains – The Late Mesozoic/Cenozoic record of North Dakota (12–14 October). Further details of the meeting can be obtained from <**http://www.vertpaleo.org/**>.

First International Conference on Palaeontology of Southeast Asia (ICPSEA)

Mahasarakham University, Thailand *27 – 30 October 2003*

For further details visit the conference website at <**http://www.msu.ac.th/bpc/index.html**>.

The Measurement and Origin of Biodiversity

Dunedin, New Zealand *5 December 2003*

A one-day meeting to be held in association with the Australasian Association of Paleontologists / Geological Society of New Zealand annual conference. Understanding the origin, history and controls of biodiversity remains one of the primary goals of paleontology and biology. The measurement and interpretation of biodiversity data, however, is fraught with problems. In this meeting we will bring together paleontologists and biologists to explore some of the perplexing questions surrounding biodiversity. Using New Zealand and global examples of living and fossil clades, we will examine topics such as species-area effects, onshore-offshore diversity gradients in the marine realm, latitudinal gradients, and distortions of the paleobiodiversity record related to preservational biases. The meeting has been scheduled to allow attendees to also participate in field trips associated with the Geological Society of New Zealand conference. Some of these trips will have a paleontological focus.

For further details contact <**j.crampton@gns.cri.nz**>.

26th Nordic Geological Winter Meeting

Uppsala, Sweden *6 – 9 January 2004*

We invite talks and posters for the following session at the Nordic Winter Meeting in Uppsala: Session 15. Late Precambrian – Early Palaeozoic biotas: origins, diversifications and extinctions, organized by Lars E. Holmer and David A.T. Harper.

The late Precambrian – Early Palaeozoic was a critical and exciting interval in the history of life on Earth. During a period of some 750 million years a range of metazoan phyla originated, diversified and suffered at least two major extinctions against a background of dramatic climatic changes. These key biotic events set the agenda for much of marine life on the planet. This multidisciplinary session aims to combine phylogenetic and taxonomic data together with the ecological and environmental aspects of these events. We hope to attract a diversity of contributions ranging from analyses of the fossil record to the interpretation of changing geochemical signals through this important interval. Further details of the meeting are to be found on <**http://www-conference.slu.se/nordgeo/**>. The deadline for abstracts is 10th September 2003.

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**>.

International field seminar

Kerman, Iran *14 – 18 April 2004*

Iran has a rich and varied geology, but much of it remains little-known outside the country. In Kerman Province (east-central Iran) there are especially well exposed and extensive sequences of Cambrian-Ordovician-Silurian-Devonian rocks, Jurassic-Cretaceous sediments, and Cenozoic rocks including sediments, metamorphic complexes and extensive volcanics. This notice is the first announcement of plans to hold a field-based seminar programme centred at the University of Shahid Bahonar, Kerman City. Estimated costs are US $950 to include registration, accommodation, all meals and field transportation (students US $600). Day 1: Introductory lectures on the geology of Iran. Days 2,3,4,5: Fieldwork covering four separate themes (Lower Palaeozoic-Devonian stratigraphy and faunas; Jurassic-Cretaceous geology and faunas; Cenozoic sediments, volcanics and structure; Economic geology including ore mineralogy and regional metamorphism). Each theme will run separately over the full four days of fieldwork, with co-ordination and guidance by local experts. For further details contact either Assoc. Prof. Mohammad Dastanpour (Department of Geology, Shahid Bahonar University, P O Box 76169-133, Kerman, Iran, Fax: [+] 98 341 2267 681, <**dastanpour@mailuk.ac.ir**>), or Prof. Michael G. Bassett (Department of Geology, National Museum of Wales, Cardiff, CF10 3NP, Wales, U.K. Fax: [+] 44 2920 667 332, e-mail <**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 that works on biomechanical interpretation of extant or fossil organisms? Will an anthropologist contribution on human faeces or footprints be welcomed? Could a zoologist working on bioerosion or benthic bioturbation contribute to this meeting? The answer to all these questions is YES, and we wish further to extend the invitation to petroleum geologists/engineers, wildlife biologists, reef biologists, trackers, entomologists, and any other scientist working on Ichnology-related issues.

The meeting will be held at the Museo Paleontológico Egidio Feruglio (MEF), located at the city of Trelew, in the Argentine Patagonia. The MEF is a modern Museum engaged in research and educational activities essentially related to the rich 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 – 28th 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**>.

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**>), and on the Congress website at <**http://www.11ipc.org/**>.

Computer techniques in the modelling and analysis of biological form, growth and evolution
Firenze, Italy *22 – 28 August 2004*

The 32nd International Geological Congress will take place in Firenze, Italy, in August 2004. The first circular is available on-line on the Congress website, at <**http://www.32igc.org/home.htm**>. The first of the general symposia planned in section G17 (Palaeontology) is entitled "Computer techniques in the modelling and analysis of biological form, growth and evolution". Organisers are Enrico Savazzi (Uppsala University <**enrico.savazzi@pal.uu.se**>) and Richard A. Reyment (Swedish Museum of Natural History <**richard.reyment@pal.uu.se**>). The symposium 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. We encourage the submission of volunteered abstracts and expressions of interest in participating by other scientists. Submission of abstracts by invited and volunteering speakers and/or poster proposers should meet the deadline in late November, 2003.

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. Contact the organizers (Savazzi and Reyment) for more information.

Chemosynthetic communities through time. This is session T-18.4 within the Topical Symposium: T -18 “Geosphere-Biosphere Interactions” at the 32nd International Geological Congress, Florence, 2004. The aim of the 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**>), Roberto Barbieri (<**barbieri@geomin.unibo.it**>) and Kathy Campbell (<**ka.campbell@auckland.ac.nz**>). 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).

The second circular for the 32nd IGC is on the Web <**http://www.32igc.org/home.htm**>. This lists registation 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**>.

The Organizing Committee will help individual scientists mainly from developing and East-European Countries to attend the Congress by partially subsidising their expenses via the GeoHost Programme; see <**http://www.32igc.org/circular-gen07.htm**>.

>>*Future* Meetings of Other Bodies

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 Mikulá, Institute of Geology, Czech Academy of Sciences, Rozvojová 135, CZ–165 00 Praha 6; e-mail <**mikulas@gli.cas.cz**>.

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

Meeting REPORTS

Sixth International Congress on Rudists
Rovinj, Croatia *29 September – 5 October 2002*

Since their inception in Belgrade in 1988, the international rudist meetings have succeeded in assembling most of the world's devotees of these engagingly baroque fossil bivalves. This latest meeting, held in the scenic old town of Rovinj in Istria (the peninsula that juts out into the northern end of the Adriatic), was no exception, fully living up to its 'international' billing. At least seventeen nations were represented, by just over fifty participants, ranging from Mexico to Japan and from Germany to Saudi Arabia, though, as might be expected, with a preponderance of folk from the Mediterranean countries.

In established tradition, the Congress celebrated the memory of the region's foremost rudistologist. This time it was the turn of Ante Polšak (1930–1990), whose seminal studies of Istrian rudists made a major contribution to rudist biostratigraphy in general, as well as providing the stratigraphical basis for work in the region today.

The 27 oral and 20 poster presentations given at the meeting, together with a few further abstracts submitted by those who were unable to attend, covered a wide diversity of topics. I will treat the contributions under five thematic headings, mentioning just a few highlights to convey a sense of that variety.

(1) Systematics and evolutionary patterns

Modern approaches to the low level taxonomy of rudists are (at last!) beginning to take root, with increasing emphasis on the morphometric discrimination of inherently variable populations. This certainly involves more work per publication than the mere typological naming of every slight variant (a habit that is, alas, not entirely extinct), but it does offer the promise of getting closer to the real biological species, hence the foundations for any serious palaeoecological or evolutionary analysis.

Group photo of (most of) the world's rudistologists

Examples presented at the meeting covered the rudists' stratigraphical spectrum, from the Upper Jurassic to the Upper Cretaceous. Especially memorable was the report from **Dietrich Schumann** (Darmstadt) on his haul of spectacular specimens of *Torreites* from southern Oman – beautifully illustrated, as always. This genus has a curiously disjunct distribution. Besides Arabia, it has also long been known from the Caribbean region, where it has nevertheless only ever been found in small numbers. On account of its strange distribution, as well as an aberrant morphology (even by rudist standards), for many years it enjoyed the accolade, usually accorded only to dinosaurs and the like, of being the subject of more papers than there were known specimens. However, Schumann has found it to be very abundant at certain horizons in Arabia, allowing him a good insight into its variability, which strongly reflects the constraints of individual growth attitude and accommodation to neighbours. It was also gratifying to see **Simon Mitchell** (Kingston, Jamaica) tackling the wild jungle of the smaller Upper Cretaceous Jamaican radiolitids, while **Tvrtko Korbar** and **Ivan Guši** (Zagreb) did battle with the *Praeradiolites* of Bra Island, both using a similar approach. All good, solid, much-needed, taxonomic gardening.

(2) Palaeoecology

Recent critiques of the text-book caricature of rudists as 'reef-builders' has led to a fruitful proliferation of studies aimed at elucidating what their palaeoecology really was like. The richly illustrated poster of **Gabriele Carannante** and colleagues from the 'Neapolitan school' demonstrated the relationship between various kinds of rudist lithosome in the Upper Cretaceous of southern Italy and their original hydrodynamic setting on unrimmed, channellised shelves. In a more quantitative vein, **Jean-Pierre Masse** and **Muguet Fenerci-Masse** (Marseille) combined volumetric estimates of carbonate in Upper Barremian rudist beds in SE France with the time-scales of the Milankovitch cyclicity considered to have yielded them, to calculate ky-scale rates of carbonate production.

Intriguing results also came from smaller scales of observation. **Tvrtko Korbar** and **Vlado Jelaska** (Zagreb) documented preferred life orientations in radiolitids that suggest entrainment of the radial bands with respect to ambient currents. **Stefan Götz** and colleagues from Karlsruhe built up a breathtakingly detailed 3D computer image of individual settlement and growth within a hippuritid cluster, based on closely spaced serial section-grinding. In this instance they found no relationship between available settlement space and juvenile survival, but they did detect a correlation between number of co-eval settlers and later survivorship, suggesting a predominant competitive control on eventual cluster density. They also found a strong hint of annual (seasonal) spatfalls. Meanwhile, **Iván Regidor-Higuera** and colleagues from Bilbao presented an exquisitely well resolved sclerochronological study of radiolitid shells. Such careful, highly detailed studies of rudist settlement, survivorship and growth promise fascinating insights into their palaeoautecology. They will also provide much-needed quantitative data on the contribution of rudists to the sedimentary budget of Cretaceous carbonate platforms.

(3) Geochemical investigations

Geochemical analyses of rudist shells, especially of their isotopic compositions – a field in which, incidentally, Ante Polšak was also a pioneer – have provided many valuable new data in recent years. Topics addressed at Rovinj ranged from correlation based on strontium-isotope ratios (**Riccardo Cestari**, AGIP, Ravenna; **Thomas Steuber**, Bochum) to diagenetic effects (**Regidor-Higuera** *et al*.; **Ahmed Mansour**, Alexandria), thus proving the value of isotopes from the stratigraphical to the petrographical scales of investigation.

The Cenomanian clinoforms of Frasker Island

(4) Biostratigraphy and Palaeobiogeography

Studies of the rudists themselves, as described above, were well balanced by those of their distribution in time and space, and the implications of such patterns. Naturally, it was here that the broad international scope of current rudist research was most evident, with descriptions of faunas from nearly every corner of the rudists' empire. Besides the chemostratigraphical correlations mentioned above, useful progress is being made in the biostratigraphy of rudist limestones through the integration of different taxa. A notable project in this respect is that of **Bob Scott** (Cleveland, Oklahoma), who reported on continuing progress with his massive graphic correlation scheme for the Barremian-Turonian, which now integrates 1,800 taxa, as well as geochemical event-, magnetochron- and sequence stratigraphical levels. **Sacit Özer** (Bornova-Izmir) also deserves a medal for his patient retrieval of cryptic stratigraphical information from marbles in the Menderes Massif of SW Turkey, where rocks that were formerly considered Permo-Carboniferous now turn out to be Upper Cretaceous, based mainly on the identification of hippuritid rudists.

(5) Miscellaneous

A few presentations dealt with yet other issues. **Ann Molineux** (Austin, Texas) explained how modern curatorial methods are being applied at the Texas Memorial Museum of Science and History, where a number of important rudist collections are housed, with on-line access to the data-base and specimen illustrations a major objective. It was heartening to see this essential work being properly supported. Too often, museum collections – the 'family silver' of palaeontology – lose out to high-profile (and big-appetite!) machine-based science in the funding game. Also in pursuit of maximising data-retrieval, **Wyn Hughes**, with colleagues from Saudi Aramco, demonstrated how computer tomography and Formation Microscanner Imaging can reveal the distribution and orientations of specimens in unslabbed cores and uncored wells, respectively. These non-destructive methods will make it much easier than before to map out distinct associations (*e.g.* elevator-, or recumbent-dominated) in the sub-surface. Finally, **Mileva Sladi-Trifunovi** (Belgrade) looked back over the preceding international rudist meetings by way of a build-up to announcing the long-awaited publication of the proceedings from the first meeting, in 1988. A few honoured delegates received their copies there and then from the small supply that she had been able to bring with her. The rest of us eagerly await ours.

Other aspects

The meeting was conveniently held in the well-appointed hotel where delegates were accommodated, and our Croatian hosts on the organizing committee did an excellent job of ensuring flawless multimedia projection facilities. Delegates also enjoyed several lively social gatherings, the highlight of which was the conference dinner, held in a rustic village setting. There, we were greeted by a display of traditional dances and treated to a wonderful meal of local produce, finishing up with the now also traditional home-grown *eisteddfod* (for some curious reason, rudist researchers seem to be an unusually musical, even operatic lot!).

Those who were fortunate enough to be able to stay on after the meeting enjoyed a dream field-trip around this virtual paradise of rudist limestones, in superb weather, and guided by the richly informative field-guide edited by (the seemingly ubiquitous) **Igor Vlahovi** and **Tvrtko Korbar**. The highlight was a boat trip that provided us with both spectacular views of clinoforms of rudist debris filling in a Cenomanian intra-platform depression, along the coast of Frašker Island, and a landing on Fenoliga Islet, where we were able to see a trail of dinosaur footprints right across the top of a rudist biostrome! Needless to say, our Croatian hosts also saw to it that we were treated to a variety of local culinary delights along the way.

In all respects, then, the meeting was a great success, for which the Croatian organizing team deserves the congratulations of the rudistological community. The next international rudist meeting is to be held in Austin, Texas, in 2005, convened by **Bob Scott** <**rwscott@ix.netcom.com**> and **Ann Molineux** <**annm@mail.utexas.edu**>. And of course, in Texas the rudists are, well…. So, if you have the slightest affinity for them, you won't want to miss it.

Peter Skelton
Open University, Milton Keynes, UK
<P.W.Skelton@open.ac.uk>

'Walking with dinosaurs', on Fenoliga Islet

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

Geological Society, London 24 February 2003

The annual Lyell Meeting, sponsored by the British Joint Committee for Palaeontology to foster exchange of ideas and research information between fields in actualistic geology such as palaeontology, sedimentology and stratigraphy, this year focused on recent advances in applied ichnology. Generous sponsorship by international oil companies enabled an impressive programme of ten speakers from eight counties and six posters to be presented to 80 participants with excellent organisation by Duncan McIlroy and Geological Society staff. About a half of the audience was from universities, staff and postgraduate students, and museums, research institutes and the oil industry.

The meeting opened with a review by McIlroy and Taylor of relevant trace fossil concepts, including ichnofacies, ichnostratigraphy and bioturbation analysis, recent developments of ichnofabric analysis and sequence stratigraphy, and suggestions for new frontiers in integration of many disciplines, new technologies and experimental studies. The importance of establishing genetic stratigraphic sequences was stressed by George Pemberton in a worldwide review of the application of substrate specific ichnofacies to oilfield problems and supremacy claimed for rocks and trace fossils over "squiggly lines on paper" (geophysics?)!

The remaining talks and posters fitted well into the themes of the meeting. The ichnology of major depositional environments was covered from palaeosols (Genise *et al.*), estuaries and tidal flats (Mangano & Buatois ; McIlroy), deltas (Bann & Fielding), clastic shorefaces (Bann *et al.*; Schlirf), hardgrounds (Bromley), to deep sea (Uchman). Many of these case histories demonstrated the value of trace fossils for high resolution palaeoenvironmental analysis including possible climatic (latitudinal) zoning of crustacean and echinoid burrows, recent and fossil (Goldring *et al.*).

Problems of using trace fossils for true time stratigraphy 'ichnostratigraphy' were discussed for Neoproterozoic–Cambrian of Norway (McIlroy), Cambrian transgression in Grand Canyon (Baldwin & Strother), relationship of *Cruziana* to mixed layer development and substrate firmness (Droser *et al.*), identificaton of extinction and recovery ichnofaunas (Twitchett & Barras) and evolution of deep-sea graphoglyptids (Uchman). The only contribution to the meeting on vertebrate ichnology was from Phil Manning who showed from experimental laboratory studies the importance of preservation analysis to the palaeoenvironmental and palaeobiological interpretation of trackways. Richard Bromley presented us with a masterly illustrated overview of diverse borings of many ages, leaving the detailed stratigraphic documentation to the published paper.

The final theme, the use of ichnology in sequence stratigraphy, was well covered for both substrate related ichnofacies (Pemberton) and recognition of key stratal surfaces and ichnofabrics (Bann *et al.*; McIlroy & Taylor; Schlirf). In his concluding remarks to this highly successful meeting John Pollard drew attention to palaeoenvironmental and stratigraphic references to trace fossils by Charles Lyell in his writings, particularly how his description of the famous marine bivalve bored marble pillars of the Roman temple at Puzzuoli in Italy, anticipated the link between *Trypanites* ichnofacies and sea level change by more than a hundred years!

The authors and titles of papers and posters are listed below with further details in Bibliographica Ichnologia 2003 in Ichnology Newsletter 25, in McIlroy, D. (ed.) *The Lyell Meeting 2003, Application of Ichnology to Palaeoenvironmental and Stratigraphical Analysis.* Abstract volume, 24pp. (unpaginated). Geological Society, London, and in forthcoming Geological Society Special Publication (in press).

Programme

BALDWIN, C. and STROTHER, P. Traces and spores from the base of the Sauk transgression in the Grand Canyon (Tapeats Sandstone-Bright Angel Shale- Mauve Limestone). (Poster)

BANN, K. L. and FIELDING, C. R. Ichnological distinction between non-deltaic shoreface and delta front facies : examples from Permian reservoirs of Eastern Australia.

——, TYE, S. C. and FIELDING, C. R. Ichnofacies analysis and high-resolution sequence stratigraphy of a complex coastal and shallow marine succession, the Early Permian Pebbley Beach Formation, Sydney Basin, Australia. (Poster)

BROMLEY, R. G. A stratigraphy of borers and borings

DROSER, M. L., JENSEN, S. and GEHLING, J. G. Development of the early Palaeozoic mixed layer: implication of event beds, trilobite trace fossils and distribution of siltstone.

GENISE, J., BELLOSI, E. and GONZALEZ, M. G. Ichnofabrics and palaeosols.

GOLDRING, R., CADEE, G., D'ALESSANDRO, A., GIBERT, J. DE., JENKINS, R. and POLLARD, J. E. Climatic control of trace fossils in the marine realm.

MANGANO, M. and BUATOIS, L. A. Ichnology of Carboniferous tide-influenced environments and tidal flat variability in North American mid-continent.

MANNING, P. L. Vertebrate palaeoichnological approaches to palaeoenvironmental and palaeobiological analysis and interpretation of vertebrate ichnocoenoses. (Poster)

MCILROY, D. A comparison of the ichnology of estuarine and non-estuarine tide-dominated depositional systems. (Poster).

—— Stratigraphic ichnology of the Neoproterozoic–Cambrian transition in Finnmark, Norway. (Poster)

—— and TAYLOR, A. M. Review of concepts, recent advances and frontiers.

PEMBERTON, S. G. Stratigraphic application of substrate specific ichnofacies: delineating discontinuities in the rock record.

SCHLIRF, M. The characterisation of depositional environments and identification of key surfaces of relative sea level change with the help of trace fossils : examples from the Upper Jurassic of the Boulonnais (northern France). (Poster).

TWITCHETT, R. J. and BARRAS, C. Trace fossil in the aftermath of mass extinction events.

UCHMAN, A. Palaeoenvironmental and evolutionary problems of deep-sea trace fossils.

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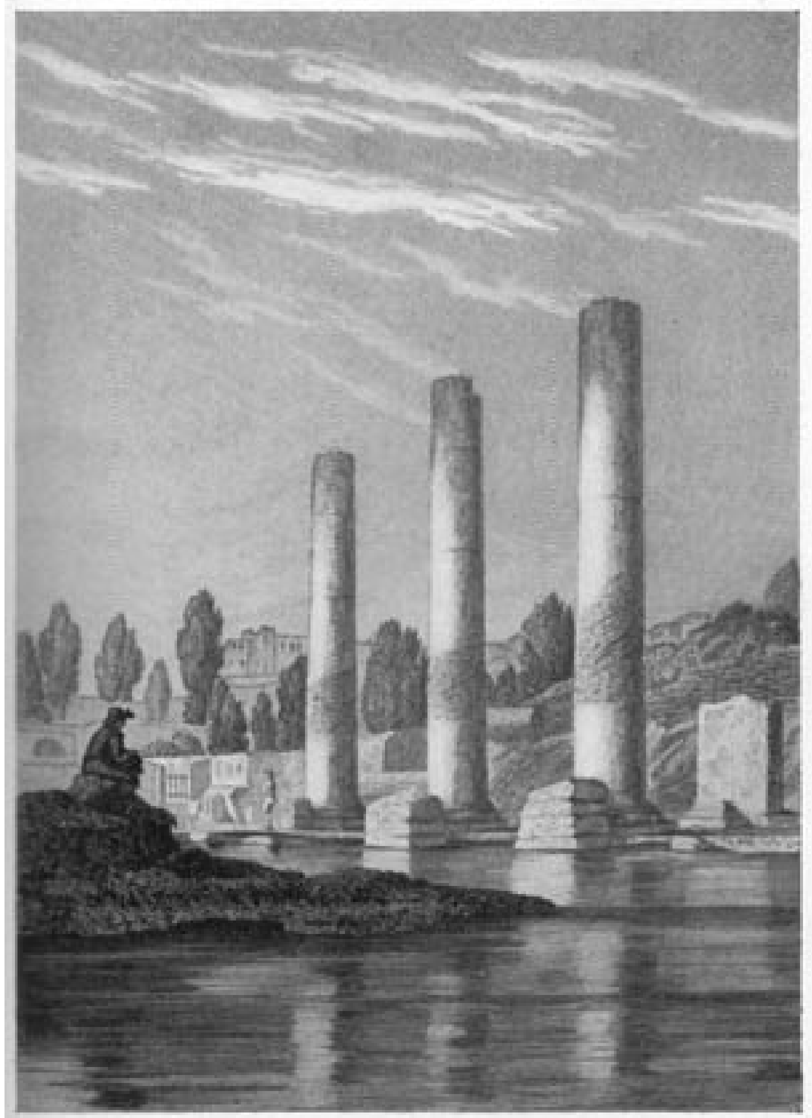

Plate 10 Lyell's sketch of the Temple of Jupiter Serapis at Pozzuoli.

Lyell's illustration of the 40ft high marble pillars of the Roman temple of Jupiter Seraphis at Pozzuoli in Italy showing the 12ft high zone of boring by marine bivalves the top of which is now 23ft above present sea level. He cited this as evidence of periods of uplift and submergence of the Italian coast in historic times. (In modern ichnological terms borings Gastrocoenolites belonging to Trypanites ichnofacies of an uplifted hardgroud indicating sea level change). Original Frontispiece to Volume I of "Principles of Geology" by Charles Lyell 1830, published by John Murray, London.

Progressive Palaeontology 2003

Division of Earth Sciences, Glasgow University *10 – 11 June 2003*

The annual Progressive Palaeontology Conference got underway with a reception at the Hunterian Museum annexe. The whisky tasting was ably hosted by David Brown, a fellow postgraduate at Glasgow, and an honorary palaeontologist for the day. Five fine whiskies were enjoyed, or perhaps not in some cases.

Tuesday's programme commenced with an erudite introduction by Sir Alwyn Williams who reminded us all of the importance of communicating in the same language in a subject that incorporates scientists from many different backgrounds with a wide variety of interests. He illustrated his point by using the only method of communicating to postgraduate students – cartoons!

Session 1 chaired by Jennifer England began when **Jessica Pollitt** (Bath) set a high standard with her talk on the phylogeny of the unique, extinct Phlangiotarbid arachnids, emphasising the affinity of the Phlangiotarbida to the Palpigradi and the Tetrapulmonata based on cladistic analysis. She showed us some lovely images of these indeed enigmatic creatures. **Sarah Stewart** (Glasgow) went on to discuss biodiversity in the Ordovician sedimentary succession of the Girvan district of SW Scotland. **James Wheeley** (Cardiff) continued with the Ordovician theme with his work on 'missing' aragonite molluscs and possible large-scale taphonomic skewing. **David Jones** (Leicester) gave us an insight into the aims of his work on conodont apparatus where morphometric analysis is to be applied to the conodont morphospecies *Ozarkodina excavata*.

After a break for coffee Session 2, chaired by David Parkinson, started with **Laura Braznell** (Birmingham) and an introduction to her work on the palaeoecology and taphonomy of the Carboniferous lagerstätte from Coseley, West Midlands, introducing us to a wide variety of exceptionally preserved plant and animal material. **Jennifer England** (Glasgow) detailed a contemporary study looking for common mechanisms of calcium carbonate precipitation from disparate biomineralisation regimes. She ably illustrated the different crystal make-up of several natural systems and showed us the variation in organic and inorganic components within the shells of two organisms living one atop the other. At this point 'Big Dave', the session chair, decided to acknowledge defeat and let **Rachel Moore** (Bristol) introduce her own talk on synziphosurines. Rachel went on to present unique specimens that have undergone exceptional preservation showing detailed appendages and soft tissues. **Erik Tetlie** (Bristol) then discussed the difficulties in determining the phylogeny of Silurian eurypterids, many of which have been described from incomplete specimens.

Despite a delayed lunch the delegates were set to start again with much enthusiasm. The third session, chaired by Sarah Stewart, again provided an array of different subjects. **Colin Barras** (Natural History Museum) examined the ichnofossil record across the Triassic/Jurassic boundary, detailing changes in bioturbation, burrow size and ichnofabric index. **Richard Forrest's** (New Walk Museum) passion for plesiosaurs was apparent in his detailed talk regarding two distinct groups of 'long-necks', determined from his analysis of the vertebral columns. **Claire Pannell** (Glasgow) gave us an enthusiastic account of her fieldwork in Tenerife with some lovely findings, and did her best to convince us she doesn't just lie on the beach. **Lucy Wilson** (Cambridge) gave a well-illustrated account of the gut morphology of enigmatic hyolithids.

More tea and coffee was followed by **Liz Boulter** (Cambridge), who began the final session chaired by Claire Pannell, and provided us with a candid account of her challenging research into the Burgess Shale 'worms'. **David Parkinson** (Glasgow) gave a fascinating talk on the use of stable isotopes from brachiopod shells in palaeoenvironmental reconstruction, bringing together palaeontology and mass spectrometry techniques. **Tom Challands** (Bristol) animated his talk using the remains of lunch to illustrate the preservation of bones from fissure fills, and provided a chance for the delegates to get their own back by asking him some questions for a change! **Jeff Liston** (Hunterian Museum) concluded the day 'briefly' with 100 plus slides (!!) accompanied by sound effects and even Deep Purple's 'Smoke on the water,' detailing his find and attempts to excavate a stegosaurus skeleton. Or was it a fish?

A poster session with more wine was followed by a highly enjoyable evening at Di Maggios' Italian restaurant, including an impromptu performance by a magician who bemused the delegates with his amazing multiplying bunny rabbits.

The next day a rather reduced number of delegates (3 out of 18; was it due to the night before?) assembled outside the Gregory Building for the field trip to Trearne Quarry led by Neil Clark and John Faithful of the Hunterian Museum. The quarry contains important Carboniferous fossils and some interesting minerals. Everyone found something of interest including the famous jellyfish and also bivalves, brachiopods, gastropods. After a spot of lunch we headed back to Glasgow and rounded up the day with a quick visit to see Fossil Grove, Victoria Park – preserved *in situ* Carboniferous trees.

Everyone on this year's committee would like to thank all the delegates for their attendance and making the symposium an enjoyable event. Thanks also to everyone who helped with the organisation and to the Geological Society of Glasgow for a donation of funds.

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Delegates of Progressive Palaeontology 2003

——OBITUARY——

Michael House (1930–2002)

The universities central to the academic life of Michael House, who died on 6th August 2002, can be appropriately traced on the geological map of England. From his birthplace on the Chalk at Blandford Forum, Dorset (1930), near the south coast, draw a line to Durham (Lectureship, 1954–1963) in the far north. From Durham follow the broad arc near the base of the Chalk, southeastward to Hull (Professor and Head of Department, 1967–1988) and around and southwestward to Cambridge (first class honors, 1954) and Oxford (Lectureship, 1963–1966) and, with a detour to Southampton (1988–2002), back to the south coast and official retirement in Weymouth (1993). Stratigraphic palaeontology has lost one of its finest and most productive students, the Ambassador for the Devonian with ammonoid portfolio. Butcher (2002) and Neale (2002) captured his life and career in splendid memorials for The Geological Society and Yorkshire Geological Society. This tribute is a view from America.

Michael House's geological roots were quite literally in the Jurassic and Cretaceous of Dorset. One of his earliest papers, *The Structure of the Weymouth Anticline* (House, 1961) maps the area of his boyhood, where ammonites introduced him to the world of cephalopods and his hero, Arkell, to the world of stratigraphy. Early on he developed extraordinary skills in geological mapping, outcrop sketching and draftsmanship of charts, the essentials for a life of bed-by-bed fossil collecting. In this age of computer graphics he will be remembered as one of the last to have preferred pen-and-ink.

It was in the Devonian of South West England and North America that Michael began his life-long study of ammonoid (goniatite) cephalopod systematics and biostratigraphy. Out of the tangled mass of slate and nodule in Devon and Cornwall he brought to light an ammonoid sequence which showed that the major zones of the classic German succession could be recognized in England (House, 1963). Similar discoveries in North America, from the Appalachians in the Eastern U.S. (House, 1962, 1965, 1978) to Western Canada (House and Pedder, 1963), set the stage for a programme of research that radiated across the globe with special focus on New York, Montagne Noire (France), Canning Basin (Australia), Timan Basin (Russia) and Tafilalt Platform (Morocco). The collaborations and friendships are too numerous to list but his correspondences alone included virtually all the players in Devonian biostratigraphy, major and minor, of his era.

In coming to North America in 1958 Michael followed the route of Lyell, travelling from Cambridge, Massachusetts (Harvard Museum) to Albany (New York State Museum and Geological Survey). But he was tracking Devonian ammonoid type-specimens, and the quest required visits to New York City (American Museum) and Washington, D.C. (U.S. National Museum) and countless other museums, grand to obscure, across the continent. At Cornell University in Ithaca, New York, John Wells introduced Michael to the Devonian of New York, a succession with great potential for biostratigraphic refinement. He took me on as an assistant to re-examine the classic Upper Devonian Naples Fauna of J.M. Clarke. Starting with the 1965–66 field seasons, this project expanded over the years to become the still-unpublished monograph (our Opus) outlined in Kirchgasser and House (1981) and House and Kirchgasser (1993).

Michael was a pioneer in the work of the International Subcommission on Devonian Stratigraphy (SDS) and by his own reckoning participated since 1960 in all International Union of Geological Sciences (IUGC) committees charged with defining mid-Palaeozoic stage, series and system boundaries and visited "all sites considered important." His leadership of the SDS intertwined with Willi Ziegler, the great German pioneer of Devonian conodont systematics and biostratigraphy, who by incredible coincidence died two days after Michael. These rivals guided the SDS to define the Series and Stage boundaries and the Global Stratotype Sections and Points (GSSPs) for the whole of the Devonian. Their joint paper, House and Ziegler (1977), was an important step in the integration of the conodont and ammonoid zonations.

The dissolution of the University of Hull Geology Department, a consequence Mrs Thatcher's experiment, was of course a terrible blow to Michael but he found new colleagues and friends at Southampton and the teaching and research continued uninterrupted. He was sad to see Hull's geological family dispersed. Among his papers is a notebook with tiny photographs with annotations of every Hull geology student of his tenure. Perhaps some former members of the student Harker Geological Society (in conjunction with the Hull Geological Society or Yorkshire Geological Society) could organize a reunion field excursion in his honour, perhaps to his favourite sections on the Yorkshire coast between Whitby and Scarborough. Similarly the Ussher Society should consider organizing a field excursion in Devon and Cornwall.

It was inevitable that the ammonoid investigations of Michael House and R. Thomas Becker would intersect. In 1985 the master met the young prodigy from Germany and an extraordinary partnership commenced. Their expeditions to Australia, France, Russia and Morocco initiated a dramatic refinement and internationalization of the Devonian ammonoid zonation. Paralleling the biostratigraphic work, they introduced a major revision of Devonian ammonoid systematics (*e.g.* Becker and House, 1993) in which megagenera (such as *Manticoceras* and *Tornoceras*) are separated, by details of shell and suture, into smaller monophyletic and biostratigraphically significant groups of species, with many assigned to new genera. Their prolific collaboration is finalized in Becker and House (2000), in which some sixty international ammonoid genozones are recognized. The new systematics will be incorporated into the revised ammonoid section of the *Treatise* with Thomas Becker (Münster) taking over Michael's contribution.

Michael had a long fascination with the environmental controls of sedimentary and evolutionary processes. He believed that orbital or Milankovitch cycles are responsible for the small-scale sedimentary microrhythms that pervade the stratigraphic record, and that by counting such rhythms it would be possible to calculate absolute ages for intervals in the chronostratigraphic scale (House, 1985b, 1991). He also advocated episodic sea-level and temperature changes as principal controls of major evolutionary events (extinctions and originations) as exemplified by the twenty or so major Devonian events (House, 1985a). His final publication on these complex issues (House, 2002) includes his final chart of the Devonian System, his legacy to the succession that was so much a part of his life's work (Figure 1).

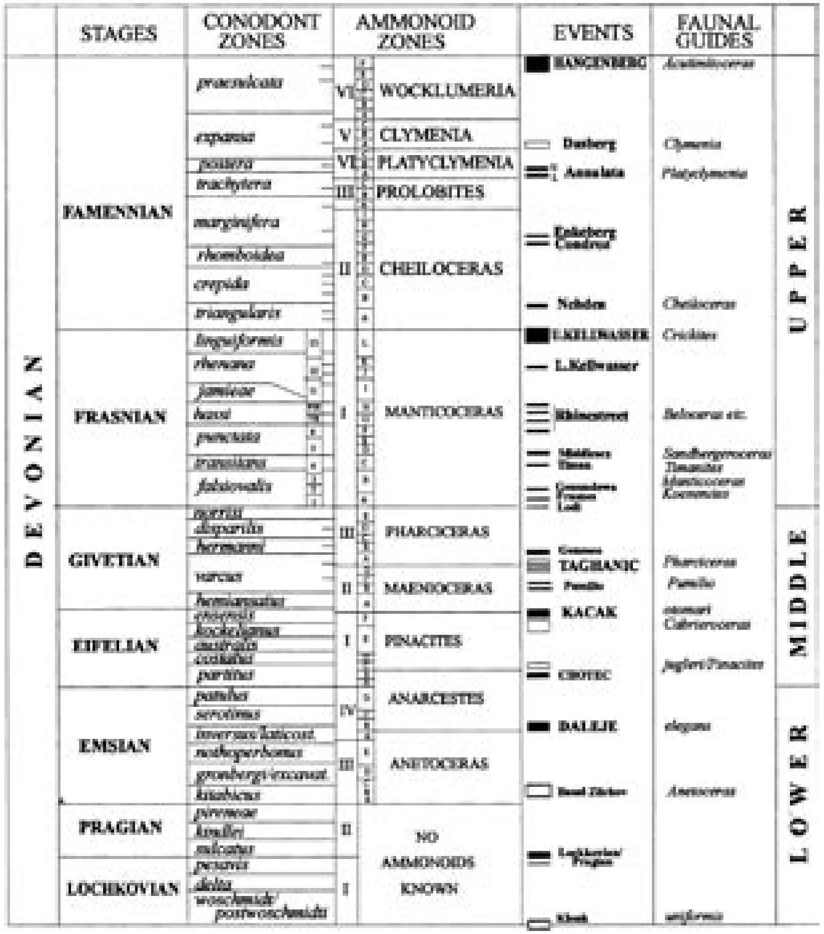

Figure 1. Chart showing correspondence of main evolutionary 'events' recognized in the Devonian with chronostratigraphic stages and conodont and ammonoid zonations. Black rectangles represent events characterized by short-term dysoxic and anoxic facies in their named areas. Frasnian conodont zone correlation based on Klapper and Becker (1999).
From House (2002, fig. 1) with permission.

Always the gentleman, Michael balanced work and family life beautifully. He was devoted to his loving wife, Felicity and to their children, Sue and Jim, and his grandson, Matt. Felicity ('Flick') was the bedrock support of Michael's academic and research career. Generations of geologists from around the world are thankful for their generous hospitality and loving friendship.

Looking northward from the office window in his retirement cottage one can see the steeple of the parish church of St. Andrew, Preston, were the funeral was held, and on a clear day the great White Horse in the Chalk downs of Hardy Country beyond. Walk out the garden gate and follow the footpath southward past the Roman Temple to the bluff overlooking Weymouth Bay, the Isle of Portland straight ahead. You will be standing near the axis of the Weymouth Anticline, in the area where geology began for Michael House. Westward is Weymouth in the direction of Lyme Regis. Eastward, past Osmington Mills, the classic Mesozoic sections continue toward Ringstead, White Nothe, Lulworth, Kimmeridge and St. Alban's Head, the magnificent Dorset Coast, designated a Natural World Heritage Site through the efforts of geologists like Michael House. On weekends shortly before his death he was still leading field excursions for locals, doubtless using his own Geologists' Association field guide (House, 1989), living a geological and family life fully to the end. His Devonian papers, maps and specimens will be housed in Oxford, and Jurassic ones in a room in the County Museum, Dorchester, to be named in his honour.

As for the Opus monograph, *Late Devonian Goniatites from New York*, I was able to tell him, two weeks before he died, that it had passed reviews for publication in the *Bulletins of American Paleontology* of the Paleontological Research Institution (PRI), Ithaca. The manuscript is sitting on my desk as I write this. I still tinker with it, but in my heart I know that soon I must let it go.

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Friends of the Devonian, Southwestern New York, 1966.
From left: John Huddle (U.S. National Museum), Ed Buehler (State Univ. of New York at Buffalo), Larry Rickard (N.Y. State Geological Survey), the author and Jon Harrington (Cornell University) and Michael House. Photo taken by John Wells (Cornell University.)

Middle-Upper Devonian Series Boundary and Global Statotype Section and Point (GSSP) (hammer), Col du Puech de la Suque, Montagne Noire, France, 1983.

Michael House and Geoffrey Wade (University of Hull).

Canning Basin, Western Australia, 1990.

From left: Gil Klapper (University of Iowa), Thomas Becker and Michael House (University of Southampton).

From our Correspondents

“Laws” of animal evolution and evolutionary folk wisdom

The reconstruction of animal phylogeny is immensely challenging. In order to elucidate the broad patterns of evolutionary relationships within the animal kingdom, the deepest splits of which go back more than half a billion years ago, we are chiefly working with scattered information that is imperfectly preserved in the complex structure, development and molecular architecture of living animals. For certain taxa crucial information from the fossil record may help this endeavour, but in general fossils have not played a central role in the reconstruction of metazoan genealogy. Despite the fact that our knowledge of the details of animal morphology and genetics is limited to a very small sample of the bewildering array of extant and extinct forms, we have only to look at the ever increasing number of gene sequences deposited daily at Genbank, and the size of published morphological data matrices (the largest to date with more than 16,000 entries) to see that we are constantly working to diminish this factual deficit.

However, certain gaps in our knowledge cannot so “easily” be fixed by the accumulation of new facts, and it is here where interpretations and assumptions complete the scientific mix of observation and theory. It is also here that we can identify a veritable Lagerstätte of conceptual fossils, in addition to the ones that I identified in the previous issue of the *Newsletter* (PAN52). There I designated one category of conceptual fossils as true fossil concepts, *i.e.* ways of thought that have become so entrenched in the common practice of a discipline that their validity has become unquestioned, despite the fact that they have outlasted their utility (if they ever had one). Here I will focus on a group of conceptual fossils that might be called “laws” of animal evolution. These “laws” can be seen as assumptions about evolutionary processes and patterns that are posited, frequently without empirical support, in order to create sensible order out of chaotic data. However, the empirical support for these “laws” of evolution is frequently scanty, if present at all, and these “laws” therefore qualify as evolutionary folk wisdom. Like all folk wisdom they are tenaciously embedded in our belief system, often with little more value other than offering psychological solace in our often frustrated attempts to understand a complex world.

Increasing complexity in evolution

Anyone who has taken an interest in zoology in university has sooner or later come across the work of Libbie Henrietta Hyman (1888-1969) (for details of her life and work see Schram, 1993 and Winston, 1999). Several generations of biology students have used the various editions of Hyman’s *A laboratory manual for comparative vertebrate anatomy* as a guide in their vertebrate dissection practicals, and those with an interest in invertebrate zoology and phylogeny could always rely on her magisterial six volume synthesis of invertebrate biology *The invertebrates*. Hyman wrote this series during her long career at the American Museum of Natural History in New York, and it was published between 1940 and 1967. This most comprehensive work on invertebrate zoology written in the English language by a single person was a real work of love, and it remains as the mainstay of her continuing fame. Her work on the vertebrate anatomy manual, on the other hand, was a result of the need for a suitable laboratory manual for the course in vertebrate comparative anatomy that she taught at the University of Chicago. The royalties on the sales of the vertebrate manual together with those for her *Laboratory manual for elementary zoology* brought her financial independence, but a work of love these works apparently were not. This becomes painfully obvious when one reads her prolonged correspondence with the University of Chicago Press about the need for a revision of the 1922 original. In 1936 the Press first suggested that a revision might be appropriate, and after working on the revision she wrote in December 1938: “As I have repeatedly told members of the Press, vertebrate anatomy is not my field of work at all, and further I dislike the subject violently.” Then in 1943 when she received her first royalties for the second edition, which was published in 1942, she wrote the Press: “Not only am I not a student of vertebrates but I hate the subject with the most violent hatred.” Then in 1951 the Press felt the need to discuss a third edition of the vertebrate text. Not entirely unexpectedly, Hyman’s response was spicy: “Your letter was certainly very unwelcome news. Fifteen years ago the Press began pestering me to death to revise my … manual.” If that didn’t get the message across, she let the Press know, once more, that the manual “was an agonizing and hateful job, because not only is vertebrate anatomy not my field but I detest the subject with the utmost violence.” Yet, the Press didn’t back off, and correspondence continued for some time. We can only guess how it ended because the correspondence between Libbie Hyman and the University of Chicago Press after 1956 is still protected by privacy laws. Under the guidance of an appointed editor the third edition finally hit the shelves in 1979, ten years after Hyman’s death.

In sharp contrast, until the very end of her life she kept intensely busy with her invertebrate treatise. Unfortunately, old age prevented Hyman from completing her work. The series ends with a volume on molluscs as she became too weak to work. Many think that the quality of this final volume was not up to the standards of the earlier volumes, partly because she didn’t have the personal experience with molluscs that she had with the groups covered in the other tomes, and partly because her health was deteriorating. She pushed herself to her absolute limits working at the end of her career. A graduate student colleague of my former PhD supervisor Fred Schram watched Dr Hyman one day in the library of the American Museum of Natural History. Hyman was sitting on a chair slumped forward over the table, motionless. After some time he became worried that Dr Hyman might not be all right, and he walked up to her to check. She was OK, but for the longest time she had been trying in vain to push her chair away from the table in order to get up. She was simply not strong enough to do that! Such determination to work despite the frailty of old age should be an inspiration to us all.

Now finally to the theme of this section. Although phylogenetic reconstructions formed only a modest part of Hyman’s work, her comprehensive knowledge of invertebrate structure and development nevertheless placed her in a unique position to comment on animal phylogeny. She did so in particular in the first volume of *The invertebrates* in chapter II entitled “Classification,” a chapter that was concluded with the only drawn phylogeny in her synthesis. Ironically, despite Hyman’s statements that “there is no such thing” as a “’correct’ final classificatory arrangement," and that "any text simply represents the best opinion of some zoologist," which "necessarily changes as knowledge of anatomy, embryology, distribution, and palaeontology increases," her views have subsequently become set in stone as the traditional Anglo-Saxon view of animal phylogeny. This situation persists to this day as both books and papers continue to refer to her phylogenetic views as the canonical textbook view of the recent past. There is of course nothing wrong with this situation if Hyman's views are accurately reflected in recent commentaries, and if her views have up to now been the best estimate of animal phylogeny based on non-molecular data. In that case her views are simply a venerable conceptual fossil. However, this is not the case for two reasons.

First, as detailed elsewhere (Jenner, 2000) Hyman's views have been almost universally misrepresented in recent works. In particular recent authors have labelled Hyman's phylogenetic scheme as a "glorious saga of progressive increase in complexity" that arose from an "intellectual bias for increasing complexity in evolution." In particular, the common textbook phylogeny that arranges animal relationships according to a single linear progressive increase in complexity of body cavities, from acoelomate to pseudocoelomate to coelomate organizations, has been attributed to Hyman. Detailed reading of Hyman's phylogenetic hypotheses presented throughout the different volumes of *The invertebrates* shows that this is clearly a misreading of her views. Hyman did indeed distinguish between compactly organized acoelomates, pseudocoelomates with a more spacious non-coelomic body cavity, and coelomates, but she did not envision these as a phylogenetic series. Instead, throughout *The invertebrates* Hyman argues for a diphyletic theory of bilaterian relationships, with one lineage leading to the coelomate deuterostomes, and another lineage leading to the acoelomate, pseudocoelomate, and coelomate protostomes. Hyman's only drawn phylogeny closely corresponds to her explanation in the text by showing the acoelomate, pseudocoelomate and coelomate protostomes as closer together than the protostome and deuterostome coelomates. This phylogenetic topology contradicts the Coelomata as a monophyletic pinnacle of complex bilaterian organization that is misleadingly drawn in all recent works citing Hyman. Hyman herself argues clearly against this false attribution of a later age: "Although some groups of animal are obviously 'higher', *i.e.*, structurally more complex, than others, many groups are difficult to evaluate, for they may rank high in some organ systems, low in others. If animals had evolved in a straight line, they could be arranged in a linear series of increasing complexity of structure, and each group would be higher than the preceding one. But all the evidence indicates that groups evolve by branching from preceding groups so that the animal kingdom must be graphed not as a line but as a branching tree" (Hyman, 1940: 39). I was unable to trace in Hyman's work any conscious use of a notion that evolution necessarily leads to an increase in organismic complexity as a guiding principle for her phylogenetic speculations. Unfortunately, it is this false distillate of Hyman's views that has become ensconced as a fossil concept in later works. When Hyman does speak of morphological complexity, she is only referring to organizational grades that do not reflect a phylogenetic pathway.

Second, far too commonly one sees Libbie Hyman's contorted views used in papers and professional talks as merely a convenient jumping board to showcase the revisionist views of molecular systematics. Other views of metazoan phylogenetics have been advocated since her works, and especially the use of explicit cladistic methodology has produced a series of alternative views that are all too easily brushed over when new molecular results are presented. A typical sketch of the history of metazoan phylogenetics that one finds in molecular phylogenetic papers and reviews follows a fixed set of three steps: 1) Hyman's alleged views are heralded as the canonical view of animal phylogeny prevalent until very recently; 2) Hyman's views of animal phylogeny are unfortunately based on a misguided principle of a linear increase in complexity in animal evolution; 3) the new findings of molecular systematics reveal a new and better understanding of animal phylogeny, which breaks dramatically with the received wisdoms of the traditional morphological tree. Typically no attention is given to phylogenetic views proposed by other workers than Hyman in the pre-cladistic era, and recent morphological cladistic analyses are similarly ignored.

Of course, there is only so much space available in the introduction of a new paper to outline the historical development of our discipline, and admittedly morphological cladistics of the Metazoa has not yet produced any clear consensus that can be contrasted with molecular results. However, we have to worry when this Whig interpretation of history is uncritically presented as state-of-the-art knowledge in commentaries intended for a non-specialist audience (see for example Graham, 2000). A proper reading of Hyman is sufficient for the demise of the acoelomate-pseudocoelomate-coelomate phylogeny, and modern morphological cladistic analyses provide as little support for it as molecular phylogenetics. Ironically, the most recent "real" support for the acoelomate-pseudocoelomate-coelomate progression is not a morphological fantasy, but the result of the first generation of molecular phylogenetics. The earliest 18S phylogeny that I know that included acoelomates, pseudocoelomates, and coelomates shows a neat acoelomate-pseudocoelomate-coelomate progression (Bergström, 1991), exactly the linear phylogenetic progression in body cavity complexity falsely attributed to Hyman. Incidentally, Bergström doesn't mention Hyman's work at all.

If Hyman did not exhibit an overt commitment to a simple progressive increase in complexity during animal evolution, have there been others who have done so? Obviously, the answer is yes. Let us consider just some points in the history of evolutionism and then look at current practice. Notions of biological progress in geological time have been present ever since the birth of evolutionism. In a delightful exposé of the history and current status of the relationship between cultural and biological progress Ruse (1996) claims that there has always been, and continues to be in modern evolutionary science, a cross-fertilization between notions of biological progress and cultural progress. In particular he identifies a transfer of beliefs in cultural progress (in the form of increasing scientific knowledge, technological ability, moral and social behaviour, *etc.*) into convictions about biological progress, which are often manifested as ideas about increasing complexity in evolution. One of the earliest convincing examples of this cross-fertilization is the theorizing of Jean Baptiste Lamarck (1744-1829) (see Burkhardt, 1977; Ruse, 1996; and Gould, 1999 for explications of Lamarck's views). At the core of Lamarck's original evolutionary theory there were two causes of change. He hypothesized one cause to lead to the uninterrupted progressive complication of organic structure in time from the simplest beginnings of spontaneously generated life, to the most perfectly organized animal. This upward thrust in complexity could be deflected from its linear path by a second cause, which is widely known as Lamarckism, or adaptation by the inheritance of acquired characteristics through the principle of use and disuse. When one considers Lamarck's views on human improvement, one can see that his belief in the force that incessantly pushes organisms toward greater complexity is joined with his progressive personal philosophy of the desirability of change and reform in social and political conditions. In other words, Lamarck's conceptions of biological and cultural progress were tightly linked. He envisioned social improvement to be most easily attained through installing philosopher-kings as heads of state with an important role for scientists as well. Of course, these leaders had to be Europeans, which Lamarck considered to be the superior human race because they are the oldest, and have therefore moved upwards to perfection more than other human races.

When we jump from the beginning of evolutionism to the beginning of Darwinism, we see that a progressive increase in complexity in evolution is no longer baked into the mechanism of evolutionary change. Nevertheless, an undeniable impression of progress can still be seen in certain phylogenies drawn at the time. The first phylogenies drawn by Ernst Haeckel, for example, were branching trees expressing diversity of forms, but they retained a central or main stem to indicate linear anatomical advance. Yet, we might think that in our enlightened world of cladograms without central axes we have completely done away with attempts to introduce progress in complexity in our accounts of evolution. Although strong concerns for progress in evolution indeed no longer seem to play a guiding role in most of evolutionary biology, a notion of increasing complexity in evolution still raises its head here and there in various guises.

Biggelaar *et al.* (1997: 367) in a paper on the embryology and evolution of spiralian protostomes state "ontogeny as well as phylogeny are associated with a progressive increase in complexity." With this guideline they determine primitive and derived character states in trying to resolve spiralian relationships using developmental data. For example, they argue that a uniform distribution of maternal determinants in an egg cell is primitive to a heterogeneous distribution; synchronous cleavage divisions are primitive relative to asynchronous divisions; external fertilization is primitive and internal fertilization is derived. Utilizing a similar argument that simple equals primitive, Nielsen (2002: 686) concludes with respect to different types of larval settlement in the entoprocts that "settling with the frontal organ appears to be the ancestral type, because it involves the least morphogenetic change." In similar vein, it has been proposed that in segmented animals such as annelids and arthropods the general rule is that homonomy is primitive relative to heteronomy. For example, in trying to systematize Lower Cambrian arthropods Hou & Bergström (1997: 107) state that "if we try to polarize character states in arthropods without the use of outgroups, specialization of segments and tagmosis in general must be considered more advanced than a state in which segments and podomeres are similar throughout."

The above ideas may be a helpful guide in a vaguely defined and limited context, but surely they cannot be used "in general." When a certain level of organismic complexity is attained, all directions of evolutionary change are open. Simplifications of morphology, and changes on the same level of complexity do occur, and mosaic evolution of different features in an organism seriously compromises the value of this reasoning. The principle of increasing structural (and functional) complexity during evolution might be helpful for understanding the evolution of certain characters for certain taxa. However, there is no reason at all to claim that such a guide is infallible in most cases, or even helpful at all. For example, whereas external fertilization may be primitive for some spiralian phyla such as annelids, when all spiralians phyla are considered the picture may change drastically. Various published analyses show basal positions for taxa for which fertilization is primitively internal, such as the gnathostomulids, platyhelminths, and entoprocts. This would indicate that within the spiralians external fertilization might be derived. Only the phylogenetic distribution of features can yield an objective basis for assessing primitive and derived character states.

The mechanism of natural selection does not necessarily produce increasing complexity of structure, and so far no convincing documentation has been presented for a progressive increase in complexity as a prime signature of evolution across diverse times and taxa (*e.g.* McShea, 1996). Even if it can be concluded that a particular group of organisms has tended to increase their overall complexity (by some definition) through time, then this finding can simply not be extrapolated to other organisms living in entirely different circumstances with different morphologies. If increase in complexity had such fractal properties, we would have established it as an immutable law of evolution long ago. Therefore I think that a belief in the increasing complexity in evolution to guide the reconstruction of phylogeny merely represents unquestioned folk wisdom (just as the principles of inheritance of acquired characteristics, and of use and disuse were folk wisdom in Lamarck's time) that has been retained as a fossil concept from an earlier time in history when ideas about progress in evolution and culture were much more visible than is currently the case, and where transfer of cultural beliefs to scientific values was more common. As an antidote we may simply posit another folk wisdom of opposite significance: the often-stated belief among evolutionists that it is easier to lose than to gain complex structures. This bias in character transformation would yield the opposite expectation, namely that simpler morphologies are typically derived, and that evolution must therefore be predominantly degenerative.

I wanted to discuss several other "laws" of evolution and evolutionary folk wisdoms, but unfortunately space is running out. As an appetizer (I hope…) for the next *Newsletter*, three riddles: what has been a shared major impediment to understanding the evolution of turtle and molluscan body plans, why was Darwin wrong in determining the ancestral nature of the sexual system in cirripedes, and how can a phylogenetic pattern in plain sight be clouded by evolutionary process assumptions?

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Dusting off bone ontologies; considering skeletons in the palaeo-closet

Vertebrate researchers routinely utilize "the skeleton" as a primary source of phylogenetic, biomechanical and ontogenetic data (Hall, 1978). Although the skeleton may include a diverse assemblage of tissues, ranging from hyaline cartilage to enamel, bone typically constitutes the main topic in the majority of skeletal discussions. Certainly bone and bone development have a long history in biological investigations – by 1736, Nesbitt had observed that bone could develop via two distinct modes: "[t]he bony particles in *foetuses* begin to be deposited or to shoot either between membranes or within cartilages" (quoted in de Beer, 1937, p. 1). But, whereas interest in bone, like an embryonic diaphysis, continues to grow, the 'ontology' of bone is often overlooked. Consequently, the terminology used to describe bone development and structure(s) remains befuddled. In this contribution, we provide hard, crystalline (albeit probably controversial) descriptions for terms or designations commonly associated with bone to stimulate discussions about skeletons and how biologists conceptualise them.

What is bone?

Bone is simultaneously a tissue, an organ, and an organ system (Patterson, 1977; Hall, 1997). In its most common form, bone as a *tissue* includes unique cell types (*e.g.*, osteocytes, osteoclasts) as well as extracellular matrices of inorganic ions, proteins, glycoaminoglycans, *etc.*; serves a physiological role as a reservoir of calcium, phosphorous, and other necessary elements that can be released in a controlled fashion; and functions as a building material. Bone as an *organ* forms the scaffolding for soft tissues and may harbour haemopoetic and fat cells, as well as immune system components. Bone as an *organ system* comprises the entire assemblage of (bone-) organs formed from (bone-) tissues; this organ system is usually considered to be synonymous with the 'vertebrate skeleton', although, as noted previously, this constitutes an incomplete summary. The vertebrate skeleton also includes various non-bone elements and tissues, such as tracheal and articular cartilages. Bone may be atomized histologically, systematically, functionally and developmentally (none of which are mutually exclusive).

How many types of bone are there?

Whereas various types of bone tissue exist, most are relatively obscure. Disregarding osteoid (unmineralized bone), acellular bone, chondroid bone (bone matrix with cartilage cells), and alveolar bone, all mature bone tissue, regardless of embryological or phylogenetic origin, is similar histologically. Admittedly, there are differences in cellular and matrix composition, the amount of remodelling, vascularisation, porosity, and the presence and appearance of enveloping membranes (periostea and endostea) between various elements in various taxa and bone palaeohistologists are frequently able to retrodict the biology of fossil taxa on the basis of bone histology. Overall however, it would be virtually impossible to identify confidently the element and species from a particular portion or fragment of bone tissue. Histologists studying modern bone therefore conventionally subdivide bone by considering (as Nesbitt did) modes of ossification – endochondral versus intramembranous.

During development, bone tissue may develop either *indirectly*, by endochondral osteogenesis, replacing a preformed model (usually cartilage), or *directly*, by intramembraneous osteogenesis. Considering these prominent differences in the modes of ossification, it is tempting to organize bone tissue into bone organs by an extension of the same dichotomy, *e.g.*, endochondral versus intramembranous bones. Regrettably things are not so simple.

A stereotypical textbook interpretation of endochondral ossification relies primarily on data gleaned from mammalian long bone development. To summarize: formation of a cartilage model, chondrocyte hypertrophy, mineralization of the cartilage matrix, invasion by blood vessels and osteoprogenitor cells, and (endochondral) deposition of bone. However this is nowhere near the whole story. Cells below the perichondrium (surrounding the cartilage model) also deposit bone tissue. As this bone tissue is laid down on the surface of the cartilaginous model and is *not* replacing the cartilage *per se*, it is not formed endochondrally. It is perichondral by position and intramembranous by mode of ossification.

Furthermore, the pattern of long bone ossification described for mammals is by no means typical for all tetrapods. In birds the majority of long bones form perichondrally as a sleeve around the cartilage model. Thus the development of long bones in avians is essentially intramembranous, with the 'membrane' being the perichondrium transformed into a periosteum. Only in adult birds does 'endochondral ossification' begin. Among teleosts the pattern differs further, with resorption/replacement of the cartilage model usually occurring along a straight front and no calcified cartilage trabeculae forming (for surfaces of bone deposition).

Well-documented examples exist of the formation of homologous bone organs by different ossification processes in closely related species. In the aquatic frog (and laboratory denizen) *Xenopus laevis*, the larval cartilages giving rise to the sphenethmoid are resorbed, and an intramembranously derived bony element forms in their place. In other anurans larval cartilages are replaced endochondrally (Trueb and Hanken, 1992). Another example is the orbitosphenoid. In the amphisbaenian *Leposternon microcephalum* the orbitosphenoid develops intramembranously, associated with cartilage nodules, while in most other vertebrates the orbitosphenoid develops strictly via endochondral ossification (Bellairs and Gans, 1983).

Patterson (1977) and Smith and Hall (1990, 1993) helped to clarify the terminology of bone tissue versus bone organs. Replacement bone is preformed in connective tissue and thus will ossify in part (but not exclusively) via endochondral ossification; dermal bone is not preformed in connective tissue and thus will not undergo endochondral ossification (ossification is associated with an ectodermal basement membrane).

So what of bone organ systems? It is common to consider the skull and postcranium as the major groupings of bone organ systems. Whereas the skull is widely recognized as a composite structure, integrating both replacement and dermal bones, the postcranium is generally regarded as a collection of replacement elements. Again, exceptions are the rule. In all tetrapods some element(s) of the postcranium (*e.g.* the wishbone [furcula] of birds, the interclavicle of crocodylians, and the collar bones [clavicles] of mammals) are dermal bones.

Skeletons

Given these lessons from *bone*, what about *skeletons*? Just as bone can be considered on multiple levels, considering skeletons also involves hierarchial complexities. Even consensus on a definition of what constitutes a skeleton remains elusive. Hall (1997) defined the 'skeleton' as an organ system of cartilages and bones that supports and protects the body, provides attach[e]ment sites for muscles, and houses the marrow from which blood-forming cells arise." However in some vertebrates (*e.g.*, chondrichthyans and some teleosts), blood-forming cells reside external to the bone marrow (if and when a marrow core exists). For palaeontologists, the skeleton is commonly conceived as the parts of an animal that typically fossilize (*i.e.* are mineralized), including bones and teeth but not most cartilages. This conception of the skeleton also excludes other unmineralised elements, such as the actinotrichia of osteichthyans, or osteoid (unmineralised bone). Once defined, we are then faced with the issue of how to partition all the various constituent skeletogenous parts. Depending on one's interests, the same 'skeleton' may be subdivided on the basis of phylogeny, position/topography, or development.

If we compare a vertebra with a limb bone, we note that both are postcranial elements derived from mesoderm, and both are considered part of the endoskeleton. However, by adopting different criteria for classification, the vertebra is a component of the axial skeleton, whereas the limb bone is a component of the appendicular system. Furthermore, while both come from the same germ layer, the vertebra is derived from paraxial somitic mesoderm, while the limb bone is lateral plate mesoderm.

More differences occur if we consider modes of ossification. As was previously noted, the femur may develop via different ossification processes in different taxa. Similarly in some vertebrates, vertebrae develop via endochondral ossification (tetrapods), while in others they develop intramembranously (some teleosts). The inductive influence of adjacent structures (*e.g.*, the notochord, epithelia) has also been used as a mechanism for distinguishing various parts of the skeleton, although applicability of this method is limited due to fluctuations in the effects that these 'inductive structures' impact throughout development. Thus, while the skeleton may be disarticulated (conceptually) in a multitude of ways, evaluations must occur at comparable, internally consistent levels.

These issues are relevant to palaeontologists! Terminology and classification schemes are essential tools for the comparison and study of organisms and their evolution; quagmires develop when simplifications or generalizations become widespread. The various levels of meaning for the terms *bone* and *skeleton* leave plenty of room for confusion. Palaeontologists who study mineralized remains of organisms must be prepared to acknowledge that these may or may not reflect the entirety of the skeleton. Other skeletal data (including the mode of ossification) are usually difficult to interpret from fossil remains. However, as more palaeontologists use histology in broad studies, the importance of terminology and classification of bone tissues, organs, and ossification processes becomes ever more important to 'dig out of the closet'. We will continue to pick away at the issue of skeletal segregation in the next column…

Note: We are encouraged by the many interesting responses we have received to our previous columns. We intend to present (and address) some of these comments in future articles to stimulate further interactions between developmental biologists and palaeontologists. This contribution was inspired, in part, by Smith's reply (*Palass Newsletter* **52**: 34–37) to one of our past columns (*Palass Newsletter* **51**: 27–30), and our different opinions on how to subdivide the skeleton.

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Coping with creation

You might recently have received an invitation, on elegant cream-coloured paper, to a national conference to debate the origin of life, no less. It's a magnificent topic. Who could resist? There was just a little work to do first: a short, and very curiously worded, questionnaire. Caveat completor: *you* are being targeted for ammunition to help the creationist cause. How, as a palaeontologist, should you react?

The questions fall into a number of categories. First, there's the deliriously garbled. That's question one: for the origin of life there is a choice of (a) Darwinian evolution; (b) punctuated equilibrium; (c) the Big Bang; (d) Special creation; or (e) Other. Now, as carbon-based life-forms requiring liquid water are unlikely to be entirely comfortable in a plasma of subatomic particles at several million degrees centigrade, the Big Bang may be safely discarded. And punctuated equilibrium is quite compatible with Darwinian evolution (in either Darwin's meaning or the modern synthesis), and both are usually applied to the evolution of life-forms, post-origin. Can either have a role in the transformations of complex but essentially abiotic compounds into simple organisms? A great topic for discussion over a couple of beers after the Pal Ass Annual Dinner, but can you confidently tick these categories on this sheet of paper? Then you have Special Creation (perhaps at ca 4 Ga around some hydrothermal vent, for added verisimilitude): a simple option but unproveable. And the 'Other' may take you some time, as you discuss simple amino acids in space, the Urey-Miller experiments and those hydrothermal vents, of course.

Then there's the loaded question. Do you know of any naturally occurring mechanism by which any living organism can develop into greater complexity? Here's profundity, and *deep* profundity at that. First, define complexity. Even a bacterium is amazingly complex. And is a rabbit more complex than a dandelion than a human being? A marvellous topic for research, but be careful here to make sure that your honest uncertainty doesn't get translated into the 'No' category. And votes for 'no', of course, will be a demonstration that scientists are baffled as to how complex organisms arose (enter Deity, stage right). There are, of course, fine documented examples of how complex geometrical shapes of, say, animal shells, have developed gradationally over time from relatively more simple shells (and also of the converse process). But then, that isn't what the question asked. Normally, of course, you have to be a stratigraphical palaeontologist to be familiar with many such examples. Which brings us to…

The very loaded question. Do you know of any fossils which are without doubt a (sic) transitional form? If so please state which and how you know of them… There was some coffee room discussion of this one. It's a tricky one for, say, igneous geochemists (another danger of a 'no' statistic here), just as I would be found wanting if suddenly asked for chapter and verse of the helium contents of mid-ocean ridge basalts. Meat and drink for stratigraphical palaeontologists, though. Personally, I've hammered lots of transitional forms out of the rock, peered at them, measured them, drawn them, now and then published them. Most of the graptolite taxa that I work with can be sensibly (if not always uniquely) fitted into lineages, and when anyone takes the trouble to look really closely (Margaret Sudbury, say, on the triangulate monograptids, a work comparable in its way to Peter Sheldon's demonstration of gradual evolution in the Shelve trilobites) then these lineages become quite convincing.

And finally the punchline question. Should alternatives to Darwinian theory be given more consideration on the National Science education Curriculum? Reasonably phrased – but no mention of which alternatives, exactly, might be considered. There's the Lamarckist alternative, reasonable and influential in its day. Lamarckism should certainly go into any decent course on evolution, if only for its historical importance. Then there's genetic drift, which isn't terribly Darwinian *sensu stricto*, but which has been indicated as an effective driver of inherited change, and also well worth including in any decent curriculum. Presumably the alternative meant, though, is Special Creation or its evolutionary successor, Intelligent Design.

Is there a danger, US-style, that such creation science be given equal weighting with mainstream evolutionary theory on school curricula in UK schools? Unlikely, one might think. Nevertheless, this questionnaire suggests that there is at least one organized attempt in that direction. Does one engage with the questions on it, ignore it or what?

I wonder if the most effective way might be not so much direct response to such questions, especially as they're not easily answered by snappy soundbites, but to think more strategically about how, long-term, to help disseminate understanding of current ideas of global and biological evolution, and what might help bring the really important aspects of Earth history into focus.

Some aspects of geological history are widely popularised, while others are not. Most ten-year-olds, for instance, can correctly identify far more dinosaurs than I can. But dinosaur fossils are rare, while unglamorous invertebrates are common as muck, and their evolutionary history is often much better preserved. There's also the current media obsession with meteorite impacts, erupting supervolcanoes, suffocating oceans and mass extinctions. These have profoundly affected the course of evolution, to be sure. But a close focus on near-Armageddons can almost make one forget about the huge, if more humdrum intervening spans of non-Armageddonish Earth history, readable from good old-fashioned strata.

Strata! Crucial, of course, to determining Earth (and biological) history. But so much part of the backcloth of geology that it's often neglected to explain them: the general public recognition of fossils is still often, it seems, of animal remains somehow buried in the ground, or lying about in caves. Even within the science, the idea of stratal successions as more or less complete and testable records of the biological evolution of skeleton-forming organisms hasn't always been secure. Old textbooks stressed the *incompleteness* of strata, likening them to 'a book with most of the pages torn out'. It's a lovely,analogy, but it's often plain wrong. Sure, in most shallow-water successions, erosion alternates with accumulation as sea level rises and falls. But deepwater strata, particularly in the bottoms of sedimentary basins, can often comprise an essentially complete sedimentary record of time. Where else is there for the sediment to go to?

The minor revolution that is Milankovitch-based stratigraphy, racing into ever-older successions, is eloquent testimony to this relatively new recognition of the essential completeness of many stratigraphic successions. Beautiful combinations of, say, isotopic and palaeontological data are now being published in journals, showing superbly detailed pictures of significant segments of global and biotic history (but if they don't include at least one catastrope they don't usually make it on to the TV screens).

It's a crucial advance, not just scientifically, but as an essential key to dealing, on a human scale, with the huge monster in geology and palaeontology that is Time itself. The standard units we use, millions of years, represent spans so vast that they are pretty well unimaginable, and so are essentially meaningless to the general public: simply abstract numbers. But a Milankovitch cycle, now, say, of 20,000 years. That's a scale the human mind can cope with, just. Stretch one back from the present day. The ice-sheets retreated half-way back such a cycle. The pyramids began to be built one quarter of the way back. The birth of Christ happened one-tenth of the way back along this scale. The start of the Industrial Revolution represents just one per cent of such a unit. Even this smallest of Milankovitch units is still a vast great chunk of time: 600 human generations. Now begin to stack the cycles on top of each other, in the wiggle curves produced by Nick Shackleton and his colleagues. 50 add up to a million years, and the backcloth to biological change, to the evolution from one species to another, will comprise tens to hundreds of such cycles.

It's just one aspect of the new geology, and the resurrection of stratigraphy and palaeontology in the last couple of decades. But it might just, as a psychological link between human and geological timescales, help get across the very big and very complex story of how the Earth and its inhabitants have changed. It also provides a backcloth of humdrum normality (all those stripes in the white cliffs of Dover) against the succession of geo-disasters on TV. And it marvellously allows integration of data, understanding and insights from all of the earth sciences, of linking the story of biological change to that, say, of climate change. No panacea, of course. But it might help palaeontologists to set an agenda, rather than reacting to one.

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CORRESPONDENCE

Reconstructing fossil mammals: strengths and limitations of a methodology

Introduction

A recent review of Jordi Agustí's and my book "Mammoths Sabertooths and Hominids" has seriously questioned the accuracy of my reconstructions of fossil mammals (Jenkins 2003). Facing such commentary, the reader may legitimately wonder if there is any solid methodology behind my artwork. Traditionally, very little has been published about the methodology of restoring past life, in part because the scientific exercise of reconstruction is a rather restricted field. This situation, together with the hybrid nature of the reconstruction work – which is and will remain an art as much as a science – has contributed to keep it in a sort of conceptual limbo, where subjective opinions are often confused with scientific judgements. Things are changing, and several seminal papers published over the last fifteen years (Bryant and Seymour 1991; Bryant and Russell 1992; Witmer 1995) have contributed to lay a firmer theoretical ground for reconstruction. But if we are to reassure the general and specialized readers alike about the reliability of our work, it is up to the reconstructors to provide comprehensible explanations about the working method.

Methodological overview

Anatomical reconstruction proceeds in a series of steps from the inside out, adding layers of tissue as in a "reversed dissection", but the process does not end with the rendering of the animal´s appearance: other aspects, including locomotion and ecology, are incorporated, especially in full environmental representations. My working method is discussed extensively elsewhere (Antón 1996; 1998; 1999; 2003; Antón *et al.*1998; Jablonski *et al.* 2002; Turner & Antón 1997) but a brief summary is opportune here.

1. The first step is to reconstruct and assemble the skeleton of the extinct animal with all its elements in feasible, life-like articulation.
2. The second step is to create an image of the life appearance of the animal with all its soft tissue. This second step can in turn be sub-divided into several layers, starting with the reconstruction of deep muscles and tendons, and continuing with the more superficial musculature, cartilage, fat and skin, and ending with such external details as inferred coat patterns.
3. The third step is the reconstruction of the animal´s pattern of locomotion, and other forms of behaviour.
4. The fourth step involves the reconstruction of the vegetation, landscape, and the environment in which the fossil animals lived.

Criticism of my illustrations has centered on anatomical aspects, so I will concentrate here on steps 1 and 2, with little further discussion of steps 3 and 4.

Reconstruction and phylogeny

Before dealing with the steps of anatomical restoration, it is useful to comment on the phylogenetic aspects of reconstruction. Whether we are filling in some missing vertebrae in a fossil skeleton, or deciding about coat colour pattern of a fossil mammal, we need to refer to related taxa, extinct or extant, in which the unpreserved attribute that we want to reconstruct is better known. An intuitive perception of this principle already informed the working method of Charles Knight in the late 19th century, but modern developments in phylogenetics allow us to refine this procedure considerably.

The most useful theoretical approaches to the use of phylogeny in reconstruction are those of Bryant and Russell (1992) and Witmer (1995). Both programmes are based on one essential concept: that the closest extant relatives, or extant outgroup, of an extinct taxon provide the reference for the most conservative hypothesis about the status of unpreserved attributes. As an additional control, both approaches insist on the necessary reference to the next closest group, that is, the outgroup to the clade formed by the fossil taxon and its closest extant relative.

The programme of Bryant and Russell (1992) includes two major steps: 1), phylogenetic inference of attributes, based on the cladistic distribution of known features in related taxa, and 2), extrapolatory analyses, such as form-function correlation, that infer the unpreserved attributes from the known features of the fossil. The inherently conservative phylogenetic inferences are given priority, and they should only be overturned when the functional or other extrapolatory evidence is compelling. Extrapolatory approaches provide the only means of inferring or interpreting autapomorphies in fossils.

The Extant Phylogenetic Brackett approach (Witmer 1995), was conceived originally as a methodological tool for reconstructing soft tissue but it is applicable to virtually any unpreserved trait in a fossil taxon. This method makes explicit reference to at least the first two extant outgroups of the fossil taxon of interest, and is firmly based on the relation of biological homology. It provides a means of establishing the limits of inferences, allowing the construction of a hierarchy of inference.

One consequence of using these approaches is that one has to refer to updated classifications in order to make founded decisions about unpreserved attributes. One example is the extinct carnivore family Nimravidae, which according to the reviewer is "firmly placed in the dog branch of the Carnivora" (Jenkins 2003), warranting, in his view, a more dog-like restoration of the nimravid *Eusmilus*. A close relationship of nimravids to the Caniformia was proposed over two decades ago (Flynn and Galiano 1982) but that interpretation lost favour as further cladistic analyses were conducted. When I prepared the head reconstruction of *Eusmilus*, the leading studies (Bryant 1991) classified the Nimravidae as part of the Aeluroidea (the "cat" branch of the Carnivora), but more recent analyses (Peigné 2003) suggest that they may actually be the sister group to both branches of the modern carnivores. Regarding reconstruction (figure 1), the two latter interpretations would moderately affect choices about coat patterns and details of the rhinarium (in my recent restorations of nimravids I show them without hair in the dorsal part of the rhinarium, a widespread carnivoran condition, instead of giving them more cat-like noses with hair reaching the anterior margin). None of these two hypotheses would lead us to transfer coat patterns of dogs to nimravids, and even if that were done, coat patterns alone would not make the animals look especially dog-like; as will be made clear in the following sections, the general shape of the head is determined by skull morphology, and by the reconstructed shape of the musculature and the cartilages of ears and nose, all of which are essentially independent of the systematic position of the nimravids within the Carnivora. Consequently, the reader should not be misled to thinking that the reconstructor has the choice to make a fossil carnivore like *Eusmilus* (which has a high skull and a cat-like, shortened rostrum) look "dog-like" by some sleight of hand. If there were such choice, then the reliability of the method would leave much to be desired.

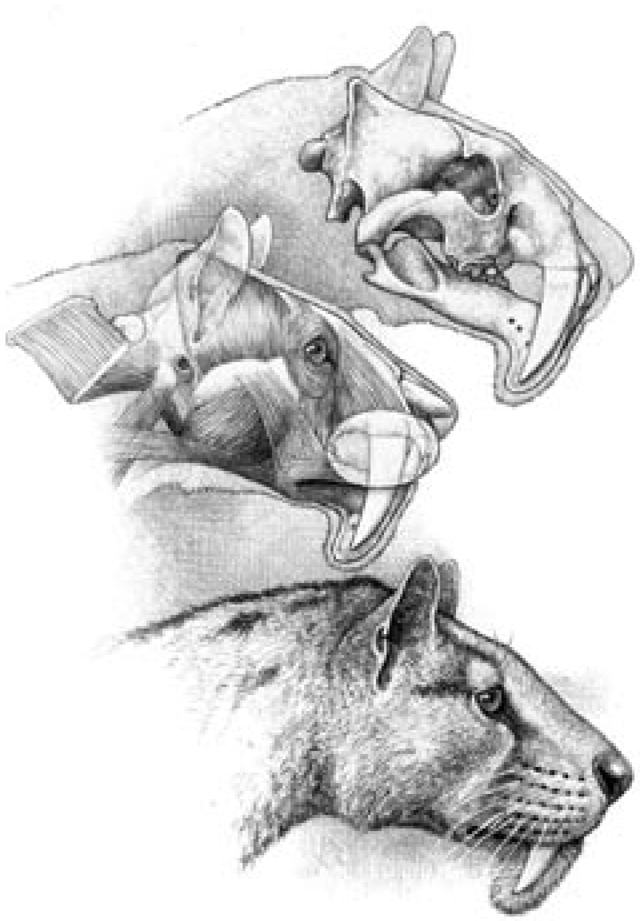

Figure 1. Reconstruction of the head of Eusmilus bidentatus. *The addition of succesive layers of tissue, each traced on translucent paper over the skull reconstruction on top, ensures that the final result is congruent with cranial morphology. The rhinarium is shown without hair on top, differing from most modern cats but resembling most other carnivores. The ears are of a generalized carnivore type, and the coat pattern is a combination of those observed in several modern viverrids, which are among the most primitive aeluroids.*

Steps of anatomical reconstruction

Step 1 (skeletal restoration). This step of the reconstruction is facilitated in the case of exceptional findings of complete, articulated skeletons, like those preserved in Lagerstäten such as Höwenegg, or Messel (Agustí & Antón 2002). However, in the majority of fossil species the skeleton must be restored from dissarticulated, often isolated bones, which may come from individuals of different body size and need to be reduced to a similar scale. The next step then is to articulate the skeleton in a life-like, natural pose, which requires choices about the angles of articulation and the ranges of flexion, extension, abduction and so on. A study of the articular surfaces and an exercise of comparative anatomy are necessary to assess the pose of an extinct animal.

Since the relationships between bone and soft tissue are rather uniform among mammals, the "uniqueness" of a fossil species is already defined at this stage, and soft tissue reconstruction cannot usually add to the "weirdness" of an extinct animal. If the restorations of creatures like the chalicotheres (figure 2) look weird, that is because the relative proportions of their skeletons differ so radically from any modern relative.

To ensure accuracy, osteological features must be studied directly from the fossil material, casts, or at least original descriptions of the fossils, rather than trusting traditional reconstructions which in some cases may be grossly misleading. One example is the paleotherid *Paleotherium magnum*, which has been restored since Georges Cuvier's times as a tapir-like animal, with short neck, short forelimbs and a level back. While preparing the restoration of *Paleotherium* for our book, we reviewed modern literature on paleotheres (Franzen 1995), studied the original description of a complete skeleton (Roman 1922) and examined a cast of that skeleton housed at the Paleontological Institute in Sabadell. This process resulted in a radically different image of the animal, with a long neck, long forelimbs and a sloping back, which actually resembles a combination of an okapi and a heavy horse (figure 3) more than a tapir.

The skull is the single most important element of the skeleton for the restoration of fossil mammals, as it embodies so much of an animal's "personality". It is essential to access the best possible graphic information in order to get a satisfactorily three-dimensional picture of the skull. Working with casts or original fossils has the additional advantage of allowing us to draw the skull from any different angle, but in cases where the fossils are deformed or incomplete, a reconstructed scale model is sculpted and used as reference for drawing non-orthogonal views. When the fossil is simply not available for study, a model can still be sculpted if enough orthogonal views are provided. Many plates in the book show combinations of several views obtained with this procedure.

Step 2 (soft-tissue restoration). Muscle reconstruction requires a study of the insertion areas in bones, as determined by crests, ridges or rough areas. Not all muscles leave marks on bone, and among those that do, muscles with aponeurotic attachments leave more distinct marks than those with fleshy ones (Bryant and Seymour 1990). Muscle restoration implies the recognition of the homology of each muscle in the fossil taxon with that in the referred extant taxa. Establishing homology is simpler for fossil species with close extant relatives, or in those with generalized musculo-skeletal systems. In fossil taxa without close extant relatives or which display obvious autapomorphies in their skeletons, deciding about homology becomes more difficult. In such cases, the phylogenetic approaches become especially useful.

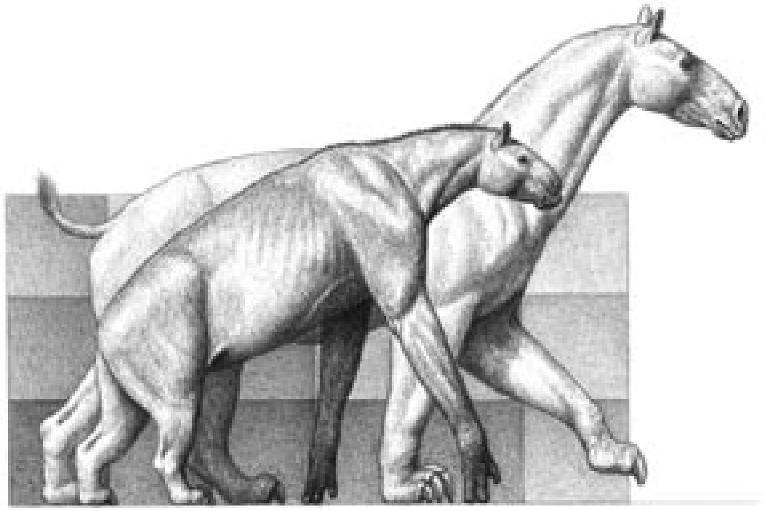

Figure 2. Reconstruction of two chalicotherids from the Miocene of Europe: Chalicotherium grande *(foreground) and* Ancylotherium pentelecicum. *The unfamiliar appearance of these ungulates is just a reflection of their unusual skeletal proportions.*

The skeleton also provides clues for restoring other soft tissues such as cartilage, which is essential for restoring noses and ears. Among mammals, an extremely retracted nasal opening is often associated with a proboscis of varying length, as in the cases of tapirs and proboscideans. The nasals of deinotheres (an extinct group of proboscideans) were enormously modified and retracted, unambiguously indicating the presence of a trunk. However, some specialists have proposed that they should be reconstructed with a short, tapir-like trunk (Tassy 1998). In fact, the morphology of the nasal cavity differed from that of true elephants in several details suggesting that the muscular control of trunk movements in deinotheres was less sophisticated, but those features tell us nothing about actual trunk length, and the modification of the nasal region is certainly much more profound than in tapirs. Looking at the postcranial anatomy, we find that deinotheres had an elephantine body with tall, columnar limbs, and although the neck was longer than in true elephants, it was not nearly long enough to allow the animal to pick objects from the ground, or more importantly, reach standing water, if it had only a tapir-like trunk (Antón, 2003). With these reasons in mind, we have restored deinotheres with trunks of moderate length, shorter than in modern elephants, but long enough to at least allow them a drink without forcing their elephantine limbs to uncomfortable strains (figure 4). This choice may contribute to make deinotheres look too "familiar" for some observers (Jenkins 2003), but it is based on anatomical and palaeobiological reasoning.

The external ear or pinna has a fixed position relative to the auditory meatus in the skull, facilitating its reconstruction, but aspects such as size and detailed shape of the pinna require the use of phylogenetic inference and functional extrapolation. Returning to deinotheres, the only reference for restoring the morphology of their external ears are modern elephants and woolly mammoths, all of which share the same ear shape, with variations in size. The next closest relations would be hyraxes or sirenians, which are too distant and different to provide any helpful clue to ear morphology. Since deinotheres lived in tropical or subtropical climates, we would not expect them to have small ears like the cold-adapted mammoths, so the most conservative hypothesis remains to give them broadly elephant-like ears, again making them look rather familiar, but again fitting with what we know of deinothere relationships and palaeobiology.

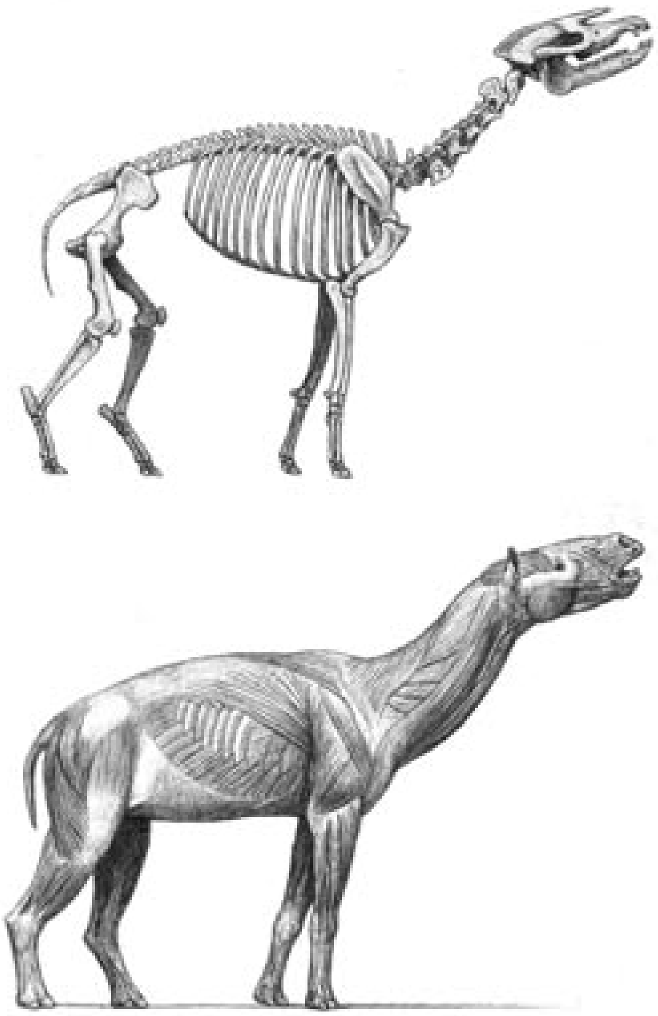

Figure 3. Reconstruction of the Eocene peryssodactyl Paleotherium magnum. *The study of the osteology of this ungulate, traditionally depicted as a tapir-like animal, resulted in a very different restoration.*

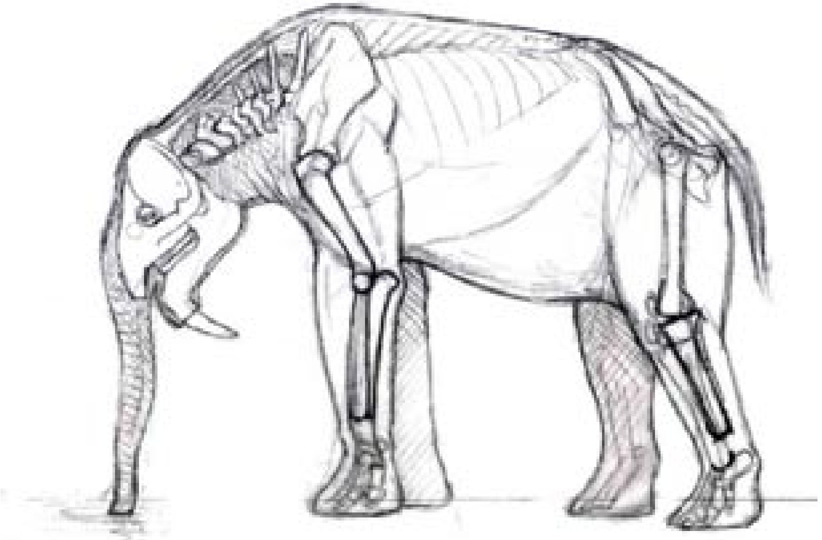

Figure 4. A deinothere drinking. This working sketch shows the neck of the animal in ventral flexion, and the trunk is restored with just enough length to clear the distance to the ground or to standing water. Depicted here is the african species Deinotherium bosazi*, in a study previous to the reconstruction shown in a monograph about the Lothagam fauna (Antón 2003).*

Colour patterns are one of the most speculative aspects of restoration, but one which cannot be eluded when recreating extinct mammals. Some functional reasoning can be applied: predators often display camouflage patterns to conceal their approach to prey; and very large animals usually do not display very bright or contrasting coats. On the other hand, phylogenetical considerations can be superimposed with functional reasoning. So, if we reconstruct a fossil mammal which belongs to an extant family, we can look at living species for widespread patterns of coat colouring, so that the pattern we create for the fossil taxon is a feasible variation within the range of patterns of the larger group, while being consistent with inferred habitat or behaviour patterns. For instance, if we reconstruct an extinct carnivore belonging to the Ursidae (bear family) or Canidae (dog family) we would avoid spotted or striped coat patterns, but if we are reconstructing a fossil member of the Felidae (cat family) whose anatomy indicates marked climbing abilities and thus a forested habitat, then the inference of a spotted pattern would be doubly supported, because such patterns are widespread, and likely primitive for, the felids, and they provide a useful camouflage in wooded habitats. For fossil species belonging to wholly extinct families or orders of mammals, phylogenetic inferences obviously provide increasingly vague results.

One aspect of muscle restoration which may lead to confusion is the use of graphic conventions in myological drawings. Anatomists divide muscles in layers from deep to superficial, and in many cases, muscles of one layer are shown as “cut”, to reveal relevant tissues underneath. Consequently, some muscles appear not to reach their natural end in insertion or origin, and would seem to lead nowhere. This shortcut is the only alternative to using a dozen drawings to illustrate the musculature of a single animal. Also, some superficial, paper-thin muscles, may be drawn as somewhat more solid, to emphasise their presence and the direction of the pull of the fibres. The use of such conventions in my reconstruction of the Miocene pig *Microstonyx* (Agustí and Antón 2002, figure 5.10) implied that the *Levator naso labialis* – an important facial muscle in mammals, whose presence is perfectly well documented in suids (Barone 1989) – is shown "cut". It actually inserts on the skin of the upper lip, but that external layer was omitted in the drawing, in order to keep visible the bony growth over the canines as a landmark reference to the skull drawing. This led the reviewer to perceive it as "a muscle that moves nothing", and then he could not identify the muscle in an anatomical preparation. It is feasible that it was indeed absent from the preparation, because these thin muscles inserting on the dermis are often inadvertently peeled-off while skinning the animals.

The graphic restoration of soft tissue proceeds as a series of drawings in translucent paper, with each layer traced on top of the previous one. This very simple procedure guarantees that gross errors, such as having a restored jaw drawn thinner than the bony mandible, are very unlikely to happen, but that is precisely what the reviewer claims to have observed in my reconstruction of the hyeana-like carnivore *Dinocrocuta*. In fact, the drawing of the *Dinocrocuta* head with open jaws was preceded by a working sketch of the skull with the corresponding gape, and the soft tissues were added over the bony outline as usual (figure 5). In the published version, any reader need only to take a reference measurement, such as the vertical distance between the base of the crown of p3 and the inferior outline of the fur in the mandible in the top drawing, then take the same measurement in the bottom drawing, to find that the measurements are identical down to the nearest millimetre.

Figure 5. Head reconstruction of Dinocrocuta gigantea. *This working sketch is an intermediate stage between the top and bottom drawings in figure 5.6 of "Mammoths, Sabertooths, and Hominids". The skull is traced again with the mandible rotated around the glenoid articulation, the masses of the main mastication muscles are indicated and the external outline of the head is drawn around the skull. Such intermediate stages are not shown in this and many other plates of the book for space limitations.*

"Weird" vs. "familiar" reconstructions

The beauty of this method resides in its conceptual simplicity: once the skeleton is assembled and the necessary phylogenetic considerations are cleared, it is basically a matter of adding layers of soft tissue and watching the creature grow. Yet no matter how robust the method, the artist will always be only human and thus fallible. I have been privileged to collaborate with many leading experts on the various groups of mammals I have reconstructed, and they have often pointed to errors which I had overlooked. Even when the illustration gets the approval of the whole team, it will have to stand the test of time, and as more fossils are discovered and our tools for studying them improve, some interpretations are likely to get outdated.

I am thus well aware that we shouldn't love too well the creatures that we made, but one thing that keeps puzzling me is the reaction of some viewers who appear disappointed when a reconstructed fossil mammal looks more "familiar" than they expected. I think there are several causes for such expectations.

One likely reason is that comparisons of bare bones can be misleading about the likely differences between the corresponding live animals. The habit of comparing skeletal elements trains our eyes to perceive the smallest differences which may help us tell apart different taxa. For instance, there are differences in detail between the skull of a nimravid and that of a true felid, especially in the ear region, which allow us to classify them in different families, but that cannot keep us from perceiving the similarity in overall design. The palaeontologists who classified nimravids as just a subfamily within the Felidae during the first half of the 20th century were competent scientists, and yet those similarities were enough to deceive them. Or let us consider kangaroos; if they were known only from fossil skeletons and an artist would manage to prepare an absolutely correct restoration of their facial appearance, it is likely that some critics would doubt that an animal which was a whole infraclass away from our familiar, placental deer, could look so similar to them in the face. But that resemblance is just a consequence of the relationship between skull shape and soft tissue in mammals.

Expectations of "weirdness" may also stem from misinterpretations of the fossils. The giant creodont *Megistotherium* was described from an isolated skull, considerably larger than those of the largest living carnivores, which led early authors to imagine the whole beast as a gargantuan monster, much bigger than the largest bear or tiger (Savage 1973). But eventually a partial skeleton of *Hyainailouros* (a close relative of *Megistotherium*) was discovered, showing that the animal had a disproportionately large head for its body size (Ginsburg 1980). Although the size of the known cranial elements in *Hyainailouros* is comparable to that of *Megistotherium*, the associated limb bones are no larger than those of a large lion or tiger (figure 6). That was really no great surprise, because other, smaller members of the family hyaenodontidae had been known for decades to have similar proportions. The twofold implication of this is rather frustrating for some previous expectations: on one hand the body mass of giant creodonts was not nearly as large as once imagined, and on the other hand the body proportions of the living animal would have differed from those of modern big carnivores, being more similar to those of some small mustelids.

Yet another factor behind expectations of weirdness can be a psychological need to be surprised, shocked or scared by extinct animals. This is the kind of impulse which led Spielberg's team to turn the coyote-sized theropod dinosaur *Velociraptor* into the tiger-sized predator of "Jurassic

Park", and to embellish *Dilophosaurus* with a clamidosaur-like frill on its neck for which there is no fossil evidence and no real justification. To put it simply, *Velociraptor* was not deemed big and scary enough, and *Dilophosaurus* was not judged weird enough for the film, so they were re-invented.

Our own motivation for undertaking a project like "Mammoths, Sabertooths and Hominids" was, to a large extent, curiosity. I experienced it as an opportunity to learn as much as possible about the palaeobiology of Tertiary mammals, and with such a goal in mind, there would be little point in trying to cheat the readers; I would be the first one cheated. Many years ago, at the beginning of my palaeoart career, finding a book like this one would have been a little like a gift from heaven, and I am sure there are lots of curious people out there, just as eager as I was to see as many as possible of those beautiful, bygone beasts between two covers. Ultimately we are unlikely ever to know the exact size of the ears of deinotheres or the length of the fur of giant creodonts, but what we can do is an honest effort to get as close as possible to restoring their life appearance. I for one will certainly keep trying.

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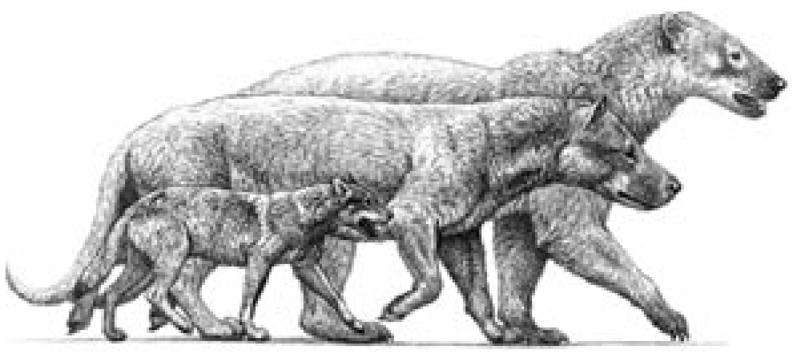

Figure 6. Reconstructions of Hyainailouros sulzeri *(centre) and* Amphicyon giganteus *(background), drawn to scale with a modern gray wolf. In spite of their enormous skulls, giant creodonts like* Hyainailouros *had relatively small bodies, not larger than a large tiger or lion. With big heads and short legs, their proportions differed considerably from those of large true carnivores, such as the amphicyonids.*

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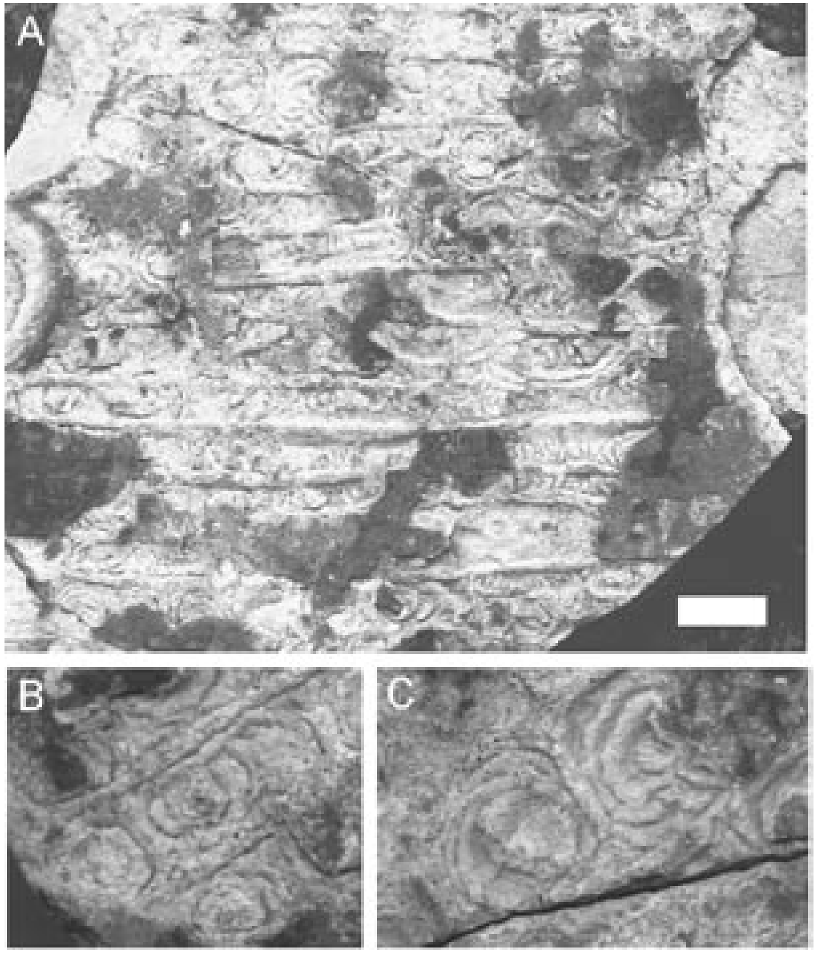
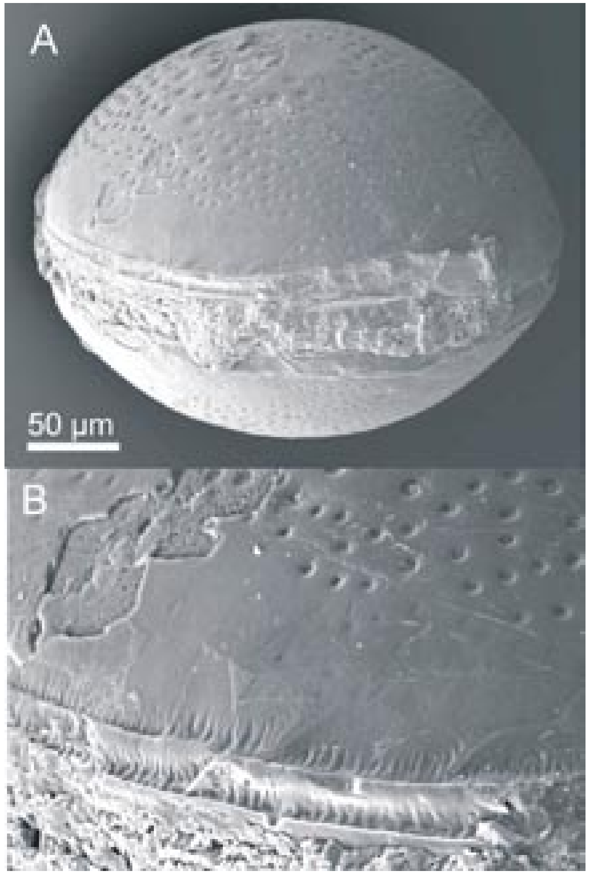
The Mystery fossil

Ever been in the field and picked up a fossil that completely stumped you? Ever been picking through acid residues and thought "What on Earth is that?". Ever had the idea that your mystery fossils might be important, but not have the foggiest who to ask to identify them?

Mystery Fossil Two (Fig 1a-c). This specimen comes from the Lower Purbeck Formation on the Isle of Portland and the alternating limestone and clay shales from which it was found represents cyclic deposition in a lagoonal/playa lake/sabkha setting. The scale on image A is 1 cm. Images B and C are details of A showing 'rings' and 'lines', and 'rings', respectively.



Have you got the faintest of ideas of what this is? Is it even a fossil? As ever, answers in an email to Cris Little <**c.little@leeds.ac.uk**>.



Mystery Fossil One (Fig 2a, b) was a globular microfossil from the Oligocene Lincoln Creek Formation hydrocarbon seep carbonates, Olympic Peninsula, Washington State, USA. Two respondents sent in their ideas as to its identification. John Whittaker from The Natural History Museum (London, UK) suggests the fossil is a marine polycopid ostracod, a group being characterised by their nearly circular carapace. David Williams, also from the NHM, suggests instead that the mystery fossil is a diatom, perhaps belonging to the genera Hyalodiscus or Podosira. Both point out that the oblique-edge view of the fossil makes it rather difficult to be certain about either of these two identification possibilities. Marvellous.

If you have a fossil that you want identifying, please send in an image to <**c.little@leeds.ac.uk**>, as hard copy or in JPEG format (preferred; please ensure that electronic images are at least 1,200 pixels across their long axis and use no more than medium compression).

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Sylvester-Bradley REPORTS

Trace fossils from the Tumblagooda Sandstone of Western Australia

Trace fossils provide important evidence on the timing of the conquest of the land by arthropods – a major milestone in the evolution of life. Recent research, focused on Lower Palaeozoic terrestrial trace fossil assemblages, has shown that the earliest landfall by arthropods was in the late Cambrian, significantly extending the invasion of land by around 40 million years; the Nepean Formation of south eastern Ontario (which includes a distinctive facies characteristic of an aeolian dune deposit) has produced large (up to 12 cm wide) arthropod trackways, attributable to euthycarcinoids (MacNaughton *et al*. 2002).

The Tumblagooda Sandstone of Western Australia, originally dated as Late Silurian (*e.g.* Trewin & McNamara 1995), has recently been re-dated as late Ordovician in age (Iasky *et al*. 1998), based on conodonts from overlying rocks. A highly diverse ichnofauna (*e.g. Heimdallia*, *Diplocraterion*, *Skolithos*, *Beaconites*, *Didymaulyponomos*, *Cruziana*, *Didymaulichnus*, *Diplichnites*, *Palmichnium*, *Tumblagoodichnus*, *Lunatubichnus*, *Rusophycus*, and *Tigillites*) occurs in an aeolian sandsheet and pond facies (Trewin & McNamara 1995). This revised age, together with the amazing diversity of trace fossils, supports the interpretation that the land was colonized much earlier than is indicated by the body fossil record, and correlates with the recent data from Ontario. Indeed, the *Diplichnites* trackways are very similar to those from Ontario, and were probably also produced by euthycarcinoids.

This Sylvester-Bradley award enabled the Tumblagooda trace fossil collections in the Western Australian Museum to be studied in detail. Previous work on this ichnofauna (e.g. Trewin & McNamara 1995) has “scratched the surface” of the total ichnodiversity apparent – unstudied specimens reside in the collection and considerable material remains to be collected in the field. Computer modelling has proved a powerful tool to clarify the producers (and their behaviour) of fossil arthropod trackways, and elucidate the concept of a ‘functional threshold’ (i.e. a transition from in-phase to more stable out-of-phase gaits amongst arthropods as they moved onto land). Computer modelling will be applied to data gathered on the Tumblagooda trackways. In addition, Tumblagooda trace fossil occurrence data will be integrated into analyses of the palaeoenvironmental distribution of Palaeozoic terrestrial trace fossil assemblages (e.g. Draganits *et al*. 2001), as part of on-going studies to “keep track” of the earliest animals on land.

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The Potential Utility of Cranial Arterial Canals and Foramina in the Resolution of Problems in Turtle Systematics

Turtles have long been considered to be representative of the primitive amniote condition and have been used to polarize characters in phylogenetic analyses of other groups of amniotes (Gaffney, 1984). There has been much recent debate surrounding both the relationships of turtles to other vertebrates, and relationships amongst turtles themselves (*e.g.* Lee, 1997; Shaffer *et al*., 1997; Rieppel, 1999). The employment of various suites of characters, both morphological and molecular, has resulted in the production of alternate phylogenies (*e.g.* Bickham and Carr, 1983; Shaffer *et al*., 1997; Wu *et al*., 1999). The inclusion of fossil taxa in phylogenetic analyses has posed the additional problem of the treatment of missing data. The difficulty of dealing with fossil forms has led to uncertainty about the relative positions of such taxa within turtles and the relationships of turtles to other vertebrates.

It has been proposed that the cranial arterial canals and foramina of turtles are useful in determining systematic relationships. Previous studies (*e.g.* McDowell, 1961; Albrecht, 1976), relying heavily on dissection of latex-injected specimens, have found that meaningful differences exist in the relative sizes of various canals and foramina associated with the internal carotid artery. However, these differences have not been quantified, which is a potential source of concern

Figure 1: a dorsal view of Portlandemys mcdowelli (the specimen is BMNH R2914, Holotype)

Figure 2: a ventral view of Portlandemys mcdowelli (the specimen is BMNH R2914, Holotype)

in a systematic study. With this in mind, the goals of this study are three-fold: firstly, to show that there are quantifiably meaningful differences in the canals and foramina of turtle skulls; secondly, to show that meaningful phylogenetic characters can be drawn from these structures; and thirdly, to extend this utility to the fossil record in order to improve our understanding of the phylogenetic position of extinct turtles with respect to extant forms, and the position of turtles within Amniota.

Receipt of a Sylvester-Bradley Award enabled the undertaking of a preliminary research trip to Europe in the fall of 2002, with stops in England and Austria. Three days were spent at the British Museum (Natural History) (BMNH) studying fossil specimens. The BMNH collection contains a number of important fossil turtle specimens and casts, including the type specimen of *Portlandemys mcdowelli* and several examples of *Kallokibotion bajazidi*. Additionally, visits were made to the Oxford University Museum of Zoology (OUMZ) to study the type specimen of *Plesiochelys planiceps*, and to the University Museum of Zoology, Cambridge (UMZC), to study the type specimen of *Mesochelys durlstonensis*. Reconstructions of cranial circulation were created based upon these observations, and a number of interesting patterns with potential phylogenetic implications were revealed. These reconstructions, along with measurements of canal and foramen diameter taken from the specimens, will provide the framework for investigating turtle origins and relationships within turtles once the extant phase of this study is completed.

The Naturhistorisches Museum in Vienna, Austria (NMW), contains a taxonomically broad and important collection of extant turtles. In addition to the breath-taking quality of specimens in the Siebenrock collection, there is an extensive collection of cranial material representing the majority of extant turtle taxa. This museum was therefore ideal to begin the collection of data from extant skull material. Five days were spent studying this collection, and data were collected from 70 specimens representing 31 genera. Canal and foramen diameters were measured by inserting surgical needles of varying gauges until the tightest possible fit was obtained. Canal lengths were determined by probing with a bristle. A suite of skull measurements were also collected from each specimen. A preliminary phylogenetic analysis of data collected from the NMW revealed a phylogenetic signal grouping the Trionychoidea and Testudinoidea, indicating that previously-described qualitative differences are indeed present, and lend themselves to a quantitative re-assessment. Based upon these results, further collection of data from extant specimens is proceeding. Computed-tomography, radiography, and corrosion-casting are being employed in order to gain a more thorough understanding of patterns in extant turtle

cranial circulation. This in turn will enable higher measurement precision and accuracy, and consequently facilitate retrieval and enhance the reliability of morphometric characters from the cranial circulation of extant and extinct testudines.

It is anticipated that this study will provide new information in helping to resolve problems in turtle systematics. The methods employed in this study will be broadly applicable to amniote systematics, and will provide a useful tool to help in deciphering relationships of fossil amniote taxa.

Acknowledgements

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Ontogenetic determination of a new specimen confirms Terrestrisuchus to be a junior synonym of Saltoposuchus

Sphenosuchians occupy a basal position in the evolutionary history of the Crocodylomorpha. These Late Triassic and Early Jurassic carnivores were gracile, cursorial and well adapted for a terrestrial mode of life. This is in contrast to the extant crocodylomorph families (Crocodylidae, Alligatoridae and Gavialidae) that comprise only semi-aquatic forms. *Saltoposuchus* connectens and *Terrestrisuchus* gracilis are closely related sphenosuchians known from the Late Triassic of present-day Western Europe. All *Terrestrisuchus* specimens were excavated from the fissure-filling lagerstätten of south-west Britain whereas all *Saltoposuchus* specimens derive from the fluvial deposits of south-west Germany. German specimens are significantly larger than those from Britain, although the material is identical in appearance except for four key morphological differences that separate these genera in a recent cladistic analysis (Clark, Sues and Berman 2000). These differences concern the proportional size of the maxilla, squamosal ridging, the presence/absence of a sagittal crest, and the relative length of tibia versus femur.

A newly described partially articulated postcranium (BMNH R.10002) from the Slickstone Quarry of Cromhall in Britain shows evidence of open neurocentral sutures in the six most proximal caudal vertebrae. Significantly these sutures close prior to, or shortly after hatching in extant crocodilians (Brochu 1996). The Slickstone Quarry specimen is therefore confirmed to be a juvenile. A simple linear plot of tibia and femur lengths of four representative specimens from Britain and Germany shows that the relative increase in tibia length is greater than that for the femur. BMNH P.47/21 (the *Terrestrisuchus* holotype) is shown to be smaller than BMNH R.10002 and can thus also be considered to have been a juvenile. Limb lengths of the German specimens are consistent with a scenario where they were at an adult stage of growth.

The analysis of Clark, Sues and Berman (2000) included the four conflicting characters, and the resultant cladogram placed *Saltoposuchus* and *Terrestrisuchus* in separate areas of the cladogram. The differences in character coding (Table 1) appear to be the result of ontogenetic variation between the German and British samples. This is consistent with a preservation bias in favour of juveniles at the fissure-fill sites although such bias has yet to be adequately demonstrated. *Saltoposuchus* was named first and therefore takes priority. *Terrestrisuchus* should be considered a junior synonym of *Saltoposuchus*.

Omitting the four ontogeny-related characters from the 33 characters used by Clark, Sues and Berman (2000) effectively removes all disparity between *Saltoposuchus* and *Terrestrisuchus*. A single parsimony-uninformative character (character 26) was also removed from the character-taxon matrix. Four characters ran ordered in the analysis (13, 16, 18 and 19), as was the case in Clark, Sues and Berman (2000). A branch and bound search implemented using PAUP version 4.0 (Swofford 1999) yielded four equally most-parsimonious trees of 48 steps (Figure 1), with a consistency index (CI) of 0.688 and a retention index (RI) of 0.741. This compares favourably with the analysis of Clark, Sues and Berman (2000) which found three equally most-parsimonious trees of 60 steps each with a consistency index (CI) of 0.633 and a retention index (RI) of 0.707. *Saltoposuchus* forms part of an unresolved polytomy with *Pseudohesperosuchus* and *Hesperosuchus* at the base of the ingroup clade. The Sphenosuchia are paraphyletic with the inclusion of the crocodyliforms.

This Sylvester-Bradley award made it possible to visit the collections of the Natural History Museum in London (UK) and the Staatliches Museum fur Naturkunde in Stuttgart (Germany).

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A.

2 Facial portion of maxilla anterior to anterior edge of antorbital fenestra equal in length to or longer than posterior portion posterior to anterior edge of fenestra (0) or shorter than posterior portion (1)

12 Squamosal without ridge on dorsal surface along edge of supratemporal fossa (0) or with ridge (1)

17 Medial extent of supratemporal fossa on lateral surface of parietal separated on midline by broad, flat or gently rounded area (0) or by "sagittal crest" (which may be divided by interparietal suture) (1)

31 Tibia:femur length ratio: less than 1 (0) or more than 1 (1)

B.

	2	12	17	31
Saltoposuchus	0	1	1	0
Terrestrisuchus	1	0	0	1

Table 1. A, descriptions of the four ontogeny-related characters of Clark, Sues and Berman 2000. B, the coding from Clark, Sues and Berman 2000 of each character relating to Terrestrisuchus *(British specimens) and* Saltoposuchus *(German specimens). The designation of juvenile character states to* Terrestrisuchus *is indicated by the shaded coding.*

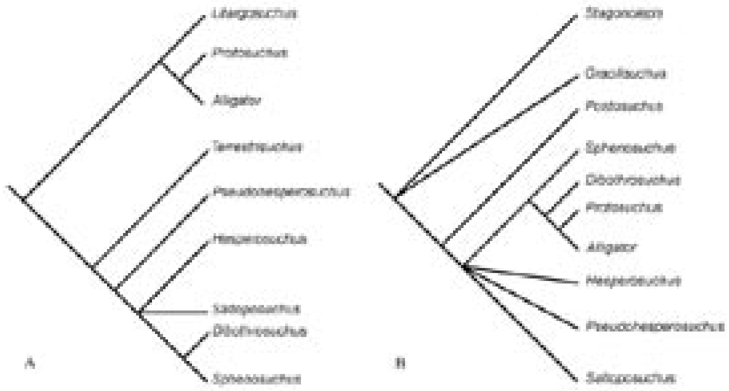

Figure 1. Strict consensus trees resulting from: A, Clark, Sues and Berman 2000. B, the present analysis (the reduced matrix of 28 characters).

A review of fossil felid specimens in the collections of the Naturalis Museum, Leiden, The Netherlands

The Naturalis Museum contains the Dutch national natural history collections and curates and displays both modern and fossil material. The palaeontology department has a wide range of specimens, which includes the famous Dubois Collection from Indonesia and a very large collection of Pleistocene vertebrate fossils from the Netherlands and North Sea.

The purpose of my visit was twofold: first, to see and draw the previously unreported material of *Panthera gombaszoegensis* (Kretzoi, 1938) from the Pleistocene site of Tegelen, the Netherlands and second, to study the Dubois collection of fossil tigers (*Panthera tigris* L.) and compare them to the modern cats.

The trip was even more fruitful than I had originally planned as, during my visit, some of the missing type specimens for *Felis (Panthera) Schreuderi* Von Koenigswald 1960, were found in the collections of the Amsterdam Zoological Museum. These specimens are now referred to *P. gombaszoegensis,* but eight of the type series had been mislaid. This turned out to be due to a cataloguing error from the 1940s, when they were originally identified as *Hyaena* and the catalogue entry had not been changed. As my PhD thesis had involved a discussion of these, presumed lost, specimens I was glad to have the opportunity to study them. In addition, at the Naturalis Museum, the first cast was made of an empty natural mould in which one premolar of a large cat could be seen. This resulted in a positive cast of a very large felid mandible which initially seemed much bigger than any of the other early Pleistocene cats. However, having reviewed all of the available cat measurements, it does appear to fit into the series of *P. gombaszoegensis*, although it was obviously a very large individual. This work has now been submitted for publication.

The opportunity to work on the modern and fossil tigers also proved interesting. The Naturalis Museum has an excellent collection of skulls of the endangered Sumatran tiger, the recently extinct Javan tiger, and an extremely rare specimen of the Bali tiger (this sub-species is also now extinct and only eight skulls are known to exist in museum collections around the world). This material was compared to the Dubois collection of fossil tigers from Java and the results will form the basis of a future study of variation in the tiger.

I should like to thank the Palaeontological Association for granting me a Sylvester-Bradley Award which allowed me to undertake this research visit. The data collected will not only be of use to studies mentioned above, but also for future work on big cats, their biogeography and their evolution. I am also grateful to John de Vos and Lars van den Hoek Ostende for facilitating my visit to the Palaeontology Department, and to Chris Smeenk for his help in mammalogy at the Naturalis Museum. I also wish to thank Minke Det for finding the missing *P. gombaszoegensis* specimens and Adri Rol for allowing me to visit the Amsterdam Zoological Museum collections at very short notice.

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Geographic and temporal intraspecific variation in African mammalian taxa: a comparison of modern and fossil conspecifics

This study examines intraspecific variation in four mammalian species which co-occur in East and southern Africa from the late Pliocene (ca. 3 million years ago) to the present. Specifically, this study explores body size variation within extant species in order to interpret past body size changes. The species chosen for this study are: the spotted hyaena, *Crocuta crocuta* (Erxleben, 1777), the Plains zebra, *Equus burchelli* (Gray, 1824), and the impala *Aepyceros melampus* (Lichtenstein, 1812). The fourth species is the extinct Reck's Springbok *Antidorcas recki* (Schwarz, 1932). These species are suitable for the study of modern and past body size changes as they represent a range of mammalian orders (Carnivora, Perissodactyla and Artiodactyla) and are relatively abundant in the East and southern African fossil record.

Craniodental measurement data were collected, since cranial dimensions are taken to be good proxies of overall body size (Janis 1990). Crania and dentitions are often the most identifiable sections of the skeleton and are most commonly found in museum collections. Measurements were taken on wild-caught specimens of known geographic provenance to compile a modern dataset. Modern variability in cranial and dental morphologies is assessed by morphometric comparison of specimens from East and southern African regions. Multivariate analyses and statistical comparisons of modern samples were used to identify and quantify significant differences across the range of each species. These modern baseline data are then used to investigate temporal variation by examining fossil conspecifics. Identical measurements were taken on fossil material previously assigned to the chosen species. Temporal variability is assessed by comparing modern and fossil specimens from East and southern African Plio-Pleistocene (3.0 – 0.25 million years ago) sites to assess the nature and extent of differences in these species through time.

These results have implications for interpretation of fossil body size and the identification of fossil species, in which size can play an important part. Potentially, this study may also have implications for our understanding of evolutionary changes of fauna in East and southern African sites. Results of this study demonstrate that modern conspecifics follow a size-cline with larger-bodied animals in southern Africa relative to East African conspecifics. This was previously noted for modern *Equus burchelli* subspecies (Klein & Cruz-Uribe 1996) and also in modern *Crocuta* (Klein & Scott 1989). However, comparison of modern and fossil datasets has revealed that fossil conspecifics do not follow the same size cline. This study demonstrates that body size variations occur in modern conspecifics of all four species examined in this study. Likewise, body size shifts between modern and fossil conspecifics have been identified in all four species. However, the nature and extent of this temporal variability is different within each species, as are intraspecific differences within East and southern African regions.

Body size is an important attribute of any animal (Schmidt-Nielsen 1984). Mammalian body-size is influenced by climatic and environmental factors, especially in colder environments where larger body sizes offer a thermoregulatory advantage (Bergmann's Rule). Therefore geographically widespread conspecifics may exhibit body size clines over their range as a response to climatic gradients. Correlations between climate and body size have been well-documented in spotted hyaena. European *Crocuta* body size shifts during the Pleistocene have been attributed to glacial/interglacial cycles (Kurtén 1957; Klein & Scott 1989) and a similar pattern has been recorded in Pleistocene *Crocuta* from southern Africa (Klein 1986).

An alternative hypothesis for the explanation of intraspecific body size changes is that of fasting endurance, where large-bodied conspecifics have the energy resources to survive in more arid, seasonal environments (Linstedt & Boyce 1985; Millar & Hickling 1990). Body size changes through time may therefore be as a result of climatic or environmental shifts. The results of the study thus far seem to indicate that the nature and extent of body size changes in East African fauna are greater than changes in southern African conspecifics. Climatic shifts throughout the Plio-Pleistocene are a likely explanation for the disparity of fossil and modern body sizes in these mammalian taxa. This may indicate that the East African region has undergone a greater degree of climatic change from the late Pliocene to the present.

The Sylvester-Bradley award presented to the author was used to collect data for this study and is gratefully acknowledged by the author.

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Late Permian tetrapods from the Sahara

Based on the presence of common genera in southern Africa, India, Europe, and Russia, the Late Permian has been interpreted as a time of broad cosmopolitanism among terrestrial vertebrates. In particular, the Beaufort Group of South Africa has shaped our understanding of late Palaeozoic and early Mesozoic terrestrial ecosystems because of its thick sedimentary sequence and long history of palaeontological study.

Recent fieldwork in the Upper Permian Moradi Formation of northern Niger suggests that this more equatorial region of Pangea hosted an endemic tetrapod fauna with a community structure remarkably different from that of the Beaufort Group. In contrast to the dicynodont-dominated faunas known elsewhere, the herbivores of the Moradi Formation are predominantly captorhinids, represented by

J. Sebastien Steyer cleaning the vertebral column of a new pareiasaur from the Upper Permian of Sahara; photograph courtesy of C.A. Sidor.

Moradisaurus, and pareiasaurs, represented by a new genus possibly related to *Elginia*. The latter taxon is known from abundant cranial and postcranial material and is characterized by globular bosses over the external naris, orbit, and temporal region. Faunal dissimilarity also extends to the amphibians. Beaufort temnospondyls are rare and low in diversity, with *Rhinesuchus* and *Laccocephalus* representing the only Permian genera. The Moradi Formation has yielded the remains of at least three new taxa, including one possible rhinesuchid and two larger forms that represent families not known from the Permian of southern Africa. Most surprisingly, therapsids are only tentatively present in the Moradi Formation; several isolated maxillae and caniniform teeth possibly belong to a gorgonopsian or therocephalian predator.

Our research in the Moradi Formation suggests that West Africa may not conform to the model of faunal homogeneity previously considered for the Late Permian. The rarity (or potential lack) of dicynodont herbivores, coupled with a unique reptile and amphibian fauna, instead indicates a previously unsuspected area of biogeographic isolation and endemism in the centre of Pangea.

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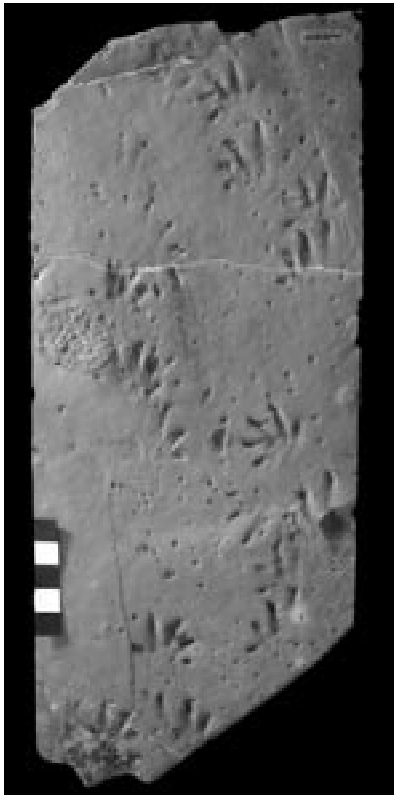
Ichnological Evidence for the Development of Late Carboniferous and Early Permian Terrestrial Tetrapod Faunas

The Late Carboniferous to Early Permian represents a key stage in the evolution of tetrapod faunas. The amphibious assemblages of the Carboniferous declined with the appearance of the amniotes during the later stages of this period, producing a transition to predominantly terrestrial communities that continued into the Early Permian. My Ph.D. aims to chart this transition with the use of terrestrial tetrapod ichnofaunas. A Late Carboniferous (Westphalian D) ichnological assemblage from the Salop Formation (former Keele Beds) of the Warwickshire Group, southern Shropshire forms the principal data set for the project. This ichnofauna comprises the traces of predominantly stem-lissamphibian (recent) tetrapods of the paraphyletic group 'temnospondyli', with a minor early synapsid ('pelycosaurian'), amniote component (Tucker and Smith in press). These biotaxa are represented by the ichnogenera *Limnopus* (*Limnopus*) Marsh, 1894, *Limnopus* (*Batrachichnus*) Woodworth, 1900, *Dimetropus* Romer and Price, 1940, *Hyloidichnus* Gilmore, 1927, and *Ichniotherium* Pohlig, 1885. In comparison, Early Permian ichno-assemblages across Europe (for example, within the Rotliegend of Germany and the sedimentary basins of southern France) suggest a shift within terrestrial tetrapod faunas from predominantly amphibious communities to those with a higher proportion of reptilian amniotes. Ichnogenera such as *Amphisauropus* Haubold, 1970, *Chelichnus* Jardine, 1850, *Dimetropus*, *Dromopus* Marsh, 1894, *Hyloidichnus* and *Varanopus* Moodie, 1929 predominate, representing more derived, 'reptilian' diapsid and synapsid forms. Amphibians are still present, but their abundance and diversity is greatly reduced.

The majority of terrestrial tetrapod body and trace assemblages of the Late Carboniferous and Early Permian are found within an area that stretches across central North America, through Britain, into southern France, Germany and the Czech Republic. This region closely mirrors the position of the Permian equator in relation to pre-drift Europe and North America, indicating a palaeotropical distribution of terrestrial tetrapods along the southern margin of the single Euramerican continent, Laurasia, during this period. An absence of aquatic boundaries enables the uniform distribution of these faunas across this region (Milner and Panchen 1973), and in consequence, North American and European faunas are highly comparable. Therefore, in order to construct a comprehensive, detailed picture of the development of terrestrial tetrapod faunas through the study of ichno-assemblages, comparison of the North American ichnofaunas with those in Europe provides significant complimentary interest. However, despite the similarity of these assemblages, separate ichnotaxonomies have developed in Europe and North America, thereby impeding identification from the literature of North American ichnotaxa that are equivalent to those in Europe.



Type specimen (YPM 304) of Hylopus hermitanus Gilmore, 1927. Courtesy of the Peabody Museum of Natural History, Yale University, New Haven, USA.

This award enabled these problems to be addressed through the examination of many North American vertebrate ichno-assemblages, in particular, holotype material, and the extensive collections of the New Mexico Museum of Natural History. Not only has this allowed a clearer comparison of discrete European and North American ichno-assemblages, it has also clarified the taxonomical situation; many typically 'American' ichnotaxa have been found to be synonymous with 'European' ichnotaxa, at both ichnospecies and ichnogenus level (Tucker and Smith in press, in prep., *a*). Additionally, the large collections of North American material from single sites (such as the Robledo Mountains, New Mexico) allowed an examination of taxon abundances and relative proportions of taxa within these early vertebrate communities. As the detailed study of a large amount of type material has also enabled a partial revision of previously described material from Europe, this data has been synthesised to examine the development of terrestrial tetrapod communities across the Late Palaeozoic faunal transition, looking at aspects of tetrapod community development such as taxon replacement and displacement, and adaptive radiation (Tucker and Smith in prep., *b*). This novel use of trackway data in conjunction with body fossil data has the potential greatly to increase our understanding of terrestrial community dynamics, as well as offering insight into periods of evolutionary transition from a completely new perspective.

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A new shorebird from the Green River Formation of Wyoming and its implications for the phylogeny of the order Charadriiformes

The traditional avian order Charadriiformes ('shorebirds') is a large and disparate group that includes a large number of very familiar coastal birds such as the gulls, puffins and waders (Sibley and Ahlquist 1990). It is currently the only major extant clade of birds for which a large amount of independent data for phylogenetic reconstruction has been collected (*i.e.* osteology, morphology, behaviour, DNA and feathering). Although some of this data has been considered by use of modern cladistic methods, most has not (*e.g.* Strauch 1978; Mickevich and Parenti 1980). The phylogenetic relationships of Charadriiformes are of importance because this is a large group of modern birds (343 species, 91 genera [Hoyo del *et al*. 1996]).

The published fossil record of Charadriiformes is extensive, extending at least to the Lower Eocene and possibly into the latest Cretaceous (*e.g.* Olson 1985; Unwin 1993). Although well-represented fossil material is known from the earliest Tertiary (Olson 1985; Mayr 2000), some incomplete remains have also been considered 'charadriiform' from the Cretaceous (see Olson and Parris 1987); however, all of this material is fragmentary and likely of uncertain taxonomic affinities. Despite this apparent diversity, the fossil record of Charadriiformes has never been investigated within the context of a cladistic morphology-based character analysis.

In order to study a likely new fossil charadriiform specimen (FMNH, Geology Department Collections [PA]718) (see fig. 1) and have access to sufficient extant osteological material for phylogenetic analysis and comparive purposes it was nessecary to travel to the American Museum of Natural History, New York. The travel expenses were funded entirely by a Sylvester-Bradley award, for which the author is extremely grateful.

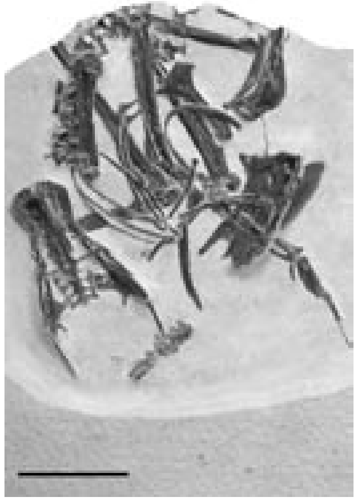

FIG. 1. The preserved elements of FMNH, Geology Department Collections (PA)718. Scale bar equals 50mm.

An extensive character matrix (using most genera in the order Charadriiformes) was constructed and a detailed description of the new fossil specimen was written whilst in New York. The fossil specimen (PA718) described is not named here as the description is, as yet unpublished (Waterhouse, in review).

PA718 (see fig. 2 for reconstruction) was diagnosed as follows: A plover-like shorebird distinguished by a small brachial tuberosity of the coracoid, which does not hook distally, and a straight distal margin of the coracoid. Overall, the preserved skeletal morphology of the fossil compares well with that of modern 'shorebirds'. As a group, Charadriiformes share a number of osteological features considered unique within modern birds (Mayr 2000; Dyke *et al*., in preparation) including six sternal costal processes on the sternum (for the attachment of ribs), absence of a distinct fossa on the medial sulcus of the sternum, and a processus acrocoracoideus of the coracoid that does not point cranially. All of these characters are preserved in PA718 allowing for unambiguous referral of this fossil to the order.

FIG. 2. PA718 right lateral reconstruction. Preserved elements are white, missing elements are grey, feathering and soft tissue are black. Scale bar represents 50mm.

All phylogenetic analyses showed PA718 to be a crown-group member of Charadriiformes (not basal as perhaps would be expected of a fossil about 50 million years old [Lower to Middle Eocene]). From this albeit limited data, it is possible to infer that the charadriiform radiation occurred at, or before, 47–54 million years ago.

PA718 is nested firmly amidst a clade comprising the plovers (Charadriidae *e.g.* the Pacific Golden-Plover, *Pluvialis fulvis*, and the Magellanic Plover, *Pluvianellis socialis*). If PA718 is taken out of this analysis and it is run again, no differences in the phylogenetic relationships of the taxa are recovered.

More details will be presented in a separate publication, which is currently in review. PA718 is at present held in the Field Museum of Natural History, Chicago, Illinois, USA.

I am very grateful to Dr Gareth Dyke for his help and support whilst this work was being carried out, also to everyone in the American Museum of Natural History who are too numerous to name individually.

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Faunal comparisons of Wenlock (Silurian) Crinoidea

The occurrence of British Wenlock crinoids is restricted to only a few localities of very abundant and diverse assemblages. Globally, the Wenlock marks a time of huge diversity and the dominance of crinoids in carbonate environments. Principal outcrops for crinoid faunas are in North America, Gotland and Dudley, and although the bulk of the Ph.D. study was concentrated on the exceptional faunas of the Wenlock of Britain, direct comparisons were made with the other two faunas. The funding that was granted by the Palaeontological Association through the Sylvester-Bradley award allowed direct study of the Gotland fauna in order to relate it to information already gathered from the specimens of North America and the West Midlands, particularly in areas of systematics, ecology and phylogeny.

There is a certain amount of co-occurrence of genera and species across the three global faunas, but with little or no communication between older researchers there is a large degree of assumption involved when accurately identifying species. As such direct reference to type material is an essential part of any study. This was the main purpose of the work carried out at the Riksmuseet, Stockholm.

One of the principal works on Swedish crinoids was carried out by Angelin (1878). Yet despite his groundbreaking monograph, and the large number of new species and genera that it designated, his text was not accompanied by accurate illustrations. In some cases, it is impossible to match the original specimens with the figures that are supposed to portray them. This was partly down to the preference for pretty illustrations rather than accurate ones, often combining the calyx and arms of representatives of entirely distinct classes. Direct study of type specimens of Angelin (1878) and of other important authors at the Riksmuseet, however, highlighted the need for several new genera for the Gotland species, one of which is described and named in Widdison (2001) as *Pleuroptyx.* This genus was erected to classify a single Much Wenlock Limestone Formation species *Pleuroptyx punctatus* (Hisinger), which was originally included in the cladid genus *Enallocrinus* and has erroneously been considered a junior synonym of *E. scriptus* (Hisinger). Re-examination of Hisinger's (1827, 1828, 1837) original material at the Riksmuseet highlights the major differences in the proximal arrangement of fixed brachial plates and necessitates the separation of the *Apiocrinites? scriptus* Hisinger and *Actinocrinites? punctatus* Hisinger into their original species and further into distinct genera. Further taxonomic study of specimens resolved a number of complex synonyms in genera and species that co-occur in the Much Wenlock Limestone Formation and in Gotland, and helped to resolve numerous misidentifications.

Without cladistics, identifying evolutionary trends in Palaeozoic Crinoidea is largely dependent on the appearance of particular morphologies in the fossil record. One of the major morphological trends that has been claimed to occur is the reduction in the number of plates in calyces to the primary building blocks – the radial, basal and infrabasal circlets. This has certainly been concentrated on for camerates (Ubaghs, 1978) but it is generally accepted that all Palaeozoic crinoids possess features that are considered to be both primitive and advanced, and as such there is no derived taxon that signifies the ultimate goal of crinoid evolution.

The classification of Wenlock higher taxa has previously followed that published by Moore and Laudon (1943) and Moore and Teichert (1978), with little evidence to substantiate the groupings. It was thus thought that a cladistical study could be made on the crinoids from the Much Wenlock Limestone Formation in an attempt to test suprageneric classification of the fauna and provide some evidence toward the phylogenetic framework of Silurian crinoids.

The recognition of possible ecophenotypes in crinoids and the vast differences in morphologies of faunas associated with the bioherms and non-reef areas of the Much Wenlock Limestone Formation led to eliminating certain global faunas from the list of possible outgroup taxa. Initial theories that the Gotland fauna was more closely comparable in its diversity to that of the Much Wenlock Limestone Formation led to the study of specimens first-hand, with a view to their use as outgroup taxa. Accurate data sets were compiled only from available material; there was no reliance on the published descriptions. On running the analyses, however, the taxa invariably plotted as part of the ingroup, despite apparent 'primitive' morphologies. In order to resolve the problems of identifying the outgroup, only taxa from within the Much Wenlock Limestone Formation were included, unrooted analyses were run with limited success.

Pleuoptyx punctatus (Hisinger), a cladid crinoid from the Much Wenlock Limestone Formation of Dudley. BMNH 57479, scale bars are 1mm.

In Wenlock crinoids there are no visibly apparent trends in overall morphology, so recognising these trends would identify common ancestry and help perceive a

primitive morphological state that is otherwise difficult to determine. Overall, there is a good consensus between the existing systematic classification scheme and the one suggested by the cladistics. This is particularly relevant in the camerates and the Cyathocrinida (Cladida). The phylogenetic results support the prior erection of two camerate subclasses based on the number of plate circlets in the calyx. There is also good support for most of the multispecific genera (for full results see Widdison 2001).

The results show that the peculiarity in morphologies of flexibles and cladids is not suitably distinct to erect two separate subclasses. They certainly share trends to reduce the number of calyx plates whilst increasing the effective food gathering potential through increased arm number or the development of endotomy. In camerates, although individuals with greater arm numbers are positioned crownward, there is no comparative trend in reduction of calyx plates. It would suggest that the trends of the camerates and that of the flexibles and cladids are independent of one another and do not follow an ultimate design.

Cladistic analysis will help to provide a fuller picture of diversity across the three principal crinoid faunas of the Wenlock, and will finally answer the question of whether any is more advanced than the other. But, most importantly, there is the lengthy process of a systematic review of both Swedish and American faunas before such analysis can proceed. Studies of specimens from the Wenlock of Gotland and North America have highlighted the high degree of over-speciation by previous workers of both faunas, and the somewhat ignored overlap of genera and species between these faunas and that of the Much Wenlock Limestone Formation. In following previously published synonymy lists for British species, it has been noted that incorrect identification, in particular of Swedish crotalocrinids (Cladida) and North American eucalytocrinids (Camerata), disguises a large number of new species yet to be correctly assigned taxon names. What is clearly required is a comprehensive review of all Silurian taxa in order to provide more accurate systematic descriptions and classification.

This research has served to highlight the level of work required to bring crinoid palaeontology up to date. The publication of monographical studies into specific faunas, not just those of Britain, would go a long way to solving many of the taxonomic and nomenclature problems that workers face. Such research would pave the way for studies of phylogenetic relationships between crinoids of the entire Wenlock and allow the formation of an up to date, and more accurate classification system.

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A comparative study of Early Triassic gastropods from Italy and Oman

Gastropod faunas in the aftermath of the Permian-Triassic (P-Tr) extinction event (*'when life nearly died'* Benton 2003) are usually impoverished and many P-Tr genera are Lazarus taxa. A typical fauna from the Palaeo-Tethys is preserved in the Lower Triassic Werfen Formation that crops out in the Italian Dolomites. In contrast to this, the Griesbachian (Lower Triassic) Al Jil Formation of Oman from Neo-Tethys has yielded a new and partially silicified diverse gastropod fauna, uncharacteristic of this time interval (Krystyn et al. 2003).

Erwin (1996) attributed the abundance of Lazarus genera at this time to the absence of silicified faunas. Any of the genera present in the silicified fauna (Oman) and not in the unsilicified fauna (Italy) could therefore be reappearing Lazarus taxa. A study of these two contemporaneous faunas was conducted with the following aims. Firstly, to test Erwin's hypothesis; does the Oman fauna contain Lazarus taxa that are not found in unsilicified contemporaneous assemblages (Italy)? Secondly to gain knowledge of the nature of typical Early Triassic gastropod faunal preservation and generic diversity in a field setting.

The gastropod fauna from the Mazzin and Siusi Members of the Werfen Formation (sampled at Passo San Pellegrino, Sass de Putia and Siusi) is taxonomically impoverished compared to that of the Oman. The fauna is composed of the genera *Bellerophon*, *Coelostylina* and one unidentified mid to high spired form. These gastropods are preserved as internal and external moulds, with little evidence of original shell material. Fossil occurrence seems to be restricted to a number of sedimentary facies; notably thin-bedded, Fe-rich red siltstones, mollusc coquinas, oolites and muddy carbonate slump deposits.

The depauperate nature of the Italian fauna contrasts with that of the Oman Al Jil Formation. This is very diverse and is composed of at least eleven genera: *Ananias*, *Bellerophon*, *?Byzantia*, *Chartronella*, *Coelostylina*, *Naticopsis*, *Omphaloptychia*, *?Soleniscus*, *Strobeus*, *Worthenia* and *?Zygopleura*. 105 specimens out of 350 recovered from Oman material have been identified to generic level. Coarse silicification precludes further precise identification as characteristic features are obliterated and even a few of the generic identifications are tentative. The Oman gastropods are preserved as silicified casts and more rarely silica filled internal moulds.

The greater diversity of the Oman fauna compared to the Italian fauna is interpreted as being partly taphonomic; early silicification often 'captures' significant aragonitic components of faunas otherwise missing from unsilicified equivalents (*e.g.* Cherns and Wright 2000; Wright *et al*. 2003). The Italian fauna may originally have been more diverse, but some of the gastropods have been lost from the fossil record through early aragonite dissolution. Original shell composition (possibly calcite layers in shells/low organic content), as well as abundance of a particular genus may have secured its entry to the fossil record but there is no direct evidence for this.

If the lack of silicified faunas at this time was the main cause for the Lazarus effect through the P-Tr interval (Erwin 1996), then we would expect some of the missing taxa to be present in the Oman fauna. However, with the possible exception of *Ananias*, all the Oman gastropods identified are known from Griesbachian deposits elsewhere (see Gastrobase <**http://www.earth.cf.ac.uk/people/summaries/GASTROBASEdoc.htm**>). Therefore Erwin's silicification hypothesis for Lazarus genera seems to be only part of the story.

The other reason for the greater diversity of the Oman fauna is environmental. The Oman fauna, the most diverse Griesbachian assemblage yet known, was living under well-oxygenated, shallow marine conditions. Oceanic anoxia was the norm for the rest of the Tethys at this time including the Werfen Formation in Italy (Wignall and Twitchett 2002). Oman was one of the few locations in Tethys free from oceanic anoxia in the Griesbachian; no sedimentological or palaeontological evidence exists for anoxia until later in the Griesbachian (Krystyn *et al*. 2003).

Comparative study of an unsilicified (Italy) and silicified (Oman) Griesbachian gastropod faunas has enabled the taxonomic diversity differences to be appreciated. The diverse nature of the Oman fauna is attributed to taphonomy (silicification) and favourable palaeoenvironmental conditions (well-oxygenated setting). The depauperate nature of the contemporaneous Italian gastropod fauna is conversely attributed to the lack of silicification and harsh palaeoenvironmental conditions (oceanic anoxia). The Oman fauna contains possibly only one reappearing Lazarus genus (*Ananias*); all other genera are known from Italy or other Griesbachian sections. This comparative study has highlighted how contrasting taphonomy along with differing ecology can result in very different faunas from contemporaneous geographically similar carbonate shallow marine settings.

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The effects of the end-Triassic extinction on the ichnofossil record of Austria

Introduction

Of the five largest mass extinction events that punctuate the Phanerozoic, the end-Triassic event is the least known, due to the limited number of complete sections spanning the Triassic/Jurassic (Tr/J) boundary. This situation is now changing, and the number of studies concerning the end-Triassic event is on the increase. However, with this increasing understanding, the general perception of the event has altered. The evidence for catastrophic extinction at the end-Triassic is now questioned (Hallam 2002) and it has been suggested that widespread facies change, rather than a real biotic extinction, accounts for the faunal turnover (*e.g.* Cuny 1995).

The advantages of studying the ichnofossil record

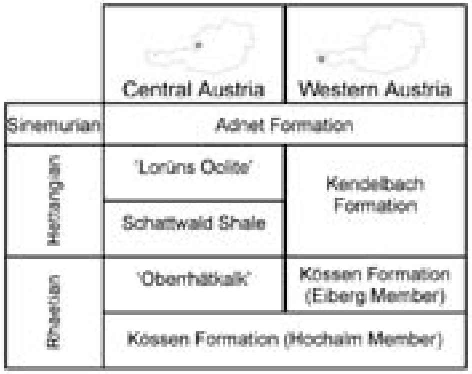
Trace fossils regularly record the behavioural activity of soft- as well as hard-bodied taxa. They therefore provide the best insight, other than through rare Konservat-Lagerstätten, into the soft-bodied benthic palaeocommunity. This is of particular importance when studying extinction events as modern day marine ecosystems are dominated by soft-bodied taxa (Allison & Briggs 1991, p26). Similar dominance in ancient marine ecosystems is shown by Konservat-Lagerstätten. Only by using a technique whereby the records of both hard- and soft-bodied taxa can be studied is it possible to evaluate the response of the benthic palaeocommunity as a whole to a perceived extinction event.

The advantages of studying the Tr/J boundary interval of Austria

Trace fossils vary in a complicated way with facies (*e.g.* Ekdale 1988). To simplify their study, it was therefore necessary to compare the ichnofauna of similar palaeoenvironments. In England this is difficult, as unusual salinity conditions existed during the Late Triassic (Hallam & El Shaarawy 1982). However, these salinity considerations do not apply in Austria, where normal salinity existed throughout the boundary interval (*ibid*. 1982).

Methods

The Tr/J boundary was logged through a shallow marine section in Western Austria and a relatively deep water succession in Central Austria (Figures 1-3). The ichnotaxa present were identified, and the degree of bioturbation was assessed using a vertical ichnofabric index (*sensu* Droser and Bottjer 1986).



	Central Austria	Western Austria
Sinemurian	Adnet Formation	
Hettangian	'Lorüns Oolite'	Kendelbach Formation
	Schattwald Shale	
Rhaetian	'Oberrhätkalk'	Kössen Formation (Eiberg Member)
	Kössen Formation (Hochalm Member)	

Figure 1: The stratigraphy across the Tr/J boundary of Central and Western Austria

Results

Western Austria

In Western Austria, a section spanning the Tr/J boundary was studied at the Vorarlberg Cement Works near Lorüns (Figure 3). A modest ichnofauna, and intensive bioturbation, is present in the shallow water limestones of the Triassic Oberrhätkalk immediately below the Tr/J boundary. Although only the ichnotaxa *Planolites* and *Skolithos* are present, ichnofabric indices of ii3-5 are common. The Tr/J boundary is located in the overlying Schattwald Shales (McRoberts *et al.* 1997), a series of deep water laminated marls and limestones that contain no ichnofauna. The Lorüns Oolite represents a return to shallow marine conditions, and the resumption of carbonate production. These rocks are generally too homogeneous for ichnofabric analysis. At only one horizon, approximately 20 metres above the Tr/J boundary, do the two ichnotaxa *Planolites* and *Skolithos* re-appear.

Central Austria

At Gaißau in the Salzkammergut of Central Austria, a section through the Eiberg Member of the Kössen Formation was examined (Figure 2). The Eiberg Member represents an intraplatform basin, bordering the carbonate platform of the Oberrhätkalk in the West (Golebiowski 1990). The limestones of the Eiberg Member contain a rich and abundant assemblage of five ichnotaxa: *Diplocraterion*, *Planolites*, *Rhizocorallium*, *Skolithos*, and *Zoophycos*. Ichnofabric indices of 3–4 (*sensu* Droser and Bottjer 1986) were recorded throughout the section. This is in stark contrast with rocks from the same Formation only 10 km west of Gaißau, in the Kendelbach Gorge, where the uppermost part of the Kössen Formation is exposed (Figure 2). Although the limestones here are similar in appearance and lithology to those of Gaißau, they contain no readily observed trace fossils. The limestones are homogeneous, possibly the result of total bioturbation, or possibly simply reflecting the homogeneity of the deposited sediment. It is also possible that the rocks in the Kendelbach Gorge have been subject to local recrystallisation, removing any original fabric.

Similarly deep water deposition continued at the Kendelbach Gorge through the Hettangian Kendelbach Formation. Limestones of the Kendelbach Formation are again too homogeneous for easy application of Droser and Bottjer's (1986) ichnofabric index. No trace fossils were found in these rocks.

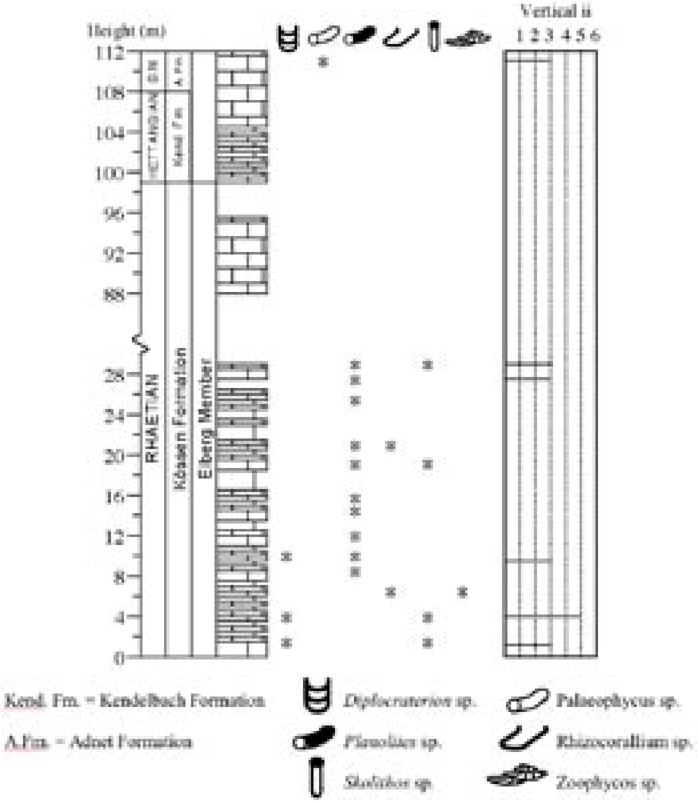


Figure 2: Sedimentary log through the Tr/J boundary of Central Austria, showing values obtained from vertical ichnofabric index analysis. Observed occurrences of ichnotaxa marked with asterisks.

Discussion

At first glance, Figures 2 and 3 show similar ichnofaunal patterns. The Rhaetian sediments, represented by the shallow marine Oberrhätkalk in Western Austria, and the deeper marine Kössen Formation in Central Austria, have a modestly diverse ichnofauna and are well-bioturbated. In Western Austria, this bioturbation continues until immediately below the Tr/J boundary, while in Central Austria, the Kössen Formation immediately below the boundary appears to be barren. In neither Western nor Central Austria is there a well-developed ichnofauna during the Hettangian, other than at one horizon within the Lorüns Oolite, 20 metres above the Tr/J boundary (Figure 2). The apparent ichnofaunal disturbances approaching the Tr/J boundary are consistent with an end-Triassic environmental perturbation.

But to what extent do these observations reflect preservational bias rather than environmental disturbance? The sediments of the Upper Kössen Formation at Kendelbach are homogeneous, as are the sediments of the Hettangian Kendelbach Formation and Lorüns Oolite. In the absence of burrows, the unequivocal evidence of bioturbation, there are a number of potential causes of

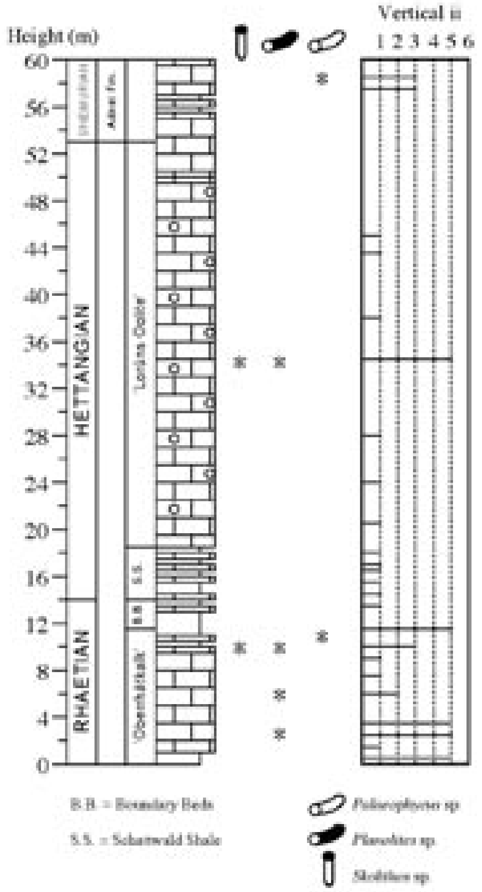


Figure 3: Sedimentary log through the Tr/J boundary at the Lorüns Quarry, Western Austria, showing values obtained from vertical ichnofabric index analysis. Observed occurrences of ichnotaxa marked with asterisks.

this homogeneity. Sediments with a similar appearance may be produced by homogeneity of original deposition, or by the subsequent re-crystallisation of the rocks. Independent evidence is necessary to clarify the situation.

Geochemical investigation provides an alternative source of evidence for end-Triassic environmental disturbance. The lower Schattwald Shale of Western Austria coincides with a negative excursion in ^{13}C and a positive excursion in ^{18}O, and these excursions may reflect a short-term decline in primary productivity coincident with the Tr/J boundary (McRoberts *et al.* 1999). Such a decline in primary productivity would support the theory that the observed decline in bioturbation approaching the Tr/J boundary was caused by environmental disturbance rather than preservational bias. It is possible, however, that these geochemical trends are the product of diagenesis (*ibid.*).

Summary

The ichnofossil record of Austria appears to record the effects of an environmental disturbance across the Tr/J boundary. In both Central and Western Austria, there is evidence of a moderately diverse ichnofauna producing well-bioturbated sediments in the Late Rhaetian. Yet in both Central and Western Austria, this ichnofauna disappears at, or slightly before, deposition began in the Hettangian, and remains generally absent throughout deposition of the Hettangian sediments. The disappearance may, however, reflect preservational, rather than true biological, factors.

Acknowledgements

The fieldwork in Austria was funded by a Sylvester-Bradley Research Grant awarded by the Palaeontological Association. Thanks to the staff at the Vorarlberger Zementwerk Lorüns for allowing access to the boundary section at Lorüns, and for their hospitality. Thanks to Will Barras for field assistance throughout the trip.

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Software Review

MacClade 4

MacClade 4.05 is the latest version of the popular phylogenetic software written by David and Wayne Maddison and published by Sinauer (**http://www.sinauer.com/**). The authors state in the really excellent manual that the aim of MacClade is “to help biologists explore the relationships between data and hypotheses in phylogenetic biology.” MacClade has been widely used to do just that. Many phylogeneticists have used MacClade to organize their data and compile matrices, to build and manipulate trees and to explore patterns of character evolution. MacClade uses the NEXUS file format and is compatible with and generally used in conjunction with other NEXUS programs such as PAUP* (Swofford, 1998). MacClade is the only software of which we are aware that implements stratigraphic parsimony (Fisher, 1991) and may be of particular interest to Palaeontologists for that reason.

The new version benefits from some major enhancement, mainly to the *Data Editor*, and mainly addressing the needs of molecular systematists. Enhancements include options for sequence

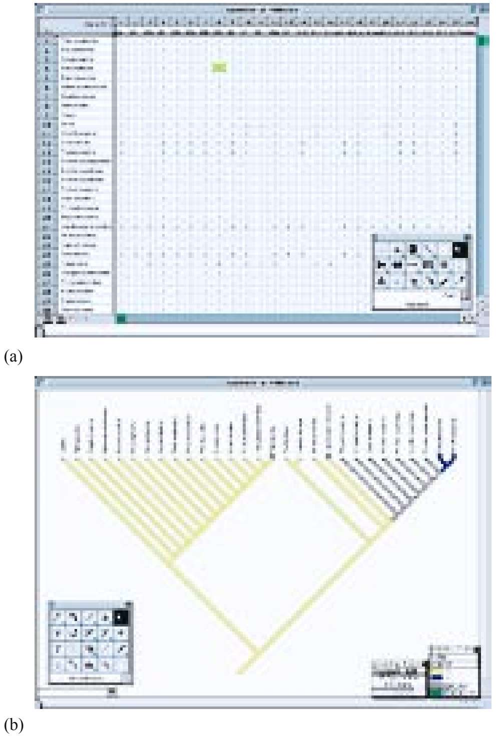

Fig. 1. Screenshots of MacClade 4.05. (a) The Data Editor. (b) The Tree Window. The data set used to take these screenshots is from Gauthier et al. *(1988).*

alignment (both manual and automated), for calculating consensus sequences, for plotting the number of nucleotide changes, on a given tree, at the first, second, and third codon position, and for plotting relative frequencies of various transitions and transversions.

MacClade 4.05 (hereafter referred to as version 4) is faster than MacClade 3.7 (hereafter referred to as version 3). We measured how rapidly these programs opened a tree file of 2,000 trees on 115 taxa. Version 4 was approximately 20% faster than its predecessor. Another improvement in version 4 is that files can now be opened with a double click also when the program is already uploaded in memory. Although only a minor change it is very pleasing. Another very timely, and much needed enhancement is represented by the option for saving data matrices in HTML format for Web publishing. Posting systematic data and conclusions on the Web makes them readily accessible, it is eminently sensible and to be encouraged. Having software that makes it easier to convert data and trees into Web pages will result in more data being available. We would encourage authors to consider making their data and trees available in central repositories such as TreeBase <**http://www.treebase.org/treebase/**> or CladeStore <**http://palaeo.gly.bris.ac.uk/cladestore/default.html**>.

While most improvements are in the *Data Editor,* the *Tree Window* has undergone minor improvement in that the *tool palette* opens together with the tree window rather than having to be dragged open. An important enhancement is the introduction of *list windows* that bring a unified interface to the management of trees, taxa and characters. Compatibility with PAUP has been enhanced in the use of taxon and character sets.

The improvements definitely make version 4 a better drive than version 3. However, for the (non-molecular) palaeontologist, the relevant enhancements are nice but not substantial. MacClade is a useful tool for phylogenetic palaeontologists. While we would advise any researcher who does not have MacClade to get it we are less convinced that a cost-benefit analysis indicates that Palaeontologist users of MacClade 3.5 or higher should upgrade to version 4.

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Book Reviews

Atlas of pollen and spores of the Polish Neogene.
Volume 1 – Spores.
Volume 2 – Gymnosperms

Stuchlik, L. (ed.). 2001, 158 pp.; 2002, 237 pp. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków. ISBN 83-85444-79-3 (pbk), US$40; 83-85444-92-0 (pbk), €48.

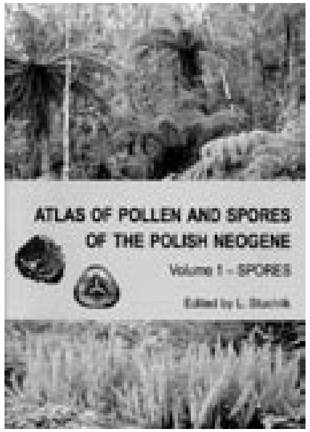
Studies in Australian Mesozoic palynology II

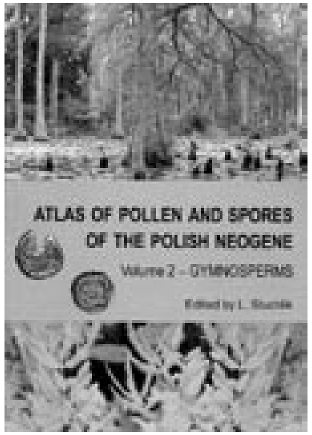
Laurie, J.R. and Foster, C.B. (eds). 2001. Memoir 24 of the Association of Australasian Palaeontologists. iv + 235 pp. ISBN 0-949466-22-0, ISSN 0810-8889. Aust.$128.

These three volumes consist largely of systematic descriptions of palynomorphs and are, therefore, primarily of value to the specialist in palynology rather than to palaeontologists in general. All are useful additions to the literature, the Polish ‘atlas’ having sorted out some of the taxonomic problems that have accumulated in the literature over the years, and the Australian memoir containing fine descriptions and illustrations of mostly new taxa of Mesozoic dinoflagellate cysts.

The spore and pollen volumes are the first two of a projected series of four on the miospores that have been recovered from Neogene deposits in Poland. Volumes 3 and 4 will deal with the pollen grains of flowering plants and are due to be published within the next three years. The aim of the series is to provide a synthesis of the taxa that have been described from the succession during the past half century. The contents are based on both the published literature and unpublished documents, the latter housed in the archives of Polish geological institutes and the W. Szafer Institute of Botany. The authors [L. Stuchlik, M. Ziembi ska-Tworzydło, A. Kohlman-Adamska, I. Grabowska, H. Wałyłska, B. Słodkowska (vol. 1 only), and A. Sadowska] express the hope that the ‘atlas’ will be of value to palynologists concerned with the Neogene stratigraphy, palaeobotany, palaeoecology and palaeophytogeography of Europe.

Both of the large format (A4) volumes contain a short introduction, some observations on the morphological terminology used, and a map on which all of the localities of the ‘profiles’ (sections) mentioned in the text are indicated. Volume 2 also includes a figure showing the stratigraphic coverage of the sections plotted alongside chronostratigraphic, lithostratigraphic and generalized lithological columns. The bulk of each volume consists of systematic descriptions and plates (56 pp. + 42 pls in vol. 1, 54 pp.+ 82 pls in vol. 2). Almost all of the figures on the plates in volume 1 are of specimens that have been photographed in transmitted light and reproduced at the convenient magnification of x1000; only four are scanning electron micrographs. Rather more use of the latter has been made in volume 2.





In the past, too many subspecies and subgenera have been erected to accommodate minor morphological variations in European Cenozoic pollen and spores. The opportunity has thankfully been taken to elevate many of the subgenera to generic rank and to regard most of the subspecies as being within an acceptable morphological range for a species, though a few have been raised to specific rank. The descriptions of all of the species are preceded by synonymies. These list non-Polish papers that contain important taxonomic changes and all Polish publications. The descriptions themselves are presented in a standard format, and the taxa are grouped according to their presumed botanical relationships at order or family level. Within this grouping the taxa are arranged alphabetically according to genus and the species each includes. The botanical affinities and geographical occurrences noted are based on morphological resemblances to the spores and pollen of extant taxa, and present-day distributions of these plants. All of the species or genera to which the miospores have been assigned are classified as Palaeotropical for tropical and subtropical components, and Arctotertiary for warm- and cool-temperate elements. The stratigraphic distributions are based on data from the general palynological literature and their distribution in Poland again according to both published and unpublished national records.

Unfortunately, missing from both volumes is an abstract that includes a list of the new taxa and revised combinations of genera and species. This would have been useful, especially since the taxonomic indexes provided also lack this information. It is necessary to check through the text or plate explanations to determine how many of each are involved. Volume 1 contains descriptions of 176 species of spores referred to 48 genera; of these, one of the genera and five of the species are new, 28 are in new combinations, one species has been renamed, and one subgenus has been elevated to generic rank. The second volume is concerned with 97 species referred to 20 genera. Six of the species and two of the genera are new, one subgenus is elevated to generic rank, the diagnoses of four genera are revised, and there are 20 new combinations.

Although also largely comprising systematic descriptions of palynomorphs, the Australian memoir differs markedly in its physical appearance (smaller page size, photographic illustrations of very uniform appearance) and in the approach adopted by the authors. Apart from a brief introduction to the volume by the editors (pp. i–iii), all but four of the 235 pages consist of eight papers by J.B. Riding and R. Helby; the single exception is by Helby and A.D. Partridge on a new genus (*Bonbonadinium*) and species (*B. granulatum*) from Tithonian (uppermost Jurassic) deposits on the North-West Shelf of Australia. The papers range from those that concern species of particular genera (*Bonbonadinium*, *Phallocysta* and *Wanaea*) to those that contain descriptions of a variety of taxa from particular zones or stages. They are arranged in stratigraphic order from oldest to youngest (Toarcian–Aptian and Albian).

The collection is intended to provide the taxonomic foundation for some of the Jurassic and Cretaceous zones that are widely identified on the North-West Shelf. It is based on palynological assemblages recovered from numerous wells that have been drilled on the shelf together with some encountered in well sections from further afield (*e.g.* South Australia, New Zealand), and it supplements the contents of a paper by Helby *et al.* in an earlier (1987) publication of the Association of Australasian Palaeontologists on Mesozoic palynology; hence the ‘II’ in the title. Thirteen genera and 55 species are described as new, and the diagnoses of a further six species and nine genera are emended. A full description of the criteria on which the impressively detailed biozonation of the succession relies is currently being prepared by Helby and Partridge. Such precision is critical to the demands of production and development geology in a mature hydrocarbon province. It is expected that in due course there will be further publications devoted to descriptions of dinoflagellate cysts on other parts of the succession.

There is no question that good taxonomy is essential if biostratigraphy of high resolution is to be achieved, and this volume is a fine example of how to describe and illustrate dinoflagellate cysts. Each paper contains biostratigraphic observations on the taxa, and some also include notes on other topics, such as palaeoenvironments. Almost all of the photographs that make up the composite figures are of high quality with clean backgrounds, though a few (*e.g.* five of those on p. 207) are dull and lack contrast. This volume can be recommended to all palynologists who work on fossil dinoflagellate cysts.

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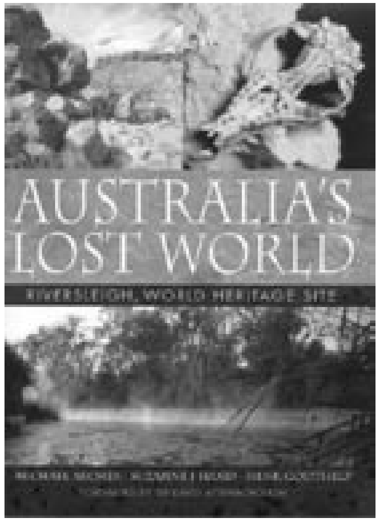
Australia’s Lost World: Riversleigh, World Heritage Site

Michael Archer, Suzanne J. Hand, and Henk Godthelp (2000), Reed New Holland: Sydney, Auckland, London, and Cape Town. USD$39.95.

It is usually a treat for a scientist, particularly a palaeontologist, to visit Germany. The reason is not the Bavarian beer, the rolling landscape, or the picturesque university towns, but the books. German popular scientific books, especially palaeontological ones, are unusually rich in their detail, their depth, and their illustrations. Multitudes of colour pictures of fossil specimens, artful reconstructions, detailed maps, historical tidbits, and genuine artwork are combined with generous text in books that are a delight to peruse, regardless of whether the reader is old or young, scientist or amateur. Indeed, the books are so generously illustrated that even the person who does not read German can spend hours absorbed. Recent examples of this genre include *Lebendige Eiszeit* by Wighart von Koenigswald (2002, Theiss) or *Vom Schwarzwald zum Ries* by Elmar Heizmann (1998, Verlag Dr. Friedrich Pfeil). Visitors to Germany may well ask, “Why can’t we have this kind of book?”



Anglophone publishing has gone a rather different route than German. We have no lack of popular scientific books, despite the unbreakable cultural truism that scientists do not communicate their work in accessible form to a non-scientific audience. Funding councils invest in trying to reverse this mythic trend. British and American publishers clamour for science books to replace their lines of history, art, and travel, certain in their conviction that the move towards science will turn their company around. The sad truth, however, is that even though there are so many of them, English language popular science books are seldom very interesting. Part of the reason is that scientists have a strong tradition of the journal article as the primary medium of communication, rather than the book which is the mainstay of the humanities. Most scientists simply do not publish books, and those who do often do so with the goal of supplementing their income or increasing their fame rather than exploring new intellectual pathways. Science writing is thus left in the hands of a small group of scientists and a larger group of non-scientists. Publishers shepherd their writers to write to their audience, who is always imagined as an eleven-year old boy with mild attention deficit disorder. We end up with science books whose overcharged, bipolarized plots often more resemble a noisy 3-D computer war game than an engrossing intellectual read. Andy Clark’s *Natural Born Cyborgs* (2003, Oxford University Press; we feared them, now they’re here…), Robert Aunger’s *The Electric Meme* (2002, Free Press; “thought gene” are electric buzzing in the brain…), or Walter Alvarez’s *T-rex and the Crater of Doom* (1999, Bt Bound; big rock smashes half the life on earth…) are notable examples. But as 3-D computer war games, most scientific books can’t compete with *GameBoy*. So the pre-teens go to Sony, and the rest of us walk through the ever lengthening Border’s science shelves, thoughts of the *Schwarzwald* in our minds, wondering, “Why can’t we have this kind of book?”

Australia’s Lost World by Michael Archer, Suzanne J. Hand, and Henk Godthelp is an island in the sea of Anglophonic cacophony. Originally published in 1991, it was republished in 2000 by Reed New Holland. The book was written as a visitor’s companion to the Riversleigh World Heritage Site, a terrestrial sequence in Queensland spanning almost 24 million years, from the late Oligocene through the Holocene. Terrestrial Cenozoic sites are rare in Australia, and Riversleigh is their keystone.

The authors do considerably more than give us a picture book of a few fossils (though good pictures of fossils are generously supplied). Australia’s palaeontology is contextualized in a wide ranging account of living biodiversity and ecosystems, continental drift, taphonomy, and the historical contingencies of scientific recovery. We find reconstructions of the palaeoenvironments recorded at Riversleigh, we can peruse a bestiary of Australia’s former vertebrate inhabitants, we get a synthesis of the Australian fossil record, and we even find a quantitative comparison of vertebrate communities through the Australian Cenozoic lurking in one of the appendices. The book occasionally panders, offering action-packed epithets for its extinct beasties: “Marsupial Lions: Magnificent Meat Merchants of the Miocene” or “Diprotodontoid: Doomed Vegetarians of the Forests and Plains” (interlaced with some not so caffeinated like “Wombat-like Beasts Aplenty: Anticipating the Grasslands to Come”). The book often teaches (“Excavation and Collection in the Field”, or “Techniques for Dating”), sometimes preaches (“Why Riversleigh is Significant? Ten Good Reasons”), but really does not disappoint. Like *Lebendige Eiszeit*, *Australia’s Lost World* is detailed and varied enough to engage the child, the undergraduate, and the professional palaeontologist. Hopefully it may even get an eleven year old boy to slow down for a minute or two.

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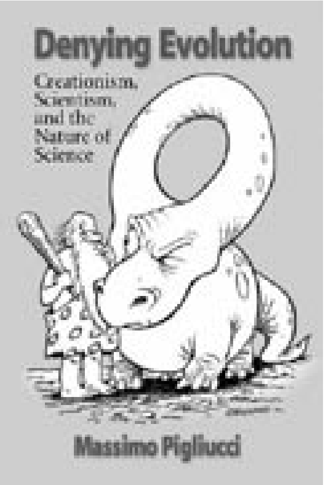
Denying Evolution; Creationism, Scientism and the Nature of Science.

Massimo Pigliucci. Sinauer Associates, Sunderland Massachussetts. 2002. £19.99.

This is an extremely detailed and authoritative review of what in the United States, at least, is a very serious problem: the growth of anti-evolutionism, creationism, and other –isms that threaten to erode the teaching and popular acceptance of a whole range of sciences.

Anti-evolutionism takes many forms, only one of which is the religious fundamentalist (Biblical literalist) creationism that insists the world is 6,000 years old. Some anti-evolutionists are more or less willing to accept a very ancient Earth and even the fact of evolutionary change over time. The one point that all of them have in common is the insistence that the initial origin of life – the process or processes that produced the first self-replicating molecule – must have been the work of a super-natural Intelligent Designer. The modern version of this belief centres around the term “irreducible complexity.”



“Irreducible complexity”, as expounded by people like Michael Behe (Darwin’s Black Box, 1996), actually consists of two concepts, confused. The first is that a system is irreducibly complex if removing or disabling of any part causes the whole to cease function. The human body is irreducibly complex with respect to the heart, lung and liver, but not toe-nails, hair, some proportion of the fingers and toes, or even the spleen.

The second element of ‘irreducibly’ is the more obvious one, and somewhat redundant: a system is irreducibly complex if its functioning cannot have arisen (evolved) through the operation of simpler systems. The human body is irreducibly complex in this sense if it cannot be created out of bits of a mouse and a drosophila. For anti-evolutionists, if one were to trace a retrospective *reductionist* analysis of human evolution over time back to ever-simpler micro-organisms, a point would be reached at which normal scientific material phenomena no longer “work” and something super-natural is needed. The link between the two meanings is none other than our old friend “natural theology.”

Of course, all these sorts of argument depend first on positing the existence and operation of non-material phenomena; and that cannot be tested scientifically (as far as I know). Secondly they depend on pure unquestioning belief, not backed by any empirical evidence, in a negative – that there was originally something that not only did not evolve, but could not have evolved. But the anti-evolutionists would argue that evolutionary scientists also merely *believe* in reducibility: they haven’t seen it, so it is a matter of *faith*. They have merely seen that everything else has proved reducible.

Just writing the above means venturing into waters that are uncharted for most working scientists and locking horns with a group of people who, whatever their shortcomings in our eyes, are superbly prepared and skilful debaters. Getting into an argument with one of these zealots can be like mounting a bronze shield against a cruise missile. Pigliucci is a professor of evolutionary biology at the University of Tennessee, the State that gave us the Scopes trial (Dayton, TN, 1925). He decided to brief himself thoroughly in this complex and increasingly sophisticated subject. His book is essentially a “how to” guide: all the information you would ever need if you ever had to deal with challenges such as: “evolution is only a theory”, “evolution violates the laws of thermodynamics”, and other shibboleths. It may also be useful if, like me, you have found your work being quoted by anti-evolutionists as evidence that the whole subject is a sham (because you have had the honesty to point out that there is still work to be done in perfecting our knowledge of evolution). To see if this has happened to you, try this website: <**http://antievolution.org/people/wre/quotes/**>. Look at that site anyway and you will see what a nasty, cut-throat business this is turning out to be.

All this may seem a million miles away to us in the UK. But it isn’t. With the proliferation of “faith schools,” encouraged and subsidised by a Government that seems always to be looking for a quick fix rather than a deeper philosophy, various forms of fundamentalist teaching and thinking have the potential to spread. Equally, however, I worry about the extreme scientism expressed by, for example, at least two of my Oxford colleagues. Provocative (and scientifically indefensible) assertions to the effect that all of philosophy, ethics, art and religion are, or will be, reduced to science do no-one any good and do the cause of scientific literacy and dissemination a great deal of harm. What may be admirable as a personal philosophy for one person looks like another form of ugly fundamentalism when aired too fanatically in public, and is best saved for when the battle has been won. Meanwhile, the price of liberty still is eternal vigilance. Pigliucci has done a massive amount of homework for everyone else.

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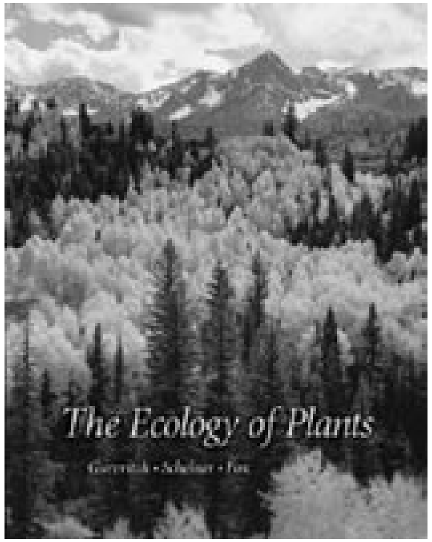
The Ecology of Plants

Jessica Gurevitch, Samuel M. Scheiner, Gordon A. Fox (2002). Sinauer Associates Inc. 0-87893-291-7. £ 40.99 (hardback).



This book presents a well-written synthesis of plant ecology that is accompanied by informative and easily understandable illustrations. It has been logically divided into five sections that progress in physical scale through the book, dealing with (1) the individual and its environment, (2) evolution and population biology, (3) from populations to communities, (4) from ecosystems to landscapes, and (5) global patterns and processes. The content is on the whole good, and I was impressed by the amount of information contained. For this the authors must be congratulated, particularly on presenting it in such a way that the information is informative, useful and entirely accessible. Each section concludes with references segregated into ‘classic references’, ‘contemporary research’ and ‘additional resources’, although these are highly selective and include only a small amount of the information written on individual subjects. As with all too many textbook treatments, references and citations in the body of the text are rare, and points raised throughout the text are not referenced to enable readers to follow up individual points with ease. This citation/reference style clearly delimits the book as a student text rather than constituting a research resource of any kind.

Rather than listing the full contents in detail (which anyone can do for themselves by looking at the publisher’s website at <**http://www.sinauer.com/**>) and discussing merits/limitations of each section, this review focuses on the books relevance to students and researchers in palaeobiology. After all, that’s why this review is appearing in the Palaeontological Association’s Newsletter. This review may therefore appear more critical than it would otherwise be for other audiences, from which it is apparent that the book’s content is not targeted to palaeontologists.

The diagrams are clear and directly relate to the text. I think it is fair to say that several palaeontological authors could benefit from adopting a style similar in their own books! In many cases these illustrations would make ideal learning aids for those teaching plant ecology and its related subjects. The most useful of these to palaeobotanists and palaeoecologists will be those elaborating processes or models founded on neo-botanical evidence that have a specific relationship to the fossil record. Examples include diagrams on global cycling, plant lifecycles, climate and physiognomy, and ecosystem processes. Unfortunately, the book is not accompanied by supplementary information or associated merchandising, and this would have presented an ideal opportunity for the publishers to distribute a CD of images for teaching purposes.

By far the most obvious limitation of the book, and one that as a palaeobotanist would have put me off purchasing it, relates to its intended neo-botanical/ecological audience. The palaeoecological chapter is woefully inadequate, and detailed information presented on plant palaeoecology is generalised and highly selective. More comprehensive palaeoecological treatments exist elsewhere (*e.g.* Bateman 1991; Behrensmeyer *et al.*, 1992 and references cited therein), but are typically example-based, where this book is primarily process-based in its approach. My view is that this book represents a missed opportunity to integrate the fossil record into a process-based treatment.

While neo-botanical coverage is on the whole excellent, specific examples from the geological record are lacking. This is clearly something that would be of benefit to the book in providing a broader, and not time limited, coverage to the subject. Despite the book containing a wealth of information on global and climate change, the focus is on recent historical records with little mention of well-known palaeontological examples (see Chaloner and Creber, 1990). For example, Berner's work on palaeoatmospheric compositions developed through the Geo-Carb models that show long term changes in CO_2 composition (Berner and Kothavala, 2001), is not included despite its obvious relevance. Although containing a wealth of information on plant: climate relationships, the book ignores well-known methods developed for (and from) the geological record. These include the Climate Leaf Analysis Multivariate Program (Wolfe, 1993; Wolfe and Spicer, 1999), Leaf Margin Analysis (Wolfe, 1979; Wilf, 1998), Nearest Living Relative (NLR) methods (Mosbrugger, 1999), the Coexistence Approach (Mosbrugger and Uttescher, 1997), and stomatal parameters (Beerling, 1997). Each of these methods is based on neo-botanical relationships that can also be applied to fossil data, and demonstrate limitations to the scope of the book. This is a fundamental problem for readers interested in plant palaeoecology, and at the same time this information would surely be of interest to botanists. If a second edition is ever considered (as I would hope it will be), the addition of a palaeobotanist/palaeoecologist to the authorship would make a significant advance to the scope of the book, covering some of the important omissions that exist in the present content.

Sections within the book that stood out as being of palaeontological importance are scattered throughout the text. Although much of the text relates indirectly to forms/processes observable in the fossil record, the authors did not recognise or emphasise these such that the information is in most cases unavailable to palaeontological readers. For instance, information presented on disturbance and succession has palaeontological importance, as do the examples given of climate: physiognomic relationships. For palaeontologists these kinds of omissions are unfortunate.

In summary, this book's main audience will be students, primarily in North America, who require an overview of plant ecology. It will be of more limited use to palaeoentological audiences and almost no use to specialist researchers in plant ecology or palaeoecology. Notwithstanding, at a price of £40.99 for the hardback, it still represents good value for the content contained, although probably not for palaeobotanists.

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Lebende Fossilien – Oldtimer der Tier- und Pflanzenwelt, Zeugen der Vorzeit

Erich Thenius. 2000 [2nd edition]. [in German]. 228 pp., ~100 partly coloured figures. 21,3 x 24,5 cm. Hard cover ISBN 3-931516-70-9 €15 / US $ 20.

Emeritus Professor Erich Thenius, vertebrate palaeontologist at the University of Vienna, is known to the scientific community by his numerous articles and also to the public by his more popular books. His most recent work deals again with one of his favourite themes, "living fossils." Admittedly, many people use this term in the one or other way, but I teach my students that there are no such things as "living fossils" in the living world. Having the following phrase in mind "*This term, which is by no means un-problematic (indeed it is self-contradictory…*" I started reading the book, interested in what Dr Thenius would make out of the theme and if he could finally persuade me of the existence of such animals. It was also interesting to learn which group of readers he wishes to attract most.

After outlining some definitions, including a short explanation of modern phylogenetic systematics, Thenius – though not in the title – states clearly that the term is kind of difficult and

should always be used in apostrophes, but then continues to find "living fossils" in the same way important and useful. In chapter 2 he explains what should be understood by a "living fossil", a rather difficult section with several jumps back and forth between taxa and arguments. Building upon this, chapters 3–16 contain a wealth of information on all the different kinds of organisms, historically classified as "living fossils", and reinterpreted by Thenius. Here, he does not restrict himself to classic examples but delves deep into the concept, discussing also the fossil relatives of many extant species or groups. All very interesting to teachers such as myself.

Thenius's inclusion of bacteria and uni-cellular eukaryotes in the "Pflanzenreich" (plant kingdom) shows immediately a very traditional view of the system, which becomes even more apparent when looking at the "phylogenetic schemes" accompanying the text (missing for mammals) and in the overview of the system at the end of the text. These are reminiscent not only of the old days, but many have been proven outdated. Only a few examples of Eukaryota did not radiate 530 million years ago because the photosystems evolved much earlier, and also data are demonstrating increasingly that poriferan metazoans, at least, predate the Precambrian-Cambrian boundary (see refs. below). Again, archeans are, according to the scheme figured in fig. 3.1, the sistergroup of Eukarya and not to bacteria and Eukaryotes. There are no longer any "coelenterates", and I shiver a little when reading names like "reptiles" and "mammal-like reptiles." And there is simply no bifurcation within vertebrates into cartilaginous fishes and bony fishes, but "fishes" are paraphyletic and the sistergroup relationship of the ray-finned fishes (Actinopterygii) and the Devonian *Eusthenopteron* plus the kinocranians, which include the tetrapods, is long known and well-embedded into more modern textbooks (ref. below); dipnoans are not ancient "osteichthyes." There are more such examples. This retention of the old classification greatly hinders, in my view, the direct relationship between the evolution of taxa and their character development. Taken for granted that no one can overlook the whole world of organisms – and Thenius collected information for all major lineages –, there are several taxa, which I know a bit more of, that would have really benefited from inclusion of more recent literature. Arthropoda, just as an example, are apparently not the area Thenius is too much into. Favourites of Thenius are more up-to-date, such as monoplacophorans, coelacanths and certain other vertebrate taxa while, for example, the famous Chengjiang fauna (few examples of literature on it below) is completely missing when discussing the velvet worms (Onychophora, with approximately 300 living taxa are not a very small group, which has so many modifications from either presumed marine ancestors that even the term "modified living fossils" would not hold) and chordates. The more we know of early Palaeozoic fossils from exceptional lagerstaetten such as Chengjiang (or the Orsten), the more we have to add, and all this dilutes the value and necessity of the term "living fossils." Again one misses a word on all the "worm" taxa, whether nemathelminthes and their long-existing in-groups (ref. below); at least for priapulids we know that they remain morphologically very similar to their Cambrian counterparts. It would also have been interesting to see how Thenius would have handled the single species *Xenoturbella bocki*, which some place in a sister-group position to all Bilateria (ref. below).

The largest problem with this book on "living fossils" remains, for me, the failure to adopt phylogenetic systematics. This is a pity, because Thenius otherwise discusses matters very clearly and extensively, proving information on organisms from morphology (not always acceptable however; *e.g.*, cephalocarids have no eyes, neither compound nor naupliar, at any stage of their development) to distribution patterns, distribution history and behaviourial aspects. Admittedly, traditional thinking and the existence of "living fossils" are accepted, the argumentation is quite consistent and clear. There can be no question that Thenius has a broad knowledge and provides high quality discussion. So back to the definitions according to which organisms can be classified as "living fossils" if they fulfil criteria like *presence of many plesiomorphic character states, compared to the recent sistergroup, and generally only few inconspicuous autapomorphies, existence of only one or few recent species, compared to numerous fossil species of the same clade or at least a similar grade, relict type of distribution of the recent representatives, often a disjunct distributional pattern, Recent sistergroup with relatively numerous species, apparently an intermediate position between two different Recent groups (Darwin's original idea) or an extinct group and a Recent group, caused by symplesiomorphic similarity with one group and a synapomorphic similarity with the other group*. To me these criteria are subjective, and I understand from this why Thenius presents solutions for only part of the many forms he mentions. Many open questions remain. I sometimes could not readily follow why forms are or are not "living fossils", and sometimes are "modified living fossils" – to me a little trick to accept them still. Being isolated in a system is a weak argument, and also Thenius does not accept it as a sole argument, and when considering a number of Recent forms, there is always one taxon that is the phylogenetically oldest. It is also difficult to classify organisms on their amount of plesiomorphic characters – even we "still" have five fingers.

Slightly aside the main topic, Thenius has added a chapter on extinction, strategies for survival and areas of recovery, which I found very stimulating because it critically discusses various aspects, from the demise of individuals and species (here a cladistic view would also have pushed the arguments much further), mass extinctions, survival strategies and the distribution of taxa through time – apparently Thenius's favourite topic. I liked this part because I am always searching for such kinds of summaries for my lectures, and this chapter helps much in listing the points. Yet, in the end I was still unsure why I should really need the term "living fossils" and how it should be applied to taxa. It is fun to see "old" taxa in the extant world, but they are surely not survivors but simply descendants in a continuum of speciation events where, starting from a stem species, many species extinguished (Willmann 1988, fig. 9). These taxa did not escape from anyone, nor did they hide themselves in the dark, or in holes, until today. At least, this is not my view of looking upon opportunistic evolution.

So summarising my points: I am a little lost. For people who have little connection to the topic but like a summary of information about candidate "living fossils" this book is very helpful and surely worth the money. People who like the "living fossil" concept will find more examples and a clear discussion of a wealth of organisms on the basis of given definitions, and this may be enough to persuade them to buy the book (but please be careful with the phylogenetic interpretations!). Others might particularly be interested in the historical record of taxa mentioned – though not based on very recent data in most cases. If one is a phylogenetic systematist, the book is simply disappointing and does not help much further – with the exception of the wealth of information concentrated in the book. So everyone has to "classify" himself and consider buying it. At least it is worth a look.

Looking at the formal aspect, the book has a nice hardcover and contains on 227 pages numerous well-printed illustrations, from drawings of organisms to schemes and various photographs, many in colour (strangely not *Triops cancriformis* in spite of the vicinity to Erich Eder and Walter Hödl, the two Austrian branchiopod specialists). The space taken up by the flawed and outdated could have been used much better for illustrating more of the example taxa. I would have liked to see some of the seemingly important taxa because I did not know about them. There remains the question about the clientele for this book and the problem of the language – it is in German. At first sight I thought it would be for a broader audience. The usage of many taxonomic names and scientific terms – in many cases either not explained at first mention, or never explained at all – told me after a few pages, however, that only the *cogna scenti* would be able to read the text. And sentences like "*Eine Erfahrung, die so mancher Badegast bei unfreiwilligem Kontakt mit Quallen gemacht hat.*" (an experience, which the one or other swimmer in the sea has made by accidental contact with jellyfish) are rare as well as superfluous, since too much populistic. Therefore the book is not too easy to read and not for a non-native (German) amateur. More experienced students and interested colleagues, from biology as well as palaeontology, might be able to understand much of the text yet. Therefore I would recommend the book only for professional scientists.

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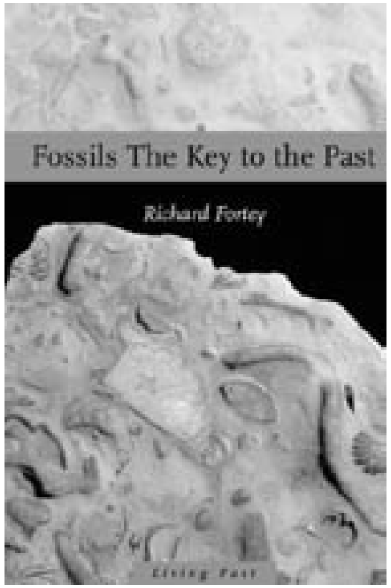
Fossils: The Key to the Past

Richard Fortey. Third Edition. 2002. Natural History Museum, London.
232pp. ISBN 0 565-09163-8. Paperback £16.95.

The first edition of this engaging book was published some 20 years ago, and its continued popularity is evident in the production of a third edition. In the preface the author sets out his remit, which is to provide "a straightforward introduction to the study and meaning of fossils: how they help us understand the geological past, how their fascination is more than just 'stamp collecting'." I was rather glad to see this last comment, since we palaeontologists are still occasionally plagued by the fallout from the crudely misplaced assertion by an eminent physicist (was it Rutherford?) that there are only two branches of science, physics and the said 'stamp collecting'. This beautifully illustrated and clearly written book, aimed at a young, or at least non-professional audience, should make clear that there is much more to palaeontology than that alone.

The book consists of eight chapters, with a brief glossary, bibliography, and index.

Chapter 1, *Buried in the Rocks*, is a simple introduction to what fossils (including trace fossils) actually are, while in Chapter 2, *Setting the stage: time and change* touches on basic concepts in stratigraphy and the subdivision of geological time. Radiometric dating, moving continents, changing sea levels and fluctuating climates are all mentioned here, all testifying to evolutionary change against the backdrop of constantly, if slowly, fluctuating environments. Chapter 3, *Rocks and fossils*, is concerned with sedimentary facies, with specialised environments such as reefs, deep sea habitats, and with the role of microfossils of various kinds in palaeontology. Chapter 4, *Bringing fossils to life*, is about how fossils can be reconstructed and their habits objectively analysed. Examples include swimming trilobites, dinosaur locomotion, the life of graptolites, and how brachiopods and bivalves live today and in the past. And, of course, the customary, but still entertaining story of how *Hallucigenia* turned upside down from a weirdie into a respectable onychophoran.



In Chapter 5, *Origin of life and its early history*, the palaeontological evidence is fitted to the overall picture; Precambrian microfossils, stromatolites, Ediacarans and small shelly fossils. *Evolution and extinctions* form the subject of Chapter 6, and here we find Sepkoski's Evolutionary Faunas, the evolutionary stories of *Micraster* and of *Globigerina*, an engaging treatment of human evolution, and the importance of major extinction events, which are both destructive and creative in clearing the field for new innovations. Chapter 7, *Fossils in the service of humans*, mainly concentrates upon micropalaeontology as used in the oil and gas industry, but there is also a short section on fossils forming decorative stone. And finally Chapter 8, *Making a collection*, ranges through where to find fossils, what kinds of sedimentary rocks are most likely to yield them, what tools to use, how to record a section, how to use comparative collections and guidebooks for identifying, and how to store your fossils properly.

Obviously this book is aimed at amateur geologists, keen lay people, and as I would envisage, particularly for young people just starting out on palaeontology. Yet the 32 coloured plates (of excellent quality), showing the immense diversity of the fossil record, make this book a delight for all palaeontologists, whatever their level of erudition. Moreover, the author has the ability to write no less effectively at a relatively simple level, as he has in his more advanced and profound works, and with the same enthusiasm, the same entertaining flair. Inevitably the examples chosen to illustrate particular points will be favourites of the author, and indeed why not? In a work of this scope one cannot cover everything; what is remarkable is that so much has been covered, and so well. It is very good value, for the price.

I wish, when I had started out as a neophyte palaeontologist some fifty years ago, that I had then had this book as a companion. If it stimulates keen young persons to higher things, then surely it will have served its main purpose. But old fossils, such as I, can read it with pleasure even now.

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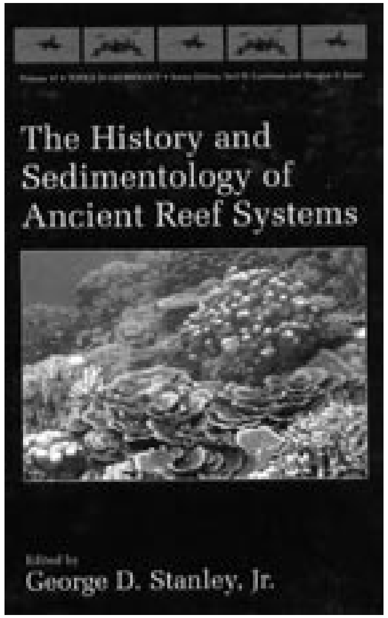
The history and sedimentology of ancient reef systems

Stanley, G. D. (ed.). 2001. *Topics in Geobiology*, volume 17. Kluwer Academic/Plenum Publishers, New York, 458 p. ISBN 0 306 46467 5 (hbk), £66 ($95).

Ever since Darwin, reefs have sorely taxed the minds of ecologists, palaeontologists and sedimentologists. Given current scientific understanding, reefs present us with more than their fair share of paradoxes. How are modern reef communities able to flourish in what are effectively nutrient deserts and yet show such phenomenal biodiversities and rates of gross primary production? What ecological forces structure and maintain these unique communities? What controls the substantial production of reef calcium carbonate and its redistribution as sediment? And how can we combine these to make sense of how palaeoecology, biodiversity, and carbonate production have changed through geological time?

The straightjackets of uniformitarianism and scale of enquiry have always hampered the study of reefs. This is because many of the defining characteristics of modern reefs – such as the underpinning of the ecosystem by photosymbiosis, and the ecological and sedimentological importance of reef fish – are relatively recent evolutionary innovations. In addition, it is these very phenomena that are highly problematic or impossible to detect with any certainty in the fossil record. This has meant that we cannot simply confer the ecological properties of modern reef communities to ancient representatives. Even more importantly, most ecological and physicochemical phenomena can only be observed on human timescales, so we still have little understanding as to how measurable events such as periodic storms, episodes of nutrient enrichment, or even ecological interactions, can explain the longer-term ecological and evolutionary trends in reef communities seen over geological timescales. This has meant that the gulf between those who study ancient and modern reefs has remained to a large degree depressingly insuperable.


The History and Sedimentology of Ancient Reef Systems

Edited by
George D. Stanley, Jr.

This volume is part of the impressive *Topics in Geobiology* series, and joins the ranks of a spate of publications on reef evolution in recent years. The eleven chapters are arranged in a traditional format following stratigraphic age, starting with a broad introduction to reef ecosystems by George Stanley (who also edited the volume) and an analysis of broad trends using the 'Paleoreef' data base by Wolfgang Kiessling, followed by eight chapters detailing successive geological intervals from the Proterozoic to Modern, and ending with an essay by Pam Hallock on modern reefs as the major source of calcium carbonate and the harbingers of global change. As such, this book is written almost wholly by palaeontologists, and is unashamedly targeted at that audience.

All the chapters are written by experts in their field. Many are single-authored contributions, so often present an individual perspective that highlights outstanding controversies. They are for the most part descriptive. Inevitably some lack of consensus emerges, but in sum they offer a fine resource of up-to-date reviews for almost all ancient reef communities. But while this format presents the reader with a clear sense of the evolutionary changes that have taken place through the 3 billion years of reef history, with some notable exceptions, it does not allow for any deep analysis of the underlying driving mechanisms of such change.

Greg Webb presents a very thoughtful chapter on the 'evolution' of non-skeletal biological calcium carbonate production through time. He explores, for example, the role of supersaturation with respect to calcium carbonate. This now appears to be a major control on a whole range of carbonate production-related phenomena, from determining the rate of individual coral growth, to controlling relative carbonate production over the Earth's surface, and even as a major determinant of regional scleractinian coral species diversity. Greg Webb also offers hope by highlighting how secular trends in marine carbonate saturation may be quantifiable as $_{p}CO_2$ data become better constrained and more accurate models of the carbon cycle appear. This in turn will allow investigation of the effects of changing carbonate saturation with respect to the evolution of calcifying biota and reefs as a whole, so opening up a new and exciting line of enquiry.

Pam Hallock presents a useful summary chapter explaining the nutrient paradox and the significance of photosymbioses on modern reefs. It is photosymbiosis that allows the successful biological harvesting of calcium carbonate in nutrient-depleted environments, and the regional distribution of nutrients can control the type of carbonate producing community as well as the relative propensity for drowning of carbonate platforms in different oceanographic areas. But how can we now weave what is now understood as to the effects of increased sedimentation, nutrification, and global climate change on modern coral reefs into our analysis of the record of ancient reefs?

In summary, this volume has strengths and weaknesses: it offers one of the best descriptive synopses of the changing nature of reef communities through geological time, and as such this reference volume should be placed on every geological library shelf. But many of the questions we really want answered are not broached. For this we must await a future volume that probes the unexplored territory between disciplines that is so necessary if we are to understand the true, multifaceted face of reefs.

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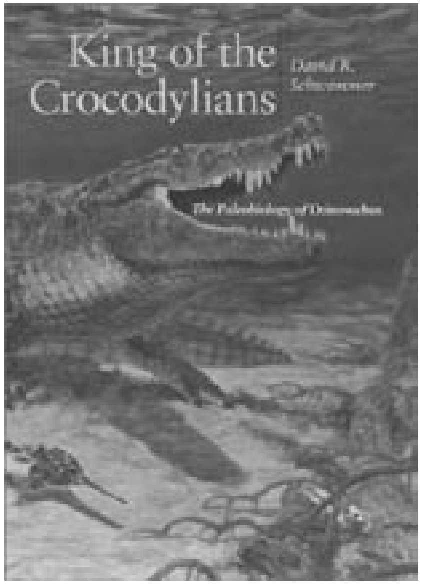
King of the Crocodylians: The Paleobiology of *Deinosuchus*

David R. Schwimmer, Indiana University Press. ISBN 0-253-34087-X. £34.50.

The back of the dust jacket of this offering from Indiana claims it to be a biography of one of the largest carnivores that ever lived. This grandiose claim to fame for *Deinosuchus* is presumably the excuse needed for writing the book, but it is a dubious claim and *Deinosuchus* must share it with a large number of aquatic and terrestrial animals both living and extinct. Of course, the marketing men at Indiana Press needed something to brag about to enhance sales, but they really do need a lesson in hyperbole. Come on guys, this splendid croc ate dinosaurs for breakfast. I thought all publishers knew the golden rule: dinosaurs on the front cover = 25% more sales.

Deinosuchus was a very large crocodile (forgive me for using the term crocodile, *Deinosuchus* is in fact a very large alligatoroid, but I intend to use the vernacular *croc* in the remainder of this essay, and I know purists will take umbrage) from the Late Cretaceous of North America. It appears to have grown to lengths of eleven, and perhaps even twelve metres; a little over half the size of the Jurassic pliosaur *Liopleurodon*, and lived on both sides of the North American Interior Seaway. It had a massively constructed, blunt snouted skull armed with ferocious caniniform teeth anteriorly and numerous blunt, crushing teeth in the back of the jaws. Some quite spectacular specimens of the skull are known that clearly demonstrate that *Deinosuchus* was an awesome beast. Sadly, no complete skeleton has ever been discovered, and in some respects, this adds to the animals' mystique and enhances the book. It appears that *Deinosuchus* is not an especially rare fossil, and Schwimmer notes many places where fragmentary remains have been collected; the characteristic teeth and osteoderms occur frequently in some bone rich accumulations in the south eastern United States of Alabama, Georgia and North Carolina among others.



Schwimmer's offering does tell us pretty well everything that is known about this croc, and happily, he provides references within the text in the standard form. Lay readers, for whom sections of the book are clearly intended, might find this a little irritating, but I applaud this approach. We get to learn about its preferred prey, distribution and evolutionary history. There is a graphic account of this super croc eating breakfast and chapters on the croc's palaeontological history, its size and its age. Unfortunately, in this chapter the author felt the need to explain all the principles behind biostratigraphy and radiometric dating and I began to get the feeling that I had been here just one time too many.

Much more entertaining are Schwimmer's discussions on how knowledge of *Deinosuchus* has come about using a sobre mixture of logic, palaeontological and sedimentological data and geological occurrence of the croc. In one nice example Schwimmer describes an important anomaly in the geographic distribution of *Deinosuchus* and explains why this anomaly is worthy of investigation. Essentially, fossil assemblages of this mega croc occur on both sides of the North American Interior Seaway (NIS), and it is unclear how the two populations came about. Further, he considers whether the size differences between the two assemblages are of taxonomic importance. It is not the end result here that is of great concern (well, to me anyway), but the methodologies used to attempt to understand this bimodal distribution. Schwimmer does a great job to explain clearly how palaeontologists attempt to answer important questions using a wide range of data. I have to say that I enjoyed this discussion most, and found myself trying to knock down his arguments with little success. My only disappointment is that Schwimmer leaves little room for the bizarre, and we know that nature can be very bizarre. So I tentatively offer this hypothesis; Western *Deinosuchus* populations frequently followed migrating turtles heading for isolated islands and sand flats to lay their eggs. Well, it could have happened! Data? I have none!

Some chapters are a little turgid and require high levels of concentration, and often a little rereading, but I am less convinced that this is the authors' fault, and more to do with the plethora of taxonomic names and the various vernaculars that go with them. But I persevered, and I now know that *Deinosuchus* is not a croc, but is an eusuchian mesoeucrocodylian archosauromorph. I just hope I attend a dinner party where I can regurgitate this little gem.

All in all, I enjoyed this book, and although I am not sure *Deinosuchus* merits an entire book's worth (it would have provided an excellent, and large chapter in that imaginary book *The Big Girls and Boys Encyclopaedia of Very Large Fossil Animals*) it is surely better to have this book, than not to have it. My criticisms are trivial; the photographs are shit (b & w photography is an art form and the photographs in this offering provide a lesson in how not to do it; surely Indiana Press can reproduce a photograph in focus and with some contrast), and there should have been a cladogram.

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Palaeobiogeography and Biodiversity change: the Ordovician and Mesozoic-Cenozoic Radiations

Crame, J.A. and Owen, A.W. (eds) 2002. Geological Society, London, Special Publication No 194: 206 pp. ISBN 1-86239-106-8. £65.

As concerned with the question of evolution of life, the choice of J.A. Crame and A.W. Owen is very accurate: the two main periods of bio-radiations on Earth, ending in episodes of glaciations. However, the two periods are very different in nature: the Ordovician is ca. 65 My long vs. 203 My for the Jurassic to Cenozoic; the end-Ordovician glacial event is short in time (ca. 1.5 My for the Hirnantian) *vs*. the end-Cenozoic one beginning at least in the Oligo-Miocene (~ 34 My ago). So, both periods of radiation have probably been "pacemakered" (Schopf in Owen and Crame, p. 1) by very different series of geological events. This choice relates to several "scientifically correct" topics: biodiversity, climate change, large databases, *etc.*, which claim for a new way of making palaeontology, that is (1) integrating as much information as possible from biology (either palaeo- or neo-) and geology, (2) trying to inter-relate them in an intelligible scheme, leading to (3) eventually new scenarios of spreading of life on Earth. "If the patterns can be comprehended, then the processes that drive them can be addressed" (Owen and Crame, p. 2). The ultimate hope is to provide predictions on what will happen in the near future; *e.g.*, is the present global warming natural or anthropic in origin? But this is not said in the preface.

75 scientists attended the 2001 Lyell Meeting at Burlington House, London, whose proceedings give here a Special Publication of the Geological Society. After what I already said more than ten years ago (Blieck, 1990), has the field of palaeobiogeographical science changed? From McKerrow and Scotese's (1990) volume on the Palaeozoic palaeogeography and biogeography, it was quite evident that biogeographers were using a wide, diverse, heterogeneous spectrum of methods (which have been shortly reviewed by Hugot, 2002), making difficult any inter-group and inter-period comparisons. And this is typically the aim of this volume: relations, if any, between biodiversity change, palaeogeography, plate tectonics (orogeny, volcanism), climate, depositional environments, plus biases introduced by datasets and sampling in large databases.

M.G. Bassett, L.E. Popov and L.E. Holmer give an ecological interpretation of the spreading of brachiopods from the Early Cambrian to the Middle Ordovician. The brachiopod-dominated communities of the low-latitude northern- and peri-Gondwanan margins first inhabited shallow water, inner shelf environments. These elements of the Palaeozoic Evolutionary Fauna then dispersed outside Gondwana, and had comparable adaptive evolutions on the inner and outer shelves of Baltica, Laurentia, Siberia, and Gondwana. The migrations from Gondwana to the other landmasses took place when they were in relative proximity until the Early Ordovician, but dispersal of brachiopods may also have taken place through emergent volcanic arcs which formed "island hopping bridges" between the major continents (Bassett *et al*., p. 21). This typically recalls the "staging posts for the dispersal of shallow-marine biota"of Talent *et al*. (1987) concerning the contemporary marine zoogeographic context of the Indo-West Pacific tropical province as applied to the Devonian brachiopods.

Such an important role is also given by D.A.T. Harper and C. Mac Niocaill to the many reconstructed intra-oceanic island sites of the "Greater Iapetus Region" to explain the dispersal of rhynchonelliformean brachiopods in Early Ordovician time. These oceanic island terranes are here qualified as "cradles and museums" of brachiopods for the following radiations on Laurentia, Baltica, Gondwana, and the numerous intermediate micro- and mini-terranes. The diversification of brachiopods appears to be diachronous on those palaeocontinental elements, occurring earlier on Perunica (in the earliest Caradoc) than on Avalonia and Gondwana (in the early Caradoc). The scenario of Harper and Mac Niocaill is in phase with Bassett *et al*.'s one. Both interpret the brachiopod diversification as a consequence of the Ordovician spreading of continents, with a burst in Caradocian time.

The interpretation of J.C.W. Cope of the Ordovician bivalves is also ecological. Late Cambrian bivalves are still unknown, but they are supposed to have been restricted to Gondwana because they are endemic to Gondwana (including Avalonia) in the Early Ordovician. At that time, they show a greater diversity in low latitude Gondwana (*e.g.*, Avalonia) than in high latitude Gondwana (*e.g.*, Montagne Noire), and they were facies-controlled, being mostly collected in originally shallow-water siliciclastic sediments. Bivalves migrated to Baltica and Laurentia in the Middle Ordovician, and reached all the continent shelves in the Late Ordovician. This dispersal resulted in two major phases of adaptive radiation: mostly infaunal taxa in the Middle Ordovician siliciclastic sediments, and development of semi-infaunal and epifaunal taxa in the Late Ordovician siliciclastic and carbonate sediments. The high latitude, Late Ordovician bivalve faunas are very impoverished, which is interpreted by Cope as due to much lower temperatures in the Ashgill.

Contrary to the three previous ones, the paper of S.T. Turvey is a phylogenetic-biogeographic analysis. It is concerned with an Ordovician subfamily of calymenid trilobites, *i.e.*, the Reedocalymeninae, including the 22 species of *Neseuretus* and all other reedocalymenine genera. This subfamily is endemic to Gondwana. The cladistic analysis of 32 species/25 characters by PAUP results on a strict consensus tree where *Neseuretus* appears to be polyphyletic. Most nodes have low bootstrap values. The corresponding area cladogram leads Turvey to define four main nodes. After comments on the palaeogeographic location of some peri-Gondwanan terranes (as, *e.g.*, S. and N. Turkey), and a redefinition of the geographic nodes, he concludes that no significant environmental barriers existed across the shallow-water inner shelves of Gondwana, because the cladogram contains four subclades each containing a wide range of both eastern and western Gondwanan areas. However, the consensus area cladogram presented in Turvey's Fig. 5c, and supposed to support a "faunal cline across the palaeocontinent during the Early Ordovician" (*viz*., from S. America to Australia-SE Asia-Cimmeria-Sardinia/Turkey, and to N. Africa-France/Spain-Avalonia) is not so clear. The topologies of the area subclades are not congruent, the bootstrap values of the taxa cladogram on which they are based are low (as recognized by Turvey himself), and the number of characters analyzed is weak as compared to the number of taxa. Nevertheless, such an analysis is rare among Early Palaeozoic palaeontologists, and, as proposed by Turvey, his result should be tested on other trilobite groups. It should also be tested on other higher taxa such as brachiopods, bivalves, *etc*.

The paper of M.P. Smith, P.C.J. Donoghue and I.J. Sansom is on the Early Palaeozoic vertebrates (in fact chordates, including tunicates, cephalochordates, "cyclostomes", and their total-group gnathostomes created to include conodonts and jawless fishes!). It is also based on a phylogenetic-biogeographic analysis. The "out-of-Gondwana" scenario of Elliott *et al*. (1991) for early vertebrate evolution is dismissed and replaced by an "out-of-Laurentia" scenario by Smith *et al*. "In contrast, an 'out-of-Gondwana' radiation for many invertebrate groups is a recurring theme" (Owen and Crame, p. 4), and thus in agreement with Elliott *et al*.'s (1991) and Blieck and Turner's (in press) hypotheses. The out-of-Laurentia scenario is based upon the proposed cladogram where conodonts are included within the vertebrates (classical meaning, that is, lampreys + "ostracoderms" + gnathostomes), and the Gondwanan arandaspids are the sister-group of heterostracans. So that basal vertebrates being either cosmopolitan (conodonts) or endemic to Laurentia (*Eriptychius* and *Astraspis*), an out-of-Laurentia scenario is favoured. However, if conodonts are not considered as vertebrates (Turner *et al*., in press), if arandaspids are not the sister-group of heterostracans (Gagnier, 1995), and taking into account the presently known stratigraphical distribution of Ordovician taxa (Turner *et al*., in press), an out-of-Gondwana scenario is more probable.

With H.A. Armstrong and A.W. Owen's paper on Late Ordovician euconodont generic diversity, we come back to ecological biogeography. The question they address is fundamental in evolutionary biology: is the diversification of Ordovician euconodonts due to intrinsic properties of the clade or to external, physical factors, including biogeography and environments? For that, they proceed with a genus/locality matrix analysis of the trans-Iapetus areas (Laurentia, Avalonia, Baltica) as to define various oceanic and continental shelf biofacies. However, we are faced with a linguistic problem. Armstrong and Owen's Oceanic Biofacies are composed of "pelagic" taxa, their Shelf Biofacies being made of "nektobenthic" taxa. If I remember well, in oceanic biology, "pelagos" equals "plankton + nekton" *vs*. "benthos". So, taxa may be considered as either pelagic (planktonic, nektonic) or benthic; and I suppose that the "pelagic" taxa of Armstrong and Owen are "planktonic." They develop a model of biofacies superposition from the late Middle Ordovician ("Llandeilian") to the Early Silurian which leads to the conclusion that the southern margin of the Iapetus ocean (the "western" peri-Gondwanan terranes as, *e.g.*, Avalonia) was characterized by upwelling currents during the Ashgill, and its northern margin (the Laurentian shelf) during the late Ashgill; this is deduced from the vertical distribution of the cold water Oceanic Biofacies 3 from a deeper setting in the Mid-Ordovician to a shallower setting in the Ashgill. I must say that this model seems to be very sophisticated (and I am not sure to have understood all).

J.P. Botting's chapter is on the role of pyroclastic volcanism in the Ordovician faunal diversification as tested from the Welsh Basin's ostracodes and inarticulate brachiopods. The model implies a correlation between ash flows and subsequent blooming of planktonic and benthic taxa, through varying environmental conditions (from aerobic to anoxic), and the application of population genetic concepts. Five ecologically defined groups of organisms are proposed by Botting. Ostracodes and inarticulate brachiopods fall within his group 1 which would show complete eradication by ash deposits, followed by rapid recolonization in high-amplitude blooms. I must say that if this seems to be the case for the "Llandeilian" (end-Darriwilian) ostracodes, it is not so clear for the Early Ordovician ostracodes and inarticulate brachiopods for which the blooms are weak. Nevertheless, Botting encourages "Readers … to present additional data as a test of the hypothesis, in order to establish its validity."

The paper of M.B. Hart, M.J. Oxford and W. Hudson opens the series of papers devoted to the Meso-Cenozoic, with a chapter on the Jurassic and Cretaceous planktonic foraminifers. Their stratigraphical range chart (Fig. 2) clearly shows an "origination" in the Middle Jurassic (Bajocian), a low generic diversity through to the early Cretaceous (Hauterivian), followed by a radiation all along to the latest Cretaceous (Maastrichtian). This pattern is related to the biogeographical distribution of the group, which is restricted to the mid-northern areas of the Tethys ocean during the Jurassic and most of the Early Cretaceous, and attained a wide circum-global distribution in the warmer waters (between ca. 45°N and 45°S latitudes) of the latest Early Cretaceous (Albian). The radiation which began in the late Early Cretaceous (Hauterivian to Albian) is correlated to the strong increase in ocean crust production (which caused the Late Cretaceous continental fragmentation), and to the resulting sea level rise (which caused more widely inundated continental shelves and a more deeply stratified ocean) (*e.g.*, Kauffman and Hart, 1996). Such a causal chain at such a wide time slice does not open to question and is probably classical among Mesozoic planktonic foraminifer experts.

The question that M. Aberhan addresses is concerned with the extinction of a group of marine benthic organisms and its recovery, as illustrated by the Early Jurassic bivalve biodiversity of the Andean basins and NW Europe. Both areas have been supposed to be communicating as early as the Early Jurassic through a so-called Hispanic Corridor seaway between E. Pacific and W. Tethys. This seaway would have been the cause for the extinction of Pliensbachian-Toarcian bivalves in the Andean basins (by immigration of competitive cosmopolitan species), and for the recovery of Toarcian-Aalenian bivalves in NW Europe (by immigration of spreading Andean species) [compare this to the Great Faunal Interchange of Cenozoic mammal faunas between N. and S. America]. Aberhan calculated the specific diversity of both the Andean and NW European Early Jurassic bivalves, and compared their extinction, immigration, and origination rates. His general conclusion is that his results dismiss the two above-mentioned hypotheses: recovery from the end-Pliensbachian extinction event is best explained by an increase of the specific origination rates both in the Andean and NW European basins. So, I presume that this paper keeps the question of the Hispanic Corridor unsolved, even if it is not said in Aberhan's conclusion. I think that this paper is based upon a simpler method than some of the preceeding ones, and his result is rather elegant.

With D.J. Cantrill and I. Poole, we turn for the first time in this volume towards terrestrial organisms: they analyze the role of the Antarctic Peninsula (AP) on the biogeographic relationships of W. and E. Gondwanan angiosperm floras in the Cretaceous. The palaeogeographic reconstruction used (R.A. Livermore, unpublished; not so different from earlier reconstructions, *e.g.*, Owen, 1983) shows the potential "strategic" role of the AP in floral migrations through Gondwana. However, Cantrill and Poole refute the pivotal role of the AP and propose an ecological scenario. The peak of angiosperm radiation in the AP postdates appearances elsewhere in Gondwana (Australia, S. America; S. Africa and India being less known) and cannot be considered as a "centre of origin" (my wording). The highest diversity of angiosperm macro- and micro-remains is reached in the Coniacian, just after the peak of greenhouse effect in the Turonian, and Cantrill and Poole propose that this Turonian warming has been "the forcing mechanism for the radiation of angiosperms into the Peninsula", from low latitude understorey niches to high latitude understorey, and later overstorey niches. This scenario cannot yet be followed precisely in all its steps because of uncertainties both in the palaeogeographic reconstructions of the southern landmasses (timing of sea-floor spreading *vs*. transcurrent faulting), and in the dating of the fossil record (mostly in S. Africa and India). In this topic, the fossil record of terrestrial organisms is still crucial to help reconstruct the palaeocontinental positions. But, I disagree with Cantrill and Poole when they say (p. 143) that "The recent discovery of Late Cretaceous dinosaurs in Madagascar …, and their occurrence in South America and India, also suggests that these landmasses were still connected (via Antarctica) in the Late Cretaceous …" It is not so simple. If the Malagasy, S. American and Indian taxa are considered as co-specific, either we suppose that the dispersal was "instantaneous" and we accept their proposal; or we suppose that the duration of that species (several million years as a mean) is enough for migrations to take place between Madagascar, India and S. America, and we need precise datings of both the fossil sites and opening of the Indian and Southern oceans. The latter scenario is valid if the various taxa of Madagascar, S. America and India are treated as different ancestor-descendant species. However, if those taxa are considered as sister-groups, their occurrence in the three continents does not date their persistent land-connections; it just means that their ancestral species was living somewhere on the general track [Madagascar + India + S. America], at a time when these landmasses were connected together, and *older* than the corresponding fossil sites (so, either in the early Late Cretaceous or in the Early Cretaceous). This depends on the methodoly used (stratophenetic *vs*. cladistic).

The paper of J.A. Crame and B.R. Rosen is at a global scale; they look for a "convincing integrated theory or model to account for the origins of large-scale biodiversity patterns in both time and space" to explain the rise of modern biodiversity in relation to the Cenozoic palaeogeographic evolution. Taking into account the present latitudinal gradient of taxonomic diversity on Earth, the higher diversity in the tropical realm, and the heterogeneity of this tropical realm both in the marine and terrestrial domains, they try to link those facts to external, physical forcing factors of the Cenozoic. Plate tectonics with the motion of Antarctica towards the South Pole and its co-occurring glacial event, orbitally forced range dynamics, and climatic cycles are thus advocated. I just have the feeling being at the limit of my knowledge to critically evaluate such a wide-looking paper. But the query for the origin of the tropical centres of biodiversity looks like the query for "centres of origin" of taxa, and we know that it is by force strongly dependent upon the known fossil record. All "centres of origin" are "berceaux à roulettes" ("roulette cradles"?), as I have been taught while a student in Paris University.

As P.J. Markwick and R. Lupia say, "The fossil record is the only direct evidence about the biological evolution of life on Earth", but this record is very heterogeneous, so that the large databases settled to evaluate the past and present day patterns of biodiversity are largely biased. Markwick and Lupia thus evaluate the problems of database structure, of their spatial and temporal scales, and of taxonomy (*e.g.* synonymy), and they make three suggestions to improve the quality of databases.

This procedure is certainly applied by Markwick in the following paper where he uses a large dataset of Recent non-avian tetrapod fauna to examine the macroscale relationships between climate, biogeography and species diversity. The result seems very complex, integrating strategies for procuring energy (sun for reptiles [?], food for mammals), past history of the taxa, relationships between latitude (temperature) and percentages of ectotherm or endotherm animals, *etc*. However, it is based on a GIS which contains data from "only" N. America, Europe, S. Africa, and Australia, and we may wonder how wide is the validity of this model. Just add Bolivia to the latter series of geographical areas, and you get exactly the same situation as concerned with Ordovician vertebrates (Blieck and Turner, in press): most data come from the most developed countries (MDC), or from countries where people from the MDC went for sampling and collecting, and all our models are biased by this heterogeneous record. In such a situation, either you think it useless to settle a sophisticated model for a very incomplete fossil record, even if you are convinced that the external, physical factors have forced the evolution of life (Blieck and Turner, in press), or, in case of a wide dataset, you try to produce a model (this paper by Markwick).

In conclusion, it appears that, in (palaeo)biogeographical studies, different methodologies lead inevitably to different interpretations, and it is presently difficult to escape this issue. Most of the papers are based upon ecological analyses at different spatial and temporal scales. Phylogenetic biogeographical analyses are once more needed to test the ecological scenarios proposed in several of the papers. The subject of this book is very complex. Each group of organisms and each palaeocontinent had a different history. Who or what system is able to embrace the whole story? As concerned with Ordovician, the answer will perhaps emerge from the volume of Webby *et al*. (in press) which results from six years of international collaboration under the banner of IGCP 410. Strangely, none of the authors of the papers of this book was seemingly concerned with this programme. Finally, I think that the topic of this book is highly interesting, but that the different chapters are heterogeneous, some being at very wide scales, some at more regional ones. It seems that this is difficult to avoid for the proceedings of a meeting. And the retail cost of £65 for the volume is too high.

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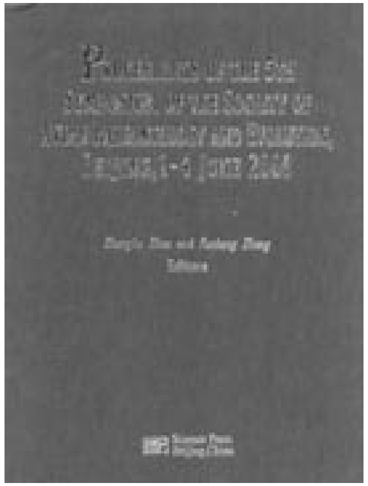
Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution, Beijing, 1-4 June 2000

Zhonghe Zhou and Fucheng Zhang (editors). 2002. 311pp. Science Press, Beijing China; ISBN: 7-03-010551-6/P·1338 (hbk).



This book is a collection of papers presented at the 5th International Meeting of the *Society of Avian Paleontology and Evolution* (SAPE) held during the Summer of 2000 in Beijing, China. All in all, and as discussed in the preface, this meeting was a great success – 110 participants from 17 countries contributed 66 oral and 8 poster presentations covering all aspects of the palaeobiology and evolution of birds (including theropod dinosaurs and discussion of the Jehol biota, famous of course for its 'feathered dinosaurs'). However, given the international publicity that this meeting received at the time (*Nature* 2000, **405**: 992; **406**: 930–932 and *Science* 2000, **288**:1721), we found this volume a little disappointing because in the end only 23 papers comprise the published SAPE proceedings for 2000.

About half of the contributions to this book present descriptions of fossil birds, ranging considerably in age – from Cretaceous through Palaeogene up into the recent past – making this volume primarily of interest to specialists in this area. In contrast to the published abstract proceedings from this SAPE meeting (*Vertebrata PalAsiatica* 2000 suppl. 38), the scope of this volume is somewhat limited; few papers will generate interest in the wider palaeontological community simply because they are so specialised within the systematics of fossil avians. Six papers deal with the specific taxonomy of individual genera or families of fossil birds (*e.g.*, new description of a teratorn, fossils within the genus *Athene*, relationships of Tertiary anhingas, systematics within fossil cathartid vultures), a few deal with avifaunas from particular localities (*e.g.*, the German Middle Eocene Geiseltal and the North American ?Cretaceous Navesink and Hornerstown Formations) while the latter one-third of this volume focuses on species evolution, palaeogeography and stratigraphy (*e.g.*, speciation in the Quaternary avian fossil record, the early history of just some 'chosen' groups of birds). This collection of papers is not much fun to read!

One exception to this, a highlight, and perhaps the most exciting and controversial paper included in this volume, is Chatterjee's long-awaited (page 125) description of *Polarornis*, a claimed Cretaceous-age loon (Gaviidae) from Antarctica. As readers of this newsletter will be aware, the timing of the evolutionary radiations of modern birds and mammals remains much debated in the recent literature; in the case of birds, very few convincing records that can be assigned to the extant orders have to date been described from the Cretaceous. *Polarornis* was first mentioned by Chatterjee (1989) in a conference abstract and avian palaeontologists have waited since then for a more comprehensive description of this tantalising specimen – is this fossil really a loon from the Cretaceous? Is the Formation whence it comes really Cretaceous in age? One thing is for sure: *Polarornis* is an exceptionally interesting fossil, easily the best record of a possibly 'modern' bird ever found from the Cretaceous. This paper eclipses the rest of the SAPE 2000 volume and much debate looks sure to follow!

We recommend that serious students of avian palaeontology check-out the published proceedings of the 2000 SAPE conference; we are just not sure this volume holds much of interest for the generally inclined palaeontologists out there!

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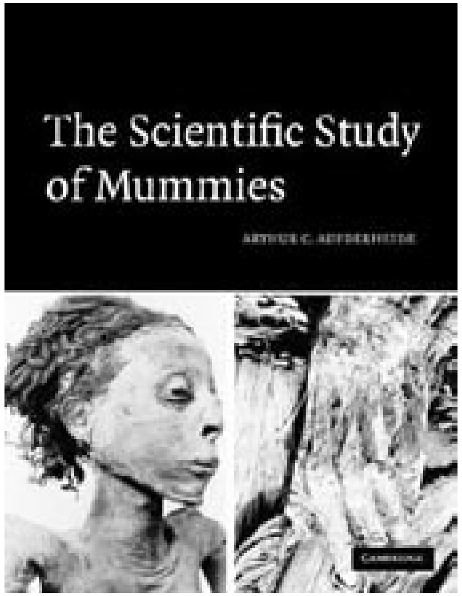
The scientific study of mummies

Arthur C. Aufderheide 2003 Cambridge University Press Cambridge xvii plus 608pp. ISBN 0-521-81826-5 (hbk) £100.00.

This is an extraordinary book by the doyen of American palaeopathologists, Arthur Aufderheide, who founded the Paleobiology Laboratory at the Department of Pathology of the University of Minnesota, Duluth, and edited the *Cambridge Encyclopedia of Human Paleopathology*, published in 1998. His own particular research interests are patterns of disease in ancient populations and the cultural anthropology of the Arctic. Aufderheide's purpose in this new book is no less than the provision of a basis for the structuring of the science of mummy studies. In doing so he has created the essential purchase for all those interested in palaeopathology, archaeology and anthropology, but there is much here of interest to the palaeontologist as well.

The scientific study of mummies covers the entire gamut of the subject (the contents and first chapter can be downloaded from the CUP website). Aufderheide defines the term mummy broadly as ‘a corpse with soft tissues sufficiently preserved to resemble a once-living person’ (p. 1). Thus he covers natural as well as anthropogenic processes of mummification. An introduction on the history of the investigation of mummies is followed by an account of the purpose and methods of mummification. A major survey of the global distribution of mummies, including data on the relationship between types of mummification and various environmental and cultural factors, makes up over one third of the book. This systematic review, as far as I can judge, considers any mummy from anywhere worth remarking upon – from frozen sailors in the Canadian Arctic to the desiccated remains of the Chinchorro people of the Atacama desert region of Chile, from bog bodies in Ireland to the pharaohs of Egypt, interspersed with accounts of singular examples such as the bodies of Elmer McCurdy (an Oklahoma outlaw), Eva Peron, Vladimir Ilych Lenin, and even the head of Oliver Cromwell – now interred somewhere in my alma mater (and his), Sidney Sussex College, Cambridge.

Aufderheide may be the first to apply the term taphonomy to mummies, as their interpretation requires an understanding of ‘the effects of postmortem processes that altered the decay mechanism sufficiently to result in mummification’ (p. 287). Mummies may be distorted as a result of taphonomic artefacts – what Aufderheide terms pseudopathology. The most striking are facial expressions – surely the inspiration for the physiognomy of the orcs in Peter Jackson’s *Lord of the Rings*. “Much nonsense has been written in efforts to relate a mummy’s expression to the emotions experienced by that individual at the moment of death … yet all are artefacts of decay processes” (p. 337). This is no less important a message for the palaeontologist interpreting the soft tissues in a Palaeozoic invertebrate – the preserved morphology is to some degree a product of decay.



The chapter on soft tissue taphonomy will be of most interest to palaeontologists. Much of the focus is on biomolecules – proteins, nucleic acids, lipids, carbohydrates. The literature is reviewed comprehensively – investigations by organic geochemists and molecular palaeontologists are summarized and there is even mention, for comparison, of amber and dinosaur bone. Lipids are the most decay-resistant of these molecules and have been investigated in bog bodies and Egyptian mummies (much of the work by Richard Evershed’s group in Bristol) to provide evidence of preservation processes and diet.

Aufderheide considers the nature and formation of adipocere, fatty acid deposits associated with soft-tissue preservation, which may in part explain the preservation of brain tissue about 8,000 years old in a Florida peat bog. The diagenesis of bone is treated only briefly, but its importance as a possible means of assessing the potential of archaeological bone as a source of DNA has only just been realized. Aufderheide himself acknowledges, however, that only limited generalizations can be drawn from “isolated observations and profoundly limited experimental studies dealing with the chemical mechanisms of postmortem … degradation?” (p. 292, on protein studies). More research is required – the field of molecular preservation in mummies has yet to progress as far as its importance warrants.

The second part of the chapter on taphonomy reviews current understanding of the factors that influence the preservation of soft tissues in humans. Dehydration, which must proceed fast enough to prevent soft tissues being consumed by decay, has been investigated in Aufderheide’s laboratory using animal carcasses. Such experiments revealed, for example, that clothed tissue loses water faster than unclothed (whether buried or not) presumably because fabrics draw water off the carcase. Desiccation may lead to the preservation of skin while the internal tissues continue to decay. Metal ions also inhibit decay, and the association of soft tissues with arsenic, mercury, copper or lead may promote soft tissue preservation. The influence of bacteria, fungi and insects is also considered, and there are many observational data that confirm the influence of temperature on rate of decomposition. The final section of this chapter deals with what palaeontologists describe as preservation potential – some of the information based on experimental data and observations by forensic scientists, some on Aufderheide’s studies of spontaneously mummified human bodies from the Atacama Desert. There are some surprises here: hair and nails have a predictably high preservation potential, but eyes are more frequently preserved than either! This review of mummy taphonomy provides a fascinating and comprehensive account of chemical and anatomical decay in terrestrial (mainly subaerial) settings. The drawback, which is a reflection of the stage that the discipline has reached, is that the treatment is largely a catalogue of case histories without any real synthesis.

An extensive chapter on mummy study methodology sets out detailed procedures and protocols for dissection and other analyses. Studies of mummies are linked inextricably to pathology and the science has capitalized on innovative techniques. X-radiography was applied to a mummy in 1897 only two years after Roentgen announced his discovery. Perhaps the best known project on mummies in the UK was that based at the Manchester Museum – initiated by Margaret Murray in the first decade of the 20th century and continued by Rosalie David in the 1970s. But technology has moved on from x-radiography to CT scanning. Organic geochemistry has been used to determine the source of bitumens used in mummification and DNA has been sequenced to identify pathogens. Attempts to amplify DNA from Egyptian mummies, however, have been largely unsuccessful (see Maroata & Rollo, *Cell. Mol. Life Sci*. **59** (2002), 97–111).

The investigation of mummies has always been a sensitive area, leading to potential conflict between scientist and curator: “while investigative dissection of mummies usually generates new information … dissection is often seen to be in conflict with preservation interests” (p. 324). Aufderheide advises that mummies are rarely made available for investigation without the involvement of curator as collaborator and coauthor. Similar considerations often apply to fossils held in private collections.

The remaining chapters deal with the mummification of animals, with human soft tissue palaeopathology (here the more squeamish may wish that the book was not quite so well illustrated!), and with issues of museology. Aufderheide uses the final chapter, on the use and abuse of mummies, to accommodate a miscellany of information that does not sit easily elsewhere in the volume. Mummies have been looted for artefacts, particularly during the 18th century, when there was a major market for Egyptian memorabilia. This trade even led to the production of forgeries; hoax mummies have been revealed by x-radiography in, for example, the British Museum and the Field Museum in Chicago. (The parallels in palaeontology have been well publicized.) I was surprised to learn that ground-up mummies were once sought after for their medicinal qualities, and that mummies have been used for fuel. Aufderheide even supplies a list of mummy-inspired movies, the most famous probably the 1932 original *The Mummy* starring Boris Karloff.

Exceptionally-preserved fossil deposits (Konservat-Lagerstätten) have been incorporated largely into the mainstream of palaeontological research, and are no longer considered mere curiosities. Mummies are the Konservat-Lagerstätten of bioanthropology. Their investigation is increasingly interdisciplinary and involves cutting-edge technology. Aufderheide argues that, with the demonstration that "unique, recoverable information is resident in mummified tissue and that it can be integrated with the general biomedical and bioanthropological database, the scientific study of mummies appears to have come of age" (p. xv). In writing this book he has provided a landmark against which the future development of the discipline will be measured.

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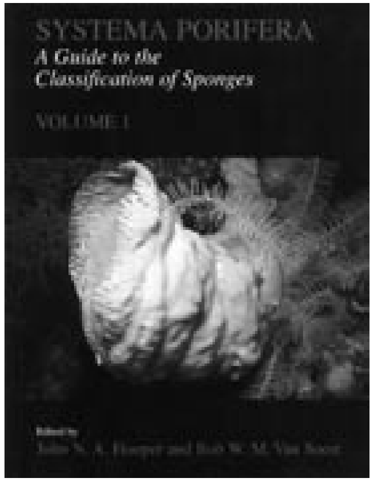
Systema Porifera

Hooper, J.N.A. and van Soest, R.W.M. (eds) Hardcover 1,810 pages (September 2002) Publisher: Kluwer Academic / Plenum Publishers; ISBN: 0306472600. £398.

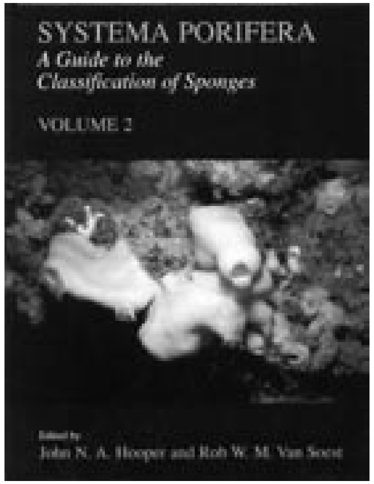
It's hard to know where to start with a beast like this. Seventeen hundred pages of taxonomy is enough to make anyone blanch, irrespective of the benefits for propping open doors or, for that matter, convergent plate margins. It is undoubtedly extremely impressive, but my initial reaction to seeing something of this scale is to ask whether it justifies the huge amount of work put into it (and the four hundred pound price tag), given that it is, essentially, a summary of previously published knowledge. So the first question must be why anyone would be barmy enough to do it.

It is probably fair to say that it could only happen with sponges, and this does explain the perceived need. Sponge taxonomy is a complete nightmare; the 15,000 or so modern species are dominated by demosponges, which are the most diverse group, morphologically and structurally. There is no fixed taxonomic basis for the demosponges, with severe doubt even over the orders, and definitely over the families. In fact, so few characters are both stable enough and useful enough to form a framework that the task sometimes seems impossible.



Even on the level of species, there are severe problems. Only recently, with the advent of molecular identification, have the distributions of even the best known species started to be understood. All this means that the contributors to these volumes are fully aware that they are not presenting a completed phylogenetic taxonomy. That is not the aim. Rather, it is perhaps twofold – firstly, to slice through the morass of invalid taxa, unrecognisable species and synonyms to give an authoritative description of the known genera, and secondly, to synthesize the modern view of sponge taxonomy in such a way that it can form a basis for future revisions. We may not all agree on how the revisions should appear, but at least we can agree on what we're revising. Almost, it sounds like making a fresh start. Hopefully this gives some idea of why the project took place, and believe me, with sponges it's a worthwhile cause!

It must be said immediately that this is primarily devoted to extant faunas. Fossil taxa are treated, but in much less detail – that is the role of the forthcoming Treatise revision. The fossil sections are designed for modern biologists as the audience. Unfortunately, palaeospongological taxonomy is almost completely decoupled from the Recent taxonomy below class level, particularly in the Palaeozoic, so you may wonder why they are included. Ironically, I think this could have been the greatest benefit of the *Systema*, if more attempt had been made to correlate the two. For example, the chapter on fossil non-lithistid demosponges by Reitner and Wörheide consists of a series of short sections discussing the main groups, in which they use terms such as "'Axinellid'-type arrangement." This is fine, but where the rest of the volume is explicit in stating categorical interpretations of the systematic position of each group, it leaves things sadly open. This section is certainly a useful summary of previous data, and even includes some previously unreported information, but that's all.



The chapter on fossil hexactinellids (Krautter) is fine for the Mesozoic and later taxa, but for the Palaeozoic, merely summarizes the present palaeontological taxonomy, in places stating that the taxa are not monophyletic. Worse, the taxonomy used is not a very widely accepted one, including such features as the Hintzespongiidae being subsumed into the Protospongioidea, rather than constituting a superfamily of their own, placing *Cyathophycus* in the Hintzespongiidae, and including the Brachiospongioidea within the Reticulosida. The discussions of each family are also rather weak, and I found this section, which is among the most relevant to palaeontologists, to be a little disappointing. While it forms a basis for future work, I can't help thinking that it will not be long before this classification is redundant. Time will tell. Pickett's account of the Heteractinida is more interesting, and is a comprehensive summary. However, there is no proposed relationship to modern taxa, and they also are left floating.

The lithistids are treated with more coherence, which is unsurprising, given that both extant and fossil groups were dealt with primarily by Andrzej Pisera. This section, once again, is comprehensive and impressive, and includes the laudable suggestion that the term "Lithistida" be abandoned once and for all.

There are additional sections on archaeocyathans, sphinctozoans, and practically every other group of fossil sponge is treated at least in passing. I couldn't find any omissions at high taxonomic levels, and the Archaeocyatha in particular are treated in great depth (160 pages) by Debrenne *et al*. Some, however, are treated very briefly, such as the two pages on stromatoporoids by Cook. Finally, there are five pages of unrecognisable taxa and unavailable names (three pages authored by Haeckel!), including fossils.

So that's the situation with the fossils, but the emphasis of the volume is on living sponges – and that's where the work becomes truly impressive. Each genus is discussed in terms of synonymy, type species (with detailed description), definition, diagnosis, distribution, and usually remarks. They don't quite manage to list every species, but do give references to reviews of each genus, where available. Practically every genus is illustrated, either by photographs or drawings, or both. Although the authors' own preferences undoubtedly become incorporated into the taxonomy of their respective families, I'm pretty sure no two authors have claimed the same genus; with sponges, that's a noteworthy achievement, and must have involved a lot of work by the editors.

On the subject of editors, although the volume is admirably produced and profusely illustrated, there are some unfortunate typos; these include generic names, such as "*Vaurelispongia*" instead of *Vaurealspongia* and "*Twenhofella*" instead of *Twenhofelella* (both p.1,214). I've also spotted several frustrating omissions and inconsistencies in the reference lists (implying that there are probably many more), which is unexpected in a work of this professionalism. However, I suppose the odd mistake is bound to slip in, in a work of this size. I just hope that there aren't too many more of them, because misspelling of taxonomic names is not ideal for readers unfamiliar with the taxa.

This great rambling review of a similar book should probably be given a conclusion, unlike the latter. For sponge biologists, it will become an essential basis for taxonomy. For palaeontologists, the palaeontology sections will be of limited use, except for those new to the group, in which case they can be reservedly recommended. However, the biological component is the greatest benefit for palaeontologists, in that it is essential, for the future study of the group, that we try to integrate the Palaeozoic into the modern framework (I bet the reverse won't happen, after all). On this basis, I would recommend it as a reference for anyone actively pursuing sponge palaeontology – it just makes life so much easier than trying to sift through hundreds of obscure journals. Should you buy it? If yes, the chances are you already have, while it cost a fraction of the price as a pre-print order. Is it worth £400 now? Well, let's just say I'd recommend you find some journal that wants a review of it, or find a library. Actually, unless you're really keen, make it the latter – but make sure you can get it on long loan.

As a last word, despite the criticisms: congratulations to all concerned, for producing something truly monumental.

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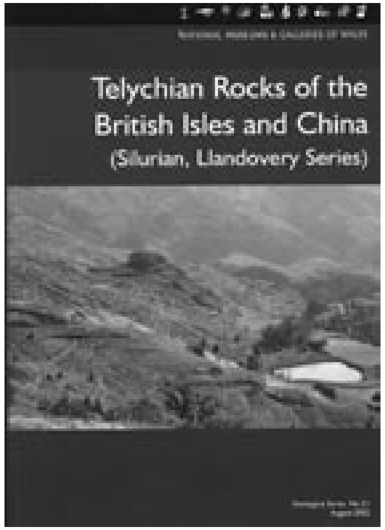
Telychian rocks of the British Isles and China (Silurian, Llandovery Series): an experiment to test precision in stratigraphy

Holland, C.H. and Bassett, M.G. (eds) 2002. 210 pp. National Museum of Wales Geological Series No. 21, Cardiff, ISBN 0-7200-0455-1 (pbk) £14.99.

This long awaited volume describes the development and presents the results of 'Project *Transhemisphere Telychian'*, a collaborative programme that will be familiar to a number of the Silurian workers in the British Isles. The *Transhemisphere Telychian* was set up through the Royal Society to facilitate collaboration between the Nanjing Institute of Geology and Palaeontology and a cohort of Silurian experts from the British Isles. The development of the project teamed sixteen co-workers (eight from Nanjing matched with eight from the British Isles) to focus in on eight fossil groups deemed appropriate for enabling precision in stratigraphic correlation, with Charles Holland the figurehead. The fieldwork in China was carried out in the Yangtze Region in 1988, whilst the Chinese collaborators have been frequent visitors to the British Isles in subsequent years.



The volume presents, logically, an outline of the Telychian of the Yangtze Region, including many detailed descriptions of key field sections – this part of the volume is particularly well thumbed in my review copy as it provides an invaluable source of information on the lithostratigraphic units of the Silurian of South China. This is augmented by a similar description of the Telychian of the British Isles. The latter will no doubt provide the basis for many field guidebooks and fills an important gap now that Siveter *et al*. (1989) is increasingly hard to find.

Description and correlation of macrofossil and microfossil groups by the paired teams of the project forms the bulk of the rest of the volume, with Rickards and Chen dealing with graptolites; Aldridge and Wang the conodonts; the late Charles Downie describing the acritarchs and, with Geng, the chitinozoans; Scrutton and Deng, the corals; Bassett and Rong, the brachiopods; Chen and Holland, the cephalopods; Bassett and Xu, the bivalves; and Lane and

Wu discuss the trilobites. This section includes many high-quality illustrations of the specimens, added by the high-gloss paper on which the whole volume is printed, and includes analysis of the palaeobiogeography, potential facies control on occurrences as well as numerous range charts for most of the groups.

Summary chapters on facies and palaeogeography and a synthesis of the palaeobiogeography provide a conclusion to the work, together with a wealth of references. But, and this is potentially a big but, it's very much a product of the late eighties and early nineties, as is especially evident from the reference list. It's not clear what has caused the delay in publication, but this has left many of the sections out of synch with some subsequent developments (for example Verniers *et al.* 1995). This is a pity and dates the volume, although, whilst I'd suggest that it will primarily be of use to those with an interest in Silurian biostratigraphy and palaeobiogeography, particularly in South China and the British Isles, it's rare that you get a bargain in academic publishing, and the amazingly low price for such an elegantly presented volume probably means the potential market deserves to be much wider.

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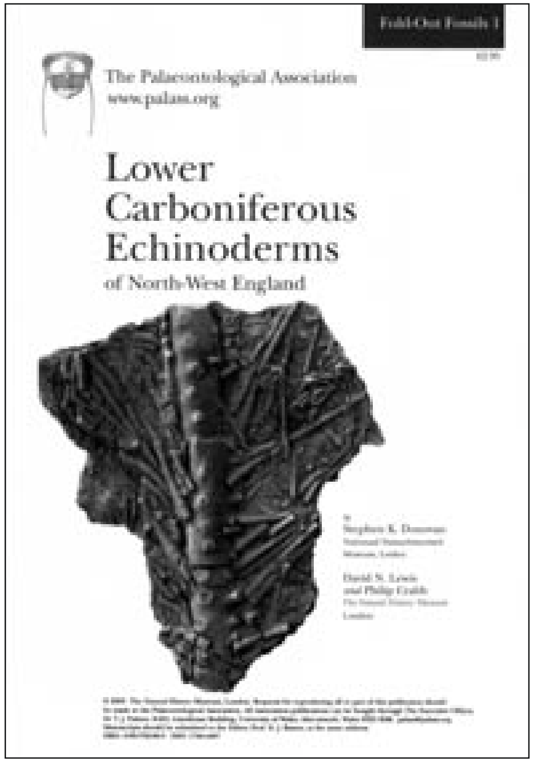

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Special Papers in Palaeontology No. 69. 213pp. ISBN 090170279X. £60
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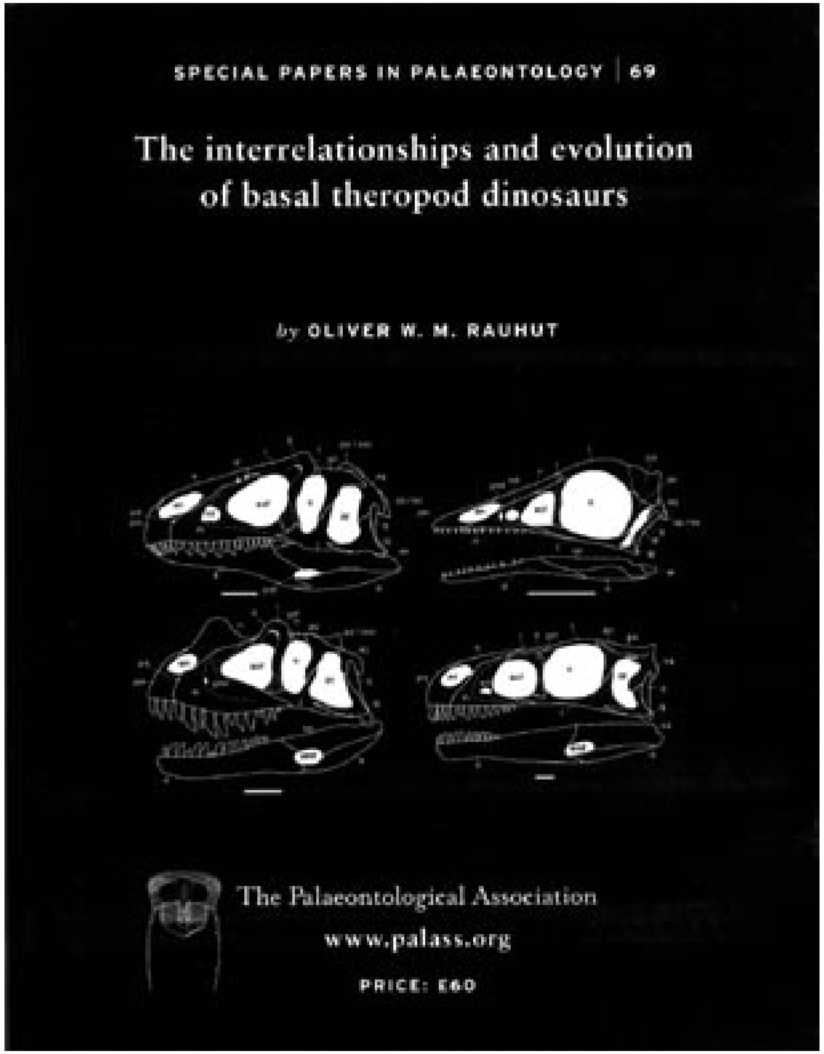
by Oliver W. M. Rauhut

Abstract

Many recent studies of theropod relationships have been focused upon the phylogeny of coelurosaurs and the question of the origin of birds, but the interrelationships and evolution of basal theropods are still poorly understood. Thus, this paper presents a phylogenetic analysis of all theropods, but focuses on the basal members of this clade. The result supports the inclusion of *Eoraptor* and herrerasaurids in the Therpoda, but differs from other recent studies in two main aspects: (1) The taxa usually grouped as ceratosaurs form two monophyletic clades that represent successively closer outgroups to tetanurans. The more basal of these clades, the Coelophysoidea, comprise the majority of Late Triassic and Early Jurassic theropods. The other clade of basal theropods that are usually included in the Ceratosauria comprises *Ceratosaurus*, *Elaphosaurus*, and abelisaurids. (2) Two monophyletic groups of basal tetanurans are recognized: the Spinosauroidea and the Allosauroidea. In contrast to other recent phylogenetic hypotheses, both clades are united in a monophyletic Carnosauria. The branching pattern of the present cladogram is in general accordance with the stratigraphic occurrence of theropod taxa. Despite the differences in recent analyses, there is a significant level of consensus in theropod phylogeny. At least four different radiations of non-avian theropods can be recognized. These radiations show different patterns in Laurasia and Gondwana, and there are increasing differences between the theropod faunas of the two hemispheres from the Triassic to the Cretaceous.



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