The Palaeontology Newsletter

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Reminder: The deadline for copy for Issue no 48 is 4th October 2001

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

Editorial

Post-graduate opportunities in Palaeontology 2002— call for PhD project titles

For a while, Pal Ass has been awarding membership to the best students in palaeontology in UK Earth Science and Zoology Departments. Thus, we have direct access to the most promising aspiring-palaeontologists in the country, through the journal and this Newsletter, and have the opportunity to convince them that a future in palaeontology is for them. To this end, we intend the next issue of the Newsletter to contain a digest of postgraduate opportunities in palaeontology, including related MSc courses and PhD topics available to begin Autumn 2002. It is also my intention that this issue should contain potted biographies of palaeontologists in various employments, explaining how they got to be where they are today!

In order to achieve this, I need your help. I need you to send me all palaeo-related PhD topics on offer by your departments, to begin Autumn 2002, including the project title, a list of supervisors and their affiliation, and an indication of the first point of contact. Please also send details of MSc courses, and any short courses of related interest. This request is by no means limited to the UK. The newsletter will be distributed to the membership and additional copies of this list will be sent to departments and posted on the Association Web site. This will happen in the Autumn 2001 term, just as finalists are beginning to think about their future.

Please send all copy to me at <**newsletter@palass.org**>. *Copy deadline for the next Newsletter is 4th October 2001.*

Philip Donoghue
Newsletter Editor

Association Business

Secretary's business

One of my first and most pleasant duties as your new secretary is to thank the retiring members of Council for their sterling efforts over the past years and welcome new members to Council. Potential applicants for the Sylvester-Bradley Award, Hodgson Fund, the Mary Anning Award and grant aid to attend the Annual Meeting are reminded of the conditions and deadlines listed in this Newsletter. It is also customary in this edition of the Newsletter to announce the forthcoming Lyell Meeting (2002); however the meeting is still in the early stages of planning and at present no title or date is available.

Howard A. Armstrong
Secretary

Council Members 2001-2002

President: **Prof. C.R.C. Paul**, Department of Earth Sciences, University of Liverpool, Brownlow Street, Liverpool L69 3GP.

Vice Presidents: **Dr M.J. Barker**, School of Earth, Environmental & Physical Sciences, University of Portsmouth, Burnaby Road, Portsmouth PO1 3QL. **Dr M.P. Smith**, School of Earth Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT.

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Other Members of Council: **Prof. S.K. Donovan**, Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD. **Dr S. Gabbott**, Department of Geology, University of Leicester, University Road, Leicester LE1 7RH. **Dr E. Harper**, Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ. **Dr D.K. Loydell**, School of Earth, Environmental & Physical Sciences, University of Portsmouth, Burnaby Road, Portsmouth PO1 3QL. **Dr C. Milsom**, School of Biological and Earth Sciences, Liverpool John Moores University, James Parsons Building, Byrom Street, Liverpool L3 3AF. **Dr I.J. Sansom**, School of Earth Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT.

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.

Nominations for Council 2002-2003

At the AGM in May 2002, Dr Barker (**Vice President**), Prof. Harper (**Editor**), Dr Wood (**Editor**), Dr Pearson (**Newsletter Reporter**), Dr Purnell (**Publicity**), Prof. Donovan (**Ordinary member**) and Dr Loydell (**Ordinary member**) will come to the end of their terms of office.

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. Nominations must be accompanied by the candidate's written agreement to stand for election and a single sentence describing his/her 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, 28th September 2001. They should be sent to the Secretary.

Grant aid to attend the Annual Meeting

Grant aid is available to assist postgraduate palaeontologists attending the Association's Annual Meeting. This is available for those travelling from outside the country hosting the meeting (England, Scotland, Wales and Northern Ireland are regarded as constituent members of the UK for this purpose). Awards are limited to those making an oral or poster presentation. Applications for grant aid to attend this year's meeting (no form necessary) should be made to the Executive Officer: Dr Tim Palmer, Institute of Geography & Earth Sciences, University of Wales Aberystwyth, Aberystwyth, Ceredigion SY23 3BD.

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.

Applications consist of a CV, one A4 page account of research aims and objectives, and a breakdown of the proposed expenditure. 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. Application forms can be downloaded from the Web site (<**www.palass.org**>) or from the Secretary. The deadline is 30th November, 2001.

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, with a short statement (up to one page of A4) outlining the candidate's principal achievements, should be sent to the Secretary. Members putting forward candidates should also be prepared, if requested, to write an illustrated profile in support of their nominee. The award comprises a cash prize plus a framed scroll, and is usually presented at the AGM. The deadline is 30th November, 2001.

Hodson Fund

This is conferred on a palaeontologist who is under the age of 30 and who has made a notable early contribution to the science. The nomination must be supported by at least two members of the Association and an appropriate academic case. Nominations should be sent to the Secretary by 30th November. Nominations will be considered and a decision made at the January meeting of Council. The Award will comprise a fund of £1,000, presented at the Annual Meeting.

Dr H.A. Armstrong
Secretary
Department of Geological Sciences, University of Durham, South Road, Durham DH1 3LE
e-mail <**secretary@palass.org**>

news

Palaeontologia Electronica – *Your CD-ROM*

With this Newsletter, Individual Members (Ordinary; Student; Retired) will have received a CD of Volumes 1–3 of *Palaeontologia Electronica*, the highly-acclaimed electronic journal of which the Association is a Tier 1 sponsor.

Council considered offering this for sale to members for between £1 and £2. In the end we decided to send it to everyone free of charge, in order to avoid the horrendous administrative and VAT implications of doing otherwise.

All members are reminded that, when they come to filling out their subscription payment form in November of each year, they have the opportunity to make a modest and entirely voluntary contribution to the Sylvester Bradley Fund.

The CD-ROM will allow fast access to all the papers published in Volumes 1–3 of *Palaeontologia Electronica* (1998 to 2000). In order to read the papers you will need a Web browser (Netscape 3 or higher, Explorer 4 or higher); to access the PDF files, you will need Acrobat Reader (available as a free download from Adobe, <**http://www.adobe.com/products/acrobat/readstep.html**>).

The easiest way to access the papers is to insert your *Palaeontologia Electronica* CD-ROM into the CD-ROM drive of your computer and open the file called **index.html**. If this fails, launch Netscape or Explorer, and open the file from within the browser. More information is included in the "readme" files on the CD.

Palaeontographical Society Monographs
Backpart discount offer to members of the Palaeontological Association

In order to try and ease the problems of storing monograph parts that go back to the origins of the Palaeontographical Society, Council has decided to offer to Members of the Palaeontological Association a 25% discount on all parts prior to those published in 1996. This is the current discount rate for Palaeontographical Society Members. Any number of differently numbered parts may be ordered subject to availability, but only one of each part may be ordered. The sale discount offer is made to Palaeontological Association Members on a first-come, first-served basis, is effective immediately, will continue while stocks last and will be withdrawn after 31st December 2001. As it is not possible to produce a stock list, due to the long period of publication since 1848, you are advised to contact the Marketing Manager with your wants: he will let you know the availability of the required monographs and will give you a quotation which will include postage, packing and handling. The Marketing Manager is Jim Bryant, 27 The Crescent, Maidenhead, Berkshire, SL6 6AA (tel/fax +44 (0) 1628 631705, <**http://quercus.ge.man.ac.uk/PalSoc.html**>).

Reduced prices for Paleobiology *for Pal Ass members*

We have recently agreed with the Paleontological Society in the USA that the other society's members should be offered the same reductions on publication costs as home members. This means that henceforth, as in earlier times, Pal Ass members will get a reduction on the cost of a subscription to 'Paleobiology'.

The annual subscription will be $39 to ordinary members, and $23 to student members, plus an additional $5 for an online subscription as well as the paper copy. This payment should be made to the Paleontological Society Subscription department in the normal way, *not* to the Pal Ass. If you want to take advantage of this deal, you will be required to send evidence of Pal Ass membership along with your subscription request. Such evidence can either be a copy of a confirmatory e-mail note from Tim Palmer <**palass@palass.org**>, or the mailing label from a current issue of *Palaeontology*, which bears the PA member's name and membership status.

In future, Pal Ass members will also be offered any further deals that Paleo Soc members may receive on any future special sales etc. of Paleo Soc publications (plus postage and packaging at cost). Details will be announced in the Newsletter from time to time, or on the Pal Ass Web site at <**www.palass.org**>.

'A Future for Fossils'

edited by M.G. Bassett, A.H. King, J.G. Larwood, N.A. Parkinson, and V.K. Deisler. National Museums and Galleries of Wales Geological Series Publication No 19, 156 pp. ISBN 0 7200 0479 9

This splendid publication is the record of a meeting that was held in Cardiff in the Autumn of 1998 to discuss issues relating to the collecting of fossils. It is a compilation of 25 short papers organised into four sections: National Perspectives and Policies; Policy into Practice – Case Studies; Users of Fossils as a Resource; a Sustainable Approach to Valuing the Resource. The meeting was sponsored by the Association (among others), and deals with examples and case histories from Europe, the USA, and (predominantly) the British Isles. It is hoped to have a review in a future issue of the Newsletter, but this is a must for the libraries of all individuals and institutions that hold fossil collections or have an interest in the issues raised by fossil collecting.

The Cover Price is £14.50, but members may buy their own copy for £12.00, including P & P within the UK. Cheque payable to the Palaeontological Association. Overseas prices (orders using Credit Card preferred; we shall convert to Pounds on the day of processing) are: Europe €24.00 including mailing costs; Rest of World $24.00 surface, $36.00 Air Mail. Order from the Executive Officer (<**palass@palass.org**>, or see inside covers for address etc).

2001 Sylvester-Bradley Award Winners

Mr Peter Alsen (University of Copenhagen), £1,000
Palaeobiogeography and ammonite biostratigraphy in the Valanginian (Lower Cretaceous) of East Greenland.

Dr Howard Falcon-Lang (British Antarctic Shelf Program), £975
Forests in a mid-Jurassic desert?

Ms Susan Hammond (Cardiff University), £1,000
Fossil plants from the Middle to Late Devonian of the Yangtze region, central China.

Mr George Iliopoulos (University of Leicester), £750
The Upper Miocene locality of west coast South Africa. Comparisons with the Upper Miocene of Kerasia, Greece.

Dr Ian Jenkins (University of Bristol), £900
The Gorgonopsidae.

Mr Alistair McGowan (University of Chicago), £800
Triassic ammonoid morphological evolution, mass extinction and recoveries.

Mr Lance Morrissey (University of Bristol), £705
The biological affinity of the enigmatic trace fossil Beaconites.

Dr Ireneusz Walaszczyk (University of Warsaw), £1,000
Taxonomy, biostratigraphy and biogeographic relationships of the Campanian and Maastrichtian (Cretaceous) inoceramid bivalves of South Africa.

Dr Adam Yates (University of Bristol), £450
The first melanosaurid (Saurischia: Sauropodomorpha) from continental Europe and the origin of sauropod dinosaurs.

Michael Zuykov (St Petersburg State University), £587
Morphology, taxonomy and morphogenesis of Ordovician brachiopods of the genus *Platystrophia* (Orthida, Plectorthidae) from East Baltica.

IPA Directory of Fossil Collections of the World

I would like to remind everyone that the IPA Directory of Fossil Collections of the World is currently on-line, but its success depends upon curators and collection managers entering information about their particular collections.

Please visit the site at <**http://ipa.geo.ukans.edu/Fossil/fossil.html**> and take a few minutes to fill out the New Record page. While you're there search the 50 records that are currently in the database or browse through the more than 1400 records in the Directory of Paleontologists of the World at <**http://ipa.geo.ukans.edu/Directory/directory.html**>

Also watch for the new IPA Web site coming soon to <**http://ipa.geo.ukans.edu/**>

Michael Cormack
Paleontological Institute, 1475 Jayhawk Blvd., Room 121 Lindley Hall, The University of Kansas, Lawrence, KS 66045 USA

Colour Postcard set

Our new collection of postcards has been enthusiastically admired wherever it has been received, yet many members have not yet taken the opportunity to buy a set at the specially reduced members' rates. Now is your chance, and below we reproduce the announcement that first appeared in Newsletter No 46.

The Association, in a joint venture with The Lapworth Museum at the University of Birmingham, has produced a series of 16 high-quality colour postcards. They are sold in shrink-wrapped sets and are suitable for use with or without envelopes. They are ideal for offprint requests, teaching, and all general uses. They may be retailed and the images may be reproduced for teaching purposes.

The captions are:
Venerid, bored by clionid sponges and encrusted by corals. Tertiary. U.S.A. x1.1
Thallograptus, a dendroid graptolite. Wenlock, Silurian. Dudley, England. x1.2
Hemicyclaspis murchisoni, an osteostracan agnathan. Pridoli, Silurian. Dudley, England. x1.2
Lepidodendron leaf cushions on stem (external mould). Westphalian, Carboniferous. Dudley, England. x1.3
Brachiopods. M. Jurassic. Normandy, France. x1.1
Spines of *Balanocidaris*, a regular echinoid. U. Jurassic. Portugal. x1
Acervularuia ananas, a rugose coral. Wenlock, Silurian. Dudley, England. x1.2
Pecten. Tertiary. Sicily. x0.9
Skolithos (Pipe Rock). Early Cambrian. Assynt, Scotland. x1.1
Viviparus (Purbeck Marble). L. Cretaceous. England. x1.7
Silicified araucariacean cone. Jurassic. Argentina. x2
Placocystites forbesianus, a carpoid. Wenlock, Silurian. Dudley, England. x4
Calymene blumenbachii, trilobites. Wenlock, Silurian. Dudley, England. x1.6
Dragonfly wing (part and counterpart). Westphalian, Carboniferous. Dudley, England. x2
Stromatolite showing seasonal banding. Purbeck, U. Jurassic. Portland, England. x1.5
Crinoid columnal gravel. L. Carboniferous. Derbyshire, England. x1.4

Sets can be obtained from The Executive Officer (see address inside front cover; for further details e-mail <**palass@palass.org**>). Costs include Air Mail Postage and Packing. UK 1–5 sets, £2.50 each; more than 5 sets, £2.00 each. Europe 1–5 sets, £3.00 each; more than 5 sets, £2.50 each (Credit Card payment preferred). USA and Canada 1–5 sets, $5.50 each; more than 5 sets, $5.00 each (US Dollar cheque preferred, or Credit Card). Rest of World 1–5 sets, £3.50 each; more than 5 sets, £3.00 each (Credit Card payment preferred).

Persuade your Museum Shop to stock them for sale as sets or individually, and receive a free set for your own use

Subscription information

Would supervisors and advisors of Ph.D. students starting in October 2001 please tell them that they can now join the Association for the whole of their three year studentship for a single one-off fee at the start. The cost will be £25, representing a further 16.6% reduction on the normal student subscription rate for three years.

Translation and Editing of Scientific Texts

'Translations Group' is a group of translators that are able to handle work in any subject, but who specialise in scientific and technical translations and editing. Furthermore, since the translators have trained as scientists (including some with doctorates or post-doctoral experience in micropalaeontology) they thoroughly understand the importance of accuracy and deadlines. For more information see <**www.translations-group.com**>.

Baldwin's Scientific Books: closure of Fossil Hall Bookshop

Fossil Hall Bookshop is closing down so that the proprietor, Stuart Baldwin, can work from home on a smaller basis to give him time to concentrate on a PhD. In the meantime he has several thousands of books to dispose of, many of which are reduced to £1 each. The book sale will last as long as stocks do. Stuart is still buying, however, and visitors will be able to see many shelves of stock just arrived. Topics cover the whole of geology, palaeontology, earth sciences and the sciences from astronomy to zoology, plus natural history, biography and numerous other subjects. Visitors will also be able to see prints, minerals and other items for sale at reduced prices. Contact Stuart at <**sbaldwin@fossilbooks.co.uk**>.

New Software for Palaeontologists

PAST is a free, easy-to-use data analysis package aimed at palaeontologists. It is an ideal teaching and research tool. The package was inspired by PALSTAT and was developed by Øyvind Hammer (University of Oslo) with assistance from David Harper (University of Copenhagen) and Paul Ryan (National University of Ireland, Galway). It includes most common statistical, plotting and modelling functions:

- A spreadsheet-type data entry form, graph, scatter, histogram, ternary and survivorship plots
- Curve fitting: Linear (Standard and Reduced Major Axis), lin-log (exponential), log-log (allometric), logistic, von Bertalanffy, sum-of-sines, B-splines.
- F, T, Chi-squared, Kolmogorov-Smirnov, Mann-Whitney, Shapiro-Wilk, Spearman's Rho and Kendall's Tau tests, correlation, contingency tables, one-way ANOVA.
- Diversity statistics, rarefaction. Dice, Jaccard and Raup-Crick similarity indices.
- Multivariate statistics: Principal Components (with Minimal Spanning Tree), Principal Coordinates, Correspondence analysis with detrending, Cluster analysis (three algorithms, nine distance measures), seriation, discriminant analysis, Hotelling's T-squared.
- Time series analysis: Spectral analysis, autocorrelation, wavelet transform.
- Geometrical analysis: Directional statistics, rose plots, point distribution statistics, Fourier shape analysis, elliptic Fourier shape analysis.

- Simple parsimony analysis (cladistics): Exhaustive, branch-and-bound and heuristic algorithms, Wagner, Fitch and Dollo characters. Bootstrap, strict and majority rule consensus trees.
- Biostratigraphy using Unitary Associations

Included in the distribution are 14 real data sets for educational use, together with extensive documentation and case studies. The package may be downloaded from <**www.toyen.uio.no/~ohammer/past/**>, and the approach and methodology of the package are summarized in Hammer, Ø., Harper, D.A.T. and Ryan, P.D., 2001 (see *Palaeontologia Electronica*). Users should sign up with Øyvind (email <**ohammer@toyen.uio.no**>) for news of updates and cite the *Palaeontologia Electronica* article if the package is used for published research.

David A.T. Harper

Geologisk Museum, Denmark
<**dharper@savik.geomus.ku.dk**>

AGM and Annual Address 2001

The 2001 Annual General Meeting of the Palaeontological Association was held in the Wellcome Suite of the Royal Society, London, on Wednesday 2nd May. Two Association awards were conferred upon three palaeontologists in recognition of their work in the field.

Mary Anning Award

J.S.H. Collins is the recipient of the Mary Anning Award for 2001. He is a leading expert on fossil crabs and barnacles in the British Isles, and has published extensively in a wide range of internationally cited journals since 1961. Joe has described over 250 new crab taxa and he has greatly expanded the collections of the Natural History Museum. Joe has previously received the Fullerton Award of the Geological Association and the Worth Prize of the Geological Society.

Joe Collins receiving his award from the Association President Prof. Chris Paul.

news...

Hodson Fund

Due to the very high calibre of the applicants Council agreed to sanction two awards.

Paddy Orr is a lecturer at the National Museum of Ireland, Galway. His portfolio contains 14 publications in a wide range of internationally cited journals and includes a number of substantive monographs. His work has focused on Silurian arthropods, exceptional preservation (including work on the Burgess Shale) and trace fossils. The latter has included novel computer-based models for the generation of traces.

Ivan Sansom is a lecturer in Palaeobiology at the University of Birmingham. In the last ten years he has become a leading figure in the debate over the origin and early evolution of vertebrates through his work on conodonts and fish. His work ranges from histological to systematic and phylogenetic studies. He is currently actively collaborating with a large number of international scientists investigating the divergence of jawed vertebrates. His portfolio of publications includes three *Nature* papers, book chapters and a variety of systematic works.

The annual address was given by Prof Richard Fortey FRS of the Natural History Museum, London, on the subject of '*Deducing life habits of trilobites: science or scenario?*').

Association Meetings Programme

Molecules and Pal Ass at the Systematics Association Biennial

Imperial College, London 3-7 September 2001

This year's Biennial Meeting of the Systematics Association will include a one-day symposium sponsored and organised by the *Palaeontological Association*. The symposium *Telling evolutionary time: molecular clocks and the fossil record* has been organised by Phil Donoghue and Paul Smith (University of Birmingham) under the auspices of *The Association* and features invited speakers, both national and international, who will discuss aspects such as the mechanics of molecular clocks, the quality of the fossil record, and the use and abuse of palaeontological data. The symposium will also include a series of case studies in which speakers will address match and mismatch between palaeontological and molecular estimates of the timing and tempo of major evolutionary radiations, most notably, within animals and plants. A list of papers is given below. Discounted registration rates are available to members of the Palaeontological Association; registration is also available on a daily basis. Further details regarding the meeting, as well as registration forms for attendance can be obtained from <**www.systass.org/biennial2001/index.html**>.

- Molecular Clocks: Whence and Whither (Francisco Ayala *UC Irvine, USA*)
- The quality of the fossil record and reconciling differing molecular and morphological dates (Mike Benton *University of Bristol, UK*)
- Placing constraints on divergence times using the fossil record: problems and prospects (Andrew B. Smith *Natural History Museum, UK*)
- Towards an integration of molecular clocks, Earth history, and the fossil record (Blair Hedges *Pennsylvania State University, USA*)
- Ghost ranges: real or imaginary? (Chris Paul *University of Liverpool, UK*)
- Episodic evolution in foraminifera, evidence from molecular and fossil data (Jan Pawlowski *Universite de Geneve, Switzerland*)
- Molecular clock calibration from comparing molecular and stratophenetic phylogenies of coccolithophores (Jeremy R. Young[1], Alberto Saez[2], Linda Medlin[2], Ian Probert[3] ([1]*Natural History Museum, UK*; [2]Alfred *Wegener Institute, Germany*; [3]*Université de Caen, France*))
- Dating the origin and early diversification of land plants: evidence from fossils and molecules (Charles Wellman *University of Sheffield, UK*)
- Integrating ancient fossils and new methods of analysis in estimating the age of angiosperms ([1]Susana Magallon, [2]Peter Crane, [1]Michael J. Sanderson, [1]Patrick Herendeen *([1]University of California at Davis, USA; [2]Royal Botanic Gardens at Kew, UK*))
- Angiosperm divergence times: What use are molecules? (Niklas Wickström *Natural History Museum, UK*)
- Metazoan divergence: evidence for the phylogenetic fuse (Richard Fortey *Natural History Museum, UK*)

- Written in stone? Fossil evidence for the origin of animals (Graham Budd *Uppsala Universitet*, *Sweden*)
- Origin and early evolution of chordates: reconciling molecules and fossils (Philip Donoghue, Paul Smith & Ivan Sansom *University of Birmingham, UK*)
- Bones, clocks and crown tetrapods origins (Mike Coates[1], Blair Hedges[2] & Marcello Ruta[1] ([1]*University of Chicago,* [2] *Pennsylvania State University*))
- Molecular clocks and the fossil record: the radiation of modern birds (Gareth Dyke *AMNH, USA*)
- Origin and spread of anatomically modern humans (David Goldstein *University College London, UK*)

Annual Meeting of the Palaeontological Association

Geological Museum, University of Copenhagen 15th-19th December 2001

The Annual Meeting of the Palaeontological Association, 15th-19th December 2001, will be held in the Geological Museum with field trips to Bornholm (pre-conference), Stevns Klint and Faxe Quarry (one-day post-conference excursion, 18th December). (Delegates intending to visit Bornholm should contact Richard Bromley directly to make arrangements: <**rullard@geo.geol.ku.dk**>). The technical sessions will consist of two days of talks and posters (16th–17th December) on all aspects of palaeontology, supplemented by a series of social events in the capital city of jazz and design, of smørrebrød and Danish beers, and intimate bars and restaurants. Lectures will be held in the museum's lecture theatre (16th and 17th December) and space will be provided on the adjacent galleries for poster displays. Presentations on any aspect of palaeontology are welcome. Talks are scheduled for 15 minutes with a further five minutes for discussion. The museum has also substantial collections of Palaeozoic, Cretaceous and Paleogene fossils; type material will be available for study by prior arrangement.

Copenhagen is a relatively small and compact European capital but with many attractions. Cultural aspects of the city are described on the Wonderful Copenhagen Web pages <**www.woco.dk**>. The Geological Museum <**www.geological-museum.dk**> is Denmark's National Museum for geology; but it also forms a network within the Science Faculty of the University of Copenhagen together with the Botanical Gardens, Botanical Museum and Zoological Museum. The museum is also part of the Copenhagen Geocentre that combines the museum, the Geological Institute and Geological Surveys of Denmark and Greenland (GEUS) together on Øster Voldgade, adjacent to the King's Gardens, the Botanical Gardens, the Art Gallery and the Rosenborg Palace.

The museum is a 15 minute train journey from Copenhagen's international airport, Kastrup, but is also accessible by rail and road from other parts of mainland Europe. There is now a fixed link to Sweden across the Øresund Bridge. There are flights from many European cities. Cheap flights from the UK are available with GO from Stansted (<**www.go-fly.com**>).

Accommodation, near the museum, is being reserved in the 'Cabin Inn Scandinavia' group of hotels. The following prices include breakfast. Further information about alternative accommodation at a wide range of prices is available on the Wonderful Copenhagen Web pages.

Intending contributors should forward an abstract, preferably by e-mail, of not more than 200 words to the local secretary <**palass2001@savik.geomus.ku.dk**> before 1st September. The format for abstracts should follow the style adopted in the Association's Newsletter number 45 (2000), also available on the Association's Web pages <**www.palass.org**>. Please also indicate if your abstract is for an oral or poster presentation. Presenters under the age of 30 on 15th December who are members of the Association and wish to be considered for the President's awards for best talk or best poster should inform the local secretary when submitting their abstracts. Special group meetings before or after the meeting may also be arranged.

Completed booking forms together with full payment should reach the local secretary before 1st September.

Further booking forms can be downloaded from the Association's <**www.palass.org**> and Museum's <**www.geological-museum.dk**> Web pages.

The deadline for abstracts of 200 words or less (preferably by e-mail to <**palass2001@savik.geomus.ku.dk**>) is 1st September.

Dave Harper (chair), Walter Kegel Christensen, Finn Surlyk, Svend Stouge and Nina Topp.

The Association runs a programme of grant aid to assist overseas palaeontologists who are presenting talks or posters at the Annual Meeting with their travel costs. For the Copenhagen meeting, awards of up to £100 are available to registered full-time students whose presentations are accepted and who are travelling from outside the host country. Payment of these awards is given as a disbursement at the meeting, not as an advance payment. Students who wish to be considered for one of these travel awards should contact the Association directly (Executive Officer, Dr Tim Palmer <palass@palass.org>), not the local secretary.

—— OBITUARY ——

DENNIS CURRY
1912-2001

Dennis Curry was the outstanding combination in the 20th century of a non-professional geologist who was both a brilliant researcher and a generous philanthropist.

As a businessman he was a director of the high-street chain Currys Ltd for 46 years; he published more than 50 scientific papers and for many years was Visiting Professor of Geology at University College London; and as a philanthropist he provided the capital for the Geological Society of London to set up its own publishing house, and for the Geologists' Association to establish the largest charitable trust for geology in Europe. All this was combined with a quiet incisive modesty, which made him more influential.

Dennis Curry was the eldest son of Albert Curry and grandson of the founder of a one-man cycle-making operation in a Leicester garden shed. He was himself born in Leicester, in 1912, but moved with his family to Bournemouth when he was 14. He joined Curry's in 1934. It had become a public company in 1927 but was still dominated by the Curry family.

Curry used his knowledge as a scientist to build up the sales of electrical goods, particularly radios. This expertise was put to use when he served in the RAF in the Second World War and trained airmen in the latest developments in radio and radar. In later years he became President of the Radio Industries Club.

After the war Curry realised the commercial future of electrical goods for ordinary households: televisions, fridges and washing machines. As a joint managing director, he built up his field in Curry's shops. Following the death of the chairman, he took over the post in 1967, finally retiring from the company in 1984, by which time he had seen the number of branches rise from 150 to 550. In one week in 1972 the shares rose in value by more than 22 per cent.

When he was a small boy, Dennis Curry would accompany his father who was a keen fisherman. One day at Newhaven he became bored with the fishing and happened to notice fossils in the Chalk. His early interest in butterflies then started to turn to fossils. Having moved to Bournemouth, and helped by his younger brother Donald, he was able to extend his collecting to the wonderful coastal exposures of rocks at Barton and in the Isle of Purbeck.

At school he was always ahead for his age. His father had rashly promised him a motorbike if he passed his School Certificate when he was 14. Of course, he did pass, and then drove (illegally?) to school on the motorbike. After Higher School Certificate he had a whole year to spare to spend entirely on geology.

His father now expected him to join the family business but Curry obtained a scholarship to Jesus College, Cambridge. In a year of outstanding undergraduates, he not only obtained a First but was awarded the Harkness Scholarship (of £159.25) which enabled him to stay on for a further year doing geological research. He could now have started a university career.

He always pretended that it was quite automatic for him to join Curry's; in fact there was a tremendous family row. Businessmen at the time assumed that the eldest son would follow

his father in the business. In the Curry family all the men stayed in the family firm. Dennis acquiesced but, although he worked hard for the company, he continued to put as much time as possible into geology.

At the start he used to work in a London hotel, returning to Bournemouth at weekends. Later he set up two workrooms in his house at Northwood. Family "holidays" touring Europe were contrived to get past brick-pits and quarries. The family was told he would be "back in 20 minutes", but often he had not returned after two hours. The three children had to perch themselves on lumpy bags of rock samples in the back of the car. And, of course, there was always a halt at any new roadworks.

In warmer countries he would visit the fish market early in the morning, then dissect his purchases in the hotel bedroom to extract the otolith (the "ear-stone" in bony fishes) for his friend Fred Stinton, another enthusiastic amateur geologist. This practice was not popular with Dennis's wife, Joyce.

Dennis Curry's first field of research was the British Lower Tertiary. Publications on the benthic foraminifera, cephalopods and pteropods, were followed by major syntheses which included detailed comparisons with the equivalent rocks in Belgium and France, free of earlier stultifying hypotheses. He then turned his attention to the rocks on the floor of the English Channel. With the help of the Marine Biological Research Station at Plymouth, he was able to use their research vessel, the *Sarsia*, to obtain some 70 cores from the Channel. His mapping revealed structures hitherto unsuspected.

He had long been collecting samples from the Chalk. He now showed how extensive post-depositional solution had been by comparing the planktic foraminifera preserved in flints compared with the surrounding Chalk. This work led to demonstrations of how far flints from the Chalk had been transported before incorporation in the overlying Palaeogene sediments.

Collaboration with French geologists (he spoke French fluently and had a working knowledge of German and Russian) resulted in major improvements in the radiometric dates for the Early Tertiary. This extraordinary breadth of research was only possible because he had no constraints of a professional career in a university or as an industrial geologist, nor did he have to worry about the expense.

Generosity to professionals and other amateurs, both individually and collectively, went through Dennis Curry's life. I recall in the late Fifties, when Norman Peake and I were surveying the Chalk of Norfolk, but neither of us had a car, Curry would drive us round either in the Jaguar or the Rolls. He invited a range of geologists to join him on the *Sarsia*, ostensibly to help him but really to give them free research experience.

At the centenary of the Geologists' Association in 1958 he gave the Association a block of shares in Curry's Ltd which was the largest gift in the history of the Association. In 1986 the Association used the capital to set up a charitable trust in the name of Dennis Curry to support geology and geologists anywhere. Curry hoped that it would be particularly used for the preservation of quarries which would otherwise be filled in and the exposures lost.

Around the same time he gave a similar sum to the Geological Society of London which they used to set up their own publishing house. Without the income from this, the Society might

now well be bankrupt. He also established a charitable trust which has helped the Maritime Trust, several environmental organisations and the local hospital. His enormous collections have been given to the Natural History Museum, together with funds for the cost of curating them. Even without his scientific publications, the name of Dennis Curry will be remembered for a long time.

Dennis Curry, businessman, geologist and philanthropist: born Leicester 18th May 1912; director, Curry's Ltd 1938-46, joint managing director, 1946-68, chairman 1968-84; president, Geologists' Association 1963-65; Visiting Professor of Geology, University College London 1971-84; married 1937 Joyce D'Arcy (one son, two daughters); died Chichester, West Sussex, 3rd March 2001.

Jake Hancock
Bleke House, Shaftesbury, Dorset SP7 8QA, UK

(Reproduced from *The Independent*, 30th March 2001, with permission.)

What's all this fuss about PhyloCode?

Readers of this Newsletter will have heard of the PhyloCode <**www.ohio.edu/PhyloCode**>; some may have read it at length, and some even may have put the contained recommendations into practice. This contribution is for those who may not have examined it in detail, or appreciated the implications for nomenclature and, in particular, the potential impact for our everyday palaeontological work. There is copious literature and I will only concentrate on those areas where, in my opinion, there may be potential confusion with our standard practice of naming taxa under the conventions of Linnean Taxonomy (herein abbreviated to LT) with which we are all familiar.

The PhyloCode is a new system of Biological Nomenclature which provides rules to govern the naming of clades across all of biology. It is intended to be used concurrently with, or to replace the International Code of Zoological Nomenclature, the International Code of Botanical Nomenclature and International Code of Bacteriological Nomenclature. The PhyloCode is the formalisation of the ideas of Phylogenetic Nomenclature (herein abbreviated to PN) which has been discussed in a series of papers beginning with de Queiroz & Gauthier (1990). Terms such as Phylogenetic Taxonomy and PN were freely interchanged in the earlier papers on PN. The two are not the same. Phylogenetic Taxonomy is effectively phylogenetic systematics. We can have Phylogenetic Taxonomy without PN and indeed we could have PN without Phylogenetic Taxonomy since the only requirement is that we have a phylogeny before us, irrespective of how that phylogeny was derived (phenetics, evolutionary taxonomy or even maximum likelihood).

A near comprehensive bibliography of PN is given following the Preface at the PhyloCode Web site. It has been discussed, refined and argued over in three symposia, with the formal proposals being set out as a result of a meeting in 1998 at Harvard. At present the recommendations are in draft form and incomplete in the sense that rules for governing the naming of species have not yet been written, primarily because the species problem is a harder nut to crack (see Cantino *et al*. 1999 for some 13 alternatives, some of which abandon the binomial in favour of uninomials). Names erected under PhyloCode rules will be registered and PhyloCode will officially 'go live' when the Registration Committee of the International Committee on PN is established.

Why do we need Phylogenetic Nomenclature?

Proponents of PN argue that there should be congruence between phylogenetic hypotheses and nomenclature. LT, structured as it is around Types and Rank (Genus, Family, Order etc.) is not compatible with this objective and indeed the instability introduced by insisting on rank operates against any attempt to reflect changes in ideas about the phylogenetic relationships. Types simply provide the focus point for the name and say nothing about the evolutionary relationships of taxa.

The principles of the PhyloCode are stated under six headings (*PhyloCode Division I. Principles*):

"1. Reference. The primary purpose of taxon names is to provide a means of referring to taxa, as opposed to indicating their characters, relationships, or membership.
2. Clarity. Taxon names should be unambiguous in their designation of particular taxa. Nomenclatural clarity is achieved through explicit definitions.
3. Uniqueness. To promote clarity, each taxon should have only one accepted name, and each accepted name should refer to only one taxon.
4. Stability. The names of taxa should not change over time. As a corollary, it must be possible to name newly discovered taxa without changing the names of previously discovered taxa.
5. Phylogenetic context. The PhyloCode is concerned with the naming of taxa and the application of taxon names within a phylogenetic context.
6. The PhyloCode permits freedom of taxonomic opinion with regard to hypotheses about relationships; it only concerns how names are to be applied within the context of a given phylogenetic hypothesis."

Thus, PN is based on ontological definitions of ancestry and descent rather than epistemological diagnoses of taxa. The divorce of characters from naming is seen as the strength of PN:

> "The use of phylogenetic definitions liberates biological taxonomy from a 2,000-year-old tradition of basing the definitions of names on characters."
>
> de Queiroz & Gauthier (1990: 310)

PN claims clarity, uniqueness and stability as advantages. Since these are also goals of the other (Linnean-based) codes we may be entitled to ask questions as to whether there is improvement and how it is achieved. Divorcing names from characters, relationships, or membership may seem extreme, but naming under PhyloCode is done with reference to a particular definition which describes evolutionary history in different ways. There are basically three **definitions**: node-based, stem-based and apomorphy based (there can be subtle variations on these—see legend to Fig. 1). These ways are shown in Figure 1 with respect to a phylogeny leading to birds (Aves) where the definition of Aves under the three definitions of naming are given. The particular taxa and character chosen (*e.g. Struthio camelus*, *Corvus corax* and feathers) are called **specifiers** (see below). Here we meet the first potential confusion between PN and our current practices. Many of us will be familiar with the concepts of stem, crown and total groups used in phylogenetic systematics. The crown group (Jefferies 1979) is the latest common ancestor plus all descendants of a Recent group. This corresponds to the node-based definition of PN except that the group can consist of entirely extinct members. The total group (Hennig 1966) consists of the crown group plus all species more closely related to the crown group than to the Recent sister group. The stem-based definition of PN is similar to the total group concept except that it can be used for an entirely extinct clade. The stem group of Hennig (1966) is, by definition, composed of extinct members only and, unless composed of a single species or a single monophyletic group, will be paraphyletic. Under PN the stem group does not exist but will be contained within the taxon named under the PhyloCode stem-based definition.

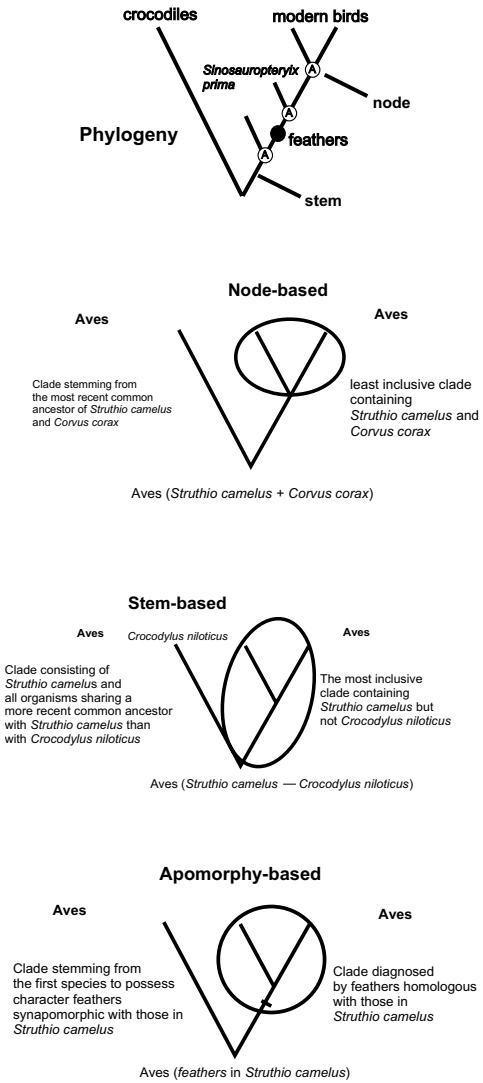


Fig. 1. PhyloCode uses three types of definition in naming. A phylogeny is shown at top left and the node-, stem- and apomorphy-based alternatives are shown alongside. To the left of each definition a description is given which includes reference to ancestors, to the right direct reference to ancestors is omitted but implied. Below each is the shorthand notation suggested by PhyloCode. The definitions may be extended so that there could be a stem-modified node-based definition (Wyss & Meng 1996).

Apomorphy-based definitions are the same under PN and LT in the sense that characters are used as the defining attribute. Historically, under LT apomorphy-based names are those which have caused most confusion as Rowe & Gauthier (1992) point out in the context of the naming of Mammalia, where they show that different authors have used different characters to define Mammalia and different taxa have thereby been included or excluded. But the situation is not avoided by adopting PhyloCode. Characters may be defined differently by different authors. For instance, we might use 'feathers homologous with those in *Corvus corax*' as the specifier to be used in an apomorphy-based definition of Aves. The feather may be considered as just the filament, the filament and the barbs or the filament, barbs and barbules (Xu, Zhou & Prum 2001). Thus, different authors may code the same character differently with resulting different taxa included. In this instance the feather can be seen to be a structure developing through several evolutionary steps and the question for naming becomes at what stage does a feather exist. However, fossil taxa very often do form a pectinated series of taxa displaying sequential development of complex characters—and this is one of the advantages of studying fossils (*e.g.* Smith 1984 on the Aristotle lantern in echinoids and Forey & Fortey 2001 on the teleost tail). Additionally, different but equally parsimonious ways of optimising a character on the phylogenetic tree (*e.g.* ACCTRAN and DELTRAN) may mean that the character can be regarded as homologous or non-homologous (Forey 2001: fig. 4). Therefore it may be necessary to specify under what optimising procedure the name has been erected. Another problematic area is particularly relevant to fossils where the taxon may be unknown for that particular feature due to poor preservation, but the simple optimisation of question marks may arbitrarily include or exclude those taxa from the named clade. The fourth reason is that, should future phylogenetic work show the original theory of homology to be incorrect (*e.g.* that the synapomorphy appears independently on the tree in at least two places), then there would be two taxon names potentially sharing the same specifier.

Specifiers, definitions and stability

PN claims greater stability in the event of changing ideas of phylogenetic relationships (de Queiroz & Gauthier 1994: box 3). By using two specifiers linked to a particular definition of how those specifiers are genealogically related PN claims, quite correctly, stability of the name. But most practising taxonomists seek stability of content of the group which is named. PN recognises this. However, in using different definitions and, at least, two specifiers this has created a complex and, to my mind, an equally subjective chain of decisions which have to be made as with the choice of Linnean types.

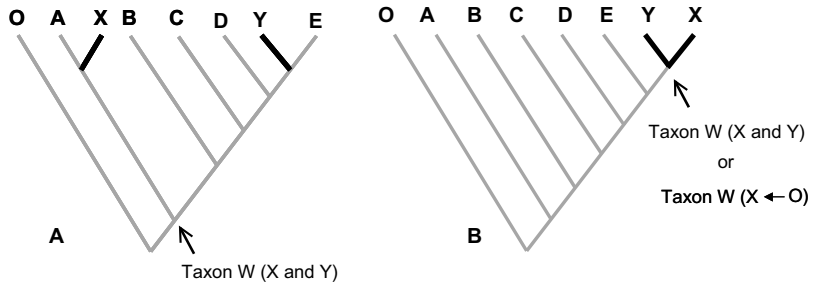


Fig. 2. Choosing specifiers and definitions. Choices have to be made as to what taxa to choose as specifiers and what definition. Rogue taxa which are unstable in their phylogenetic positions can cause drastic changes in stability of taxon membership. A. Node-based group using taxa X and Y as specifiers. B. Phylogenetic revision which places these two as a cladistically derived sister group can result in all other taxa being excluded. One way around this is to use a stem-based definition. These choices often depend on the support for various parts of the phylogeny current when the name is coined.

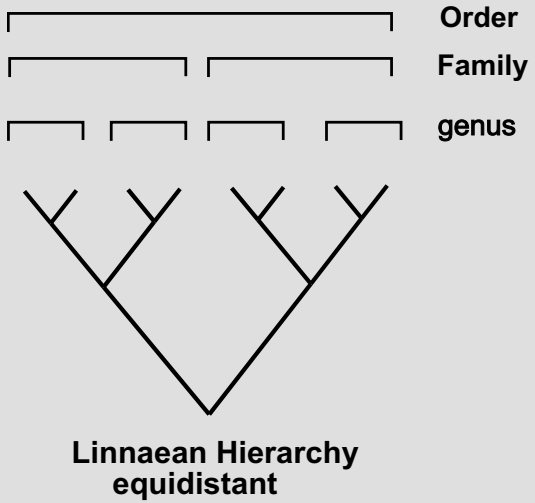
Consider Fig. 2A in which we may erect a node-based group—Taxon W (X and Y). This might be considered reasonable since these taxa are about as cladistically distant from each other as they could be and we might expect the name to be pretty resistant to phylogenetic revision. However, on phylogenetic revision (Fig. 2B), should X be considered the sister group of Y the stability of the content of the group is drastically altered such that there are many clades now left un-named. One way in which phylogenetic changes may be absorbed under the same name is to use a stem-based definition. For instance, if the Taxon W was defined as "all taxa more closely related to X than to 'O' (a taxon outside of the group)" then all permutations of taxonomic revision involving taxa A-E, X, Y would still be possible under the same name. However, should X be resolved subsequently as the sister group of O, the content of the name would be substantially different. Unfortunately, fossils are notoriously variable in their phylogenetic placements, and using them may mean very unstable contents of the PhyloCode name.

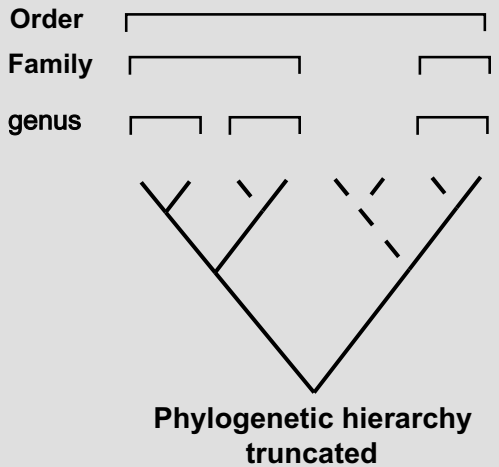
For this reason a substantial part of PN literature has been devoted to suggesting criteria which should be considered when choosing both the specifiers and the type of definition to be used (*e.g.* Sereno 1999; Lee 1998, 1999a, b). These criteria really condense down to the support (ie: Bootstrap, Bremer Support, Jacknife, Implied Weighting etc.) for parts of the original phylogeny in place when the name is coined. How useful this will be in choosing specifiers and/or definitions is debatable, considering the questionable value any of these support indices have in justifying the strength of phylogenetic signal (Kitching *et al*. 1998)

Box 1. Problems with Linnean Rank

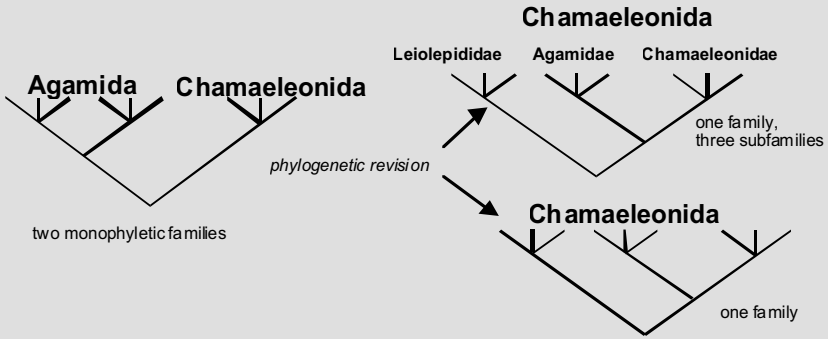
Linnean rank can cause difficulties in three areas:

1. The Linnean hierarchy is symmetrical and the Zoological and Botanical Codes insist that species be referred to every rank up to and including family. This can result in redundancy of information in instances where evolution or extinction result in monospecific families etc.

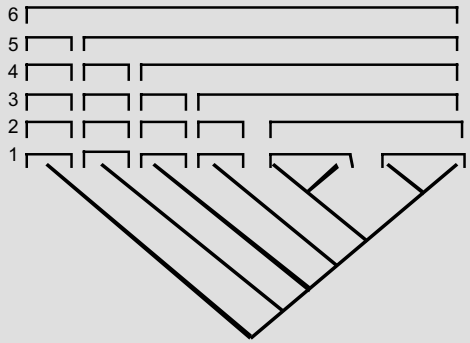




2. Insistence on rank can mean that there is synonymy, inflation of names or loss of phylogenetic information caused when splitting or lumping. One particular area in which this happens is the elimination of paraphyletic taxa (from de Queiroz & Gauthier 1994).



3. If sister groups are required to take equal rank (numbered below) in order fully to depict the phylogenetic tree we would very soon run out of traditional ranks and resort to complex modifiers (e.g. Farris 1976). This problem is exacerbated in highly pectinated trees which are often those discovered by palaeontologists.



Ranks

One of the main advantages of PhyloCode is seen as the abolition of ranks. There are certainly problems with Linnean ranks (Box 1, overleaf). However, under PhyloCode the rank-free system can lead to (familiar) names switching their inclusivity with changing ideas on phylogeny (Fig. 3C) as well as leading to names becoming synonymous (Fig. 3B).

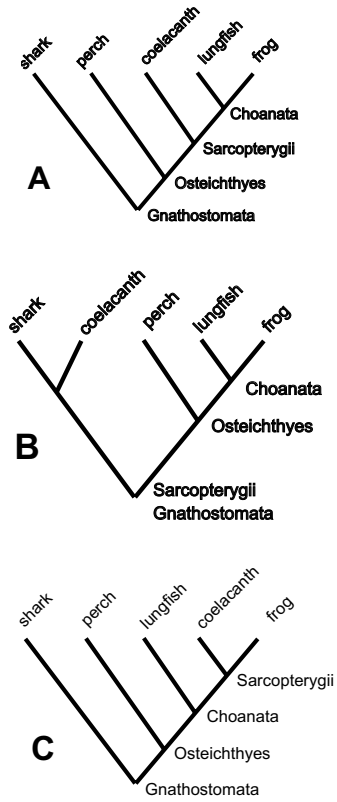


Fig 3. Stability and synonymy. In this diagram three hypotheses of the relationships of coelacanths to other vertebrates are given. That shown in the left column after Forey (1980), centre column after Lagios (1979), and that in the right column after Schultze (1987). The effects of the different taxonomic content of the names Choanata and Sarcopterygii can be mapped across a node based of Sarcopterygii and Choanata. Note in B Sarcopterygii becomes synonymous with Gnathostomata while in C Choanata and Sarcopterygii change relative status of inclusivity as compared with their usage in A. Further effects on taxonomic content under stem- and apomorphy-based definitions of this same phylogeny are illustrated in Forey (2001: fig. 2).

The latter instance can happen under LT. Dispensing with rank is perfectly possible under LT using a few conventions such as sequencing and the plesion 'rank', and this has been done on more than one occasion (Patterson & Rosen 1977, Crane & Kenrick 1997). The Linnean ranks may still be maintained for those people who feel them desirable. And there are some advantages of rank, although few have anything to do with classification. There have been arguments suggesting that ranks can indicate both inclusiveness and exclusiveness (Dominiguez & Wheeler 1997, Schander & Thollsson 1995). Thus Clupeini is included within Clupeidae and some hierarchical information of inclusivity is given through the names and the rank endings. Conversely, a member of Order A cannot be a member of Order B, therefore exclusivity is implied. Parenthetically, it should perhaps be noted that the latter situation will only hold if both Orders are monophyletic.

Another reason for retaining ranks is as sampling items in compilation of diversity indices, particularly in species diversity studies involving fossils, where the chance of detecting a representative of a family or a genus in the fossil record and for calculating lineage duration is greater than detection at the species level (Smith & Patterson 1988, Patterson & Smith 1989). Similarly, it is common practice in biodiversity inventories simply to note the existence of a representative of a family because the organism may be new and can only be recognised initially on family characters. Under PhyloCode it would be difficult, if not impossible, to apply counts since there is no implied comparability of membership species numbers or morphological diversity implied in clade names. Under LT, rank has been used to signify level of morphological divergence either in amount or in kind. The limits of Genus, Family, Order etc. are traditionally judged on degrees of morphological similarity and difference, and these degrees have grown up with the study of the particular group. In a practical sense the rank Family etc. does mean something to specialists within the group and this may be useful in making comparisons between faunas in time and space. But it remains true that it is virtually impossible to justify the comparison of a trilobite family with a fish family, unless we followed Hennig's (1966) suggestion and tied rank to age of origin of the group.

Monophyly etc.

LT can name monophyletic (Class Aves), paraphyletic (Class Reptila) and polyphyletic (Class Vermes) groups. Whether we would want to name the last two is debatable but it is possible that some people would wish to name ancestral (paraphyletic) groups. There does seem some confusion in PN as to whether such is possible. In the early days of PN a suggestion, albeit cumbersome, for naming paraphyletic groups was put forward (Fig. 4). However, PhyloCode is perfectly clear that "Rules are provided for naming clades" … " a clade is a monophyletic group of species" (PhyloCode: *Properties item 2*), or a "group of species sharing an exclusive common ancestry" (de Queiroz & Gauthier 1994: 27). PhyloCode may therefore be restricted to naming only a small fraction of organismal diversity, and therefore the impact of PN on biological nomenclature may be minimal.

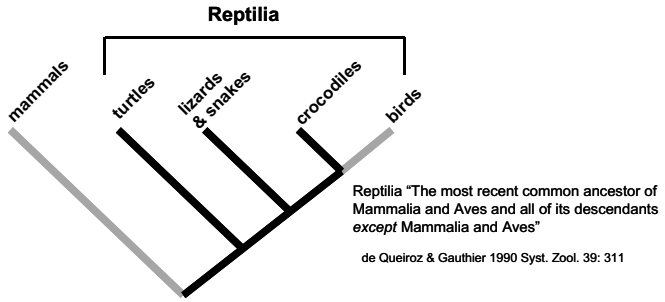


Fig. 4. Suggestions for naming paraphyletic groups have been made within PN. Here, Reptilia is named with the original PhyloCode definition (right) and a modern PhyloCode definition (below) that makes explicit reference to species. Whether this is helpful or even allowed within PhyloCode (see text) is a moot point.

Naming and synonymy

There can be considerable potential confusion introduced in choosing names under PhyloCode as compared with LT. There are two sources of confusion. The first is the use of the same name to mean very different taxonomic entities under the two nomenclatural systems. The second is synonymy. PhyloCode recommends using LT-based names where possible and Articles 10 and 11 detail conditions to try to maintain the original LT usage. However, this is a minefield demanding a careful path to be trodden. One example of a real PN application may exemplify this. A little history may be in order. In 1934 Save-Söderbergh erected a fossil group—Anthracosauria—based on the genus *Anthracosaurus* as type under LT. Save-Söderbergh thought that the Anthracosauria were the closest relatives to the rest of the Amniotes (reptiles, birds, mammals and all their extinct hangers on). He called this combined group the Reptiliomorpha. The modern amphibia were regarded as the living sister-group to the Reptiliomorpha (Fig. 5A). Laurin (1998) revised the phylogeny (shown here in its very simplified form in Fig. 5B) by suggesting that Save-Söderbergh's Anthracosauria was cladistically more primitive than first thought and that the sister-group to the Amniota was the modern Amphibia plus some stem lineage fossils which did *not* include *Anthracosaurus*. He gave the PN name Anthracosauria to a stem-based group that includes all taxa more closely related to Amniotes than to Amphibia. The specifiers are *Amniota included and Amphibia excluded*. This means that the PhyloCode name Anthracosauria no longer includes the type genus *Anthracosaurus* under LT. This is not very helpful.

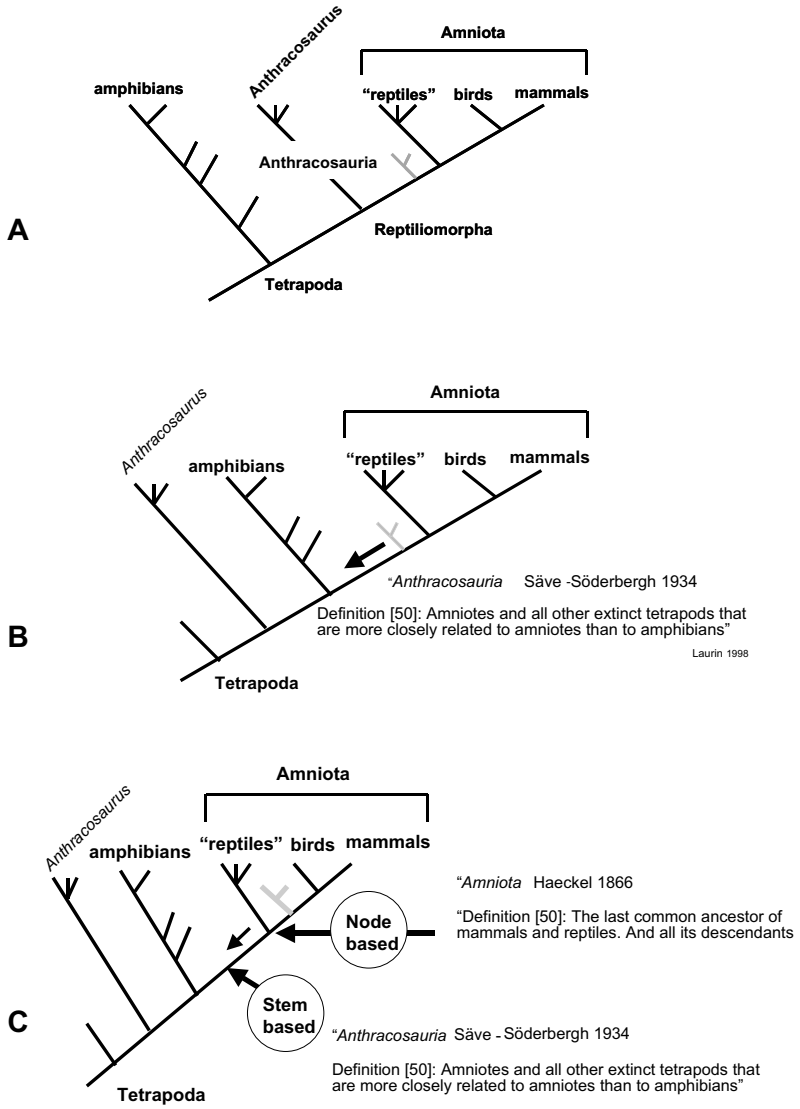


Fig. 5. Linnean types and PhyloCode synonymy. A. The Linnean name Anthracosauria was originally based on the genus *Anthracosaurus*. B. A new phylogeny (simplified from Laurin 1998) now places *Anthracosaurus* below Amphibians but the PhyloCode name Anthracosauria has been coined for a stem-based definition of taxon including Amniotes plus a small extinct group (grey) (the arrow is a convention suggested by Sereno 1999 to signify a stem-based name). C. Should future phylogenetic revision place the grey group inside Amniota the PhyloCode names

Anthracosauria and Amniota would be co-extensive but would not be synonymous (see text).

The soup gets a little more cloudy here because, under PhyloCode, we run into problems of synonymy. The reason why these names Anthracosauria and Amniota are different under PN is that they do not potentially include the same taxa *because* they have been defined in different ways. Now let us imagine that the fossil group shown in grey here which was previously outside Amniota had now moved inside the Amniota on subsequent phylogenetic analysis (Fig. 5C). Now these names Anthracosauria and Amniota specify the same taxa—they are co-extensive. But would they be synonymous? And if so, what name should be applied?

Under PN, names established under different definitions (node-based and stem-based in this case) are not regarded as synonymous. This means we have two legitimate names specifying the same group. Neither can be sunk because neither is a synonym of the other. Is this clarity or uniqueness?

We might of course decide to take the sensible way out of this and regard these names as synonymous, and then we have to take on the problem of which we choose. Laurin credited Haeckel and Save-Söderberg with the names Amniota and Anthracosauria respectively, but neither of those original authors applied those names in the sense that Laurin has. They are effectively Laurin's names and there is a convention in PhyloCode that puts a "[P]" behind the name to suggest that this name has been coined under PhyloCode conventions (as opposed to [L]). And page precedence in Laurin (1998) here would make Anthracosauria the name for the group including Recent "reptiles birds and mammals"—a group known as Amniota under Linnaean taxonomy since 1866. Is this clarity or uniqueness?

Conclusion

Nomenclature, Linnean or Phylogenetic, is the interface between systematic research and the wider biological sciences. As palaeontologists we play a significant and vital role in discovering relationships between organisms, and so are key players at that interface. At the same time we accept the challenge in trying to convey our ideas of relationships through names in written classifications, or we leave the diagrams to speak for themselves. As de Queiroz & Gauthier remark (1992: 457) "…given that the primary task is to represent phylogeny—and acknowledging that there are already more names than anyone can remember—then naming clades seems preferable to leaving them unnamed…". Palaeontologists (and perhaps molecular systematists) often have need of new names to denote those newly discovered clades. Therefore, the subtleties of PhyloCode most urgently need to be appreciated, assessed, accepted or rejected. Are we serving the wider biological community by switching from a Linnean system of character-based names—where we can refer a newly found fossil to the family Clupeidae because it shows a recessus lateralis—to one where Clupeidae is "*Clupea harengus* and *Alosa sapidissima*"? I am not convinced. Is it important for an ecologist, behaviourist or physiologist to understand the theoretical foundations of the establishment of a name? Hopefully, this brief note has introduced some of the strengths and weaknesses of PhyloCode or, at least, has encouraged further reading at <**www.ohio.edu/PhyloCode**>.

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If you have any comments on this article, please send them in to <**newsletter@palass.org**>.

Deep Time, Palaeontology and Stamp Collecting

I should like to take issue with Paul Pearson's review of my book *Deep Time: Cladistics, the Revolution in Evolution* (Newsletter no. 44). In the review, Pearson writes that cladistics "is firmly established across the life sciences as the best way to infer relationships among *distantly related* organisms or fossils given *very incomplete data*" (my emphasis). As far as I am aware, cladistics can be used to infer relationships between any organisms irrespective of the quality of the data or prior ideas about degree of relationship. What is the source of Pearson's very specific misinterpretation of cladistics?

A criticism sometimes levelled against cladistics is that it is just fine for vertebrate palaeontologists, whose material is scarce and scattered, but unnecessary for palaeontologists fortunate to have richer concentrations of material at their disposal. The worries about the nature of ancestry and descent that preoccupy vertebrate palaeontologists, claim the critics, need not apply in cases when fossils are common and densely sampled. So whereas it might be questionable to claim an ancestor-descendant relationship for—say—two fossil mammals, known only from teeth and separated by many metres of sediment, it is acceptable to infer ancestor-descendant links for a pair of forams sitting next to each other in a stratum that consists exclusively of forams.

But it is not acceptable. By what measure can such judgements be reached, other than a qualitative assessment of sampling density in a record whose underlying distribution is unknown and whose completeness, therefore, is impossible, to assess? At what stage of qualitative, subjective completeness do such critics judge the use of cladistics acceptable, or not? To claim that you can safely assert ancestor-descendant links in some circumstances but not others is special pleading.

Pearson takes me to task about the difference between 'testability' and 'falsifiability'. When I describe a hypothesis as a proposition that is testable, I mean exactly that—for it to be falsifiable, an hypothesis must at first be testable. In other words, an hypothesis should imply a way that it might be tested, so that it might then be falsified. Proposed ancestor-descendant relationships do not meet the criterion of testability, let alone falsifiability.

The same applies to any assertion of cause and effect in deep time. Pearson suggests that the discovery of Palaeocene dinosaurs would falsify the impact hypothesis of the end-Cretaceous mass extinction. But this is not so, for the technical reason that we cannot test the impact hypothesis. We do not have replicate Mesozoic Earths in which the asteroid missed, or in which volcanoes erupted instead, and so on. So, were we to discover Palaeocene dinosaurs, we would have no idea which hypothesis of mass extinction we would have falsified, if any. However, following this line of thinking, Pearson suggests that when I say something is 'testable', what I really mean is that it is 'provable'. I do not claim to be so ambitious. When I say 'testable', I mean 'testable' and nothing else. "Absolute truth is something that belongs to the priests and politicians, and they can keep it" says Pearson: I couldn't agree more, and say so several times in the book. This is why I am puzzled when Pearson asserts propositions as fact when they can be neither falsified nor tested: the principal problem of cladistics, Pearson claims, is that "a cladogram will not depict one fossil as being ancestral to any other even if that was in fact the case". But let's look at Pearson's statement—why should Pearson regard this as a limitation of a cladistic, rather than a traditional (or stratigraphic) approach to phylogeny? How can Pearson actually know, for a fact (remember, 'fact' is the word he uses), that one fossil is an ancestor of another? Is there, perhaps, any experiment that can be devised that can even outline this posited ancestor-descendant relationship as a possibility, let alone a certain fact? I challenge Pearson to invent one, because nobody else has succeeded. Were he to succeed in this task, he would violate his own statement that 'absolute truth is something that belongs to the priests and politicians.'

Pearson's misreading of cladistics is further revealed by his investigation of the thought-experiment in which I invite readers to study the next fossil they see, and consider whether this fossil could be their ancestor. "The next fossil I saw was a Jurassic ammonite" says Pearson. "I could plot a cladogram (but I won't) showing that it cannot be my ancestor, at least not with any degree of parsimony." But that's just the point. Cladograms are not meant to demonstrate ancestor-descendant relationships, for the simple fact that such demonstrations are logically impossible.

There is also the charge levelled at cladists that because they question the utility of the fossil record, they are in bed with creationists. I suspect that such critics protest too much, because their own approach to science does not differ materially from that adopted by the creationists themselves.

The aim of cladistics is to reconstruct phylogeny free from any assumption of the tempo or mode of evolution. However, no cladist would doubt that the subjects of phylogenetic reconstruction are the products of evolution. The problem comes when palaeontologists assert that they can use the sequence of fossils to trace phylogeny directly, and even discern evolutionary trends. Such claims go beyond the evidence. They can be supported only by repeated assertion, personal prejudice and appeals to authority. Significantly, this way of thinking, in which a statement is perceived as true as it is authoritative, is precisely congruent with that used by creationists. The creationists, indeed, have an advantage in that they can always assert an authority that is divine rather than merely darwinian.

In my book, I raise questions about the security of hypotheses of adaptation based on fossils, given that extinct organisms lived in ecosystems we cannot know even fractionally; that the adaptive pressures exerted by other organisms (including competitors, congeners, parasites, predators and prey) on an extinct organism can only be guessed; and because fossil organisms are often very different, morphologically, from any creature alive today, so their behaviour and function can never be known with any certainty. Worse, there is no easy way to estimate the degree to which one's guesses are in error. But perhaps more importantly, no amount of functional morphology will ever tell you anything about the processes of evolution. Just because birds are adapted to flight, this fact says little about how birds evolved this facility. In *Deep Time* I spend a whole chapter establishing that very point—but Pearson misses it. "Gee takes evident pride in deriding those old-time palaeontologists and their adaptive ideas. But I put it to him that this tale shows how new scientific evidence has allowed us to test and reject a sensible hypothesis using adaptive reasoning!" The point is not that scenarios are wrong, but that they are founded on unscientific reasoning that is closely akin to the reasoning used by creationists.

I apologise for the following caricature, but it serves to make the point: proponents of scenarios might start with *a priori* statements (for example, that the evolution of birds was necessarily connected with the origin of flight in reptiles that lived in trees); proceed to select evidence that supports such *a priori* statements (the claws of *Archaeopteryx* suggest arboreal habit); and complain when contrary evidence (feathered dinosaurs) is announced. Pearson says, perhaps meaning to be sarcastic, that he hesitates to call the proponents of adaptive scenarios 'scientists'. He would be right. I put it to Pearson that this kind of reasoning is neither more nor less scientific than creationism, in which one starts with an *a priori* axiom (that the Bible is literally true); tries to select evidence in support of this view (Noah's Ark on Mount Ararat; Precambrian human footprints); and complains when contrary evidence is announced (the manifold evidences for evolution.) So when I make my provocative (Pearson calls it 'fanatical') statement that palaeontology without cladistics is as scientific as the one that proclaimed that the Earth was 6,000 years old and flat, I mean precisely that.

Other critics of my book look at my reasonable demand that any science, including historical sciences, should—to deserve the name of science—be based on rigorous hypothesis testing: and accuse me of 'physics envy'. But this is no counsel of despair, because cladistics offers a practical means of hypothesis testing ideally suited to palaeobiology. If palaeontologists want to be taken seriously by the rest of the community, and not be dismissed as stamp collectors, they should take note not just of cladistics but of the scientific principles on which it is based. Palaeobiology is dead—long live palaeobiology.

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Paul Pearson replies…

Henry Gee invites me to respond to a number of points, which I am pleased to do. Let me be clear at the outset that I am no opponent of cladistics. I see it is a useful tool for determining phylogenetic relationships and indeed I occasionally indulge myself. One of the attractive features of the method is that once a character matrix has been constructed the analysis is repeatable from that point onward. Also one can forge ahead with very small data sets, which is good news to palaeontologists. But the method also has well known limitations, which are especially evident in my own field (marine micropalaeontology). So whereas Gee seeks to portray cladistics as the one factor that has turned the study of fossils into an acceptable science, I see palaeontology as a rich and fascinating arena in which good work can be done even without plotting a cladogram.

Gee is right to point out that, in essence, adaptation is the flip side of selection and we can never know even fractionally all the selective events that conspired to produce a particular feature in a particular organism. But if I say the teeth of *T. rex* were used for slicing meat rather than chewing foliage it is not just random guesswork. My inability to put a quantitative error bar on the assertion simply shows that not everything in science can easily be quantified. Richard Fortey made a similar point regarding trilobite function in his 2nd May keynote address to the Annual General Meeting of this Association, as a specific riposte to Gee's characterisation of such efforts as so much cocktail party chatter.

As regards cladistics, the day we start treating any particular methodology as sacrosanct is the first day of a new dark age. Therefore I welcome the opportunity to acknowledge briefly some of the more important practical limitations of the method as I see them, while underscoring that I am, in fact, a keen supporter of the approach. (Incidentally, one criticism I have not made and would not make is that cladists are somehow "in bed with creationists".)

1) Cladistic analysis of fossils relies on the construction of character matrices, but organisms are not composed of "characters" as such. Ideally characters should be unambiguous and independent of one another but this is difficult to achieve in practice. Constructing defensible lists of characters for my foraminifera can be a hellish business when fine species-level discriminations are usually based on qualitative shape criteria and detailed morphometrical discrimination of populations.
2) Idiosyncrasies of character choice can have a big impact on the final result (especially if no weighting procedure is applied).
3) The ambiguities inherent in character selection mean that a nefarious taxonomist might subtly manipulate their character matrix in order to get the desired "result", and then slink away under the smokescreen of cladistic objectivity.
4) Computing power means that one can only analyse a limited number of Operational Taxonomic Units at once. If I have a tray full of thousands of specimens where do I start? The answer is, like any taxonomist I have to first divide the specimens into OTUs on phenetic grounds. But even species level taxonomy in planktonic foraminifera is a 500-taxon problem.
5) In cladistics as generally understood there is no place for stratigraphical information although it is evidently informative with regard to possible phylogenetic hypotheses. A particular problem involves the calibration of cladograms against time, which will exaggerate the frequency of "ghost ranges" if one has sampled ancestors.
6) The actual path of evolution is unlikely in principle to be the most parsimonious path as regards the evolution of characters. To make matters worse, we have evidence of striking iterative homeomorphy in the foraminifera and other fossil groups, which amounts to "coordinated homoplasy". In these cases, the cladistic approach is well and truly scuppered for those taxa.
7) Who says evolution has to work by continual branching and re-branching of permanently isolated species? Horizontal gene transfer and even occasional hybridism of distantly related organisms might in principle occur. So cladistics as an exercise in phylogenetics (rather than just classification) is not free from assumptions about the process of evolution.

Those theoreticians who hold the view that stratigraphical information has no place in phylogenetics should at least consider the three taxon problem (A (B,C)). One test of this hypothesis is that a stratigraphic level exists in which taxon A or its ancestor exists alongside a single population that turns out ancestral to both B and C. With a dense well-dated record and pandemic species we can go to the right level and apply this test using population counts.

The use of stratigraphical data and the tracing of ancestor-descendant lineages is regarded with deep suspicion by most phylogeneticists who do not regularly experience the joys of working systematically through long time-series from deep sea cores that are full of microfossils. (When I say full of microfossils, I mean literally that I can sample anywhere at will within the stratigraphical range of a common species and recover abundant specimens.) There is nothing wrong with healthy scepticism, of course, but I suspect part of the problem is different workers' experience with the groups they study, and I encourage critics to consider how they would respond to such very high density data.

Specifically, would they A) name a new species for each stratigraphical level they sample, even for effectively indistinguishable populations, or B) extend the phenetic grouping of individuals into taxa across time by acknowledging that a single taxon can have a stratigraphical range? If they choose the former route they would be instantly lost in an ever-sprouting taxonomic jungle that no cladogram will ever resolve and, incidentally, concede any possibility of doing something useful with the fossils, like date rocks. If, more sensibly, they were to choose Option B, then in effect they will have already acknowledged the applicability of a working hypothesis of ancestry and the spell is broken. They might find that the mean morphology of the species shifts gradually with respect to stratigraphic level. And what if a single unimodal population that they have traced for sample after sample begins to show evidence of divergence, and eventually gives way to two populations? Would they poke out their eyes in disbelief?

(By ancestry I mean that a Population A from one level may contain specimens that are literally in the distant family tree of Population B from a higher level. Or if it does not, it is a feature of sexual reproduction that an individual from A cannot be very far removed in terms of generation number from the common ancestor relative to an individual from B. Hence the older population contains information about probable ancestral character states.)

It is wrong to say that stratophenetic hypotheses are untestable or can only be supported by personal prejudice and appeals to authority. For example, Gingerich (1999) has formally outlined the stages in the development of a stratophenetic hypothesis and how it can be tested by further data collection. In Bristol we are currently applying this method to an Eocene planktonic foraminifer called *Turborotalia* that shows substantial gradual evolution over about ten million years. Back in the 1960s it was suggested that late Eocene *T. cerroazulensis* was a direct descendant of middle Eocene *T. pomeroli* to the exclusion of another closely related taxon from the middle Eocene. Our collection currently consists of over 10,000 well-dated specimens, on each of which about 10 measurements have been made. On publication, the data will be made public and the collection deposited in a museum. Or if somebody prefers they can re-sample the cores and repeat the study. In fact the original hypothesis has not so far been rejected in our study, and therefore can be regarded as strengthened by having withstood a large amount of data gathering.

Even within a purely cladistic approach an hypothesis of ancestry can be tested and rejected. For example, I can easily reject *Australopithecus robustus* as a likely human ancestor because it exhibits multiple autapomorphies, but I have a harder time rejecting *A. afarensis*. Indeed it is common practice for palaeontologists to present "A-trees" in which taxa that lack autapomorphies are depicted as ancestors on the tree (Smith 1994).

My response to Gee's challenge then is contained in my original review. No, I will never be able to prove beyond any doubt that an hypothesis of ancestry is correct, but provability is not a prerequisite of scientific investigation. And the source of my "very specific misinterpretation of cladistics", as Gee puts it, is that I would prefer to combine evidence from all 10,000 well-dated specimens of *Turborotalia*, taking into account the variation in populations and their observed temporal changes, rather than boil the issue down to a three-specimen problem and run it through PAUP.

Gee asks the interesting question at what point of fossil record completeness is a cladistic approach "acceptable" or not. The answer is that it is always acceptable, but it may not always be optimal. All workers have to judge what methods are best to answer the questions they are interested in. Gee's comment that making the decision involves "special pleading" sounds impressive but means nothing.

I acknowledge that in something like 99% of palaeontological problems there are insufficient data to test an ancestry hypothesis using stratophenetics and therefore cladistic analyses are optimal. The problems listed above will remain, however, and we would do well to keep them in mind when assessing how likely it is that a particular cladogram reflects the true phylogenetic pattern. It is a fact of life that most of the fossil record is very incomplete and there is a lot we shall never know. But there are also fossil groups with much more complete historical records than is generally admitted and it would be a shame not to use every tool in the box to investigate them, including investigating hypotheses of ancestry and functional morphology.

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Henry Gee has the final say……?

Most of Paul Pearson's problems stem from his confusion between ancestors and sister-groups and his failure to understand that ancestry, in the fossil record, is formally impossible to establish. I shall take Pearson's catalogue of errors in the order in which they are presented.

Pearson agrees with me that "adaptation is the flipside of selection". I wrote no such thing. Indeed, the statement is meaningless. He does, however, grasp my point that we can never know the selective events that conspired to produce a particular feature in a particular organism. But he spoils it by saying that an assertion that the teeth of *T. rex* were not used for chewing foliage is "not just random guesswork". But what else is it? The carnivory of *T. rex* can be inferred using many lines of evidence, including the shape of its teeth. But *T. rex*'s teeth could have been used for many other things besides eating meat. As Gould and Lewontin demonstrated in their famous 'Spandrels of San Marco' paper, it is always a

mistake to assume that we can be sure about the purposes of organic structures. (For example, nobody would ever guess from the anatomy of a dead goat that its living relations are very capable climbers of trees.) The only guide to assertions such as these are the parochial and subjective prejudices of those making the assertions. The fact that Pearson's "inability to put a quantitative error-bar on the assertion simply shows that not everything in science can easily be quantified"—which he advances as a boast—compounds the error. If it is not quantifiable, what, then, is it? A guess? This touchy-feely-sticking-fingers-out-of-windows exercise certainly isn't science. Worse, it suggests that it is an assertion supported by nothing more than an appeal from an authority, who, faced with no valid alternative, seeks to defend his position by appeals to subjective notions of plausibility rather than any dispassionate inspection of the evidence. Pearson's invocation, in his support, of Richard Fortey's own attack on my position, should be enough demonstration of this unfortunate tendency in action. In Fortey's own review of *Deep Time* (in the London Review of Books), Fortey says words to the effect that I have never published a cladogram, as if this accusation, even if true (which it is) should have any bearing at all on the soundness of my argument (which it does not). And then Pearson has the gall to say that "the day we start treating any particular methodology as sacrosanct is the first day of a new dark age". Tu quoque.

Moving on to Pearson's numbered points:

(1)-(3) Pearson notes that organisms are not composed of independent characters, and that this creates a problem for cladistics. True enough, but the "hellish business" of constructing character lists for his forams is no fault of cladistics, and, for all that constructing character lists may be difficult, the process is at least transparent. This makes Pearson's opinion of cladistic taxonomists as "nefarious" and engaged in deceit all the more scandalous. I shall throw that back at him—how transparent is the logic on which he bases his assertions, for example, of the purposes for which *T. rex* teeth are adapted?

(4) Computer power is no longer a limiting factor. There exist methods of phylogenetic reconstruction, and technological work-arounds, that can (or soon will be able to) analyze as many taxa as you please. These techniques—developed by systematists and adopted by researchers in the genomics business—need not involve cladistics or parsimony, but the point is made.

(5) Stratigraphy and phylogeny make uneasy bedfellows. There are two clear reasons for this. First, a specimen does not wear its stratigraphy in the same way as a morphological feature. This is as true for a well-controlled foram as for a dinosaur. Second, to use stratigraphy as phylogenetic information and then to use the resulting phylogeny to make statements about stratigraphy (ghost ranges, and so on) is to form a circular argument. Pearson makes the specific point that "A particular problem involves the calibration of cladograms against time … if one has sampled ancestors". And there's the rub: as Pearson consistently fails to grasp, you can never know if any fossil you have sampled is the ancestor of any other. The most you can ever know is that you have discovered a sister-group. Now, speaking as one who has never published a cladogram, I should say that someone who has "indulged", albeit discreetly, should know better—at least to the extent of understanding the principles on which his methodology is based.

(6) "The actual path of evolution is unlikely in principle to be the most parsimonious". Pearson is correct. What is more, I explicitly make the point in *Deep Time*, saying that cladograms give a minimum estimate of evolutionary change—not dogma, not truth, but merely a place to start. Indeed, parsimony makes cladograms ideal as tests for homoplasy. Palaeontologists often fail to understand this point, so I shall use another example, the famous Hardy-Weinberg (HW) Equilibrium from population genetics. In the HW Equilibrium model, alleles spread through a model population that is infinite in extent and in which matings are random. Of course, no real population is like that—the measurable deviations from the HW Equilibrium recorded from real populations therefore tell us interesting things about the effects of population size and assortative mating on the spread of alleles. In the same way, cladists use the assumption of parsimony to see how characters for real creatures deviate from the ideal, maximally parsimonious state. This reveals much about homoplasy. Therefore how it is that Pearson can assert that his forams show a "coordinated homoplasy" that "scuppers" a cladistic approach is hard to fathom. How did he discover this homoplasy, if not through cladistics?

(7) Traditionally, cladistics assumes that organisms evolve in a dichotomously branching pattern. Pearson advances this—again—as if I had never thought of it, but I discuss this assumption in my book. These days, however, cladistics need not be restricted to this model, and I believe that software exists to allow for reticulate models of evolution.

One test of a hypothesis, Pearson says, is that "a stratigraphic level exists in which taxon A or its ancestor exists alongside a single population that turns out ancestral to both A and B". But what manner of science is this "turning out?" More specifically, how can Pearson know, test, falsify, still less prove, that any taxon is the lineal, genealogical ancestor of any other? The fact is that he cannot. Of course ancestors exist—but we can never know that we have discovered them, or even test this proposition. Again, the most we can say is that we have found a relation, in some degree.

Pearson then bemoans the rich stratigraphy with which micropalaeontologists are blessed and asks how critics would approach data of such high density. He offers two alternatives, which I shall examine.

A—name a new species for each stratum sampled, even for effectively indistinguishable populations, or B—extend the phenetic grouping by acknowledging that a single taxon can have a stratigraphical range.

Pearson suggests that option A would result in a taxonomic nightmare, and removes any option for "doing something useful with the fossils like date rocks". Pearson is confusing taxonomy with systematics, for in systematics there is no necessity to name anything—the topology is the important thing. And I would also doubt that fossils are of any use in dating rocks. This may sound heretical, but techniques of absolute chronology are increasingly pushing biostratigraphy as a method of dating into the background.

Pearson then swoons into the seductive arms of option B, in which he can see gently shifting Gaussian distributions of characters in neat stratigraphic order that practically scream 'ancestry' at him—with no mention of geographic control, environmental variation, continuity versus replacement, estimations of completeness (itself a chimaeric concept that must be saved for another day) or any other issue that confounds the neat reading of the

rocks as a picture of straight ancestry and descent. Now, as a personal aside, my postgraduate work involved the quantification of variation in populations of Ice-Age bison and cattle, with a view—initially—to working out evolutionary trends. Bison are not as abundant as forams, to be sure—but they are abundant enough for statistical purposes. It soon became clear to me that I was on a hiding to nothing, simply because there was no way to know, test, falsify or prove any hypothesis claiming that one population was ancestral to another—even in strata as well known as the Upper Pleistocene. The most one could do was to establish 'statistical' populations in which the presumption of ancestry was played down to the point of extinction (I never got as far as drawing up cladograms for my populations, partly because I was dealing with known species with modern representatives, but also because I could never be certain of the biological reality of the OTUs I was dealing with.) For Pearson to claim that the very richness of his data transcends such worries suggests to me that he is in thrall to his data to the extent that he has forgotten the problems of interpreting fossil evidence. The possession of billions of perfectly characterized specimens can never get round the theoretical obstacle that ancestry can never be known, only sisterhood inferred.

His misconception about ancestry deepens with his aside about hominids. "Even within a purely cladistic approach", he says, "an hypothesis of ancestry can be tested and rejected." That this statement is complete rubbish is demonstrated by his suggestion that he can reject *Australopithecus robustus* as a possible human ancestor but would have a harder time of it with *A. afarensis*. The fact is that no cladistic approach would posit either as an ancestor—what cladists are interested in is relative sisterhood, not ancestry, and Pearson's failure to appreciate this difference shows that despite his indulgence in cladistics, he does not understand what he is doing.

Pearson admits that, despite all his evidence, he would never be able to prove that an hypothesis of ancestry is correct "but provability is not a prerequisite of scientific investigation". True indeed—as I say repeatedly in *Deep Time*. The problem that Pearson cannot grasp is that hypotheses of ancestry are in fact no hypotheses at all.

We come, at last, to the crux of the matter. Pearson seems to think that if one's data are, for whatever reason, unsuitably made for cladistics, then alternatives in which one might invoke ancestry might do instead. He responds to my suggestion that "you can safely invoke ancestor-descendant links in some circumstances but not others is special pleading" with the comment that "All workers have to judge what methods are best to answer the questions they are interested in" and that my invocation of special pleading "sounds impressive but means nothing."

Let me, therefore, be more explicit. Pearson goes on to say that in perhaps 99% of problems in palaeontology there are insufficient data to test an ancestry hypothesis. The figure is 100%, and there is no 'perhaps' about it—hypotheses of ancestry are untenable in principle, and to claim that if cladistics fails to find ancestors for you (which it cannot, because no way exists, logically, whereby ancestors can be traced) then something else will.

So why, then, is Pearson indulging in special pleading? I think it is because most of his work, along with that of many other palaeontologists, is based on the presumption that hypotheses of ancestry have a logical foundation, and that ancestor-descendant links are

readily tractable from the fossil record. In which case, the demonstration by cladists that hypotheses of ancestry have, in truth, no logical basis whatsoever, will only be perceived as a threat. The reaction, therefore, has been predictable—some palaeontologists try to distort, belittle and misrepresent what cladists are about. Some whisper that cladists are in bed with the creationists (it happened to the late Colin Patterson, for example). Others (such as Richard Fortey) try to pull rank. Most, I fear, will respond to the threat by pretending it doesn't exist. But the truth will out, and to use a well-worn metaphor, palaeontology will have to adapt or become extinct.

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If you have any comments on this discussion, please send them in to <**newsletter@palass.org**>.

Meeting REPORTS

Acritarch and marine microflora discussion meeting

Sheffield, UK, 21st March 2001

The Palynology Group of the British Micropalaeontological Society <**www.bmsoc.org**> held its first meeting for several years at the University of Sheffield in March. Ken Dorning hosted this successful event that brought together members from across the U.K. and as far afield as Eire and Norway. The twenty-five people who attended came from various universities, the British Geological Survey, oil industry operating companies and service companies.

The morning session dealt mainly with dinoflagellates. Martin Head (University of Cambridge) began proceedings with his talk entitled, "Dinoflagellates and hydrography of the SW Baltic during the last interglacial (Eemian, ca. 130ka)". Rex Harland (Dinodata Services) and K. Grosfjeld (Geological Survey of Norway) reported "The distribution of dinoflagellate cysts from inshore areas along the coast of southern Norway (from Kragero to Kristiansand)". Paul Dodsworth (University of Sheffield, current address Ichron Ltd.) gave the first of three presentations dealing with phytoplankton changes across postulated faunal mass extinction intervals, "Palynology of the Cenomanian-Turonian boundary succession in Crimea, Ukraine". We broke for lunch at the University's '197 Club'.

The afternoon session was devoted to acritarchs. Dan Fiucane and Ken Higgs (University of Cork) discussed, "Microphytoplanktonic decline in the Devonian-Carboniferous boundary beds at Riescheid, Northern Rheinisches Schiefergebirge, Germany". Dave Gelsthorpe (University of Leicester) spoke about, "Microplankton changes across a mass extinction interval: preliminary results from the Early Silurian Ireviken Event". The meeting then changed to a less formal format of discussion sessions. Gareth Hughes (University of Cork) outlined his doctoral research undertaken to date and his plans for future work, "Biostratigraphic correlation of the new Devonian timescale using palynology". Ken Dorning (Pallab Research) initiated debate on anomalous high recovery of acritarchs in the Tremadoc and their extensive stratigraphical and geographical reworked distribution. Craig Harvey (University of Sheffield, current address Ichron Ltd.) summarised his doctoral research on the Devonian Campo Chico Formation in Venezuela, leading to debate on palaeogeographic floral realms and the identification of marine incursions in predominantly terrestrial environments. Ken Dorning and Craig Harvey initiated a discussion on the importance of acritarch size in taxonomy and the problems of standardising sieve mesh size in studies of samples. Ken Dorning continued discussion on biozonations in general with reference to specific Silurian acritarch schemes in the Welsh Basin. Dave Gelsthorpe threaded together a lively debate on acritarch morphology and its possible functions.

The Palynology Group was joined by a number of other geologists for the Sorby Geological Forum lecture by former Sheffield graduate Jason Hilton (Royal Museum of Scotland) who

spoke about "Strange things from Chinese coal seams; a guided tour of the coal swamp plants of China and their significance". Both groups retired to the 'Red Deer' for refreshments.

The next Palynology Group meeting, possibly to be held at the Natural History Museum in London, will take place in early 2002.

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Third International Conference on Trilobites and their Relatives

Oxford, UK, 2-6 April 2001

Compared with those who work on some other fossil groups, trilobite workers have organised few dedicated conferences. In July 1973, an International Conference on Evolution and Morphology of the Trilobita, Trilobitoidea and Merostomata was held as a NATO Advanced Study Institute in Oslo. The proceedings volume, *Fossils and Strata* No. 4, reports that 60 participants from 13 nations attended. There was then a 24-year interregnum before the Second International Trilobite Conference was held in St. Catharines, Ontario, in August 1997. Papers arising from that meeting were published by *Journal of Paleontology* **73** (2) 1999. In early April 2001 some 120 delegates assembled in the magnificent Victorian stone and wrought-iron setting of the Oxford University Museum of Natural History for The Third International Conference on Trilobites and their Relatives, and we are now hopefully on track to hold a symposium every four years.

In his welcoming address, Keith Thompson (Director, Oxford University Museum of Natural History) told us about the museum's history and pointed out some of its notable features, before the technical sessions got underway. Here I have taken the liberty of organising the presentations into broad themes, although many of the lectures could be classed under more than one of the headings I have chosen. Within each paragraph, lectures are mentioned in no particular order. I have underlined the speaker's name in multi-authored contributions.

There were several talks that dealt with diversity and major events in trilobite history. Peter Jell (Queensland Museum) tackled Cambrian trilobite phylogeny, key to the systematics of the whole group. He argued that the polarity of a character on which current thinking on higher taxonomy is heavily based (that the attached hypostome is primitive and the detached condition is derived) should be reversed. This leads to evolutionary pathways that differ from currently used models. Jonathan Adrain (University of Iowa) and Stephen Westrop (University of Oklahoma) discussed the 'cryptogenesis' problem, the apparent phylogenetic discontinuity between Cambrian and post-Cambrian higher trilobite taxa, striving to bridge the gap using evidence from silicified growth series from the Marjuman of Nevada. They postulated the first Cambrian records for the orders Proetida and possibly Phacopida as well as proposing a new order, the Aulacopleurida. In a later presentation they addressed the decoupling between taxonomic (in terms of alpha diversity) and ecological (in terms of abundance) 'success'. Alan Owen (University of Glasgow) and Tim McCormick (British Geological Survey) used a high-

resolution database (in terms of taxonomy, geography and stratigraphy) to critically assess trilobite diversity change during the middle Ordovician radiation in the British Isles. One result not suggested by earlier compilations was that in this part of the world at least the rise to dominance of the so-called Whiterock Fauna was already well underway prior to the major taxonomic radiation event.

Informal session in St John's College. Left to right: Brian Chatterton (Alberta), unnamed person!, Greg Edgecombe (Sydney) and Kristina Manson (Sweden)

A number of presentations dealt with trilobite palaeobiology and behaviour. David Bruton (Paleontologisk Museum, Oslo) and Winfried Haas (Institut für Paläontologie, Bonn) took a very close look at the ventral and internal morphology of Mid Devonian *Phacops* using evidence from careful dissection and X-ray studies. They also analysed the animal's eye, concluding that images were built up from small units contributed by each lens ("puzzle-vision"). They suggested that the Huygensian interface previously claimed to be present in the schizochroal eye was in fact a preservational artefact. Euan Clarkson, Cecilia Taylor (University of Edinburgh), Per Ahlberg (University of Lund) and John Ahlgren (Floby, Sweden) showed spectacularly spiny olenids from the Upper Cambrian Alum Shales of Sweden, and discussed possible life habits and feeding strategies. Richard Fortey (The Natural History Museum) discussed trilobite feeding habits as indicated by hypostomal morphology. He also described hydrodynamic experiments carried out using scale models of *Eobronteus* which suggest that dorsal terrace ridges on pelagic trilobites helped to reduce drag at relatively high speeds. Jana Slavícková (National Museum, Prague) showed how knowledge of the exuviation process in some trilobite species has been enhanced by study of three-dimensionally preserved specimens from siliceous nodules in the middle Ordovician Sárka Formation, Prague Basin. Brian Chatterton (University of Alberta) showed some intriguing examples of "cryptic behaviour" in trilobites, including agnostid and eodiscid carcasses inside empty *Selkirkia* worm tubes in the Burgess Shale, always with their heads towards the narrow end of the tube, and collections of *Acernaspis orestes* moults inside burrows made by other organisms in the Lower Silurian of Anticosti Island. Brian speculated that the animals were hiding from hazards such as turbidity flows or predators, especially during exuviation. Raimund Feist (Université de Montpellier) described concentrations of Devonian trilobite carcasses and moults found in sheltered sites beneath coral colonies and within cephalopod body chambers. The trilobites

were possibly feeding on nutrients concentrated in the shelter as well as using it for protection. Joanne Kluessendorf (University of Illinois) and Donald Mikulic (Illinois State Geological Survey) described flume experiments to determine hydrodynamic controls on formation of trilobite concentrations in Silurian reefs, and showed that recognition of intact exuviae can provide evidence about behaviour and depositional conditions.

Jon Drain (Iowa) and Harry Whittington (Cambridge)

Kenneth McNamara (Western Australian Museum), Yu Fengy and Zhou Zhiyi (Institute of Geology and Palaeontology, Nanjing) showed growth series of four species of the oryctocephalid trilobite *Arthricocephalus* from the Early Cambrian of Ghuizhou Province, SW China and argued that species-species evolution in the genus was through dissociated heterochrony, involving both paedomorphoclines and peramorphoclines. Yuan Wenwei, Zhou Zhiyi (Institute of Geology and Palaeontology, Nanjing) and Zhou Zhiqiang (Xi'an Institute of Geology and Mineral Resources) described ontogeny in the Arenig pliomerid trilobite *Ovalocephalus primitivus* from southern China, and suggested that paedomorphosis played an important role in the subsequent evolution of the genus. However Mark Webster (University of California, Riverside) argued for caution in interpreting evolutionary patterns as heterochronic. He used landmark-based morphometrics to show that an ancestor-descendant pair of species of the Early Cambrian olenelloid *Nephrolenellus*, previously interpreted as an example of peramorphic evolution, in fact show different ontogenetic shape change from each other, so that the descendant ontogeny differs in spatial rather than just temporal characteristics. This may indicate that heterochrony is being overused (or inadequately defined?) in evolutionary studies. Catherine Crônier (Université de Rennes) used elliptic fourier analysis to compare ontogenies of two species of Famennian phacopines, interpreting the differences as the result of ecological adaptations. Nigel Hughes (University of California, Riverside), Giuseppe Fusco and Alessandro Minelli (University of Padova) tackled the tricky question of why, when trilobites are supposed to have added new thoracic segments at each moult stage during the meraspid period until they reached the full adult compliment and then stopped adding them, apparently adult Middle Silurian *Aulacopleura konincki* range in segment number between 18 and 22. They suggested that there was variation in the timing of the meraspid-holaspid switch leading to the polymorphism. Brenda Hunda and Nigel Hughes (University of California,

Riverside) introduced their nice study of morphometric variation in *Flexicalymene* sampled from a succession of life assemblages smothered during storm events in the upper Ordovician Cincinnatian Series, which promises to yield very interesting results about intra-populational variation and microevolutionary change. Richard Robison (University of Kansas) argued in favour of hybridisation to explain intermediate morphs between two species of the Middle Cambrian agnostid *Ptychagnostus*. If borne out this would be the oldest such example known, but it seems likely to be a controversial suggestion.

Wren's Nest field/social excursion. Left to right: Andrew Sandford (Australia) and Zhou Zhiji (China)

More theoretical approaches to trilobite palaeobiology were taken by Øyvind Hammer (Paleontologisk Museum, Oslo) who considered lateral inhibition as a possible developmental mechanism for spatial organisation of structures like granulations, terrace ridges and visual ommatidia on the trilobite exoskeleton, and by Alessandro Minelli, Giuseppe Fusco (both University of Padova), Nigel Hughes and Mark Webster, who discussed post-cephalic segment specification in trilobites. They noted that trilobites appear to be unique among arthropods in that the identity of post-cephalic segments changed during ontogeny: segments formed in the transitory pygidium were later released into the thorax. This raises the question of whether trilobite segmentation is strictly comparable with that in other arthropods.

There were many presentations on phylogeny, biostratigraphy and taxonomic practice. Terrence Fletcher (Edinburgh) discussed the correlation of Cambrian olenellid and paradoxidid sequences using agnostids, bridging the gap between these two distinct associations and possibly opening the way for the first global correlation of Cambrian rocks. James Loch (Central Missouri State University) argued that new trilobite collections show that there is no major faunal break in the upper Ninemile Formation at Whiterock Canyon, Nevada. If true, this would remove a major objection to acceptance of this section as basal stratotype for a global Middle Ordovician Series. David Brezinski (Maryland Geological Survey) presented a nice phylogenetic analysis of the Carboniferous-Permian trilobite *Paladin* (Proetida) revealing clades of palaeobiogeographical and palaeoecological significance. J. Stewart Hollingsworth (Grand Junction, Colorado) described the biostratigraphy of Holmiidae and related trilobites in the Early Cambrian of Nevada. Igor Korovnikov (Oil & Gas Geology Institute, Novosibirsk) did the same for Early Cambrian Protolenidae from the Siberian Platform, relating morphotypes to facies and postulating derivation of the Paradoxididae from the Protolenidae. Hans-Hartmut Krueger (Museum für Naturkunde, Berlin) used the asaphid hypostome as a biostratigraphical tool. Robert Owens (National Museum of Wales) assessed the biostratigraphy and extinctions of Permian trilobites. Taxonomic revisions were presented by Petr Budil (Czech Geological Survey) on the Ordovician-Silurian Dalmanitidae and Acastidae of the Prague Basin; Dong-Chan Lee and Brian Chatterton (University of Alberta) on the Hystricuridae (lower Ordovician); J. Keith Ingham (Hunterian Museum, Glasgow) on the Ellipsotaphrinae (Ordovician); Shanchi Peng (Institute of Geology and Palaeontology, Nanjing), Loren Babcock (Ohio State University), Nigel Hughes and Huanling Lin on Upper Cambrian Shumardiidae from western Hunan, China; Helje Pärnaste (University of Tartu, Tallinn) on the Cyrtometopinae; Andrew Sandford (University of Melbourne) on Homalonotidae from the Silurian-Early Devonian of southeastern Australia and New Zealand. Historical reviews of taxonomic practice were given by Peter Jell, who spoke on the history of erecting genus names in Cambrian trilobites and noted that many synonyms probably remain, and by Michael Cuggy (University of Saskatchewan) who presented some analyses of the stability of the trilobite species described by Resser and Rasetti.

Talks focusing on trilobite associations and palaeoecology included that by J. Javier Álvaro and Daniel Vizcaïno (Université de Lille) who discussed environmental conditions and relative taxonomic turnover in blind and normal-eyed trilobites in the Middle Cambrian conocoryphid biofacies. Zhou Zhiyi (Institute of Geology and Palaeontology, Nanjing), Zhou Zhiqiang (Institute of Geology and Mineral Resources, Xi'an) and Yuan Wenwei (also Nanjing) presented four late Llanvirn–early Caradoc cyclopygid-dominated trilobite biofacies from Shaanxi Province, China, representing an environmental gradient from inner shelf to outer shelf slope with correlated diversity reduction. Samuel Turvey (University of Oxford) also recognised successive associations along a deepening environmental gradient in Arenig–Llanvirn rocks of Shaanxi, Hubei and Hunan provinces. Nigel Hughes, Shanchi Peng (Institute of Geology and Palaeontology, Nanjing), O. Bhargava and S. Parcha (Wadia Institute of Himalayan Geology) showed us the oldest and youngest known Cambrian trilobites from the Himalaya, which extend the previously known stratigraphical and geographical ranges.

Four presentations dealt specifically with trilobite palaeobiogeography. Malte Ebach (University of Melbourne) applied the technique of area cladistics to harpetids to elucidate Palaeozoic palaeogeography. Bruce Lieberman (University of Kansas) also took a phylogenetic approach, evaluating the relative importance of dispersal and vicariance in the diversification of Early Cambrian clades. Wayne Henderson and Nigel Hughes (University of California, Riverside) evaluated the taxonomy of the saukiids and dikelocephalids with a view to reassessing Late Cambrian endemism and biogeography. Duck Choi (Seoul National University) discussed the palaeogeographical relationship between the Sino-Korean and Yangtze blocks during the Early Palaeozoic as indicated by Cambrian and Ordovician trilobite faunas.

Non-trilobite arthropods were an important feature of the conference, as they had been at the 1973 and 1997 meetings. David Siveter (University of Leicester), Dieter Walossek (University of Ulm) and Mark Williams (British Geological Survey) described their recent find of the earliest known "Orsten-type" material, consisting of two specimens of phosphatised phosphatocopid arthropods from the Lower Cambrian of Shropshire. One of these, a larval stage, is the earliest known example of an animal preserved in three dimensions with all limbs intact. The material shows that the Crustacea were already present in the Early Cambrian, possibly indicating a Precambrian date for the radiation of the Arthropoda. Burgess Shale taxa featured in talks by Desmond Collins (Royal Ontario Museum) who described three new onychophorans from that deposit (and suggested that *Hallucigenia* was probably also an onychophoran—the spines

pointed upwards in life but it is still not known which end of the body is which), and Diego Garcia-Bellido (Universidad Complutense de Madrid) and Desmond Collins, who have carried out a study of the anatomy, functional morphology, and behaviour of the famous *Marella splendens*. They argued for the presence of sessile eyes on this animal, and interpreted the second pair of appendages as swimming legs. Derek Siveter (University of Oxford), Derek Briggs (University of Bristol), David Siveter (University of Leicester) and Mark Sutton (University of Oxford) described a new Herefordshire fossil Lagerstätte that yields remarkable non-mineralised Wenlock fossils preserved in three dimensions within carbonate concretions. Derek described the novel process of serial grinding, digital photography and 3D computer visualisation used to study these forms, and we were shown the results as applied to Offacolus kingi, a new soft-bodied fossil interpreted as a basal chelicerate. Derek Briggs, Matthew Wills (University of Bath) and Christoph Bartels (Deutsches Bergbau-Museum, Bochum) described some new arthropods from the Lower Devonian Hunsrück Slate whose "rather basal" morphologies indicate that arthropod taxa not assignable to trilobites or to the modern groups were still in existence long after the Cambrian. Paul Selden (University of Manchester) and Derek Siveter reported on arachnids, including some new ones, from the Carboniferous (Westphalian D) of Somerset, and illustrated the usefulness of computer-aided restoration of deformed fossils, which revealed that there are fewer morphotypes present than previously thought.

Left to right: Mrs and Pfr Peter Jell (Australia), Nigel Hughes (Cincinnati) and Sanshi Peng (China)

Two presentations dealt specifically with higher relationships within the Arthropoda. Gregory Edgecombe (Australian Museum, Sydney) and Gonzalo Giribet (Harvard University) presented an analysis of extant arthropod phylogeny combining eight molecular loci with morphological characters. Using 48 arthropod phena plus tardigrade and onychophoran outgroups (and 256 Pentium III processors), they discovered monophyly of the clades Pantopoda + Euchelicerata, Mandibulata, Myriapoda, and Hexapoda + Crustacea. Comfortingly for the palaeontologist, the analysis suggested that purely morphological and morphological + molecular analyses seem to be converging in this area. However Alberto Simonetta, Marta Pacini and Lavinia Tinalli (Universita di Firenze) argued that phylogenetic studies of arthropod systematics are

compromised by parallel and convergent evolution (especially in functionally significant characters), and by uncertainty in character polarity. They argued that classical comparative anatomy is a more profitable route to arthropod relationships than cladistics.

Last but not least there was what I call the "Wow look at that!" category. Kevin Brett and Brian Chatterton (University of Alberta) described the new genus *Parabolops*, an asteropygine trilobite represented by two species from the same locality in the Lower Devonian of southern Morocco, and characterised by the possession of an amazing trident-like anterior cephalic process. Possible functions for this structure include sexual recognition or defence, and Kevin noted that the presence of two morphologies in the same strata at this locality may be the result of sexual dimorphism, something not yet convincingly demonstrated for any trilobite species so far as I know. David Rudkin (Royal Ontario Museum), Graham Young (Manitoba Museum of Man and Nature), Robert Elias (University of Manitoba) and Edward Dobrzanski provided the arresting title "The world's biggest trilobite". It is a complete articulated carcass of a new species of *Isotelus* from the upper Ordovician of northern Manitoba, measuring 683 mm in length (and that with an estimated 37 mm broken off the anterior). This is almost 70% longer than any previously documented complete trilobite, and suggests a 1200-fold length increase from protaspis to final size!

The presentations took place in a lecture theatre whose size was ideally suited to the conference, and whose projection facilities, including multimedia, ran for the most part flawlessly. Coffee breaks, poster presentations and some buffet meals were held in the upstairs gallery of the museum, and there was ample opportunity to explore the exhibits and conference posters. Additional events included a half-day excursion to Dudley, where we were able to spend an hour or so successfully hunting the "Dudley bug" (a.k.a. *Calymene blumenbachii*) in talus at the classic Wren's Nest Wenlock Limestone locality. We repaired to Dudley Museum for tea and a welcome from the Lord Major of Dudley, whose ceremonial chain bears an engraving of said "bug". Thence to Dudley Living Museum where we were treated to a narrowboat ride through the tunnels and caverns beneath Castle Hill, created during limestone mining operations in the eighteenth and nineteenth centuries—with a little "legging" by some brave souls. The evening was completed by some fine Black Country hospitality—sausage, mash and mushy peas, and a convivial tipple or three in the Living Museum's pub the Bottle and Glass Inn. Another event worthy of mention is the fine conference dinner in the dining hall of St. John's College which rounded off the symposium. The highlight of this evening was a spontaneous standing ovation for Harry Whittington. Few would disagree with Richard Fortey's statement that this conference was, as much as anything, dedicated in recognition of Harry's work over the years.

This conference covered a huge breadth of subject matter, and a variety of study methods were on show. Phylogenetics, not in evidence in the 1973 Oslo conference, now dominates systematic work on fossil arthropods at all taxonomic levels, effectively providing the framework within which all other studies progress. Molecular evidence from extant animals is of increasing importance in underpinning our work, especially at higher taxonomic levels. Great strides are being made in elucidating the higher-level systematics of trilobites and their relationships to the other arthropods. Morphometrics, which made but a single appearance in Oslo, has greatly advanced, principally with the introduction of "geometrical" and "thin plate spline" techniques, and is now used as a research tool in a variety of contexts. Another new

technology is that of computer-aided reconstructions like the ones shown by Siveter *et al.*, and these are likely to become more common in future. We are at last beginning to come to grips with fossil arthropods as living, functioning animals with complex biology and behaviour.

Congratulations and thanks are due to Derek Siveter and the organising committee for a superbly arranged and run conference. Papers from the conference will be published in a dedicated issue of *Special Papers in Palaeontology*. It is unfortunate that the foot and mouth disease outbreak meant that the pre- and post-conference fieldtrips covering classic Palaeozoic geology of southern Scotland, northern England, Wales and the Welsh Borders had to be postponed, but it is planned to run these trips in 2002 subject to interest, and the fieldtrip guides (Owen *et al.* 2001; Owens *et al.* 2001) are available. The next conference is scheduled for 2005. At time of writing the venue has yet to be finalised but is likely to be in either Spain or Australia. They have a tough act to follow.

Speech time at the conference dinner. Left to right: David Bruton (Oslo), Derek Siveter (Oxford), Richard Fortey (London), Alan Owen (Glasgow) and Dick Robison (USA).

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Photographs courtesy of Helje Parnaste (Geological Institute, Tallinn, Estonia <**helje@gi.ee**>) who has made a gallery of images from the meeting available at <**www.gi.ee/~helje/**>

Progressive Palaeontology

Liverpool, UK, 16-17 May, 2001

Progressive Palaeontology 2001 was held at the Peter Jost Centre at Liverpool John Moores University. This year around 40 people attended and there was a truly international feel with people from as far afield as Zurich and the talks taking us around the world from the UK, to Antarctica, Venezuela and the Amazon.

Following registration and coffee, the morning's talks began with JMU's own Mike Carr, who gave a talk about foraminifera distributions in salt marsh environments in the River Alt estuary. He discussed how this could be valuable in the quantitative interpretation of regional coastal Holocene sequences. Next, an alternative study of the late Quaternary Amazonian savanna-rainforest interaction was presented by Phil Metcalfe. He outlined a range of palaeoecological techniques he hopes to apply to the understanding of the long-term dynamics of the Amazonian savanna-rainforest boundaries and the possible influence of orbital forcing. One of the most interesting and well presented talks of the morning was given by Jodie Howe. She introduced her Antarctic fieldwork and discussed her palaeobotanical reconstructions of Cretaceous forests there. The last talk of the morning was presented by one of the organisers, Hannah O'Regan. She highlighted the possible biases in museum palaeontology collections, particularly those of big cats established from game hunting, and commented on the considerations that should be taken when interpreting results.

Hosts and Association President Chris Paul at Progressive Palaeontology 2001, flanked by the organisers Hannah O'Regan (left) and Sally Reynolds (right)

After an enjoyable lunch Susan Hammond began the afternoon session with a talk outlining her project and the preliminary results from her field trip to Venezuela. She discussed the types of fossil plant found and the possible implications for the earliest seed. On a different slant Liam Herringshaw discussed his work on weird and wonderful problematica from the Wenlock Limestone, which he hopes will aid the understanding of the Silurian marine palaeoecology. Next, tracking invisible dinosaurs was the subject of Daniel Elvidge's talk. He emphasised the complexities involved in studying the morphometrics of footprints and the lack of consistency of the measurements in the literature. The theme was continued with Lauren Tucker's talk about Late Carboniferous Tetrapod footprint assemblages from south Shropshire, marking the transition from amphibious tetrapods to amniotes. Next Chris O'Connell gave an eye-opening talk on reconstruction of the evolution and dispersal of Macaca. The final talk of the day was given by Raoul Mutter on Triassic actinopterygian genus *Colobodus*. He outlined his work on scale histology and gave a brief summary of his initial results.

Poster displays generated much interest and discussion: they varied from dinosaurs, to trackways, both ancient and modern, to well preserved invertebrate faunas.

The whole day's proceedings went smoothly and a high standard of presentations were given by all. The evening progressed with a wine reception, a meal at a Chinese restaurant and then on to a local pub for lighter palaeontological conversation.

Due to the bad weather, the field trip to Hilbre Island had to be cancelled, but the JMU organisers were ready with an alternative trip around the collections at the Liverpool Museum. Progressive Palaeontology 2001 attained a high standard of organisation and was felt of benefit to all who attended. We look forward to seeing many of the same faces at Leicester for Progressive Palaeontology 2002!

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Sylvester-Bradley Award report: Wooded oases of an Early Jurassic desert erg

The Early Jurassic (Toarcian) Navajo Sandstone Formation of southwestern USA is known worldwide as the classic example of sandy desert deposition in the Phanerozoic record. Across a huge outcrop belt 500 km long by 300 km wide and spanning the states of Utah, Arizona, Colorado, and New Mexico, thick sandstone units occur containing gigantic dune slip-face deposits in excess of 25m high. Until recently the Navajo erg was considered an extremely arid, inhospitable region at the heart of Jurassic Pangea, devoid of many traces of life. It was therefore with great excitement and gratitude that I accepted one of this year's Sylvester-Bradley Awards to follow up the enigmatic claims of some local geologists that large fossil trees were common in parts of the Navajo Sandstone Formation.

This is a preliminary report of fieldwork undertaken in conjunction with Judy Parrish (University of Arizona) between 19th May and 28th May 2001 in SE Utah. More details can be found in a forthcoming journal paper in preparation with Parrish, and at the Web site <**www.lakepowell.net/navajowet.html**>.

Eight sites exhibiting well-preserved trees, documented over the past ten years by local geologist Fran Barnes, were studied. They occur in spectacular high desert canyonlands near the town of Moab, and are only accessible with a four-wheel drive vehicle across very difficult country. Four major sedimentary facies occur in intimate association at all eight localities:

(1) Fine-grained sandstone units containing large-scale cross-stratification are interpreted as the deposits of gigantic aeolian dunes.

(2) Horizontally-bedded siltstone/fine sandstone units represent clastic interdune deposition.

(3) Fine-grained unstructured sandstone units containing metre-sized intraclasts are believed to be the product of mass-flows.

(4) Thin discontinuous limestone beds also occur, and locally exhibit 2m high tufa domes associated with a vertical cataclastic pipe mineralized by chert. Lateral to the domes, limestone beds rapidly decrease in thickness to c.15-20cm and assume a dark grey, crystalline lithology. At a still greater distance from the domes, soft carbonates begin to interdigitate that possess a saccharoidal texture, gypsum pseudomorphs, rip-up clasts, and enterolithic bedding. The limestone units are interpreted as being spring-deposited, the tufa domes represent the spring loci themselves, the grey limestones were formed in freshwater pools around the springs, and the soft carbonates represent evaporite deposition (now calcitised) further from the freshwater source.

At two of the sites, perhaps more, silicified coniferous trunks occur, rooted in carbonate-cemented sandstone immediately below the spring-deposited limestone units. Due to poor exposure only a very small number of upright trees are demonstrably in growth position, and no unequivocal paleosols could be identified. At the majority of localities tree trunks are prone or have weathered out the cliff-face. The largest trunk recorded was 93cm in diameter

but most fall in the range 17-48cm. In addition to the wood, the impression of a coniferous, leafy shoot was found at one site. The fossil plant assemblage is interpreted as the product of wooded oases that developed around isolated spring seeps between the desert dunes. Growth rings are apparently absent in the woods over tens of centimetres, indicating growth under an equable tropical climate. The lack of annual rings makes estimates for the average life-time of an oasis community difficult, but assuming a maximum tropical radial growth rate of c. 1cm per year, a conservative estimate may be in the order of 50-100 years. Silicified woods also occur abundantly in the mass flow units, where large logs are randomly orientated. This second fossil plant association records the periodic destruction of wood oases by high-energy flash flood events.

Considerable research is needed to document further the wooded oases of the Navajo Sandstone Formation, and this project just represents a small step in a much larger ongoing research program. In addition to the fossil plants, extensive vertebrate and invertebrate trackways and burrows are also associated with the limestone units. These may provide further details about the diverse desert communities of Jurassic southern USA.

Anyone interested in contributing to future work on these Navajo sites should contact Judy Parrish (e-mail <**parrish@geo.arizona.edu**>) for further details.

Dr Howard Falcon-Lang
Dalhousie University, Nova Scotia, Canada

From our Correspondent

Are there trilobites in space?

"No topic is too vain not to be included in this confused medley of mine"

Michel de Montaigne, Essays

There are certain topics, sometimes interesting to palaeontologists, that have a quite unbalancing effect on their students. To name names: such topics include the species concept; the homology concept, and the question of life on other planets. Each question has been furiously argued over for years, yet seems no closer to resolution. As people seem to get rather upset over these issues, I humbly offer the services of my next few columns here as a sort of therapeutic aid to calm the breasts of those suffering from life-, homology- or species-angst. To anticipate: all of these problems are largely self-generated by trying to find things 'out there' which properly only exist in our own heads.

Let us then start with one of the big questions: does life exist elsewhere in the universe? Who would have thought that the PalAss Newsletter would be the organ finally to bear the definitive answer to this question? Surprisingly, the answer, with one excepting circumstance, is straightforward: certainly not. The fact that we think there could be comes about, strictly, through linguistic confusion. To see why, consider the related, and perhaps equally important question, *are there trilobites elsewhere in the universe?* The closest we have come in recent years to an alien landing is the notorious Martian meteorite ALH84001. The latest flag-bearers for traces of life are nanometric crystals of magnetite that are apparently terribly similar to those produced by some terrestrial bacteria. I do not know what the general view on these crystals is. But suppose that one had cracked open a meteorite and had found, in the place of tiny mineral grains, a trilobite. Actually, the Russian palaeontologist Timofeev described some acritarchs from a chondritic meteorite in the 1960s (*e.g.* Timofeev 1963), so it is not completely out of the question. Here is a trilobite from outer space; and it looks rather like, say, *Asaphus expansus* (Wahlenberg, 1821). After all, if magnetotactic bacteria, why not trilobites? There would appear to be two possibilities for its origin. Either it really was an *Asaphus*, or was a completely alien life form that had evolved to look like one. And both of these scenarios show up the flaws in 'life-on-other-planets' scenarios.

Take the first possibility, that this trilobite was a genuine *Asaphus*, and thus an interplanetary space traveller, as required by the 'Panspermia' theory. Then, astonishing though the find would be, one would be forced to conclude that life had originated elsewhere and been ferried to Earth. One obvious difficulty with such a theory, and not one that is often aired, is a phylogenetic one. A space trilobite would imply that all branches on the tree of life connected to its own ancestral lineage would also have evolved somewhere else, and would therefore have to have been brought to Earth independently (see figure 1). A trilobite from space would imply a truly gigantic number of transfers, together with the oddity that selective forces on the Earth would not have shaped any of the organisms

involved. Of course, a further consequence would be a lack of correspondence of the fossil record with a global phylogeny of life. Even a magnetotactic bacterium is astonishingly derived relative to the last common ancestor of all life on Earth; and would also imply an implausible number of transfers. On these grounds, if none others, I find it hard to believe that magnetite crystals from Mars point to a genuine transfer of life from one to the other. I suspect few do.

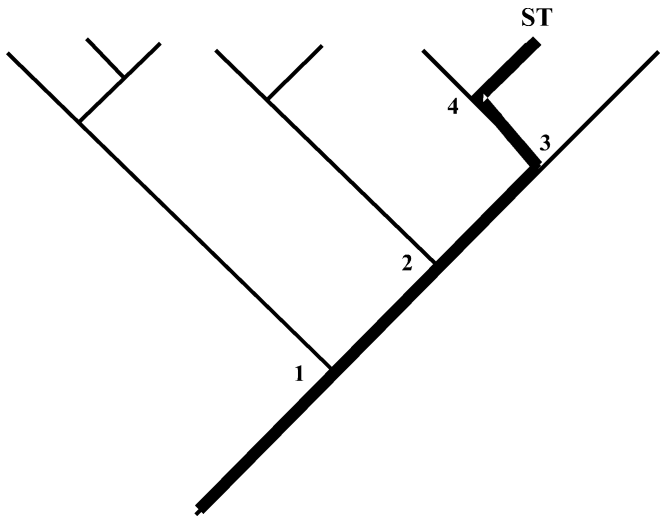

Figure 1.

A somewhat simplified rooted universal tree of life. ST: space trilobite, our intrepid interplanetary explorer. The heavy line marks its line of descent, and the numbered nodes represent the independent seedings of Earth required to account for present and past Earth diversity.

Let us turn to the other scenario, then: could trilobites independently evolve? And to the answer that is obviously, if a trifle pedantically, no. We have struggled for centuries to rid our taxonomic language of polyphyletic groups, and have largely succeeded, except, strangely, for life on other planets. Indeed, the more similar the members of a polyphyletic group are, the more important it is to insist on its destruction, because of its pernicious appeal. The point is that what goes for worm-shaped organisms and convergent sorts of beetle also holds for intergalactic trilobites. There might be rather trilobite-like things out there, of which more below; but in the same way that we don't consider the marsupial wolf really to be a wolf, we should ruthlessly exclude segmented and scuttling invertebrates from planets around Barnard's Star from our concept of 'trilobite'. You should be able to see the extreme and unreasonable conclusion I am heading for here: this argument goes for 'life' itself. There simply is not life on other planets unless it is monophyletic with our own. This also shows how counterproductive trying to define 'life' is. Astrobiologists have struggled

over coming up with just such a definition—something with DNA, perhaps? Or subject to natural selection? Or something 'self-replicating'? This has always struck me as an odd way of proceeding. Surely the thing to do is describe rather than define life, something which after all we are very clear about. No one ponders their pet dog in the evenings, wondering whether it is alive or not, and what it is that makes it 'alive', as if one might suddenly realise that one has been mistaken about it all these years. For the one thing that all life shares is that it is monophyletic and related to us. That is why we feel inclined to call viruses living, and inclined to call prions non-living, because the genetic code of viruses makes us think there is a shared ancestry with all other life. If one really wanted a definition, then one could list the characters at the base of the crown group. Unless Panspermia is correct, nothing else in the universe can fit into this phylogenetic scheme, so nothing else is alive, in the same way that we do not think that a 'definition' of a mammal is perfectly serviceable for a string of other clades too. Keeping this in mind would stop the utterly futile arguments, when a complex chemical process on another planet is eventually discovered, about whether it is 'really alive' or not: not that, I predict, anyone will.

If one's extra-terrestrial trilobite neurosis has been calmed, one can then survey the likelihood of complex, or DNA-containing, or self-replicating chemical processes being found on other planets. This is a question of convergence. Given the same starting conditions, will evolution generate the same sorts of structures, including DNA and so on, or are the events of the future balanced on a pin head, with contingency the only rule that counts? As the Montaigne quotation at the beginning is from his whimsical essay on 'ceremonial at the meeting of kings', let me give two royal examples, and not the tiresome shooting-in-Sarajevo First World War one usually trotted out. On 25th November, 1120, William the son of Henry I, the heir to the English throne, drowned in the wreck of the White Ship. There had, by all accounts, been a little too much merriment amongst the crew. For England, the loss of the male heir was a disaster, and led directly to the chaos of the 12th century civil war between Stephen and Matilda, complete with Robber Barons and the rest. It might be possible to argue that if this event hadn't happened, the entire course of English history would have been completely different: no Magna Carta or parliament, perhaps. Now let us consider another similar case: the death of Arthur, the eldest son of Henry VII, on 2nd April 1502. This time, no civil war, no slide into chaos. Contingency rules OK? The trouble for the contingency theorists is that it is always possible to ask the analytical question: why not? And then one might wish to enquire about the balance of power between Court and Barons; the availability of another male heir (the Henry VIII to-be) and so on. Such an analysis gives succour to the opposed view that nothing happens without a cause, and that historical—or evolutionary—events, even if random, occur within a matrix that determines the effect they have. Assessing the degrees of freedom and constraint that important evolutionary events have is critical to deciding whether or not events similar to those that gave rise to life on Earth would occur on other planets, and if so, what they would turn up.

It is, I suppose, possible to divide the sorts of issues involved into two: generalities that will apply to all sorts of life-like processes, and ones that are environment-specific. For example, in one entertaining effort, Barkow (2000) argues that life-like processes are

extremely likely to evolve exactly two sexes, because whichever explanation one adopts for sex—efficiency of evolution, elimination of harmful mutations or outmanoeuvring parasites—it will apply wherever life-like processes appear. Furthermore, he presses the case that, given sex, sexual selection will come along too before you know it, ending up with all sorts of other things including intelligence. Rice pudding and income tax would then be only just around the corner. Such features might therefore be inherent in any life-like system. Furthermore, one can think of the environment of evolutionary adaptiveness (EEA) any organism evolved in and consider how much control that has exerted on its particular features—what effect the oxygen content of the air, the strength of gravity and the viscosity of water has had on our numbers of limbs, heads, guts and so on. Naturally enough, as organisms evolve over millions of years, there is no single environment that accounts for all of their features, so one must think in more limited terms of adaptively relevant environments (ARE) for each one.

The palaeontological record is, in theory, a glorious repository of information for investigating just these sorts of issues. However, convergence is a little unfashionable at the moment, with some noble exceptions (*e.g.* Conway Morris 1998), partly because phylogenetics is not very interested in uninformative characters. But over the vast grid of time and space that the fossil record is found in, every combination of same-environment-different-organisms, different-environment-same-organisms, etc etc, can be found, presenting endless possibilities for the investigation of chance and necessity. Purely anecdotal evidence, from sabre toothed cats, say, suggests that AREs and EEAs hold organisms in a vice-like grip, which leads to questions like: if convergence is so strong, why doesn't everything look the same? If some organisms resist evolving sex on Earth, couldn't they do it on a different planet?

I started by arguing that life could not possibly exist on other planets, and end by thinking there could be some pretty passable imitations. It's not life, Jim, but…?

Graham Budd
Uppsala University

References and further reading

Conway Morris, S. (1998). *The crucible of creation*. OUP.

Timofeev, B.V. (1963). Lebensspuren in Meteoriten; resultate einer microphytologischen Analyse. *Grana Palynologica* **4**; 92_99.

Barkow, J.H. (2000). Do extraterrestrials have sex (and intelligence)? *Annals of the New York Academy of Science* **907**, 164-181.

>>*Future* Meetings of Other Bodies

Recent Advances in studies on Elephants and other Proboscideans
Sun City, South Africa *12 – 17 August 2001*

This symposium is planned during the 8th International Theriological Congress (ITC); the co-organizers are Jeheskel Shoshani <**hezy@eol.com.er**>, William J. Sanders <**wsanders@umich.edu**>, and Pascal Tassy <**ptassy@mnhn.fr**>. Please write to any of us as soon as possible with your topic/title on evolution, ecology, and conservation of proboscideans to allow us to plan this symposium expeditiously. Selection of participants will be based on a diversity of topics and on a first-come, first-served basis.

The registration form is available at <**www.eventdynamics.co.za/itc/**>. Otherwise, please contact Dana Plotz or Sandra Collier, Event Dynamics, PO Box 98009, Sloane Park, South Africa 2152; Telephone: 27 11 706 5010; Fax: 27 11 463 7195; e-mail <**dana@eventdynamics.co.za**>, Web <**www.eventdynamics.co.za/**>.

Third International Meeting on Mesozoic Fishes
Serpiano, Switzerland *August 2001*

Systematics, Palaeoenvironments and Biodiversity

We are pleased to host the third international meeting on Mesozoic Fishes in one of the most famous sites for these fossils, the Monte San Giorgio-Besano area. The organization of the meeting is supported by the Dipartimento di Scienze della Terra of the Milano University (Andrea Tintori), the Museo Cantonale di Storia Naturale in Lugano (Markus Felber), and the Palaeontologisches Institut und Museum der Universitaet Zuerich (Heinz Furrer).

Prof. Andrea Tintori, Dip. Scienze della Terra, Iniversità degli Studi di Milano, Via Mangiagalli, 34 I-20133 MILANO, tel: +39.02.23698202, fax: +39.02.70638261, e-mail: <**andrea.tintori@unimi.it**>.

8th Congress of the European Society for Evolutionary Biology
Aarhus, Denmark *20 – 26 August 2001*

The eighth Congress of the European Society for Evolutionary Biology will be held in Aarhus, Denmark, from 20th to 26th August 2001. The structure of the Congress will be similar to previous meetings, each day starting with a plenary keynote speaker, followed by parallel symposia. Besides, there will also be a few contributed paper sessions. The Congress will cover the field of evolutionary biology in a wide sense but with emphasis on processes and mechanisms of evolutionary phenomena.

Details are at <**www.biology.au.dk/eseb/**>.

Spore-Pollen Subcommission of the Commission Internationale du Microflore du Paleozoique

Cork, Ireland *3 – 7 September 2001*

The first meeting of the Spore-Pollen Subcommission of the Commission Internationale du Microflore du Paleozoique (CIMP) will take place at University College Cork, Cork, Ireland in September, 2001.

The conference itself is from 3rd to 5th September, 2001, inclusive, and is followed by a field excursion to South Waterford and South Wexford, on the 6th and 7th, to examine Cambro-Ordovician and Devonian-Carboniferous sections.

University accommodation will be available in the Castlewhite Apartment Complex at a cost of IR£24 for single room and continental breakfast (per day). There is plenty of other accommodation close to UCC: a list will be provided so that participants may book their own if they wish. Approximate costs are, for Guest Houses, IR£35 B&B per day, and Hotels from IR£50 to £100 B&B per day.

The approximate cost of the field excursion is IR£50, which will include return travel by coach to South Wexford along with accommodation, evening meal and breakfast in Fethard on Sea, Co Wexford.

Please submit expressions of interest and/or titles for presentations in the first instance to Duncan McLean <**d.mclean@sheffield.ac.uk**>.

Systematics 2001

London *3 – 7 September 2001*

The biennial conferences of the Systematics Association are intended to provide a forum for systematists from different disciplines to present and discuss their research. The Third Biennial Conference, to be held at Imperial College, London, will continue in the spirit of previous meetings by providing a mixture of open and focused thematic sessions. The organisers are keen to stress that the conference is open to everyone, and especially research students and younger post-doctoral fellows, whatever their chosen subject.

Thematic sessions currently under preparation include "*Milestones in Systematics*" (Organisers: Peter Forey & David Williams), "*Telling the evolutionary time: molecular clocks and the fossil record*", (Organisers: Philip Donoghue & Paul Smith), "*From macro to micro: the challenge of soil biodiversity*" (Organiser: Paul Eggleton), and "*Organelles, Genomes and Eukaryote Phylogeny*" (Organisers: Robert Hirt & David Horner). However, please remember that contributions can be on any topic whether submitted as talks or posters. Substantial prizes in the form of book tokens will be awarded to the best talk and poster by a student at the conference.

Conference organising committee: **Gordon Curry** (Treasurer of the Society, University of Glasgow), **Peter Forey** (The NHM, London), **Julie Hawkins** (University of Reading), **Chris Humphries** (Chairman of the Organising Committee, The NHM, London), **Paul Kenrick** (The NHM, London), **Andrew Milner** (Birkbeck, University of London), **Russell Seymour** (The Institute of Zoology, London), and **David Williams** (The NHM, London).

Timetable

Monday 3 September 2001

14.00-17.30 Registration – Mechanical Engineering Concourse, Level 2, Booking into accommodation at Linstead Hall.

Tuesday 4 September 2001

8.30-9.30 Welcome; tea, coffee

9.30-17.30 Scientific presentations, including "Milestones"

19.00-21.00 Evening Reception at the Linnean Society of London

Wednesday 5 September 2001

9.30-16.00 Scientific presentations, including "*From macro to micro: the challenge of soil biodiversity*" and "*Telling the evolutionary time: molecular clocks and the fossil record*"

19.00-21.00 Evening Reception at the Natural History Museum

Thursday 6 September 2001

9.30- 17.30 Scientific presentations – including contributed papers

19.30 Conference Dinner

Friday 7 September 2001

9.00-12.00 Closing Scientific presentations – including "*Organelles, Genomes and Eukaryote Phylogeny*"

12.00 Award presentations

12.15 Concluding Remarks and Departure

Contact

For more information including registration and booking details see <**systass.org/biennial2001/**>, or e-mail <**systematics.association@nhm.ac.uk**>, or fax +44 (0)20-7942-5529.

The 49th Symposium of Vertebrate Palaeontology and Comparative Anatomy (SVPCA) and the 10th Symposium of Palaeontological Preparation and Conservation (SPPC)

The Yorkshire Museum, York *3 – 7 September 2001*

The SVPCA is from 3rd to 5th September 2001, and the SPPC is on the 6th and 7th September. Details and booking form: Jane Clarke, 65 Oakmount Road, Chandler's Ford, Hampshire SO53 2LJ UK (tel 023 8025 2309, Fax 023 8090 4364, e-mail <**jane@geoden.demon.co.uk**>).

Two hundred years of Pterosaurs: a symposium on the anatomy, evolution, palaeobiology and environments of mesozoic flying reptiles
Toulouse, France *5 – 8 September 2001*

This occasion seems a good opportunity to take stock of recent developments in the study of pterosaurs and to discuss current problems concerning this group of extinct vertebrates. The symposium will deal with all aspects of pterosaur palaeontology: anatomy, phylogeny, palaeobiology, ichnology, palaeoecology and the history of pterosaur research. Accommodation is available in numerous hotels with a large range of prices (details will be sent in the second circular).

Excursions to: The Late Jurassic 'Pterosaur Beach' at Crayssac (Lot), where both pterosaur footprints and bones have been found. The Esperaza Dinosaur Museum (Aude), which houses remains of Late Cretaceous pterosaur bones, and to nearby pterosaur localities.

Organising committee: **Jean-Michel Mazin** (Poitiers), **Jean-Paul Billon-Bruyat** (Poitiers), **Eric Buffetaut** (Paris), **Francis Duranthon** (Toulouse), **Michel Bilotte** (Toulouse).

For more details and the second circular please contact: Jean Michel Mazin, Laboratoire de Geobiologie, Universite de Poitiers, 40 avenue du recteur Pineau, F-86022 Poitiers Cedex <**jmmazin@univ-poitiers.fr**>.

Early Palaeozoic Palaeogeography and Palaeobiogeography of Western Europe and North Africa
Lille *22 – 29 September 2001*

The Laboratory of Palaeontology of Lille invites you to participate in and contribute to a conference on early Palaeozoic Palaeogeography at Lille in September 2001. A pre-conference field trip to visit the Lower Palaeozoic of Belgium and a post-conference field-trip to the southern Montagne Noire (Languedoc, southern France) will be organized.

The conference topics are designed to address various subjects related to the Lower Palaeozoic palaeogeography and palaeobiogeography of western Europe and north Africa, and include:

1- The geodynamic and tectonostratigraphic framework of western Europe and north Africa during early Palaeozoic times.
2- Relationships between the northwestern Gondwana margin and related terranes (Ossa-Morena, Armorica, Perunica, Avalonia, etc.).
3- Palaeomagnetic versus palaeobiogeographical data.
4- Biostratigraphic improvements of the Proterozoic-Cambrian transition and the Lower Palaeozoic (Cambrian to Silurian).
5- Lower Palaeozoic geochemical anomalies and palaeoclimatology.
6- Palaeogeographical controls on biodiversity patterns.
7- Volcanoclastic events and geochronological framework.

8- Evolutionary trends in early Palaeozoic ecosystems.
9- Event stratigraphy and radiation/extinction turnovers.
10- Sea-level changes, cyclicity and palaeoenvironments.

Dates:

Conference: (3 days) Université des Sciences et Technologies de Lille, Villeneuve d'Ascq, 24-26 September, 2001.

Pre-conference excursion: (2 days) Lower Palaeozoic of Belgium: 22-23 September, 2001.

Post-conference excursion: (3 days) Lower Palaeozoic of the southern Montagne Noire: 27-29 September, 2001.

Please send correspondence to: *José Javier Alvaro* or *Thomas Servais*, USTL – Sciences de la Terre, UPRESA 8014 CNRS, Cité Scientifique SN5, F-59655 Villeneuve d'Ascq cedex (France), tel: (+33) (0)3 20 33 72 20, (+33) (0)3 20 33 63 92, fax: (+33) (0)3 20 43 69 00, e-mail: <**Jose-Javier.Alvaro@univ-lille1.fr**>, <**Thomas.Servais@univ-lille1.fr**>.

Society of Vertebrate Paleontology 61st Annual Meeting
Bozeman, Montana 3 – 6 October 2001

In addition to platform and poster sessions, there will be six symposia held on Wednesday, 3rd October. These include *CT Scanning in Vertebrate Paleontology*, *The Archaic Ungulate Mammals: Condylartha Sauropod Evolution and Paleobiology*, *Incremental Growth in Vertebrate Skeletal Tissues: Paleobiological and Paleoenvironmental Implications*, *Advances in Bone Paleohistology and their Implications for Archosaurian Paleobiology*, and the *Preparator's Symposium*. I hope that many of you will arrive early this year to attend these fine symposia. And be sure to see what workshops we have planned for this year, too! There are four pre-conference field trips in Montana and Wyoming, and one post-conference field trip in Alberta, Canada planned. Each trip will be covering a lot of ground and there is something for everyone who wants to get out on the Northern Rockies and Plains landscape. If you have never been to this part of the west before, these are trips you will not want to miss. We expect spaces to fill up quickly so be sure to register early! For further details <**www.vertpaleo.org**>.

History of Palaeobotany 2001
London, UK *24 October 2001*

The Linnean Society's Palaeobotany Specialist Group and the Geological Society's History of Geology Group are organising a joint meeting on The History Of Palaeobotany at the Linnean Society, Burlington House, Piccadilly, London, on Wednesday, 24th October, 2001. Offers of papers have been received to date from Andrew C. Scott, Bill Challoner, Hugh Torrens, Barry Thomas and Christopher J. Cleal. There is still space in the programme for other papers on this subject. Please contact the Convenor, Richard Wilding, 175, Whitton Road, Twickenham, TW2 7QZ (tel 020 8892 3123, e-mail <**ricval@lineone.net**>).

Society for Comparative and Integrative Biology 2002
Annual Meeting
Anaheim Marriott, Anaheim, CA, USA 2 – 6 January 2002

Symposia:

- The promise of integrative biology. *Organized by: Marvalee H. Wake and John Pearse as a Society-wide Symposium*
- Symposium on comparative immunology. *Organized by: Edwin L. Cooper as a Society-wide Symposium*
- Integrative and evolutionary roles of extracellular hormone-binding proteins. *Organized by: Kevin M. Kelley and Cunming Duan for DCE*
- Dynamics and energetics of animal swimming and flying. *Organized by: Malcolm S. Gordon, Ian K. Bartol, and Jay R. Hove for DCPB and DVM*
- Ecological developmental biology. *Organized by: Scott F. Gilbert and Jessica Bolker for DCDB and DEDB*
- The Cambrian explosion: Putting the pieces together. *Organized by: Graham Budd for DEDB*
- New perspectives on the origin of metazoan complexity. *Organized by: Ruth Ann Dewel, James G. Gehling, and Julian P.S. Smith III for DEDB, DIZ and AMS*
- Physiological ecology of rocky intertidal organisms: From molecules to ecosystems. *Organized by: Lars Tomanek and Brian Helmuth for DEE*
- Integrative approaches to biogeography: Patterns and processes on land and in the sea. *Organized by: Rachel Collin and Marta deMaintenon for DEE, DIZ and DSEB*
- Retirement mini-symposium in honour of Russel L. Zimmer. *Organized by: Scott Santagata and Michael Temkin for DIZ*
- Neural mechanisms of orientation and navigation. *Organized by: James A. Murray for DNB*
- Recent developments in neurobiology. *Organized by: Richard Satterlie for DNB*
- Biomechanics of adhesion. *Organized by: Kellar Autumn and Robert J. Full for DVM*
- Tendon—bridging the gap. *Organized by: Adam P. Summers and Thomas J. Koob for DVM*

For further details: <**www.sicb.org**>

Taphos 2002 3rd Meeting on Taphonomy and Fossilization
Valencia, Spain *14 – 16 February 2002*

The "International Conference Taphos 2002" is a meeting about the problems relating to the formation of the fossil record and its dynamics. This Conference follows the two previous meetings held in Spain on these subjects under the heading "Reunion de Tafonomia y Fosilization" (Madrid, 1990 and Zaragoza, 1996 respectively). The success of the two earlier meetings (with many foreign attendants) has convinced us to give an international character to our forthcoming Conference, and we expect a high level of participation.

The "International Conference Taphos 2002" will be held in Valencia on the 14th, 15th and 16th of February 2002. The meeting will be mainly supported by the "Universidad Internacional Menendez Pelayo", in collaboration with the "Ayuntamiento de Valencia" and the "Universitat de Valencia".

We propose five broad topics and encourage contributions to them:

- Taphonomy in archaeology
- Taphonomy in analysis of patterns of evolution and extinction
- Taphonomy in biostratigraphy
- Theory of taphonomy
- Taphonomy in other fields: palaeoecology, sedimentology, exceptional preservation, and so on.

The official languages of the Conference are English and Spanish, with simultaneous translation. Oral presentation of contributions can be in Spanish or English.

Three invited lectures of one hour will take place during the Conference. There will also be eight invited talks of half an hour about the suggested topics. Ordinary contributions will be presented as posters in special sessions devoted to them. The text of the posters should be written in English. A chairman will lead each session. Discussion will follow a short presentation of the poster lasting five minutes.

Ordinary contributions will be edited in a special volume with the title "Taphonomy and fossilization" published by the Ayuntamiento de Valencia. This book will be delivered to the participants at the beginning of the Conference. Original manuscripts will include up to a maximum of eight pages of text, with 30 lines per page and 70 characters in each line. In these eight pages you must include figures, tables and bibliography. In a new circular, you will have new instructions about address and sending of manuscripts.

The price for subscriptions is about 20,000 pts. ($110/€120); students will pay about 10,000pts. ($55/€60).

Correspondence about the Conference has to be addressed to the Secretary of Taphos 2002: **Dr Margarita Belinchon**, Museu de Ciencies Naturals. C/ General Elio, s/n; Jardins del Real, E-46010 Valencia, (SPAIN), e-mail <**Taphos2002@paleopolis.rediris.es**>.

The Amateur in British Geology
London, UK 14 – 15 March 2002

This is a two-day joint meeting organised by the History of Geology Group of the Geological Society and The Geologist's Association, to be held at the Geological Society's premises, Burlington House, Piccadilly. If you are interested in giving a paper on any aspect of Geology or Palaeontology, please contact the convenor, Stuart A. Baldwin, Fossil Hall, Boar's Tye Road, Silver End, Witham, Essex, England, CM8 3QA (tel 01376 583502, fax 01376 585960, e-mail <**sbaldwin@fossilbooks.co.uk**>).

ECOS VIII Eighth European Conodont Symposium
Toulouse and Albi 13 June – 1 July, 2002

For the first time the International Conodont Symposium held in Europe (ECOS VIII) will take place in France and Spain. As well as the scientific sessions, two other important events will take place: the final meeting of International Geological Correlation Program (I.G.C.P.) 421, and a meeting of the Subcommission on Devonian Stratigraphy (S.D.S). The meeting will be hosted by the Université Paul Sabatier in Toulouse and Albi. The Scientific Conference will focus on all aspects of conodont research; a special Session on "Bias and Completeness in the Conodont Fossil Record" will be organised by Mark Purnell (Leicester, UK) and Philip Donoghue (Birmingham, UK). An eight day pre-conference field trip to visit Palaeozoic sequences of Cantabrian Zone, Iberian Chain and East Pyrenees (Spain) will take place from June 13-21, 2002. A six day post conference field trip of Montagne Noire and Pyrenees (France) will take place from 26th June to 1st July. Both excursions are planned for a maximum of 35 participants.

For further details contact Marie-France Perret-Mirouse, Laboratoire de Dynamique des Bassins, 38 rue des Trente-six Ponts, Toulouse, France (tel: +33 (0)5 61 55 84 41, fax: +33 (0)5 61 55 82 50) e-mail <**mfperret@cict.fr**> <**www.le.ac.uk/geology/map2/con-nexus/ECOS/ECOS_VIII.html**>

Jurassic Symposium 2002
Sicily *12 – 22 September 2002*

The First Circular for the 6th International Symposium on the Jurassic System has been circulated. The Symposium will be held in Sicily from 12th to 22nd September 2002. These dates include pre- and post-Symposium field trips. If you have not received the First Circular (return due by 1st March 2001) you can contact the Symposium Secretary Dr Luca Martire (Torino), e-mail <**martire@dst.unito.it**>. You can also get further information from the Web site at <**www.dst.unito.it/6thISJS/**>.

6th International Congress on Rudists
Institute of Geology and Faculty of Science, Department of Geology and Palaeontology, Zagreb, Croatia September 2002

The conference is dedicated to the exchange of knowledge on rudist taxonomy, shell structure, biostratigraphy, evolution, palaeobiogeography, palaeobiology, stable isotope analysis, palaeoecology, and modern analogues, as well as sedimentology and stratigraphy of rudist strata and associated microfossils.

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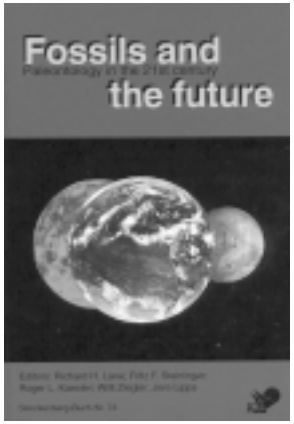
Book Reviews

Fossils and the Future: Paleontology in the 21st Century

Richard L. Lane, Fritz F. Steininger, Roger L. Kaesler, Willi Ziegler and Jere Lipps (eds) 2000. 290 pp. Senckenburg-Buch Nr. 74. Senckenbergische Naturforschende Gesellschaft, Frankfurt a. M. ISBN 3-7829-1162-8 (hbk). DM 55.00.



"Organizations are being asked to do more with less."
'Paleontology in Government' by Edwards *et al.*
Fossils and the Future, p. 73, Topic E, Section III

Major Bloodnok: "Of course I shall need special equipment."
Neddy Seagoon: "Such as?"
Major Bloodnok: "Money."
'The International Christmas Pudding'
The Goon Show, first broadcast November 1955

Fossils and the Future wants both more output of products and input of money, although the two are generally discussed separately, thus preventing those at the workface from getting greedy. That is, its central themes are that palaeontologists, particularly those who are reading it, need to spread the palaeontological word and they should also pursue greater funding from all potential sources (particularly for those who wrote it?). This volume arises from a meeting held in Germany in 1997 and is a modern attempt to write a new Moore *et al*. (1968), but without the humility of the original.

Fossils and the Future, such a potentially exciting topic, is poorly edited and patchily written. This book is too long, too dry and too sparsely illustrated to interest the non-specialist, so there is no hope of using it to sell palaeontology to a wider audience. Too many chapters are in need of critical revision. Indeed, the editors and contributors did not heed their own message; "Most manuscripts … profit from drastic surgery, and the time spent by authors and editors concentrating the message may repay itself in the shorter time [that] the … readership has to spend in deciphering it" (p. 229). In short, *Fossils and the Future* is an archetypal transactions volume from a conference, with minimal editorial input producing a rambling book lacking cohesion, rather than a focused briefing document that could have been circulated constructively amongst interested parties, including life and other Earth scientists.

The book is an agenda for palaeontology produced by a series of committees; however, 57% of the (invited) delegates represented only two countries. The terminology and points of reference, such as NSF, are entirely American. Too many chapters are compilations of lists and

bullet points, written by a series of committees. One glaring repetition (pp. 87-89) is compounded by various misspellings, such as 'interment' for 'internet' in the chapter on communicating with the media! In short, this is a difficult book to read, but it might be asked was it meant to be read and, if so, by whom? I consider it significant that, although based on a meeting held in September 1997, this volume was not published until 2000. This lack of urgency suggests that the meeting itself satisfied many agendas. The evangelical note of many chapters—palaeontologists "should strive", "… sponsor", "… participate", "… work", "… advocate", "… ensure" to give a few examples from one chapter—is also grating. Indeed, too many articles repeat too many platitudes. In short, the book is tedious to read, which is very wrong for a subject that can be sold easily for its raw scientific excitement.

The book is divided into five sections—"Introduction", 'Pan Paleontological Issues", "Organizations", "Paleontological Themes" and "Paleontological Infrastructure"—formed from 34 chapters, supplemented by three appendices. Section I includes two introductory chapters which rally the troops and includes a re-statement of Jablonski's (1999) four questions for the future. The summary of the workshop indicates that, out of 108 delegates, 41 were American and 21 German, five were 'non-palaeontologists' and only 14 were women. Although this chapter is written as a manifesto, it is readily apparent that not everyone has been asked to join the Party.

Section II (Pan Paleontological Issues) begins with two depressing chapters in which the focus isn't palaeontology, but the big bucks that I presume at least certain of the authors want in order to run their own projects. While exciting possibilities certainly do exist, this isn't a current scenario in palaeontology, although I have to wonder if NSF have taken the bait. As more than one later chapter points out, palaeontologists tend to work as individuals or small groups rather than big teams; a change of culture will involve a very major change of attitude. Even what is probably the biggest international project in the field, the Panama Paleontological Project, doesn't command the types of sums that are proposed as targets in these papers.

Section III (Organizations) looks at those places where palaeontology happens, from government bodies, universities and museums to scientific societies and the homes of amateurs. The American bias of many chapters makes them of little relevance to other audiences and some of the ideas, such as the suggestion that certain private collections might become auxiliary to those of public museums, look, at best, doomed to ridicule. The suggestion in the chapter on consultancies (p. 67) that "Perhaps a certification process for consulting paleontologists would be useful to set standards of quality and consistency" seems to be made in complete ignorance of the C.Geol. scheme of the Geological Society, which has operated successfully for a number of years. Then again, who originated the Fawltyesque suggestion that only the right sort of amateur should be allowed to join scientific societies?

At last, on p. 115, we reach Section IV (Paleontological Themes) and get some idea of what the manifesto considers to be future research directions. The selected themes vary from the broad to the less broad. I regard the first chapter as an unfortunate choice, dealing with the pie-in-the-sky, if only there were some specimens to work on, subject of astropalaeobiology. While my heart says Mars or bust, my head agrees with Lovelock's (2001) reasoning that the Red Planet is unlikely to yield either life or fossils. While astropalaeobiology is, by definition,

about future finds, other chapters are perhaps too much review (see, for example, "Macroevolution") and too little forward look, so it is palaeontology in the late 20th, not early 21st, century that dominates this section.

Section V (Paleontological Infrastructure) covers pertinent areas such as databases, collections, publications and outreach, and contains few surprises. The longest chapter is centred on an international survey of government regulations regarding palaeontology, based on delegates' replies to a questionnaire. Not even all countries represented at the conference are represented in the replies to this survey, let alone those not represented, so its worth is debatable.

The palaeontologists of the Third World receive just a little notice in the book; there were but few delegates to represent this marginal seat of the 'Party's' constituency and fewer still seem to have been involved as lead authors of chapters. Suggestions for provision of resources for them seem uninformed and I feel that prescriptions have been written without asking the patient what is ailing them. Rather, proposed initiatives involving palaeontologists in the Third World do not focus on palaeontology in the Third World, but, rather, it appears that they are to be 'globalized' to bring them in line with a North Atlantic, perhaps North American, axis. Thus, in the third chapter of Section II, more on-line resources are recommended for the 'lone' palaeontologist. However, the truly lone palaeontologist is likely to be in a Third World country with, at best, limited computer access, unreliable power supply and no IT support. Even without Web access, there are a host of avenues for getting data and information in such an isolated situation, providing you have a postman—books, journals, offprints, photocopies, letters, you name it. Information is already available, what is needed is interaction. Although the Web is seen as a panacea for too many ills throughout this volume, for the palaeontologist in the Third World, actual face-to-face communication with fellow practitioners at conferences, in the field, etc., is priceless. In my own experience, getting delegates, apart from the overseas co-workers of the organisers, to a conference in Jamaica is an uphill struggle, even with such an attractive venue. So, using travel money to go to meetings in developing countries rather than the usual venues in Europe and North America might be a wise, scientifically constructive and appreciated initiative. Only the late Jack Sepkoski seems to have realised that actual contact was required.

With the meeting being dominated by Americans, it would have been more astute to publish this volume through GSA or a similar outlet, which would give what is presumably intended to be an important contribution a higher profile. I haven't been able to discover how much *Fossils and the Future* costs and, although the front of the book includes useful information concerning the surface conditions on Venus, nowhere could I find the year of publication.

Many of the suggested directions in this book could have happened during the late 20th century. The principal reason why they haven't been implemented previously was that resources were not available, not just money, but also time and people. I see few truly practical suggestions for deforming the resource base in palaeontology's favour. If I am to pursue any of the holy grails outlined herein, what must I stop doing? The manifesto needed truly to emphasise what the excitement is and is likely to be in palaeontology, but too often the message is looking backwards, that endeavour X will correct the erosion of our credibility and get us back to where we were 30 or 40 years ago. Too much, the feeling is of palaeontologists being defensive, running scared from a faceless 'them'. I'm afraid that the overall impression is that many perceived ailments in our science have been self-induced.

Physician, heal thyself.

This is a document of potential and certainly intended importance. Who was meant to see it and who will see it? I wouldn't want funding agencies or other Earth and life scientists to read it, as their reaction will be "Oh, those stuffy palaeontologists!" I can't recommend it for individual palaeontologists. If you see a copy in a library sometime, scan through it and read those chapters that seem most applicable to you. This is the least the book deserves, but it doesn't deserve much more.

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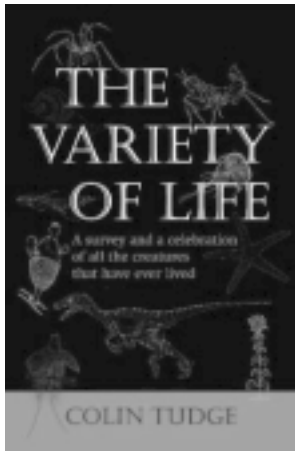
The Variety of Life: A survey and a celebration of all the creatures that have ever lived

Tudge, C. 2000. 684 pp. Oxford University Press, Oxford.
ISBN 0-19-850311-3. £24.95.



Close to the question of life, the universe and everything (which, as the late Douglas Adams taught us, has a deceptively simple answer once you understand the question), the question of the total diversity of life comes second among the Great Unfathomables. Anyone attempting to write a book about all of life must surely be either blissfully naïve or suicidal. How can you write a book about everything, even if the everything is "only" organismal biology? Colin Tudge has attempted it.

It would be unfair to criticize the book for what it isn't. Tudge's book isn't a textbook on organismal biology or biodiversity. It isn't a coffee-table piece on the Wonders of Life. It isn't a field guide to whatever you may find in a slimy pool at your holiday resort.

What is it, then? That's more difficult to answer. Maybe the book simply cannot be classified, but that way out would be too easy; after all, we're dealing with a book that has the central message that (living) things can and must be classified in order to be manageable by our minds. So let's try. Though not a textbook, it has the structure of a traditional biology text: Chapters of introduction followed by systematically arranged chapters

on each and every sort of organism. Though not a coffee-table piece, it is attractively produced indeed and contains nicely executed drawings of representatives of most major groups presented. Though not a field guide, it has brief and pregnant characterizations of most of the organismal groups. Maybe the best way to describe Tudge's book is as a work of love and respect, both for the stupendous diversity of life on earth and for the biologically oriented readers (professionals or non-professionals) who feel that they would very much like to have a better grasp of "what's out there" but just don't have the time to get into all the boring details.

As most books on systematic biology these days, this one resounds with hymns to the cladistic revolution. And as most books that try to make sense of life's diversity, it embodies an attempt to get away from the consequences of the cladists' requisition of taxonomic nomenclature for the purposes of non-graphic representation of branching-order diagrams. Tudge's attempt is called "Neolinnaean Impressionism" and is, alas, just as apologetic as it sounds: Refer to paraphyletic taxa if you have to, but mark them with a pest fla… excuse me, an asterisk, and do try to keep the number of ranks down. Not much different from other "solutions", I'm afraid. (Tudge unfortunately also renders the potentially helpful concepts of "grades", "crown groups" and "stem groups" effectively useless through sloppy definitions.) We certainly have a long way to go before taxonomic names again become tools for biological classification rather than just reflections of the latest cladogram.

The largest section of the book, the systematic one, is called "A survey of all living creatures", a somewhat perplexing restriction of the book title's "A survey … of all the creatures that have ever lived". The difference between "living" and "have ever lived" is something like one to one thousand or greater, so what is in fact intended? In the introductory sections of the book Tudge gives due credit to the well-known but often conveniently forgotten fact that almost all of the species that have ever lived are extinct. The systematic section includes most of the well-known extinct groups, but a strong pull-of-the-Recent is obvious, as in most biology textbooks. In fact, an even stronger tug-of-the-human is obvious as well: 10 chapters are devoted to chordates (two of which are to primates), eight to all other animals, three to plants, and four to all other organisms. Maybe few readers will complain (after all, it very much reflects the relative weight of research on these organisms), but these imbalances do reinforce current biases and tend to make the book look like a rather ordinary text-book, which—again—it isn't.

Despite, or perhaps thanks to, all the things this book isn't, it is likely to become quite useful. Not so much for the data and interpretations it contains, for rarely is there any reference to the original source; the text is deliberately kept free of literature references. Not for the anatomical information, for the text on each taxon is brief, and the illustrations are invariably habitus drawings of selected representatives that do not and cannot serve to characterize or describe the organisms. However, a book may be quite useful without being a data bank or key to the literature, simply by being an easy-to-grasp, impressionistic tour of a subject, in this case the main taxonomic components of Earth's multifaceted biosphere. As such, it's not so much for the professional systematists as for the non-systematists and non-biologists who may want a quick and handy chart to the profoundly complex territory they normally only catch a glimpse of on flickering monitor screens or through viewing ports.

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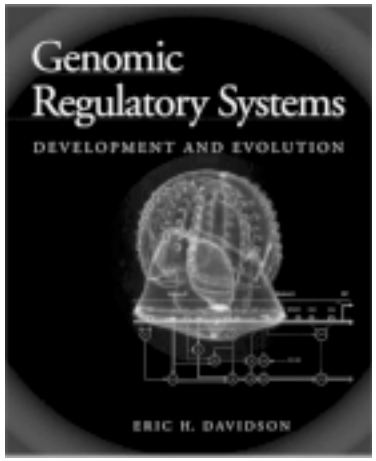
Genomic regulatory systems. Development and evolution

Eric H. Davidson. 2001. xii + 261 pp. Academic Press.
ISBN 0-12-205351-6 (hbk) £46.95.



Davidson has written a thoroughly engaging and visually attractive book that attempts to tackle a fundamental mystery in both developmental and evolutionary biology: what is the role of an organism's genome in directing morphological change in developmental and evolutionary time? Anyone interested in either of these two questions should not hesitate to read this book, but before rushing out to buy it, the potential reader should be aware that this book is not intended for casual browsing. Despite the proclamation on the back cover that it is "easy-to-read" I found it to be among the more difficult books that I have read. This is wholly due to the complexity of the subject matter, but Davidson does an admirable job in synthesising and explicating a massive and complex literature in an accessible style. However, a considerable background in molecular developmental biology and embryology is indispensable for a full appreciation of this important work.

The five chapters of Davidson's book present an in-depth study of the structure and deployment of genomic regulatory systems in the orchestration of animal development (chapters two to four), and their potential role in generating the exuberant morphological diversity that characterises the Bilateria (throughout the text and in particular chapter five). The book is a worthy celebration of a large body of elegant experimental work in molecular developmental biology performed to an important degree in Davidson's own laboratory. Handsome colour illustrations illuminate the main text in all chapters (single pictures with legends may extend as much as four pages!), and Davidson constructs his narrative around a set of well-chosen examples that form the core from which he distils his mainly abstract main conclusions.

Chapter one introduces the nature of genomic regulatory systems in bilaterian animals as the *cis*-regulatory elements that control where and when genes are expressed in development. The functional organisation of these *cis*-regulatory elements determines which transcription factors may bind within them and thereby exert their specific effect on the transcriptional activity of the regulated gene. The key organisational feature of the *cis*-regulatory elements is their modular nature. A rule of animal development is that single genes are multifunctional. That means that they are deployed in various different places and at different times during the development of an individual organism. Particular modules in the *cis*-regulatory elements of individual genes turn out to be responsible for regulating gene expression at specific places and times, so that different modules regulate gene expression with different spatio-temporal characteristics. The *cis*-regulatory elements of different genes are functionally linked to each other through regulatory interactions so that regulatory networks are formed. For example, the gene product of a gene that codes for a transcription factor may directly influence the expression of another gene through modulation of its transcriptional activity. The essential message here is that an understanding of the regulatory network architecture will ultimately yield insight into how the genome encodes the properties of organisms, and Davidson presents the first tantalising glimpses of the nature of such regulatory networks.

Chapter two looks in detail at how *cis*-regulatory logic works, by linking the internal design of *cis*-regulatory elements to the specific patterns of gene expression that they control. This clearly illustrates that *cis*-regulatory systems are the genome's integrational centres that translate a diversity of both positive (transcriptional activators) and negative (transcriptional repressors), spatial and temporal cues into a single transcriptional output: when and where and at what level a gene is transcriptionally active. Reading chapter two you quickly become fascinated with the uniform logic of the elegantly complex *cis*-regulatory systems that constitute the genetic control underlying the development of such disparate animal body parts as mammalian hindbrains and insect imaginal discs.

Chapter three specifically focuses on the nature and role of genomic regulatory systems that are active during direct cell type specification processes. Early embryogenesis in many animal groups (with insects and vertebrates as notable exceptions) proceeds according to direct specification mechanisms, where the cytoarchitecture of the egg plays a major role in specifying initial territories within an embryo composed of undifferentiated cells. An important conclusion that Davidson draws is that direct cell type specification processes are controlled by relatively shallow regulatory networks. This means that the complexity of this process chiefly resides in the internal architecture of key *cis*-regulatory elements, without the involvement of a deeply hierarchical regulatory control network. This relatively simple regulatory design is sufficient to construct a small organism with a limited number of differentiated cells, such as a swimming larva. This is in striking contrast with the complex, multilayered regulatory networks that control the pattern formation processes that eventually build the adult organism from the initial embryo or larva. That is the subject of chapter four, which provides ample illustrations of the progressive nature of adult body part differentiation, from the initial definition of successive domains of transcriptional activity to the final instalment of differentiation programs responsible for producing all the differentiated cells that build complex adult organisms. At this point Davidson has distilled from the selected examples some fundamental principles (even called "laws") of development that are applicable across a wide variety of animals. For example, the ubiquitous role of transcriptional repressors in setting the boundaries on domains of gene expression. This is particularly exciting since this evidence contributes some careful sketches to the elusive 'theory of development' that might eventually crystallise out of the findings of developmental biology.

In the final chapter Davidson addresses the significance of this developmental evidence in answering a fundamental evolutionary question: what is the cause of bilaterian morphological diversity? In its simplest form the answer may be formulated as cooptive change in developmental gene regulatory networks. For example, a gene coding for a transcription factor may gain control over the expression of a new set of downstream genes when these acquire new target sites for this transcription factor. Davidson presents some fascinating

examples of the evolutionary cooption of genes to new pattern formation processes. A corollary of the hypothesis that bilaterian diversity evolved through cooption of developmental genes (with multiple developmental functions) for new roles is that it becomes impossible to predict the nature of a morphological change on the basis of knowledge of the identity of the affected gene(s). Instead, it is the location of the affected gene within a regulatory network that determines what morphological effects a genetic change will have. This inability to say that a particular developmental gene "codes for" a given morphological feature explains why, fortunately, we don't encounter speculations about the nature of Urbilateria in Davidson's book. I consider this a great relief, because the 'evo-devo' literature of the last few years has been filled with often frustratingly speculative attempts to pin down the nature of this hidden ancestor.

However, Davidson's greatest strength may also be the source of potentially the greatest weakness of his approach: wanting to explain too much with too little. Davidson (p. 19) writes that "the objectives of both evolutionary and developmental inquiry" appear to be "so intertwined as to become indistinguishable." In an act of ultimate reductionism he states (p. 19) that "what we are now seeing is the initial phase of a major intellectual realignment, in which the study of the mechanisms by which animal body plans evolve will ultimately be regarded as a branch of regulatory genomics…" Surely such bold statements are merely reflective of the enthusiasm that Davidson obviously exhibits for his exciting subject. I certainly don't want to mount a major criticism against what appears to be an obligate symptom afflicting all major scientific changes in perspective: overextending the explanatory umbrella and redefining other legitimate fields of inquiry in terms of the preferred perspective. Additional "causes" of bilaterian diversity and animal body plan evolution will certainly have to be sought after on a multiplicity of levels, from the evolutionary genetics of populations to the epigenetic processes intervening between gene expression patterns and differentiated morphology. More importantly, however, Davidson offers enough titillating statements that can form the seeds of further research. For example, that by studying the modular nature of *cis*-regulatory systems and the functional linkage of different regulatory systems we might infer the evolutionary sequence through which a regulatory network may have evolved.

Genomic Regulatory Systems stands in contrast to various other books on 'evo-devo' that have recently been published, through the adoption of a narrow focus which allows a great depth of treatment. It will likely form a milestone for a new phase of looking at the relationship between development and evolution, advancing from the comparison of expression patterns of single genes to the comparative study of entire gene networks. We can only look forward with anticipation to what the next years of research will bring, while at the same time hoping that this work will be communicated to a larger scientific audience in an equally skilled manner as Davidson has succeeded in doing.

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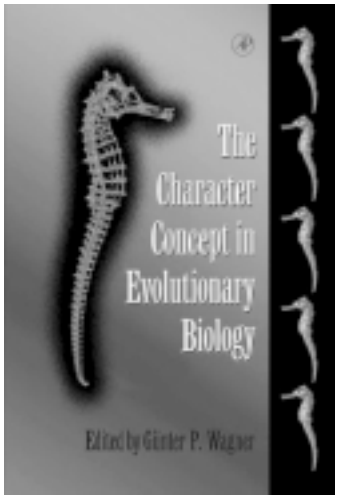
The Character Concept in Evolutionary Biology

G.P. Wagner (ed.) 2001, Academic Press, ISBN 0-12-730055-4 (hbk), £54.95



In the late 18th and early 19th centuries—at the beginning of the Industrial Revolution—organisms were regarded by many as machines that could be disassembled into their constituent parts, and perhaps even reassembled from appropriate collections of parts. The former served as a primary motivation for much systematics research (especially insofar as insight into the design of the machine was held to provide insight into the mind of its creator) while the implications of the latter spawned a rich speculative literature of which Mary Shelly's *Frankenstein* is the most well-known example. This mechanistic-reductionist world-view has been with us ever since. On the whole, it has provided an extraordinarily productive research programme for biological investigation. However, it is currently opposed, has always been opposed, and probably will always be opposed by a holistic-integrationist world-view which holds that organisms are more than the sum of their parts. Evidence for this is thought to exist as 'emergent properties' whose actions manifest themselves only over portions of the organisational hierarchy. The tension between these conceptualisations is nicely encapsulated in the very word 'organism' which not only refers to the individuals' constituent parts, but also makes reference to the musical organ as a mechanical device with—many would say—highly developed emergent properties. Günter Wagner's edited book *The Character Concept in Evolutionary Biology* is an exploration-discussion-debate on these fundamental issues as they apply to a largely unacknowledged construct that stands at the heart of most biological research, including virtually all of systematics. As such, it is a book worth paying attention to.

Whether we like it or not, whether it is appropriate or not, characters are the mental constructs we must use to abstract biodiversity from its seemingly infinite variety down to sets of observations that are manageable from a hypothesis-testing point-of-view. The role—some would say the art—of biological character recognition is to reduce the complexity of observed genotypes and phenotypes without obscuring the relations among structures within those domains, between those domains, and with external variables of interest (*e.g.*, environmental variables). In this way character-abstracted data can represent groups of real organisms for the purposes of data analysis. The obvious problems, of course, are knowing whether one has successfully achieved this goal with a particular abstraction scheme, whether alternative abstraction schemes are better (or worse) at preserving the target relations, the extent to which particular analytic results are dependent upon particular abstraction schemes, and the establishment of 'best practice' principles to ensure adequacy and consistency. The more subtle problems include issues of ontological priority, especially as these relate to the question of character origination (*e.g.*, if you don't know what a character is how can you know whether a new one has been created?).

The book is likely to prove challenging for palaeontologists who have not been following current debates on the origin of characters or who know the concept of characters only through its guises in comparative morphology and phylogenetic inference. Those topics play a minority role in the discussions of Günter's authors. Instead, the book contains twenty-five articles written by thirty-two authors and subdivided into five sections: historical roots, new approaches to the concept, character detection, architecture of characters, and evolutionary origin. This roster is completed by an introduction (written by Wagner) and a preface (written by R.C. Lewontin) along with brief introductions to each book section (written by Wagner).

Wagner is well placed to organise and edit a volume on characters. He has been singularly active in reinvigorating the subject of biological characters and has made a number of important contributions to this field. His stated purpose in assembling the book is to 'bring together results and ideas from philosophy of science, evolutionary theory, systematics, genetics, functional morphology, and developmental biology which have implications on the way we conceptually construct and identify characters.' (p. xv). As a rationale this struck me as a little dry. After all, like the concepts of 'species' and 'homology', the concept of a 'character' is a well-known intellectual minefield. This is because while virtually all practitioners of biology must routinely develop character concepts in order to pursue their science, no two biologists are (or can be) compelled to use the same character concept in any given situation. Moreover, since there is no way to measure the quality of the character-based abstraction with respect to *a priori*-defined questions at present, there is no basis on which to compare alternative abstractions other than by reference to consensus or authority. Add to this the fact that major segments of the biological community disagree as to the set of candidates available for character recognition (*e.g.*, systematists only use intrinsic features of the phenotype as characters whereas ecologists would admit extrinsic features such as guild membership) along with systematic's entrenched tradition of qualitative (rather than quantitative) analysis, and you have a recipe for serious confusion. Wagner admits to these flaws in the book, but excuses them in his Preface by only seeking to 'stimulate further discussion…and ultimately stimulate the creative replacement of [current] ideas with better ones.' (ibid).

Lewontin's Introduction sets the stage appropriately. As he (and Wagner) see it, the fundamental problem with characters lies in their uncooperative behaviour as 'quasi-independent' entities; 'small sets of objects and forces within which there are effective interactions and between which there is operational independence.' (p. xix). Characters are neither so independent as to be able to exist separately of the organism nor so tightly integrated into the organic whole that they cannot undergo unique changes. Remove the frustratingly imprecise notions of 'effective interaction' and 'operational independence' and one is left with the important insight that characters are correlations (or covariances) that cannot be observed other than through comparisons with other observations. For me, this insight served as an extremely useful reference point for understanding what many of the authors were grappling with, as well as providing a useful guide for integrating information about characters. Lewontin identifies two primary constraining forces that result in the correlations we call characters: development and function. This dichotomy agrees well with collective experience provided development is taken to include phylogenetic history. Personally, I prefer the three-fold causality of phylogeny, development, and function because alternative developmental pathways can, in principle, yield the same phylogenetic result and can be targets of selection in their own right.

The first section on 'Historical Roots of the Character Concept' contains articles by Kurt Firstrup, Manfred Laubichler and by Oliver Rieppel. Of these, Firstrup's article on 'A History of Character Concept in Evolutionary Biology' will be of the most general interest to palaeontological readers. Firstrup casts his history in terms of dichotomies that force the acceptance of different character concepts. Functional approaches to biological understanding require the subdivision of organisms into types of fundamental units that would be inappropriate for historical studies. While the differences between character concepts in functional and historical studies are usually matters of qualitative type, Firstrup correctly notes that the character-based distinctions inherent in the phenetic-phylogenetic dichotomy encompass a different, though no less historically important aspect of conceptual variation. Phenetics is based on the assumption that systematic issues could be resolved by analysing greater numbers of characters—however defined—whereas cladistics makes a fundamental distinction between generalized character types (apomorphies and plesiomorphies) and bases its results on a subset of the available characters that conform to an *a priori* distribution model. In addition to these issues, Firstrup considers a variety of interesting subsidiary issues, such as 'how many characters are sufficient?', 'what determines the importance of a character?', and 'are characters methodological artefacts?'. Firstrup's chapter is also one of the (surprisingly) few essays in this collection that review morphometric approaches to character analysis. The remaining two essays in this section—a historical consideration of the theoretical work of Oskar and Cécile Vogt by M.D. Laubichler and a discussion of preformationist and epigenetic themes in the development of morphological character concepts by O. Rieppel—are more specialised and 'historical' histories than Firstrup's excellent conceptual overview, and will probably be of interest to a relatively smaller palaeontological audience.

The second collection of essays entitled 'New Approaches to the Character Concept' represents the real heart of the book. These contributions come at the character question from a variety of different theoretical points of view (*e.g.*, natural selection theory, quantitative genetics/life history theory, organismal theory, structural theory, mathematical abstraction) and discuss the implications of these perspectives for the use of characters in generalized evolutionary contexts. The intellectual terrain covered in this section is enormous and several of the contributions are highly mathematical. Interesting insights abound for anyone with the staying power to slug their way through this material. To his credit, Wagner attempts to summarize each essay's major points in his preface to the section. However, these 'plain-language' descriptions are far too short and generalized to be considered adequate abstracts. [Note: this problem could have been alleviated if Wagner had instructed each author to provide a formal abstract to their chapter and insisted that those abstracts not lapse into techno-speak.] Highlights of this section for me included David Houle's discussion of evolutionary characters and 'phenomics', Wagner and Laubichler's essay on the role of the organism in character identification—which originally appeared in the journal *Theory in Biosciences*—, and Kurk Schwenk's essay on the evolution of functional units, with special reference to structural units, mechanical units, and evolutionarily stable configurations.

Section III gets down to the nitty gritty of character detection with four essays on operationalising the character concept. Dan McShea and Edward Venit lead off this section by asking the obvious question 'What is a Part?'. Their somewhat ambiguous answer is 'a system

that is both integrated internally and isolated from its surround'. While this definition is fine as a first-principles construct and will work for musical organs, it is unlikely to suffice for organisms for reasons well-explained in previous sections of this book. Accordingly, McShea and Venit immediately back off from this overly restrictive concept and suggest that characters can be operationally recognized as sets of hierarchical 'relationships' (should be termed relations) among phenotypic structures in a manner reminiscent of Olson and Miller's (1958) _and *F* groups. However, this construct appears to run afoul of Colless' (1985) distinction between character-parts, character-variables, and character-attributes. McShea and Venit's statements that their character concepts incorporate elements of Colless' character parts and Miller and Olson's _and *F* groups seems logically inconsistent. These concepts are mutually incompatible under Colless' (1985) classification (see also Fristrup 1992). Moreover, the large number of qualifiers these authors employ makes understanding their character concept as daunting as the task they address. This discussion winds up by presenting a series of abstract diagrams illustrating concepts like separation and inclusion (parts of which owe much to and are superseded by R.D.K. Thomas and W.-E. Reif's curiously unacknowledged 1991 article on skeletal design elements, along with a flow chart to be used by readers in making their own character analyses. An example of the application of these concepts to byrozoan morphology is included. Unfortunately, the results of this analysis only add to the aura of confusion by concluding that while the 'digestive tract' can be considered a 'part' (and presumably an acceptable character candidate), its traditional constituents (*e.g.*, mouth, anus, caceum, pylorus, and rectum) are 'non-parts'. Can a useful part-character concept really be so semantically contingent? Of the remaining essays in this section paleontologists might be interested in Ward Wheeler's comprehensive overview of the concepts of character and homology as they apply to DNA sequence data while H.N. Bryant reviews the problem of character polarity in cladograms, though both of these topics have been discussed at length in other publications.

The subject of characters' mechanistic architecture is covered in Section IV by six essays, most of which are drawn from combined genetic and morphological studies on real organisms. This section, as well as the following section, build upon Wagner's insight that through the course of evolution natural selection has likely operated to select organismal Bauplans for modularity in order to increase flexibility in the face of environmental change. On a conceptual level, these 'modules' correspond to characters. If this conjecture is correct characters should have a deep genetic basis. The six essays in this section demonstrate that while evidence for such genotypic-phenotypic organisational patterns exists, the 'characters' so defined do not always correspond to the characteristics used by systematists and functional morphologists. For example, Paul Brakenfield's essay in this collection reviews work on the eye spot pattern in butterflies and shows that the unit character is the entire pattern of eye spots rather than individual eye spots. Even more importantly, Brakenfield's essay shows that reorganisations of the spot patterns are associated with a different type of genetic change than variations in the theme inherent in each pattern type. This general theme is extended by James Cheverud's contribution that discusses a genetic marker study on mice in which it was possible not only to give more precise genetic definition to Lewontin's 'quasi-independent features' character concept (= features that share more genes in common with each other than with other features), but that also provides evidence that the pleiotropic effects of genes do tend to be restricted to functionally and

developmentally related traits. This study also suggests that the distribution of pleiotropic effects can be a target of natural selection. While the essays in this section may not be directly relevant to palaeontological data *sensu stricto*, palaeontologists must keep abreast of developments in the understanding of genotype-phenotype interactions in order to discuss intelligently the biological implications of their findings. The contributions in this section of Wagner's book provide a valuable summary of and entry to this fascinating literature.

Finally, Section V addresses the big enchilada, the evolutionary origin of characters. As Wagner points out in his introduction to this section 'the major steps in evolution often, if not always, involve the origin of new characters which then become characteristic of many descendent species' (p. 489). Studies of the origin of major characters bring all the themes in this book together. Unfortunately, though, this is one of the smallest sections in the book. A mere three essays on the origins of major phenotypic structures (flowers, by P. Endress; butterfly wing patterns, by F. Nijhout; and tetrapod limbs by J. Capdevila and J.C. Belmonte). Given the present lack of studies of this type it is too early to make generalizations about the steps involved in the origins of major character. However, Newman and Müller's essay in this section suggests that the generalized aspects of the process are two-fold, (1) an initial, spontaneous self-organization of developmental pathways followed by (2) a stabilisation phase in which the genetic apparatus for producing the phenotypic trait is consolidated and stabilised. The section, and the book, is then closed by F. Galis' essay reviewing key innovation types (*e.g.*, structural duplications, decouplings, increases in structural complexity, new structures).

Production of the volume achieves a high graphic standard, that is unfortunately marred by an inexplicably large number of printing inconsistencies. For example most of the bibliography for Wagner's introductory chapter is missing. Even more curiously, top and bottom page margins tend to bounce around in an almost random manner in some chapters. And, of course, insufficient room has been left along the side margins for notes. For the prices Academic Press are charging for this volume they could have paid more attention to holding up their end of the publishing bargain. However, this in no way detracts from the overall quality of the authorial and editorial effort. This is a useful book that has fulfilled Wagner's goal of summarizing information on this topic and stimulating discussion. Read it as soon as you can (certainly before Wagner and colleagues publish their next books on this topic) or risk being left behind as an area that is fundamental to all we do as systematists takes off.

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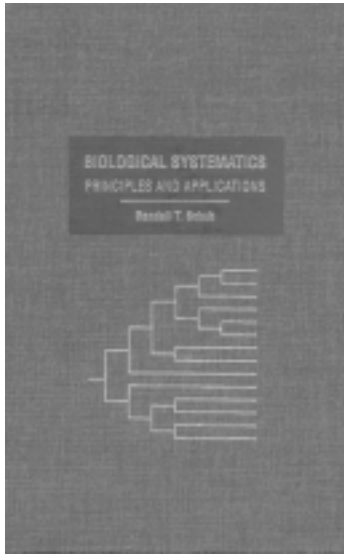
Biological Systematics: principles and applications

Schuh, R.T. 2000. ix + 236 pp. Ithaca: Cornell University Press.
ISBN 0-8014-3675-3 (hbk). £27.95



This is an excellent book. Written by a practising systematist with a keen interest in the theoretical development of systematics, it has a blend of theory and empiricism which results in a very authoritative treatment. It is entitled *Biological Systematics* but in reality it is about cladistics and parsimony analysis with phenetics, evolutionary taxonomy and maximum likelihood being brushed aside with increasing degrees of impatience. Interestingly, Schuh dates modern taxonomy as starting in 1950 (p. 4) and therefore literature prior to this date are not considered. Schuh gives particular acknowledgement to Gary Nelson and Steve Farris in the formulation of his view of systematics. Given the current bipolarity of these two influential people the contents of the book have surprising coherency such that the new reader will have no need to delve into one or the other's philosophical standpoint. But it is a disappointment that 3-taxon statements (Nelson) is only given one eight-line paragraph!

So what about the mechanics of the book? After an introduction to the science of systematics in which distinctions between evolutionary, phenetic and cladistic schools are very clearly presented there is a chapter devoted to formal classification (returned to in Chapter 8). Here, the Linnaean ideas of typification are given sympathetic if not uncritical airing in the face of current moves to remove rank and binomials. Schuh, may be forgiven for dismissing the move to introduce uninomials as receiving " little attention at the time of its introduction into the literature and now seems to have disappeared from consideration." (p.41) since the publication of the *PhyloCode* <**www.ohio.edu/PhyloCode**> and all the possible mayhem this will cause postdated the preparation of this book.

There then follows a chapter on homology (and rooting) which is always the most contentious of systematic subjects. Schuh handles this very well; he ties the modern concepts of primary and secondary homology together with the tests for homology very well, and his table 5 (adapted from Rieppel 1988) is an insightful compendium of ideas.

The middle book section of Chapters 5-7 covers the basic mechanics of cladistic analysis (character analysis, optimisation, fitting of characters to trees, tree support and evaluating the results). This section will interest the practising cladists and be used to judge against other descriptions of cladistics. Here we find there is a strong defence of the total evidence (simultaneous analysis) approach which continually refers back to Chapter 3 (Systematics and the Philosophy of Science) for justification.

Short chapters 8–11 deal with the practical application of cladistics through formal classifications, biogeography, plotting ecological features onto phylogenetic trees and the relevance of systematic to biodiversity studies. Taken individually, these chapters are minute vignettes into the respective applications which in other separate books may be explored in greater depths but taken together they round out the importance of systematics to a wider biological community.

Schuh's stye of writing is sympathetic to the degree that he is careful to give the original source of the idea. Too often textbooks cream off the latest, most fashionable or idiosyncratic viewpoint leaving little idea that there may be counterviews. At the same time he expresses a very strong opinion for one or another alternative and dismisses other avenues. On occasions I felt that this was a detriment to the book that was entitled *Biological Systematics* as opposed to 'Parsimony Analysis'. The dismissal of maximum likelihood in a book on biological systematics seems to me a bit harsh. As a morphologist, like Schuh, I am sceptical of ML (after all—what models of evolution can we apply?). But, like it or not, there is a world of molecular systematics that does have empirical justifications for applying models of evolution to phylogenetic reconstruction.

The book ends with a handy glossary and a list of computer programs, what they do and their availability. This, of course will be the most epheremal part of the book.

Schuh adopts a discursive style with argument and counterargument which makes you feel you are in the classroom with him—almost hammering out the issues with pencil and paper and specimens—and his dialogue on the ontogenetic criterion is particularly instructive. The one annoying feature of the book I could not get to grips with is the use of "sidebars". These are greyed footnote boxes which I presume are there to supplement the main text and beloved by modern publishers. But many are curiously out of place and only casually referred to (sometimes in adjacent chapters). I hope this book will go into a second edition and the 'sidebar' material will be incorporated into the main body of the text where it truly belongs.

In total, I thoroughly recommend this book, steeped as it is in the New York–Stockholm *Cladistics* axis. This recommendation does not come lightly from a reviewer who co-authored a similar and possibly rival book on parsimony analysis (Kitching *et al*. 1998). The systematic community is particularly well-served at present with a number of books airing the many issues confronting problems within phylogenetic systematics. This book demands to be read as much for its readability as its content.

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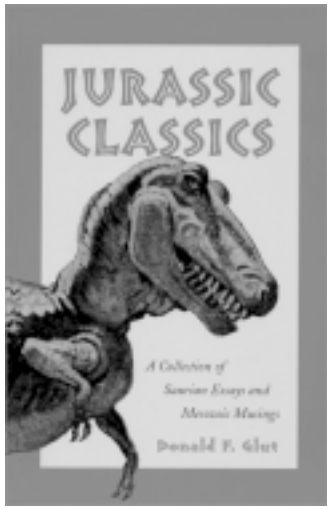
Jurassic Classics: A Collection of Saurian Essays and Mesozoic Meanderings

Donald F. Glut. 2001. 282 pp. McFarland & Company Inc.
ISBN 0-7864-0961-4 (pbk) £27.10.



Dinosaurs are more popular than ever and there is an apparently insatiable demand for books, videos, toys and other related merchandise. "Jurassic Classics" represents yet another popular book on the subject, albeit a rather quirky one. The book is a compilation of previously published essays (some of which first appeared in print over 30 years ago) written by a freelance writer and director who possesses a passion for dinosaurs. The essays fall into three broad categories: the author's reminiscences of his formative experiences in palaeontology and palaeontological movie making; articles written for a lay audience that outline the palaeoecology of various geological periods or the history of discovery of various dinosaurs; and many (too many) articles on dinosaurs in film, comic strips and other printed media.

Perhaps the most surprising aspect of this volume is how little dinosaurs actually feature in it. Sure, there are several pieces that do deal with palaeontological themes in reasonable depth, but most of the other essays contain only tangential references to the science, and are concerned mainly with fictional depictions of dinosaurs or with the author's reactions to the portrayal of these animals in either museum displays or the popular media. Indeed, the one unifying theme in the book appears to be self-referencing capability of the author. In every chapter we are told something about what *he* did, how *he* was involved or what *he* wrote. This seems rather bizarre, given that this is not meant to be a memoir or an autobiographical work, but simply a collection of assorted, topical writing. The volume smacks of self-aggrandisement. Glut sees himself as an informed source of palaeontological information, though it should be noted that he is neither a professional palaeontologist nor one by training, and all of his 'authority' is second-hand. As a self-proclaimed 'righter' of popular dinosaurian 'wrongs', he could at least have checked the proofs thoroughly—taxon and stage names are often spelt incorrectly, something which, according to the text, the author finds immensely irritating.

Glut has been an active populariser of dinosaur studies in the US and was also involved in several charitable schemes to funnel much needed money into dinosaur research. His contribution in these fields has generally been beneficial. However, this volume does him, and these causes, a great disservice. With the exception of one or two general, factual essays, this volume will neither appeal to the palaeontological novice nor to the dinosaur expert—it is two-dimensional, repetitious and highly restricted in content (both the title and the dust jacket are rather misleading as they suggest more depth and range). There simply isn't enough about

palaeontology to appeal to its target audience, whereas a limited body of Hollywood 'B movies' and comic strips are covered, in some cases, in three or more separate essays. The book will probably appeal to sci-fi buffs, however—there is so much information on movie making techniques and plot lines that it will probably be *de rigeur* for the dinosaur-groupie equivalents of 'trekkies' or Dr. Who fans. Moreover, to ask £27 for such a book is wildly optimistic on the part of the publishers—I can't imagine anyone except the most hardcore (and unselective) dinosaurphile or science fiction fan ever wanting to own a copy of this tome.

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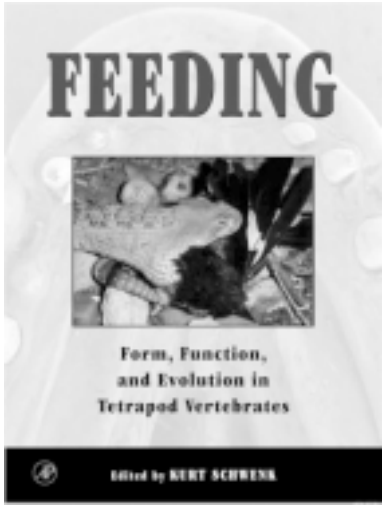
Feeding: form, function and evolution in tetrapod vertebrates

Kurt Schwenk (ed) 2000. 537 pp. Hardback. Academic Press London.
ISBN. 012-632590-1 (hbk) £74.



The evolution of the craniofacial skeleton and dentition in fossil vertebrates has always been an area of particular fascination for palaeobiologists. This is probably because jaw movements can be looked at as the lever system they actually are, and subsequently assessed in a 'how-things-work' way; it is a theme that many people find interesting. Additionally, teeth preserve superbly well and the sight of a gleaming enamelled surface that appears pristine, but may be many millions of years old, has a huge appeal. Teeth themselves come in a vast array of shapes and sizes and many are highly impressive. However, for many people, the interest goes far deeper, and the study of feeding mechanisms and strategies in living animals is the main focus of their scientific endeavour. For those vertebrate palaeobiologists who have a major interest in the evolution of craniodental anatomy, this book is an utter godsend. Really good palaeobiological analyses of putative feeding strategies in extinct animals are nowadays dependent upon experimental data from living animals and biomechanical principles. This book provides a huge wealth of information on feeding in most groups of living vertebrates. It is a vitally important and immensely interesting addition to the literature in its own right, but as a tool for furthering palaeobiological research into feeding styles it is a key publication.

The introduction to the book is a two-part section: the first deals with tetrapod feeding in the context of vertebrate morphology and the second part is an introduction to tetrapod feeding.

Both these sections give excellent overviews of evolutionary aspects of tetrapod feeding in general. The remainder—and bulk—of the book covers practically all the tetrapod groups in considerable detail. All groups of amphibians are discussed and the major clades of reptiles—lepidosaurs, snakes and crocodilians—are treated in depth. Mammals naturally receive a huge amount of attention, and it is excellent to see specific chapters devoted to myrmecophagy (ant/termite eating) and feeding in marine mammals. Admittedly, the latter chapter suffers from rather poor illustrations. Birds receive a surprisingly large amount of coverage, and this is extended to palaeognathous birds as a specific chapter. The one really large deficiency is a reflection of the great lack of study into a particular group of tetrapods—the testudines (tortoises and turtles). The 'chapter' on testudines is limited to a bibliography of turtle feeding and runs to half a page of text and two-and-a-quarter pages of bibliography. This is a shame as testudines can be used as meaningful analogues for feeding in a wide range of 'primitive' reptiles, which extended from the Late Carboniferous to the Late Triassic.

The information that is packed into this big, quarto sized monster derives from experimental approaches, observational data collected in the field and behavioural studies; all set into an evolutionary context. Most of the chapters are written by acknowledged experts in their fields with enormous experience of their subjects. It is well illustrated, although I felt that the 'illo' count could have been even higher, cladograms are evident in many places and provide good phylogenies in which to view many of the changes seen in tetrapod feeding. Functional anatomists and biomechanicists such as myself will probably love this book; it is interesting, well-edited, well-written, full of crucially important information for palaeobiologists, and likely to become a success. The price tag reflects superb production and although high, must not be allowed to prevent appropriate libraries from obtaining a copy.

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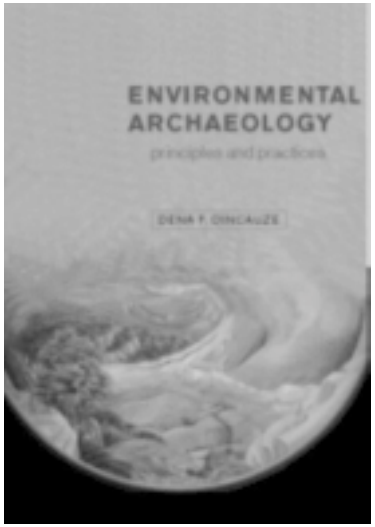
Environmental Archaeology—Principles and Practice

Dena F. Dincauze (2000) Cambridge University Press.
ISBN 01521325684 (pbk). £25.00.

As a discipline environmental archaeology covers a wide range of subjects. Many people working in the field are specialised within a particular area, with only a vague knowledge of changes in other spheres. It is only in the last two years that books have appeared that synthesise much of the recent information. This book represents an ambitious attempt to review the broad scope of this subject and much of its background in 522 pages.

Many archaeological books are focused on how to study particular types of material, *e.g.* faunal remains, diatoms. This book concentrates on answering the theoretical why question—why am I studying this and what are the reasons behind it? It is a useful addition to the environmental archaeology literature for this reason. The text is comprehensive, covering aspects of climatology, dating, faunal analysis, etc., providing a synthesis of literature and ideas from all these areas and how they relate to archaeology. In addition many of the classic

archaeological texts are referenced so that those who wish to study areas further can find the core material and read on from there.



It is hard to tell who the book is aimed at: there are several case studies which all archaeology students would be familiar with such as the Elm Decline and Star Carr, but the text is too heavy even for the keenest of undergraduates. Each sentence requires consideration before beginning the next; although there is a useful glossary at the start, no concessions are made to people without a thorough knowledge of the vocabulary of each area.

It is a subject that required synthesis and this is a book that needed to be written. However it is not a book that is easy to read and this is a shame considering the wealth of information and knowledge that has gone into it. As an overview of many aspects of environmental archaeology and related subjects it is hard to beat, but it is simply impenetrable to all but the most determined of readers. It is best suited as a reference book for those working in environmental archaeology, who wish to improve their knowledge of areas outside their expertise. I would recommend it to anyone who had to write a lecture course on the subject, but not as a direct source for undergraduates. It certainly is not something to sit and read from cover to cover!

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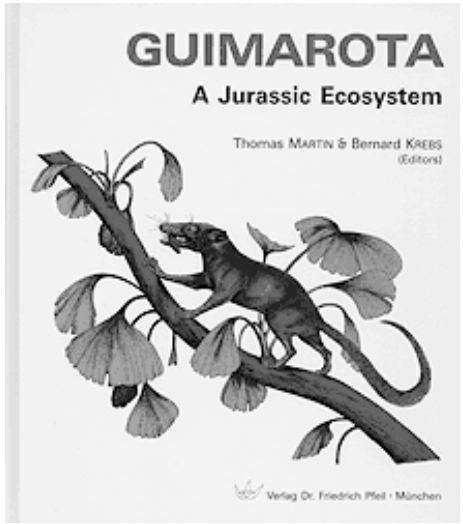
Guimarota: A Jurassic Ecosystem

Thomas Martin and Bernard Krebs (eds). 2000. 155pp. Dr Friedrich Pfeil, München. ISBN 3-931516-80-6 (hbk). 120 DM <**www.pfeil-verlag.de**>

Small terrestrial vertebrates (mammals, frogs, salamanders, lizards, etc) are under-represented in the Mesozoic fossil record. You don't stumble over a fossil mammal or lizard skeleton as you might a dinosaur. The most complete skeletons come from fine-grained ('lithographic') limestones like those of Solnhofen in Germany, or the Yixian Formation of China, but these exceptional horizons cannot provide enough data for an accurate reconstruction of the temporal and geographic history of the groups in question. A crucial contribution comes from microvertebrate sites (*e.g.* caves, fissures, channel fills), where depositional conditions act to preserve and concentrate the remains of small animals—albeit, frequently, as disarticulated elements.



The German palaeontologist, Walter Kühne, pioneered a systematic search for microvertebrate sites in his quest for early mammals, and he left a valuable legacy. Based in Britain during and after World War Two, Kühne was responsible for the discovery of the mammal-rich Lower Jurassic fissure fillings of South Wales. Returning to Berlin, he then initiated a hunt for potential mammal-bearing localities in Continental Europe. In the lignite mine of Guimarota, Portugal, he hit a treasure trove, a patchy but productive horizon deposited in a small brackish lagoon during the Late Jurassic (Kimmeridgian, c. 150 million years ago). To date, the site has yielded invertebrates (mainly molluscs and ostracods); a diversity of plants; and tens of thousands of small bones from fish, amphibians, turtles, lizards, crocodiles, pterosaurs, dinosaurs and birds. For mammals, Guimarota must have exceeded Kühne's wildest dreams, producing two nearly complete skeletons; more than 20 compressed skulls; 1,000 jaws; and at least 10,000 isolated teeth.

Guimarota—a Jurassic Ecosystem is a celebration of decades of work on this remarkable assemblage. It was edited by Thomas Martin and Bernard Krebs, and translated from the original German by Oliver Rauhut. Sadly, it is now also something of a memorial volume to Bernard Krebs who died in March of this year. Krebs was responsible for getting the site reopened after commercial work there had ceased (and Kühne had lost interest) and, from his base at the Freie Universität Berlin, he coordinated the research effort over more than thirty years.

The book is generally clearly written and well illustrated, with plenty of figures and plates. A history of the discovery and early exploration of the site is followed by short chapters on all aspects of the assemblage, and a representative bibliography. While this is very much an interim report, at least for the non-mammalian components of the Guimarota assemblage, it does provide a comprehensive review of current knowledge. At 120DM, this slim book is relatively expensive, but for anyone interested in Mesozoic ecosystems, it is certainly useful to have the existing data summarised in one place.

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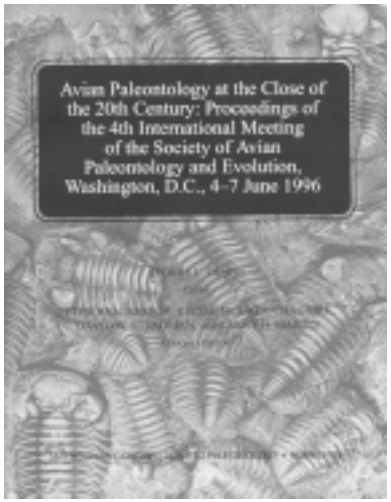
Avian Paleontology at the close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, D.C., 4-7 June 1996.
Smithsonian Contributions to Paleobiology 89.



In 1999, the Smithsonian Institution (Washington) published the proceedings of the 1996 conference of the Society of Avian Paleontology and Evolution (SAPE) in its *Contributions to Paleobiology Series* (number 89). The volume comprises a series of 28 papers on fossil birds and the minutes of a number of "roundtable discussions" on the origins of birds and their flight, neatly divided into several sections—"Quaternary Insular Birds", "Quaternary Avifaunal Studies in Continental Europe", "Large Raptors from the Late Cenozoic of the New World", "Three New Genera of Paleogene Birds", and "Mesozoic Birds and Avian Evolution".

The volume opens with a series of papers discussing birds from the relatively recent past, island faunas that have been influenced by the colonization of humans. These include reviews of the avifauna of Réunion Island (Mascarenes – Mourer-Chauviré *et al.*), Amsterdam Island (Indian Ocean – Worthy & Jouventin), faunas from the western Mediterranean and Hawaii (Segui & Alcover), a new species of extinct Barn Owl from Barbuda (Lesser Antilles – Steadman & Hilgartner), a resumé of the history of the Chatham Islands avifauna over the last 7,000 years (Millener), a discussion of the role of climate change and human impacts on South Island (New Zealand – Worthy), and a list of the fauna from Spingallo Cave (Middle Pleistocene of Italy – Pavia). Next, three papers give descriptions of birds and their environments from the Quaternary (Potapova & Panteleyev, Tyberg, and J. Stewart), and Campbell *et al.*, Tambussi & Noreiega, and Emslie & Czaplewski present papers on late Cenozoic raptorial birds.

In one of the more interesting parts of the volume for me, a number of new taxa of Palaeogene birds are described: Boles & Ivison describe a new genus of megapode from the Oligocene of Australia; Karhu presents additional material assigned to the extinct apodiform (swifts and relatives) family Jungornithidae (Upper Eocene of the Caucasus); Peters discusses a beautiful specimen of early fossil mousebirds named *Selmes* from the Middle Eocene of Germany; fossil anseriforms (waterfowl) are presented in papers by Alvarenga and Olson respectively; and new material referred to the fossil flamingo taxon *Juncitarsus* is described by Ericson. Tacked onto the end of this section, Hope then describes material representing a new species assigned to the enigmatic late Cretaceous taxon *Graculavus* from the Lance Formation of Wyoming.

In the latter section of this volume, a number of papers on more primitive types of Mesozoic birds and the early evolution of Aves appear. Dzerzhinsky discusses the implications of the detailed cranial morphology of palaeognaths to the evolution of birds, Kurochkin outlines the relationships of the taxa *Ambiortus* and *Otogornis* to the other known groups of Mesozoic birds, Bochenski presents evidence that the well known and diverse clade Enantiornithes may have diverged at an earlier time than *Archaeopteryx*, Zhonghe & Martin consider the morphology of the hand of *Archaeopteryx*, and lastly Martin & J.D. Stewart re-evaluate patterns of teeth implantation in birds. These latter two papers carry the implication that birds are not part of the theropod dinosaur clade.

However, by far the most interesting part of this volume are the pages at the end: edited minutes of three discussions centring around the origin of birds. This SAPE conference (the volume took almost three years to appear) was held shortly after the appearance of what would turn out to be one of the most controversial publications in recent times: the suggestion of Perle and colleagues (1993–1994) that the bizarre theropod *Mononykus* was a flightless bird, occupying more derived position within the avialan phylogeny than *Archaeopteryx*. For those who followed the exchange of views at the time this idea was first tabled, these roundtable reports (edited by Chiappe, Witmer and Goslow) make fascinating reading. Feelings ran so high among various workers on this issue that these roundtable meetings must have been tense affairs!

This volume is available from the Smithsonian Institution (Washington D.C). In my view it represents a valuable, although somewhat specialized in places, addition to the palaeontological literature (especially if you spend your time working with birds!).

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Encyclopedia of Paleoherpetology, Part 12A: Sauropterygia 1

Olivier C. Rieppel 2000. 134 pp. ISBN 3-931516-78-4 (hbk).
DM 125,00 / Euro 63,91 / US$ 83.00 <**www.pfeil-verlag.de**>

Olivier Rieppel has spent much of the last decade revising the anatomy, taxonomy, and biogeography of non-plesiosaur sauropterygians, rewriting the metaphorical book on this group of Triassic marine reptiles. With the welcome publication of the first sauropterygian volume of the *Encyclopedia of Herpetology*, Rieppel has written the literal book as well. At a price of US$83, this 134-page, 80-figure volume is a great reference for all interested in sauropterygians, and for vertebrate paleontologists in general.

The previous literature on non-plesiosaur sauropterygians spans almost two hundred years, back to the Victorian era and the birth of vertebrate palaeontology as a science. Much of this literature is rare and difficult to find today, and is largely written in German, with other contributions in Italian, French and English. Rieppel has assimilated this literature and done the detective work to locate the many holotypes and other historically important material in museums across Europe. In many cases important fossils have not survived the upheavals of the twentieth century. Rieppel has diligently untangled the resulting taxonomic problems, as well as those stemming from the taxonomic exuberance of the Victorian era. The results of these labours are published in no fewer than 50 publications authored by Rieppel and co-workers over the last 14 years. Rieppel's *Paleoherpetology* volume is a much-needed summary of this work.

The volume begins with a nice historical review of the relevant literature, continues with a phylogenetic section where Rieppel presents his view of sauropterygian relationships, and moves to a short primer on post-cranial anatomy. The bulk of the book is comprised of taxonomic reviews of all non-plesiosaur sauropterygians. Perhaps the most useful aspect of Rieppel's volume is the illustrations; Rieppel's drawings are clear and informative, striking a good balance between representation and schematic clarity. They amply illustrate the cranial characters listed in Rieppel's taxonomic reviews and diagnoses. Figures of post-cranial elements are rare, but are generally adequate for the needs of the taxonomic review. The taxonomy itself has been extensively revised by Rieppel, and this book will be required reading for anyone doing descriptive research on non-plesiosaur sauropterygians.

The book does have some drawbacks; Rieppel is a transformed cladist, and his rather extreme philosophical views sometimes colour his presentations and interpretations. For instance, Rieppel often speaks of certain nodes in his various cladograms as being stable or unstable given different sets of included taxa. However, he never includes tree statistics of any kind with his cladograms. He also does not include bootstrap values or decay indices, both of which are established methods for measuring the stability of nodes. Rieppel states that his topologies often change with the inclusion of new taxa; this type of instability is a red flag indicating that the topology as a whole is unstable. Measures of cladogram instability would illustrate this, and also indicate which of Rieppel's nodes are likely to last through his next publication. This is important because Rieppel names and diagnoses many internal nodes in his cladograms. When the cladogram changes, the definitions and diagnoses change as well, leading to a long and confusing history for his taxonomic terms. The main cladistic conclusions in this volume are hopefully stable; however, the reader should be aware that these conclusions may change with the inclusion of new Chinese taxa. The lack of cladogram support statistics is a major defect of this book.

There are several other quibbles of which the reader should be aware. Rieppel does not specify his outgroups in his cladograms, and while this information is available from the primary literature it would be convenient to have it included here. Also, Rieppel tends to make anatomical generalizations about 'all Sauropterygia' when he actually means all non-plesiosaur sauropterygians only. For instance, Rieppel states that all sauropterygians have two

cervical rib heads and a free anterior process on each rib; however, derived plesiosaurs lack both of these characters. Readers interested in specific character states in plesiosaurs should take such statements with caution.

Overall, Rieppel's book is a much-needed and very informative review of recent work on non-plesiosaur sauropterygians. The quality of the anatomical and taxonomic work is very high throughout, and the modernization of two hundred years of sauropterygian palaeobiology is a great service to the field. I recommend this book to anyone working on marine reptiles, those teaching courses in vertebrate palaeontology, and anyone interested in this group.

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Dinosaurs of Darkness

Thomas H. Rich and Patricia Vickers-Rich. 2000. 222pp. Indiana University Press. ISBN 0-253-3373-9 (hbk). £24.95.

A number of vertebrate palaeontologists, primarily dinosaur workers, have taken to writing memoirs of their scientific experiences in field and laboratory. This practice, perhaps exemplified by the works of Victorian natural historians and explorers, has in the past led to the production of some great works of travel writing (and science) that could, in some cases, be regarded as literature. Such works were (and are) generally aimed at a non-specialist, lay audience and often have the explicit aim of communicating both scientific information and the actual process of scientific investigation and discovery via the vehicle of an exotic locale or bizarre animal. (They often had the less noble aim of cashing in on the public's desire to read about the fabulous and fantastical, though the funds raised were sometimes ploughed back into research as funding for the next expedition). This genre, a travelogue/natural history/autobiography amalgam, seems to be attempting a comeback of sorts as evidenced by the proliferation of accounts on palaeontological expeditions and long-term research projects, including: "The Little Dinosaurs of Ghost Ranch" by Ned Colbert (dealing with the discovery and study of the theropod *Coelophysis* in New Mexico over the past sixty or so years), "Dinosaur Impressions" by Philippe Taquet (recounting the author's dinosaur excavations in the Sahara and southeastern Asia) and "Quest for the African Dinosaurs" by Lou Jacobs (describing the expeditions to the Dinosaur Beds of Malawi). "Dinosaurs of Darkness" is the most recent addition to this corpus.

Until the work of this husband and wife team, the terrestrial faunas of Mesozoic Australia were known from only a handful of localities, each of which had yielded relatively small amounts of useful material. The chance discovery of bone fragments during a prospecting trip along the Victoria coast led to the development of several productive vertebrate-bearing sites, the most famous of which is the eponymous 'Dinosaur Cove'. Diverse vertebrate faunas, including dinosaurs, other reptiles, fish and mammals, were recovered from two late Early Cretaceous units at these sites, challenging and augmenting our perception of Gondwanan dinosaurs and palaeoenvironments. "Dinosaurs of Darkness" recounts the circumstances surrounding the discovery, exploration and excavation of these localities and also provides some insights into the subsequent study of these important specimens.

Following events in strict chronological order, the Riches set out to document the trials and tribulations of work in a number of difficult, and often dangerous, locales. All of their quarries were situated in sheer sea cliffs, requiring much ingenuity to get equipment and people in and fossils out, preferably in one piece. In some ways, the book can be read as a 'how to' manual for those with limited resources, but lots of determination, to pull off some interesting fieldwork in unfavourable conditions. Certainly, the Riches have devoted the last twenty years of their lives to this endeavour with no small measure of success. Techniques used to get at the fossils ranged from digging with pick-axes to the use of explosives; we hear how they rigged a DIY cable-car to move equipment in and out of the site; and how they often drove hundreds of kilometres in a day to get a spare part for that pesky pump or generator. During their numerous field-seasons the Riches were ably assisted by a huge number of individuals, ranging from local store owners to major corporate sponsors, and all of these contributors get their mention in the book. Special tribute is paid to the bands of dedicated volunteers who gave their time to help in the project and were the mainstay of the palaeontological labour force. These mentions are all well deserved, but at times the book does tend to read like an extended list of acknowledgements making these passages worthy but rather uninspiring reading. Much information is provided in a simple and easy to read form, but the prose can be a little telegraphic and dry. Little is made of the 'travelogue' aspect of the work, a pity given that the localities were situated in areas of outstanding natural beauty. Perhaps this is because the authors didn't actually have to travel that far to get to their sites, or maybe it's because southeastern Australia is not regarded as particularly 'exotic' by the majority of North American or European readers.

The title might lead the reader to expect that they would find out lots about the animals and plants of Early Cretaceous Australia, but here they would be disappointed. Most of the animals recovered from the digs are mentioned in passing, with a few comments regarding their palaeobiology and their possible significance to larger scale problems such as phylogeny and palaeobiogeography. However, the rightful stars of the book are relegated to cameo appearances. Much more was needed on the animals, plants and their environment, as each raises a number of fascinating questions. How did the bizarre relict temnospondyl *Koolasuchus* survive in polar Australia? What are the phylogenetic and biogeographical implications of the controversial mammal *Ausktribosphenos*? How were the dinosaurs adapted to live in an environment with both a long polar night and low ambient temperatures? This is not so much a book for people who want to find out about dinosaurs, or any other extinct

animals, but for those interested in the mechanics of organising and running a long-term palaeontological project. Still, this book should appeal not only to a large number of 'dinosaur groupies', but also to those interested in exploration and discovery.

The book is reasonably priced for a hardback volume of this size, and the format, which is also used in all of the other Indiana University Press dinosaur volumes, is attractive. However, in all of these cases, with the exception of a few nicely produced colour plates, photographic figures are abysmal—surely IUP should invest in some better technology to rectify this. Some wonderful shots of both fossils and landscapes have been ruined by their poor, grainy reproduction.

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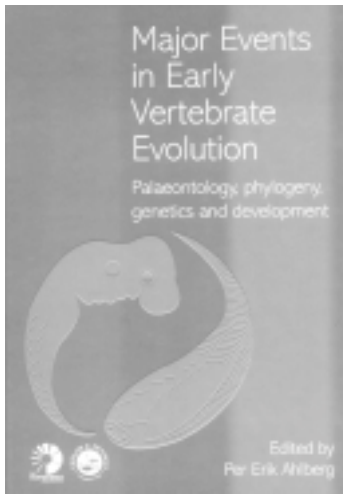
Major Events in Early Vertebrate Evolution

Per Erik Ahlberg (ed.). Taylor & Francis, London, 2001. 418 pp.
ISBN 0-415-23370-4 £55



On the 8th and 9th of April, 1999, a group of developmental biologists, molecular systematists and palaeontologists met at the Natural History Museum in London to explore the recent impact of these fields on early vertebrate evolution. This volume is essentially a record of that meeting. Although not formally divided into sections, the chapters fall into four major areas: 1) the origin of vertebrates; 2) the molecular evidence for the phylogeny of early vertebrates; 3) the history of early vertebrate radiations; and 4) the fish-tetrapod transition. The chapters on these topics contain a wealth of new information that will be welcomed by anyone interested in the origin and early evolution of vertebrates. Equally important, however, many of these chapters reflect the emergence of a new interdisciplinary approach, termed evolutionary developmental biology, which promises to reveal how gene expression and developmental pathways are changed over time to generate new morphologies.

Earlier attempts to understand the origin of vertebrates suffered from the absence of a well corroborated hypothesis of deuterostome phylogeny and a paucity of early vertebrate fossils. Both obstacles are now being surmounted, however, by the application of molecular techniques and the discovery of new additions to the fossil record.

Henry Gee reviews new molecular studies that support Metschnikoff's 19th Century hypothesis that echinoderms and hemichordates form a monophyletic group termed the Ambulacraria.

This hypothesis is in sharp contrast to the usual textbook assertion that echinoderms are the sister group of all other deuterostomes and that hemichordates are, in turn, the sister group of the chordates. In the latter scenario, which is essentially the hypothesis espoused by Al Romer and Bobb Schaeffer, the pharyngeal slits and, possibly, even the stomochord of hemichordates were believed to be homologous to the pharyngeal slits and notochord, respectively, of chordates. Recent molecular studies have not supported the putative homology of the hemichordate stomochord to the chordate notochord, and one would think that the ambulacrarian hypotheses would also have as a corollary that the pharyngeal slits of hemichordates and chordates can not be homologous. Surprisingly, however, Gee proposes that gill slits are, in fact, a primitive feature of all deuterostomes. His assertion is based on Dick Jefferies' claim that the extinct cornutes, such as *Ceratocystis* and *Cothurnocystis,* possessed pharyngeal slits. If this were the case, then at least some members of each deuterostome group would have possessed these pharyngeal slits, which could be interpreted as a primitive feature of deuterostomes. What is particularly troubling about this claim, however, is that to this reviewer's knowledge, *Ceratocystis* and *Cothurnocystis* are the only "stem-group echinoderms" that may have possessed pharyngeal slits, and even these genera must be removed from consideration if they are "stem-group chordates", as Jefferies insists.

The contentious carpoids again take centre stage when Dick Jefferies claims that a minuscule groove near the base of the appendage in *Ceratocystis* is a homologue of the tunicate atrium and the left inner ear (otic vesicle) of vertebrates. The impetus for this assertion appears to be the recent claim that the tunicate atrium and the vertebrate inner ear are homologous because each arises from an ectodermal invagination, expresses *Pax* homologues, and contains ciliated sensory organs. Since Jefferies initially claimed that mitrates possessed atria, his essay is essentially a search for the conute homologue of the mitrate atrium, which he believes is the unpaired groove in *Ceratocystis*. Jefferies proposes the following scenario for the origin and evolution of the "acustico-lateralis" system: the unpaired groove in cornutes such as *Ceratocystis* was essentially a mechanoreceptive "lateral line" which subsequently invaginated in mitrates to form an atrium whose primary function was as an acoustic organ.

This scenario is an old one, in which only the names of the players have changed from hypothetical protovertebrates to carpoids, with the added twist of an atrium. There is no palaeontological evidence that the inner ear of vertebrates arose by the invagination of a lateral line of neuromasts, as all fossil vertebrates, including some of the newly discovered Chengjiang vertebrates, have inner ears. Furthermore, neurophysiological data indicate that the inner ear of vertebrates arose as a vestibular organ, as there is no evidence that the inner ears of hagfishes and lampreys have acoustic abilities. Speculation on the origin(s) and initial function(s) of atria are also suspect. The atrium of amphioxus forms from longitudinal ectodermal folds that initially develop dorsal to the pharyngeal slits and then fuse at the ventral midline, rather than forming ectodermal invaginations as in tunicates. It is possible that atrial formation in tunicates differs from that in amphioxus due solely to the size of the larvae, and/or that the formation of an atrium occurred independently in two chordate lineages. Finally, the cupular organs within the atria of tunicates are almost certainly an example of parallel homoplasy vis-à-vis the cupular neuromasts of vertebrates, as the lateral line receptors in hagfishes and lampreys do not have cupulae.

Jefferies' contribution to this volume is the latest in an extensive and often scholarly series of publications, but his version of the acustico-lateralis hypothesis, like so many others, is difficult to test. The only valid test of any of the corollaries of his calcichordate theory is, as Gee and others have noted, a phylogenetic one. In this context, the contribution of Paul Smith, Ivan Sansom, and Karen Cochrane is particularly welcome. They review recent attempts to test Jefferies' theory cladistically, and note that most tests are biased by whether characters are coded according to the calcichordate or the non-calcichordate hypothesis. Two tests, however, appear to bypass this bias. The calcichordate theory proposes that tunicates, rather than cephalochordates, are the sister group of vertebrates, whereas a majority of all recent cladistical analyses involving both molecular and morphological features place tunicates as the sister group of cephalochordates-plus-vertebrates. Equally important, as Smith *et al*. note, unmineralized crown vertebrates are now known from the mid-Early Cambrian, some 100 million years prior to Jefferies' proposed sister group to these crown vertebrates.

Until a decade ago, it was assumed that vertebrates first appeared in the Ordovician and subsequently radiated during the Silurian and Devonian Periods. The fossil evidence for these earliest known vertebrates has been very limited, however. That for *Anatolepis*, for example, comprises only small scrapes of tubercles connected by sheets of apatitic tissue. This situation changed with the discovery of well preserved but non-biomineralized vertebrates from the Early and Middle Cambrian in the Chengjiang and Burgess Shale Lagerstätten, respectively. Smith *et al*. catalogue these discoveries, which include animals that appear to have had cartilaginous cranial skeletons that included nasal capsules, otic capsules and branchial cartilages. These fossils clearly indicate that vertebrates arose much earlier than the Ordovician, perhaps as early as the Late Neoprotozoic, given the complexity of their features in the Early Cambrian. Despite the existence of these non-biomineralized vertebrates from the Early Cambrian, however there is no evidence of a mineralized exoskeleton for another 25 to 30 million years. Smith *et al*. speculate that this long gap between the origin of vertebrates and the development of biomineralized exoskeletons may indicate that the earliest vertebrates did not have the developmental capacity to produce enamel and dentine.

Many tissues of the head, including much of the dermal skeleton, teeth and numerous neural tissues, are either derived from neural crest or require an inductive signal from neural crest. A number of years ago, Carl Gans and I postulated that the origin of vertebrates was dependent in large part on the development of neural crest and neurogenic placodes. This theme continues to be explored in a chapter by Linda and Nick Holland (the American Hollands) and chapters by Peter Holland (the British Holland), Hiroshi Wada, Miguel Manzanares, Robb Krumlauf, and Sebastian Shimeld. Linda and Nick Holland summarize recent studies on the distribution of a number of gene expression patterns associated with the development of the neural tube in amphioxus. They conclude that amphioxus lacks a definitive neural crest but that many of the genes expressed in the premigratory neural crest of vertebrates are also expressed at the boundary of the neural plate and general ectoderm in amphioxus. The expression of these genes, however, appears to be insufficient to confer on these cells the properties associated with vertebrate neural crest.

Peter Holland *et al*. ask what properties cells must possess in order to be defined as neural crest; they conclude that the position of origin, the ability to migrate, the ability to differentiate into a number of distinct cytological cell types, and the ability to be patterned differently along an anteroposterior body axis are all hallmarks of vertebrate neural crest. They also conclude that neural crest does not exist in amphioxus, despite the expression of a substantial number of developmental genes that characterize neural crest in vertebrates. Their discussion ends with an interesting speculation. In vertebrates, Hox genes pattern the neural tube and crest, but in amphioxus, these genes are expressed only in the neural tube. They speculate that Hox genes were used to pattern only the neural tube in ancestral chordates but later in vertebrate evolution were incorporated to pattern neural crest and mesoderm also.

It is widely appreciated that neural crest cells differentiate into a number of very distinct tissues, but there has never been substantial agreement on the phylogenetic chronology of these tissues. It has been generally assumed that the earliest vertebrate skeleton was a cartilaginous endoskeleton, which became mineralized after the phylogenetic origin of a mineralized dermal exoskeleton. Phil Donoghue and Dick Aldridge, however, present evidence that conodonts are the sister group of all other vertebrates that possess a mineralized skeleton and, as such, are the first vertebrates to develop mineralized tissue in the form of dentine. What is most exciting about their report, however, is that this mineralized tissue occurs as denticles, located within the oropharyngeal cavity of otherwise naked conodonts. If this claim is further supported, a considerable change in our ideas about the origin and evolution of vertebrate cranial skeletons will have to occur.

Turning to the molecular evidence for the early history of vertebrates, three different chapters address interrelationships of the early vertebrates based on molecular data. Jon Mallatt, Jack Sullivan and Christopher Winchell expand their earlier 26S rRNA data set and readdress the relationship of lampreys and hagfishes. Their expanded data set continues to support cyclostome monophyly, and Blair Hedges reached the same conclusion as Mallatt *et al*., based on the sequences of a number of nuclear protein-coding genes rather than mitochondrial protein-coding genes. In yet a third study involving both nuclear and mitochondrial genes, Rafael Zardoya and Axel Meyer generate very different phylogenies, depending on which molecular data set is used. When the nuclear 28S rRNA set is used, the resulting phylogeny closely agrees with the phylogeny generated with morphological characters, with the exception that hagfishes and lampreys again form a monophyletic group. When the mitochondrial tRNA data set is used, however, the result is phylogenies with a number of bizarre vertebrate groupings (*e.g.*, snakes and hagfish as a group). Zardoya and Meyer interpret these anomalies as due to non-random, misleading noise in the data set. Thus, at present, cladistic analyses based on morphological and physiological characters yield one phylogeny, in which lampreys are the sister group of gnathostomes, with hagfishes, in turn, being the sister group of the lamprey-gnathostome clade, whereas analyses based on molecular data support the monophyly of hagfishes and lampreys. With the possible exception of tunicate-cephalochordate-vertebrate interrelationships, there is probably no other single case where the resolution of two opposing hypotheses would so fundamentally affect our understanding of early vertebrate evolution. When the morphology-based hypothesis is accepted, a large

number of hagfish characters are interpreted as being primitive for vertebrates; when the molecular-based hypothesis is accepted, a large number of hagfish characters are interpreted as being derived (degenerate). It is difficult to see how this situation can be resolved. Morphological and molecular based approaches usually generate congruent phylogenies, but clearly both can not be correct in this case. If and when a resolution occurs, we will have not only a better understanding of the interrelationships of early vertebrates but also a better approach to reconstructing phylogenies in general.

The history of vertebrates is covered in some 11 chapters and constitutes at least half of the volume. Topics range from documentation of the Ordovician vertebrate radiation to detailed discussions of the systematics or anatomy of each of the major groups of the early vertebrates.

Ivan Sansom, Moya Smith and Paul Smith document the growing evidence that the first major radiation of vertebrates occurred in the Ordovician. Although this evidence consists primarily of microremains (fragments of dermal armour, tubercles, scales, and teeth), it exists in sufficient quantity to indicate that a wide range of pteraspidomorph, arandaspid, thelodont, placoderm, chondrichthyan, and acanthodian taxa already existed. The authors note that this initial radiation of vertebrates coincides with changes in global sea level and suggest that the expansion of the epicontinental nearshore environment greatly increased the number of potential niches that could be utilized.

Two aspects of "ostracoderm" biology are covered in chapters by Philippe Janvier and Mark Purnell. Janvier reiterates his position that the armoured "ostracoderms" are more closely related to the gnathostomes than they are to hagfishes and lampreys. Here he focuses on the galeaspids and osteostracans, and argues that approximately half of the characters likely to be preserved in gnathostome fossils also occur in these ostracoderms. Thus both the phylogenetic position and morphology of galeaspids and osteostracans provide important information on the origin of gnathostome cranial organization.

Mark Purnell focuses on major transitions in early vertebrate evolution and provides thoughtful insights into two major ecological explanations of the decline of Paleozoic jawless vertebrates and the rise of gnathostomes. His analysis of familial diversity does not reveal any simple relationship between these phenomena, particularly as the rate of agnathan extinction peaked in the Early Devonian, whereas gnathostome diversity peaked in the Late Devonian. He concludes that there is therefore no evidence that agnathans declined as a result of competition with gnathostomes. He suggests that the anatomy of conodonts supports the hypothesis that the origin of vertebrates was related to the rise of predation, but he also argues that very little is known about the feeding habits of the other groups of fossil agnathans, and that it is presently impossible to determine whether the origin of gnathostomes was related to increased levels of activity and predation.

Five chapters focus on various groups of early gnathostomes and their interrelationships: placoderms (Daniel Goujet), chondrichthyans (Mike Coates and Sandy Sequeira, and John Maisey), osteichthyans (Zhu Min and Hans-Peter Schultze, and Hans-Peter Schultze and Stephen Cumbaa). These chapters contain a wealth of information that can not be summarized easily in a short review but will be of considerable interest to specialists who focus on a particular taxonomic group. Not surprisingly, the nature of the braincase and fins

in ancestral gnathostomes is a theme that appears again and again but whose resolution remains disappointingly elusive.

Three additional chapters each focus on a particular aspect of gnathostome anatomy: dentition (Moya Smith and Mike Coates), caudal skull (Willy Bemis and P.L. Forey), and the caudal (tail) fin (Brian Metscher and Per Ahlberg). Each of these chapters considers both ontogenetic and phylogenetic aspects of a specific organ and exemplifies (as do others) the hoped-for synthesis that was the impetus for this meeting.

Moya Smith and Mike Coates examine the evolution of vertebrate dentition and, in an amazing tour de force, reject the classical theory that teeth evolved from dermal denticles. They document the profound patterning differences between dermal and oral denticles and suggest that these differences must have arisen very early in vertebrate phylogeny. They then propose a new theory, that the developmental program responsible for the whorl-like sets of oropharyngeal denticles was co-opted for mandibular dentition in primitive gnathostomes.

Bemis and Forey continue the developmental evolutionary theme by examining the developmental bases for phylogenetic variation in the occipital region of the skulls of actinopterygians. They do a remarkable job of clarifying a topic initially introduced by Fürbringer (in a most confusing manner) by surveying the occipital region of the skull in both embryonic and adult actinopterygians, in order to determine the number of vertebral segments that are incorporated into the skull, then examining the distribution of this data within the context of an already established hypothesis of actinopterygian phylogeny. They conclude that three vertebral segments were already incorporated in ancestral actinopterygians and that a complex pattern of additions and deletions characterize the various actinopterygian groups. This analysis demonstrates how relatively simple techniques can reveal complex phylogenetic patterns, whose development can then be modelled experimentally by choosing a species such as the zebrafish.

Metscher and Ahlberg perform the same type of analysis by examining the ontogeny and phylogeny of the homocercal teleost tail. This tail appears to be derived from a heterocercal tail in basal actinopterygians, where the vertebral column extended to the posterior tip of the caudal fin, which was capped dorsally by fulcral scales and the fin-ray field restricted ventrally. By examining the development of the median fin patterns of sturgeons and other nonteleost rayfinned fishes, they were able to hypothesize that the dorsoventrally symmetrical fin-ray pattern in teleost tails probably evolved due to a homeotic duplication of the ancestral ventral fin-ray field, rather than progressive realignment of the fin-rays to form a symmetrical field.

The final section of this volume consists of three chapters on the fish-tetrapod transition. In a short chapter, Jean Joss and Terry Longjurst re-examine the development of the pectoral fins of the Australian lungfish and are able to augment and correct details of earlier accounts by employing a much more complete set of developmental stages. Of particular interest is their claim that there is no evidence of bifurcation events involving each axial element and its preaxial radial, as proposed in the Shubin-Alberch model of tetrapod limb development.

In a second chapter, J.R. Hinchliffe, E.I. Vorobyeva, and J. Géraudie address the question of whether a single developmental pattern underlies limb evolution in tetrapods. They were able to map prechondrogenetic patterns in zebrafish, two salamanders, and the clawed frog, using

an antibody against chondroitin. Their observations do not support the widely held view that the proximal skeletal elements in fin buds are homologous to the proximal skeletal elements in limb buds, because both the chondrogenic patterns and processes differ between the two bud types. The authors conclude the following, based on their results. These results do not preclude the possibility that molecular control of teleost fins and tetrapod limbs are similar, but if they are, this cannot be true for the downstream processes. Also, a tetrapod developmental bauplan does exist and can be characterized by a number of similarities.

In a final chapter on the fish-tetrapod transition, Jenny Clack returns to the otoccipital region of the skull. While many parts of the skull changed gradually during this transition, she notes that there was a radical restructuring of the otic and mid-region of the braincase with the origin of tetrapods. Taking the results of recent developmental studies of embryogenesis and craniofacial patterning in living vertebrates, she attempts to apply this knowledge to the changes in the braincase that marked the fish-tetrapod transition. Clack notes that the ventral cranial and metotic fissures divide the braincase of gnathostomes into three separate divisions, and she postulates that each of these divisions is composed primarily of different tissue domains involving neural crest and cephalic and somitic mesoderm in a rostrocaudal sequence. Each of the regions that are radically restructured, however, appears to involve an increase in tissue domains involving neural crest. This is a novel and important insight into the developmental mechanisms underlying cranial restructuring that is certainly amenable to experimental verification. Clack does not speculate on why these remodelling events should have involved neural crest rather than any other cranial tissues. It is possible, however, that given the migratory and rostrocaudal regional specialization of neural crest, this is the cranial tissue that is most malleable developmentally.

It is rare for an edited volume arising from a symposium to have an important effect on a field. Most such volumes are already dated and of little interest to anyone but their contributors by the time they are published. I believe that this volume is the rare exception and that it will have a profound effect on a number of fields for some time to come. It is well worth reading and an important addition to the library of any serious scholar of vertebrate evolution.

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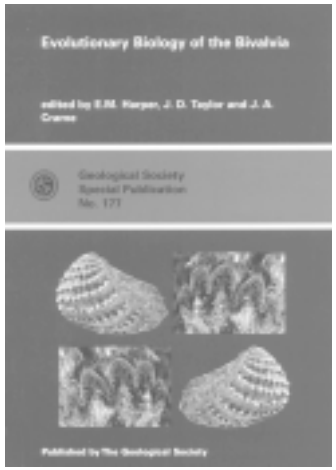
Evolutionary biology of the Bivalvia

Harper, E.M., Taylor, J.D. & Crame, J.A. (eds) 2000. 494pp Geological Society Special Publication no. 177. ISBN: 1-86239-07602

Despite their richness and diversity in much of the Phanerozoic record and their great value in palaeoecological and palaeobiogeographic studies, bivalves have not received the attention given by palaeontologists to many other invertebrate groups. Probably this is because their stratigraphic value is rather limited, and hence there has been less incentive for detailed taxonomic work. This may be a major reason why modern phylogenetic studies involving cladistics and molecular biology have lagged behind that of some other groups. A good start has nevertheless been made, as indicated clearly in this volume, which is an outcome of a meeting at Cambridge in 1999 organised by one of the editors, Liz Harper. Attended by nearly 120 scientists from across the world, this was the first international bivalve meeting for zoologists and palaeontologists to be held for over 20 years.



Steiner & Hammer have used an analysis of 18S rDNA sequences in order to tackle the phylogenetic relationships of the pteriomorphs. Their researches support the monophyly of the Protobranchia, Heteroconchia and Pteriomorpha; within the pteriomorphs, there is strong support for two major clades, ([Pinnoidea (Ostreoidea + Pterioidea)] and [(Anomioidea + Plicatuloidea) + (Limoidea + Pectinoidea)]. Further molecular studies by Campbell, also using the 18S gene, deal with the relationships between a wide range of bivalve superfamilies, orders and subclasses. Gratifyingly he found that all superfamilies, which have been established on morphological grounds, appeared monophyletic, as were most orders. Carter *et al*. have undertaken a cladistic analysis of Palaeozoic taxa, using a surprisingly large number of characters, which produced embarrassingly numerous parsimonious trees. Nevertheless there are some interesting conclusions, such as supporting Waller on the basal position of the Mytiloidea among the pteriomorphs. They also put forward the iconoclastic view that the Bivalvia were not derived, as generally believed, from the rostroconchs, preferring instead a monoplacophoran origin. In a review of early bivalve phylogeny, Cope considers the evolution of the filibranch gill, which he identifies from dental changes, as providing the initial impetus for the diversification of the group in the latest Cambrian or earliest Ordovician. Skelton and Smith report the results of the first cladistic analysis of the rudists, coming to the major conclusion that many of the phylogenetic relationships established by pioneer workers such as Douvillé were sound. Thus an outer shell layer of fibrillar prismatic calcite is a diagnostic synapomorphy for all rudists, and the attachment to the substrate by one or the other valve provides a fundamental division into two stocks. Harper *et al*. use a cladistic analysis of the

Anomalodesmata; among their more interesting conclusions is that carnivory has arisen independently within two separate clades. Two groups of zoologists have undertaken molecular analyses of two groups of the important freshwater unionids.

By no means all the chapters are devoted, however, to phylogenetic matters, for there is a wide range of subjects dealt with involving bivalve form and function, biodiversity, biogeography and ecology. I shall give just a sample of the diverse topics dealt with, which I found particularly interesting. Taylor and Glover have analysed the mechanism of chemosymbiosis in the lucinids, all of which appear to harbour sulphide-oxidising bacteria within their gills. Morton has studied the pallial eyes of pectinids and concluded that their true purpose remains unknown—they certainly do not appear to help in escaping predators. A new analysis of regional bivalve faunas by Crame shows that both latitudinal and longitudinal gradients are not as regular in form as supposed. There is a distinct step between 20 and 30°N in the latitudinal diversity gradient for the northern hemisphere and in the southern hemisphere the bivalve fauna of Australia forms a distinct hotspot of diversity.

The causes of these large-scale patterns appear to be multiple and complex, and involve a significant historical component. Jablonski *et al*. have analysed the diversity gradients on the eastern Pacific coast, with results differing from Crame's in some respects. Johnson *et al*. have studied both growth rings and stable isotope fluctuations in Late Cenozoic Queen Scallop shells in the North Sea, and demonstrate that the growth rings may be a more reliable climatic indicator than oxygen isotopes for Pliocene times. The final chapter, by Seed *et al*., is devoted to the most familiar and well studied of all bivalves, the marine mytilid mussels. Because of their abundance and accessibility, as well as their importance as food, mussels have been widely used as sentinel indicators of environmental change and pollution. Seed *et al*. demonstrate, by detailed studies of shell growth and trace element analysis, how mussel shells can be used as chronometers of environmental change.

This excellently produced book, conforming well to the high standard set in the Geological Society series, is required reading for all researchers on living and fossil bivalves, and also provides much of potential value to others.

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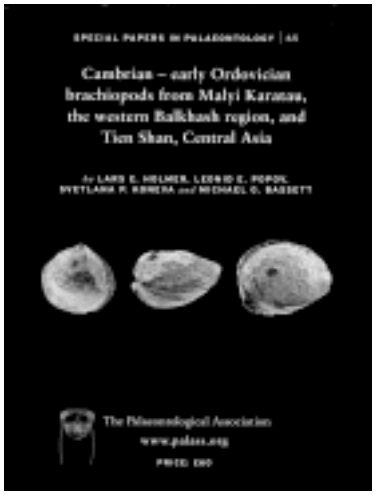
Special Papers in Palaeontology No. 65

Cambrian-early Ordovician brachiopods from Malyi Karatau, the western Balkash region, and Tien Shan, Central Asia

Lars E. Holmer, Leonid E. Popov, Svetlana P. Koneva & Michael G. Bassett (2001). pp. 1-180, 51 plates, 27 tables, 19 text-figures. ISSN 0038-6804; ISBN 0901702 71 4. £60/$120 non-members, £30/$60 members. Postage and packing extra (£2 within UK; £4 or $8 per item surface mail overseas; £8 or $16 airmail overseas).

Abstract



Carbonate platform deposits of the Shabakty Group in the Malyi Karatau Range of southern Kazakhstan contain rich brachiopod faunas of early Cambrian (Botomian)-early Ordovician (Arenig) age. Seven biostratigraphically successive assemblages are defined across this interval. Four further discrete microbrachiopod assemblages occur in Middle-Upper Cambrian sequences of various adjacent Central Asian regions, including Suukadyr Mountains of the southern Betpak-Dala Desert (Darbaza Formation), the western side of Lake Balkhash (Zhalgyz Formation), north-west Balkhash (Sarykumy Formation), the Kostek Range of North Tien Shan (Karagajly Formation), and the Moldotau Range in Central Tien Shan (Karadzhorga Formation). Linguliformean (organophosphatic-shelled) stocks are dominant, comprising 74 of the 88 described species. In a total of 55 identified genera, 47 are linguliformeans and eight are rhynchonelliformeans. *Diencolobus* is identified as a new linguliformean genus, and there are 11 new species of linguliformeans, referred to the lingulides *Notiobolus indefinites, Canalilatus? major, Mirilingula postuma, Diencolobus simplex, Canthylotreta atasuica, Dactylotreta septata, Picnotreta karakichiensis, Stilpnotreta minuta, Pomeraniotreta obtuse, Kleithriatreta kostekensis*, and *Eoscaphelasma? delicata*. Twenty-four taxa are described under open nomenclature.

Brachiopods from different segments of the Central Asian tectonic collage have different biogeographic signatures. In the early Cambrian, Malyi Karatau was probably part of the Yangtze Plate (South China). Middle Cambrian affinities were with East Gondwana (eastern Australia), but by the end of the mid Cambrian westward drift introduced links with Baltica and Laurentia. Balkhash and Tien Shan terranes retained East Gondwanan relationships throughout the Cambrian.

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