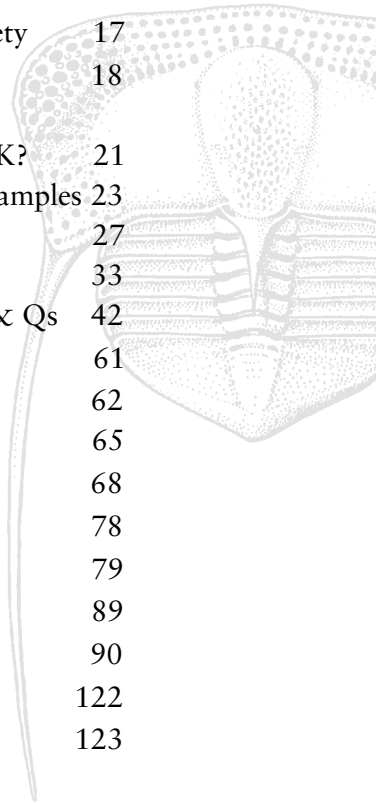


The Palaeontology Newsletter

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Reminder: The deadline for copy for Issue no 62 is 23rd June 2006.

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

ISSN: 0954-9900

Editorial

As noted by the President during the AGM in Oxford, Phil Donoghue has retired from his post as Editor of this *Newsletter*. I say “newsletter”, but the University of Plymouth’s library services actually lists this publication in its database of accessible electronic *journals*. Plymouth University is not alone in holding our *Newsletter* in such high regard. The reason for this, without doubt, is the transformation that we have seen in the contents and style under Phil’s expert guidance and vision over the past few years. As also noted by the President at the AGM, Phil’s will be a hard act to follow. The *Newsletter* is a top class publication of which we can be very proud indeed. I would like to take this opportunity to thank Phil for all the hard work he has put in over the years, and more recently as he has guided me through the first few weeks on the job.

Of course, the *Newsletter* would be a very thin and little read publication were it not for the efforts of the correspondents, reporters and others who work so hard to produce copy for each edition. The mix of scholarly, thought-provoking, witty, entertaining, useful and highly readable contents means that – I hope – there remains in the *Newsletter* something for everyone. If you feel that this is not the case or if there is something you wish to see more of (or perhaps even less of!) then feel free to contact me.

Finally, I need to mention a small change to our team of contributors: Graham Budd has left his post as Newsletter Reporter and Maggie Cusack has given up her role of compiling the list of future meetings. I am relieved to see that apparently only two – at least so far – have felt that life without Phil in charge is so unbearable that resignation is the only option! I would like to thank both Graham and Maggie for their service over the years, and would like to take this opportunity of welcoming Al McGowan into the fold, on whose broad shoulders both tasks now rest.

Richard Twitchett

Newsletter Editor

<newsletter@palass.org>



Association Business

Awards

Lapworth Medal awarded to Professor William G. Chaloner FRS



As announced at the 2005 AGM in Oxford, Council has awarded the Lapworth Medal to Professor William (Bill) Chaloner FRS in recognition of his lifetime contributions to palaeobotany over more than 50 years. Bill Chaloner has had an enormous influence on the development of palaeobotany in this country and abroad, always seeing the bigger picture – and always striving to expand the relevance of palaeobotany to questions of broader biological and geological significance. Some of the areas in which he has pioneered new approaches are: integration of the palynological and macropalaeobotanical record by studies of *in situ* pollen and spores, the early application of scanning electron microscopy to studies of plant fossils, the use of fossil plants in determining ancient climates – including the history of carbon dioxide in the atmosphere, and the study of plant–animal interactions in the geological record. In addition, he is a world authority on Palaeozoic plants and especially lycopods.

Bill was unable to attend the Annual Meeting in Oxford, but we plan to present him with the Lapworth Medal at this year's meeting in Sheffield in December. Bill Chaloner served as President of the Palaeontological Association from 1976–1978. By extraordinary – but appropriate – coincidence Bill is also related, through his maternal grandfather, to Professor Charles Lapworth.



Sir Peter Crane

Hodson Fund awarded to Dr P. J. C. Donoghue

Phil's scientific track record speaks for itself. His publications, which already number in excess of 30, include significant papers on conodont palaeobiology, early vertebrate phylogeny, the evolution of skeletal development, and metazoan palaeoembryology in *Nature*, *Biological Reviews*, *Philosophical Transactions of the Royal Society*, *Proceedings of the Royal Society*, *Palaeobiology* and *Palaeontology*. He has also edited two books.

The quality of Phil's research has been recognized by high-profile awards, including the Murchison Fund of the Geological Society (2002), and a Philip Leverhulme Prize (2004). Recently, Phil was



awarded a NESTA (National Endowment for Science, Technology and the Arts) Fellowship. He has obtained funding from NERC through a Postdoctoral Fellowship, a New Investigators Award, and a large grant.

Not surprisingly, he is also well respected by senior colleagues, and comments from nominees included statements such as “I cannot think of anyone his age who comes even close to the quality and quantity of his contributions to palaeontology,” “the most impressive palaeontologist in his age group working in the UK today,” and “I know of no palaeontologist under the age of 35 who more richly deserves the Hodson Fund”.



Phil has also made time to contribute to the wider palaeontological community through a number of professional activities. These include several years as editor of *The Palaeontological Association Newsletter*, during which time it has gone from strength to strength. He was previously editor of the *Newsletter of The Micropalaeontological Society*, and has served on the councils of the Systematics Association and the Palaeontographical Society.

Mark Purnell

Mary Anning Award – Andrew Yule

Andy Yule of Cowes is unique amongst the many fossil collectors on the Isle of Wight. Despite the lure of the fame and sometimes fortune that accompany the collecting of dinosaurs from the Island’s south-west coast, Andy has stuck with his passion for collecting from the late Eocene to early Oligocene Solent Group which outcrops along the Island’s north-west coast.

Andy, a true local lad, now in his fifties, has spent his entire working life in the building industry. He was inspired by the old ‘Victorian’ style displays of fossils at the old Geological Museum in Sandown and through talks and field trips of the local Natural History Society. From the 1970s



Andy Yule receiving his Mary Anning Award

he started looking for fossils in the then largely forgotten Gurnard–Thorness Bay and Quarr Abbey sections. He was soon finding pieces of turtle and alligator, which rapidly turned to complete carapaces of turtles and one of the most complete alligator skeletons ever to come from the Island. Andy realising the importance of his finds was quick to donate them to the museum, where he felt they belonged. Andy’s turtle finds became part of the display at ‘Sandown’ and now in the new Dinosaur Isle Museum. Along with these spectacular finds Andy started finding new sites which have fed research into mammals and palaeoenvironments.

Andy made just the one change of emphasis when he moved onto the insect bed, an exceptional preservation of early Oligocene insects and plants exposed in the cliffs near his Cowes home. Andy developed the knack of knowing



just how to break open the blue limestone blocks, and revealing their fabulous fossil content. Andy has since freely passed on to the museum the pick of his finds which now included spiders and bird feathers. Despite eye cataracts Andy has continued to make super finds from the insect bed which this year have been fed to the assembled experts of INTAS Project 03-51-4367 on the terrestrial fauna and flora of the Insect Bed; this meeting comprised 33 scientists from six countries. For this benchmark study Andy made all his finds available, many of which have travelled off with the participating experts. Recently, a water spider *Vectaraneus yulei* Selden (2001) (*Palaeontology* 44, 695–729) from the insect bed was named in his honour.

Andy stands out for being completely generous and self-effacing. He has kept alive interest in the geology of the Island's north coast despite all the attention the dinosaurs have gained. He has a unique knowledge of where and how to find fossils. His many finds comprise not just the highest quality museum specimens but also discoveries which have contributed to, and will continue to expand our knowledge of, late Eocene to early Oligocene biota and environments well into the future.

Martin Munt

Mary Anning Award – Steve Etches

Over the last thirty years Steve has collected fossils from the Kimmeridge Clay from exposures throughout the British Isles. He has become proficient in preparing, conserving and displaying his finds, and his advice on conserving Kimmeridgian fossils is sought worldwide. His collections are of global importance.



Steve Etches entertaining school children during a Rockwatch event (photograph courtesy of Susan Brown, of Rockwatch)



Despite running his family plumbing business, Steve tried to make his time available to palaeontologists and interested parties to view his collections – but this is difficult during working hours. Plans are currently afoot to open a museum to contain the collection which will make access available throughout the year. It is Steve's wish to share his knowledge and enthusiasm with as many people as possible – be they professors, students or school children.

Steve has invested a lot of his time, effort and finances into amassing and preserving his collection, and he considers himself a guardian of the geological heritage which he hopes will be preserved for posterity.

Jane Clarke

Sylvester-Bradley Awards for 2005

Jennifer England (PDRA, Glasgow), Crystallography and chemistry of fossil craniid brachiopods: £760

H. Falcon-Lang (Lecturer, Bristol), Terrestrial palaeoecology of a Late Carboniferous intramontane basin, Czech Republic: £970

R. Irmis (PhD student, Berkeley), Reappraisal of the phylogeny of early dinosaurs: £1,000

Marc Jones (PhD student, UCL), Morphometric analysis of sub-fossil *Sphenodon*: £1,000

Tim Kearsey (PhD student, Plymouth), High-resolution palaeotemperature curve through the P/Tr extinction horizon: £887

Ben Kotrc (MSc student, Bristol), Size changes in radiolarians and their effect on global silicate cycles: £894

Claire McDonald (PhD student, Leeds), Herbivory in Chilean forests: £1,000

Daniel Oakley (PhD student, Bristol), Analysis of charred angiosperm woods from the Cenomanian of the Czech Republic: implications for early angiosperm radiation: £865

Rob Raine (PhD student, Birmingham), Palaeogeography of tropical domain conodont faunas from the Cambro-Ordovician of Laurentia: £998

Leyla Seyfullah (PhD student, Birmingham), Chinese Permian seed ferns: diversity and abundance: £1,000

Bridget Wade (Research Fellow, Rutgers), Taxonomic and geochemical analysis of pristine forams from Puerto Rico: £1,000



Nominations for Council

At the AGM in December 2006, the following vacancies will occur on Council:

- President
- Vice-President
- Book Review Editor
- Publicity Officer
- Webmaster
- at least one Ordinary member

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 their interests.

All potential Council Members are asked to consider that:

“Each Council Member needs to be aware that, since the Palaeontological Association is a Registered Charity, in the eyes of the law he/she becomes a Trustee of that Charity. Under the terms of the Charities Act 1992, legal responsibility for the proper management of the Palaeontological Association lies with each Member of Council.” Responsibilities of Trustees can be obtained from <secretary@palass.org>.

The closing date for nominations is **Monday 4th October 2006**. They should be sent to the Secretary: Dr Howard A. Armstrong, Department of Earth Sciences, University of Durham, Durham DH1 3LE; e-mail: <h.a.armstrong@durham.ac.uk> or <secretary@palass.org>.

Awards and Prizes

Nominations are now being sought for the Hodson Fund and Mary Anning Award.

Hodson Fund

This award is conferred on a palaeontologist who is under the age of 35 and who has made a notable early contribution to the science. Nominated by at least two members of the Association, the application must be supported by an appropriate academic case. The closing date for nominations is **1st September 2006**. Nominations will be considered, and a decision made, at the October meeting of Council. The award will comprise a fund of £1,000, presented at the Annual Meeting.

Mary Anning Award

The award is open to all those who are not professionally employed within palaeontology but who have made an outstanding contribution to the subject. Such contributions may range from the compilation of fossil collections, and their care and conservation, to published studies in recognised



journals. Nominations should comprise a short statement (up to one page of A4) outlining the candidate's principal achievements. Members putting forward candidates should also be prepared, if requested, to write an illustrated profile in support of their nominee. The deadline for nominations is **1st September 2006**. The award comprises a cash prize plus a framed scroll, and is usually presented at the Annual meeting.

Sylvester-Bradley Award

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

Council will also consider awards in excess of £1,000, particularly for pilot projects which are likely to facilitate a future application to a national research funding body.

Electronic submission of applications, through the website, is preferred and will comprise a CV, an account of research aims and objectives (5,000 characters maximum), and a breakdown of the proposed expenditure. Each application should be accompanied by the names of a personal and a scientific referee. Successful candidates must produce a report for *Palaeontology Newsletter* and are asked to consider the Association's meetings and publications as media for conveying the research results. **Deadline: 1st November 2006.**

The Golden Trilobite

Nominations are sought for the "Golden Trilobite Award" for prestigious websites.

The award is for the best institutional and amateur websites that promote the charitable and scientific aims of the Association, the promotion of palaeontology and its allied sciences. The award will take the form of a statement of recognition that can be posted on the winning sites. Nominations are sought from the membership, and should be sent to the Secretary at <secretary@palass.org> by **1st September 2006**. The websites will be judged by Council members.



Grants in Aid

Applications for sponsorship for scientific meetings should be sent to <secretary@palass.org>. Funds typically will cover speaker expenses, attendance of students or scientists, who would normally be unable to attend meetings for financial reasons, and other expenses associated with the running of scientific meetings. Awards will be considered at a full Council meeting and will typically be up to £2,000.



Palaeontology back issues online

The Palaeontological Association is making issues of the journal *Palaeontology* from volume 1 (1957) to volume 41 (1998) available to the palaeontological community, without restriction or charge. To enter this system, click on the trilobite image on the [palass.org](http://www.palass.org) homepage, which will take you directly to the back issue portal.

Article availability: Articles from Volume 48 (2005) to Volume 1 (1957–9) will ultimately be available through this portal. At present articles from Volume 41 (1998) to volume 14 (1971) are available, and can be downloaded. Older volumes are being prepared at present, and will be added sequentially as the project is completed.

Issues from Volume 42 (1999) to the present time can be obtained through the Blackwell's Synergy website where they are free to Members of the Association and subscribing institutions, and available for purchase by non-members and non-subscribing institutions on an individual basis.

File format: All files are in Adobe Acrobat Portable Document Format (.pdf) and are compatible with Adobe Acrobat Reader version 6 or higher. Adobe Acrobat reader is available for free from Adobe at <http://www.adobe.com/>. Note that *Palaeontology* files are not guaranteed to work in older versions of Acrobat, and users are hence advised to update their software before using this service.

File size: File size varies considerably, longer papers or those with more plates or photographic text-figures are larger being larger than smaller documents without images. Typical file sizes range from 1 to 8 Mb, with the search engine informing users of file size before individual files can be downloaded. Users with low-bandwidth Internet connections, such as home users with modems, are advised that even relatively short papers may take many minutes to download; first try small documents with relatively few pages to assess download capability. Please note that the Palaeontological Association will not be making smaller files available for low bandwidth users as this has major implications for document quality. As technology improves we anticipate that the effect of file size will become less noticeable.

Status of online articles: The Palaeontological Association is providing this service to aid the dissemination of palaeontological literature in line with the Association's charitable objectives. Online versions of Volumes 1 to 41 are not intended to replace printed copies where high quality reproduction is required; they are intended as a supplement rather than a replacement for the printed versions.

File quality: All pages have been scanned from printed pages rather than direct from any digital source files; within the file, text is thus represented in raster format, and is hence not selectable or editable, and images cannot be extracted directly.

Image scale: Please note that the Association cannot guarantee that images within the online documents are produced at exactly the same magnification as in the printed version, although errors are likely to be small. It is also important for users to be aware that re-scaling images when printing (e.g. using 'fit page size' or similar options) will also change the printed scale of images. Users are advised to check the printed text of the article where precise measurements are required.



Search engine: A powerful online search engine is provided which can locate online articles from data such as volume number, year of publication, words in title or author's name. Abstracts are not currently included in the searchable dataset, and cannot be searched. Wildcards (*) are supported, as are Boolean searches for the title field using the symbols '&' for 'and', '+' for 'or'. A link to a brief tutorial on advanced search techniques is provided on the search engine page.

Citation format: Results returned from the search engine provide full citation details for articles, although a condensed format is available for searches likely to return many results. Each citation acts as a hyperlink; clicking it will open the full online version of the article. Citations for articles prior to 1999 that lack a link may represent errors in our data (*i.e.* unavailable files). Note that citations of articles published after 1998 will link to files hosted on Blackwell's Synergy website, and can be accessed freely by members of the Palaeontological Association (including institutional members) or subscribing institutions, and otherwise can be individually purchased through Synergy.

User demand: The Palaeontological Association hopes that this system will be adopted as an important resource within palaeontology and related disciplines. However, as this system is provided free, without restriction, at times it may experience high user demand and work slowly; although we intend to assess demand and adjust the system accordingly, some congestion may prove unavoidable. If you have speed problems and are confident that they are not the fault of your Internet connection, we recommend that you try again at a different time of the day when usage levels may be lower. Please report any problems with the service to the site administrator (e-mail: <webmaster@palass.org>).

Supported browsers: The search engine and portal should be fully compatible with all web-browsing software. However, Internet Explorer users may find that they need to enable file downloads to access PDF files. Under Windows XP the relevant setting can be found by opening the Control Panel, then 'Internet Options', then clicking the 'Custom Level' button in the 'Security' tab. Aggressive pop-up blocking software can also disable downloads; if problems occur, Internet Explorer users should ensure that the 'Filter Level' of the built-in pop-up blocker is not set to 'High', and users of other browsers or third-party pop-up blocking software should check equivalent settings.

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Acknowledgements: This project has been realised with the help of the Lapworth Museum of Geology at the University of Birmingham, including numerous volunteers and weekend workers scanning pages and making pdf files. Tables of contents for *Palaeontology* have been compiled in electronic form by Larry Bowlds.



Using the new Secure Payments pages

The new cart-based secure payments pages at <<https://www.palass.org/catalog/>> have now been operating since the Summer of 2005 and have been largely successful. Over 700 people have so far used them for membership payments, publication purchases, and payments for the Oxford conference last December.

The system that we are using has been adapted from existing freeware for our own particular uses by Alan Cole, a former Jurassic sedimentologist / palaeoecologist who now runs Pixelwave, a web design company (<<http://www.pixelwave.co.uk/>>). All submitted card details are broken down and posted to different sites from where they can only be retrieved and reassembled by the person with all the keys (*i.e.* me). I then process the payments manually. This is somewhat time-consuming, but it does mean that if people have particular requirements, changes of address, *etc.*, then they can tell me about them by writing a message in the Comments box. Any gripes can also be sent to me at <palass@palass.org>. Users get an immediate automatic acknowledgement that their submission has been made.

The only problem that some people are having is that they do not realise that, on the first time of use, they have to register with the system by giving it delivery and Card addresses, an e-mail address and a password. These are chosen by the user at the time of first use, and the password is used at each subsequent use. We do not know these details, and none of the information that is used for communication between the program and the user interacts with any of the information that the Pal Ass holds about members on its Membership database. Therefore, if people can't remember their registration details there is nothing we can do to jog their memories. In this case, it is best to register again as a new user.

All payments are now taken in GB pounds, so overseas users will see the GBP amount and the amount in their own currency appearing on their Card statements. The system accepts both Credit and Debit cards (some of the latter, particularly in the UK, ask for 'valid from' date and Issue Number). We are not set up to accept Amex, because they are very expensive for us. We no longer charge an additional figure to UK users to cover the costs that we incur for accepting a payment by Card.

The Credit Card company has just told us that, in the next couple of months, it will no longer be possible for us to accept 'cardholder not present' transactions from users who do not give us their CVV number (the card security code – the last three, occasionally four, numbers printed on the signature strip). Therefore we have recently modified the payment page to request this information from the user. This piece of information is deleted as soon as the payment is recorded, adding yet another piece of security to the system.

Tim Palmer



Other news

Lyell Meeting 2007

The choice of topic for the Lyell meeting 2007 falls to the Association. Members wishing to propose topics and convenors should contact the Secretary (<secretary@palass.org>) as soon as possible.

Honorary Life Memberships

The following members have been elected Honorary Life Members:

- Prof. W. G. Challoner
- Prof. A. Hallam
- Prof. Harry Whittington
- Dr Robin Cocks

Electronic submission of manuscripts

Please note that manuscripts can now be submitted for publication. Details (including “Notes for Authors”) can be found on <palass.org>.

Newsletter Reporter

Dr A. McGowan (Natural History Museum) has been co-opted to Council as Newsletter reporter.

Progressive Palaeontology: call for abstracts

22–23 June 2006

Department of Earth Sciences,
University of Cambridge

Abstracts are invited for the forthcoming *Progressive Palaeontology*, an annual conference for postgraduate students who wish to present their results at any stage of their research. Presentations on all aspects of palaeontology are welcome.

The Itinerary will include:

- One day of oral and poster presentations
- Reception at the Sedgwick Museum, Cambridge
- Dinner at Selwyn College
- Fieldtrip to the Oxford Clay of Cambridgeshire

Online registration and abstract submission are at <<http://www.palass.org/>>.

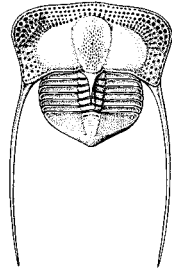
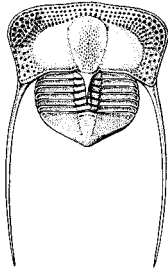
Deadline for abstract submission: 14th April 2006.

Deadline for registration: 12th May 2006.

For further information contact:

- Susannah Maidment <smai03@esc.cam.ac.uk>
- Tom Harvey <thar04@esc.cam.ac.uk>

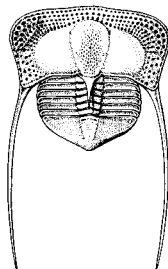
Supported by Oxford University Press and the Sedgwick Museum.



Palaeontology: **CALL FOR SHORT PAPERS!**

From January 2005 *Palaeontology* has been published in A4 size with a new layout. In line with this development, space is reserved for rapid publication of short papers on topical issues, exceptional new discoveries and major developments that have important implications for evolution, palaeoclimate, depositional environments and other matters of general interest to palaeontologists. Papers, which should not exceed six printed pages, should be submitted in the normal way, but they will be refereed rapidly and fast tracked, on acceptance, for publication in the next available issue.

Submission of longer review papers is also encouraged, and these too will be given priority for rapid publication. While *Palaeontology* maintains its reputation for scientific quality and presentation, these developments will ensure that the Impact Factor of the journal reflects its status as a leading publication in the field (rising to 1.19 in 2003).





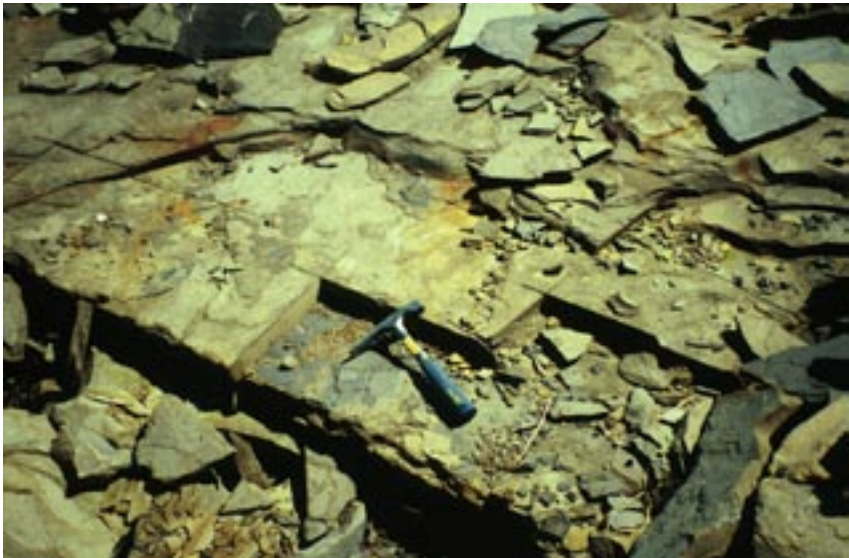
news



Announcing the preparation of the Scottish Fossil Code

Scotland has a tremendous fossil heritage that spans at least 800 million years of Earth history. Scotland's rocks have yielded the world's oldest known vertebrate, some of the earliest amphibian and reptile remains, some of the oldest known plants, the oldest known insect, the smallest dinosaur footprints and some of the earliest mammal remains. Scotland's fossil heritage has therefore had a crucial role in evolutionary studies, and it is expected that significant discoveries will continue to be made, many of these by responsible amateur collectors for whom fossil collecting is a hobby.

As a hobby, fossil collecting is quite often the route through which children and others develop an interest in Earth science and the natural environment. Amateur collecting tends to be small-scale and impinges little upon the fossil heritage. However, not all fossil collecting is benign. For many years Scotland's fossil heritage has been hacked and hammered at with impunity by folk that collect in a thoroughly irresponsible manner, for the purpose of either amassing a private collection or for commercial gain. Irresponsible collecting has seen the destruction and removal of important fossil horizons to the point that in a few SSSIs, de-notification of the geo-feature has been considered. Unscrupulous collectors, some of whom are based in mainland Europe, have caused tremendous damage, with rock saws, mechanical diggers and explosives being used to extract rare and precious



The aftermath of irresponsible collecting activity at Cruaday Quarry in Orkney. A rock saw has been used to remove fossil fish from a slab of rock that had been used for educational purposes.



A fossil foray for schoolchildren in Caithness in 2002: a media event that highlighted the need for responsible fossil collecting.

fossils. Generally the fossils end up in private collections, though a significant number are sold to museums. Although a museum destination is the ideal home for fossil material, it does not alter the fact that more often than not the fossil has been stolen and that its inexpert removal has meant that crucial contextual details have not been recorded.

Ignorance also damages the fossil interest, as exemplified by the depressing fact that most of the dinosaur bone finds on Skye have been partially destroyed by fossil or curio hunters, before rescue has occurred. One would hope that the damage to these fossils has been in error! In the Skye dinosaur case, the possibility of deliberate destruction is evidenced by one scene that took place in a quarry in the north of the country, where a collector from mainland Europe smashed to pieces the excess fossil material that he had collected because he was unable to transport it all home!

SNH has always promoted responsible fossil collection, but at the same time the organisation has struggled with the issues of irresponsible collecting and adequately protecting vulnerable palaeontological sites. The Nature Conservation (Scotland) Act 2004, which increases the protection of Scotland's natural heritage – including its rocks, fossils and landforms – is therefore a welcome addition to the statute books. It is hoped that in time we shall see the curbing of the reckless and damaging behaviour of thoroughly irresponsible fossil collectors.

In addition to the provisions that will help safeguard sites, the Act gives SNH the duty of preparing a code to be known as the 'Scottish Fossil Code', that will set out recommendations, advice and information relating to Scotland's fossils. The code will contain information on activities that are likely to damage fossil resources, the circumstances in which fossils should not be removed from land and the manner in which fossils removed from land should be kept or otherwise treated. SNH will publish the code and promote an awareness and understanding of it. The code is to



be reviewed from time to time and if the need is required, be revised. The code is therefore an additional means available in the effort to curb the damage being inflicted upon Scotland's palaeontological heritage, with encouragement for the responsible collecting and use of fossil specimens. The code also offers a wonderful opportunity for raising an awareness of Scotland's tremendous fossil heritage.

A group has recently been constituted that in consultation with others will draft and prepare the code. Known as the 'Fossil Code Working Group' (FCWG), and chaired by SAC board member Professor Nigel Trewin, the FCWG consists of a group of individuals from a variety of backgrounds each with a distinctive stake-hold in, and perspective of, Scotland's palaeontological heritage. Academics, museum curators, amateur and commercial collectors, and landowner interests are all represented. The draft code will be ready for public consultation at the start of 2006 and it is hoped that it will be launched late in 2006.

Although local codes have been produced in the past in various areas of the UK such as Dorset and the Isle of Wight, with general codes in leaflet form produced by the likes of the Geologists' Association, the Scottish Fossil Code will be the first national and fully comprehensive geological code of its type anywhere in the UK or abroad.

The Scottish Fossil Code is not only an opportunity to help consign irresponsible collecting to history, but will also promote responsible collecting and the continuation of the amateur collecting tradition, that will inevitably lead to the discovery of further spectacular fossil finds.

Colin MacFadyen

Main SNH contact in the production of the Scottish Fossil Code

For further information contact:

Dr Colin MacFadyen
Scottish Natural Heritage
2 Anderson Place
Edinburgh
EH6 5NP

Telephone: 0131 446 2055
E-mail: <colin.macfadyen@snh.gov.uk>



Scotland's first dinosaur bone find, reconstructed from fragments after being smashed (in ignorance?) by a collector.



The Micropalaeontological Society

The Micropalaeontological Society

was founded in 1970 to further the science of micropalaeontology.

We organize a number of specialist meetings through the year, on aspects of research into foraminifera, palynology, ostracods, silicofossils, nannofossils & microvertebrates.

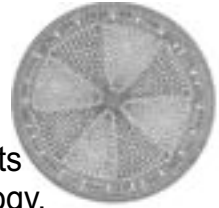
The society holds its AGM in the Autumn of each year, & this year the theme of the meeting is on '**Microfossils & climate change**' (November 15th, 2006).

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ASSOCIATION MEETINGS



50th Annual Meeting of the Association
Sheffield, UK 18 – 21 December 2006

The 50th Annual Meeting of the Palaeontological Association will be held at the University of Sheffield, under the auspices of the Department of Animal & Plant Sciences.

The meeting will begin on Monday 18th December with a special full-day symposium on “Macroevolution” (details below). This will be followed by an evening reception at the Sheffield Botanical Gardens. The technical sessions will consist of two days of talks on Tuesday 19th and Wednesday 20th December in the Auditorium located in the Students’ Union on the main campus, together with poster presentations situated adjacent to the lecture theatre. The talks and posters will be open to all aspects of palaeontology. The talks will be scheduled for 15 minutes inclusive of questions and there will not be parallel sessions. Depending on submissions for oral presentations, some talks may have to be re-scheduled as posters. On Thursday 21st December there will be a field excursion collecting Carboniferous plant fossils from a local opencast pit, and incorporating a visit to The National Coal Mining Museum for England, with a trip descending 140m underground into Caphouse Colliery, one of Britain’s oldest working mines.

Venue and travel

Information about the city can be obtained from <<http://www.sheffield.gov.uk/out—about/tourist-information>>, and about the University from <<http://www.sheffield.ac.uk/>>. Sheffield is easily reached by road and rail links from London and all other major UK cities. The most convenient airport is Manchester, with a direct rail link to Sheffield (1 hour 15 mins.). Sheffield may be reached from London airports via underground plus overland rail links that take a minimum of 3 hours 30 mins.

Accommodation

This will be at Tapton student hall of residence, which is situated 10–15 minutes’ walk (or a short bus ride) from the main university buildings. Details of how to get to the meeting venue on the main university campus and how to get to Tapton student hall of residence are available on the university website at <<http://www.sheffield.ac.uk/visitors/travel>>. There will be a range of accommodation with different facilities and prices.

Registration and Booking

Registration and booking (including abstract submission) will commence on **Monday 1st May**. Abstract submission will close on **Wednesday 13th September**. Abstracts will not be considered after this date. Registration and booking after **Wednesday 13th September** will incur an additional administration cost of £15, with the final deadline on **Friday 24th November**. Bookings will be taken on a strictly first come, first served basis.

Registration, abstract submission, booking and payment (by credit card) will be from online forms



available on the Palaeontological Association website <<http://www.palass.org/>> from Monday 1st May.

Programme:

Monday 18th December

One day symposium on “macroevolution” (details below).

Evening reception at Sheffield Botanic Gardens.

Tuesday 19th December

Scientific sessions followed by Annual Address at the Auditorium in the Students' Union of the University of Sheffield.

Annual Dinner, the Cutlers' Hall, Sheffield.

Wednesday 20th December

Scientific sessions at the Auditorium in the Students' Union of the University of Sheffield.

Presentation of awards.

Thursday 21st December

Post-conference field excursion to an open cast coal pit and the National Coal Mining Museum.

Travel grants to help student members (doctoral and earlier) to attend the Sheffield meeting in order to present a talk or poster

The Palaeontology Association runs a programme of travel grants to assist student members presenting talks and posters at the Annual Meeting. For the Sheffield meeting, grants of up to £100 (or the Euro equivalent) will be available to student presenters who are travelling from outside the UK. The amount payable is dependent on the number of applicants. Payment of these awards is given as a disbursement at the meeting, not as an advance payment. Students interested in applying for a PalAss travel grant should contact the Executive Officer, Dr Tim Palmer, by e-mail at <palass@palass.org> once the organisers have confirmed that their presentation is accepted, and before 8th December 2005.

Details of symposium

Special one-day seminar: Macroevolution (18th December 2006)

Macroevolutionary perspective

Todd Grantham (College of Charleston, USA): “*How does philosophical work on mechanism and emergence bear on the relation between micro- and macro-evolution?*”

Species and Species Interactions

Mark McPeck (Dartmouth College, USA): “*Phylogenetic patterns resulting from species interactions*”

Richard Bambach (Harvard University, USA): “*Autecology, ecospace and change in the realized ecospace through the Phanerozoic*”



Tempo and Mode

Kevin Peterson (Dartmouth College, USA): “*Tempo and the macroecological impact of early animal evolution*”

Nick Butterfield (University of Cambridge, UK): “*Mode and the macroevolutionary history of metazoans*”

Diversity

Brent Emerson (University of East Anglia, UK): “*Molecular phylogenetic approaches to understanding the origins and maintenance of community level species diversity*”

Mike Benton (University of Bristol, UK): “*How did life get to be so diverse?*”

Disparity

Mike Akam (University of Cambridge, UK): “*Is disparity just skin deep? A developmental perspective*”

Doug Erwin (Smithsonian Museum of Natural History, USA): “*Why so many gaps? Morphologic disparity in the fossil record*”

Macroevolutionary Synthesis

David Jablonski (University of Chicago, USA): “*Hierarchy and scale in macroevolution*”



From our Correspondents

Should Eagle Owls be considered native to the UK?

The role of palaeontological evidence

“What has palaeontology got to do with anything?” asked Tea Leoni’s character in ‘Deep Impact’. I’ve never seen the film (honest), but Gene Hunt used to have the quote on his office door. Many conservation bodies are rapidly shifting their efforts towards ‘evidence-based conservation’. The recent award to Dr Kate Vincent for her dedicated work on studying the decline in house sparrow populations should remind us just how much excellent research is carried out by scientists working for, or in collaboration with, various environmental non-governmental organizations (NGOs) and governmental bodies such as English Nature (soon to be Natural England). I think palaeontological data should start to contribute to the evidence base for conservation biology.

Palaeontology is often only called upon to provide a toll of extinction, and as a source of dire predictions for the Sixth Mass Extinction. The palaeontological perspective ties in well with the need of conservation biologists to think beyond the time horizon of the human lifespan into ‘deep’ time, but the two groups tend not to interact much. We do though have many challenges in common, including sampling problems, changes in the geographic distribution of organisms, and understanding the potential for competition among different taxa.

An excellent example of why conservation biology should pay attention to the fossil record is the heated debate generated by the BBC ‘Natural World’ programme on the eagle owls of Yorkshire (16th November 2005), and a follow-up article in the December issue of the BBC Wildlife Magazine. Indications from ringing studies are that eagle owls have started to breed in the area. Having experienced the reintroduction of two raptor species to Scotland, the osprey and the white-tailed (sea) Eagle, I expected the eagle owl to be welcomed, and reports of this species breeding in the UK as a conservation success. However, there has been some ambivalence towards the appearance of these large predators. They are impressive, with a six-foot wingspan, but there was concern that they might affect other birds of prey in the area, both indirectly by



An Eagle Owl in captivity at the Combe Martin Wildlife and Dinosaur Park, North Devon, England. Escapes of captive owls are thought to be the source of populations such as the one in Yorkshire. Photo taken by Adrian Pingstone in July 2004 and released to the public domain.



competing for food, and directly by predated the smaller raptors. Invasive species are a major concern to conservation biology, with invasion biology representing a specialist, and growing subdiscipline. Examples of biological invasions that have entered the wider culture would include the grey squirrel, zebra mussels, and mitten crabs. In Australia the introduction of the cane toad proved to be a major mistake, despite the worthy aim of attempted biocontrol of pests.

I don't wish to rehash the arguments that have broken out over the Yorkshire eagle owls. A web search will reveal the acrimony over both the programme, and the wider issue of what constitutes a 'native' species. The Royal Society for the Protection of Birds (RSPB) has felt compelled to issue a clarification of their position on their website. Their statement is well considered, and mentions a range of sources they have examined, including the fossil record. The crux of the eagle owl story is that the British Ornithological Union (BOU) have indicated that, based on their records, they do not regard the eagle owl as part of the native UK avifauna. They acknowledge that eagle owls have escaped and are capable of surviving in the wild in the UK, and may be establishing breeding populations. The BOU has a scheme for coding birds, and the current evidence has been ruled insufficient to include the eagle owl in categories A–C, the 'British List'. The criteria for inclusion on this list can be found at <<http://www.bou.org.uk/recbrlst.html>>.

However there is a wider point at stake in all of this, which we, as palaeontologists, should be interested in; namely the role of fossils in deciding whether a species is native. It struck me that eagle owls probably had a fossil record in the UK, and a trip three floors down to see Andy Currant led me to what I was looking for. I thank Andy for his help with this article. Mine was not the first enquiry about the eagle owl. He had already taken about ten calls from members of the public on the subject. A specimen, on loan to the Natural History Museum (NHM) from Wells Museum, has been identified by the late Wilfred Jackson as *Bubo bubo*. Other workers agree with this identification. The specimen is from post-glacial deposits, near Cheddar in Somerset. This find partly contradicts the RSPB statement, which does specifically mention breeding populations, but raises the question of how many more specimens are either already in museum collections, or preserved in cave deposits.

I consulted some palaeornithologists for further information. Dr John Stewart, a visiting scientist to the NHM with a strong interest in palaeornithology, is doing some active research on the issue. His view was that the eagle owl is missing from a similar area of NW Europe as the white-tailed (sea) eagle and osprey. Human persecution has probably played a major role in excluding the



Figure 2. Radius and ulna of an Eagle Owl from a post-glacial site near Cheddar in Somerset. The specimen is about 100mm long. Thanks to Andy Currant for help with photographing this specimen.



Eagle Owl from the most populous parts of NW Europe, although its range is expanding rapidly through Belgium and Holland. John explained this was not the first time the fossil record had been called upon to adjudicate about an issue of public concern. The spread of cormorants inland was viewed as unnatural by some people involved in stocking ponds for angling. The fossil record of cormorants in the UK shows that they ranged inland long before the stocking of flooded gravel pits for anglers.

Dr Jo Cooper, another palaeornithologist based at Tring, where much of the NHM bird collection is housed, also spoke to me about the Eagle Owl story. She had already had around half a dozen enquiries about the eagle owls. Her view concurred with that of John, and she pointed out just how large, and frankly scary, an eagle owl is to most people (see <<http://news.bbc.co.uk/1/hi/scotland/4206031.stm>> for a 'shaggy owl' story). Jo also told me that the Swedes have begun to adopt an approach to bird listing that encompasses historical records and the fossil record of extant birds.

I think that as palaeontologists we should be pushing for a 'deep time' view of these matters. Change over time, local extinction and range re-expansion are part of the palaeontological worldview, and I think the palaeontological viewpoint has something to offer in these debates. Periodically there are schemes for re-introducing large mammals such as the wolf, the beaver, and the lynx to the Scottish Highlands. These reintroductions are backed by abundant fossil evidence and historical documentation to prove that these animals are 'native'. Shouldn't the whole fauna and flora receive similar scrutiny?

A depressing postscript to this article is that a female Eagle Owl living in the area featured in the BBC documentary was later shot, and died of starvation due to losing the ability to fly. Another data point for John Stewart's persecution theory.

Al McGowan

Natural History Museum

Modularity in Palaeontology Subunit 2: Examples

In our last column (subunit 1), we outlined modularity, a concept used by evolutionary developmental biologists. The two columns were designed to spark interest amongst palaeontologists in the concept of modularity and to make us all think about our research areas from a different angle.

To recall, modules as independent yet interactive units of development and/or evolution may be structural, developmental, physiological or behavioural. New modules evolve by one of three processes – dissociation (a new function is taken on), duplication and divergence (new function taken on by the duplicate), or co-option (new modules incorporate functions from other modules) (see Subunit 1: An introduction to Modularity, *Pal Ass Newsletter* 60: 10–12 for details).



In this column we present some examples of how the concept of modularity is being used by palaeontologists, although not always recognized and cited as such. Our examples include mammalian inner ear ossicles, body patterning in trilobites, teeth, and appendages.

Ear ossicles: It has long been agreed amongst palaeontologists that elements composing the reptilian jaw joint (*viz.*, the quadrate and articular) are homologous with the incus and malleus (both first arch derivatives), respectively of the mammalian middle ear. Supporting evidence comes from various independent sources, including the fossil record, embryology and developmental genetics. The fossil record shows us a virtually complete series beginning with the reptilian lower jaw, passing through various 'intermediate' stages of non-mammalian synapsids (in which there is an increase in dominance of the dentary and a reduction in the postdentary elements) and ending with the modern mammalian condition. Developmentally, the reptilian articular bone and a large portion of the mammalian malleus can be seen to form by ossification of one end of Meckel's cartilage; the middle portion of Meckel's, the embryonic cartilage of the lower jaw, then atrophies leaving the incus and malleus (and ectotympanic) attached to the ear region of the skull. Some of these transitional stages are visible in the embryogenesis of extant marsupials. More recently, it has been argued that developmental genetics has shown that gene knock-outs can reveal ancestral patterns in the mutant phenotype (although see Smith and Schneider [1998] for an alternative interpretation). This is a classic and remarkable example of evolutionary transformation.

The middle ear ossicles lie at the junction of the first and second branchial arch, which is an evolutionarily important region. One can consider the elements of the reptilian lower jaw as entities or modules that can evolve (into ear ossicles), which undergo dissociation (assuming a new function in mammals) and which shift in space (migrating to the middle ear in mammals). Evidence that this module can also evolve independently comes from a recent description of the dentary of the oldest known monotreme, the Early Cretaceous *Teinolophos*, in which Rich *et al.* (2005) show that the mammalian middle ear evolved independently in living monotremes and therians (marsupials and placentals) at least twice. This module is under the control of master developmental genes, the Hox genes. Knocking out Hox genes in mouse embryos results in malformations of this region, specifically the duplication of elements, which are often regarded as resurrected reptilian bones. For a further discussion of the evolution of the lower jaw elements in reptiles and the middle ear ossicles in mammals, and more discussion on the molecular regulation of these elements, see Box 13.1 in Hall (2005 and references therein).

Trilobites: Nigel Hughes of the University of California published an insightful paper on body patterning in trilobites (Hughes, 2003), which exemplifies how the concept of modularity illuminates the evolution of tagmosis in arthropods. Tagmosis is the process by which an animal body is subdivided into tagma (segments), which, either individually or as groups, exhibit structural and functional distinctness and can thus be considered modules. Ten thousand species of trilobites extending over a 270 Myr history is an astonishing database for such analyses. By coupling an analysis of tagmosis in trilobites with work on Hox gene expression in modern arthropods, Nigel was able to infer how Hox genes may have been employed in trilobites. He concentrates on the trunk region, demonstrating that several derived clades of trilobites independently evolved functionally-distinct trunk tagmata, based on what Hughes calls "two-batch" trunk regionalization. He makes the case that trilobites 'took advantage of



the flexibility of segment numbers in the trunk – a flexibility that is manifest both in ontogeny and over phylogenetic lineages – that allowed evolution of independence of regions within the trunk; much as gene duplication provides the flexibility to free up a gene(s) for a new function. This is another example of modular dissociation. His approach illustrates the lack of congruence between boundaries of Hox gene expression in modern arthropods and the morphology of the same animals; and how our emphasis on segments with different morphologies (rather than numbers) and groupings of segments without boundaries that define between segment classes, has limited our ability to link body form with developmental control. As Hughes notes in concluding his paper: “Cases such as trilobite trunk evolution..., in which fossils provide the empirical record of the development of a major evolutionary innovation, demonstrate palaeontology’s unique and integral role within evolutionary developmental biology” (p. 395).

Teeth: A third example of modularity. The fundamental unit from which teeth and early vertebrate scales arose is the odontode. The basic odontode consists of three subunits – a dentine cone with internal pulp cavity, a base of laminar bone and a cap of hypermineralized tissue (*viz.*, enamel). These three modules are often considered as one fundamental unit of tooth development. However, each module can interact during developmental, and can be separated over the course of evolution. Delving into the fossil record reveals many examples of animals that do not have all three subunits of the basic odontode. For example, galeaspid scales only have two modules – the base of laminar bone and the enameloid cap; some heterostracans (psammosteid) have the basal bone and the dentine-covered cones but lack any hypermineralized tissue. As revealed by the fossil record, the three tissues in each module of the basic tooth (skeletal base, dentine, and enamel) have evolved in different ways and at different rates. These subunits can therefore be viewed as three separable evolutionary modules, a notion introduced by White (2004).

Appendages: Through time, appendages of invertebrates and vertebrates have been modified as feeding, locomotory, reproductive and sensory structures. The multiple functions didn’t necessarily evolve in any order but are commonly found within one individual. Lobsters, for example, have podia modified for feeding, reproduction, defence and locomotion. It could be argued that the appendage developmental module is the most labile module considering the astounding diversity of appendage structures and functions that arose from a similar developmental module. The evolutionary flexibility of the appendage module was apparent early on in life history; the Cambrian was replete with invertebrates exhibiting many sets of paired appendages that were used for different functions. The Burgess Shale fauna is rich with creatures with many types of appendage structures undoubtedly tailored for different functions.

The diversity of animal appendage structures is due largely to the modification of the expression of the gene package (appendage developmental module) responsible for patterning the appendages (Shubin *et al.*, 1997). These authors comment how the paired appendages of vertebrates and invertebrates cannot be considered homologous as they do not share a common ancestor with paired appendages; they also develop completely differently (limb buds *versus* imaginal discs). However, by applying the concept of modularity to appendages we are provided with a meaningful way with which to compare serially homologous structures and those that arise through convergent evolution. We can compare the evolutionary histories of appendages in diverse groups because they have a developmental module in common. Given



the astonishing diversity of appendages, it is perhaps not surprising that their evolution appears to have progressed through all three of the evolutionary processes modules can follow, namely dissociation (fins evolved into limbs with a reduction of the distal-most portion of the module), duplication and divergence (the duplication of the appendage developmental module facilitated the evolution of distinct locomotory and feeding appendages in arthropods), and co-option (some suggest that the origin of vertebrate fins is due to the co-option of the gut patterning genes into the paraxial mesoderm to form the appendage developmental module [Coates and Cohn, 1998]).

Different parts of vertebrate limbs (stylopodium, zeugopodium and autopodium) are structural modules arising from the developmental appendage module. We can discuss the evolution of the autopodium, for example, distinct from the developmental appendage module, knowing that the variability in autopodium structures in vertebrates is due to the modifications of the appendage developmental module. The compliment of genes involved in the development of the autopodal structures can also be considered a developmental module. In other words the autopodium is a structural module that has a structure determined by the appendage developmental module and the autopodium developmental module.

Vertebrate limbs are a fantastic biologic system to which the concept of modularity is applicable. Palaeontologists can use the concept of modularity in their studies of highly modified limbs that are only found in the fossil record, *e.g.*, most agnathans, plesiosaurs, ichthyosaurs, mosasaurs, *etc.* The concept of modularity provides evolutionary biologists, including palaeontologists, a construct in which to examine evolutionary process from evolutionary pattern.

We hope to have inspired you to use the concept of modularity in your studies and that modularity will be referenced more in the palaeo-literature in the near future.

Tamara A. Franz-Odenaal*, Brian K. Hall, Lisa A. Budney, and Matthew K. Vickaryous

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IN DEEP WATER

Purely professionally, one should, perhaps, be glad to be living in such interesting times. If palaeontologists had evolved long ago, in one of the less ostentatious intervals of geological time, then one could seemingly look forward to a good few million years when nothing very much happened. The sober progression of Milankovitch stripes in the Chalk cliffs or on those Mediterranean Tertiary sections, and the placid background rate of species appearances and extinctions, suggest a world so ordered and fine-tuned that tiny changes in incident sunlight patterns could truly shape the world. An ambitious palaeontologist of those times might have longed to see a little more action in the great global physico-bio-geochemical amphitheatre of the world's surface.

Well, it's now the late Holocene/Quaternary/Neogene, *aka* the early Anthropocene (select hierarchical level of chronostratigraphy to chime with chosen level of actuoenvironmental significance). Rates of change in global geochemical parameters and in terrestrial and marine biodiversity are changing so fast that one could almost write a daily diary of progress. The Heath Robinson machine of climate has been belted amidships with the monkey wrench of an extra few hundred billion tons of carbon, and, with a regulatory biosphere under new management, we wait to see which of the several thousand possible feedbacks are going to click and whirl into action.

The world outside, sleepwalking as it is into likely geo-drama, barely registers this in the normal life of the day. From time to time, it does signal it with fanfare and brass band and Greek tragic chorus rolled into one, when the headlines – briefly setting aside Rula Lenska¹, bowls of milk and feline parliamentarians² – proclaim the latest on Kyoto, or Antarctica, or the rain forest. And, of course, in the citadel of dreams, any flavour of Armageddon can be converted into pleasure and profit via an epic of the silver screen. A true aficionado will always be watching for choice examples of this quite particular genre.

So... there it was, in the sale racks of the multimedia store. A pearl to add to the list of Great Stratigraphic Cinematic Disasters. The story of the grand-daddy of all marine transgressions, the maximum flooding surface that jumped clear of the Exxon curve, the sea level event that carried on where Derek Ager's global Chalk sea had left off. It was Kevin Costner's folly, *Waterworld*: the film that broke the hearts of a thousand Hollywood accountants. I had missed it the first time round. Now, just after Christmas, the ideal turkey had come my way. Poetic. Irresistible.

I parted with a modest sum – oh, perhaps the equivalent of an air ticket to a fashionable central European capital city – and took my trophy home. Settling in the armchair with the mug of tea and thin biscuits (for prize hokum like this, one pulls out all the stops), I prepared to savour.

The environmental setting is spelt out, virtually in words of one syllable, in the introductory voiceover. It is the future. The icecaps have melted. The tattered scraps of humanity eke out an existence on makeshift rafts, upon one of which is Kevin Costner as Our Hero, a superevolved

¹ Actress and siren device for the felinization of parliamentarians within the strange, other-worldly ecosystem of British reality TV.

² No one can say, though, that contemporary science is not trying to catch the popular mood. Being generally interested in matters of technical nomenclatural revision, I was struck by the suggestion, as reported in *Nature*, that astronomy would gain popular appeal if Orion's Belt were to be re-named Chantelle's Thong.



mutant who has acquired gills but lost all sense of irony, while on another is arch-villain Dennis Hopper, complete with rolling eyeballs³, fiendish grin and an inexhaustible supply of bottles of bourbon. They are racing to reach the one remaining island on earth, the location of which is, in defiance of all principles of cartographic rigour and at one-to-eighteen-billion scale, tattooed on the back of a stray Cute But Plucky Waif, who in turn is under the protection of the Lissom Heroine. There are sundry perils and piraticalities. Our Hero undertakes a metapsychological journey from male chauvinist neptunist to caring sharing new mer-hunk under the influence of Waif and Heroine, and all ends happily in the wake of a gigantic supertanker explosion.

Given that this is arguably the first blockbuster global warming movie, the science is quite as characterful as that in *The Day after Tomorrow*. While the latter plays fast and loose with any and all of Newton's laws, this one cheerfully tramples over primary school geography. Melting icecaps to drown the whole earth, bar one remaining island? Well, the Greenland and Antarctica icecaps are big, but not that big. About 70 metres worth of sea level, all told and all melted, which will still leave quite enough land to be easily located and terrorised by the Dennis Hoppers of the future.

Even the low rolling countryside of the English Midlands won't submerge wholly, but will become a wonderfully elaborate chain of archipelagos. Mine own home will reside smugly a good ten metres above the waves; a nook then to be shaded, I trust, by a small stand of palm trees. Just down the road, the offices and labs of the British Geological Survey will nestle in picturesque fashion by the seaside. Nottingham airport, true, will have to be converted to take seaplanes, while at Trent Bridge some slight changes to the rules of cricket might need to be carefully deliberated. In sum, the terra will be lessa but still firma. No matter. One supposes that mere physical impossibility cannot be a constraint to script development when one has a cinematic McGuffin as potent as a Waif-borne tattoo to push the action along.

The take on marine ecology in *Waterworld* is just as idiosyncratic. Throughout, there is *not one fish* to be seen, even in the underwater scenes. Has the ecosystem been degraded to bacterial level? No, because the pinnacle of the food chain suddenly appears: a gigantic sea monster hoves into view, luckily just as our gallant trio are feeling peckish. Our Hero allows himself to be swallowed whole on the end of a line. He then seems to admonish the poor beast sharply (the details are a little unclear), and in the next scene our three protagonists are happily tucking into monster steaks. All the while, meteorologically, we have reached the End of Weather, being firmly stuck in idyllic mode, with blue skies, sunshine and the gentlest of breezes. There's not even the tiniest of greenhouse-hurricanes; all that atmospherically trapped energy was evidently needed to drive narrative credibility.

Well, of course, the whole shebang was pure, gloriously unreconstructed tripe, and I suppose one shouldn't expect any different. As so often, the gross domestic product of a small country was lavished on the special effects and the rather fetching sackcloth-and-leather outfits on view, leaving but small change for the scriptwriter, while the science advisors must have been led out through the back door at some early stage in the proceedings and put out of their misery.

There are, rarely, more intelligent cinematic takes on ecodisaster around. A couple of columns ago, I gave honourable mention to Miyazaki's animated fable *Princess Mononoke* in this respect.

³ Literally rolling eyeballs, as it happens.



One of our undergraduates e-mailed me a short while later – had I seen another Miyazaki film, *Nausicaa of the Valley of the Wind*? Well, no, I hadn't. So I sought it out. It's an earlier work, without quite the technical finesse or nicely shaded realpolitik shown by *Mononoke*, but in its own way it is quite as remarkable. Wearing its heart prominently on its sleeve, the film places the eponymous heroine in a ravaged, post-apocalyptic landscape, where human communities are fragmented into small enclaves, variously peaceful or warlike, amid wastelands and poisonous forests.

The forests are inhabited by monstrous, phantasmogoric arthropods, spawned out of the Burgess Shale via a Carboniferous coal swamp, that, when provoked, turn violently anti-human. So, will Nausicaa rescue the humans, Costner-style, from these over-sized creepy-crawlies? Here the story veers sharply from the standard shoot-'em-up script. A militant pacifist, Nausicaa doesn't lay waste to the fearsome crustacea. She defends them, to the death, against competing human armies. She defends them because she realises that the earth would not function without them, and because they are inherently valuable as living creatures.

The message would be familiar to James Lovelock or David Attenborough: a stable, self-regulating ecosystem needs a diversity of living things, among which many-legged horrors and ugly bugs are just as important as fluffy bunny rabbits or doe-eyed deer (or humans, for that matter). Similarly, a palaeontologist is fascinated, not repelled, by, say, the well-nigh two-metre eurypterid that left its footprints for Martin Whyte to discover a little while back in Scotland.

It's thoughtfulness fighting back. While the writ of Hollywood rules virtually worldwide, Miyazaki gives it a run for its money at the box-office in Japan, where he seems to be well-nigh revered. Not just because his symbolism is rarely banal and reaches out to some large questions, but because he's a born storyteller who manages to breathe life into his literally paper-thin creations, a little as the likes of Callas, Jurinac and Gobbi imbued even the creakiest of stock operatic characters with a reality that could seem more than human.

So where is this discussion taking us, other than up an unconscionably twisty and weed-strewn garden path? Well, while palaeontology as a science is resurgent, it is also subject to a peculiar kind of scrutiny: because, as a minor throwaway implication of the science, it suggests that the human species possesses, in the grand scheme of three billion years of evolving biology, no more inevitability or importance than, say, a duck-billed platypus or a fruitfly. And that perspective is often, from the inside of a human cranium and looking out, uncomfortable.

Hence the hot air and fur and feathers that have been flying, ever since Darwin, over our relationship to brute creatures. And from there it's but a short step to casting aspersions at the mechanism that would posit us within such an undignified relationship, even though it's the relationship of brute creatures to other brute creatures that is, in any spirit of zoological democracy, essentially the whole story. The infinitesimal twig that is us is statistically insignificant. And, given that the science of such as *Waterworld* does not instantly attract volleys of tomatoes from affronted audiences everywhere, there's obviously still some way to go as regards explaining, to a wider audience, the sheer scale and inter-relatedness and antiquity of life and environment on earth.

One could, perhaps, argue that the debate of evolution *versus* intelligent design *versus* creationism is a question of philosophy and personal preference. Following Voltaire's dictum,



the debate could be debated heatedly but harmlessly and even honourably, until the cows have either come home or have mutated into a new variety of non-returnable ruminant.

The argument, though, might run deeper than the validity or not of a particular biological mechanism. Perhaps it stretches beyond the question of whether an eye or a bacterial flagellum can evolve unaided or whether they need help that might range from a nudge or two along the cladogram right down to complete pre-fabricated assembly. The argument might encompass no less than the controls on the basic parameters at the planetary surface.

Let's take the extreme creationist line of believing that earth is ten thousand, rather than four and half billion years old. Then the world becomes simply a designer home for the human species, and not an entity that has emerged from the wreckage of the early solar system through the complicated, evolving and capricious interplay of tectonics and biosphere. If, yet, life is Intelligently Designed (time-span optional), then it might also be tempting to think that climate must also be held in place via an Intelligently Regulated Thermostat. So, safely enclosed in our purpose-built garden, we can go forth and multiply both ourselves and our industries, secure in the knowledge that a little bit more carbon dioxide is good for plants and good for us⁴, and it was all meant to be. If there is in reality any significant conflation of these themes, even if subliminal, then that surely raises the stakes in the debate.

It also renders the debate more complex, of course. Believing that you live in a purpose-built garden doesn't necessarily prevent you from doing your best to look after it, while good old humanism itself isn't bereft of a strand that regards the earth as something that we fell into the lap of and that should be vigorously exploited for our benefit. Nevertheless, looking to place the present in the truest possible past must surely be a prerequisite to steering our way through into the least worst future.

So we must simply keep on relating the history that we observe, to try to prevent it from repeating itself in its more dramatic modes. Just as the most compelling evidence for evolution – or descent with modification – lies in the fossil record, so too does that fossil record, directly and indirectly, give the fullest and most accurate record of how climate and environment have changed on earth. The twists and turns of Quaternary climate would be impossible to decipher without those foraminifera in the deep-sea muds, whose chemistry was so ably and brilliantly exploited by the late Sir Nick Shackleton. And global warming events in the earth's past – such as that Toarcian temperature hike – are recognised as phenomena through fossils (those gigatons of decaying plants, big and small, that make the shale jet-black): phenomena whose effects are also seen in the fossil record, as evolutionary radiations and extinctions.

Now, the sheer reality of this kind of evidence is obvious to any palaeontologist who has put in numberless hours at the coalface of standard biostratigraphy. In my days at the British Geological Survey, I hacked through many rock sections, alone or in the incomparable company of Steve Tunnicliff, Dennis White, Adrian Rushton *et alii*, to retrieve some few hundred thousand graptolites; probably we managed a few million between us, now stored in thousands of trays in the hangar-like store of the BGS. From those same rocks Stewart Molyneux and Hugh Barron

⁴ Something I discovered while gathering material for a lecture, upon innocently typing "CO₂ science" into Google.

⁵ Something very similar happens on typing in "global warming". It's now an org. And it says, at some length, that it itself, as it were, doesn't really exist.



extracted countless acritarchs, all smaller than the graptolites and all with longer names. Here and there, a trilobite turned up, or sundry brachiopods, or nautiloids (the latter, alas, mostly undeservedly ignored). A couple of years back Thijs Vandenbroucke came across to those same rocks and hauled out a fine collection of the chitinozoans that had skulked within them.

From such as this, I know in my bones the reality of descent with modification, of both life and environment. It's documented in yards of massive yellow-bound museum registers, kilograms of BGS Open-File Reports, précis'd in the usual journals. One could take enthusiasts and doubters alike to, say, the 60-metre Whitland road section through Caradoc strata in south Wales. There's a nice wide safe road verge, and lots of rock, albeit now a bit weathered. For lunch, there's a good pub down the road (where I recall Richard Fortey once telling the Great Welsh Air Pie story⁶).

A few hours hammering and one can show the beasts that appear and disappear. There's *clingani* and *quadrimucronatus*, floating (or swimming?) on and off the stage, and evolving somewhere, elsewhere. There's *harknessi* and *calcaratus*, and a horde of *morrisi* hitting town at 36 metres. And the star of the show, that most morphologically unassuming Alec Guinness of graptolites, the numberless shoals of *Normalograptus* sp.: so many and so variable that one joins with Peter Sheldon in spirit and hesitates to give them a name. Through more than thirty metres they get a little wider here, or narrower there, through time and rock. Then, at 39 metres (the paint mark might still be on the rock) something happens and this morpho-temporally elastic graptolite supersizes, virtually doubling in girth (in response to the appearance of fast food microplankton, one might imagine⁷). As neat a punctuation as one will see (and one day I'll publish it, honest).

This is how evolution appears in the rock; maybe not testable as such, but pretty well – and with due respect to Messrs Signor and Lipps – reproducible. And, there's Hart Fell and Dob's Linn and, for apparent gradualistic change on best behaviour, the Rheidol Gorge and those inter-morphing triangulate monograptids, superbly described by Margaret Sudbury. Beyond, there are the ammonite-haunted cliffs of Dorset and the dinosaur-trampled Isle of Wight shoreline and much, much more. It's the infinitely interrogateable evidence for the world as it was and as it worked, and it's so obvious that maybe we take it a little for granted.

But to anybody who has not done this sort of work it probably is not at all obvious, and it might seem that dinosaur bones somehow come from somewhere underground. It is just as, say, the innards of a computer are bafflingly mysterious to the 99.x% of the population who have never designed, built or assembled one of these strangely wonderful devices. The difference here is that, among the great masses of cybernetically baffled, few think that all of that hyper-quick calculation is really done by a team of tiny captive imps, fingers a blur on their microscopic abaci.

There never has been, though, any justice. Still, what to do? Well, I've sometimes wondered whether one couldn't exploit all those systematically catalogued SSSI/RIGS sites a little further, or those projects aimed at documenting classic British stratigraphic sections so that future researchers can precisely key in their data with all that had been obtained before.

This is all useful, indeed indispensable stuff for the pursuit of our science. But perhaps one could adjust the idea a little and assemble, from all that locality information, just *one* historical

⁶ It's a good story.

⁷ Though, agreed, one shouldn't.



line of earth history, a composite section going back to the beginning of metazoan life, using the best, most accessible and longest section for each time interval. Within the UK, one could start, say, from the Severn estuary, where tidal mud strata accumulate and can be traced back (using pollution layers) to the Industrial Revolution; and thence to the Holocene fen deposits, and then skipping through sundry Quaternary localities to the pre-glacial Crag sites, with their changing mixture of extant and extinct species, and from there leapfrogging further all the long way back via the Yorkshire coast and such to the Ediacaran quilt-creatures of Charnwood Forest.

There are gaps, of course, and one could suggest nice places abroad to fill them (a Mediterranean seaside holiday to the Miocene, or a jaunt to the K/T boundary at Gubbio). And there are more or less continuous and more or less condensed successions, and the problems of stratigraphic resolution bequeathed us by millions of generations of mud-eating, strata-disrupting invertebrates. It's all part of the evidence, though, warts and all, to be explained, discussed, argued over.

Why a single time line? After all, we have a staggering number of fossiliferous sections where change in fossil assemblages through time can be demonstrated. Here, it might just be that their staggering number *is* the problem, as the poor human brain is singularly susceptible to information overload, and all too ready, when faced with imminent confusion, to give up and go down to the pub. It's also quite susceptible to symbolism, and the concept of a single track of history plunging into ever stranger landscapes might help assimilate the sheer hugeness of the whole story.

For real effect, one could complement these hundreds of local segments of stratigraphy with just one single uninterrupted stratal span. At the bottom of the ocean floors – before subduction cuts off the record – one can, and the Ocean Drilling Project does, go down to two hundred million years-worth of oozes: Rachel Carson's near-eternal submarine snowfalls of plankton skeletons. Now, wouldn't it be a splendid thing to display a continuous core sliver in a single column, many hundreds of metres long, as tangible record of all of that time and of all that happened, and of the connection between the present and the deep past. As a work of art and symbol and evidence rolled into one, why, it might even rival the Angel of the North or the London Eye...

Enough! This is all getting out of hand. I rest safe in the knowledge that the idea is completely impractical, and is thrown into the pot for amusement rather than consideration, not least (and here emerges the grim truth of column-writing) as the editor's deadline looms.

Perhaps, perhaps, though, if some hypertrillionaire might be persuaded to let fall a little loose change to help the cause along? With a proper budget, one could organise the material, write the guide book. And then, of course, the whole thing would have to be done virtually, on the web. Then, naturally, as a computer game (got to catch them young). And then maybe as a film of the book. That'll need someone with pizzazz and brio, so the whole thing unfolds with a swing and a sweep and a couple of exploding supertankers, perhaps. Come back, Kevin, all is forgiven...

Jan Zalasiewicz



Cladistic characters

Any variation between individuals and taxa may be considered as characters to be used in reconstructing phylogeny. Such variation may be morphological, physiological, behavioural, ecological or molecular. For present, palaeontological purposes I will stress morphological variation as characters. Some palaeontologists, who are also cladists, additionally use stratigraphic variation of taxa as characters in order to reconstruct phylogeny: this is a more contentious issue to which I will return in another article. Stratigraphy has also been used to choose between equally parsimonious trees, as well as to root the tree, but since these are activities that we do *after* cladogram/tree construction I will leave these issues until later.

The delimitation of characters – how they are coded to be used in phylogenetic analysis – is not the sole province of cladistics: it extends into evolutionary taxonomy and phenetics (numerical taxonomy). However, the parsimony algorithms used in computer-generated cladograms do impose certain constraints on how we code variation, and how we interpret the consequences of particular ways of coding.

The main point to be made in this article is that the selection and coding of characters is *the* key stage of cladistic analysis. The way we code characters can influence the phylogenetic hypothesis. Once the data matrix of taxa against character codes is constructed, the analysis is done. That which flows from the matrix is maths (and maybe some special pleading). It is the construction of the data matrix that is the key advantage of cladistic analysis because it forces the investigator to think about how the variation is to be described; it forces the investigator to look for variation in *all* taxa, to be precise in the translation of variation to codes for analysis, and to understand the consequences of their actions. Here endeth the sermon!

The subject of characters – even as to what constitutes a character – has been discussed extensively and has generated a vast literature. In part this is because it is characters that enable us to recognise groups (taxa), so the idea of a character is intimately tied with the most fundamental concept in biology – homology.

Here are some definitions of characters:

“A character in systematics may be defined as any feature which may be used to distinguish one taxon from another.” (Mayr et al. 1953)

“A character is a feature of an organism that can be evaluated as a variable with two or more mutually exclusive and ordered states” (Pimentel & Riggins 1987)

“A character is a theory that two attributes which appear different in some way are nevertheless the same.” (Platnick 1979)

These ideas can be illustrated as in Figure 1 that illustrates the structure of a crustacean appendage.



Same but different



crustacean maxilla



amphipod maxilla

Figure 1. These two structures are deemed to be the same even though they look different. They are the 'same' because they are formed on the same serial segment of the head, formed of the same tissues etc. They are different in their shape and complexity. Therefore they can be thought to be part of the same character, but to show different states (e.g. endopodite smaller/larger than scaphopgnite etc).

So, characters concern identity or otherwise of the observation as well as the notion of homology (theory of sameness). There are two stages in this argumentation. The first is to suggest that each of the observations is somehow *the same* and each allows us to recognise a group; the second is to put that theory to the test. Some people speak of primary and secondary homology. Primary homology is the initial assessment of identity – is it the same thing? Similar topographic position, similar ontogeny and similar histological structure may be factors helping us make this decision. Phylogenetic analysis allows us to recognise secondary homology and establish characters of groups. For most people the delimitations of characters and states of characters is the domain of primary homology, and for all investigators it is the first thing that is done. Therefore we will concentrate on this.

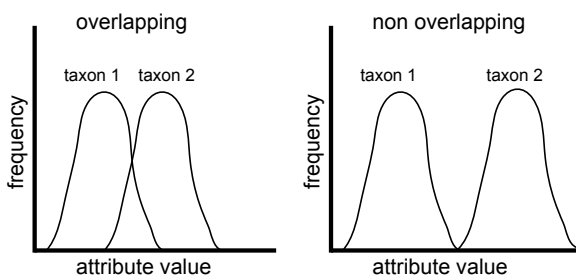
Nearly all modern cladistic analyses are computer-driven, simply because of the scale of the problem (see next article on tree building). Any morphological variation is translated to discrete integers or symbols (1, 2, 3, 4 *etc* or a, b, c, d *etc*). This differs from phenetics (numerical taxonomy) where continuous variables can be accepted in raw form (1.342, 1.784, 2.345 *etc*). Morphological variation can be described under two contrasting forms – qualitative or quantitative; discrete or continuous. You can, of course, have a character in which the states can be both discrete and quantitative.

Qualitative variation may be exemplified by 'leaves round' and 'leaves ovate', whereas a quantitative character may be 'eye comprising at least half head length *etc*'. We are naturally inclined to prefer the first kind over the second as being more clear cut. However, many so-called qualitative characters are, in fact, quantitative, and in reality we have placed some observational filter to convert quantitative into qualitative. For example, amongst those taxa deemed to have round leaves there may well be some where not all diameters of a leaf are equal (round) and may be more appropriately described a nearly ovate. In other words there may be some overlap in attribute features. Morphometric techniques may help here in being able to describe shapes mathematically, and give numerical justifications for separating round from ovate. They can also critically divide up morphological variation into a number of states. An example is given by Macleod (2002).

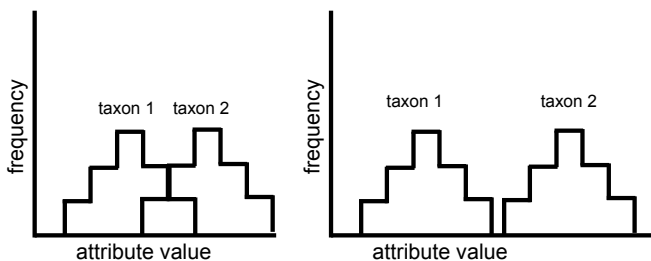
Another way in which we may describe variation in states of a character is discrete or continuous. Discrete variation is that which may be coded in single integers: presence/absence (0, 1) or two digits, four digits, five digits (0, 1, 2). There can be no logical intermediates. Continuous data is that which has infinite potential numbers. Classic examples are ratios – head length vs. head breadth (biometric data), or numbers of vertebrae (meristic data).

No matter what the kind of data is, we need to evaluate the degree of overlap in the sample that we have in order to separate it to two or more states (Figure 2). Where the individuals showing two or more values are completely separate from one another – disjunct – there is no problem. The difficulty comes when there is overlap. How much overlap are we to allow before we can no longer recognise two (or more) states?

Continuous variables



Meristic variables



Binary variables

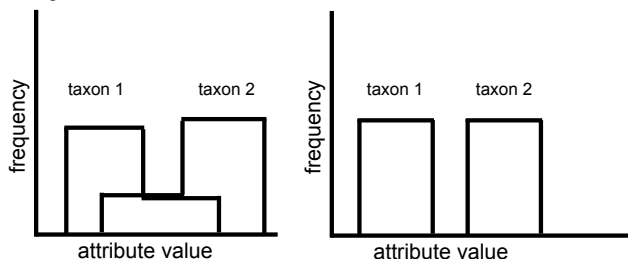


Figure 2. Morphological variation can be divided into two or more states very easily if there is no overlap (right-hand column). The difficulties occur when there is overlap (left column); some individuals of taxon 1 show feature attributes more commonly associated with individuals of taxon 2.

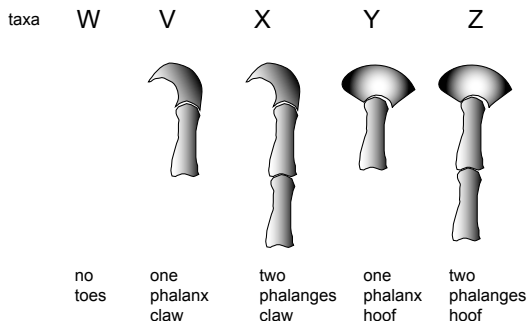


Discrete variables

These come in two basic forms, binary and multistate. Binary characters (*e.g.* absence/presence) have just two states, usually coded as '0' and '1'. They are relatively unambiguous. Multistate characters have more than two states '0', '1', '2', '3' *etc* (the PAUP* computer program allows up to 32 states).

For much of our variation there may be obvious and limited ways of coding. But for some variation there are some tantalising choices. These dilemmas usually exist where the variation is linked and conflicting. For example, let us assume that we had a group of vertebrates, some of which had fingers and some did not. Amongst those that had fingers some had one bone in a particular digit and others had two. Let us further assume that some of those with one-boned fingers had claws and some had hooves, and some of those with two-boned fingers had claws and some hooves. Here we are dealing with three variables that may all be ascribed to a single structure – the digit (either the fingers are there or not; if they are there they may be one-boned or two-boned, and they may be clawed or hoofed). I use this example because Jerry Hooker tells me this is a real situation in mammals (I've added the total absence – which could be a snake, for instance). Figure 3 shows several ways of coding this variation (there are other ways – see Forey & Kitching 2000). In all but the first method of coding (the pure multistate character) the coding results in the variation being split into more than one character. That's OK, but remember that in cladistic analysis every column of data contributes to the final hypothesis of relationship – indeed it is expected that each column of data will be independent of any other. We could argue that this is not the case in methods B and C. In the most extreme example (method C) this variation in the digit has been translated into five characters – and more importantly those taxa that do not have fingers have been scored as such five times! It also means that taxon W, that has no toes, is scored the same as taxon V, that has toes but no hooves. Method B is interesting in that those taxa that do not have fingers have been scored as question marks – meaning here “not applicable”. Question marks can be problematical as we will learn later.

Coding methods



Method A. Formula coding. Each overall condition given one code (linked states)

Character 1. absent (0), one phalanx with nail (1), two phalanges with nail (2), one phalanx with hoof (3), two phalanges with hoof (4)

Method B. Hierarchical coding. Presence/absence, Number of phalanges and terminal structures treated as three independent binary characters, additional codes for presence and absence and inapplicable code for conditions where codes are illogical (where there are no phalanges).

Character 1. Features absent (0), features present (1)

Character 2. One phalanx (0), two phalanges (1)

Character 3. nail (0), hoof (1)

Method C. Independent coding. Every attribute is given a separate character.

Character 1. Features absent (0), features present (1)

Character 2. One phalanx absent (0), one phalanx present (1)

Character 3. Two phalanges absent (0), two phalanges present (1)

Character 4. Nail absent (0), nail present (1)

Character 5. Hoof absent (0), hoof present (1)

taxa	Coding method		
	A	B	C
W	0	0 ? ?	0 0 0 0 0
V	1	1 0 0	1 1 0 1 0
X	2	1 1 0	1 0 1 1 0
Y	3	1 0 1	1 1 0 0 1
Z	4	1 1 1	1 0 1 0 1

Figure 3. Given the variation in digit structures shown amongst five taxa at top, there are several different ways of coding the variation (three methods are shown here). The method of coding can influence the outcome of phylogenetic analysis because it is assumed that each column of data provides an independent hypothesis of relationship.



Continuous variables

In order to incorporate continuous variables with discrete variables the former are usually recoded as discrete characters. This recoding usually takes the form of some gap-coding method whereby the variation is segmented where there is a gap or low frequency of overlap of observation.

Several ways have been devised for doing this and a good review of strengths and weaknesses of various methods is given by Ried & Sidwell (2002). One common way of coping with a broad range of variation in any one variable (e.g. snout length) is to use gap-weighting devised by Thiele (1993). This method uses standard gap coding but imposes a weight as well, meaning that it is going to ‘cost a lot of steps’ to go from the shortest to the longest but much less to pass between adjacent lengths – and the width of the gaps is taken into account (Figure 4).

Continuous variables are almost always coded as multistate characters.

Coding continuous variables

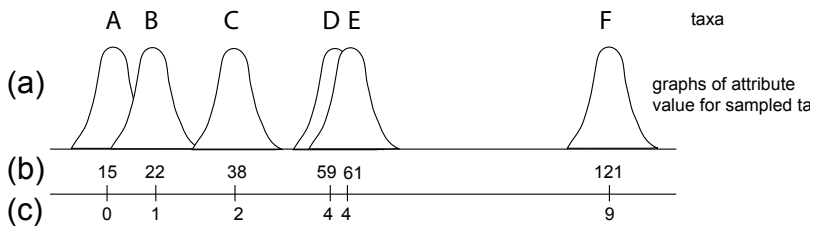


Figure 4. The gap weighted method of Thiele (1993), used to give codes that reflect not only the value of the attribute but also the distance between adjacent values. (a) frequency distribution curve for six taxa. (b) means or medians (you would normally range-standardise the data). (c) the total range is then partitioned to a set number of equal units (in this case ten) and codes given according to the position into which the taxon means fell. The character is then considered as an ordered multi-state character with states ranging from 1 to 9 (states 3, 5, 6-8 are unrepresented).

Ordered and unordered characters

Characters may be ordered or unordered in their transformation between states. This choice will only affect multistate characters. In a multistate character with three states 0, 1, 2, then to pass between state ‘0’ and state ‘2’ is going to cost two steps (0 ↔ 1, 1 ↔ 2); that is, it is incremental. And this can happen in any direction. In an unordered character, any transformation between any state costs one step. You may decide to order a character such as limb with two segments (0), three segments (1), four segments (2) if you believe that the evolutionary transformation from two segments to four segments *must* have gone through the three segment stage. Imposing order will select some trees shorter (more parsimonious) than others (Figure 5).

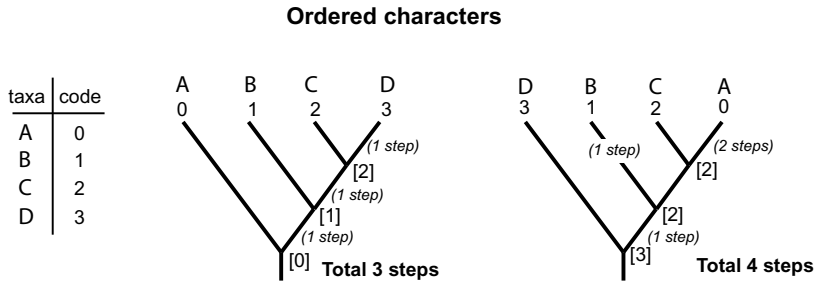


Figure 5. When using ordered characters you should be aware that some cladograms will be shorter than others and will be preferentially selected simply because of optimisation of character states. Here are two trees involving four taxa with character states of a single character given at left. The character states can be optimised on to each of these trees (two of 15 possibilities) such that the tree on the left is more parsimonious (fewer steps) (we will deal with the precise way of optimising characters in the next article). The reconstructed node states (ancestral states on trees) are in square brackets.

If the character were unordered there would be no difference because any transformation is made with equal cost in numbers of steps. Both trees would be retained as equally parsimonious.

Polarisation of characters

Here the investigator can impose a *direction* of transformation between states. In other words we can specify, *before* the analysis, which state is to be regarded as plesiomorphic and which is apomorphic. Referring back to Figure 2 in the first article then taxa are only grouped on the apomorphic state. There have been several criteria used to determine which is the plesiomorphic and which is the apomorphic state. Here are some of the common ones.

Ingroup commonality: the plesiomorphic state is that which is most common in the ingroup (the group of interest).

Stratigraphic: the plesiomorphic state is automatically that which occurs in the earlier fossil. Of course, this should be true but it depends on assessments of the quality of the fossil record *etc.*

Biogeography: the state of the character found in members occupying the presumed centre of origin are to be regarded as plesiomorphic with respect to the state found in the members most widely removed from the centre or origin. This assumes that the plesiomorphic species sits tight and more derived species are to be found more distant. The alternative – that the more derived species have literally pushed out the plesiomorphic species – is not allowed.

Ontogenetic criterion: the state of the character occurring in earlier growth stages is to be regarded as the plesiomorphic condition. This is often justified in terms of Haeckel’s law of recapitulation but is actually more closely aligned with Von Baer’s law that general characters appear before the special characters (*e.g.* the egg appears before the neural tube).

Outgroup criterion: that character state which occurs in the outgroup taxon is to be regarded as the plesiomorphic condition.

In modern cladistic analyses it is usually only the last that is used to polarise characters, and this is effectively done automatically. If you wish to impose polarity using the other criteria then you



would make a hypothetical ancestor that incorporated all the plesiomorphic states and use that as the outgroup (root).

Therefore there are at least two ways (order and polarity) in which we may constrain the behaviour of a character with three or more states (Figure 6). Constraining the possibilities may reduce the number of equally parsimonious trees, but remember that this action requires independent justification. The most obvious situation in which there may be justification is where different ontogenetic stages are linked into a multistate character. The order is given by the ontogenetic trajectory and the polarisation is given by the earliest ontogenetic stage.

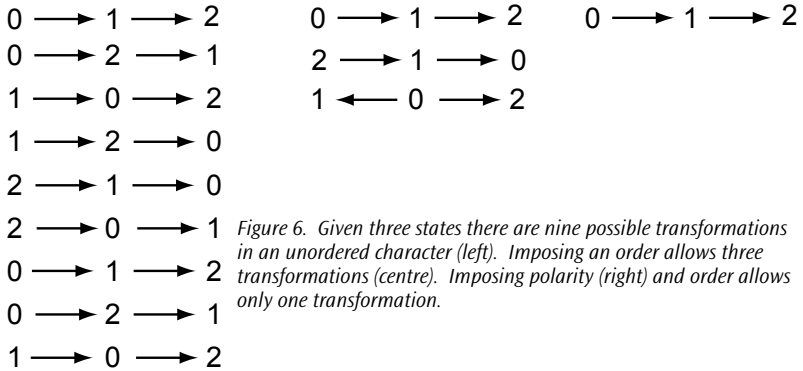


Figure 6. Given three states there are nine possible transformations in an unordered character (left). Imposing an order allows three transformations (centre). Imposing polarity (right) and order allows only one transformation.

Data input

Once you have decided what variation is to be coded for, whether to use multistate or binary, in what way the variation is to be divided into characters and character states, then we need to get the information into the PAUP* program. PAUP accepts Nexus files. You can write such a file in a word processor and save it as a text file. You can open up the PAUP program and write a new file directly. The PAUP manual gives you the precise syntax.

By far the easiest way is to use a separate program. If you are Mac-based then the MacClade program is the one to use. For PC users then Nexus Data Editor is the one for you (see Nerd Notes at the end for details). Both of these programs open up a spreadsheet in which you enter taxa names and character numbers and the relevant character codes. Normally these codes will be 0, 1, 2, 3 etc. You will need a code for missing data (usually '?'). You can also enter polymorphic codes. For example if a particular taxon had components (individuals, species) some of which showed the '0' state and some showed the '1' state, this could be entered as such. Personally I would shy away from this because the output is difficult to interpret. You can also enter codes for 'not applicable' (usually 'N' is used). This is useful in the data matrix stage which will be published and conveys to the reader the precise nature of the ambiguity, but computationally these are simply translated to question marks in the tree-building phase.

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- WILLIAMS, D. M. (2004). Homologues and homology, phenetics and cladistics: 150 years of progress. In WILLIAMS, D. M. and FOREY, P. L. (eds). *Milestones in Systematics. The Systematics Association Special Volume Series 67*. pp 191–224. Boca Raton, CRC Press. [An excellent article on the history of views on homology and how it impinges on modern systematics.]
- WILLS, M. A. Morphological disparity: a primer. In ADRAIN, J. M., EDGECOMBE, G. D. and LIEBERMAN, B. S. (eds). *Fossils, Phylogeny, and Form – an analytical approach*. Pp. 55–144. New York: Kluwer Academic. [Although this chapter is about morphological disparity it does contain some clearly written discussion on discrete and continuous characters and it is packed with references for further reading.]

Nerd Notes

Here are a few details on commonly used computer programs.

Nexus Data Editor (NDE), written by Rod Page, is a spreadsheet data editor that interacts with the Windows PC version of PAUP*. It is virtually self explanatory. It allows you to annotate your data with text and pictures. It is free to download.

Web address: <<http://taxonomy.zoology.gla.ac.uk/rod/NDE/nde.htm>>

MacClade 4 is a data editor as well as a tree manipulator. It was written by Wayne and David Maddison. It interacts with the Mac version of PAUP*. It allows you to enter data into a matrix and provides a limited capability for annotating the characters. It is far more powerful than NDE because it also has capabilities for manipulating trees and character optimisation, and to output



trees graphically. It comes with a manual. It must be purchased (\$125 when I last looked). It is distributed by Sinauer Associates: <<http://www.sinauer.com/>>.

PAUP 4.0 Beta*, written by David Swofford, is the key parsimony program to construct trees and get data output (although it does other things that molecular systematists like to play around with). It is only available in beta version – no idea when it will be finished. You buy a program and an updater (supplied on the same CD, both of which have to be loaded). It comes in three versions. One is for the PC (Windows or DOS). This is command line driven, which sounds a bit cumbersome but is quite easy to get used to. The Mac version requires either Mac OS 9 or OS X with Classic installed, and is either command line driven or by means of pull down menus. The last version is the Linux version but I know of no one who uses this. It must be purchased (Windows version \$85, Mac version \$100 when I last looked). It is distributed by Sinauer Associates: <<http://www.sinauer.com/>>.

PAUP* does not come with a manual but one can be downloaded from the PAUP website at <<http://paup.csit.fsu.edu/>>.

PAST (PAleontological STatistics) by Øyvind Hammer, of the Paleontological Museum of the University of Oslo. This may already be familiar to many of you. It does a variety of things, one of which is parsimony analysis. I have tried it and find it OK for small, clean data sets but some of the heuristic addition sequence options found in PAUP* do not appear to be there, and there is a danger of missing alternative and more parsimonious trees. It can be downloaded free with manuals from <<http://folk.uio.no/ohammer/past/index.html>>.

If you want more information on a variety of phylogenetic programs and associated tree manipulators then try this site, which has details of 101 programs: <<http://evolution.genetics.washington.edu/phylip/software.html>>.

PalaeoMath 101

Minding Your Rs and Qs

All the methods we've been discussing to this point in the *PalaeoMath 101* essays have exhibited an underlying similarity. No, it's not only the fact that all have made extensive use of the four canonical arithmetic operators (+, -, x, /). Rather, our discussions of bivariate regression, multiple regression, principal component analysis (PCA), and factor analysis (FA) are united by the fact that each technique has focused its mathematical sights on relations between variables, the sets of observations or measurements we make on specimens, at localities, *etc.* In particular, all these methods have operated on values, or matrices of values, of the covariance or correlation coefficients.

Recall the definitions of these quantities. The variance (first discussed in the Regression 2 column, *Newsletter 56*) is the sum of the squared deviations of the measurements from their mean, divided by one less than the number of measurements in the sample. The covariance (*Newsletter 56*) is the joint variation of two variables around their common mean, and the



correlation coefficient (*Newsletter 58*) is the ratio of two variables' covariance to the product of their standard deviations. All these quantities can be used to make statements about the character of the distribution of measurements in populations, provided the samples used in the calculation of these quantities provide accurate representations of the underlying population of possible measurements. Thus, the structure of variance–covariance relations among the three variables of our trilobite dataset ...

Table 1. Trilobite data

Genus	Body	Glabella	Glabella
	Length (mm)	Length (mm)	Width (mm)
<i>Acaste</i>	23.14	3.50	3.77
<i>Balizoma</i>	14.32	3.97	4.08
<i>Calymene</i>	51.69	10.91	10.72
<i>Ceraurus</i>	21.15	4.90	4.69
<i>Cheirus</i>	31.74	9.33	12.11
<i>Cybantyx</i>	36.81	11.35	10.10
<i>Cybeloides</i>	25.13	6.39	6.81
<i>Dalmanites</i>	32.93	8.46	6.08
<i>Deiphon</i>	21.81	6.92	9.01
<i>Ormathops</i>	13.88	5.03	4.34
<i>Phacopidina</i>	21.43	7.03	6.79
<i>Phacops</i>	27.23	5.30	8.19
<i>Placopania</i>	38.15	9.40	8.71
<i>Pricyclopyge</i>	40.11	14.98	12.98
<i>Ptychoparia</i>	62.17	12.25	8.71
<i>Rhenops</i>	55.94	19.00	13.10
<i>Sphaerexochus</i>	23.31	3.84	4.60
<i>Toxochasmops</i>	46.12	8.15	11.42
<i>Trimerus</i>	89.43	23.18	21.52
<i>Zacanthoides</i>	47.89	13.56	11.78
<i>Minimum</i>	13.88	3.50	3.77
<i>Maximum</i>	89.43	23.18	21.52
<i>Range</i>	75.55	19.68	17.75
<i>Mean</i>	36.22	9.37	8.98
<i>Variance</i>	346.89	27.33	18.27

... can be represented by the covariance and/or the correlation matrices of those measurements, as shown in Table 2 overleaf ...

**Table 2. Relations between trilobite variables**

	Covariance			Correlation		
	Body Length	Glabella Length	Glabella Width	Body Length	Glabella Length	Glabella Width
Body Length	329.892	87.191	68.416	1.000	0.895	0.859
Glabella Length	87.191	27.333	20.315	0.895	1.000	0.909
Glabella Width	68.416	20.315	18.266	0.859	0.909	1.000

... and the structure of these relations—including representations of between-specimen relations—can be summarized numerically and even portrayed graphically in the form of scatterplots along either variable or composite variable axes.

There is another way of looking at the problem of summarizing structural relations within this dataset, however. Suppose we're not really interested in the structure of the variables' relations with one another, but instead wanted to know about the structure of similarity relations between individual trilobite specimens. Of course, this is not an idle consideration. In many instances relations among objects—or populations that can be represented by a specimen or locality—are precisely what we do want to know about. From our previous discussions you will recall that placement of the PCA and FA axes we used to portray inter-specimen relations was determined entirely on the basis of the structure of the covariance or correlation matrices. The tables of eigenvalues we generated as part of those operations tell us what proportion of the observed variance is being represented along the various PCA and FA axes. That's all more-or-less straightforward. But how 'good' were those pictures of inter-specimen similarities and differences that were presented on those plots of specimen points projected onto the PCA and FA axes? Those PCA and FA axes reproduce the structure of the covariance or correlation matrices. They do not sense, much less optimize, inter-specimen relations *per se*. Should we always believe the picture they paint of inter-specimen relations? How can we determine whether the analysis introduced sufficient distortion to bias any interpretation we may wish to make? Are we always restricted to using the covariance or correlation matrix as a proxy for measuring inter-object similarity?

Interestingly, a realization of what PCA and FA actually do implies that there exists a 'parallel universe' of methods, similar in form to PCA and FA, but different in that their focus would be directed to summarizing inter-specimen relations. Such a parallel universe does indeed exist within numerical data analysis, and with it tantalizing questions about the particular strengths of the methods that populate that universe and the character of the mathematical interface between those two universes. It is this alternative universe of specimen-based (as opposed to variable-based) methods we'll explore in the next few essays.

As with all things scientific, this new universe must be given a name. When we are basing a multivariate procedure on the structure of relations among variables, data analysts say they are working in the *R*-mode. Up to now we have been concerned exclusively with *R*-mode data-analysis techniques. With this essay I'll introduce some of the methods data analysts use to undertake investigations based on the structure of relations among specimens or localities. This



is work undertaken in the 'Q-mode'. Where did these terms come from? They are mathematical symbols for the two different types of structure matrices. The 'R' in *R*-mode refers to the **R** that linear algebraists use to represent the correlation matrix in equations. At least this makes some sense insofar as r_{ij} is the standard symbol for the correlation between variables i and j . Why 'Q' for the matrix of relations among objects (across variables)? As it turns out, **Q** is the symbol mathematicians use to represent a distance or association matrix. Most *R*-mode techniques have *Q*-mode counterparts, though in this essay we'll see that sometimes this apparent correspondence is more a matter of rhetoric than reality. In any event, I'll focus on the *Q*-mode counterparts to PCA and FA in this essay. Once we're comfortable with these we'll go on to consider even more interesting techniques that provide properly trained investigators with the power to perform *R*-mode and *Q*-mode analyses simultaneously.

The first thing—some would say the main thing—to understand about *Q*-mode analyses is that there are a far larger selection of similarity indices available for assessing the structure of relations between objects than for assessing the structure of relations between variables. Literally hundreds of *Q*-mode similarity indices have been proposed. Discussing in detail even those one sees referred to repeatedly would be an essay in itself, and reviewing the entire literature would require a particularly tedious book. In this essay we'll focus on just three of these *Q*-mode indices to give a flavour of the available range.

Before we do that, though, it might be good to consider the question "Why not just regard the specimens as variables, the variables as specimens—in other words, transpose the data matrix—and use the normal covariance or correlation coefficients as the basis for a normal PCA or FA analysis?" After all, those methods are well established, the characteristics of these indices well understood, and, so long as one is willing to make the concept transpositions mentioned above, the calculations are possible. What's the problem with calculating the covariance between objects?

Most authors of data analysis textbooks either don't consider this question at all or tend to dismiss it with cryptic comments like "The reasoning behind such a measure is at best obscure." (Davis 2002, p. 540). The actual reasons are simple to understand but may not be as obvious to neophytes as some experienced practitioners might believe. The covariance coefficient is derived from the variance coefficient which is itself a statement about the character of a group of observations. The sample variance of glabellar length is a proxy summary of all observations of this quantity that could have been made available to the observer. In calculating the variance one presumes the units of measurement are the same (or have been made the same) for each observation. One could calculate the 'variance' of such a set of observations, some of which had been made in centimetres, some in millimetres, some in inches, and some in feet. The result, though, would indicate more about differences in the units of measure within the dataset than about any biological reality. While it is relatively easy to control for this obvious source of inconsistency within the context of a single variable, it is much more difficult, sometimes impossible, to undertake such standardizations for a group of intrinsically different variables. In such instances it is necessary to select an index that takes differences between variables into consideration in known and logical ways. Another reason why a special class of *Q*-mode similarity indices are necessary is that a single set of observations from a population can be expected to be drawn from a frequency distribution of known, or at least ascertainable, shape. The variance



index of a sample can be related directly to the shape of a distribution of observations in the sample's parent population (see the Regression 3 essay, *Newsletter 59*). A 'variance' calculated from a mixture of samples from different distributions, often without scale or unit in common, will obey Chebychev's theorem, but not its corollary for more normal samples. The final reason is the simple, practical expedient that in some cases one may want to use a similarity index that differentially weights some aspect of the data known *a priori* to be relevant to the problem at hand. For all these reasons, the blind use of covariance or correlation indices as the structural basis for a *Q*-mode analysis is ill-advised. Unfortunately, both public-domain and commercially available data analysis packages cannot prevent the use of inappropriate similarity indices. Since the responsibility for selecting the correct method always lies with the data analyst, practitioners (and reviewers of practitioners' work) should always state the nature of the basis matrix and the reasons they chose the similarity index used to determine that matrix.

So, what are some of the more typical *Q*-mode similarity indices, and when should they be used? Perhaps the most straightforward *Q*-mode index is the squared Euclidean Distance.

$$d_{ij} = \sum_{k=1}^p (x_{ik} - x_{jk})^2 \quad (7.1)$$

In this equation *i* represents the *i*th specimen, *j* represents the *j*th specimen, and *p* represents the total number of variables measured on each specimen. Geometrically, this quantity represents the simple straight-line distance between two specimens in multivariate space. Using equation 7.1 to assess the structure of distances between the first three taxa listed in Table 1 yields the following matrix.

Table 3. Squared Euclidian Distance Matrix (3 Taxa)

	Acaste	Balizoma	Calymene
Acaste	0.000	78.109	918.313
Balizoma	78.109	0.000	1488.770
Calymene	918.313	1488.770	0.000

Note the difference in the structure of this matrix from those we've dealt with previously. The trace of the matrix is filled with zeros because the distance of any object from itself is 0.0. Large distance coefficients (*e.g.*, the distance between *Balizoma* and *Calymene*) indicate specimens that are very different from one another, while smaller coefficients (*e.g.*, the distance between *Acaste* and *Balizoma*) indicate specimens that are comparatively similar, at least in terms of the measurements taken or observations made. This is very different from the covariance and correlation matrices where large values meant high degrees of similarity and small values meant substantial difference. Distance matrices are often referred to as 'dissimilarity' matrices because the magnitudes of the values express relative degrees of difference rather than similarity. This distinction having been made, distance matrices, like similarity matrices, are all symmetrical about their trace.

The squared Euclidean Distance is perhaps the most commonly used *Q*-mode distance index, and is used primarily for data composed of continuous variables of the same type (*e.g.*, distances



between landmarks) and measured in the same units (e.g., mm). Still, many data matrices one might want to analyze are composed of different types of variables, often measured in different and incompatible units. In *R*-mode analyses we handle this situation by using the correlation coefficient because this index standardizes the data for differences in magnitude (and hence the variance) of the measurements. Standardization is often desirable in *Q*-mode analyses, but the mathematical operations are more complex and can be applied at different points in the analysis.

At the level of the similarity index, if we want to stick with a distance-based similarity measure we need to apply a scaling correction to the different variables during calculation of the component differences between all pairs of specimens. The most popular of the scale-corrected distance indices is the Gower Coefficient.

$$S_{ij} = \frac{\sum_{k=1}^p 1 - |x_{ik} - x_{jk}| / R_k}{p} \tag{7.2}$$

In this expression R_k represents the range of the k^{th} variable. The Gower index is based on a distance index ($|x_{ik} - x_{jk}| / R_k$) but subtracting this distance from 1.0 forces its range to fall within an interval from 0.0 to 1.0 with 1.0 representing perfect identity. *Q*-mode matrices in which the trace is occupied by 1s are called association matrices. Although the Gower matrix may look like a correlation matrix, the calculations are very different and, unlike the correlation coefficient, there is no mirroring of the index across the scale origin to represent inverse similarity (though the Gower Coefficient can be adjusted easily to incorporate this feature). Table 3 illustrates values of the Gower matrix for the first three taxa in Table 1.

Table 4. Gower Coefficient Matrix (3 Taxa)¹

	Acaste	Balizoma	Calymene
Acaste	1.000	0.947	0.618
Balizoma	0.947	1.000	0.593
Calymene	0.618	0.593	1.000

An interesting and useful feature of the Gower index is that it can be used not only with incompatible continuous variables (say, distances and volumes), but with sets of variables of any type (e.g., continuous measured variables, ratios, integer counts, nominal variables) with the only constraint being that all variables must be represented in numerical form. Of course, the manner of coding and relevance of all variables always needs to be justified, and inter-variable differences always need to be kept in mind when interpreting a Gower matrix or summaries of its structure (see below). Nevertheless, the ability to include diverse sets of variables in the same analysis should the need arise is a powerful and attractive feature of Gower matrix-based *Q*-mode analyses.

¹ These values were calculated using the variable ranges for the entire trilobite dataset (see Table 1). See the PalaeoMath 101 Spreadsheet, PCoord Worksheet for full details.



Although the Gower index approaches the concept of the *R*-mode correlation coefficient in terms of imposing limits on the index's range, it retains a degree of sensitivity to the magnitude of the observations. For example, analyses of a set of fossils that were very similar in shape, but differed in size, would produce a Gower matrix that was structured according to those size differences. A different *Q*-mode similarity index is needed if we are to eliminate differences in the magnitude of constituent variables from consideration entirely. The most popular index that performs this task, called the Cosine θ or 'Cosine theta' index, employs a geometric concept identical to that of the correlation coefficient.

The Cosine θ index is calculated as follows.

$$\cos\theta_{ij} = \frac{\sum_{k=1}^p x_{ik} \cdot x_{jk}}{\sqrt{\sum_{k=1}^p x_{ik}^2 \sum_{k=1}^p x_{jk}^2}} \quad (7.3)$$

The Cosine θ index equation is actually a generalized expression for determining the angle between two vectors in multivariate space. As such, it focuses its assessment of similarity entirely on the directionality of the vectors and ignores differences in their length. It is also numerically equivalent to the Pearson product-moment correlation coefficient if there are only two variables and if the data are mean-centred and standardized against the standard deviation.

The effects of this partitioning of the similarity into magnitude-related and non-magnitude-related parts can be striking. Table 4 illustrates values of the Cosine θ index for the first three taxa in Table 1.

Table 5. Cosine θ Matrix (3 Taxa)

	Acaste	Balizoma	Calymene
Acaste	1.000	0.987	0.998
Balizoma	0.987	1.000	0.996
Calymene	0.998	0.996	1.000

First, note that the Cosine θ index, like the Gower index, does not express dissimilarity (as all distance indices do), but true similarity with values close to the upper limit of the index (1.0) representing data patterns that are almost identical to one another. The trace of the matrix is filled with 1s, denoting the perfect identity of any specimen with itself. The Cosine θ index also allows inverse similarity to be represented insofar as its natural bounding interval stretches from -1.0 to +1.0. Perhaps even more surprising, though, is the manner in which the Cosine θ index has represented similarity relations in our trilobite data. In both the Euclidean and the Gower matrices (Tables 2 and 3, respectively) the most similar specimens were identified as *Acaste* and *Balizoma* while the least similar identified as *Balizoma* and *Calymene*. The Cosine θ matrix shows similarity relations among these taxa to be reversed. Why is this? Inspection of Table 1 reveals the answer. The absolute magnitude of the three measurements for *Calymene* is more than twice



the magnitudes of the corresponding measurements for *Acaste* and *Balizoma*. Thus, if the scale of the measurements is considered important, *Acaste* and *Balizoma* are more similar to each other than either is to *Calymene*. But if scaling differences are deemed to be nuisance factors and differences in the magnitude of the measurements eliminated from consideration, *Acaste* is more similar to *Calymene* than to *Balizoma*. This reversal of fortunes, so to speak, illustrates the power that comes from being able to 'fine-tune' the representation of similarity that is characteristic of *Q*-mode analysis. It also shows how important it is to get the similarity index right in designing a *Q*-mode data analysis. Alternatively, if one simply wants to probe the role of scaling factors in controlling patterns of overall similarity, a Cosine θ approach, in conjunction with a distance-based approach, would be indicated.

Once you've decided which *Q*-mode similarity index is appropriate for your data, the steps necessary to summarize the structure of this matrix, achieve dimensionality reduction, and produce images of the dominant similarity relations, should begin to look familiar. Say, for example, you wanted to perform an analysis that focused on reproducing the matrix of similarities among specimens, portray that structure in a space of reduced dimensionality, and ensure the variables comprising that space were uncorrelated with one another. This would imply use of the *Q*-mode analogue to principal components analysis (PCA), which is termed Principal Coordinates Analysis (PCoord). Since all the trilobite measurements are distances I'll choose to preserve scaling distinctions among taxa by basing my analysis on the squared Euclidean Distance matrix.

One disadvantage of *Q*-mode analyses is that, because one usually collects data from more specimens than variables, specimen-based similarity matrices are larger than variable-based matrices and thus entail more computations. This was a much more serious problem in the past, when computer memories were far smaller than they are today, but one still sees allusions to the 'inefficiency' of *Q*-mode methods in published discussions. One limitation that is still with us, however, is the space required to show various data matrices. Accordingly, please see the *PalaeoMath 101* Spreadsheet: Rs & Qs Worksheet (downloadable from the *PalaeoMath 101 Web Site*) for a full listing of the squared Euclidean Distance matrix for all 20 trilobite species.

Once the squared Euclidean Distance matrix for the dataset has been obtained it is usually standardized according to the following equation.

$$a_{ij} = \frac{\bar{d}_i + \bar{d}_j - \bar{\bar{d}} - d_{ij}}{2} \quad (7.4)$$

This ensures the origin of the resulting PCoord axis system will coincide with the centroid of the data's point cloud in multidimensional space, and 'closes' the similarity matrix by forcing the values of all rows and columns to sum to 0.0. The transformed similarity matrix is then decomposed using eigenanalysis in a manner identical to that used for PCA.

The eigenvalues obtained from the trilobite dataset using this method are listed overleaf.

**Table 6. Eigenvalues obtained from the scaled EDM for the trilobite data**

Principal Coord.	Eigenvalue	Percent	Cum. Percent
1	7,278.440	97.601	97.601
2	141.677	1.900	99.501
3	37.217	0.499	100.000

There are several things to note about this matrix. First, although the Euclidian Distance matrix has a dimensionality of 20 rows and 20 columns, there are only three positive eigenvalues. These mirror the three eigenvalues obtained from the *R*-mode covariance matrix for these data (see *PalaeoMath 101, Principal Components Analysis (Eigenanalysis & Regression 5)*, Table 5, *Newsletter 59*). The smaller-than-expected number of positive eigenvalues is due to the fact that, despite the number of taxa included in the dataset, only three measurements were taken. It is generally the case that the eigenanalytic decomposition of a *Q*-mode distance or association matrix will yield only as many positive eigenvalues as variables actually measured.² Second, the magnitude of the eigenvalues themselves are much larger than the corresponding eigenvalues for the *R*-mode PCA analysis of these data. This also reflects the difference in the nature of the similarity matrices subjected to eigenanalysis. In the case of the *R*-mode analysis of these data the covariance values ranged from 18.27 to 346.89, whereas the corresponding figures for the standardized distance matrix are -1,306.79 and 3,179.42. Third, despite these clear and easily appreciated differences, the percent contribution of each principal coordinate to characterizing the squared Euclidean Distance matrix is precisely the same as the percent contribution of each principal component to the characterization of the covariance matrix for these data. This identity conforms to Gower's (1966) proof that a PCoord of a *Q*-mode squared Euclidean Distance matrix is an exact mirror, or 'dual', of the covariance-based PCA for the same data. In passing, it is also worth mentioning that by moving to an analysis of relations between specimens as opposed to variables we are no longer using eigenanalysis to summarize variance, but multivariate distance. In a sense this is simply a rhetorical distinction. The calculations used for summarizing the contribution of each principal component-coordinate to the basis matrix are identical in PCA and PCoord. Nevertheless, the nature of the similarity matrix always needs to be kept in mind.

Since there are only three positive eigenvalues that can be extracted from the matrix of squared Euclidean distances between trilobite taxa, we only need to consider the eigenvectors that correspond to these positive eigenvalues.

² Usually application of Equation 7.4 reduces the number of positive eigenvalues to one less than the number of variables measured. That hasn't happened in this analysis due to the small number of variables measured, coupled with rounding error. Note the relative contribution of the third principal coordinate is very small.

**Table 7. Eigenvectors obtained from the scaled EDM for the trilobite data**

Genus	PCoord-1	PCoord-2	PCoord-3
<i>Acaste</i>	0.17	-0.29	-0.03
<i>Balizoma</i>	0.27	-0.01	-0.08
<i>Calymene</i>	-0.18	-0.22	0.10
<i>Ceraurus</i>	0.19	-0.10	-0.08
<i>Cheirurus</i>	0.04	0.28	0.37
<i>Cybantyx</i>	-0.01	0.16	-0.08
<i>Cybeloides</i>	0.14	0.00	0.02
<i>Dalmanites</i>	0.05	-0.12	-0.26
<i>Deiphon</i>	0.17	0.23	0.22
<i>Ormathops</i>	0.27	0.07	-0.17
<i>Phacopidina</i>	0.18	0.13	-0.06
<i>Phacops</i>	0.11	-0.05	0.32
<i>Placopania</i>	-0.02	-0.06	-0.03
<i>Pricyclopyge</i>	-0.07	0.45	-0.12
<i>Ptychoparia</i>	-0.30	-0.52	-0.25
<i>Rhenops</i>	-0.26	0.28	-0.48
<i>Sphaerexochus</i>	0.17	-0.23	0.03
<i>Toxochasmops</i>	-0.11	-0.20	0.47
<i>Trimerus</i>	-0.66	0.11	0.20
<i>Zacanthoides</i>	-0.15	0.09	-0.08

Unlike PCA, in which the eigenvector values can be interpreted in terms of the geometry of the data, the eigenvectors of a PCoord analysis are simply scaling coefficients, useful only for representing the structure of the distance relations among taxa on the mutually orthogonal eigenvectors. This difference is underscored by the manner in which the PCoord scores are determined. Instead of using the eigenvector loadings to project the original data into the space defined by the new principal component axes (as is the case in PCA), the PCoord scores are determined simply by scaling the raw eigenvectors by the square root of the corresponding eigenvalues.

**Table 8. PCoord scores obtained from the scaled EDM for the Trilobite data**

Genus	PCoord-1	PCoord-2	PCoord-3
<i>Acaste</i>	1Table 2. Relations	-3.41	-0.21
<i>Balizoma</i>	23.07	-0.15	-0.97
<i>Calymene</i>	-15.42	-2.59	0.61
<i>Ceraurus</i>	16.24	-1.22	-0.52
<i>Cheirurus</i>	3.67	3.37	2.25
<i>Cybantyx</i>	-1.26	1.92	-0.48
<i>Cybeloides</i>	11.68	-0.05	0.15
<i>Dalmanites</i>	0.00	-1.48	-1.61
<i>Deiphon</i>	14.29	2.77	1.34
<i>Ormathops</i>	23.18	0.89	-1.03
<i>Phacopidina</i>	15.05	1.53	-0.38
<i>Phacops</i>	9.69	-0.57	1.95
<i>Placopania</i>	-1.79	-0.75	-0.17
<i>Pricyclopyge</i>	-5.84	5.30	-0.71
<i>Ptychoparia</i>	-25.32	-6.19	-1.54
<i>Rhenops</i>	-21.89	3.29	-2.96
<i>Sphaerexochus</i>	14.46	-2.69	0.18
<i>Toxochasmops</i>	-9.58	-2.35	2.86
<i>Trimerus</i>	-56.36	1.27	1.23
<i>Zacanthoides</i>	-12.65	1.12	-0.47

In other words, while PCA uses its eigenvectors as a means to calculate its representation of the relations between objects or specimens, in PCoord analysis the eigenvectors are the representation of those relations. The rescaling operation is only needed because most eigenanalysis algorithms artificially adjust the lengths of the eigenvectors to a unit value. In a sense, this calculation simply restores the eigenvectors to their proper form.

Now, let us return to the question I asked at the beginning of the essay; how good are these scores at depicting structure of the original distance matrix? This can be assessed by calculating a new squared Euclidean Distance matrix based on the PCoord scores and comparing that to the original distance matrix. The first few entries for the distance matrix reproduced from scores on the first two PCoord axes are shown below.

Table 9. Reproduced squared Euclidian Distance matrix for first two PCoord axes (3 Taxa)

	<i>Acaste</i>	<i>Balizoma</i>	<i>Calymene</i>
<i>Acaste</i>	0.000	78.027	917.634
<i>Balizoma</i>	78.027	0.000	1487.537
<i>Calymene</i>	917.634	1487.537	0.000

Comparison of this 'reproduced' distance matrix with Table 2 (above) shows that the first two PCoord axes provide a very good estimate of overall distance relations among specimens. A quantitative assessment of this 'fit' between the original and reproduced matrices can be gained by calculating the correlation between the two matrices. For this analysis that value



is 0.9999. Finally, an image of these relations can be constructed by creating a scatterplot of scores on the first two PCoord axes (Fig. 1).

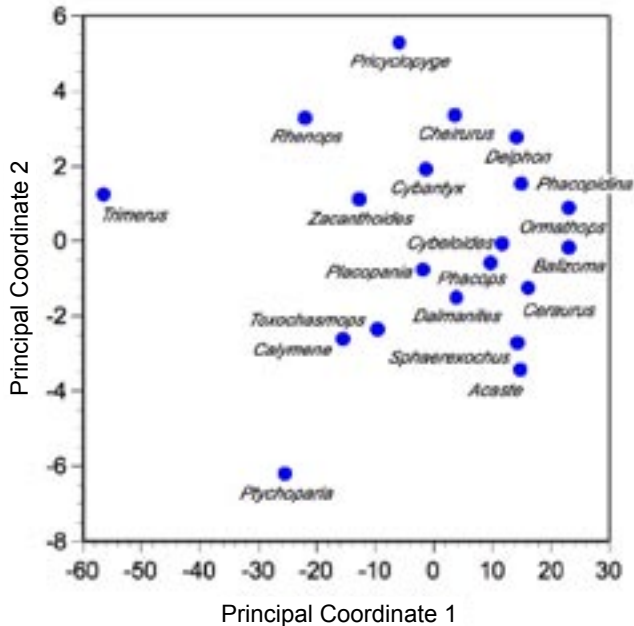


Figure 1. Scatterplot of the first two principal coordinates of the trilobite Euclidean Distance matrix.

If you've been following the column closely, this plot might look familiar. Indeed, it's almost identical in form to the plot we obtained for the space defined by the first two principal components of these data (see Fig. 7A, *PalaeoMath 101, Principal Components Analysis (Eigenanalysis & Regression 5), Newsletter 59*). There are a few differences, though; some trivial and some important. If you go back and inspect Figure 7A of the PCA analysis essay you'll see that the relative positions of all taxa shown on that plot are preserved by the PCoord results, but both axes have been reversed. This is a trivial difference. Remember, in eigenanalysis the direction of the axes is arbitrary, a result of the algorithm used to implement the eigenanalysis procedure, not the eigenanalysis concept itself. If we wished to change the direction of any PCoord or PCA axis we can simply multiply the scores along that axis by -1.0. It's perfectly 'legal' to do this, and often facilitates the comparison of plots obtained from different datasets. The positions of the point clouds along the axes are also different for the PCoord and PCA results. This is another trivial difference. The axis system of the PCoord analysis is centred on the centroid of the trilobite data because the scaling step we undertook by applying Equation 7.4 to the raw squared Euclidean Distance matrix forced it to be so. Because we did not apply this transformation to the covariance matrix used as a basis for the PCA results, the PCA point cloud is located well away from the origin of the PCA coordinate system. Once again, bringing the



coordinate systems into conformance would simply require that we mean-centre the PCA scores, another operation that is eminently legal.

If we reversed the direction of the PCA axes and mean-centred the PCA scores for the trilobite taxa we'd notice another similarity, this one somewhat perplexing. We'd find that not only does the coordinate system change to a comparable position in both plots, but the scores of the trilobite taxa in the PCA space become identical with the scores of these same taxa in the PCoord space. Even though we've now approached the analysis from two diametrically different points of view and used different matrices (embodying different definitions of 'relation'), we've obtained an identical result. What gives? If this is always the case, what's the point of a PCoord analysis?

To answer this question we need to go back to the beginning of the essay and return to first principles. As Gower (1966) showed—and as I mentioned above—a PCoord analysis based on the squared Euclidean Distance index is the dual of a covariance-based PCA analysis. These methods are inter-changeable and will always produce the same results in terms of the ordination of objects within the space of the new axes. This relation also extends to data that have been standardized prior to PCA or PCoord analysis. The point of a PCoord analysis, however, is that whereas one is pretty much stuck with always performing a PCA analysis in this mode, PCoord analyses are much more flexible because they're not confined to being undertaken only using the squared Euclidean Distance metric.

For example, let's add a count of the number of pleural lobes on our trilobite specimens to the mean-entered trilobite data matrix.

**Table 10. Trilobite data³**

Genus	Body Length (mm)	Glabella Length (mm)	Glabella Width (mm)	Pleural Lobes
<i>Acaste</i>	-13.08	-5.87	-5.21	11
<i>Balizoma</i>	-21.90	-5.40	-4.90	11
<i>Calymene</i>	15.47	1.54	1.74	13
<i>Ceraurus</i>	-15.07	-4.47	-4.29	9
<i>Cheirurus</i>	-4.48	-0.04	3.13	12
<i>Cybantyx</i>	0.59	1.98	1.12	9
<i>Cybeloides</i>	-11.09	-2.98	-2.17	12
<i>Dalmanites</i>	-3.29	-0.91	-2.90	11
<i>Deiphon</i>	-14.41	-2.45	0.03	-
<i>Ormathops</i>	-22.34	-4.34	-4.64	9
<i>Phacopidina</i>	-14.79	-2.34	-2.19	10
<i>Phacops</i>	-8.98	-4.07	-0.79	11
<i>Placopania</i>	1.93	0.03	-0.27	12
<i>Pricyclopyge</i>	3.89	5.61	4.00	5
<i>Ptychoparia</i>	25.95	2.88	-0.27	12
<i>Rhenops</i>	19.72	9.63	4.12	10
<i>Sphaerexochus</i>	-12.91	-5.53	-4.38	11
<i>Toxochasmops</i>	9.90	-1.22	2.44	10
<i>Trimerus</i>	53.21	13.81	12.54	12
<i>Zacanthoides</i>	11.67	4.19	2.80	9
Minimum	-22.34	-5.87	-5.21	5
Maximum	53.21	13.81	12.54	13
Range	75.55	19.68	17.75	8
Mean	0.00	0.00	0.00	10.47
Variance	346.89	27.33	18.27	-

Because this matrix mixes continuous variables and integer counts it could be argued that the Euclidean Distance index is not an appropriate means for estimating the among-specimen distance structure. The Gower index, however, is suited to *Q*-mode analysis of any data type or combination thereof.

Use of the Gower index results in a very different result from that of the previous analysis. First, the eigenvector decomposition of an appropriately scaled Gower matrix yields 18 positive eigenvalues, though note the step difference in terms of magnitude and percent contribution between eigenvalues 1–3 and 4–18.

³ *Deiphon* measurements were taken on a specimen that only consisted of a cranidium. Accordingly, this taxon will be eliminated from the four-variable analysis.



Table 11. Eigenvalues obtained from the scaled Gower matrix for the Trilobite data

Principal Coord.	Eigenvalue	Percent	Cum. Percent
1	2.03	41.44	41.44
2	0.78	15.90	57.34
3	0.61	12.46	69.80
4	0.27	5.61	75.41
5	0.22	4.40	79.80
6	0.20	4.17	83.97
7	0.15	3.16	87.14
8	0.12	2.40	89.54
9	0.10	1.98	91.52
10	0.09	1.78	93.30
11	0.08	1.61	94.90
12	0.07	1.37	96.27
13	0.05	1.10	97.37
14	0.05	0.93	98.31
15	0.04	0.72	99.03
16	0.02	0.50	99.53
17	0.02	0.32	99.85
18	0.01	0.15	100.00

Analysis of the percent contribution of each principal coordinate to accounting for the association matrix suggests either a 3-axis or a 4-axis solution is appropriate. Subsequent calculation of the reproduced Gower matrix using scores on the first three PCoord axes results in a 92.4 percent replication of the observed structure. This means that the plots shown in Figure 2 represent a highly accurate picture of the distance-relations among our taxa on the basis of the four variables.

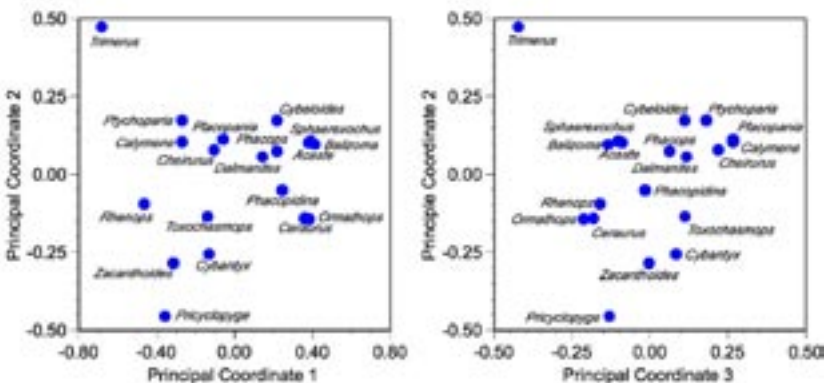


Figure 2. Scatterplot of the first three principal coordinates of the four-variable trilobite Gower matrix.



While it could be argued that these results are not strictly comparable to those of the three-variable analysis due to the absence of *Delphion* from this dataset and addition of the extra variable, inspection of Figure 1 suggests these changes did not have a strong influence on the overall character of the result. Compared to the previous ordination this result appears to confirm *Trimerus* and *Pricyclopyge* as outliers as well as exhibiting a comprehensive firming up of close correspondence (with respect to these variables) in several subsidiary groups (e.g., *Acaste–Balizoma–Sphaerexochus*, *Ceraurus–Ormathops*).

Whereas PCoord analysis can, at least in some forms, be considered an exact mirror or dual of PCA, Q-mode Factor Analysis (Q-FA) is definitely not the dual of classical or R-mode Factor Analysis. Once again, there are both trivial and an important reasons for this distinction. The trivial reason is that most textbooks recommend use of the Cosine θ association index as the best estimator of structural relations for Q-FA. Cosine θ is a safe choice as a basis for any Q-mode analysis in that it represents geometric relations between specimens in a way that is not sensitive to the magnitudes of the different variables used in their measurement-description and can even handle compositional data (data that have been artificially recalculated to sum to a constant value, such as proportions or percentages) effectively. The Cosine θ index is not, however, the only index that can be used in this context. Indeed, as with PCoord analysis, any distance or association index that produces a symmetric Q-mode matrix can be analyzed with the Q-FA procedure.

The important reason Q-FA is not the dual of R-FA is that, for all intents and purposes, Q-FA is nothing more than a PCoord analysis undertaken using the Cosine θ (or other) index. Recall my discussion of FA in the last newsletter. There I argued the only attribute truly unique to FA was the manner in which the scores of objects (e.g., specimens, localities) projected onto the FA axes were calculated. This complication is related to the statistical model on which FA is based, and requires that only those aspects of variation that covary or are correlated with the FA model be used in the determination of the FA scores. In this way, the picture of relations among specimens obtained as a result of an FA analysis represents but an aspect of the variation exhibited by the data. In Q-FA none of this applies because—like PCoord—the scores are determined not as a result of a scaling of the original data, but as a result of the scaling of the eigenvector coefficients. Since no statistical model is used as the basis for a Q-FA analysis, the accepted Q-FA procedure is simply a routine variant of the procedure used in principal coordinates analysis; a PCoord analysis based on the Cosine θ association index.

This having been said, there is merit in taking a brief look at the results of such an analysis. Returning then to the original, three-variable trilobite data, the eigenanalysis decomposition of the Cosine θ matrix yields three eigenvalues, as follows.

Table 12. Eigenvalues obtained from the Cosine θ matrix for the trilobite data

Principal Coord.	Eigenvalue	Percent	Cum. Percent
1	19.87	99.33	99.33
2	0.11	0.54	99.87
3	0.03	0.13	100.00



Note this is the most extreme decomposition we've seen yet, with all but 0.67 percent of the observed structural information being represented on a single axis. Such somewhat lopsided decompositions are often seen in PCoord results, and you shouldn't be frightened by them. Just remember you're trying to understand the system of measurements, not use the mathematics to obtain a result that looks like someone else's results or (even worse) use numbers to paint a picture of your own pre-conceptions. In this instance the extremely large signal that's being pulled out by the first principal coordinate is due to the fact that (1) there are only three variables in the system, (2) all the variables are very highly associated with each other (see the fragment from the Cosine θ matrix, above), and (3) the Cosine θ index is essentially ignoring the component of inter-specific variation represented by size differences among the specimens, which is a very large component of this dataset.

Since there are only three coordinates (or 'factors', whichever you prefer) we'll take a look at all combinations in the plots (Fig. 3). There's no reason to calculate a reproduced Cosine θ matrix because everything there is to see about this result is shown below.

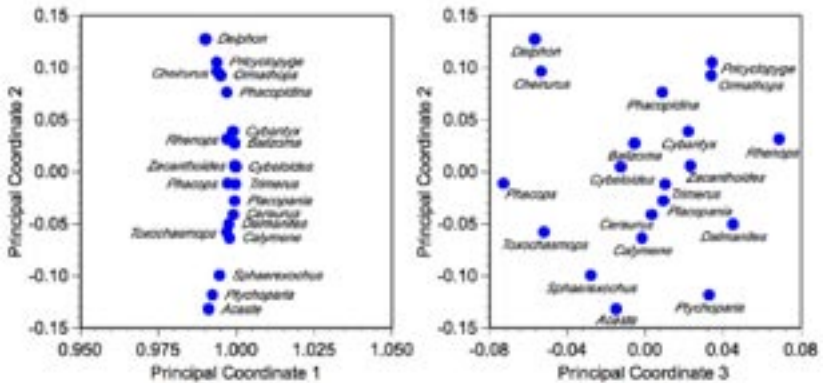


Figure 3. Scatterplot of the first three principal coordinates of the trilobite Cosine θ matrix

The unusual character of the principal coordinate 1-2 plot is also often seen in Cosine θ -based PCoord analyses, especially for low-dimensional data. Somewhat counter-intuitively the data are arrayed along a well-defined arc centred on the coordinate (1,0). This arc represents a communality of 1.0 (see previous Factor Analysis essay, *Newsletter 60*). All points that fall on the arc have their positions determined by only two axes of the three-axis solution to this matrix. Those points plotting a bit behind the arc (e.g., *Cheirurus*, *Phacops*, *Rhenops*) exhibit a more complex pattern of variation that requires all three axes to place accurately. You can think of this arc as defining the surface of a clear, hollow sphere centred on the origin of the axis system. The plot of principal coordinates 1-2 is the image you'd see if you stood outside the sphere at a position tangent to its surface and at right angles to the mean data vector, while the principal coordinates 3-2 plot is the image you'd see if you stood in the centre of the coordinate system and looked out at the distribution of points on the surface of the sphere. Effectively, principal coordinate 1 is expressing that component of variation all the trilobites have in common, whereas coordinates 2 and 3 express aspects of inter-sample difference.



Finally, note these plots are similar in some respects, but different in others to the previous representations of inter-specimen structural relations we've seen in this essay. Which representation is correct? The only reasonable answer is 'They all are!'. But that question is not specified in a very useful manner. The pertinent question is which of these indices best captures the distinctions between the trilobite specimens in which we are interested. Since this particular trilobite dataset exists only as means to illustrate mathematical techniques to a palaeontological audience, the 'which is correct' question has no answer in the context of the conversation we are having through these essays. Nevertheless, if you have data you wish to analyse by these methods, one presumes you collected the data for some purpose or to test some hypothesis. Selection of the appropriate Q -mode index will depend on the nature of the data you've collected and purpose(s) of the investigation. The decision will determine whether any PCoord result will be interesting or useful in the context of real data analysis situations. Everything else is just mathematical machinery.

Because principal coordinate analysis is not used as often as it should be, it's usually covered as an afterthought—if at all—in textbook treatments of data analysis methods. Add to this a genuine confusion among many authors as to what principal coordinates is and how it differs from other methods, as well as, more-often-than-not, all but impenetrable mathematical presentations, and it's little wonder few palaeontologists understand, use, or even know about this method. The literature really is inordinately hard going. If principal coordinates analysis is not covered as a side issue to the presentation of PCA methods, it's usually discussed as an approach to multi-dimensional scaling (MDS). This is particularly unfortunate insofar as classical metric and non-metric MDS employs mathematical techniques that are wholly unrelated to those I've presented here, though in the end they try to accomplish something very similar. We'll take a look at MDS in an upcoming essay. Despite what you might read, though, MDS is very different from PCoord. Unfortunately, this general level of confusion is, if anything, elevated in the few statistical packages that implement PCoord analysis, or at least claim to. Of these, the only implementations I'd recommend are those included in NTSYS (<<http://www.exetersoftware.com/cat/ntsyspc/ntsyspc.html>>) and Syn-Tax (<<http://www.exetersoftware.com/cat/syntax/syntax.html>>). Likely there are other good principal coordinate programs out there. If you know of any, let me know and I'll share the pertinent urls with the readership. I have PCoord routines I've written in *Mathematica* and would be happy to share with anyone who's interested. Drop me a line and let me know. Indeed, if there's sufficient interest within the PalAss community I might even be talked into coding and making available some simple applications for Windows and Mac platforms.

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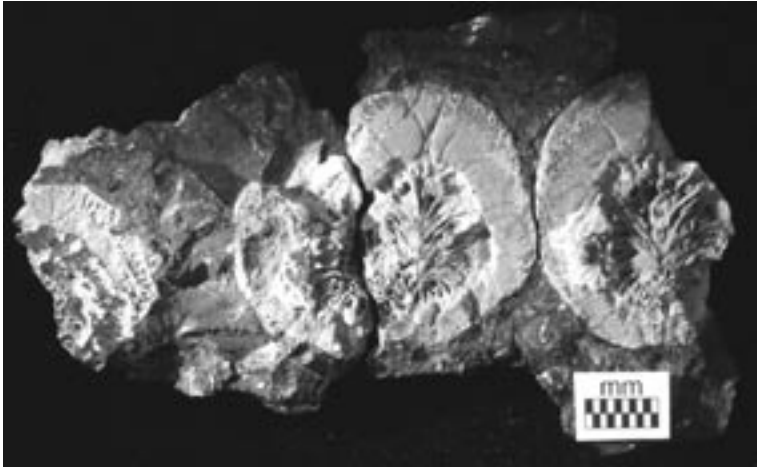


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Don't forget the *Palaeo-math 101* web page, now in a new home at
<http://palass.org/modules.php?name=palaeo_math>



MYSTERY FOSSIL



Mystery Fossil number 9 was sent in by David Cantrill, Department of Palaeobotany, Swedish Museum of Natural History. David says the material was originally described by Plumstead as angiosperm fruits from the Permian of South Africa. The structures occur in a coal and are largely composed of carbonate, which David says is a little strange when you consider that the rest of the plant material has been turned to coal around them. He would appreciate ideas what they might be.

Update on previous Mystery Fossils

The two specimens figured in Mystery Fossil Number Six from Eocene-aged continental lacustrine sediments in the Catalan Pyrenees have attracted a few guesses as to their identification, including serpulids and brain casts. Tom Yancey from Texas A&M is more certain that they are small coprolites, corroborating one of the original identifications. Tom states that the twisted form and striations are typical for aquatic coprolites and that the Catalan specimens are not too different from the famous late Miocene Wilkes Fm. coprolites in Washington State, USA. The occurrence in lacustrine sediments is appropriate for this type of coprolite. Tom suggests that their white colour suggests they are replaced by siderite, as most of the twisted coprolites are siderite replacements.

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Soapbox

Nothing new: three recurrent failings of 'soft rock' manuscripts

The stereotypical scientist hates writing. It is a widely disseminated myth that scientists hate to write up their research for publication (e.g., Yates *et al.* 2005), which somehow fails to explain just how *circa* 8,700 journals listed on the Science Citation Index (Testa 2004), plus the very numerous other journals that are not documented therein, plus books, websites, *etc.*, continue to receive sufficient copy to remain viable. It is hard to believe that all these publications are

kept in business by a group of wholly reluctant contributors. It is probably much fairer to say that, as in any group of writers, scientists represent a spectrum of authors, from the reluctant to the enthusiastic, and even those with something new to say aren't necessarily in a hurry to get it down on paper (or otherwise converted to readable electrons).

I would add a further axis to this continuum. There are those scientists who learn a little about the process of authorship every time they write, so their papers evolve in style and their presentation improves with time; and there are, frankly, those who never stop writing the same way, and badly (Donovan 2005). The latter group exists despite the wealth of literature available to help scientific writers develop their skills (e.g., Alley 1987; O'Connor 1991; Matthews *et al.* 1996; Day 1998; Lipscombe 2004).

As an editor and reviewer with some 20+ years experience of different geological journals, I see three common failings in manuscripts on palaeontology, sedimentology and stratigraphy, where the colloquialism or sloppiness that infects oral communication, at least now and again, is carried over into the written research paper. This happens at all levels in science, from the undergraduate report to the accomplished paper by a leading scientist; recently, editing one of the latter has encouraged this short communication. These errors are well-known to editors, but can be easily corrected by authors.

Is it a Formation or a Town?

To the north and east of Kingston, Jamaica, is a major half-graben structure called the Wagwater Belt, trending northwest–southeast (Draper 1998), and named after the Wagwater River. It is bounded on its southwestern side by the Wagwater Fault. Its fill, the Palaeogene Wagwater Group, includes the Wagwater Formation, a thick sequence of red-bed conglomerates (Robinson 1994). This extreme example emphasizes the importance of precision in written stratigraphy. I was formerly a lecturer at the University of the West Indies in Kingston, Jamaica. Undergraduate fieldwork included at least one exercise in this area and invariably draft reports referred indiscriminately, at least in part, to the 'Wagwater'. Which 'Wagwater'? The same imprecision is true of many established authors in their submitted manuscripts, in which the Anonymous Unit contracts to merely Anonymous in the latter parts of their report. Scientific accuracy and consistency require that it is called Anonymous Unit in full wherever it is mentioned.



Grain size

I have read many draft documents that refer to sandstones as fine, medium or coarse. I always presume that a fine sandstone wears a top hat and tails, a coarse rock tells lewd jokes in an offensive manner and a medium sandstone attempts to reach the spirit world, perhaps trying to contact the ghosts of the fossils within it. Of course, these should be fine-, medium- and coarse-grained, but it isn't only undergraduates who make this sort of error.

Sediments or sedimentary rocks?

Perhaps my most contentious criticism is that many authors use sediment and sedimentary rock interchangeably. Any good dictionary or textbook can clarify this point. For example, Phillips (1995, p. 196) defined sediment as “Rock fragments which have been formed by weathering or erosion ... they are moved by water ... ice or wind ...”, which agrees well with Brown (1993, p. 2755), “(A layer of) unconsolidated material composed of particles deposited from a suspension in air, ice, or water, or from solution.” Yet this same term may be used for a sedimentary rock – “Any rock formed by deposition of sediment ...” (Phillips 1995, p. 196) – which is poorly lithified or unlithified (e.g., Whitten with Brooks 1972, p. 405; Whittow 1984, p. 477).

It is surely poor practice to apply a term to both a Recent, perhaps ephemeral, deposit of unlithified sediment and part of a sedimentary rock sequence without, at least, adequate explanation of the author's usage. Best practice would be to use terminology such as poorly lithified or unlithified sedimentary rock, as appropriate. Poor usage can lead to confusion; I mistakenly used unlithified to describe a poorly lithified sedimentary rock (part of a Late Pleistocene raised reef) in the original submission of a manuscript and was challenged by a reviewer as to whether it might be Recent. Certainly, sediment should never be applied to a well-lithified sedimentary rock.

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—OBITUARY—

Jack A. Wolfe

10 July 1936 – 12 August 2005

On 12th August 2005 the world of palaeobotany lost one of its greatest research minds of the last half of the 20th Century. Jack Wolfe was not only an extraordinary systematist with an encyclopaedic knowledge of angiosperm leaf architecture, but he went where few palaeobotanists dare to go; he ventured into the realms of multivariate statistics in pursuit of quantifying the relationship between foliar physiognomy and climate. His ability to go well beyond botanical observation and description into using fossil leaves as tools for understanding environmental change through time has defined an area in modern palaeobotany that has found application in fields as diverse as meteorology and crustal dynamics.



Born and raised in Portland, Oregon, Jack Albert Wolfe attended Franklin High School where, with the encouragement of his biology teacher Anne Bohlen, he first developed his interest in palaeobotany. Anne was the adviser to the school Science Club and in 1952 she arranged a club visit to the fossil museum that Lon Hancock, a retired postal worker, had made in his home. Lon was an amateur who had helped furnish localities and material to both Ralph Chaney and Chester Arnold, and was a founder of the Oregon Museum of Science & Industry (OMSI). Lon, under the auspices of OMSI, started a Summer field camp in the John Day Basin of central Oregon. Looking for a research project to write up for the Westinghouse Science Talent Search, Jack attended the second year of the OMSI field camp and became fascinated with two classic palaeobotanical sites near the camp: the Clarno nut bed and the Bridge Creek leaf flora. Jack's project must have been impressive because, as one of 40 finalists, he won a trip to Washington and one of the contest judges, the Harvard astronomer Harlow Shapley, encouraged Jack to apply to both Harvard and Princeton. Unfortunately the application and scholarship deadlines had both passed, but still Shapley made encouraging noises. Jack finished in the top ten of the Westinghouse Science Talent Search and went to Harvard in 1953 on a full scholarship.

At Harvard Jack did his undergraduate research under the direction of botanist Elso S. Barghoorn and, almost every day for three years, Jack had lunch and coffee with the group that included I.W. Bailey, Don Whitehead and Margaret Davis, among others, and visitors such as Sherwin Carlquist. With the stimulation of such company, and building on his avid collecting in the Pacific Northwest, Jack had his first palaeobotanical publication only a year after being admitted to Harvard. It was on the Collawash flora of the upper Clackamas River Basin and appeared in the Newsletter of the Geological Society of Oregon. During the Summers at Harvard Jack gained further field experience – joining, on separate occasions, Roland Brown, Dallas Peck and J.F. Smith who



were all with the US Geological Survey (USGS). In this way Jack gained a breadth of experience that went way beyond palaeobotany and saw him mapping Cenozoic volcanic rocks of the Cascades and Palaeozoic sedimentary rocks in Nevada.

In 1957 Jack began his graduate studies in palaeobotany at Berkeley under Wayne L. Fry, A.S. Foster and Herbert L. Mason, and in 1959 was awarded an M.A. in Palaeontology after writing a thesis on the Tertiary Juglandaceae of Western North America. At Berkeley Jack was particularly influenced by J. Wyatt Durham, the mollusc/echinoderm worker. Jack realised that mollusc workers had rigorous criteria for identifying their material and this prompted him to try the same approach with angiosperm leaves. With the encouragement of Adriance Foster (an I.W. Bailey connection) in 1958 Jack started chemically clearing leaves to reveal venation patterns, and by 1969 this had evolved into a project to survey modern dicots using cleared leaves. Eventually the USGS cleared-leaf collection (now housed at the Smithsonian Institution in Washington) represented around 15,000 species and Jack had become, in his own words, “the largest herbarium beetle known to exist”. His rigorous approach was one of the major foundation stones of modern leaf architectural analysis in fossil angiosperm leaf identification and comparative studies.

In 1960 (when still only 23) Jack completed his PhD dissertation on the early Miocene floras of northwest Oregon. This rapid academic advancement was achieved alongside reporting on referred fossils for the US Geological Survey under the supervision of Preston E. Cloud. Jack’s industry was rewarded with a post that led him to being Research Geologist with the US Geological Survey, Menlo Park, California. Jack remained with the USGS throughout much of his career, mostly at Menlo Park, but with spells in Washington DC (1961–1965) and Denver (1982–1992).

In 1969 Jack produced his first major work on fossil floras: it was a synthesis of his findings on the Late Tertiary floras of the Pacific Northwest, which he published in *Madrono* in time for it to be handed out to attendees of the International Botanical Congress in Seattle that year.

In the 1960s Jack also began work on the Tertiary floras of Alaska. In publications and fieldwork with David Hopkins, Clyde Wahrhaftig and Estella Leopold, he presented a first cut on dating the younger floras of the Kenai Lowland as Late Tertiary in age. Before this biostratigraphic work, many prominent geologists considered the rocks of the Kenai Group as being of Palaeogene age. Jack continued and produced in 1977 a monumental and thoughtful work on the Palaeogene floras of Alaska and Wrangellia, which still stands as an exceptional monograph. One of the reasons it was so notable is that he established for the first time that truly subtropical floras existed as far north as 60° N. Lat.

Jack’s primary role at the USGS was to use plant megafossils for biostratigraphic and palaeoenvironmental determinations, but through his collaboration with Elso Barghoorn he also factored the pollen record into his deliberations. He not only undertook fieldwork himself, primarily in the western US including Alaska, but also identified material brought in to him by scores of geologists working throughout the United States. After a long and highly productive career at the USGS Jack retired to an adjunct position with the University of Arizona in 1992, where he remained an active researcher and, as at Berkeley, actively supervised research students, most of whom have continued working in palaeobotany and have co-authored papers with him.

One of his important monographs, published in 1979, was the climatic analysis of the forest types in eastern China described by Wang Chi Wu in the 1960s. He adapted the quantitative comparison of



mean annual temperature with seasonal range of temperatures in different forest types. It resulted in his development of nomograms that sketch out the climatic parameters of the forest types, not only for eastern China but also for eastern and western North America and Australia. His nomogram models are widely used by botanists today.

While Jack's reputation as a systematist and biostratigrapher will be remembered for a long time, probably his most innovative work was in quantifying the relationship between leaf form and environmental conditions, primarily climate. Following on from the pioneering work of I.W. Bailey and E.W. Sinnott, Jack recognised that leaf form is controlled by an interplay between the genotype honed through evolution and a spectrum of environmental factors. As early as the late 1970s he realised that the best way to decode the complex form/climate relationship was through multivariate analysis. He set about building and testing a unique database of foliar physiognomic characters derived from leaves of woody dicots growing in vegetation for which the climate (weather-station data) is quantified through long-term observation. His rigorous collecting methodology incorporated the full observable morphological range, rendering the approach remarkably robust in the face of taphonomic filters. The technique, which he named CLAMP (Climate Leaf Multivariate Programme), has found application not only in North America and Japan where the calibration datasets have their origin, but in Russia, Europe, South America and New Zealand. Most spectacularly, the technique yields data on enthalpy, a property of a parcel of air that can be used to estimate palaeoelevation. In recent years this approach has been applied to the uplift of Tibet and the Andes. However for some years Jack had an interest in the uplift history of the western US, and it was here that he tested the technique, something he was still working on

when he died falling from an outcrop in the eastern Sierras.

Jack always had an eye for detail, and abhorred what he regarded as sloppy work. This, coupled with a tendency to be fairly brusque, a trait that he sometimes resorted to in order to disguise his innate shyness, led to feuds with some colleagues. Moreover he was a critical reviewer. Nevertheless those who became his close friends discovered a man of great intellect, loyalty, warmth and generosity.

Jack Wolfe is already sorely missed by his colleagues and students. We have lost a singular leader and scholar of palaeobotany. We are privileged to honour his life by following where he led in the study of the major evolutionary and stratigraphic problems, and the relationship between plants and climate: areas of endeavour where Jack blazed an important trail.



*Photo of Jack at Teapot Dome
courtesy of Margaret Collinson*

Bob Spicer and Estella Leopold



Meeting REPORTS



49th Annual Meeting of the Palaeontological Association

Oxford 18 – 21 December 2005

Probably wisely, I don't write annual meeting reports in the expectation of reward. However, more than two years have elapsed since the Newsletter Editor promised me extraordinary bounty (half a pint of shandy and a plastic dinosaur) for stepping in to cobble one together at short notice, so I decided I would document nothing of the Oxford meeting until the debt had been paid. Shandy I can live without, but novelty toys are a different matter.

It was then I discovered that an editorial changeover was imminent, and began to feel slightly guilty that the new incumbent would be left in the lurch. Perhaps I should take notes at the meeting, draft a report, and then blackmail him with my childish demands instead. Well, I have to say it worked a treat. With the copy deadline looming, I became the lucky recipient of a detailed and extremely lifelike plastic insect (*Podalonia hirsuta*, apparently), courtesy of a Japanese soft drink promotion. Not quite what I expected, but incentive enough.

So here it is (the report, not the insect). If sections of it read as though infused with the demented spirit of Lewis Carroll (*Alice's Adventures in Gondwanaland*, perhaps), I can only plead that it was nearly Christmas, I was in Oxford, and that my persistent demands for replica animals had caused a short-term re-wiring of my brain. Either that or it's just the same old nonsense I churn out every year.

Are you sitting comfortably? Then we'll begin. And where better to begin than at the beginning, with a special seminar on the Ediacaran? **Dan Condon** (MIT) kicked things off with a detailed investigation into the chronology of the period, now defined as stretching from 635 Ma to 542 Ma. Perturbations in the carbon cycle appear to tie in with at least some of the major turnovers in fauna, innovations discussed in greater detail by **Doug Erwin** (NMNH). It appears the diversity of Ediacaran morphologies was mainly controlled by the appearance of new ecological niches. **Guy Narbonne** (Queen's, Ontario) then introduced the audience to the very earliest Ediacaran fossils from Mistaken Point, Newfoundland. Dated at between 575 and 560 Ma, the fauna represents a deep water ecosystem preserved by volcanic ashfalls, and is markedly different from later Ediacaran assemblages. Rangeomorphs are the dominant group, interpreted as an early group of radial organisms that were subsequently out-competed by the evolution of more sophisticated animals.

The post-tea presentations started with **Shuhai Xiao** (Virginia Tech) and the palaeobiology of the Doushantou Formation, China. Peering through three diagenetic windows – chert, shale, and phosphorite – provides different information on the fauna of the time, although there are problems distinguishing between biological and diagenetic structures. Closer to home (especially mine in Leicester), **Martin Brasier** (Oxford) has been reinvestigating the classic fauna of the Charnwood area, mainly using a laser system disguised as a microscope on a tripod. Much greater detail of the fossils has been gathered, and it is clear that *Charnia* cannot be related to sea pens, having grown



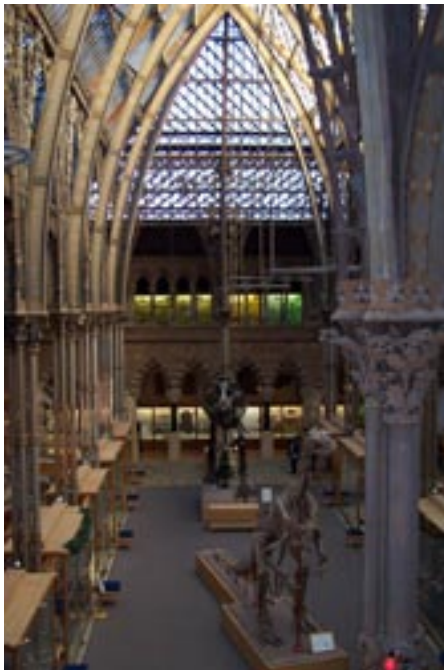
in a fundamentally different way. **Mary Droser** (UCR) then brought the seminar to a close with a dash of ichnology. Trace fossils may be the only incontestable evidence of the earliest bilaterians, but many so-called traces turn out to be rather dubious. Furthermore, taphonomic bias and spatial heterogeneity make the picture yet harder to unravel, though it is clear that complex tiering was present in these early ecosystems.

There was then just enough time to march briskly to the accommodation in St. Anne's College and get changed, or else dive into the nearest pub, before a wine reception in the University Museum of Natural History. There can be few settings more splendid for palaeontological perambulations, but PalAss delegates are unashamedly mercenary where alcohol is concerned and when the wine ran out, so did many of my colleagues. It was a Sunday evening though and, bar one or two diehards, even the most dedicated of drinkers were forced to call it a night before twelve. The revolution of English licensing laws has a way to go yet.

Monday morning saw **Graham Budd** (Uppsala) given the privilege of opening the meeting proper with his presentation emphasizing the value of the fossil record in understanding the evolution of morphological novelty. Spores in the Rhynie Chert caught the attention of **Charlie Wellman** (Sheffield), not least some examples of exceptional(ly bad) preservation of sporopollenin. Still, fossilized callose has been discovered for the first time in land plants, so the taphonomy is not universally unhelpful. **George Sevastopulo** (Trinity College Dublin) then instructed us to ignore his abstract as he tried to unravel the affinities of salebrids. They might be weird bryozoans, but they might not: any promising suggestions will be gratefully received by George.

As enthusiastic as ever, including an audacious bid to leap ahead of George in the schedule, **Giles Miller** (NHM) examined biases in the conodont fossil record. P1 elements are always over-represented, but in a highly productive new locality from Russia, priniodinid samples appear to contain elements in their original percentages, providing new reconstruction potential.

Paul Barrett (NHM) then found that a relatively unremarkable-looking Lower Jurassic sauropod from China was phylogenetically very informative, its unique combination of primitive and derived characteristics marking it out as a basal sauropod. The session was completed by **Daniela Schmidt** (Bristol), who revealed that by 2030, if current trends continue, Southern Ocean pteropods will be unable to form aragonite shells. Planktic foraminiferans, meanwhile, showed a dramatic size decrease after the K–T event, but have now become polarized, with small species getting smaller and large forms getting larger.



The elegance of the University Museum



After a coffee break where failure to observe proper queue etiquette was most definitely frowned upon, **Aoife Braiden** (UCD) demonstrated the value of using small field assistants to get into inaccessible sampling sites (perhaps a use for ASBO-wielding, pint-sized miscreants?). And, after sifting through 208 kg of sediment, Aoife unearthed approximately 2g of shrimp. Not just any old shrimp, mind, as calcium phosphate had preserved even the muscle fibres, showing that 3-d preservation is possible in high energy environments. Middle Cambrian stylophorans from Morocco enabled **Sébastien Clausen** (Lille) to determine that carroids are stem-group pre-radial echinoderms, before **Neil Davies** (Birmingham) had a look at some exceptionally preserved fish from the Ordovician of Bolivia. Four ichnofacies were recognized, with the fish found only in one, a restricted *Skolithos* ichnofacies interpreted as representing an upper shoreface environment. Preservation by obtrusion seems most plausible, with silt perhaps having clogged up the fishes' gills.

One Brummie followed another, as **Beth MacDonald** (Birmingham) presented her work on microfossils across the Triassic–Jurassic boundary. Straight nodosariids are taken as indicating deeper water conditions, whilst abundant platycopid ostracodes suggest low oxygen levels, possibly as a result of transgressive episodes. After **Christian Klug** (Zurich) described soft-tissue attachment structures in Palaeozoic cephalopods, **Phil Donoghue** (Bristol) found himself in the naughty corner, maybe because he uses a Mac, or maybe because he doesn't provide dinosaurs for newsletter reporters, who can say? With a parade of dead fish, Phil showed that biological models of gene acquisition only work if you ignore the fossils, and that apparent bursts of innovation are often simply artefacts of extinction. **Al McGowan** (NHM) brought matters to a close with an investigation of what happened to ammonoids across the P–T boundary. New phylogenetic analysis indicates that extinction may not have been quite as severe as has previously been suggested.

Lunch in the Eagle & Lamb over-ran somewhat, and I was then so delighted to find someone to talk to about macheridians that I missed the whole of the next session. Returning to the auditorium after coffee, I did at least get to see **Jonathan Adrain** (Iowa) measure the diversity of Laurentian trilobites in the Lower Palaeozoic. Ignoring the post-extinction faunas (such as those of the Late Steptoean, son) it seems richness and evenness don't change from the Cambrian to the Silurian, and that the trilobite record is primarily taphonomic. **Thijs Vandenbrouck** (Ghent) then tried to establish whether chitinozoans could be used to link the conodont and graptolite biostratigraphical records, before **Sue Rigby** (Edinburgh) made the case for a wider palaeontological application of computational fluid dynamics. If such models can reveal much about graptolite hydrodynamics, they should be useful in studies of other pelagic organisms.



Jim Kennedy delivering the Annual Address

And, after **Dick Aldridge** had exhorted us all to attend IPC 2006 in Beijing, it was time for **Peter Crane** to chair the AGM. Various committee changes were approved, 11 Sylvester-Bradley awards were made, 23 IPC grants dished out, Mary Anning awards presented to **Andrew Yule** and **Steven Etches**, the Hodson Fund given to **Phil Donoghue**, and the Lapworth Medal awarded to **Bill Chaloner**. All of which was followed seamlessly by the annual address, given this year by **Jim Kennedy** (Oxford) on the extraordinary life of



William Buckland. Jim told us this was a very serious lecture about an Anglican Richard Dawkins, before going on to inform us that, in Buckland's time, Oxford fellowships could only be acquired by the death of a fellow, or his expulsion due to carnality. In 1821, Buckland's work on the Kirkdale Cave bones (an ancient hyena den, not a relic of The Flood) earned him the Copley Medal, whilst in 1824 he described the first dinosaur, *Megalosaurus*. In 1825, he was made Canon of Christ Church, but his palaeoecological work continued, with proof that Lyme Regis fossils were coprolites, and studies of the functional morphology of *Megalotherium*. He was appointed Dean of Westminster Abbey in 1845, but four years later was admitted to Clapham asylum, where he died in 1856. His creepy son Frank did a paternal post-mortem (and, just for good measure, dissected his mother the following year) and it seems TB may have been the cause.



The Annual Dinner at Hogwarts (All photos courtesy of Tim Kearsey)

A reception in Blackwell's preceded the annual dinner at Christ Church College; another fabulous location that I am reliably informed also passes for Hogwarts (of *Harry Potter* fame) in its spare time. Whether this makes a Dumbledore of Sir Peter Crane I am unsure, but after being directly quoted in his after-dinner speech I really shouldn't poke fun at our glorious leader. Instead I should poke fun at the unfortunate souls who left their seats at inopportune moments and found that the wine waiters had been and gone in their absence. Peter told us to look forward to a Christmas Day television battle between his very own *A Year At Kew* (BBC2) and the more populist *Little Britain* (BBC1), although one of my colleagues misheard Peter and thought he was referring to the stuffed little bitter on display outside the museum auditorium. Off back to St. Anne's we then trooped for a late-night bar and a jukebox full of Johnny Cash songs, which is never a bad thing.

The bar closed at one, but anyone in need of further refreshment didn't have to move far. Outside, a multinational circle had formed, and a bottle of whisky was making its way around in somewhat



haphazard fashion. Once it was drained, many lords of the ring drifted away, but the remainder moved indoors to the sanctity of college quarters (if Alex Page's room can be described thus). Passers-by were unsurprisingly scarce but, had any been available, I suspect they might have been a little baffled. Whilst some quiet imbibing went on in one corner of the drinking den, the empty wardrobe in the other had attracted the attention of some eminent palaeontologists apparently hell-bent on gaining access to Narnia. It was time to tip-toe out of the room and quietly close the door behind you.

Tuesday morning arrived cruelly soon and brotherly love left **Dave Siveter** the pleasure of chairing the first session. For those audience members in possession of unfuddled brains, **James Nebelsick** (Tübingen) began with a puzzle: which nut did the squirrel crack? James was looking for tell-tale signs of predation in Oligo-Miocene sea urchins. Drill holes in the echinoid tests show site selectivity by predators, but rates of predation seem to have been lower than at the present day. **Thomas Hansen** (Oslo) examined Ordovician trilobite faunas in southern Norway before **Mike Benton** (Bristol) asked how many dinosaurs there are still to be found. Basing predictions on current taxonomic diversity is tough, primarily because some European workers erect a genus for every new bone found, but 1,000 taxa seems a reasonable estimate.

Christian Baars (Cardiff) then unveiled a cosmopolitan brachiopod fauna from the Ordovician of Kazakhstan, **Susannah Moore** (Cardiff) tried to unravel the development of Lower Devonian spores using spore mimics, and **Jakob Vinther** (Copenhagen) speculated whether the aesthete system of chiton molluscs derives from the hollow spicules of a halkieriid-like ancestor.

After coffee, **Emily Rayfield** (NHM/Bristol) kicked things off with some new evidence of spinosaurid feeding behaviour. Examination of the stresses involved in biting shows that *Baryonyx* behaved like a gavial, with a secondary palate resisting bending within the skull. So why did palates never evolve in any other theropods? From evolution in very large vertebrates we switched to micro-evolution in very small ones, as **Mark Purnell** (Leicester) performed some stickleback orthodontics. By studying the teeth of extant species, Mark showed that dental microwear very accurately predicts palaeoecology in Miocene forms, and that there is a direct correlation between ecology and micro-evolutionary patterns.

How to characterize complex geometries was the dilemma **Norm MacLeod** (NHM) could be found grappling with in the following talk. Eigensurface analysis might be the answer, as it yields excellent information on patterns of 3-D shape variation, enabling morphological transitions between taxa to be critically appraised. And quite how I make the jump from morphometrics to rotting whales is beyond me, even if the organizers managed it with **Cris Little** (Leeds) and his deep sea feeding bonanza. Deceased cetaceans provide nourishment for a multitude of strange creatures, often for extremely long periods of time, but how long have such communities existed? Did ancient zombie worms feast on expired ichthyosaurs in the Mesozoic? No evidence for it yet, but an intriguing possibility.

New specimens from Canada enabled **Nick Butterfield** (Cambridge) to re-visit *Vetulicola*, a mysterious Cambrian metazoan. It might be an arthropod, but it's hard to be certain, not least because it doesn't have any arthured podes (my words, not Nick's). However, it does seem to be a single taxon showing taphonomic variability, rather than a whole new phylum. **Thomas Servais** (Lille) then lamented the small size of dinoflagellates, speculating that if only they were a bit bigger



they might be able to compete for news interest with those other fossil dinos. They are thought to have evolved around a billion years ago, but dinoflagellates are presently first recognized from the Triassic, although there are possible calcified forms in the Silurian of Gotland. Back in the naughty corner sponsored by Apple Mac, **Neil Gostling** (Bristol) used a Synchrotron (a snip at just 2m Euros) to distinguish biogenic from taphonomic features in early embryos, showing *Markuelia* is a member of the Introverta. And then it was lunchtime again.

Una Farrell (Yale) kicked off the Tuesday afternoon session with some pyritized polecats. Using a CAT scan, Una was able to show that a Devonian taxon from the Arkona Shale of Ontario belongs to the crown group Phylloclodida. Miocene frogs from Spanish lake sediments caught the attention of **Maria McNamara** (UCD), not least because they include fossilized blood and bone marrow. Even more exceptionally, Maria demonstrated that the preservation was essentially independent of environment, with the bones acting as taphonomic crypts as long as they have been sulphurized first. **Rachel Moore** (Kansas) then studied the effects of anoxia on soft-bodied preservation of ecdysozoans across the Lower–Middle Cambrian boundary. Two faunas from the Pioche Shale of Nevada show different types of preservation, with conditions in the Middle Cambrian interpreted as being reducing and anoxic.

Fossil holothurians are extremely rare, so **Lucy Muir**'s (NHM) discovery of a new specimen in the Ordovician of Wales sheds new light on the early phylogeny of the group. And talking of early phylogeny, **David Wacey** (Oxford) took us back almost 3.5 billion years to see whether micro-tubes in Western Australian sandstones are of biogenic origin. Completing the penultimate set of talks, **Uwe Balthasar** (Cambridge) found that Early Cambrian obolellid brachiopods show both rhynchonelliform and linguliform features, enabling a revision of brachiopod phylogeny.

The final session was upon us, and **Sofia Wennberg** (Uppsala) introduced the audience to the ontogeny of priapulids, before **Seán Burke** (UCD) tried to establish when infaunal ecosystems first developed in deep-water environments. Evidence from Ireland and Portugal indicates that it was early in the Ordovician. Next, **Rosie Stephens** (Leeds) persuaded the Geological Society to fund a trip to Switzerland in order to bombard fantastic fossil plants with neutrons. Although the specimen (from the Eocene of Antarctica) then has to be stored in lead for two years, Rosie was able to reconstruct it as a monkey puzzle tree.

Quantifying the number of Eocene mammals on the Isle of Wight and their age of death was the challenge facing **Katerina Vasileiadou** (Royal Holloway). The fossils indicate most of the mammals were very young or old when they died, and most breakage of bones appears to have occurred in life, suggesting that they were eaten, probably by the predatory *Cynodontis*. Apparently recovered from the excess of the previous night, **Jeremy Young** (NHM) then asked what the function of coccoliths was. For such simple beasties, coccolithophores have a phenomenally complex level of construction, but it doesn't seem to represent an essential physiological function. However, asymmetrical forms may have found a means of building a thinner coccosphere. New outcrops in a potato field have enabled **Bob Davidson** (Aberdeen) to obtain new data on Lower Devonian fish, revealing fossil horizons at more than one level and suggesting the existence of multiple lakes, before **Olev Vinn** (Tartu) brought proceedings to a close. Are Palaeozoic 'spirorbids' really annelids? When did the first true serpulids appear? Were phoronids calcified in the Palaeozoic? Provocative questions indeed.



The talks over for another year, there were still presentations to be made. For her entertaining and illuminating introduction to the preservation of blood and bone marrow, **Maria McNamara** deservedly won the President's Prize, whilst **Richard Callow** (Oxford) claimed a home win in the Council Poster Prize for his work on biomineralization in the Precambrian Nama Group of Namibia. Congratulations to both. Our thanks and appreciation must also go to **Derek Siveter** and the Oxford organizing committee for an exceptionally well-managed annual meeting. When the talks run to time, the receptions have a plentiful stock of wine, and the late bar is packed to the rafters, you know someone is doing something right. And with this year's meeting in Sheffield being the 50th, we can probably assume the Association as a whole is ticking along nicely.

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Lyell Meeting 2006: Millennial-Scale Events

Geological Society, Burlington House, London 15 February 2005

The present is the key to the past, or so said Lyell in the *Principles of Geology*. Through intervening years earth scientists have modified this mantra slightly. With less emphasis on actualism and gradualism currently, the uniformitarian view still underpins the science. We no longer view sedimentation as a story of extremely gradual accumulation in which you could spend your whole life lying beneath the deep ocean, hoping to get hit by a falling flake of clay if lucky. Instead we see a story of shorter, more sudden, events; a world in which the chalk seas housed hard-grounds, in which marine canyons may have been filled in moments by mega-tsunamis. This modern uniformitarian approach is one clearly favoured by **Howard Armstrong** and **Maurice Tucker** (University of Durham), convenors of this meeting on millennial-scale events in the geological record.

The 2006 Lyell Meeting of the Palaeontological Society and the Geological Society drew a set of delegates from all around the world (North America, continental Europe and Cornwall). It took on board the many wiggles of Quaternary climate curves and looked for similar patterns through geological time. There are, after all, many more wiggles in the fossil record than those of ichnology and phylogeny. The meeting examined short-term oscillations in Earth system; though it focused mainly on recent rocks, as the day progressed we passed into the Palaeozoic to a Silurian basement. It seems that the paradigm of climate process and biosphere response is taking the plunge into the murky depths of deep time.

As the lights dimmed, an enthusiastic crowd, notepads at the ready, welcomed **Peter Clark** (Oregon State University, USA) to lay the foundations for the day in a plenary lecture discussing Heinrich events and Dansgaard-Oeschger cycles, the millennial-scale events of the Pleistocene. These have previously been viewed as an entirely North Atlantic phenomenon, and their causal mechanism has remained enigmatic. However, just as there is a collection bias in the fossil record, equally there is 'drilling' bias in the IODP legs throughout the world, leading to a North Atlantic biased view of climate.



Taking new data from the eastern Pacific, Peter proposed a mechanism whereby the Pacific Ocean mediated these cycles. In the North Atlantic, the rate of deep water formation is influenced by outwash of freshwater from the Hudson Bay. When the Laurentide ice sheet collapses icebergs raft into the high latitude North Atlantic, a Heinrich event. These events dilute the dense brine-rich surface water, slowing North Atlantic Deep Water (NADW) formation. This deep water travels around the globe and upwells in the middle of the Pacific Ocean. As upwelling in the Pacific decreases due to decreased NADW formation, the central Pacific warms and – reaching for Wikipedia™ – El Niño conditions develop. This, essentially, increases the strength of the northward warm currents. The northerly transfer of the warm waters produces increased evaporation in the mid latitudes, creating a ‘snow gun’ above western North America. This snow-gun loads the Laurentide ice sheet, which eventually collapses, causing another Heinrich event. Heck!

With warm fluids and restoration so pertinent, the delegates, especially those arriving on the early trains, were furnished with coffee in readiness for the day’s second session. **Jason Cosford** (University of Regina, Canada) illustrated a method using stalactites to show how the oceanic events manifest themselves on the continent – a test for Peter’s model perhaps. Examining 19–30 ka U/Th absolute dated speleothems, Jason showed faithful documentation of Dansgaard–Oeschger events and Heinrich events of the North Atlantic province in the caves of south-east Asia. These oceanic events manifest themselves in variations in the monsoon water from which these stalactites eventually form. Cooling in the North Atlantic generates cold, dry westerly winds that strengthen the Siberian high pressure cell, increasing the strength of the East Asian and Indian Summer monsoon. The theme of terrestrial responses to north Atlantic climatic oscillations was continued by the gesticulating **Jasper Knight** (University of Exeter at Penryn), who examined how variation of the strength of the Gulf Stream may affect erosion and deposition in the Quaternary of Cornwall. With a sedimentary record dominated by erosion, this seemed a daunting task; lacking a well-constrained stratigraphic framework, he could not unambiguously distinguish between climatic forcing and local noise. And so it was, thinking of local noise – wild nights of Cornish pasties and cider perhaps – we headed hungrily to lunch.

After lunch we moved from the glacial Pleistocene to the stadial Holocene. The inevitable surprise being that even without the Laurentide ice sheet to drive the North Atlantic system there were still extremely rapid periods of climate change, such as the 8.2 and 9.2 Ka events. These were not just confined to the seas, either. Using data of exceptional resolution from lacustrine deposits **Jim Marshall** (University of Liverpool) identified both events in micritic muds from Hawes water, Lancaster (not to be confused with its namesake that rapidly flooded the small Lakeland village of Mardale in a late Holocene reservoir construction event). Jim argued that perturbations in the $\delta^{18}\text{O}$ record in this lake represented unusual amplification of background centennial cycles due to solar forcing passing critical thresholds. This is reflected in temperature fluctuations in the lake water derived from fauna-transfer functions on the fly fisherman’s friend, the chironomid midge!

Such fine-scale records may not always be found in the marine record however, for more extensive bioturbation and slower sedimentation serves to reduce resolution. Corals may provide accurate seasonal to centennial scale palaeothermometry. However, these records are obtained from individual corals and are thereby limited to the colony’s lifespan, some ten to a few hundred years. Nevertheless, if these variations are faithfully represented in the talus that forms periplatform sediments then they may provide a high-resolution proxy applicable to geological timescales. By



comparing data from tree rings, ice cores and atmospheric indices to those from periplatform sediments, **John Reijmer** (Université de Provence, France) found that these sediments were indeed representative of Holocene climate, revealing several short period cycles of 60–600 year scale in the North Atlantic system.

As we learnt in the morning session, changes in ocean circulation and temperature also manifest themselves in continental climate, not least in the strength of monsoonal rainfall. With this in mind, **Peter Clift** (University of Aberdeen) investigated the pattern of Himalayan weathering since the Last Glacial Maximum. The Indus Delta, whose catchment includes the emergent mountains of the western Himalaya and the glacially-eroded Karakorum, provides the ideal lab to investigate this. It has continued to prograde despite the Holocene transgression, due to its high rate of sediment influx meaning it provides an accurate sample of Himalayan outwash. And although the clay mineralogy of its sediment load has remained unchanged throughout this interval, Nd isotope data reveal that the locus of weathering moved from the Karakorum to the Himalaya since the last glacial maximum, in which period the monsoon has strengthened and glacial weathering has become less significant.

Establishing such millennial-scale events in the rock and fossil record depends on the ability to differentiate regional, tectonic and global climatic signals. Though the eastern Mediterranean has been tectonically active since at least the Mesozoic, its well-studied geology provides a stratigraphic framework that allows differentiation between climatic and tectonic controls on relative sea-level. Working in the Gulf of Corinth, **Julian Andrews** (University of East Anglia) interpreted the U/Th ages of uplifted carbonates (erosion surfaces, *Lithophaga* borings, encrusting marine organisms and vadose speleothems) to produce a sea-level curve documenting suborbital changes of tens of metres magnitude within marine isotope stage 5e.

As the afternoon progressed, the audience explored the themes of the earlier talks further back in the geological record. Initially we were transported from the modern world of greenhouse effects to ice-free times of the Cretaceous oceans when black shales formed in anoxic events. Using geochemical, isotopic and molecular records, **Peter Hoffman** (University of Köln, Germany) showed that the development of anoxia was preceded by a rise in atmospheric CO₂. This rise in CO₂ led to a period of warm, wet conditions on land where increased continental run-off led to increased nutrient influx to the oceans where estuarine circulation developed. These increased both sea-water stratification and export production, forming organic rich black shales in anoxic events.

Using techniques more familiar to Cenozoic studies in deep time, the Devonian in this case, **Michael Stephenson** (British Geological Survey, Keyworth) examined a single cycle of lake sedimentation in the Orcadian Basin lakes of Caithness, Scotland. This cycle exhibited a transition from deeper to shallower facies. Carbon isotopic values became progressively more negative as the relative proportions of algae to plant matter changed within the palynomorph record, which was mirrored by changes in salinity and pH consistent with shallowing. Assuming the varved lake sediments represent annual laminae, he estimated that this deep-shallow cycle lasted 3,000 years, most likely a consequence of lake infilling rather than climate *per se*.

Such fine scale cyclicity has also been identified in Silurian sequences. **Ken Dorning** (Pallab Research & University of Sheffield) demonstrated cyclic variation in phytoplankton abundance and diversity corresponding to the deposition of limestone–mudstone couplets on shelf successions of



the Baltica palaeocontinent. The average duration for the cycles was estimated at 2.6 Ka, which – along with an observed facies control on preservation – suggested that the detailed bed-by-bed pattern represents shallow water sedimentology rather than orbitally-forced climate change.

Having traced evidence for millennial-scale events in the geological record from the Holocene through to the Silurian, it was time for **Maurice Tucker** (University of Durham) to provide a round-up. Maurice showed how ice-volume changes controlled millennial-scale events in glacial environments, as seen in the morning's talks on the Pleistocene; whereas, changes in solar radiation tend to control such events in stadials as we had heard in the afternoon's talks on the Holocene. Then, with the present being the key to the past, he applied these observations to interpret insolation and ice-sheet driven millennial-scale events in two carbonate sequences, from the Triassic greenhouse and the Carboniferous icehouse respectively – a uniformitarian approach of which Lyell would have been proud – and thus it became time for the past to be the key to the present, with delegates musing over the day's proceedings in the traditional post-meeting reception.

Tom Challands

University of Durham

Alex Page

University of Leicester



Canada Research Chair – Tier 2 (Micropaleontology)

Department of Earth and Atmospheric Sciences

Department website: <<http://easweb.eas.ualberta.ca/>>

Competition Deadline: will remain open until filled.

The Department of Earth and Atmospheric Sciences at the University of Alberta invites applications for a tenure-track position at the Assistant or Associate Professor level in the field of Micropalaeontology. Specific applications of interest include systematics, biostratigraphy, sedimentology, and palaeo-environmental reconstruction. The successful candidate will be nominated for a Canada Research Chair Tier II (<<http://www.chairs.gc.ca/>>).

The Department has exceptional research strengths in the areas of palaeontology, stratigraphy, and sedimentology, and offers an Honours programme in palaeontology in conjunction with the Department of Biological Sciences. The successful candidate will contribute to these strengths by developing an active research programme that includes the supervision of M.Sc. and Ph.D. students, by collaborating with other faculty members, and by teaching courses at the undergraduate and graduate level. Applicants must hold a Ph.D. degree at the time of appointment and have a strong research record. The closing date for applications is 1st April 2006, or when a suitable candidate is found. The start date for this position is 1st July 2006. Early applications are encouraged.

Applications should include a curriculum vitae and statements of research and teaching interests. Candidates should arrange for at least three confidential letters of reference to be sent to:

Dr Martin Sharp, Chair
Department of Earth and Atmospheric Sciences
1-26 Earth Sciences Building
University of Alberta
Edmonton, Alberta T6G 2E3

For more information about the Department and the University of Alberta, please see the Department's web page, at <<http://easweb.eas.ualberta.ca/>>.

All qualified candidates are encouraged to apply; however, Canadian and permanent residents will be given priority. If suitable Canadian citizens or permanent residents cannot be found, other individuals will be considered.

The University of Alberta hires on the basis of merit. We are committed to the principle of equity in employment. We welcome diversity and encourage applications from all qualified women and men, including persons with disabilities, members of visible minorities, and Aboriginal persons.



>>**Future** Meetings of Other Bodies



**Palaeobotany Specialist Group of the Linnean Society of London,
Spring Meeting 2006: a life of ferns and seed ferns**
Montpellier, France April 2006 (*provisional*)

This is the initial announcement for a meeting to be held in Montpellier, the city where Jean Galtier has spent his academic life. Presentations will be on topics of special interest to Jean, specifically the early radiations of ferns and seed ferns. The meeting will [hopefully] be accompanied by an excursion visiting famous fossil plant localities in the south of France. Additional details will be made available shortly. Meeting organisers: Brigitte Meyer-Berthaud (e-mail <meyerberthaud@cirad.fr>) and Nick Rowe (e-mail <nrowe@cirad.fr>) (Montpellier, France).



Development, Morphology, Evolution: The Triple Helix
Edmonton, Alberta, Canada 4 May 2006

The inaugural symposium of the newly created “Comparative Morphology & Development” section (CMD) of the Canadian Society of Zoologists (CSZ) will take place at the 45th annual CSZ meeting in Edmonton, Alberta, Canada (2–6 May 2006).

Confirmed speakers for the Symposium on 4th May include:

Dr Brian K. Hall, Dalhousie University

“Penguins, Platypus, *Peripatus* and *Polypterus*: Embryos in Evolution”

Dr Nick Butterfield, University of Cambridge

“From Microbes to Morphology: The Cambrian Explosion and Origins of the Modern Biosphere”

Dr Mark Q. Martindale, University of Hawaii

“The Evolution of Morphological Complexity: Developmental Tails (*sic*) from an Anemone Embryo”

Dr Phil Currie, University of Alberta

“On the Shoulders of Giants: Development, Size and the Evolution of Tyrannosaurid Dinosaur Crania”

Dr Mimi A.R. Koehl, University of California–Berkeley

“Sniffing with Hairy Noses: Fluid Mechanics and Convergent Evolution of Odor Capture by Antennae”

To register to attend this exciting symposium – or to submit an abstract for a talk to be given in one of the many related contributed paper sessions on Larval Biology, Biomechanics & Functional Morphology, Palaeobiology, or Evolution of Development – visit the the CSZ 2006 Meeting website: <<http://www.biology.ualberta.ca/csz2006/index.htm>>

Deadline for Early Registration and abstracts is 15th February 2006.



Don't miss this opportunity to attend the memorable and historically significant launch of the Comparative Morphology & Development section of the CSZ. To learn more about the goals, history, inaugural symposium, student awards and other activities of the CMD section, visit the section's website: <<http://www.biology.ualberta.ca/CMD/home.htm>>



Biology and Palaeobiology of Foraminifera and Coccolithophores

Liverpool, UK 25–26 May 2006

This is the Micropalaeontological Society's Foraminifera and Nannofossils groups Joint Spring Meeting 2006.

The meeting will continue the tradition of promoting contact and exchange of ideas between workers in their respective groups, and of encouraging cross-links between the disciplines and the expertise. For the 2006 meeting we will focus on the biological background of foraminifers and coccolithophores, their physiology, functional morphology, and ecology. We also encourage presentations of new approaches to study of palaeoecology and palaeoceanography based on enhanced understanding of the biology of the organisms. Whilst we would encourage people to follow this broad theme, this is an open meeting and we will still be pleased to accept presentations covering other aspects of calcareous nannofossil and foraminiferal research.

Students and professionals are encouraged to present updates of their research, techniques, industrial applications, and software. The concept is a work meeting and therefore it is especially of interest for MSc, PhD Students and PostDocs to present the status of their research. Oral presentations are welcome and posters will be on display during poster sessions and coffee breaks. The registration fee will be in the order of £20. Additional information about the meeting (abstract submission, deadlines, schedule *etc.*) and field trip will be available on The Micropalaeontological Society's web pages (<<http://www.tmsoc.org/>>). Anyone wishing to contribute a presentation or a poster is kindly asked to send an expression of interest and a title of the presentation to Daniela Schmidt (e-mail <d.schmidt@bristol.ac.uk>; Message subject: "TMS-FG& NG ABSTRACT"). Also please indicate whether you will participate in the field excursion.

The meeting will be followed by an excursion to the Lake District on Saturday 27th to Sunday 28th May 2006. The field trip will be led by Dr Richard Worden, University of Liverpool, and focus on past sedimentary environments, from deep-sea plains to mountain belts and deserts. The Lake District National Park shows a 300 million years stratigraphic record with key sections of sedimentary geology and tectonics exposed in numerous abandoned mines and quarries. This trip will provide a splendid opportunity to see how palaeoenvironmental changes left their traces in the geological record and how a landscape is formed by the oscillations of late Quaternary ice ages. The cost, including transport and accommodation, will be around £80 to £100.

Organising committee:

Jens Herrle (University of Liverpool)
Daniela Schmidt (University of Bristol)
Joachim Schönfeld (IFM GEOMAR Kiel)
Jeremy Young (Natural History Museum)

**IPC 2006: The Second International Palaeontological Congress**

Beijing, China 17 – 21 June 2006

Following the successful IPC 2002 in Sydney, the Second International Palaeontological Congress will be hosted in Beijing. The conference theme is 'Ancient Life and Modern Approaches', and there will be a wide variety of plenary sessions, general and topical symposia, short courses, workshops and special group meetings. The programme will also feature field excursions to the fossil sites that have helped Chinese palaeontology to grab so many headlines in recent years.

For further details visit the website at <<http://www.ipc2006.ac.cn/>>

First announcement: There will be a topical symposium on **The evolutionary history of vent, seep and other chemosynthetic ecosystems** at the Second International Paleontological Congress in Beijing 2006. This symposium is dedicated to the evolutionary history of deep-sea chemosynthetic ecosystems, principally hydrothermal vents and cold seeps, but also whale and wood falls. The fossil record provides direct evidence for evolutionary and ecologic changes in these environments from Precambrian microbial communities to the origin, biodiversity and biogeography of the modern vent and seep fauna. We are looking forward to an interdisciplinary symposium covering a wide range of topics including, but not restricted to, micro- and macropalaeontology, ecology, phylogeny and fossil history of vent- and seep-related groups, and geological, sedimentological, geochemical and biogeochemical aspects of ancient chemosynthetic ecosystems. This is your platform to present and discuss new ideas, new methods, and of course, new sites!

Conveners: Steffen Kiel (Smithsonian Institution), Crispin T.S. Little (University of Leeds), Jianghai Li (Peking University). If interested, let us know <kiels@si.edu>

Mark the dates in your calendar:

- 17–21 June 2006, Second International Palaeontological Congress in Beijing
- 1st March 2006, registration deadline for early birds
- A second circular about the congress will be posted by the end of October 2005

For further information go to <<http://www.ipc2006.ac.cn/index.asp>>.

**9th Symposium on Mesozoic Terrestrial Ecosystems**

Manchester, UK 27 – 29 June 2006

All aspects of Mesozoic terrestrial ecosystems, ranging from protists to plants to dinosaurs, will be covered at this international symposium, which will include over 50 platform presentations and 20 poster contributions. A pre-symposium fieldtrip will take in the classic English Cretaceous localities on the Isle of Wight and Isle of Purbeck, while a post-symposium trip will visit the Jurassic sequences of the Yorkshire Coast. Plenary speakers include David Krause (Stony Brook) on the Late Cretaceous faunas of Madagascar, Kirk Johnson (Denver) on floral events at the K/T boundary, and Xu Xing (Beijing) on the feathered dinosaurs of Liaoning.



The Fourth Circular (including the registration form) is now available online at <<http://homepage.mac.com/paulselden/MTE/>>. This contains details of the meeting (travel, accommodation) as well as a list of the accepted presentations.



Fourth International conference on Trilobites and their relatives
Queensland Museum, Brisbane, Australia 10 – 14 July 2006

Following the successful meeting at Oxford in April 2001 it was thought a good idea to spread the sequence of these gatherings to the Southern Hemisphere. Accordingly you are now invited to the Fourth International Meeting on Trilobites and their Relatives to be hosted in the Queensland Museum, Brisbane, Australia. The Queensland Museum dates from the 1860s. Although it had an emphasis on vertebrate palaeontology until the 1970s it has recently become home to the large earth sciences collections of the University of Queensland and the Geological Survey of Queensland. Most significant among its holdings is the very large amount of Cambrian trilobite material collected by Frederick William Whitehouse during the 1920s–1940s.

The Geosciences Programme is housed in an offsite annex near the airport, whereas the Museum building is in the Queensland Cultural Centre at SouthBank adjacent to the city centre. The programme will entail four days of formal presentations at the Museum and a day at the annex among the collections, and other activities. Papers on any aspect of the conference title will be most welcome as will poster presentations.

A social programme including a conference dinner will be organised for participants during their time in Brisbane.

Field trips will be available before and after the meeting but numbers may be limited due to the logistics of remote field sites. The pre-conference field trip will visit Ordovician to Devonian sites in central New South Wales and the post-conference trip will be to the Lower Cambrian sequence of the Flinders Ranges, South Australia.

The conference proceedings will be published in the *Memoirs of the Queensland Museum* as soon as practicable after the meeting. If possible papers for the Proceedings should be submitted at the meeting so the review process can begin immediately.

Organising Committee

Greg Edgecombe, Australian Museum
David Holloway, Museum of Victoria
Jim Jago, University of South Australia
Peter Jell, Queensland Museum
John Laurie, Geosciences Australia
Ken McNamara, Western Australian Museum
John Paterson, Macquarie University
Andrew Sandford, University of Melbourne
Tony Wright, Wollongong University

If you wish to receive the second circular please contact Peter Jell at the Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia, e-mail <peter.jell@qm.qld.gov.au>.



International Conodont Symposium: ICOS 2006
University of Leicester, UK 17 – 21 July 2006

For further details, see <<http://www.conodont.net/>>.



7th International Congress on the biology of fish
St John's, Newfoundland, Canada 18 – 22 July 2006

During the next International Congress on the Biology of Fish, there will be a symposium on **Biom mineralisation in Fish Bones and Teeth: from Microscopy to Design of Materials**.

This symposium will discuss all aspects of biomineralisation of the hard tissues of fish, including bone, enamel, enameloid, dentine, calcified cartilage, otoliths and scale tissues. The processes involved in biomineralisation are known in part in some mammals, but little understood in fish. Studies on immunodetection of the proteins involved in the mineralization processes of hard tissues in fish are not very widely used, and the genes coding for these proteins are not always identified. That the fine structure of fish teeth shows an enormous diversity has been known since the early studies of Owen in the nineteenth century, but little of this diversity has been studied with modern techniques of microscopy. Specific adaptations of the ultrastructure of fish dentitions, in relation to stress induced during use of the teeth, have implications for biomaterials research and for the design of more effective machinery for industrial processes. Equally, analysis of the fine structure of bone has implications for biomechanics. Improved understanding of all of these aspects of fish hard tissues also has phylogenetic implications, especially for the relationships among problematic groups of fishes, or between fish and other vertebrates. This symposium will bring together ideas from different fields, in biochemistry, genetics, developmental biology, biomaterials and microscopy, and assist in the development of productive new ideas.

For more details see <<http://www.mun.ca/biology/icbf7/>>.

Biom mineralisation symposium organizers: Anne Kemp (University of Queensland) and Gilles Cuny (Geological Museum, University of Copenhagen).



International Congress on Bivalvia
Bellaterra (Barcelona), Spain 22 – 27 July 2006

The congress with venue at the Universitat Autònoma de Barcelona calls together neontologists and palaeontologists with a research focus on bivalve molluscs. Plenary talks include population genetics, evolution of ontogeny, evolutionary palaeontology, biomineralisation and freshwater conservational biology, but contributions need not be restricted to these topics. In addition, there will be a planning session for a new bivalve treatise. Two one-day excursions – one on recent, one on fossil bivalves – will be organised.

Interested persons are asked to register and submit abstracts via the Congress webpage at <<http://bivalvia2006.uab.es>>. Further inquiries may be sent to Niko Malchus (e-mail <n.malchus@gmx.net>).



11th Chilean Geological Congress
Antofagasta, Chile 7 – 11 August 2006

The 11th Chilean Geological Congress organized by the Department of Geological Sciences of North Catholic University (Universidad Católica del Norte) will be held between 7th and 11th August 2006, and will be dedicated to the memory of Mr Renato Fernández Flores, the geologist who contributed significantly to the formation of the Geology programme of this university. The official headquarters of the congress is Universidad Católica del Norte, Antofagasta, 2nd Region, Chile. The official language of the Congress is Spanish, but publications and presentations will also be accepted in English. The programme of the Congress includes: Thematic Sessions, Symposia, Invited Conferences, Scientific Poster Sessions, Field Excursions, Special Meetings, Technical Exhibitions, and Social and Cultural Activities. For further information, including instructions for abstract submission, please visit the congress website at <<http://www.congresogeologico2006.cl>>.



IGCP Project 503: Changing Palaeogeographical and Palaeobiogeographical Patterns in the Ordovician and Silurian
Glasgow, Scotland, UK 30 August – 1 September 2006

This is the third Annual Meeting of IGCP 503, Ordovician Palaeogeography and Palaeoclimate, which aims to develop a better understanding of the environmental changes that influenced the Ordovician biodiversification, the end-Ordovician extinction and the Silurian radiation. It will focus on the changing palaeogeographical and palaeobiogeographical patterns in the Ordovician and Silurian, but contributions on any topic relevant to the aims of IGCP 503 will be welcome. The deadline for abstracts is **1st May 2006**.

The main part of the conference will comprise two and a half days of lecture and poster presentations (30th August to 1st September), a half-day local mid-conference excursion, and various social events including a whisky tasting. There will also be a pre-conference day excursion to the Scottish Southern Uplands, including the Ordovician–Silurian boundary stratotype section at Dob's Linn (29th August), and a three day post-conference trip to the classical Ordovician and Silurian successions in southern Scotland at Girvan and in the Pentland Hills (2–4 September). Further details can be obtained from the IGCP 503 website at <<http://sarv.gi.ee/igcp503/>> or from the conference organiser, Alan Owen, e-mail <a.owen@ges.gla.ac.uk>.



3rd Workshop on Ichnotaxonomy
Prague, Olomouc and Brno (Czech Republic) 4 – 9 September 2006

For further details see

<http://www.gli.cas.cz/GLU_AV/WIT_2006/3rd_workshop_on_ichnotaxonomy.htm>.



Carboniferous meeting “From Platform to Basin”: A field and research conference sponsored by SEPM-CES
University of Cologne, Germany 4 – 10 September 2006

The Carboniferous Conference Cologne 2006 will take place at the Institute of Geology and Mineralogy of the University of Cologne. The heading of this SEPM-CES research and field conference “From Platform to Basin” links a wide range of topics from very different disciplines in Earth Sciences. Field-trips to Belgium and Germany will follow a transect from the inner platform to the deeper basin. Full details, key dates, contacts, and a pre-registration form can be found on the conference website at <<http://www.ccc2006.uni-koeln.de/>>. Please have a look at the website at regular intervals for updates and new information.

Organisers: Hans-Georg Herbig and Markus Aretz (e-mail <markus.aretz@uni-koeln.de>).



The 7th European Paleobotany–Palynology Conference (EPPC)
Prague, Czech Republic 6 – 11 September 2006

For further information, see the circular which is on the meeting website (in PDF format) at <<http://www.natur.cuni.cz/eppc2006/circular.pdf>>.



PSSA 2006: Biennial Meeting of the Palaeontology Society of South Africa
Albany Museum/Rhodes University, South Africa

Every two years a meeting of the Society is arranged at a different venue in Southern Africa. The format of the meetings, usually over a five day period, is three days of conference proceedings (papers and posters, *etc.*) and the Biennial General Meeting of the Society. The last two days are devoted to a field trip to sites of palaeontological interest in the district.

If you would like to attend the PSSA'2006 meeting at Rhodes University and the Albany Museum in Grahamstown, please contact Dr Billy de Klerk (e-mail <b.deklerk@ru.ac.za>) or Dr Rose Prevec (e-mail <rose.adendorff@ru.ac.za>) for more details.

Billy de Klerk, Curator: Earth Sciences, Albany Museum, Somerset Street, Grahamstown, 6139, South Africa, tel (046) 622-2312, fax (046) 622-2398, e-mail <b.deklerk@ru.ac.za>.

For further information see <<http://www.ru.ac.za/affiliates/am/pssa/pssameet.html>>.



FORAMS 2006: International Symposium on Foraminifera

Natal, Brazil 10 – 15 September 2006

Register now to ensure your participation on field trips, workshops, and other events. Updated meeting information (Scientific Programme for Technical Sessions and Workshops, and much more), online registration forms, and information for the submission of abstracts are available now at the FORAMS 2006 websites so you may register at any time.

The Web addresses are:

New address: <http://www.fgel.uerj.br/forams2006/>

Mirror site: <http://forams2006.micropress.org/>

Please note that the final acceptance of abstracts for all presentations depends upon full payment of the registration fees, which will be opened in July 2005 and should be received by 30th June 2006. Only registered participants will be allowed to attend the meeting.



The International Symposium on Foraminifera (FORAMS 2006)

Piramide Palace Hotel, Natal 10 – 15 September 2006

Technical sessions will consist of four days of talks and posters (11–12, 14–15 September), supplemented by social events.

For further information, see the meeting website at
<<http://www.labgis.uerj.br/forams2006/general.htm>>.



66th Annual Meeting of the Society of Vertebrate Paleontology

Ottawa, Canada 18 – 21 October 2006

Location: Marriott Ottawa Headquarters Hotel (<<http://www.marriott.com/>>) and Crowne Plaza (<<http://www.crowneottawa.ca/>>), Ottawa.

For further information, see the vert-paleo website at
<http://www.vertpaleo.org/meetings/future_meetings.html>.

**The Global Triassic**

Albuquerque, New Mexico, USA 23 – 25 May 2007

This international symposium will be devoted to all aspects of the Triassic System, with particular focus on the Triassic timescale and Triassic biotic events. It will be an official meeting of the IUGS Subcommittee on Triassic Stratigraphy, and a final meeting of IGCP 467 on *Triassic Time and Correlation*. The meeting will be three days of talks and posters at the New Mexico Museum of Natural History in Albuquerque. Planning for pre-meeting and post-meeting field trips is underway, and the trips will be announced in the second circular. They will afford an opportunity to visit several classic marine sections including Fossil Hill (A–L), South Canyon (L–C), and New York Canyon (T–J), as well as classic nonmarine Triassic sections in New Mexico–Arizona. For further information please contact Spencer G. Lucas, New Mexico Museum of Natural History, 1801 Mountain Road N.W., Albuquerque, NM 87104, tel: 505-841-2873, fax: 505-841-2808, e-mail <spencer.lucas@state.nm.us>.

**40th Anniversary Symposium on Early Vertebrates/Lower Vertebrates**

Uppsala, Sweden 13 – 16 August 2007

In August 2007, Uppsala University will be hosting the Symposium on Early vertebrates/Lower Vertebrates, the latest in a series of meetings initiated in Stockholm in 1967 by the Fourth Nobel symposium, “Current Problems of Lower Vertebrate Phylogeny”. The meetings are not linked to any society, but have been hosted by institutions in different countries on a running 3–4 year rotation. In 2004, the symposium was held in Gramado, Brazil; previous symposia have included Paris 1995, Miguasha (Québec) 1991 and Beijing 1987.

The Symposia on Early Vertebrates/Lower Vertebrates are the only recurring international meetings targeted specifically at the Palaeozoic vertebrate research community. As such, they draw a broad international field of very high profile speakers, including most of the acknowledged leaders in early vertebrate research. The meetings are friendly and informal, usually with no more than about 100 delegates, making them outstanding venues for young researchers to meet the established figures in their fields and build up contact networks.

Poster and platform presentations are accepted on an open competitive basis (there is usually room for all the posters); there are normally no invited speakers. Topics of presentations usually range from the earliest chordates, through Palaeozoic agnathans and fishes, up to the origin and early radiation of tetrapods. Platform presenters are invited, but not required, to contribute papers to a symposium volume. Past volumes such as “Current Problems of Lower Vertebrate Phylogeny” (ed. Ørvig, 1968), “Early Vertebrates and Related Problems of Evolutionary Biology” (eds. Chang, Liu & Zhang 1991) and “Studies on Early Vertebrates” (eds. Arsenault, Lelièvre & Janvier 1995) have all become major landmarks in this area of palaeontology.

2007 is not only the 40th anniversary of the first Symposium, but also the 300th anniversary of the birth of Linnaeus – Professor of Botany at Uppsala University and one of the most influential biologists of all time. In this jubilee year, we are delighted to invite you to Uppsala, to attend what



we hope will be an outstanding meeting on the early evolution and palaeontology of the Vertebrata.

Symposium e-mail address: <EarlyVertebrates2007@ebc.uu.se>.

Organising committee:

Per Ahlberg: <Per.Ahlberg@ebc.uu.se>

Catherine Boisvert: <Catherine.Boisvert@ebc.uu.se>

Henning Blom: <Henning.Blom@ebc.uu.se>

Daniel Snitting: <Daniel.Snitting@ebc.uu.se>

Martin Brazeau: <Martin.Brazeau@ebc.uu.se>

Gaël Clément: <Gael.Clement@ebc.uu.se>

Rose-Marie Löfberg: <Rose-Marie.Loftberg@ebc.uu.se>



International Federation of Palynological Societies

Bonn, Germany August 2008

The next International Palynological Congress will be in August 2008, in Bonn, Germany (see <http://www.uni-bonn.de/en/The_University.html>). For further details please refer to <<http://www.geo.arizona.edu/palynology/ifps.html>>.

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

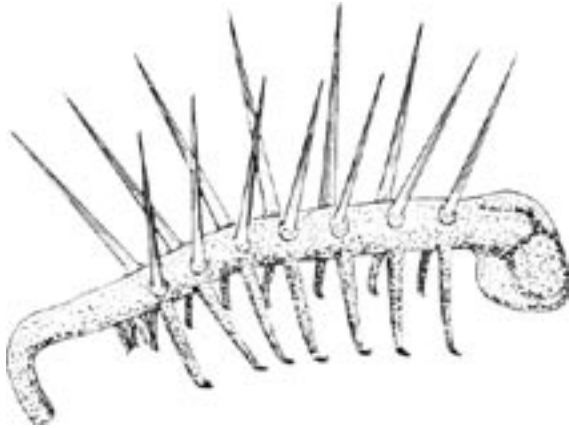


Progressive Palaeontology 2006

Cambridge

22–23 June 2006

Department of Earth Sciences,
University of Cambridge



CALL FOR ABSTRACTS

Abstracts are invited for the forthcoming *Progressive Palaeontology*, an annual conference for postgraduate students who wish to present their results at any stage of their research. Presentations on all aspects of palaeontology are welcome.

The Itinerary will include:

- One day of oral and poster presentations
- Reception at the Sedgwick Museum, Cambridge
- Dinner at Selwyn College
- Fieldtrip to the Oxford Clay of Cambridgeshire

Online registration and abstract submission at <<http://palass.org/>>

Deadline for abstract submission: **14th April 2006**

Deadline for registration: **12th May 2006**

For further information contact:

Susannah Maidment <smai03@esc.cam.ac.uk>

Tom Harvey <thar04@esc.cam.ac.uk>

Supported by Oxford University Press and the Sedgwick Museum.

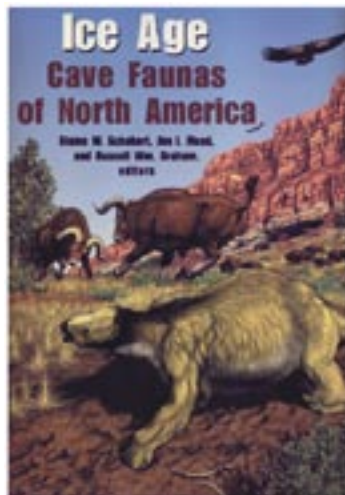


Book Reviews

Ice Age Cave Faunas of North America

Blaine W. Schubert, Jim I. Mead and Russell W. Graham (eds) (2003).
Indiana University Press, Bloomington, Indiana. ISBN 0-253-34268-6.
\$65.00 (hardcover).

Despite the comprehensive nature of the title, this publication in the *Life of the Past* series aims to gather information on several studies of North American cave faunas from the United States and Mexico. The book had its origins in a cave palaeontology symposium at the National Speleology Society convention in the Summer of 1997 in Sullivan, Missouri. It is well edited, clearly written, and focuses on descriptions of Pleistocene vertebrates and their geological settings, with emphasis on palaeoenvironmental and taphonomic analyses. The editors state that the book “should appeal to students, professional and amateur palaeontologists, biologists, geologists, speleologists and cavers.” I agree, with the proviso that the presentation is quite technical for most amateurs.



The book opens with a dedication to the late Dr Elaine Anderson, probably best known for her work with the late Bjorn Kurtén on the book *Pleistocene Mammals of North America*. Elaine worked on many cave faunas in Western United States and was a prime mover on the Porcupine Cave Project at the Denver Museum of Nature & Science. A most appropriate tribute.

Following the Contents and a list of contributors (17) there is a useful three-page Preface. The book closes with a comprehensive seven-page Index.

Of the 11 studies, each given a chapter, two provide a sense of the evolution of mammalian groups and their biogeography. For example Gregory McDonald, a well-known expert on ground sloths, deals with the extinct genera *Megalonyx*, *Nothrotheriops*, *Paramylodon* and *Eremotherium* (including the largest of North American ground sloths) from caves in the United States and Mexico. It is worth noting that the stable, dry environments in the caves since the Pleistocene have preserved soft tissues such as muscle, skin and hair, as well as dung (coprolites). Having excavated in Rampart Cave, Arizona, I (Harington, 1972) clearly recall my surprise that a section through the fossil-bearing beds consisted entirely of units of *Nothrotheriops* dung separated by stringers of bat guano! McDonald also notes the important historical connection that the first reported North American ground sloth came from a cave and was described by Thomas Jefferson, third president of the United States. And Russell Graham describes a Pleistocene tapir from Hill Top Cave, Kentucky,



and reviews the palaeoecology and Plio-Pleistocene biogeography of United States tapirs. He finds that although New World tapirs occupy tropical and subtropical environments they could tolerate relatively cold temperatures during the ice age.

Through the committed work of Ernest Lundelius and his students, many cave faunas have been studied from the karst region of the Edwards Plateau, central Texas. Lundelius provides a history of and summary of such studies which extend back to O.P. Hay's (1920) report on a fossil fauna from Friesenhahn Cave. Several archaeological sites were excavated in the region in the 1930s. Palaeontological investigations resumed in the late 1940s, when the Texas Memorial Museum of the University of Texas excavated in Friesenhahn Cave. That cave has produced a nearly complete postnatal growth series of the scimitar cat (see particularly the articulated skeleton of an adult depicted in Figure 8-3). Based mainly on these specimens, Rawn-Schatzinger (1983) has produced the "bible" on that species. It is worth noting that scimitar cats extended as far north as Alaska and Yukon in the Late Pleistocene – it and the American lion were the largest cats in Eastern Beringia during that period (Harington, 1996). No further work was carried out until the late 1950s when Lundelius and his students began a long-term analysis of bone-bearing caves in the region. Since then, 37 localities have produced faunal material extending from the last interstadial to the present. Suggestions for future work include: a better coverage of parts of the Edwards Plateau not presently represented; an investigation of some known sites that might extend the time-depth of our faunal knowledge; more radiocarbon dates on specimens from known localities; and systematic isotopic studies of specimens already collected in order to provide important information on diet and climate.

Fossils can also help in dating cave deposits. Alisa Winkler and Wulf Gose report on ice age mammal remains from two localities, Fyllan Cave and Kitchen Door, also on the Edwards Plateau, Texas. These caves are handy for study, being within the city limits of Austin. Two methods of age determination, mammalian biochronology and palaeomagnetism, corroborate an Early Pleistocene age for these cave faunas. Palaeoclimate was likely warm, more humid than at present, but lacking today's Summer and Winter extremes.

I found one of the most interesting chapters in the book was on the cave faunas of Prince of Wales Island, Alaska, probably because I am presently describing the large vertebrate remains from Bluefish Caves, Yukon (see the following section on these caves). Whereas Bluefish provides an insight into Late Pleistocene faunas of the interior of northwestern North America, Timothy Heaton's and Frederick Grady's research on Prince of Wales Island is becoming a standard for coastal marine environment in the same region during that period. A diverse fauna of fishes, birds and mammals has been identified spanning the past 50,000 years, although only the mammalian fossils have been adequately radiocarbon dated. Interestingly, a sea-ice fauna consisting of ringed seal, harbour seal, Steller sea lion and arctic fox was present during the Last Glacial Maximum – the first species being adapted to giving birth to pups on land-fast ice. A surprising record is that of a probable saiga antelope dating to before the Last Glacial Maximum (about 34,000 RCYBP). This specimen suggests an early connection with Siberia via a Bering Isthmus. Saigas did not extend south of the continental glaciers in North America. Perhaps DNA analysis of this bone would help to confirm the identification. The systematic, carefully considered study of these cave faunas, including taphonomic and isotopic analyses, and extensive (137) radiocarbon dates on bone, are exemplary. Although not discussed in this chapter, Dixon *et al.* (1997) state that two Accelerator



Mass Spectrometry (AMS) radiocarbon dates on bone from On Your Knees Cave document the oldest reliably-dated human in Alaska to about 9,800 RCYBP. These and other data (Hall, 1999) help to support the hypothesis for an early human migratory route along the Pacific coast of North America (see also the following section on Port Eliza Cave).

After the maximum glacial advance reached its southern limits between about 21,000 and 15,000 years ago, there were several marked changes [e.g. rapid reorganization of biological communities, dispersal of people into the Americas (but see the following section on Bluefish Caves for earlier evidence of people), and megafaunal extinction]. Blaine Schubert's analysis of Little Beaver Cave, Missouri, employs vertebrate fossils, especially small mammals, to reconstruct some of these events in the mid-continent. Seven radiocarbon dates on three of the 36 mammalian species represented in the cave yielded ages between 13,000 and 9,900 RCYBP. One, on an armadillo scute of $11,000 \pm 60$ RCYBP, provides the latest reliable North American date on this genus prior to the entry of *Dasyops novemcinctus* in the 1800s. As a result of his study Schubert suggests that, near the end of the Pleistocene, the Central Ozarks retained a strong boreal component; a cool, moist, and agreeable climate; and a mosaic of open coniferous/deciduous forests with intermixed grasslands.

Holocene (the past 10,000 years of earth history) cave deposits can provide an important record of the evolution of modern ecosystems. Caves containing such deposits are often studied by archaeologists rather than vertebrate palaeontologists because they may contain traces of early human activity. Following this theme, Carmen Jans-Langel and Holmes Semken report on Late Pleistocene and Late Holocene small mammal remains from Duhme Cave, Iowa. This Late Wisconsinan fauna (17 species) is radiocarbon-dated at about 22,000 RCYBP, and is dominated by boreal taxa (yellow-cheeked vole and arctic shrew) that no longer occupy the area; and a specimen of the collared lemming represents tundra associations. Analysis of the faunal composition suggests that pre-Wisconsinan climate near Duhme Cave was about 14°C cooler in Winter and 6°C cooler in Summer than at present. The best analogue (showing maximum sympatry) for this fauna is in central Alberta. Probably a mosaic of coniferous/deciduous forest with prairie (a parkland?) dominated the landscape around the cave entrance. The Late Holocene fauna began accumulating some 2,600 years ago – presumably after the cave was sealed for about 18,000 years. The greatest change in relative abundance of small mammals probably occurred since the mid-nineteenth century with the introduction of European cultivation.

There are many ways in which faunal remains get into caves. Natural trap or pit caves collect animals that inadvertently fall into the cave and are trapped. Christopher Bell and Jennifer Glennon describe aricoline rodents from Screaming Neotoma Cave, a natural trap cave on the Colorado Plateau. Their study focuses on the palaeogeography and palaeoecology of one specific aricoline rodent, the sagebrush vole, which does not occur in the area today. Although other material was collected from the surface of the cave floor, sagebrush vole and other vole (*Microtus*) remains were deposited between 30,000 and 25,000 RCYBP. Although the sagebrush vole is known from many Pleistocene localities in New Mexico, there are few fossil records from the Colorado Plateau, and the species is not found today in either Arizona or New Mexico. Estimates of regional mean annual temperatures up to 5°C lower than present fit with Harris's (1990) hypothesis that cooler Summers and more effective Winter precipitation could explain the presence in Arizona and New Mexico of populations of small mammals such as the sagebrush vole, that are typically found today in the Great Basin.



Cave taphonomy is complex, and often faunal deposits reflect several taphonomic pathways (ways in which the remains enter the cave). Jim Mead, Larry Coates and Blaine Schubert describe new finds from seven remote caves and one crevice in the eastern Grand Canyon, Arizona. These sites illustrate many of these taphonomic pathways and provide valuable information about palaeoenvironments and past communities. The remains (either directly radiocarbon-dated or coming from sediment layers with age control) extend from Mid-Wisconsinan (about 50,000–25,000 RCYBP) to late glacial (about 15,000–11,000 RCYBP) time. Five taxa (short-horned lizard, ringneck snake, sagebrush vole, ground squirrel and shrub ox – a primitive muskox) have not been previously reported from the Late Pleistocene of the Grand Canyon. Clearly the Late Pleistocene faunal communities of the region have yet to be adequately described.

The final two chapters of the book examine Mexican cave faunas. Joaquín Arroyo-Cabrales and the late Ticul Álvarez present a preliminary report on the Late Pleistocene and Holocene (30,000–500 RCYBP) mammals of Lotlún Cave, Yucatan. Sixty-eight species in ten orders are recorded, including seven that are extinct. Skeletal remains of small species were likely introduced by predatory birds, whereas medium to large mammals were likely victims of the natural trap at the cave entrance. Palaeoclimatic inferences based on the fauna indicate increased humidity during the Pleistocene. Finally, Arroyo-Cabrales and Oscar Poloro summarize the Pleistocene cave palaeontology of Mexico, providing a baseline for future work there. The remains include 173 species – more than half of the known number of Pleistocene mammal species in Mexico. The bone deposits in all these caves have been assigned to the Late Pleistocene, but only San Josecito Cave in east-central Mexico has been radiocarbon-dated. This national survey is a reminder that no Canadian cave faunas are mentioned. Indeed, the book should have been titled “*Some Ice Age Cave Faunas of North America*”, albeit that would not have been so good for marketing purposes!

To help remedy that oversight, some highlights of Canadian ice age cave faunas, as well as references to them, follow.

Caves near Saint-Elzéar and La Rédemption in Gaspésie as well as Mine and Laffèche caves in the Gatineau region have yielded fascinating glimpses of Québec Quaternary faunas (for summaries see Beaupré and Caron, 1986; and Harington, 2003).

Saint-Elzéar Cave, situated on a plateau north of Baie des Chaleurs, has produced remains of three species of amphibians, one species of reptile, four species of birds and 34 species of mammals. About 80% of nearly 4,700 fossils are fragments of small mammals. Several species no longer live in the region, and their presence seems to indicate a period of colder climate (*e.g.* arctic shrew, arctic hare, heather vole, Ungava lemming and least weasel). Due to soil chemistry, the bone seems unsuitable for radiocarbon dating (LaSalle, 1984; LaSalle and Guilday, 1980). However, maybe a few of the cold-adapted species should be sampled for AMS radiocarbon dating.

Preliminary collections of faunal remains from sediments in caves near La Rédemption (Trou Otis and Spéos de la Fée) have yielded seven mammal species (*e.g.* eastern long-eared bat, Ungava lemming, American porcupine, red fox, grizzly bear, caribou and moose). The lemming and grizzly bear are of great interest because of their rarity in the faunal record of eastern North America. I postulate that they occupied Gaspésie when patches of tundra-like habitat existed there, perhaps in early postglacial time (Harington, 1980).



Located some 20 km northeast of Ottawa, Mine Cave is partly a natural trap that has accumulated many bones and teeth which are useful for palaeoecological reconstruction. The upper 100 cm, containing a relatively recent fauna dating back to about 5,000 RCYBP, is characterized by black bear, white-tailed deer, raccoon, mouse (*Peromyscus*) and big brown bat (Carrier, 1989). The bottom 70 cm of infill dates between $8,230 \pm 80$ and $5,020 \pm 70$ RCYBP, and contains remains of fishes, amphibians, reptiles (snakes) and 23 species of mammals, but no black bear or deer. Two species, the woodland vole and Ungava lemming, no longer occupy the area. The former is found mainly in eastern United States, whereas the latter occurs in northern Québec and Labrador, suggesting Holocene range shifts to the south and north respectively. Most small mammals from the lower infill consist of boreal species (Lauriol *et al.*, 2003).

Lafèche Cave is about 27 km north of Gatineau (formerly Hull). Upper and lower levels are joined by an 18 m vertical shaft. Sandy matrix from near the lower (man-made) entrance and up to 80 cm deep has yielded four birds, and about 21 species of mammals (Harrington, 2003). Several arctic-adapted species are represented in this fauna (*e.g.* Snowy Owl, arctic hare, arctic fox, and Ungava lemming) suggesting the presence of tundra-like conditions following the retreat of Laurentide ice from the region in lateglacial time. Indeed, an arctic fox mandible yielded a date of $10,800 \pm 90$ RCYBP. (Another date from an unidentified bone is $9,310 \pm 80$ RCYBP). It is worth noting that such species retreated northward with the melting Laurentide Ice Sheet, until, at present, they survive in northernmost Québec and Labrador. Perhaps the evidence for Labrador grizzlies fits this hypothesis too (Pigott, 1999).

Two caves worth mentioning in Ontario are Elba and Kelso caves. Both are situated on the Niagara Escarpment. Elba cave is a fissure deposit in Mono Cliffs Provincial Park in south-central Ontario. The entrance is vertical. Howard Savage and crew collected 625 bones of 20 mammalian species from various ledges. Eighteen of the 20 taxa are typical of the present day fauna of Dufferin County. Only two, pika and pine marten (exterminated in the early 1900s), are not part of the local community. The single large pika (extinct giant pika?) femur was recovered on such a ledge 25 m below the surface and yielded an AMS radiocarbon date of $8,670 \pm 220$ RCYBP (Meade and Grady, 1996).

Remains of vertebrates were found in a travertine-cemented dolomite breccia from a demolished cave (Kelso Cave) in the Niagara Escarpment west of Milton, Ontario. They represent American toad, Spruce Grouse or Ruffed Grouse, varying hare, cottontail, giant pika, woodland deer mouse, muskrat, little brown bat and striped skunk. Pollen remains from the matrix with the extinct giant pika (*Ochotona whartoni*) bone suggest an age of about 10,000 years. Mead and Grady (1996) therefore suggest that the giant pika lived, possibly relictually, in southern Ontario into the Early Holocene.

In Alberta, faunal remains from January and Eagle caves are best known. January Cave, at an elevation of 2,040 m, is located on Plateau Mountain in the Front Range of the Rocky Mountains, and is about 100 km southeast of Calgary. The six most common taxa in the cave are pika, hoary marmot, Columbian ground squirrel, wood rat, long-tailed vole, deer mouse and arctic grayling. Shrew, hare, pocket gopher, several small carnivores, and bighorn sheep are also represented. Roughly 90% of all identified fossils were rodents – probably most were derived from raptor pellets and carnivore droppings. Four exotic species (brown lemming, collared lemming, Niobrara prairie



dog and black-footed ferret) were identified. The lemmings (presently occupying northern Canada) and the ferret and prairie dog (characteristic of more southern range in the United States plains) overlapped, so probably the fauna represents a cool, dry Mid-Wisconsinan interstadial according to radiocarbon dates on bone of mixed species extending from about 33,000 to 23,000 RCYBP (Burns, 1991, 2002).

Eagle Cave is situated at an elevation of 1,377 m in the Crowsnest Pass, about 10 km west of Coleman, Alberta. Like January Cave, the sediments were deposited during the Mid-Wisconsinan (more than 33,000–23,000 RCYBP). Pocket gopher and water vole are perhaps the most interesting species in the fauna. The water vole represents the oldest known fossil of the species, and its presence in southwestern Alberta suggests equable climatic conditions during the Mid-Wisconsinan (Burns, 1982, 1987).

Rats Nest Cave, a natural trap, on Grotto Mountain near Exshaw, Alberta, has yielded remains of fish, amphibian, reptile, bird, two species of shrew, two species of bat, pika, snowshoe hare, hoary marmot, two species of ground squirrel, red squirrel, deer mouse, wood rat, three species of vole, muskrat, porcupine, grizzly bear, black bear, wolf, swift fox, mink, long-tailed weasel, wolverine, badger, lynx, deer, wapiti, bighorn sheep, and mountain goat. Radiocarbon dates on bone gave ages ranging from about 7,000 to 2,500 RCYBP (Burns, 1989).

Bluefish Caves, Yukon, located 54 km southwest of the village of Old Crow at an elevation of 250 m, have yielded evidence of episodic human activity from about 25,000 to 10,000 RCYBP. I consider it to be the most significant of Canadian cave faunas because it contains: (1) evidence for the earliest people in North America; (2) a well-marked transition between Pleistocene and Holocene sediments, flora and fauna; and (3) a substantial variety of both larger and smaller mammals adapted to northern conditions. An important specimen from Cave II is a mammoth limb bone flake and its parent core AMS radiocarbon-dated to 23,500 RCYBP (both flake and core were dated, the dates overlapping at one sigma, providing the average date listed). Since the content of the caves constrain the range of taphonomic processes that could account for the breaking and flaking of a large mammoth bone, the flake and core were produced by humans. Further, a split caribou tibia, reminiscent of a broken fleshing tool, has been dated to 24,800 RCYBP. The Pleistocene fauna of Bluefish Caves includes: mammoth, steppe bison, Yukon horse, Dall Sheep, caribou, moose, wapiti, saiga, tundra muskox, American lion, cougar, brown bear, wolf and many smaller mammals including nine species of microtine rodents, birds (about ten species), and fishes. Stone artefacts, made of exotic, high-quality cherts, were mainly found in loess that contained remains of the Late Pleistocene vertebrate fauna (Beebe, 1983; Cinq-Mars, 1979; Cinq-Mars and Morlan, 1999; Morlan, 1989; McCuaig-Balkwill and Cinq-Mars, 1998).

A wealth of information about vertebrates of northeastern British Columbia spanning the last 10,800 years has come from Charlie Lake Cave which is about 7 km northeast of Fort St. John. Following the retreat of Glacial Lake Peace from this site shortly before 10,500 years ago, the gully in front of the cave began filling with sediment, ultimately reaching a depth of more than 4 m. During this process, the site was visited occasionally by people who left stone artefacts and bones as early as 10,500 RCYBP. It was also visited by predators carrying their prey and by various animals that lived in the area. The basal unit (about 10,500–9,000 RCYBP) has produced fossils including remains of suckers and other unidentified fishes. Frogs also suggest nearby lakes or streams. Of the



birds found, evidently Horned Grebe, grouse and ptarmigan, American Coot, Short-eared Owl and Cliff Swallow were most common. Other birds found were Western Grebe, medium-sized grebes, surface-feeding ducks including Green-winged Teal, Mallard, Ruddy Duck, small rail, small wader, Raven and perching birds. Among the mammals, snowshoe hare, ground squirrel, small rodents (including collared lemming) and bison were most commonly represented. Other mammals were large (possibly arctic) hare, woodchuck or marmot, deer mouse, Gapper's red-backed vole, meadow or long-tailed vole, chestnut-cheeked vole, other unidentified rodents, wolf or dog, least weasel, another small weasel and a deer. These fossils indicate that from about 10,500 to 10,000 RCYBP, the landscape was open with some water, marshes and patches of forest; changing to forest about 10,000 years ago. By 9,000 years ago, the fauna was modern (Driver, 1988, 1998a, 1998b, 2001; Driver *et al.*, 1996; Harington, 1996).

Several caves on Vancouver Island, British Columbia, have yielded vertebrate remains. Since 1985, remains of the Vancouver Island marmot have been discovered in four high-altitude cave sites: Clayoquot Plateau, Mariner Mountain, Limestone Mountain and Golden Hinde. Cut marks on bones and artefacts recovered in Mariner Mountain Cave indicate that the remains result from human hunting. Radiocarbon dates show that these sites are prehistoric, ranging from 2,630 to 830 RCYBP. The remains indicate a range decline in this marmot. Although black bear, black-tailed deer, marten and red squirrel are represented in the fauna, the predominance of Vancouver Island marmots suggests that aboriginal people travelled to these remote areas to hunt marmots (Nagorsen *et al.*, 1996).

Although the mountain goat is absent from most Pacific Coast islands, including Vancouver Island, 12,000 year-old skeletal remains were found in Resonance and Pelucidar caves east of Nimpkish Lake on northern Vancouver Island. The caves are 5 km apart and are situated at an elevation of about 800 m. Limb bones of the fossils are within the size range of modern species, suggesting a postglacial origin. Mountain goats probably became extinct on Vancouver Island during the Early Holocene (Nagorsen and Keddie, 2000).

In 1983 cavers discovered skeletal remains of three Early Holocene ($9,830 \pm 140$ RCYBP) black bears from Windy Link Pot Cave, situated at an elevation of about 900 m near Gold River on west-central Vancouver Island. The bears were relatively large. This cave system extends for nearly 10 km underground, with several steep drops in the cave floor, so there are many natural traps. Bones of three black-tailed deer were also discovered nearby. The bones showed no evidence of butchery or carnivore tooth marks so the animals presumably fell to their deaths. Pollen analysis of sediment adhering to the bones indicates that the bears lived in a mixed coniferous forest with a warmer, drier climate than today (Nagorsen *et al.*, 1995; Harington, 1996a).

Port Eliza Cave, a raised sea cave, is located on the northwestern coast of Vancouver Island at an elevation of 85 m – well above the 40 m postglacial sea level maximum. It formed along a fault trace and is 60 m long, varying in height from about 1 to 15 m. A diverse fish, amphibian, bird and mammal fauna (about 3,600 specimens) was recorded from a basal unit of silty–sandy sediment greater than 50 cm deep. The fauna, yielding ages of 18,000–16,000 RCYBP, includes: salmon, threespine stickleback, greenling, pollock, flatfish, Irish lord and possible sculpin, western toad, loon, small alcid, cormorant, duck, Horned Lark, Savanna Sparrow, Townsend's vole, marmot, American marten and noble marten, as well as deer or caribou. Fishes suggest that the seashore was close



enough for predators to have introduced this material to the cave. The terrestrial fauna indicates a cool, open environment with maximum Summer temperatures cooler than present. Humans could have survived here on a mixed marine–terrestrial diet, confirming the viability of the Pacific coastal migration hypothesis for this part of the proposed route (Ward *et al.*, 2003).

On the evidence from the foregoing cave faunas, I think that at least some should have been represented in this book. Perhaps it is reasonable to suggest that a book be published summarizing significant aspects of *most* North American cave faunas following the pithy style of West's (1996) tome on the prehistory of Beringia.

Finally for those who love puzzles, the beautiful book jacket illustration by natural history artist Carl Dennis Buell lacks a caption. My solution to animals depicted in front of a cave in what looks to be Muav limestone is: Shasta ground sloth (foreground); two shrub oxen (*Euceratherium*) jousting like mountain sheep (middleground); bison with extinct mountain goats (background); and California Condors (overhead). All but the ground sloth are represented in Eastern Grand Canyon Caves, Arizona (Chapter 4) and the ground sloth is known from Rampart Cave which overlooks the Grand Canyon (Chapter 1). So I suspect the jacket illustration depicts the edge of the Grand Canyon, Arizona with some of its Pleistocene species. Any other solutions?

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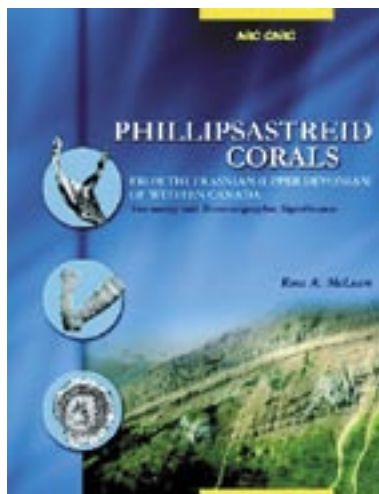
Phillipsastreid Corals from the Frasnian (Upper Devonian) of Western Canada: Taxonomic and Biostratigraphic Significance

Ross A. McLean (2005). NRC Research Press, Ottawa, Ont., 109pp.
ISBN 0-660-19364-7. \$US49.95 (paperback).

The presence of a spectacular rugose coral fauna in the Frasnian of western Canada has been well known for many years, principally through a monograph by Stanley Smith (1945). The phillipsastreids are particularly diverse and abundant, and in recent years Ross McLean has carefully revised and described them in modern terms in a series of high-quality publications of which this is the last. Massive members of the family were dealt with by McLean (1986, 1994a, b). The current monograph considers solitary and branching phillipsastreids, members of the genera *Macgeea*, *Thamnophyllum* and *Penneckiella*. As this completes the current review of the family, McLean also includes a very useful biostratigraphic review of all its members. This involves some refinement of the original zonal scheme for Frasnian rugose corals of western Canada introduced by Pedder (*in* Moore 1993) and substantially modified by McLean & Klapper (1998), who linked it to the conodont zonation originally set up in the Montagne Noire region of southern France by Klapper (1989).



The geographical area from which these faunas derive includes the Mackenzie River basin and Hay River areas of the southern North West Territories and the Rocky Mountains along the British Columbia/Alberta border. Very substantial collections have been made from these areas and a full locality register is provided. The stratigraphy and correlation of the carbonate complexes that dominate the Frasnian of western Canada have been thoroughly reviewed in recent years, largely by Ross McLean and Alan Pedder. This provides a sound basis for the revised coral faunal sequence described here. McLean discusses the biostratigraphic ranges, geographic distributions and palaeoecological preferences of the phillipsastreids with reference to this faunal sequence. Three of the rugose coral faunas in the middle and upper Frasnian are based nominally on members of the family.



In the systematic section of the monograph, McLean describes five species of *Macgeea*, two of which are new, five species of *Thamnophyllum*, three of them new, and four species of *Peneckiella*, two of which are new. As is usual in his work, McLean discusses each genus and the status of possible synonyms in considerable detail, as well as including a full list of species worldwide that he considers belong to each genus. These thorough reviews are particularly valuable to the study of these corals.

Overall this is a well written and generously illustrated monograph, which makes a valuable contribution both to the Devonian coral faunas of Western Canada and to our understanding of the Family Phillipsastreidae worldwide.

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Biogeography: An Ecological and Evolutionary Approach, 7th edition

C. Barry Cox and P. D. Moore. (2005). Blackwell Publishing, Oxford, UK.
ISBN 1-4051-1898-9. £32.95 (paperback).

This is a well written and at times engaging text book designed to form the core readings for a class or seminar in biogeography; its authors are major figures in the field of biogeography. The book falls short, however, in its treatment of a number of particularly important areas of biogeography: its treatment of the fossil record and also phylogenetic methods of biogeographic analysis. For these and other reasons I enumerate below I would have to rank it below competing books by Brooks and McLennan (2002) and Lomolino *et al.* (2005).

It is worth noting that the book does a number of things well. Even though it's in its 7th edition, having been first published in 1973, it does not have that 'long in the tooth feel.' Many of the references that are cited are up to date and current: to a great extent the book seems to have been rewritten for this edition. There are also many high-quality figures, with a few colour plates sandwiched in the middle of the book for good measure.

The introduction of the book is quite strong, arguing for the importance of biogeographic studies at a variety of spatial and temporal scales. Next follows a chapter on the history of biogeography: *de rigueur* for all biogeography texts. The chapter is thoughtful and interesting. Still, I felt there was too much emphasis on Darwin's role in the development of biogeography while other important early scientists were minimized or ignored. Also, concentrating on the flawed example of the so-called Darwin's finches from the Galapagos was a mistake; it would have been more appropriate to point to the mockingbirds and tortoises as examples that actually shaped Darwin's views.

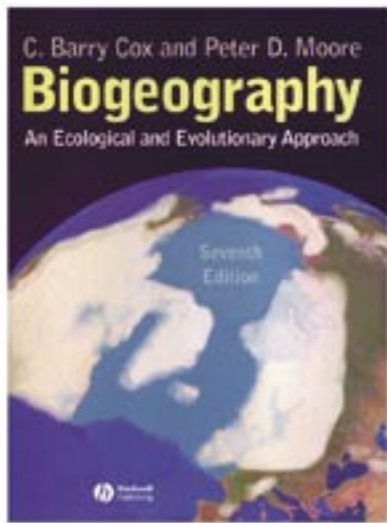
A succeeding chapter on patterns of distribution in the modern biota is useful but paid too little attention to species invasions, and ignored new predictive modelling approaches that can consider the spread of diseases and other invasive organisms using Geographic Information Systems. The view here of the Great American Interchange as a drama of competing continental biotas was also simplistic.

Chapter 5 on communities and ecosystems had several useful examples and was well thought out, but my level of perplexity rose in the next chapter which considered the source of evolutionary novelties. The authors cavalierly pronounce "the fossil record is not sufficiently detailed for us to be certain whether gradualistic evolution or punctuated evolution was involved. In any case, we have no reason to believe that either style of evolution systematically prevails over the other" (Cox and Moore, 2005, p. 158). This throw-away statement could perhaps be seen as a direct challenge to the primacy of the fossil record as our only archive of the history of life. The discussion of allopatric



versus other speciation modes in this chapter also totalled two pages, which is far too parsimonious for a biogeography text.

Meanwhile, Chapter 7 is one of the best in the text and provides a fine discussion of the theory of island biogeography and its strengths and weaknesses. Chapter 8 focuses on the importance of plate tectonics and was clearly done with palaeontologists in mind, including solid, but not detailed, discussions of the origin of mammals and flowering plants. Chapter 9 threw me for a loop as here the authors take on one of the fundamental patterns of biogeography: areas of endemism. This describes the fact that large numbers of species are concentrated in distinct areas separated by geographic barriers. This has been recognized, since the time of Buffon, as evidence that regions with distinct geological histories tend to have biotas with distinct evolutionary histories. The authors argue, however, that the only reason we see areas of endemism today is because of coincidences of current geography and recent climate change. The authors certainly do nothing to test their assertion, nor do they address why areas of endemism can be recognized in the fossil record throughout the Phanerozoic.



In spite of my issues with Chapter 9, the succeeding chapters on climate change, and the way our species is transforming the planet, are quite good. Chapter 12, on biogeographic patterns in the marine realm, focuses too much on dispersal and ecology as the primary processes explaining marine biogeographic patterns, with an absence of evidentiary support. Chapter 13 discusses the value of molecular approaches to biogeography, and in so doing takes a back-handed slap at morphological approaches to the study of evolution. For example, “the structure of organisms is not always a reliable guide to their evolutionary relationships whereas genetic constitution is a firm foundation for classification” (Cox and Moore, p. 369). Such statements might have been acceptable in the early days of molecular systematics, but it is now well known that morphological and molecular approaches often perform on par and both are essential. This section also ignores the contributions palaeontologists have made reconstructing the tree of life.

Another problem with this book is that the reader is forced to wait until the penultimate chapter (14) for a relatively cursory discussion of phylogenetic methods of biogeographic analysis. Moreover, the focus is primarily on the weaknesses of cladistic biogeography. Vicariance and dispersal are discussed here but there is no mention of congruent range expansion or geo-dispersal: involving several independent lineages expanding their ranges due to the fall of geographic barriers triggered by geological or climatic changes. A phenomenon documented to occur in the fossil record (Lieberman, 2000) and one which leaves its imprint on the extant biota (Brooks and McLennan, 2002).

The final chapter on the future of our planet's biota was a bit disappointing. Based on the good discussion in Chapter 9 on climate change and the role of humans as negative agents of biogeographic change, I was expecting an excellent recitation of the serious challenges our



biosphere faces because of our own species. Instead, the authors partly dance around the topic of human-induced global warming and take a somewhat agnostic view regarding the perils we and our cohabiting biota will face because of these and other affronts we are causing. I am somewhat concerned because each of these is backed up by all kinds of scientific data. Unfortunately, Chapter 15 read like one of those false attempts at balance. There are some scientific topics where our desire to show balance may be misguided, and represent false attempts at fairness: one need think no further than the request by some to teach intelligent design and evolution side by side in the 'interests of fairness.'

There is no doubt that this is a solid, well-written book, but its treatment of some hot-button topics in biogeography, like vicariance *versus* dispersal, phylogenetic *versus* other biogeographic methods, molecules *versus* morphology, and the current biodiversity crisis could have been better. This is not a book written with palaeontologists or those interested in systematics in mind. Still, the authors are to be commended for keeping their book up to date, and perhaps the various issues raised here might be corrected in a future edition of the text.

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Crustacea and arthropod relationships – *Festschrift* for Frederick R. Schram

Crustacean Issues 16, eds Stefan Koenemann and Ronald A. Jenner (2005). Taylor and Francis, CRC Press. Boca Raton, London, New York, Singapore. x + 423 pp and 3 colour plates. ISBN 0-8493-3498-5 (hbk \$149.95, £85.00).

Crustacean Issues 16 is dedicated to Fred Schram on his retirement from the University of Amsterdam (he has returned to the United States, where he is now an adjunct at the Department of Biology of the University of Washington, Seattle). Fittingly this is the first volume of *Crustacean Issues* to treat topics other than crustaceans, as it reflects Fred's interests in wider issues of arthropod and metazoan phylogeny. It is the latest in a series of volumes of collected papers that deal with arthropod relationships, following Greg Edgecombe's (1998) *Arthropod fossils and phylogeny*, published by Columbia University Press, and Richard Fortey and Richard Thomas's (1998) *Arthropod relationships*, published by Chapman and Hall. Unlike some volumes published in honour of distinguished individuals, the contributors to *Crustacean Issues* 16 are not limited to Fred Schram's students and close colleagues.

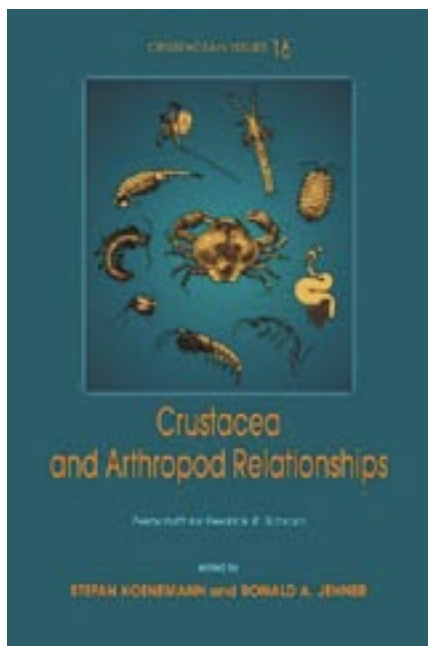
Fred Schram's scientific and other contributions have had an enormous impact. He played a central role in the founding and early organization of the Crustacean Society, becoming its third



president in 1986, the same year as his Oxford University Press book *Crustacea* was published. His most important research to date has been on Carboniferous crustaceans, crustacean phylogeny, arthropod relationships and metazoan phylogeny. Christian Baron and Jens Høeg review the development of Fred Schram's approach to phylogenetics in the *Introduction* to this book, from trenchant supporter of Sidnie Manton's view of a polyphyletic origin for the arthropods to pioneer in the application of cladistics to arthropod and metazoan phylogeny. Fred's advantage and strength has always been an ability to integrate data from living and fossil forms, allowing a total evidence approach to phylogenetic questions. Appendices to this volume provide a list of Fred's publications, and a list of taxa erected by or in collaboration with him – about 100 so far even when new genera and species are counted as one!

Crustacean Issues 16 consists of 14 papers loosely grouped into six sections. Reassuringly, perhaps, like any other multi-authored volume dealing with aspects of arthropod phylogeny, this one includes plenty that is controversial. In their treatment of Early Palaeozoic arthropods (in the section on *Palaeozoology*), Jan Bergström and Xian-Guang Hou argue that agnostids are not trilobites and provide a significant list of ways in which they differ. Dieter Waloszek and colleagues focus on new material of the Orsten arthropod *Oelandicaris oelandica*, providing a much more complete description than was possible over 20 years ago when it was first named by Klaus Müller. They regard *Oelandicaris* as the first offshoot of the stem Crustacea, and their cladogram places agnostids immediately below it – closer to crustaceans than to trilobites. Trevor Cotton and Richard Fortey, on the other hand, provide the first comprehensive cladistic analysis of agnostids (and eodiscid trilobites), and list extensive data in support of a placement of agnostids within the trilobites. Their analysis is based on features of the exoskeleton, whereas a critical element of the evidence for assigning crustaceans to the agnostids is the morphology of the limbs of *Agnostus pisiformis* as described by Müller and Waloszek. This debate is unlikely to be resolved until we know the nature of the adult limbs of agnostids and/or the larval limbs of polymeroid trilobites. In a fourth paper grouped under *Paleozoology*, Carrie Schweitzer and Rod Feldman analyse the history of decapod crustaceans across the Cretaceous–Tertiary boundary. They find a very high survival rate – only 21% of families became extinct – and they suggest that even some of these must have been pseudoextinctions. Geographic distribution is a factor in the extinction, but many taxa survived even in the Chicxulub area.

Many of the difficulties that we face in reconstructing phylogenies hinge on the identification of homology, and on an assessment of which characters are most useful for determining relationships, topics dealt with in the section on *Development and Evolution*.





Steven Hrycaj and Aleksander Popadic emphasize the potential for using genetic networks to establish homologies in limb development. Developmental studies have shown that the mandibles of all arthropods involve the limb base (they are gnathobasic), so that a 'whole-limb mandible' no longer unites myriapods and insects as hypothesized by Manton and used by her to argue for a distinct taxon Uniramia. Gerhard Scholtz and Greg Edgecombe revisit the thorny question of the homology of head segments among arthropods and, based on a new model, they argue that trilobites belong on the stem lineage leading to mandibulates (crustaceans and insects) and not on that leading to chelicerates – *i.e.* trilobites are not part of the arachnomorphs. The identification of trilobites as mandibulates is based on the homology of the trilobite antenna, the great appendage of some Cambrian forms like *Fuxianhuia* and *Parapeytoia*, the first antenna in crustaceans, and the chelicerae of chelicerates. This scheme contradicts others in which the great appendage is regarded as originating in front of the eyes and equivalent to the antenna in onychophorans. The approach, however, emphasizes how critical is evidence about the evolutionary development of the arthropod head to resolving issues of the relationships of the major groups.

In the section on *Comparative morphology* Collette and Jacques Bitsch argue that the nature of compound eyes in Myriapoda indicates a relationship to Hexapoda, although molecular studies group them with Chelicerata. Alessandro Minelli and his colleagues consider appendage regeneration, which occurs in some crustaceans but is absent in myriapods and chelicerates. While the data are not comprehensive and cannot be subjected to a phylogenetic analysis, the occurrence of a similar 'preferred breakage point' supports a relationship between malacostracan crustaceans and hexapods.

The papers in the section on *Arthropod phylogenetics* focus on crustaceans. David Horne and colleagues present a cladistic analysis of living ostracodes based essentially on soft-part morphology: including the characters of the valves introduces much homoplasy. Their data will provide a useful basis for including Myodocopa and Podocopa in analyses of wider crustacean relationships in the future to test, for example, whether ostracodes are monophyletic. Courtney Babbitt and Nipam Patel consider the relationship of crustaceans and hexapods using new 18S and 28S RNA data. The analysis suggests a sister group relationship of hexapods and a monophyletic Branchiopoda. However, more data are required to resolve crustacean relationships – this analysis did not support monophyly of Crustacea, Peracarida or Eucarida. Antonio Carapelli and colleagues use mitochondrial genes to address the same issue. Their result indicates that the hexapods are polyphyletic and that Collembola, Diplura, and other hexapods, all evolved from different ancestral crustaceans! They too concede that more sequence data from more taxa are required. Gonzalo Giribet and colleagues tackle the controversies that surround the placement of crustaceans within the arthropods, as well as the issue of relationships within the crustaceans. They use a total evidence approach (of which Fred Schram would approve!) – analysing data from both morphology and molecules. Their results show that some crustacean groups, including Branchiopoda and Malacostraca, are more stable than others, and they find strong support for a novel clade, combining ostracods and cirripedes. Interestingly they conclude that much of the uncertainty about relationships between the major arthropod groups may simply reflect how the cladogram is rooted.

Fred Schram was one of the first to apply computer-aided cladistic analyses to metazoan relationships. In the final paper in this *Festschrift*, *Playing another round of metazoan phylogenetics*, Ronald Jenner and Gerhard Scholtz explore the robustness of the molecular based Ecdysozoa



(uniting arthropods with other phyla that moult the cuticle) as opposed to the older concept Articulata (grouping arthropods and annelids). While molecular support for Articulata has not been found, the solution obtained with morphological data depends on the selection of taxa and characters coded, and the approach adopted. Issues of metazoan phylogeny remain to be resolved: as Jenner and Scholtz point out, 'phylogenetic research is composed of repeated cycles of data analysis'. This book is such a cycle, albeit one that ranks as a marker in the development of ideas on crustacean and arthropod relationships. As such it is a fitting tribute to one of the major players in this field, but the game is far from over and there are many more rounds to play.

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Trace fossils in evolutionary palaeoecology: Proceedings of Session 18 (Trace Fossils) of the First International Palaeontological Congress, Sydney, Australia, July 2002

Barry D. Webby, M. Gabriela Mángano and Luis A. Buatois (eds.) (2004).
Fossils and Strata No. 51 (containing 10 papers), ISSN 0300-9491. US \$50.00.

Ichnology, the description and interpretation of trace fossils, seems to be experiencing a growth spurt. In recent years it would be unusual for a palaeontology journal not to include several articles on traces per volume, and collections of papers such as the one reviewed here have been rolling out with increasing frequency – including both compilations with a strong biologic orientation (Miller, 2003) and collections of papers emphasizing the traditional applications in sedimentary geology (Pemberton *et al.*, 2001; Hasiotis, 2002; McIlroy, 2004). From my point of view, the more the better: it is a pleasure to see this once quiet corner of palaeontology grow into one of the most vibrant divisions of our discipline. *Fossils and Strata No. 51* extends this encouraging trend, addressing biologic significance and geologic application of trace fossils in a collection of ten important and interesting papers.

In the first contribution, Buatois and Mángano document the composition and environmental distribution of trace fossil associations in the Early Cambrian Puncoviscana Formation of Argentina. They show that a diverse ichnofauna and discernable ichnofacies associations are in place right from the beginning of the Phanerozoic. In the next paper, the same authors describe Cambrian intertidal trace fossils from the Campanario Formation, also in Argentina. The authors describe facies associations along an intertidal–subtidal gradient, tiering structure in varied settings, and properties apparently unique to early Phanerozoic intertidal ecosystems reflected in a rich trace fossil record. These papers add significantly to our knowledge of Cambrian shallow-marine palaeoecology, and would be of interest to anyone working on the Proterozoic–Phanerozoic transition.

The next two articles are devoted to deep-sea trace fossils and controls on their production and preservation. In the first of these, Uchman offers another of his well crafted and thoroughly documented studies of flysch successions, in this case focusing on trace fossil occurrences in the Lower Cretaceous of the Carpathians, controlled by oxygenation and depositional processes. In the second, Kakuwa ventures where few ichnologists have gone before, by documenting an ichnofauna



preserved in Triassic–Jurassic chert successions of Japan. The deep ocean might be viewed as the next frontier of marine palaeoecology, and the ichnologists are (and have been for some time) leading the way here.

Then we come to more familiar territory – estuaries and shorelines. Hubbard, Gingras and Pemberton describe the facies associations and crucial environmental controls on trace fossil patterns in estuarine deposits of the Lower Cretaceous Bluesky Formation of western Canada. They show that although salinity gradient and fluctuations may be an overarching control of distribution patterns, the effects of sedimentation and oxygenation have to be taken into account to explain local variations. Gregory, Martin and Campbell next describe compound trace fossils (different superimposed or interpenetrating ichnotaxa) resulting from plant–animal interactions in Quaternary shoreline-related deposits of New Zealand and Georgia (USA). This is both a kind of ichnological setting and a type of ecologic interaction that is poorly known and deserves more attention. The theme of plant–animal interaction recorded in trace fossils is continued in the contribution by Adami-Rodrigues, Iannuzzi and Pinto, who document the varieties of damage inflicted by insects on Permian plants from southern Brazil. The authors attempt to identify the trace-producing organisms based on the minute patterns and location of the various forms of leaf damage, which have been preserved in extraordinary detail.

The last three articles are rather ambitious review papers. Glaub and Vogel summarize the entire stratigraphic distribution of microborings at the ‘species’ level. The stratigraphic persistence and ecologic conservatism of these forms is truly staggering, with some appearing as early as the Proterozoic and extending to the present day. Braddy follows with a brief overview of the trace fossil evidence for earliest invasions of land by arthropods, concluding that the timing is different for different groups, apparently beginning as early as the Late Cambrian but with the major wave of colonization occurring in the Early Devonian. The volume concludes with another short overview paper in which Carmona, Buatois and Mángano outline the trace fossil record of one of the most important groups of burrowing animals – endobenthic decapod crustaceans. This contribution brings together a scattered literature, and is recommended reading for crustacean specialists, benthic ecologists and trace fossil devotees.

In general, the volume is a well-edited, nicely illustrated piece of work. The editors did us a great service making sure that the presentations in their symposium were made available to a broad readership. Ichnologists would see this collection of papers as a very useful compilation of recent work by some of the leaders in the field.

Because I spend a great deal of time sifting through the recent neobiologic literature, I can’t help but wonder how our colleagues in ecology and evolutionary biology might react to this particular collection of papers and to others like it. I think someone peering in from an adjacent discipline





would have problems understanding the special terminology and methods of ichnology, would wonder at some of the outmoded ecologic notions and in some cases the conflation of traces and trace-making organisms, and the appearance that trace fossil workers seem pretty content to talk to each other and typically do not pursue productive connections to other disciplines (other than sedimentology and stratigraphy, of course). These are issues we need to address – especially in papers and symposium volumes emphasizing biologic properties – as ichnology continues to expand and mature.

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Vertebrate Palaeontology. 3rd Edition

Michael Benton (2004) Blackwell Publishing, Oxford. ISBN 0-6320-5637-1. £31.99 (Paperback).

Twenty years ago – fresh-faced and all a-quiver at my first Palaeontological Association Annual Meeting – I, like many others, was particularly struck by an earnest young postdoctoral student who gave a splendid presentation on rhynchosaur. Not an easy task this, since these squat, tubby, rather ugly-looking creatures who, as the speaker had persuasively argued, probably spent much of the Permian and Triassic face down in the dirt, certainly could not be counted among the more charismatic of the denizens of the past. Still, the talk was rather elegant, so elegant in fact that the speaker was blessed with the President's Prize, and a blessing it proved to be. Twenty years later the one-time rhynchosaur wrangler, rather greyer upon the pate and slightly stouter, is now happily ensconced in his own Chair at Bristol University. The godfather to *Walking with Dinosaurs* (still the most successful TV science series of all time) and one of few palaeontologists whose impact has been felt beyond the narrow confines of our discipline, he is also father to a huge brood of intellectual offspring, scores of whom still ply their trade in the groves of academe, or tread the dusty depths of sunless museum sub-basements the world over. His publication list is practically unrivalled¹ and stuffed with *Nature* papers, edited volumes, a seemingly endless number of dinosaur books, and even the odd monograph on rhynchosaur. There is much worth reading here, but for my money

¹ Reputedly, the most prolific of living vertebrate palaeontologists is Spencer Lucas, of the New Mexico Museum of Natural History and Science, who is well on the way to reaching his 1,000th publication.



the best and most important contribution so far is a textbook that covers the entire field across which this palaeontological colossus has cast his long shadow. That work is entitled *Vertebrate Palaeontology*, now in its third edition, and as many readers of this Newsletter will have already guessed, its author is Michael Benton.

The first edition of Benton's *Vertebrate Palaeontology* appeared in 1991, and it was an immediate hit. Sharp, concise text and myriads of clear unfussy diagrams helped the reader through a good 600 million years' worth of evolutionary history. And what a history it was. Somewhen, down in the Cambrian gloom, something stirred. Was it a sea squirt? Or a lancelet? Or even an acorn barnacle? No one seemed quite sure, but, whatever it was, its resolve was soon to be stiffened by a notochord and, before long, its finny descendants had populated the Palaeozoic seas. Fast forward a few tens of millions of years and the first four-legged fishes could be found hot-footing it from pool to pool. Speed the tape further and their clammy-skinned progeny, encased in scales, spread across the land, and in turn climbed up onto their hind limbs and sprouted feathers, taking to the air as birds. Others sprouted hair instead and bided their time before bursting upon the world in many-splendoured forms that ravaged the plants, or each other, and one of whom erected itself upon its hind limbs and eventually evolved into you, me and Mike Benton.

Mike has the rare gift (both as an author and as a speaker) of being able to take something that is great, big and horribly complicated, like the long, complicated and often highly discursive history of the vertebrates, and turn it into nice, bite-sized lumps that anyone with an interest in palaeontology – from non-professionals to university professors – can easily digest. *Vertebrate Palaeontology* excels at this, rounding up the familiar (sharks, dinosaurs, whales) and not so familiar groups (try getting your mind, or indeed tongue, around 'phlegothontid salamanders', especially after three pints of Dogs Bollocks²) into a well mapped-out menagerie, each in its own neat, compact section. Successive chapters sort of track time because, fortuitously, the appearance of many of the major groups follows a chronological sequence, though inevitably there is some nipping back and forwards. Fish, for example, resurface on several occasions. I also found it slightly odd that the chapter on 'How to study fossil vertebrates' appeared after the chapter on 'Vertebrate origins', but this doesn't detract from the book as a whole.

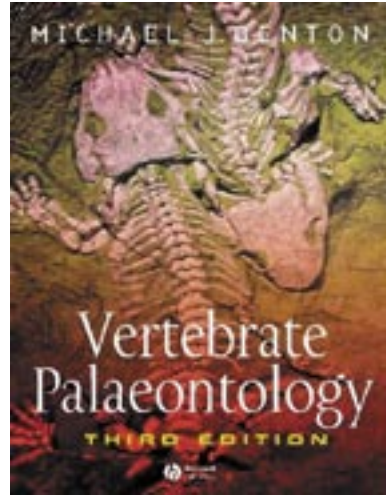
Most of the major vertebrate clades get a fair crack of the whip, although, inevitably, lack of space means that some are dealt with fairly brusquely. In earlier editions mammals were slightly wedged out by dinosaurs and their contemporaries, not that, personally speaking, I have any problem with this. In the third edition they have been given a little more elbow, horn and hoof-room and a chance to show off their once spectacular diversity – the living manifestation of which is but a sad shadow of past glories.

There are several things I particularly like about this book. First, the vertebrate story that it tells is firmly rooted in phylogenetic systematics. This approach has had a profound impact on our understanding of how vertebrate history unfolded and was instrumental, for example, in elucidating what is one of the greatest palaeontological triumphs of modern times, the discovery that birds are merely feathered dinosaurs in the sky.

² One of Mike's favourite amusements is to invite visitors for lunch in a local hostelry and, upon reaching the bar, to call out in a loud voice 'two pints of Dogs Bollocks please' and then burst into hoots of laughter at the look on his visitor's face. In English vernacular, to refer to something as 'the dogs bollocks' (a more euphonious synonym being 'the mutts nuts') implies that it is the best or exceptional, in a positive sense. It is also the name given to a popular brand of beer produced by the Wychwood Brewery in Oxfordshire, England.



Benton figures cladograms for all the main groups, and helpfully lists the apomorphies that support the various nodes. Inevitably, some have proven to be crapomorphies, one consequence being that just when we think that we have got them pinned down, problem groups such as ichthyosaurs, turtles and pterosaurs promptly splash, stagger or flit to another part of the tree. Unfortunately, this means that the sell-by date for at least some of the cladistic content of any modern vertebrate palaeontology textbook has often flown by, even before the tome has been used as the (inaccessible) foundation stone for one of those ceiling-high piles of new books in your local branch of Borders. Still, if this is the price that has to be paid for the admirable vigour of phylogenetic research, it's worth it – and, to be fair, through a blend of pragmatism and judicious choice, Benton has done



much to ameliorate this problem. Better than the cladograms, in my view, are the more traditional, but for all this very welcome and infinitely more interesting evolutionary trees – offspring of the marriage between cladistics and the fossil record. At least these diagrams give some feel for the history as it happened, something that cladograms rarely if ever do, although unfortunately one or two of the figures are marred by wiggly lines and poor rendering.

The second thing I like is the use of boxes to tell particular tales. Often these boxes are used to tidy away major cladograms, but they are also used to explain especially juicy little tidbits of vertebrate history such as the surprising discovery that some early tetrapods such as *Acanthostega* had up to eight fingers and eight toes (how would mathematics or piano playing have turned out if we had retained this condition?), the origin of snakes (digging dirt, or sailing the seas?), and the wonderful birds of Liaoning, China (since the first edition of Benton's *Vertebrate Palaeontology* appeared in 1990, the tonnage of fossil birds found in this Province and surrounding areas has far outstripped that from all other Mesozoic localities put together). Sadly, the splendid appearance of the latter is somewhat diminished by the rather poor reproduction of the photographs which, as elsewhere in the book, look as if they were taken with a Box Browning³ on a wet November day in Rhyl⁴.

Photographs aside, the remaining illustrations, copious in number and generally of very good quality, are another strong point, and the third reason why I like this book. More than any other group of organisms, vertebrates – with their complex anatomy – need, perhaps even demand, to be illustrated, partly so that this complexity can be explained, and partly because it is often aesthetically attractive in its own right. This is particularly evident in the marvellous line drawings by John Sibbick that decorate the start of each chapter.

Yet another reason for liking this book is the extensive use that it makes of the Internet. The whole work is littered with Internet addresses that lead the reader to sites where they can broaden their knowledge of fossil vertebrates. For those with lazy fingers, the entire set of web links (a useful

³ Box Browning – popular camera of the mid 1900s.

⁴ Rhyl – a Welsh seaside resort famous for its many types of rain, all of them wet.



resource in its own right) is listed on Benton's University of Bristol website (<<http://palaeo.gly.bris.ac.uk/benton/>>). Moreover, a page listing errors and corrections for the book can be found on the same site, and in the Preface the author cordially invites readers to send him any further mistakes (unavoidable in a work of this size and breadth) that they might come across. The images are all available to download, at <<http://www.blackwellpublishing.com/benton/>>.

So, how good is it then? Well, at the moment, it is without doubt the best in the field, although this claim must be tempered with the observation that there is not much competition for the title. Colbert's *Evolution of the Vertebrates* (2001) is still available, but horribly outdated (see Prothero, 2002 for an eye-watering review), and for those who really need to know, would like to tone up their biceps and have lots of readies, Bob Carroll's *Vertebrate Paleontology and Evolution* (1987) is, in all respects, the heavyweight. It's expensive though, not so easy to find, and also rather out of date, partly due to the headlong rush that the field has experienced over the two decades and partly because Carroll largely eschewed the incorporation of a cladistic approach. One could, of course, opt for more specialized works that cover major groups such as fish, basal tetrapods, dinosaurs (who hasn't written about them?) or mammals, and there are plenty of excellent works to choose from, but if you want a general text that is authoritative, eminently readable and up to date then Benton's *Vertebrate Palaeontology* is 'the dog's whatsits'.

So, should you hand over some of your hard-earned cash (or student loan) for this book? If you are thinking of illuminating the lives of your students with a little (or better still, a lot) of vertebrate palaeontology, or you are likely to be the lucky recipient of such much-needed illumination, the answer is yes. The same goes for those in related disciplines who need a quick reference to vertebrate evolution. Indeed, anyone who wants an introduction to the field could do a lot worse than start with this book. That it does the job it was intended to do is shown by its remarkable success. Earlier editions have already been translated into several languages and, I am reliably informed, a fourth edition is countenanced. And what of the rhynchosaurs, those humble grubbers of roots with a gob full of penknives and from whose backs their Boswell was to hurtle upwards into the academic stratosphere? They are there too, stumping along in several illustrations with a couple of paragraphs all to themselves – doing rather better than some, one might hazard, but it's probably no more than they deserve.

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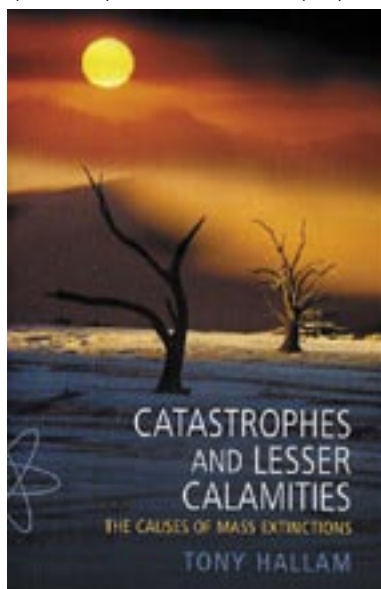
Catastrophes and Lesser Calamities

Tony Hallam. (2004). Oxford University Press, Oxford. ISBN 0-19-280668-8. £8.99 (paperback).

Dinosaurs and their demise interest the public in a way matched by few other topics in palaeontology, and far too many trees have been pulped in an attempt to satiate demand. Many of these books focus on large rocks falling out of the sky rather than alternative possibilities, and the other great biotic crises of the past have received too little attention. But now Tony Hallam has produced a wonderful short introduction to these events for the general public. Capitalizing on the *Mass Extinctions and Their Aftermath*, the survey he produced in 1997 with Paul Wignall (also published by Oxford University Press), Hallam has now written a survey for a non-specialist audience.

Although the specialist will always have quibbles about some areas in a book of such impressive breadth (and I do, see below), it must be said that Hallam has done an excellent job in introducing the reader to each of the major potential causes of biological calamities and guiding them through an evaluation of their plausibility. Following a general introduction and an excellent discussion of the history of research on mass extinctions, five of the 11 chapters consider each of the potential extinction triggers, beginning (alas) with extra-terrestrial impacts, and then proceeding through sea-level changes, oxygen deficiency, climate change and volcanic eruptions. Other factors, such as methane release, make appearances as required. Each of the chapters on triggering factors opens with a general discussion of the phenomenon, how it could cause a loss of species, and finally a reasonably up-to-date discussion of how well it may apply to the major mass extinction as well as appropriate smaller events. The final three chapters synthesize these evaluations and then look at the evolutionary significance of mass extinction before closing with a discussion of past, present and future human impacts on biological diversity. The chapter on the evolutionary impact of calamities is one of the strongest parts of the book. Hallam provides an outstanding introduction to the competing views of those favouring biotic competition versus physical disturbance as driving forces in controlling biotic diversity.

Most treatments of mass extinctions, including Hallam and Wignall's book, have focused on the events themselves, rather than the causes. I was initially a bit dubious of Hallam's approach of focusing on the causes first and then secondarily on how they have been applied to different events. Like most of us, I tend to think historically, but at least in the US it is clear that much of the public does not (and here in Washington DC evidently almost no one does!). So organizing the book in this way turns out to have been a savvy move. This allows Hallam to present enough of the geological background to these different potential causes to allow readers to grasp the issue and thus avoids much repetition.





As much as I enjoyed and recommend the book, I can't resist a few quibbles. Non-UK readers unfamiliar with UK geography will be confused by some of Hallam's comments. There are, almost inevitably, areas where Hallam's discussion is not as up to date as one might wish. He cites, for example, David Jablonski's suggestion that regressions may not have had a major impact on diversity because of the abundance of families and genera in refugia on oceanic islands, but not Gustav Pauly's (1990) studies showing that the structure of marine communities across fore-reef, reef and lagoon indicates that islands may be less effective than Jablonski argued. Similarly, Elizabeth Vrba's pulse turnover hypothesis makes an appearance, but not the later work of Kay Behrensmeyer and colleagues (Behrensmeyer *et al.*, 1997) testing and rejecting the pulse turnover model. Hallam's pattern of references is a bit unusual, so that some items that one might wish to follow up on are missing, while other, seemingly more trivial issues are cited. But this book is not intended for a scholarly audience, but for student and general readers who should greatly profit from this insightful introduction to current thoughts on mass extinctions and their consequences.

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Thunder-Lizards: the Sauropodomorph Dinosaurs

Virginia Tidwell and Kenneth Carpenter (2005). Indiana University Press, Bloomington and Indianapolis. 495pp. ISBN 0-253-34542-1, \$59.95 (hardback).

I suppose most people have lost track of how many books Indiana University Press has published on fossil vertebrates as part of its *Life of the Past* series. I have: for reviews of previous volumes, see *Palass Newsletter* 49: 95–98, 49: 101–103, 50: 91–93, 52: 85–87, 53: 110–112, 56: 128–131, 59: 118–120, 59: 131–132, 60: 79–82 and 60: 90–92 (and that's not all of them). Continuing their theme of multi-authored volumes dedicated to specific dinosaurian groups, *Thunder-Lizards* covers (or does it? Read on) the sauropodomorphs: the long-necked sauropods and their relatives. The quality of included papers varies, with some being excellent, well written and highly useful, and others being, well, not so excellent.

The book is divided into four sections. 'Sauropods old and new' provides new data on several taxa; 'Sauropods young to old' includes contributions on ontogenetic variation; 'Body parts: morphology and biomechanics' covers assorted aspects of sauropod anatomy; and 'The global record of sauropods' is made up of reviews on geographical assemblages. But while the included contributions are grouped into these sections, in terms of what is and what is not included, there is a random feel, and neither taxonomic nor stratigraphic coverage is equal. It is telling that, while the word 'sauropodomorph' features in the title, the word 'sauropod' is used in the titles of all of the



book's sections. Of the 21 included papers, only one – Galton *et al.* on *Melanorosaurus* – focuses on a taxon that has traditionally been regarded as a non-sauropod and, if some current phylogenies are to be accepted (Yates and Kitching, 2003), *Melanorosaurus* is a basal sauropod anyway. So non-sauropod sauropodomorphs – 'prosauropods' in traditional parlance – aren't really featured in the volume at all: it may as well have been titled 'The Sauropod Dinosaurs'. Why weren't 'prosauropods' represented in this volume? It most likely comes down to the fact that they've conventionally been regarded as the most boring (and hence least studied) of dinosaurs. Happily the disdain that 'prosauropods' have long received will soon be rectified, in part, by an academic volume presently in preparation, and due to appear in 2007.

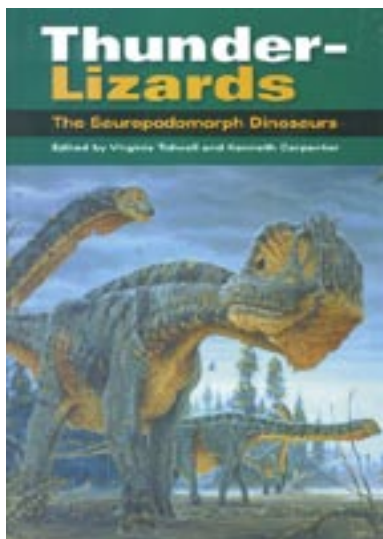
The 'Sauropods old and new' section starts with Galton *et al.* on *Melanorosaurus*. This paper provides new information on melanorosaurids and, by comparing melanorosaurid characters with synapomorphies taken from various different studies, discusses how these animals might fit within Sauropodomorpha. Unfortunately the article becomes an inconclusive progress report, rather than the definitive redescription it could have been. While these authors use the term 'prosauropod' in places, it is sometimes unclear exactly what they mean by this, given that there is more than one interpretation of this term. At its most inclusive, Prosauropoda might be almost as traditionally conceived, but if other phylogenies are favoured, and if *Plateosaurus* is used as the anchor for Prosauropoda (Serenó, 1998), then Prosauropoda is synonymous with Plateosauria.

Contributions from John S. McIntosh are always welcome, and the excellent description he provides here of *Barosaurus* is useful. Thoughts on Tendaguru material are included, as is a mention of his once-held idea that *Supersaurus* was not a distinct genus, but a large *Barosaurus*. Rather more problematic however is Carpenter and Tidwell's paper on *Astrodon* from the Aptian–Albian of Maryland. One of their primary arguments is that the name *Astrodon johnsoni* has priority over *Pleurocoelus nanus*, and that the latter should be regarded as a synonym. However, they are happy to admit that *Astrodon* is based on non-diagnostic teeth, and I can't determine how it's known that the substantial amount of referred material really does belong to the same taxon as the non-diagnostic teeth, as Carpenter and Tidwell assert it does. I am not encouraged by the fact that they switch between the spellings 'johnsoni' and 'johnstoni' throughout the text, that all the characters regarded as diagnostic come from 'very young' individuals, nor by the absence of units from the scales that accompany their skeletal reconstruction. Furthermore, while Carpenter and Tidwell regard the vertebral proportions, and extent of pneumatic excavations, of *Astrodon* as diagnostic for the taxon, a paper elsewhere in the same volume shows that 'pleurocoel size ... appears to decrease in proportion to the total centrum length when compared with that in juvenile animals' and that 'neck length increases proportionally to total body length throughout ontogeny' (Ikejiri *et al.*, p. 173). The section ends with Le Loeuff's article on *Ampelosaurus*, an Upper Cretaceous French titanosaur. Given that this taxon is now represented by over 500 bones, including an articulated skeleton that preserves a 'well-preserved disarticulated skull' (Le Loeuff, p. 136), the data provided here is, again, a provisional progress report. However, more information is provided on the taxon than has been published before.

'Sauropods young to old' includes Foster's description of new juvenile *Apatosaurus* and *Camarasaurus* specimens, Ikejiri *et al.* on ontogenetic variation in *Camarasaurus*, Tidwell *et al.* on ontogenetic features observed in a *Camarasaurus* pelvis, and Tidwell and Wilhite on forelimb ontogeny in *Venenosaurus*. Ikejiri *et al.*'s paper is particularly good in documenting the substantial



amount of variation now known for most parts of the *Camarasaurus* skeleton. Mostly this is ontogenetic and involves the development of rugosities and extra processes, but there are also indications of sexual dimorphism, and superimposed on all of this is individual variation. The new data provided by Tidwell *et al.* on *Camarasaurus* shows that characters conventionally regarded as synapomorphic for some sauropod clades (e.g., six sacral vertebrae and widely flaring ilia) occur elsewhere in the group as individual variations. Sigh: another 'cautionary note for those working with less well represented taxa' (Tidwell *et al.*, p. 185). Mostly, the take-home message from the section is a coherent and well-supported one: that sauropod growth is mostly isometric (though with some allometry occurring in the neck). This contrasts with the data from other dinosaur groups, and it's a good question as to why sauropods were so different.



Included within the morphology and biomechanics section are papers on *Camarasaurus* neuroanatomy, two on neck posture and function, one on hyposphene–hypantrum articulations, four on the morphology and evolution of the appendicular skeleton, and a review article on stress fractures. The strongest papers in this section are Matthew Bonnan's excellent, detailed review of foot anatomy and D. Ray Wilhite's on appendicular bone variation seen in Morrison Formation taxa. Bonnan shows that, far from being the 'rubber stopper on the end of a crutch' imagined by some authors, the sauropod foot was morphologically novel and uniquely flexible. Sebastian Apesteguía's two papers – one on the morphology and evolution of the metacarpus and the other on the hyposphene–hypantrum complex – are also good reviews packed with new information. As if sauropods weren't strange enough, with their columnar metacarpal arcades and reduced (or even absent) manual phalanges, Apesteguía discusses the presence of bowed 'banana-shaped' first metacarpals in some titanosaur taxa as well as evidence for a novel soft-tissue covering to the distal ends of the metacarpals. I am left wondering why a small photo of Stonehenge is included in one of Apesteguía's figures, however.

It would be an odd sauropodomorph volume indeed that did not focus at least in part on long necks. However, surprisingly little work has been done on this area, and basic questions of neck posture and orientation, and zygapophyseal movement, remain unanswered, despite the reasonable amount of work published on neck motion and orientation in extant tetrapods. Kent Stevens and J. Michael Parrish have published a couple of articles on sauropod neck posture, and, using software dubbed DinoMorph, have applied computer modelling to digitally reconstructed skeletons (Stevens, 2002, Stevens and Parrish, 1999). While there seems to be near-universal agreement that diplodocoids had a horizontal neutral neck posture, Stevens and Parrish hold the more controversial point of view that all sauropods were like this, even *Camarasaurus* and *Brachiosaurus*. Already their interpretations have been challenged by those arguing that they have not accounted for flexibility within the dorsal vertebrae, that their reconstructed neck postures



are no less speculative than the artistic reconstructions they are so critical of, and that their reconstructed necks contain misalignments and disarticulations. Rather than defending or refining the method, this paper is mostly a review of what previous authors have said about the feeding styles and neck mobility inferred for sauropods, and there is little new data or interpretation. Their reconstructed neck postures do not result from virtual modelling, but from 'using illustrations of the original material' (p. 217): in other words, drawings from monographs. Overall it is not a convincing approach to the problem. A second contribution on neck posture comes from David Berman and Bruce Rothschild, who used CT x-rays to establish the internal morphology of cervical vertebrae, and from this work out neck posture. Unfortunately the figures they provide are all but useless and may as well be anything.

The last section of the book ('The global record of sauropods') reviews sauropods from southern Europe, Patagonia and Australia, with a contribution on trace fossils from India. Fabio Dalla Vecchia's article reviews and describes sauropod bones and tracks from the Tethyan carbonate platforms of Italy, Slovenia and Croatia, and also includes interpretation of Cretaceous vertebrate palaeobiogeography across the area. While the material is not fantastic, the figures he provides (particularly of vertebrae) are highly detailed. That's tremendously useful when you have to spend time trying to interpret sauropod vertebrae, and Dalla Vecchia's figures contrast markedly with rather less satisfactory figures of sauropod vertebrae recently published in another major work on sauropods (Upchurch *et al.*, 2004). Patagonian sauropods are reviewed by Salgado and Coria, and new data on Australian forms is provided by Molnar and Salisbury. It used to be thought that Australia had a particularly poor sauropod record, comprising *Rhoetosaurus* and *Austrosaurus* and not much else. In fact the record is far richer than this – OK, it's not on par with that of North or South America, or Asia, or Europe... or, err, Africa – but it does in fact include multiple specimens, and by specimens I don't just mean isolated vertebrae. Furthermore, the old view that Australia lacked titanosaurs during the Cretaceous, and was instead home to late-surviving relict taxa, no longer seems supported.

While previous IUP volumes have been flawless in terms of editing, *Thunder-Lizards* isn't up to usual standards. We have specific names spelt incorrectly here and there, or accidentally given capital first letters. A massive shadow, looking suspiciously like that cast by a human holding a camera, looms large in one of several less-than-brilliant field photos. Mostly the figures have reproduced well however, and Todd Marshall's cover art is brilliant.

Overall, IUP has provided us with a volume similar in calibre to the other dinosaur volumes published in the *Life of the Past* series: sometimes lacking in academic rigour, and indeed flawed in places, but excellent and rewarding in others. The sheer volume of information included means that the articles of highest quality are almost swamped by the others, and for this reason it could be argued that they won't be as widely read as, or get the accolade and citation, they deserve. So there is novelty, value and excellence in *Thunder-Lizards*: for this reason this book should be owned by everyone with a serious interest in sauropods. And I do mean sauropods, and not sauropodomorphs.

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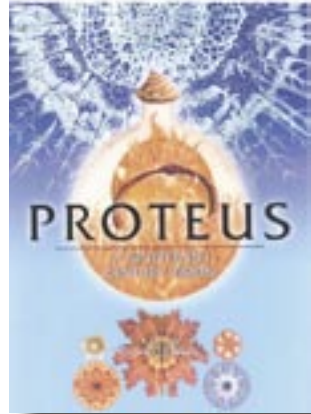


Film Review

Proteus – a nineteenth century vision

A film, director David Lebrun (released 2003). Available from First Run/Icarus Films, New York. 60 minutes, colour. Sale/video-dvd: \$US390 Rental/video: \$US125.

One of the more effective visual tricks that Apple incorporated into OS X is a screen saver which takes images and, with gentle use of pan and zoom, produces an almost hypnotic sense of animation. With a nice collection of images, some suitable background music and an occasional explanatory comment, I find this can keep people entranced for a surprisingly long time. In *Proteus* this technique is applied, with numerous variations, to produce “an animated documentary” almost entirely based on nineteenth century illustrations, paintings and photographs. The film was essentially a personal project of the director but is professionally produced and has a distinguished cast for the narration. It has been shown at various film festivals, received an Outstanding Creative Achievement award at the Santa Barbara International Film Festival, and has had some excellent reviews, notably in *Science* (Laubichler 2005). It has subsequently been shown in various museums but has not been widely released or shown on television.



The title *Proteus* refers to a Greek sea god who took on the form of various sea creatures, which is a somewhat complex metaphor for the subject of the film: the marine biologist Ernst Haeckel and his struggle to reconcile scientific and spiritual understanding of the world. Haeckel sought to show that scientific understanding of the world did not lead to mechanistic sterility. In this quest a prime influence was Goethe and “for Goethe and for the romantic poets after him it was only the shape-shifting energy of the artist’s imagination that had the power to embrace the opposites and heal the split between man and nature. They envisioned the act of creative imagination as welling up from the depth of an inner sea, to describe the power of this shaping spirit they invoked the name of *Proteus*, a Greek god of the sea capable of assuming an infinite variety of forms.” (The quote is from the film commentary). There is also a *double entendre* here, since for Haeckel the infinitely variable radiolaria were his guides from the deep sea to the understanding of evolution, his personal *Proteus*. This explanation gives an idea of the rich but somewhat obscure approach of this film – does the name *Proteus* perfectly encapsulate the subject of the film or is it a piece of obscure pretension? Is this beautiful film also useful? Fortunately the answer is yes, since the film is very well-researched and the complex interpretations are well grounded in modern understanding of Haeckel, particularly those of Robert Richards (e.g. Richards 2005) who was one of the consultants on the film. This does not make it an easy film, but it is rewarding.



Haeckel (right) and colleagues with their nets at Wurzburg

The principal story the film tells is the life of Ernst Haeckel, the prime 19th century German evolutionary biologist, king of the radiolaria, scientific illustrator extraordinaire, and metaphysical philosopher. On one level the film progresses conventionally through his life. It starts with his birth in 1834 into a family of German “liberal protestant intellectuals,” illustrated by fine family photographs. It then proceeds to his university career, which like many 19th century naturalists consisted of reluctantly following a medical course. In Haeckel’s case he was sent to Wurzburg University where scientific inspiration came from marine biology, and specifically microscopic examination of marine life – there are wonderful photographs here of Haeckel and friends proudly posing with their nets. After university his parents allowed Haeckel a year off to explore Mediterranean marine life. So, in 1859, he followed Goethe’s footsteps to Italy, staying first in Naples and Capri, where he had little success with the net and nearly gave up on science in favour of painting (lovely watercolours of complex landforms) and an artistic life. Then he moved to Messina where he finally found a superb supply of open marine material washed into shallow water, and discovered radiolaria. At the time this was a barely known group and an ideal subject for his combination of artistic ability and observational skills. His Messina studies resulted in a monograph describing some 168 new species with spectacularly beautiful illustrations based on camera lucida drawings, and equally importantly providing the first attempt at a classification of a group of organisms on the basis of Darwinian principles.

After this seminal expedition the rest of Haeckel’s career is divided in the film into three phases. First a period from the 1860s to 1870s as intellectual star at Jena University, carrying out detailed



studies of numerous marine invertebrates whilst developing evolutionary biology theories. He was immensely productive, coming up with concepts like phylogenetics, ecology, and his (notorious) biogenetic law that “ontogeny recapitulates phylogeny”. In the film this phase is skipped over swiftly to progress to the second phase, his study of the Challenger radiolaria. This started in 1876 when he was entrusted with the post-cruise study of the radiolaria collections and finished in 1888 with publication of his monograph on them. Easily said, but we are talking about a three-volume monograph of 2,000 pages, some 2,400 new species, and 140 plates each of which are masterpieces of technical drawing, and he also described the Challenger hydrozoa and Keratozoa (horny sponges). Most university libraries hold copies of the Challenger monographs, and if you have not looked at them and particularly Haeckel’s volumes I strongly recommend doing so. Actually the monograph is a slightly mixed blessing; most illustrations are somewhat artistic reconstructions of ideal form rather than objective drawings of individual specimens, and many new species are not illustrated. So at the species level radiolarian taxonomists are still struggling to sort out the legacy of ill-defined species he inflicted on the subject. On the other hand, his higher-level taxonomy has proven amazingly robust.

Finally there is the post-Challenger phase of Haeckel’s career as *eminence grise*, philosopher and science communicator. This included publication of probably his most enduringly famous book *Kunstformen der Natur* (*Art Forms of Nature*), and development of his monist philosophy.

Whilst the film progresses straightforwardly through Haeckel’s career and life, it interweaves with this two other themes. First, it provides a scientific context by looking at the development of marine science and especially the Challenger expedition. Second, it provides a psychological and artistic context to Haeckel’s work by use of Coleridge’s *Rime of the Ancient Mariner*, as illustrated by Gustave Dore. This requires a little more explanation. The Challenger Expedition is obviously important since it provided the key material Haeckel was to work on, but in the film it also symbolises man’s rational exploration of the deep sea in particular, and the natural world in general. It is characterised in the commentary as “a voyage through a sea of fact”. *The Rime of the Ancient Mariner* by contrast is an “inward journey through a sea of poetic imagination” in which the mariner “lives out the consequence of a failure of vision, of a split between man and nature.” The



Discomedusae from Kunstformen der Natur



Challenger Expedition thus parallels and symbolises the rational scientific side of Haeckel whilst the *Rime* symbolises his artistic and religious side. This approach is challenging, but provides an effective way of exploring how Haeckel endeavoured to produce a unitary spiritual understanding of nature. He rejected the more traditional dualism of natural science and an external divine creator as necessary counterparts in explaining nature. Instead he explained the evolutionary continuity of life from single-celled organisms to multicellular man as the product of an all-pervasive divine spirit, and the beauty of nature as a manifestation of this. A position which unfortunately provoked enormous hostility from both evolutionary biologists who saw no role for a soul in radiolaria and organised religion, since he vociferously rejected the concept of an external creator.

So, this is a compelling but complex film which explores the interfaces of science, art and religion. At nearly \$400 the DVD is clearly not intended for personal purchase, but could be attractive for use in teaching. Most obviously it could be used within courses in science for humanities majors exploring the different ways in which 19th century philosophers reacted to the intellectual dilemmas produced by evolutionary theory. Perhaps more interestingly, though, it could also be used as the basis of a course to educate scientists in appreciation of the humanities, and understanding of the public. The film was a 23-year labour of love by the director, David LeBrun, and represents an artist's attempt at exploring a complex scientific/philosophical topic. As such it throws up numerous questions: What was Coleridge exploring in the *Rime*? Is this a valid analogy with Haeckel's quest to reconcile spirituality and science? Are the parallels and contrasts between the Challenger expedition and the Mariner's voyage meaningful and illuminating? Does beauty in nature require an explanation? Does Haeckel deserve a re-evaluation? These are not the types of questions which we are used to addressing as scientists, but maybe we need to be more willing to balance our endeavours to educate the public in science with education of ourselves in arts-based perspectives on the world.

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Brachiopods from the Dashaba Formation (Middle Ordovician) of Sichuan Province, south-west China

Special Papers in Palaeontology 74: 1-63. ISBN 0 901702 98 6.

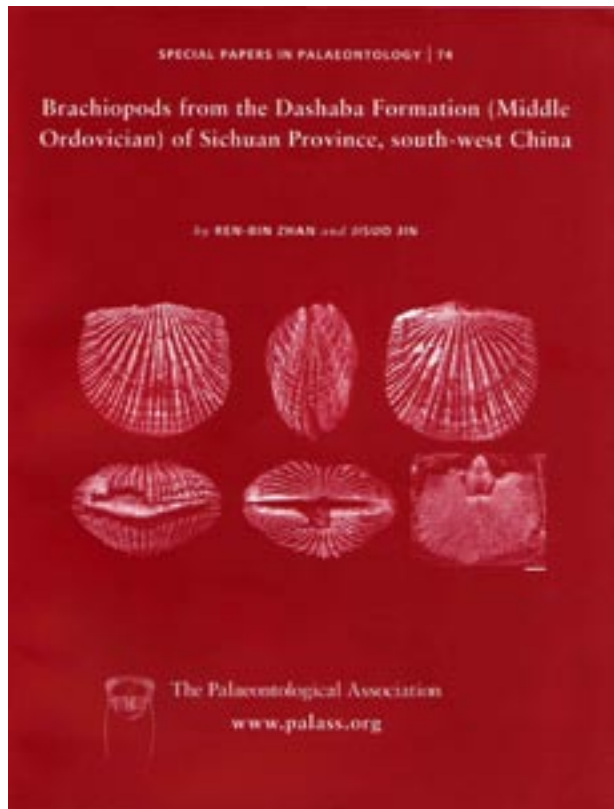
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Ren-Bin Zhan and Jisuo Jin, 2005.

The Middle Ordovician Dashaba Formation in southern Sichuan Province, China, a 50-m-thick succession of calcareous and silty mudstones with calcareous nodules and limestone lenses, contains a rich, diverse, brachiopod fauna; 19 genera and 20 species are represented by 3,018 specimens (1,257 individuals).

Four genera (*Heteromena*, *Leptastichidia*, *Parisorthis* and *Pentagomena*) and six species (*Glyptonema? rugulosa*, *Heteronema dorsiconversa*, *Leptastichidia catatonosis*, *Parisorthis dischidanteris*, *Pentagomena parvicostellata* and *Triotechia chuannanensis*) are new. Graptolites from the Dashaba Formation indicate the presence of four graptolite biozones: in ascending order, the uppermost part of the *Undulograptus austrodentatus*, the *U. intersitus*, the *Didymograptus artus* and the *D. murchisoni* biozones, which range from latest Arenig to Llanvirn in age.

Despite the relatively homogeneous lithology, cluster analysis indicates that the brachiopod fauna of the Dashaba Formation can be divided into five associations: the *Parisorthis dischidanteris*, *Saucroorthis obscura*, *Saucroorthis obscura-Parisorthis dischidanteris*, *Orthambonites delicata-Pentagomena parvicostellata* and *Calyptolepta chengkouensis* associations. Faunal differentiation may have been the result of subtle changes in water depth (between BA2 and BA3 settings) and/or reflect the variable ratios in the supply of siliciclastic mud, quartz silt and carbonate mud. The variation in sediments would have affected the substrate softness and stability, which, in turn, probably controlled the distribution of fixosessile or librossessile brachiopods.





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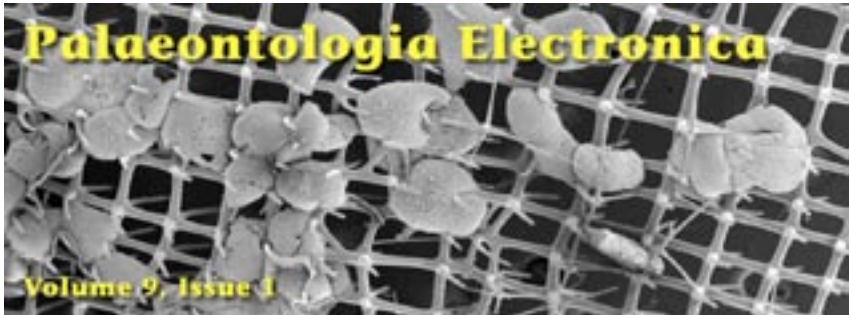


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