The Palaeontology Newsletter

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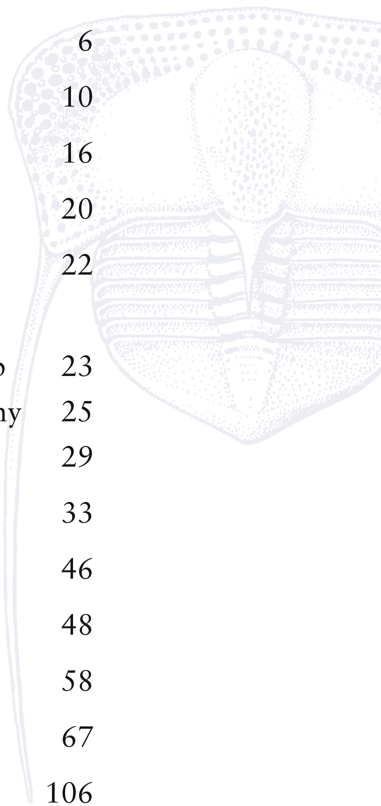

Reminder: The deadline for copy for Issue no 51 is 4th October 2002

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

Editorial

Comings, goings and the annual call for PhD titles

At fifty, *Palaeontology Newsletter* has hit middle age and, in keeping with the current academic climate, the time has come for retirement amongst its ranks. This is Paul Pearson's last issue as *Newsletter Reporter* and, as Editor, I'd like to take this opportunity to thank him for the service that he has provided to the newsletter, and particularly for the cornucopia of essays that he has provided since issue 36, following his enlistment by the previous Editor, Sue Rigby.

Paul's retirement has precipitated the enlistment of Graham Budd to the position of *Newsletter Reporter*. Graham has been a regular contributor to *Palaeontology Newsletter* since my first issue as editor (44), and this appointment ensures the supply of his musings, distilled as regular essays. Graham and I are currently hatching plans to develop the newsletter ever further and we hope that you will be free both in your suggestions for its future, and with your time when you are leant upon to contribute!

Ahh, time passes quickly, and the now annual call for PhD titles has come around much quicker than seems decent! We intend to print a distilled listing of PhD topics to be offered for the 2002/2003 academic year in the next issue of the newsletter, due out mid-November; the list will also be made available via the *Association* website. The 2001/2002 digest of PhD topics was restricted to UK institutions but there is no reason why this should continue—so I look forward to receiving topics from around the world. Remember that *Palaeontology Newsletter* gets sent to undergraduate winners of the *Palaeontological Association Prize*; these students are, by definition, the very best palaeontologists in-the-making, so don't miss your opportunity to reach out to them! If you are going to offer a PhD title, I would be eternally grateful if you could please email me the title, supervisors, and enquiry contact details, before the copy deadline for issue 51.

Phil Donoghue
Newsletter Editor
<newsletter@palass.org>

Association Business

Nominations for Council

At the AGM in May 2003, the following vacancies will occur on Council:

Vice-President, Editor

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

All potential Council Members are asked to consider that:

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

The closing date for nominations is **Friday 27th September**. 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**>.

Council Members 2002–2003

President

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Editor-in-Chief
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Awards and Prizes

Sylvester-Bradley Award

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

Applications consist of a CV, one A4 page account of research aims and objectives, and a breakdown of the proposed expenditure. Each application should be accompanied by the names of a personal and a scientific referee. All applications for support should be sent to the Secretary and a deadline for receipt of **1st November 2002** will be strictly observed. 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.

Hodson Fund

This is conferred on a palaeontologist who is under the age of 35 and who has made a notable early contribution to the science. Candidates for the award must be nominated by at least two members of the Association and the proposal must be supported by an appropriate academic case. The closing date for nominations is **1st September 2002**. Nominations will be considered and a decision made at the October meeting of Council. The award will comprise a fund of £1,000 that is presented at the Annual Dinner.

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 2002**. The award comprises a cash prize plus a framed scroll, and is usually presented at the Annual meeting.

Association Meetings

Annual Meeting of the Palaeontological Association

Department of Earth Sciences, University of Cambridge

15–18 December 2002

Technical sessions will consist of two days of talks and posters (16–17 December), supplemented by social events in the Sedgwick Museum and the University Museum of Zoology. The Annual Dinner will be held in St. John's College on the evening of 16th December.

Presentations on any aspect of palaeontology and evolutionary studies are welcome. Talks are scheduled for 15 minutes with a further five minutes for discussion. Overhead projector, slide projector, media projector and computer facilities will be available. For PowerPoint presentations, we will require a CD or zip-drive version of the presentation at least one day in advance.

On 18th December, Simon Kelly will lead a **post-conference field trip** to investigate Corallian facies of Oxfordian (Late Jurassic) age in the Upware Limestone, about ten miles north of Cambridge. Recent quarrying has advanced understanding of the local lithostratigraphy, biostratigraphy and palaeoenvironments, and it may be possible to demonstrate that the Upware Limestone is overlain unconformably by a number of Cretaceous units. Rich faunas can be collected, including corals, bivalves, echinoids, ammonites, etc. Wellington boots will be the footwear of choice on the day, and around about lunchtime we expect to find ourselves at a local pub. Depending on numbers and weather, the day's excursion might also take in a tour of the Brighton Building, the Sedgwick Museum's conservation and storage facility. *Background reading:* Wright, J.K., Kelly, S.R.A. & Page, K.N. 2000. The stratigraphy of the 'Corallian' facies Middle Oxfordian (Upper Jurassic) deposits at Upware, Cambridgeshire, England. *Proceedings of the Geologists' Association*, **111**, 97-110.

General information

Cambridge is a small university city of many museums and colleges. From Isaac Newton to Charles Darwin and more recently Stephen Hawking, the University of Cambridge has a long history of scientific achievement. In more recent years, the city has become an internationally recognised centre for technology and science. For more information about Cambridge and the surrounding area, see <**http://www.cam.ac.uk/cambarea/tourist/**>.

The Department of Earth Sciences is near the centre of Cambridge, some 15 minutes' walk (or five minutes' bus-ride) from the train station. We advise against bringing a car to Cambridge due to the shortage of parking space. Access to the Department is from Downing Street through the archway opposite Corn Exchange Street. Once through the archway turn left and enter the Department at ground level, between the stone stairs. Mind the bears!

Accommodation

Reserved accommodation for delegates is in the form of single B&B student rooms with shared facilities in Gonville & Caius and Trinity Hall colleges. Both colleges are situated in the city centre, approximately five minutes' walk from the Department. Contact information for Caius can be found at <**http://www.cai.cam.ac.uk/**> or telephone (01223) 332400; for Trinity Hall <**http://www.trinhall.cam.ac.uk/**> or telephone (01233) 332500. For alternative accommodation see <**http://www.cam.ac.uk/cambarea/tourist/**>.

The Sedgwick Museum of Geology

The Sedgwick Museum, within the Department of Earth Sciences, is both a major palaeontological research museum and a popular visitor attraction. By the time of the Palass meeting a major refurbishment of the "Palaeozoic" Oak Wing will have been completed and awaiting your generous assessment, not least on Sunday evening for the Icebreaker. General information about the Sedgwick museum can be found via the department website at <**http://www.esc.cam.ac.uk/**>. Arrangements for examining the research collections can be made by prior arrangement with Mike Dorling (tel 01223 333456, e-mail <**mgd2@esc.cam.ac.uk**>).

The University Museum of Zoology, Cambridge (UMZC)

The UMZC, within the Department of Zoology, has had a tradition of vertebrate palaeontological research since the early part of the 20th century. It has specialised in Palaeozoic and Quaternary subjects, complementing the Sedgwick's strengths in the Mesozoic. Devonian and Early Carboniferous tetrapod fossil materials will be on display, as well as permanent exhibits of extant and fossil vertebrates and invertebrates. The UMZC is open during the day, and we will be meeting here for a final glass of wine on Tuesday evening. General information about the Museum and its collections can be found at <**http://www.zoo.cam.ac.uk/museum/**>.

Registration and submission of abstracts

Registration for the meeting, the field trip, room and meal bookings, and the Palass 2002 T-shirt, are made via the accompanying booking form (additional forms can be downloaded from the Palass website at <**www.palass.org**>). Completed booking forms together with full payment or Credit Card authorisation should reach the local secretary by **6th September 2002**.

Intending contributors to the scientific proceedings should forward an abstract of not more than 200 words, preferably by e-mail, to the local secretary at <**njb1005@esc.cam.ac.uk**>; otherwise, attn. Nick Butterfield, Department of Earth Sciences, University of Cambridge, Cambridge CB2 3EQ. **The deadline is 6th September 2002**. The format for abstracts should follow the style adopted in the Association's Newsletter number 45 (2000), also available on the Association's webpages at <**www.palass.org**>. Please indicate if your abstract is for an oral or a poster presentation—note that we are planning to make a feature of the poster sessions this year. Presenters under the age of thirty on 15th December 2002, who are also members of the Association, are eligible for the President's award for best talk and Council's award for the best poster; please indicate on your abstract submission if you wish to be considered.

Organising committee: Nick Butterfield, Rachel Wood and Jenny Clack.

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

Deadline for abstracts of 200 words or less, preferably by e-mail: 6th September 2002.

Local secretary: Nick Butterfield,
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Lyell Meeting 2003

The Geological Society of London/Joint Committee for Palaeontology

Lyell Meeting 2003: The Application of Ichnology to Stratigraphic Analysis

Burlington House, London

Organised by Dr D. McIlroy (University of Bergen, Norway)

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

The meeting will combine keynote talks from Prof. R. Bromley, Prof. G. Pemberton and Dr R. Goldring, along with other lectures and a limited number of poster presentations.

Abstract deadline is 1st September 2002. Abstracts should be submitted to Dr D. McIlroy, (e-mail **dmc@liv.ac.uk**).

Authors should indicate whether they would be willing to submit a paper for publication in the conference proceedings (deadline for submission of manuscript 17th January 2003).

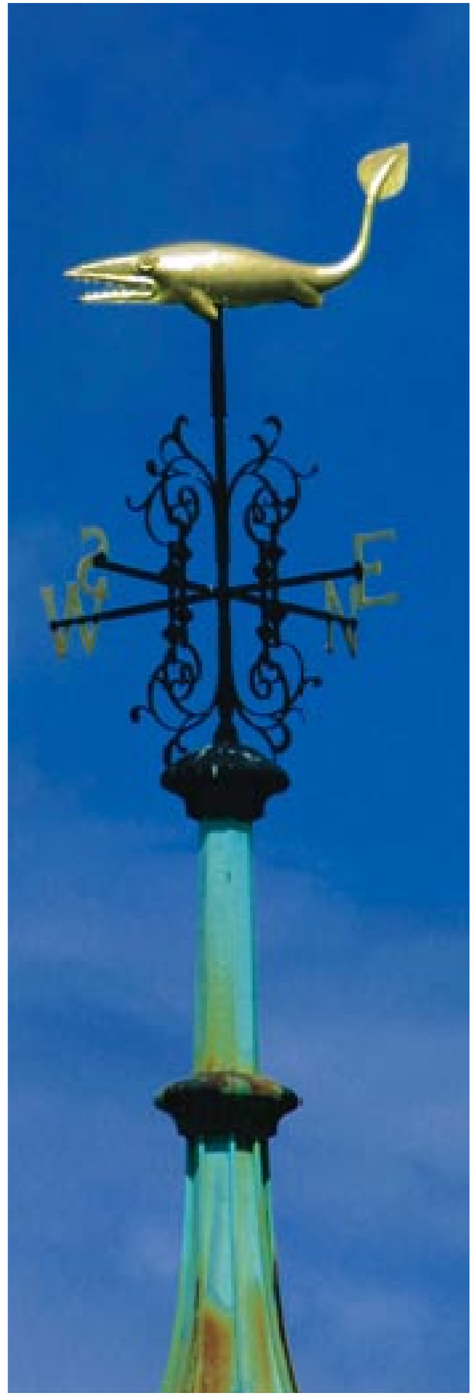
For further details contact: Helen Wilson, The Geological Society of London, Burlington House, Piccadilly, London W1J 0BG (e-mail <**helen.wilson@geolsoc.org.uk**>).

The Palaeontological Association Annual Meeting

Cambridge

15 - 18 December 2002

Department of Earth Sciences
University of Cambridge



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Meeting REPORTS

45th Annual General Meeting of the Association
Barber Institute of Fine Arts, University of Birmingham *8 May 2002*

The usual group of Council members and stalwarts gathered for the AGM. Prof. Paul extended a vote of thanks to the retiring members of Council, Dr Barker, Dr Loydell, Dr Pearson and Dr Wood. Dr Smith proposed a vote of thanks to Prof. Paul, retiring.

New members of Council for the coming year are Prof. Derek Briggs (President), Dr P. Manning (Publicity), Dr Graham Budd (Newsletter Reporter), Dr Jason Hilton (Ordinary) and Dr Maggie Cusack (Ordinary). Dr Thomas Servais, Prof. E.N.K. Clarkson and Dr Polly will stand as co-opted members for 2002-3.

The following awards and prizes were announced:

Sylvestor Bradley Awards to David Allen, Colin Barras, Simon Braddy, John Cunningham, Heather Jamniczky, Kathy Keefe, Hannah O'Regan, James Renshaw, Sally Reynolds, Blair Steel, Sebastian Steyer, Mikhail Surkov, Oive Tinn, Lauren Tucker, David Waterhouse and James Wheeley—another bumper year.

Mary Anning Award goes to Dr Fred Hotchkiss for his outstanding work and many publications on echinoderms. The photograph shows Association President Prof. Chris Paul awarding the prize to Dr Hotchkiss.

Hodson Fund awarded to Dr Graham Budd for his work on arthropods.

Formal business being completed, the Annual Address was presented by Prof. Hugh Torrens on the "Life and work of S.S. Buckmann (1860-1929), Geobiochronologist, and the problems of assessing the work of past palaeontologists." Those who were absent missed an excellent, amusing and stimulating address. Parallels were drawn between the much, but undeserved criticism of the later work of Buckmann and the current blight of "real-time" reviews of research and teaching. Much of Buckmann's work and ideas have, with only minor modifications, stood the test of time, surely the only criterion for excellent science.

Suitably edified participants adjourned to the Lapworth Museum of Geology to sample a selection of fine wines.

In 2003 the Annual Address will become part of the Christmas Meeting, in an attempt to raise the profile, and for that matter, the audience.

Howard Armstrong
Secretary, <secretary@palass.org>

Progressive Palaeontology 2002
University of Leicester *12 – 13 June 2002*

The 2002 edition of Progressive Palaeontology was held in Leicester on the 12th and 13th of June and in order that I paid proper attention to the talks being given and not seek the somnolent sanctuary of the auditorium back row, I volunteered to write the meeting report.

Now, the keen sports fans amongst you will have noticed that 12th June was also the date of the vital Group F match between England and Nigeria, so I have taken the opportunity to combine the two bastions of modern society (fossils and football, of course) and produce a World Cup themed review.

Registration was from 9.30 to 10.30am but with England's deeply thrilling 0-0 draw not finishing until about 9.20, followed by a bus journey and lengthy march across Leicester (from my parents' house on the west of the city), I arrived at approximately 10.29:59, just in time to catch Professor Dick Aldridge taking on the mantle of stadium announcer and welcoming us to the day's action.

Donning the number one jersey was **Blair Steel** (Royal Holloway), examining the phenomenon of photomovement in coccolithophores. Motile responses to stimulation by light are known in most oceanic plankton, but infrequently in coccolithophores, so Blair has been conducting lab tests to see whether they really are light or heat sensitive, discovering that photo- and thermotaxis is indeed present in certain forms. Many questions remain to be answered, and Blair noted that the probability of resolving them all is low, but still more likely than Scotland winning the World Cup.

Second in the line-up was **Kate Riddington** (Birmingham) and a selection of confusing Jurassic forams. The genus *Lenticulina* is a common element of the microfauna from the Early Triassic to the present day, but its true diversity and disparity is still deeply problematic, and Kate has bravely taken on the challenge of trying to work out just how many species there really are. Multivariate analysis of morphological characters is the way forward, but no obvious groupings have come out thus far, leading to the fascinating possibility that *Lenticulina* consists of only one, highly variable species.

Staying with forams, but moving into the Cretaceous, **Jodie Fisher** (Plymouth) presented her study into their distribution across the Cenomanian-Turonian boundary event, approximately 93 Ma. This event saw the extinction of many marine invertebrates, but its causes are not well-known. Black shale deposition suggests widespread oceanic anoxia, associated with high sea levels, whilst iridium layers imply either increased volcanism or an influx of meteorites, but the precise mechanisms remain cryptic. Jodie is using the diversity and abundance of different forams (*e.g.* surface dwellers *vs.* benthic forms) across the boundary to explain what was going on in the water column and, coupled with isotopic and geochemical analysis, what led to the extinctions.

Christian Baars (Cardiff) then reminded us that palaeoenvironments cannot be properly interpreted without examination of the influence of organisms present at the time. A prime example is the colonization of land by plants—their appearance must have had profound effects on weathering, climate and soil profiles, but can we pin down what they were? Did the first terrestrial vegetation lead to increased chemical weathering and removal of carbon from the atmosphere? Christian has been conducting controlled experiments into this, with ferns, mosses and liverworts used as analogies for the earliest land plants and their effect on leachate chemistry observed. At the moment, results are inconclusive, with hints rather than solutions, just like the left side of England's midfield.

Talking of which, Progressive Palaeo found its very own Trevor Sinclair in the shape of **Dave Gelsthorpe** (Leicester). Why that analogy, I hear you ask? Because, like Sinclair, Dave was a late replacement for a late replacement—Elizabeth Boulter (Cambridge) couldn't make it and then her substitute (me) found that his talk had vanished from its compact disc home—but still put in a fine performance stepping into the breach at spectacularly short notice. Giving an absorbing account of acritarch biostratigraphy across the Llandovery-Wenlock boundary in Gotland, Dave showed that, although the stratotype for the boundary is in Shropshire, the Ireviken extinction event from that time is seen best in the Baltic (England 1-1 Sweden?) and is a bit strange—acritarchs don't follow the same extinction pattern as the conodonts. It may well be that in lower-nutrient conditions in the Wenlock, rather than dying out, acritarchs became more specialized and actually diversified.

Sandwiches, rather than oranges, were on offer in the interval, after which Sweden came out the stronger, **Linda Wickström** (Birmingham) enquiring as to whether cladistic analysis of the Silurian conodont genus *Kockelella* could be done. It would seem suitable, with its rich fossil record, but Linda lamented that 'no-one has cared about them as creatures', which is unfortunate. That has all changed now, and the preliminary cladograms for *Kockelella* suggest that the phylogeny of many other neglected conodonts needs reassessing.

Emphasizing the importance of speciation in understanding evolution, **Dave Baines** (Leicester) took a close look at Canadian sticklebacks (possibly a team in the North American Soccer League). Two morphologies exist—one benthic, one limnetic—but how did they arise? Intra-specific competition, leading to niche and eventually phenotypic differentiation, is the likely explanation, and examination of tooth micro-wear in these forms—the limnetic sticklebacks have smooth teeth, whereas those of their benthic cousins are much more worn—can be applied to fossils to help define species.

Befitting someone occupying the number eight position, **Xavier Panades I Blas** (Bristol) entertained us with a plentiful supply of oohs. It turned out, however, that many of them were prefixes to the taxonomic sub-divisions used in dinosaur eggshell classification (*e.g.* ootaxon, oofamily). Late Cretaceous specimens from Catalunya show that the eggshells are heterogenous and different shell thicknesses probably represent different oospecies, giving a new insight into dinosaur diversity at the time.

Before **Nick Sille** (Royal Holloway) could begin his talk there was a pitch invasion as a bearded Greek gentleman hopped onto the stage and switched the PowerPoint projector to "make the audience's ears bleed" mode. Thankfully this was not sabotage but our dear friend and conference co-organizer George Iliopoulos inadvertently pressing the wrong button on the machine. Nerves unfrayed, Nick was able to introduce us to environmental changes across the Eocene-Oligocene boundary in the Isle of Wight. Finding the boundary is hard enough because it is defined by planktonic forams and the Isle of Wight sequence is terrestrial, but charophyte algae have been used elsewhere in Europe, so Nick has adopted a similar approach. Early results show no clear shifts in morphology, but further analysis, coupled with angiosperm and mammal studies, will hopefully prove more fruitful.

The Late Silurian and Early Devonian trace fossils of the Ringerike Group, Norway, have never been completely described, but **Neil Davies** (Birmingham) has been remedying that to help produce a more accurate appraisal of the palaeoecology of an early Old Red Sandstone sequence. The ichnological assemblages (*e.g.* arthropod trackways, burrows, and more bizarre forms, such as possible medusoid beachings) separate the coastal plain setting into different facies, with an abundance of forms in the near-shore lithologies and relatively few in adjacent fluvial areas—the variation can be consistently used to distinguish the two facies. Coupled with detailed sedimentology, Neil's work will provide the first integrated assessment of the depositional environment.

The fourth official then informed us that there would be a thirty minute interval before the final quartet of talks so we helped ourselves to a few refreshments.

First up in the final session was **Natalie Thomas** (Leicester) and some strange epibionts from the Bear Gulch Lagerstätte (Namurian) of Montana. *Sphenothallus* is a problematic, tube-shaped creature, found throughout the Palaeozoic but of unknown affinities, maybe scyphozoan, maybe annelid. In the Bear Gulch, specimens are found attached to cephalopod shells and the lack of pattern in their attachment sites, coupled with them not being found attached to any benthic organisms, suggests that they probably hitched a ride whilst the cephalopods were alive and up in the water column. In turn, the absence of *Sphenothallus* from the sea floor implies that conditions there were unfavourable, perhaps due to low levels of oxygen or a fast sedimentation rate.

Also floating about in the Palaeozoic oceans were graptoloids, and **Lucy Muir** (Edinburgh) examined what caused many of them to snuff it in the *lundgreni* extinction event during the Silurian. Lucy showed that geographic dispersal was not particularly important—some globally distributed species survived whilst others died—and that rhabdosome size was much more likely to be the key factor, graptoloids with large rhabdosomes dying out. This appears to fit the concept of K- and r-selection, whereby large, long-living organisms with few offspring (K-selected) are more vulnerable than their smaller, more fecund (r-selected) relatives.

Perhaps a variation on that ecological theory is taking place amongst Leicester's Ph.D. community as there appears to be a plethora of palaeontological Daves. The day's third, **Dave Gladwell**, is studying the exquisite Silurian fossils of Leintwardine, near Ludlow, a diverse assemblage that includes everything from brachiopods to xiphosurids. Whitaker (1962) interpreted the beds as submarine channel deposits, and 80% of specimens currently known come from one channel, at Church Hill. Given their rarity in the fossil record, starfish are incredibly common there, along with—according to my shambolic notes—'Arthur pods' (presumably peas grown by ancient British kings) and Dave hopes to produce a reappraisal of those and other intriguing fossils and the environment they occupied.

And bringing the fixture to an exciting conclusion, **Aaron Hunter** (Birkbeck) showed that, although complete specimens are rare in the fossil record, it is possible to use echinoderm fragments, such as individual ossicles, to interpret palaeoecology. Sampling of sediments from the Bathonian (Middle Jurassic) has proved that crinoids, echinoids, asteroids and ophiuroids lived in a range of conditions, some being more niche-specific than others—cidaroid sea urchins were present in all environments, whereas ophiuroids lived in either normal marine conditions or low salinity lagoons.

All that remained was for Chris Paul to blow the final whistle, thanking the speakers for a diverse, well-presented and scientifically innovative set of talks, before the delegates left the arena and headed for a wine reception at the New Walk Museum, courtesy of Mark Evans. That was followed by a fine curry and then a few more drinks before we slunk off into the gloaming.

For those of us still around the next day, it was fieldtrip time and a journey across the Midlands to Long Itchington quarry, near Rugby. With Andy Swift in charge, we were introduced to the Triassic-Jurassic boundary (give or take a couple of missing biozones) and began searching for evidence of life. As is often the case, the non-palaeontologists among us made the best discoveries, including a vertebra, possibly ichthyosaurian, whilst the rest of us made do with a few bits of ammonite. And once the grey muds had stopped yielding material, we retired to The Blue Lias Inn for some lunch. As an ending for a palaeontological conference, it doesn't get much more appropriate than that.

Our thanks go to Dave, Natalie, George and Dave for their hard work in making Progressive Palaeontology 2002 such a sure-fire success. We look forward to more of the same next year.

Liam Herringhshaw
School of Earth Sciences, University of Birmingham, UK
<**LGH865@bham.ac.uk**>

Colloque International Alcide d'Orbigny
Museum National d'Histoire Naturelle, Paris *1 – 7 July 2002*

The year 2002 marks the bicentenary of the birth of the French naturalist Alcide d'Orbigny. Several conferences have been organised to celebrate this anniversary, including this one hosted by the Museum National d'Histoire Naturelle. The focus in Paris was on d'Orbigny's life and works, and on stratigraphy from d'Orbigny's time to the present-day. If any of the participants were uncertain at the beginning of the conference, none will have left without being astounded by the prodigious achievements of this remarkable scientist in the 54 short years of his life. For example, d'Orbigny pioneered the study of foraminifera and is particularly well-known for the scale models of forams that he devised and sold as a young man; these are still essential teaching aids in many university courses in micropalaeontology. He took part in an epic voyage of exploration of South America between 1826 and 1834, returning to write-up the results in the form of an eight volume series covering multifarious aspects of the anthropology, archaeology, botany, zoology and geology of Brazil, Argentina, Chile, Peru and Bolivia. D'Orbigny then resumed his research on forams before embarking, in about 1840, on the ambitious *Paléontologie française* project which aimed to monograph the entire fossil biota of France. Several volumes of this work were published before d'Orbigny's untimely death in 1857, just four years after he had been appointed to the newly-created Chair of Palaeontology at the Museum National d'Histoire Naturelle.

D'Orbigny named countless new taxa, particularly of forams, bryozoans, molluscs, brachiopods and echinoids. Many subsequent generations of taxonomists have been gainfully employed trying to interpret his species and resolve some of the myriad of taxonomic problems he

unwittingly created. A follower of Cuvier, d'Orbigny extended his mentor's catastrophistic view of the history of life by recognizing 27 stratigraphical stages each populated by a unique suite of species created afresh at the commencement of the stage and suffering total extinction at the end of the stage. The catastrophic connotations of d'Orbigny's stages soon fell into disfavour but many of the stages named by d'Orbigny still survive as international chronostratigraphical units, *e.g.*, Bathonian, Callovian, Cenomanian, Turonian. Other d'Orbigny stages are now only used locally, such as the Stampien, the stratotype sections of which we visited during the mid-conference excursion to Etampes, a town with a remarkable leaning church tower.

The Paris conference was attended by some 70 delegates, dominated as might be expected by the French, but including representatives from Argentina, Australia, Austria, Belgium, Bolivia, Germany, Lithuania, New Zealand, Poland, Portugal, Russia, UK and USA. The papers read varied from historical accounts of the work of d'Orbigny, his contemporaries and other important figures in geology, to appraisals of d'Orbigny's taxonomic contributions, to reviews showing how far stratigraphy has progressed since d'Orbigny's time. Two-thirds of the 39 talks were delivered in French, too many making no concession (*e.g.* slides) to the English speakers in the audience. From a purely palaeontological standpoint, the most relevant papers were on bivalves (Dhondt and Freneix), Campanian brachiopods (Gaspard), Argentinian Tertiary molluscs (Griffin), forams (Lipps), rudists (Mace-Bordy) and bryozoans (Taylor and Gordon). Annie Dhondt noted the problems caused by the 317 new species of Cretaceous bivalves introduced by d'Orbigny in his famous, but totally unillustrated, *Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés*. While the bivalve taxa he named in the *Paléontologie française* are generally less cryptic, these too present some difficulties, *e.g.*, the figured left valve of *Pecten dujardini* is imaginary. Jacqueline Mace-Bordy showed how d'Orbigny had interpreted rudists as brachiopods based on shell similarities with the living brachiopod *Crania*. Lipps described the criticism directed at d'Orbigny by the British foram workers Brady, Carpenter, Jones and Williamson who believed that such simple organisms did not have species and therefore that d'Orbigny had grossly overestimated the diversity of the group. Darwin was apparently so influenced by his compatriots that he was led to accept the non-Darwinian notion that forams did not evolve.

In the final lecture of the conference, Agnes Lauriat-Rage told us how d'Orbigny's collection of fossil invertebrates was sold to the Museum National d'Histoire Naturelle by his widow on 25th November 1858 for 55,000 gold francs. It took a curator with the marvellous name Hippolyte Hupe just under two years to catalogue the 100,000 specimens, a work-rate that puts today's less ambitious computer cataloging targets into perspective. Hupe's handwritten ledgers, one for each of d'Orbigny's 27 stratigraphical stages, total 803 pages. The d'Orbigny Collection is now mostly housed in the Salle d'Orbigny, a very special room that the conference delegates were able to visit before the closing dinner. The hard work of the two main organisers of the conference, Marie-Thé Venec-Peyre and Philippe Taquet, ensured that everyone left Paris with an enhanced appreciation of the remarkable Alcide d'Orbigny, and happy memories of the conference convened in his honour.

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news

Dr Adrian Rushton awarded the 2001/02 Clough Medal

Adrian Rushton of the British Geological Survey, Nottingham, and the Natural History Museum, London, has been awarded the Edinburgh Geological Society's Clough Medal. The award particularly recognizes his palaeontological work on both sides of the Iapetus Ocean and with both shelly and graptolite faunas, in Wales, the English Lake District and the Scottish Southern Uplands. Adrian's work has been fundamental to the establishment in these areas of a robust graptolite-based biostatigraphy that has, in turn, allowed innovative interpretations of previously intractable structural problems.

The Clough Medal commemorates the renowned Geological Survey work of C.J. Clough (1852–1916), primarily in the Highlands of Scotland but also in the coalfields of central Scotland and northern England. It is the Society's premier award and has been presented annually, since 1935, to a geologist whose original work has materially increased the knowledge of Scotland and the north of England. The medal was presented to Adrian at a meeting of the Society in Edinburgh on 27th March 2002. After the presentation Adrian lectured on "Fossils, fashion and failure; examples from the Lower Palaeozoic of southern Scotland and northern England."

EU-supported visits to the Palaeontological Collections at the Geological Museum, Copenhagen

The palaeontological collections at the Museum form part of the Copenhagen Biosystematics Centre (COBICE), a designated EU large-scale facility that includes also the Botanical and Zoological museums together with the Botanical Gardens. The scheme offers funding (travel, accommodation and subsistence costs) to promote visits to departments in the complex. Clearly the scheme is available to support the use of our collections but the programme also allows for the use of staff expertise, specialized equipment or a combination of all three. Surprisingly, to date, relatively few palaeontologists have applied for support. The application procedure is straightforward. Intending applicants should first contact a member of the Museum's curatorial staff or myself to develop a programme. Information on both our collections and our staff are available on our website at <**http://www.geological-museum.dk/**>. Full details of the scheme, including information regarding eligibility and the simple application procedure, are posted on the COBICE website at <**http://www.zmuc.dk/commonweb/COBICE.htm**>.

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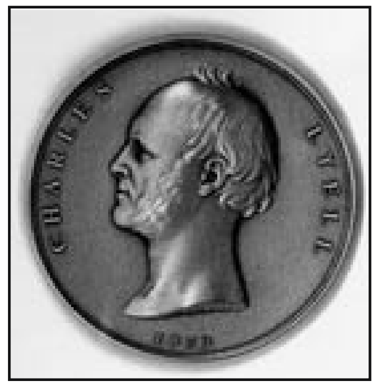
Palaeontologists clean-up in the 2002 Awards of the Geological Society of London

Contrary to the popular perception that palaeontology has a poor reputation amongst the Geological Sciences, this year's awards ceremony of the Geological Society of London witnessed a raft of awards for palaeontologists. The awards were presented by Society President, Lord Oxbrough; the supporting citations are reproduced below.

Lyell Medal: Andrew Benjamin Smith

Andrew Smith, the recipient of the Society's Lyell Medal, pioneered the application of morphological knowledge of living to fossil echinoderms. His work has shown that the tubercles and pores of the denuded tests commonly found in the fossil record precisely reflect the nature and function of the spines and tube feet that determine the animal's life-style. He has simultaneously developed his interests in echinoderm taxonomy, and his cladistic classification of the Phylum has now become the standard.



This rigorous taxonomic understanding has led Smith and his colleague Colin Patterson to elucidate patterns of extinction in the fossil record. He is responsible for a series of major monographs of fossil echinoderms from all over the world, and from the Cambrian to the Cretaceous. He has lately turned his attention to molecular taxonomy, and the study of ancient DNA. For more general audiences, Smith has authored beautifully illustrated textbooks and a website on his beloved echinoids.

Previously honoured by the Society with its Bigsby Medal (1995), by the Linnean Society's Bicentennial Medal (1993) and by Fellowship of the Royal Society of Edinburgh (1996), Andrew Smith is a worthy recipient of the Lyell Medal.

Coke Medal: John Christopher Wolverson Cope

John Cope differs from most stratigrapher-palaeontologists by virtue of his wide range of interests, covering many fossil groups and geological periods.

John made his name on the ammonites of the Upper Jurassic, where he was among the first to demonstrate sexual dimorphism throughout an entire lineage. He followed up work at home with researches on Jurassic rocks in Turkey, Albania, and Italy. He is now an internationally renowned expert on the ammonites and stratigraphy of the Jurassic System.

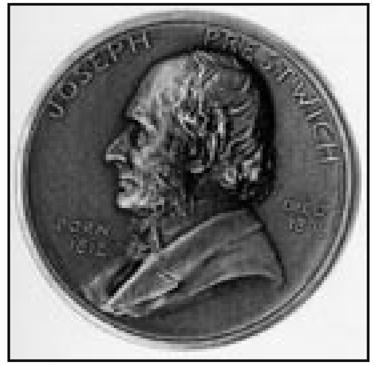
In the late 1970s his mapping in the Carmarthen area led to the discovery of hitherto unknown Precambrian rocks containing an Ediacaran fauna. He also discovered a tract of Cambrian rocks with rich faunas and the first Tremadoc rocks found in South Wales. In this overlooked area of South Wales, John discovered some of the world's richest Arenig faunas, and has since described the earliest representatives of many groups of fossils. The Arenig bivalve faunas led to work that has totally revolutionised ideas on early bivalve phylogeny. In short he has now also become the leading world authority on Ordovician bivalves.

John's demonstration of an end-Cretaceous plume under the eastern Irish Sea has elegantly explained how southern Britain was tipped up to produce the well-known geological pattern—of older rocks in England and Wales being to the north-west with a general south-eastward dip and the younger rocks to the south-east. It also explains the origin of the drainage of the southern British Isles, and his interpretation of the unroofing of the Irish Sea petroleum reservoirs has been acclaimed by petroleum geologists—a brilliant solution still not widely appreciated.

"John, you have been an indefatigable worker for the Society over many years, including a major role in the Society's palaeogeographical atlas of the British Isles, service as Publications Secretary and as Treasurer—a fact that has rendered you ineligible for a Society honour for over a decade."

Prestwich Medal: Adrian William Amsler Rushton

The Prestwich Medal goes to Adrian Rushton who, over more than 35 years, has made important contributions to Lower Palaeozoic geology, correlation and palaeontology.



His work at the British Geological Survey provided the stratigraphical control that ensured the scientific correctness of their geological maps, as will be readily acknowledged by any one of fifty or more colleagues, among whose names his was often modestly to be found. His contribution to the reinterpretation of the Lake District, Snowdonia, the Southern Uplands and the Lower Palaeozoic subcrop of the English Midlands has been immeasurable, but as his impressive list of over 140 publications attests, hardly a single area of the Lower Palaeozoic in the British Isles has been left untouched by his hand.

"Adrian Rushton, previous recipient of the Society's Lyell Fund (1977), is also a renowned scientific editor, leading expert on the Cambrian and its trilobites but legendarily knowledgeable about all fossils from brachiopods to graptolites."

Murchison Fund: Philip Conrad James Donoghue

The Murchison Fund goes this year to Philip Donoghue. Philip is an outstanding young palaeontologist who has made a major contribution to the palaeobiology of conodonts. In recent years conodonts have been shown to occupy a pivotal position in the early evolution of vertebrates. Donoghue's work, independently and in collaboration with other palaeontologists and developmental biologists, has been of particular significance in helping to determine the selection pressures driving the origin of the vertebrate skeleton and its development within the conodont clade.

"How the conodont animal fits within the vertebrate clade has been a topic of heated debate for the last ten years, and Phil Donoghue's painstaking and exhaustive cladistic research has provided by far the most thorough analysis of this question to date. He has done innovative work on conodont histology, showing how conodont elements grew, and allowing new functional interpretations of conodont microstructure. Jointly with Mark Purnell, he has led efforts to reconstruct the conodont apparatus in rigorous architectural detail and to use this information in analyses of functional morphology."

CAREERS

So you want to be a Palaeontologist…?

Enquiries regularly come in to the Association from young people in the U.K. who want to know the qualifications that they will need to become a palaeontologist. Usually they are concerned about what subjects they should choose for GCSE or A levels. Our replies are tailored to each enquiry, but assume that their interest is in a regular job in palaeontology (of which there are not that many around, as we know), rather than, say, wanting to be a professional collector. Therefore we assume that they will want to get, as a first step, a B.Sc. degree in a U.K. university.

The more usual route has been to read for a Geology or an Earth Sciences degree, or for some other single or joint honours degree that covers the general field of Earth Sciences. These subjects approach palaeontology in the traditional way, as a sub-discipline of Geology. Recently, some universities have started to offer a way into palaeontology via the biological route, and offer degrees in Palaeobiology, or in Palaeobiology with another (usually biological) subject. A few universities (*e.g.* Oxford and Cambridge) have a long tradition of exposure to aspects of vertebrate palaeontology through a Zoology degree or similar. Similarly, a few Plant Science degrees offer exposure to some palaeobotany.

Joint Honours degrees that encompass both Biology and Geology are also available at some institutions, and enquiries should be made to favoured universities. Some modular degrees provide the opportunity to do a Palaeontology course as part of a varied package within the general sciences. However, unless there is an opportunity to specialize in the final year, these programmes are not likely to be particularly useful if and when it comes to the competitive post-graduate stage of trying to secure an M.Sc. or a Ph.D. position. Routes for people interested in curatorial jobs are somewhat more flexible.

So, the hopeful palaeontologist needs to decide whether she or he wants to go down the Earth Sciences and/or the Biological Sciences route for her/his Batchelor's degree. The Pal Ass certainly doesn't recommend certain degree courses at the expense of other ones, but there is a clear history of certain departments having good palaeontologists on the staff, and turning out high-quality graduates. Departments (in alphabetical order) that go down the Earth Sciences route include: Aberdeen, Birmingham, Bristol, Cambridge, Cardiff, Derby, Durham, Edinburgh, Leeds, Leicester, Liverpool, Liverpool John Moores, London (Birkbeck, Imperial, Royal Holloway, and University College), Oxford, Portsmouth, Southampton. The palaeobiological approach is offered by Liverpool John Moores, Portsmouth, and University College London. The details of these and other courses offered differ from year to year, and the university should always be consulted for the latest news.

The choice of A levels should thus always consider which university and which course might be followed. A biological A level is appropriate for the biological approach (and useful for the others), but some of the Geology-based courses have fairly strict requirements for 'hard' sciences, such as Chemistry, Physics, and maybe Maths. Geology A level is often acceptable, but never a

strict requirement. Other courses will accept a range of science subjects and will often accept Geography or even Humanity subjects, particularly if they find themselves admitting through Clearing. It is essential to bear the usual entry requirements of particular universities in mind when choosing A levels. The new AS levels also offer the possibility of attaining a stronger portfolio of appropriate subjects, usually within the sciences.

The choice of GCSEs is usually made two years before the exams are taken, and different schools offer different combinations and subject areas depending on what can be taught at that school. Normally, the options are outside the core fields of maths and sciences (which are done by everyone), although they may include Geography, Biology, and Information Sciences. It is very unlikely that the choice (or rejection) of a particular GCSE option will ever prevent a budding palaeontologist from going on to do an A level that is necessary for any appropriate degree course, but the advice of the school should be taken in case of doubt.

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Want to help children get into your industry, or at least give them an idea of what you do…?

Science Year has recently opened a database of profiles of working scientists, engineers and technologists, science professionals, *etc.*, which is growing all the time. You can see the results of the database to date at <**http://www.scienceyear.com/nextsteps/**>.

The database is called Meet your Match and is aimed at giving young people top information about careers in a really fun way. The questionnaire takes a minimum of 20 minutes to fill in and you will be required to send a photo (you'll see on the database how much that helps). To get to the questionnaire go to <**http://www.scienceyear.com/profiles/questionnaire.html**> (username: <**CaptainCook>;** password: <**Endeavour**>).

If you have any questions or problems please contact Katie Walsh on 0207 808 1803.

CORRESPONDENCE

Epistemology matters!

I agree with Ed Jarzembowski that one of the spin-offs of cladistic analysis has been to expose the problems behind the over-conflation of pattern and process, but I must disagree with his parting comment that “the same might be said for methodology and epistemology…” On this matter, I strongly encourage Jarzembowski and, potentially, any *Newsletter* readers, not to be so immediately dismissive! On the contrary, a lucid fusion of methodology with epistemological considerations is central to the formulation of rigorous and consistent analytical techniques, especially in a historical science such as palaeontology. If we take epistemology to be “the study of knowledge, the study of how we acquire knowledge and the constraints on what can be known”, and methodology to be “the study and development of protocols that allow for some kind of analysis and hence lead to discovery,” then surely the two disciplines become intimately linked. From a methodological perspective, what analysis can detect, reveal and discover is a direct function of the epistemological constraints on the system in question.

For example, in palaeontology, as in all historical science, the most obvious constraint is the inability, in most (but not necessarily all) cases, to perform repeatable experiments which yield empirical observations that can be used to support or falsify hypotheses. This means that, to be scientific, we are compelled to confine our line of inquiry and hypothesis formulation to questions that we hope can be answered by other kinds of methods. To ignore this constraint is not “wrong”, but it would not be science. From an epistemological perspective, the methods we employ are the connections between “what it is possible to know about system X” and “what we know about system X”. It follows that, in order to do rigorous methodology, we must address the first of these statements, which effectively amounts to an *a priori* epistemological analysis of our system.

Palaeontologists are doing epistemology all the time even if they don’t realise it! This is not surprising, of course, because palaeontologists are scientists, and science and the “scientific method” are simply epistemological paradigms, *i.e.* broad schemes that describe a general approach to discovering something about, in our case, the history of life on this planet. Lying between what we can know about life on this planet and what we do know are our methods—cladistic analysis, the comparative method *etc*. In short, it is sound epistemological analysis that makes our methods scientific. This is why, for example, Hennig’s original works on cladistic theory and methodology are principally philosophical treatments that the methods “fall out” of. So I encourage readers, especially those with an active interest in methodology, to give serious thought to epistemology and not to dismiss it as dry and superfluous procrastination as it so often can seem to be, and instead see it as one of the keys that can potentially open the door to the “season of enlightenment”.

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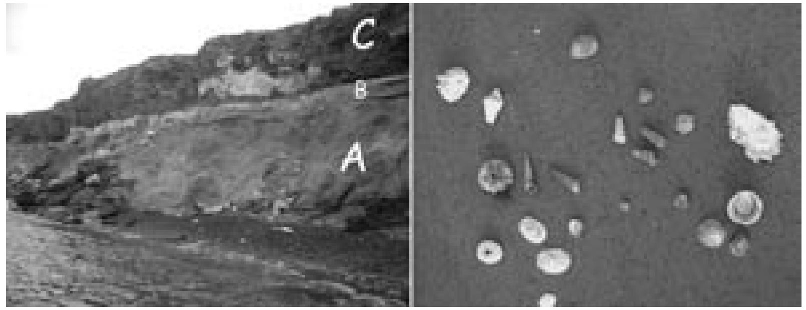
From our Correspondents

The white rock and the baobab

On 16th January 1832, HMS *Beagle* arrived in the broad bay of Porto Praia, capital of the Cape Verde archipelago in the tropical Atlantic. It was the first port call since the ship left Plymouth several weeks before. On board was Charles Darwin, aged 22, sailing as unofficial naturalist and gentleman companion to the Captain, Robert Fitzroy. As the crew set up an observatory on a small island in the bay (so Fitzroy could fix the longitude), Darwin sloped off for a spot of independent fieldwork. These were the first substantive observations he was to make on this famous voyage.

Nothing was known about the geology of Praia. Reasoning that this little islet would provide a representative geological section of the entire area, Darwin set to work examining the rocks. In essence, it is a geological sandwich, in which the massive volcanic rocks are the bread and a relatively thin band of white limestone is the cheese (as shown in the figure, with “B” being the limestone).



The white band is raised a few meters above the sea, but is easily accessible in several places. It contains abundant fossils, as I was lucky enough to confirm myself on a recent visit to Praia. Although the rock is quite hard, the shells weather proud and can easily be pulled out. Some of them retain traces of their original pigmentation. The most striking thing, however, is that an almost identical collection can be made from the modern beach at one’s feet. In the photo, the recent shells are to the left and fossils to the right.

Darwin noticed this, and discovered that he could match them up, species for species, with only a few exceptions. When he returned, he had this observation confirmed by the most eminent conchologists of Victorian Britain. From this, he reasoned that the limestone must be very recent in geological terms. However, it had evidently been raised from below sea level and covered by a substantial thickness of columnar lava. This basalt is an exceedingly hard rock, and yet a great deal of erosion had occurred since its consolidation, including the formation of the bay of Praia and the isolation of the observatory islet from the mainland.

The old citadel of Praia sits atop a rocky bluff on the mainland that is also skirted by the white limestone. A few days later, in a valley behind the fort, Darwin came across a splendid old tree, which he identified as *Adansonia* (the baobab). This tree had been named by Linnaeus to honour Michel Adanson (1727–1806), the French naturalist who first described it in the eighteenth century. Adanson had speculated that the most mature baobabs might be as much as 6,000 years old—implying that they could have sprouted on the third day of creation and been there ever since!

Darwin knew of this extraordinary claim, and remarked that "the very appearance of the tree strikes the beholder that it has lived during a large fraction of the time that the world existed". More prosaically, he also observed that it "bears on its bark the signs of its notoriety—it is as completely covered with initials and dates as any one in Kensington Gardens". A few days later he persuaded Fitzroy to visit the tree and measure it with his pocket sextant. This, the captain was happy to do, and for good measure Fitzroy climbed to the top (easy for a sailor, no doubt) and let down a string to confirm the result. It proved to be 35 feet in circumference and 45 feet high.

Incidentally, although the baobab is indeed one of the most long-lived of trees, it never approaches 6,000 years—just a few hundred for the oldest. Nevertheless the idea persists on the Internet. For example, I found a charming account of a pub in South Africa that nestles in the trunk of a supposedly 6,000 year old baobab. The same site also assures us that "pyramid power restores us to our original blueprint, unlocking our cellular memories and reactivating the 12-strand DNA structure". But I digress.

Darwin knew enough of geology (from Adam Sedgwick in Cambridge, among others) not to be misled by appearances. Instead, he used the tree in a different way to investigate the Earth's history. First of all, he argued it must be younger than the lava flow on which it had grown. This he traced to a nearby volcano called Red Hill, a substantial cone that in turn had grown atop (and was therefore younger than) a basaltic layer which correlates to the upper lava flow on the observatory islet. Are you following, dear reader? The limestone was older still, of course. There was no telling how long unrecorded intervals of time might have elapsed between these events. "To what a remote age does this in all probability call us back and yet we find the shells themselves and their habits the same as exist in the present sea".

Darwin followed his band of white rock for miles across country on the main island. Persuading one of the officers to measure it with the ship's theodolite, he confirmed that it is perfectly horizontal over areas several miles across. The uplift, he reasoned, must have been very even, such that "a town in some places might have been raised without injuring a house." To Darwin this seemed more to support the gradualist theories recently propounded by Charles Lyell than in the more catastrophic geology that was then in vogue, and taught him by Sedgwick and others. The first edition of Lyell's *Principles of Geology* had just been published, but Darwin had been warned "on no account to accept the views therein advocated."

Many years later, as an old man writing his autobiography, Darwin was "proud to remember that the first place, namely … the Cape de Verde Archipelago, in which I geologised, convinced me of the infinite superiority of Lyell's views over those advanced in any other work known to me". He also vividly remembered following the white limestone of Praia along the rugged east coast of the main island, where it "first dawned on me that I might perhaps write a book on the geology of the various countries visited, and this made me thrill with delight. That was a memorable hour to me, and how distinctly can I call to mind the low cliff of lava beneath which I rested, with the sun glaring hot, a few strange desert plants growing near, and with living corals in the tidal pools at my feet." A scientific career was launched.

The idea that the Earth is very old, and that gradual processes can operate across vast stretches of time to produce large results, underpins the science of evolution. This was the case for Darwin, and it remains just as true today. The white limestone of Praia is there for anyone with an open mind to examine—and so it will be, for millions of years to come. Sadly, no trace of the baobab can now be found, thus any hope one might entertain of finding "Fitzroy woz ere 1832" gouged into its upper branches must always be in vain.

Acknowledgments: The author is grateful to the Philip Leverhulme Prize fund for providing the means to visit Praia, and Chris Nicholas for helping with the fieldwork.

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Soapy Sam—a brief hagiography

"Beer, beef, business, bibles, bulldogs, battleships, buggery and bishops"
Ulysses, James Joyce, Ch. 12.

This pithy sound-bite by which Joyce sums up England was probably more accurate for the time than one might care to admit. More delicate readers may be relieved to learn that I intend to discuss one of the above here—which has certainly diminished in influence since then. For those of you who think that the traditional British parlour game, 'name ten famous Belgians' (the problematic nature of which says more about 'us' than 'them', one feels) is too testing after a brandy or two, here is a variant: try coming up with ten famous Victorian bishops. Tricky? Those who have passed through Cambridge at some point might scrape up Selwyn or even Westcott, but nearly everyone will have to plump for that bugbear of obscurantism, Samuel Wilberforce—'Soapy Sam'—the sometime Bishop of Oxford. Leaving aside such luminaries as Philpottts, Blomfield and Edward King, then, the one point of contact palaeontology has with the Victorian episcopacy is the hapless victim of Huxley's famous debate at the British Association on Darwinian natural selection. Wilberforce, it will be recalled, was the man who (apparently) declared the moral impossibility of at least women descending from apes, drawing from Huxley a poorly-remembered remark along the lines of how preferable this would be than to misuse one's talents in the service of obscurantism. The conventional picture is well displayed in Adrian Desmond's recent biography of Huxley: He (Wilberforce, not Desmond), in his frock-coat and sideburns, looks like the epitomy of tedious Victorian moral puritanism. But of course, the truth is far more complex than this. As this fascinating and infuriating figure scarcely gets a fair hearing in the scientific literature, I shall try to give him a run for his money here.

Samuel Wilberforce was the product of one of the most famous evangelical families: his father, William Wilberforce, was the principal campaigner for the abolition of slavery, perhaps the great moral advance of the early nineteenth century. From this extraordinary person he inherited or acquired famous oratorical skills, and although one might fail to glean it from the Huxley debate, he was one of the greatest public speakers of his day. Personable and capable, he passed through Oxford and quickly became Archdeacon of Surrey. Wilberforce, as well as being energetic, was charming and affable, and (initially) a particular favourite of Queen Victoria and Prince Albert. Thus, when the Deanery of Westminster fell vacant in 1845, Wilberforce was chosen by the Prime Minister Robert Peel for this, the most public face of the Church of England. Yet he was to stay here only a few months, as on the death of Bishop Bagot, he was moved to Oxford where he was to stay for the next 24 years. In passing, one might note that Wilberforce was a strange choice for Westminster, being mercurial and unpredictable, but Peel's choice for successor was even more peculiar: William Buckland, the notoriously eccentric Reader of Geology in Oxford. Buckland spent his time at Westminster poking around in the sewers of the school (on one occasion apparently causing a cholera outbreak as a result) and dusting the statues in the abbey (Owen Chadwick notes, however, that the feather duster Buckland habitually carried around was 'no mere sceptre of eccentricity', but a necessity in the days when the cathedrals and equivalents were mired in incompetence.

Wilberforce was regarded with some suspicion by the "Establishment" partly because he came, almost accidentally, and not entirely fairly, to be seen as being sympathetic to the Oxford Movement or Tractarians, the faction of the Church of England that was seeking to revive Catholic tradition; and partly because of his views of the relationship between Church and State. For nineteenth century England was one of the most remarkable religious crucibles the west has ever seen. Methodism, evangelism and romanticism tumbled over each other into the beginning of the century. As the romantic movement took hold of art, poetry, music and even chess, it was inevitable that religion would be affected as well. In the Church of England, this evolved into a passion for gothic architecture and an appeal to the ancient church as authorities (as opposed to a merely national church), together with calls for thorough reform of the archaic administration of the church, particularly with regard to its ambiguous relationship to the State. Many of the more prominent members of the movement eventually became Roman Catholics, including both of Wilberforce's brothers; and their transition from Evangelical to Roman Catholic was a typical one. It is perhaps hard to get a grip of the passions these sorts of sensational conversions aroused: William Gladstone was shocked to learn of his own convert sister using the pages of works by Protestant divines as toilet paper, for example. Wilberforce was firmly opposed to such tendencies, and was consistent in his defence of middle-of-the-road Church of England doctrines. So far, so unexceptional: but Wilberforce achieved a prominence far above that which might be expected for a middle-ranking bishop. First and foremost, he represented a new generation of the Episcopacy that actually did some work. Under the pressure of religious revival, bishops became expected to visit their clergy, take on a large administrative burden and carry out ordinations and confirmations on a scale that would have been unthinkable—indeed, rather distasteful—to most of their eighteenth century predecessors. Wilberforce was the absolute model of the new hard-working diocesan, as the enormous numbers of letters he wrote and committees he sat on testify. Yet he was no narrow-minded ecclesiatistic. He had a life-long interest in natural history, including geology, and in his time served on the Council of the Geological Association and as Vice-President of the British Association. William Burgon in his *Lives of twelve good men*, comments on his intimate knowledge of his home in Sussex; where he delighted in pointing out the various geological formations, plants and birds to

visitors. Perhaps the worst of him that could be said in this regard is that he suffered from that peculiarly Victorian sentimentality about animals—going so far as burying his father's favourite horse (when dead, of course) right next to consecrated ground.

Why did this charming and companiable man have such a dubious reputation preserved for posterity? Unfortunately, the reasons are partly clear. First of all, his capacities and energies made him acutely aware of his potential career—and he could not resist talking in private about "spheres of higher influence." The preface to the most recent biography puts it baldly: "Others had a less flattering explanation. They believed he was inordinately ambitious, and that he trimmed to a line dictated by that ambition" (Meacham 1970). Inevitably, many of his actions and views became seen as being careerist, and thus insincere. For example, here is Wilberforce on evolution, in his famous 1860 review of the *Origin of Species* in the *Quarterly Review*:

> *"Our readers will not have failed to notice that we have objected to the views with which we are dealing solely on scientific grounds. We have done so from our fixed conviction that it is thus that the truth or falsehood of such arguments should be tried. We have no sympathy with those who object to any facts or alleged facts in nature, or to any inference logically deduced from them, because they believe them to contradict what it appears to them is taught by Revelation. We think that all such objections savour of a timidity which is really inconsistent with a firm and well-intrusted faith".*

All very well, and indeed in his famous speech at the Oxford meeting, he dwelt not on Revelation but Rock Pigeons. But even I find it hard to believe that Wilberforce, given his strong stance not just against Darwinism, but also the other great problem of "German", liberal theology, really believed this. Perhaps he did: but the ease with which he attempted (and largely succeeded) with ingratiating himself with his opponents led the more cynical to suspect him less of integrity than smoothness. His nickname started off, indeed, as "Slippery" Sam, but was transmogrified to the even nastier "Soapy" by about 1853. In his attacks on Darwin, and on liberal theology, one gets the strong impression that, although clever, he was somehow rather cavalier in his treatment of both; that in his speeches and writings about them, he failed to perceive their heart. Rather than the stuffiness he is often accused of, his problem was the exact opposite; of flippancy. Read him again in the *Quarterly Review*:

> *"But we are too loyal pupils of inductive philosophy to start back from any conclusion by reason of its strangeness. Newton's patient philosophy taught him to find in the falling apple the law which governs the silent movements of the stars in their courses; and if Mr Darwin can with the same correctness of reasoning demonstrate to us our fungular descent, we shall dismiss our pride, and avow, with the characteristic humility of philosophy, our unsuspected cousinship with the mushrooms".*

For a Victorian bishop, that is, I submit, quite funny. But he didn't really get beyond that. Yet, let us be sympathetic: it was a time of complex change, and no-one could see where it was heading, and there were moments when the Victorians really feared that all their religion, together with the whole basis for a moral order in society, would be swept away.

Finally, the real problem with the Wilberforce and Huxley debate is that it has been taken as symptomatic of the age; when in fact the development of the reception of evolution by the church (and society as a whole) was much more stately. In the 1860s the church was largely hostile, but then, so were some scientists. In the 1870s, after the further shock of the *Descent of Man*, the opinions of the moderates (of which Wilberforce was certainly not one) began to come to the ascendency. In the pages of the *Guardian*, friend of the high church, one already has in 1868 the commendation of Darwin's "brilliant and patient research". In 1874, the official publishing house of the Church of England, the SPCK, published Bonney's *Manual of Geology;* and in 1882, when the debate was effectively over, Darwin was buried in Westminster Abbey, and the request was elicited by one of its Canons, Frederic Farrar. Finally, in 1884, Temple, who became Archbishop of Canterbury in 1896, delivered the Bampton lectures in Oxford where he assumed simply evolution to be true; and without a flicker of protest.

Meanwhile, what was Wilberforce up to? He continued to busy himself with his diocese, to fail in his ambition of Canterbury or York; continued to exasperate those who expected consistent support from him (including the high churchmen and the high Tories—after 1868, Wilberforce was effectively Gladstone's man); and eventually was shuffled up by Gladstone to Winchester in 1869. It was a tardy preferment, and one that he had hardly time for; in 1873 he dropped dead after falling off his horse, "in the very act of praising the loveliness of the landscape", according to Burgon. For whatever Wilberforce's other merits were, good horsemanship was not to be counted among them, with one correspondent sardonically remarking that "my only marvel is that the inevitable results [of his dreadful technique] did not occur sooner". I do not think I myself need to draw out any conclusions from this sad end.

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Ontogeny & Morphology, Past & Present

Palaeontologists study fossils and, so, often acquire no direct access to data that would bedazzle developmental biologists were they able to 'travel back in time' to study organisms that were to go extinct. Nevertheless, palaeontologists are privy to ontogenetic information whenever: (1) developmental stages are recorded during individual growth (*e.g.*, accreted shells), (2) developmental sequences are available from a collection of fossil specimens at different developmental stages (*e.g.*, growth series of skeletons), or (3) developmental information from extant taxa can be applied to study dead relatives. In all cases, evolutionary developmental biology studies can be conducted.

(1) Developmental Stages Recorded During Individual Growth

Mollusc shells exemplify cases wherein form recapitulates growth, because they are produced by cumulative accretion of calcium carbonate. For example, typically, a gastropod extends its mantle edge just beyond its shell aperture lip and along the periostracal groove to secrete a calcareous matrix. The mantle edge configuration depends on stress within the mantle and aperture shape; the calcareous matrix hardens onto the aperture and becomes integrated permanently into the previously accreted shell surface. Internally, the shell may be thickened or resorbed, but, once constructed, its external form remains unchanged. Consequently, shell form records shell growth. This renders gastropod shells useful for acquiring ontogenetic data and conducting developmental analyses.

(2) Developmental Sequences Available from a Collection of Fossil Specimens

Among terrestrial fossil taxa, perhaps dinosaurs provide the most comprehensive preservation of developmental stages. The large eggs of dinosaurs, protected within nests and by their rigid shells, have been found occasionally to contain preserved embryonic skeletal material. In comparison, very little (no?) embryonic mammalian fossil material has been reported in the literature. The presumed parental care demonstrated by maiasaurs or the oviraptorid sitting on its nest demonstrate how embryonic, hatchling, sub-adult, and adult growth stages associated together can enable egg or embryo identification. Bone beds containing brooding sites for species of *Maiasaurus* have made possible detailed growth-rate estimation for individuals in this group. Developmental stages are deduced on the basis of non-overlapping size classes that are exhibited among young specimens. Analyzing arrested growth lines corroborates the developmental stage and size designations.

Recently-published descriptions of Late Cretaceous embryonic material from Argentina record the first articulated cranial information for titanosaurs. Previously, the dorsal position of the nares among eusauropods was hypothesized to be coupled with braincase rotation; however, the new embryo material provides evidence that these two characters might have been uncoupled. The nares of the embryonic skulls are not located dorsally, but the braincase is rotated "slightly." Given the lack of later ontogenetic stages, nares movement during ontogeny remains possible.

Fossil developmental sequences are also available for amphibians, particularly anurans and urodeles. Mass death assemblages give rise to a wealth of information concerning ossification sequences, larval morphology and, when soft tissue imprints are available, even aspects of life history. Analyses are based largely on comparisons with extant taxa. For example, characters such as ossification state or relative proportions or positioning of skeletal elements are used to assess whether a specimen is paedomorphic or peramorphic, aquatic or terrestrial, walking or jumping. Such inferences must be drawn with caution, however. Developmental morphology tends to follow different patterns, depending on whether the structure in question (*e.g.* a skull or a limb) is functional as it develops (*e.g.* actively feeding or locomoting). Also, extant amphibians are notorious for exhibiting and exploiting developmental variation; *i.e.*, they are plastic in both their development and subsequent evolution.

(3) Applying Developmental Information from Extant to Extinct Taxa

Any study of the development of extinct taxa must, inevitably, be inferential and conducted against the background of the assumption that, although development evolves, similarities of development (whether stages, life histories, or processes) can be recognized as homologous within the context of comparative analyses.

The degree to which the development (ontogeny) of extinct taxa can be studied when no closely related extant taxa exist is exemplified by trilobites, bottom-dwelling marine arthropods of well-aerated seas of the Lower Cambrian to Upper Permian. With their segmented bodies (head, thorax, and tail), biramous appendages (one per segment save for the last tail segment and used as walking legs and gills), pair of antennae, and compound eyes, trilobites clearly reside within the arthropods. Dorsal shields are hard (sclerotized) so preserve well. Facial sutures on the head (cephalon) suggest the possibility of moulting and therefore of multiple stages in the life cycle, a suggestion confirmed by many workers over 150 years of study. Indeed, several stereotyped larval stages are identified, with evidence of 30 or more moults in many species. Early workers (back to 1849) thought that the larval stages would provide evidence for the origins of the arthropods (*e.g.*, that they might resemble the nauplius larvae of crustaceans) or evidence for ontogeny recapitulating phylogeny (larval stages of later forms appear to reproduce earlier stages in trilobite evolution). Appendage development during larval life provided information on whether arthropods were mono- or polyphyletic, especially whether those with uniramous legs formed a common group.

The first (protaspid) stage is represented by animals no more than 1 mm long in which the single dorsal shield has divided transversely into two segments. During the following (meraspid, larval) stages, the body is subdivided into distinct parts as a new segment is added with each moult until all segments are delineated (the holaspid [adult] stage) and body size has increased 6-12 fold. Any subsequent moults enable further growth but no further addition of segments. So, ontogeny is evidenced by stages (prelarval, larval, adult), segmentation, morphological diversification, and size increase. Segment number may be determined, size is not. Segment number within species may be high and variable (±50 body segments in *Emuella dailyi* from the Lower Cambrian) or low and constant (11 body segments in *Acaste downingiae* from the Middle Silurian). Such variation tends to be interspecific in early trilobites, then progressively fixed at higher taxonomic levels with progression post-Cambrian. Given such preservational evidence of ontogeny and life history stages, the clear position of trilobites within arthropods, and phylogenetic conservation of major developmental stages and/or processes (although development can evolve, as von Baer, Haeckel, Balfour, Gegenbaur, and many other 19th century evolutionary morphologists recognized), knowledge of the ontogeny of extant arthropods can be used as the *modus operandi* for analyses of trilobite evolution.

Examination of evolution by heterochrony (change in timing of development, or of a portion of development, in a descendant with respect to timing in an ancestor) has been a major focus of trilobite workers; evidence for heterochrony has also been found in echinoids, ammonites, bryozoans and graptolites. In trilobites, periods between moults are shortened and patterns of heterochrony shifted during the history of the group, from retention of ancestral juvenile characters in adults of descendants (paedomorphosis) to expression of ancestral adult characters in juveniles of descendants (peramorphosis). Identification of such patterns of heterochrony provides hypotheses to investigate mechanisms of heterochronic change in related recent taxa; one example is whether changes in segment number in trilobites during their phylogenetic history reflect increasingly constrained (invariant) developmental processes. It probably does, and it can be addressed through studies of extant arthropods.

Of course, again there are cautions. In *The Shape of Life* (1996), Raff took McNamara's work on shell indentations in sand dollars (which on the basis of visual analysis, has been interpreted as an example of pre-displacement and acceleration) and reinterpreted it as a classic case of hypermorphosis and an example of the origin of a novel morphology, leaving us with the three types of peramorphosis for the same pattern in the same organisms! Quantitative analysis of the data to account for variability and relations between variables would allow similarities and differences between ontogenies to become more apparent by taking into account that: (1) one feature (body size) might be much larger or smaller than the same feature in another group under comparison; (2) relative growth between features might differ between two or more groups being compared; and (3) absolute growth of the same feature might vary in the different groups under comparison. Operation of any one of these variables would lead to assignment of different patterns of heterochrony. Consequently, ontogenies ascribed to extinct taxa are inferential. The importance we ascribed to morphology in our first column (*Newsletter* **49**, 2002) must be tempered by careful approaches to how morphology is analysed and ontogeny of extinct taxa identified.

Application: Unfamiliar Organisms

Acquiring ontogenetic information becomes important particularly in attempts to identify unfamiliar organisms. For example, in the absence of ontogenetic data, how does one decide whether a specimen represents a new taxon or only a developmental variant or stage? This problem is not unique to palaeontologists; sceptical neontologist readers are invited to consider the ammocoete-adult lamprey discombobulation that occurred during the last century. Palaeontologists can draw more attention to these organisms by considering them to be previously unreported taxa, which generally receive greater scrutiny than do descriptions in which taxa are assimilated into pre-existing groups. However, this practice might result in superfluous and redundant taxonomy and, ultimately, misdirect subsequent evolutionary investigations.

Failure to consider different growth and developmental stages obfuscates accurate taxon recognition and is prevalent in palaeontological literature. Of course, in some situations, too few specimens are available to conduct ontogenetic studies based on developmental sequences, or developmental stage traces are effaced during growth. However, as evolutionary developmental biologists, we suggest that, even without large sample sizes or growth relics, unfamiliar taxa can convey useful ontogenetic information. The techniques and approaches of evolutionary developmental biology provide means to infer development when only morphology is available, provided that there is enough of a signal—be it histological, taphonomic, or taxonomic (comparative)—to place that morphology in context. Palaeontologists (quite happily) perform phylogenetic analyses using morphology and morphospecies. That same class of evidence—morphology—can be applied to the reconstruction of development or identification of "ontospecies." Both involve placing a taxon within a hypothesized trajectory, whether evolutionary (phylogenetic) or developmental (ontogenetic).

Given that morphology can provide palaeontologists with ontogenetic information and that the techniques and approaches of evolutionary developmental biology enable developmental inferences to be drawn, C.O. Whitman's sage observation should be considered by palaeontologists as eerily profound:

> *Ontogeny is, then, the primary, the secondary, the universal fact. It is ontogeny from which we depart and ontogeny to which we return. Phylogeny is but a name for the linear sequences of ontogeny, viewed from the historical standpoint.*
> (*Posthumous Works*, ed. H.A. Carr, 1919, p.178).

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——OBITUARY——

Stephen Jay Gould (1941-2002)

Evolutionary biologist who challenged the orthodox thinking on Darwinism and had few rivals as a populariser of science

Stephen Jay Gould was one of the most gifted evolutionary scientists of his generation. Following the publication of many eloquently written articles and books, together with numerous public lectures, he acquired a reputation as an outstanding science populariser. In the research field of evolutionary biology his reputation was more controversial because of his persistent challenging of what he saw as the conventional reductionism of the orthodoxy, with its great emphasis on Darwinian adaptation as the predominant factor in evolution.

He was born in New York, of second-generation East European Jewish emigré parents, and took his first degree in geology from Antioch College, Ohio. Four years of study at Columbia University, involving research on the biometrics and evolutionary history of Bermudan Pleistocene land snails, was rewarded with a doctorate, and in 1967 he was appointed assistant professor in invertebrate palaeontology at Harvard, and assistant curator in the Museum of Comparative Zoology. Four years later he was promoted to associate professor, and in 1974 he became a full professor at the unusually early age of 33.

After moving his principal domicile to New York following his second marriage, he took up the post of visiting research professor of biology at New York University in 1996, while maintaining his position at Harvard.

A longstanding interest in organic growth and form, inspired by the classic work of D'Arcy Thompson, led to the publication of *Ontogeny and Phylogeny*, a scholarly treatment of the relationship between the growth of individual organisms and their evolutionary history. But Gould caused a much greater stir in evolutionary circles when he and Niles Eldredge propounded the hypothesis of punctuated equilibria, which postulates that, contrary to conventional Darwinian theory, species exhibit morphological stasis over long periods of time, and give rise to descendent species by means of comparatively sudden transformations.

Just how big a change in evolutionary thought was required to account for punctuated equilibria has proved debatable but, at the very least, the hypothesis directed attention once again to the relevance of the fossil record of the study of evolution, at a time when genetics and molecular biology were making most of the running.

In the 1980s Gould went on to promote the idea of species selection to account for evolutionary trends recognised in the fossil record, and a consequent decoupling of macroevolution (evolution above the species level) from microevolution, as studied by conventional thinkers, who, following Darwin, accept only selection at the level of the individual. Species selection, although theoretically possible, was not well received by biologists, and does not receive much empirical support from the fossil record; accordingly, it is now generally disregarded.

With more success, Gould challenged other aspects of neo-Darwinism, such as the predominance of adaptive, as opposed to constructional and historical, explanations of organic form. A major theme of his writings in the later 1980s and 1990s was the key role of historical contingencies in evolution, and the lack of evident progress in general, although he was obliged to acknowledge an increase in the complexity of neural systems, culminating in our own species.

Nevertheless, he considered that human beings might not have evolved but for the chance survival of a primitive chordate ancestor in the Cambrian period. In other words, there was no historic inevitability about our emergence. This is certainly a view that challenges popular wisdom, and it was popularised in his book *Wonderful Life*. The widespread recognition during this time of deep homologies in the animal world, recognisable at the molecular level, lends support to his belief that internal constraints and channels are significant causes of evolutionary change in their own right, operating to some extent independent of the power of external selection.

Whatever the dispute that remains about his role as an innovative thinker in evolutionary research, there can be no question about Gould's success as a populariser of science, as recognised by numerous literary awards and honorary degrees, to say nothing of a large income derived from this source, which dwarfed his salary as a Harvard professor. In his abundant writings he demonstrated great verbal felicity, a rich vocabulary, and capacity for lucid and racy exposition, enlivened by anecdotes, similes and metaphors from fields of experience as diverse as baseball and Wagnerian opera. These talents were put to effective use for more than a quarter of a century in a series of monthly essays in the magazine *Natural History*, which concluded only with the publication of the 300th at the start of what he regarded as the turn of the true millennium, in January 2001. Such was the popularity of these columns that they were anthologised into no fewer than nine books.

Characteristically, Gould would seize upon some apparently odd feature of organisms, or quirk of nature, to illustrate, often with great ingenuity, some evolutionary theme. Some of these essays gave him titles for his books, too, such as *The Panda's Thumb* or *The Flamingo's Smile* or *Hens' Teeth and Horse's Toes*. Together they show an enviably wide range of learning and intellectual curiosity, ranging from homely analogies to the most arcane byways of historical scholarship.

Although predominantly concerned with evolutionary biology, a minority of them deal with what he saw as the perils of biological determinism. Always a supporter of the underprivileged, Gould was a passionate opponent of attempts, conscious or otherwise, by scientists over the past century or so to justify or bolster the entrenched power of the well-educated Caucasian protestant male in Anglo-Saxon society. He even courted notoriety in the 1970s by allying himself with politically radical groups that were not always scrupulous in their attempts to discredit the newly emergent discipline of sociobiology.

Gould's social concerns received further expression in *The Mismeasure of Man* (1981), a *tour de force* in which he endeavoured to expose the fallacies and concealed biases in a succession of purportedly objective and hence influential studies, from mid-19th-century attempts to prove by craniometry the inferiority of North American native peoples and negroes to the factor analytic studies of intelligence by Sir Cyril Burt. Yet Gould never allowed his political radicalism—which he espoused sometimes in circumstances that demanded a good measure of personal courage—to compromise his beliefs in individual human rights. Marxism is now long out of fashion but the belief he expounded in the prime of his career could perhaps best be described as those of a libertarian Marxist.

Among the books that made his reputation were *Time's Arrow, Time's Cycle* (1987), a scholarly study of the discovery of geological time, and the best selling *Wonderful Life* (1989), an account of the remarkable fossil fauna of the Cambrian Burgess Shale in British Columbia, and its evolutionary implications. For this he won the Rhône-Poulenc Prize and was shortlisted for the Pulitzer Prize.

In the following decade his books dealt with topics as varied as challenging the conventional view of evolutionary progress, establishing on good scholarly grounds why the new Millennium really began in 2001, and discussing the relationship between science and religion. His argument that the two ways of thinking belong to different domains and should be able to co-exist without conflict provoked a considerable amount of scepticism, and not just from agnostic or atheistic scientists.

At nearly 1,500 pages, Gould's most recent book, *The Structure of Evolutionary Theory*, is a summation of his work. It stands by the theory of punctuated equilibria, insisting that it is supported by such fossil evidence as the Burgess Shale, and goes on to reject Richard Dawkins' "selfish gene" account of evolution, arguing instead that natural selection occurs on many levels, from the gene to the individual organism, and even the species. Finally, it argues against the strict Darwinians that other factors—including sheer chance—also produce evolutionary change. Reviewing this "major contribution to evolutionary theory" in *The Times Literary Supplement* last week, Steven Rose called Gould "the most accomplished living scientific essayist, a match for Haldane in the 1930s and Thomas Huxley in the latter half of the 19th century."

Among his numerous honours, Gould was one of the first recipients of the MacArthur Fellowship (1981-86) and was elected to both the American Academy of Arts and Sciences (1983) and the National Academy of Sciences (1989). Perhaps the most distinguished of his many medals was the Gold Medal of the Linnean Society of London, awarded for services to zoology. He even had an asteroid named after him. He served as president of the Palaeontological Society in 1985-86, president of the Society for the Study of Evolution (1990-91) and president of the American Association for the Advancement of Science (1999-2000).

A person of strong character and natural ebullience, Steve Gould had great personal warmth and generosity of spirit: unlike some of his radical allies, he was always courteous to his opponents. His interests were exceptionally wide-ranging and his knowledge of many subjects, from medieval stained-glass windows to the history of science, was profound. He had a longstanding passionate interest in baseball, and he was able to apply even baseball statistics to his intellectual interest in the pursuit of excellence.

In 1982, when he was gravely ill with asbestos-induced cancer mesothelioma, he was greatly touched to receive a baseball signed by his boyhood hero, Joe DiMaggio. For a short period he even wrote a column on baseball for *Vanity Fair*.

He had a good baritone voice and was a keen choral singer. In 1965 he married a fellow Antioch student, Deborah, and after their divorce in 1995 he married Rhonda, a sculptor, and moved to the artists' quarter of Manhattan. He is survived by his wife and by the two sons of his first marriage.

Stephen Jay Gould, palaeontologist and popular science writer, was born on 10 September 1941. He died on 20 May 2002, aged 60.

Gould's *Magnum Opus*

To mark the publication of Stephen Jay Gould's mammoth summary of a lifetime's work, Tony Hallam and Norman MacLeod have been commissioned to produce back-to-back reviews of:

The structure of evolutionary theory

Stephen Jay Gould. 2002. Harvard University Press. 1,433 pp.
ISBN 0-674-00613-5. £27.50.

Throughout his highly productive career Steve Gould presented a succession of iconoclastic ideas challenging conventional Darwinism, and as a result provoked the ire of many researchers active in the field. Though forced to recognise the eloquence and erudition of his writings, he has been widely dismissed as a brilliant essayist who has contributed little that is novel to evolutionary theory. This monumental book, the most magnum of opera, should, in a fair world, go a long way towards repudiating such a view, because it is an even more significant contribution to scholarship than his much earlier and highly regarded *Ontogeny and Phylogeny*, and indeed is an intellectual *tour de force*. His baroque, even rococo, style will not appeal to everyone, and many might have wished for strong editing to reduce the immense length (no wonder he so enjoyed both Victorian novels and Wagnerian opera). However, I am one of those who find so much reward in what he has written that, had I been an editor, I would quite happily have indulged him to the full. He was indeed a veritable *sans pareil*.

To adopt Darwin's phrase in the *Origin of Species*, the book is "one long argument" challenging the Darwinian paradigm which asserts that the history of life at all levels, including macroevolutionary phenomena involving speciation and extinction, is fully accounted for by processes operating within populations and species. The objective is not to refute Darwinism but to extend it, to take full account of hierarchical phenomena other than individual organisms, and both historical and structural constraints. Part 1 explores the history of Darwinian logic and debate, while Part 2 addresses his revised and expanded evolutionary theory.

Less patient readers might be tempted to skip over much of Part 1, but I think that this would be a great mistake, because only by fully appreciating the historical background is one in a satisfactory position to recognise what is being attempted in Part 2. Lamarck, the most significant pre-Darwinian thinker, contrasted a primary force of linear progress with a secondary force of adaptation that drew organisms off the main line. Darwin was radical in denying the existence of such a primary force, and proposing the secondary force as an exclusivity, with uniformitarian extrapolation through time of natural selection on organisms being all that was required. There are three essential components of Darwinian logic: (1) *agency* (the "struggle for life" of organisms in natural selection, (2) *efficacy* (natural selection as a creative force for evolutionary change, (3) *scope* (extrapolation through time). Darwin acknowledged Paley's phenomenology of good design of organisms, but inverted the causal mechanism, using Adam Smith's economic arguments. Natural selection could be creative and efficaceous only if variation was both copious and isotropic, in other words undirected towards the adaptive needs of organisms. Gradualism, through time, adopted from his geological mentor Lyell, involving

both slowness and smoothness of organic change, was an essential requirement of his system, and hence huge quantities of geological time were required. The creativity of natural selection makes adaptation central, the isotropy of variation necessary and gradualism pervasive.

In the first generation of Darwinian debate, the great German biologist and Darwin champion Weismann effectively refuted Lamarckism by recognising the independence of the "germ line," but was also the first to wrestle with levels of selection. He proposed subcellular ("germinal") selection but recognised that supraorganismal selection was also possible. Darwin himself recognised the need for a hierarchical theory of selection in any full account of the phenomenology of evolution. He omitted this material from the *Origin*, but it was originally written in the unpublished long version. (We must here take note of the fact that *On The Origin of Species* was described by its author as an abstract!) According to Gould, the historian Darwin felt he needed to invoke species selection to provide a full explanation of the success of speciose clades. As Michael Caine might say, "not many people know that."

Chapter 4 is concerned with the formalist alternatives to functionalism as epitomised by Darwin, such as the theories of Goethe, Geoffroy and Agassiz. Goethe proposed that all the standard parts of flowers, sepals, petals, stamens and carpels could be regarded as modifications of a leaf archetype. The conflict between the formalist (Geoffroy) and functionalist (Cuvier) was not, as widely believed, a straightforward victory for Cuvier but a more complex "draw." Adaptationist preferences have a long anglophonic tradition, from Ray to Fisher and the Modern Synthesis. By contrast, continental traditions have favoured formalist and structuralist explanations of morphology. Owen belonged to this tradition. He was not anti-evolution, but strongly opposed Darwin's functionalism.

The next chapter deals with channels and saltations in post-Darwinian formalism, paying particular attention to the polyhedron model of Darwin's brilliant cousin Francis Galton. Although I thought I had a reasonable knowledge of the history of evolutionary thought, this was completely new to me, like much else in Gould's historical account. The essence of Galton's idea is that by rolling a polyhedral rather than a smooth wheel, there is a sharp facet flipping, implying a set of limited possibilities guided by channels set by internal constraints, and evolutionary transitions by discontinuous saltations. Orthogenesis, which came into bad odour last century, is a general term for evolutionary directionality along channels of internal constraints.

Both Bateson and de Vries promoted saltationism, with de Vries arguing for "species selection" (his term, and another novelty unearthed in Gould's book) as a mechanism for developing broader phylogenetic patterns unaccounted for by strict Darwinism. Goldschmidt, of "hopeful monsters" fame, has been generally derided by geneticists for his macromutational ideas, but can be considered as a pioneer in conceiving of genes controlling rates of morphological change. Chapter 6 is concerned with the geological evidence, which was a great worry to Darwin because of the manifest absence of gradual morphological transitions in fossil successions. Following Lyell, he attributed these to the ubiquity of gaps in the stratal record, an argument that has progressively lost plausibility over the subsequent years. From the anarchic situation that prevailed at the Darwin centennial celebrations of 1909, with confidence in the factuality of evolution linked with agnosticism about theories and mechanisms, the Modern Synthesis eventually emerged with a union of Darwinian and Mendelian perspectives. This was followed by an increasingly dubious hardening of opinion culminating in the centennial celebrations, for the *Origin*, in 1959. This substituted an increasingly rigid adaptationism for an earlier pluralism that embraced a variety of mechanisms, including genetic drift, consistent with known genetic principles, while favouring selection as the primary force.

The first two chapters of Part 2 deal with punctuated equilibria, the concept for which Gould is best known to a wide audience, and a hierarchical theory of selection. The most novel part of punctuated equilibria is the long periods of species stasis rather than the "geological instants" of sharp change, because there is more than enough time for speciation under normal genetic rules. This stasis is a direct challenge to Darwinian gradualism, and was entirely unanticipated by mainstream evolutionary thinkers, usually population geneticists. Strong empirical support from palaeontologists is thoroughly reviewed, but some gradualistic exceptions are admitted, notably from planktonic foraminifera which, with their different biology, may well follow different rules. Acceptance of punctuated equilibria allows the distinction of species as independent evolutionary individuals, and therefore amenable to selection. Selection need not operate only on individual organisms, as strict Darwinism demands, but on a hierarchy of levels—genes, cell lineages, organisms, demes, species and clades. The gene selectionism of Dawkins and Williams is strongly refuted, however, because selection depends on interaction with the environment rather than mere replication. Gould strongly promotes species selection as an explanation of trends perceived in fossil successions, with capacity to speciate being a prime reason why some clades have come to dominate over others.

Whereas, however, punctuated equilibria have been widely accepted by palaeontologists as the norm, with abundant evidential support, there has been very little positive response from them to species selection, however possible it might be theoretically; indeed it has been virtually ignored. Such few examples as have been put forward and discussed have proved to be controversial, or equivocal in their interpretation. In particular it has proved difficult to distinguish in practice between *species selection*, involving selection at the species level, from *species sorting*, where selection is at the organismal level. In 1998 I published a paper in *Geobios*, challenging Gould's species selection interpretation of trends in the fossil record, pointing out that at least many of the trends described can be readily attributable either to a combination of anagenesis and heterochrony or to phyletic size increase. This paper is cited in Gould's bibliography but is not referred to in the text. Curiously, no attempt is made at refutation, it is simply ignored. Elsewhere Gould is sceptical of the importance of phyletic size increase, commonly known as Cope's Rule. He cites favourably the work of Jablonski, whose study of numerous late Cretaceous molluscan taxa failed to reveal any net change in size up the succession. But no one seriously argues for the dominance of phyletic size increase through time, otherwise the world would be full of giants. Clearly size increase has been matched by size decrease, but the intriguing point that has emerged, and which was not addressed by Jablonski, is the apparent asymmetry through time, with more or less gradual increase through time not being matched by corresponding gradual decrease. Rather, change from a larger to a smaller, closely related, taxon is comparatively sudden. This pattern is quite common in Jurassic bivalve and ammonite taxa that I have studied, and Peter Skelton recognised the same phenomenon in Cretaceous rudists. The whole subject is worthy of much more study than that accorded by Gould who, however, was reluctant to accept evidence for gradualistic phenomena.

I think that Gould is on much stronger ground in his treatment of historical constraints and the evolution of development, or evo-devo to its devotees. Constraint need not just have a negative meaning but a positive one in terms of channelled directionality. He puts forward a triangular model for aptive structures, with functional, historical and structural vertices. Currently aptive features probably originated for conventional adaptive reasons in distant ancestors, but are now developmentally channelled as homologies that both constrain or possibly direct the patterns of changes and the inhomogeneous occupation of morphospace. As a conceptual basis for understanding the importance of recent advances in evo-devo, one must make a distinction between convergence and parallelism. There is a key contrast between parallelism as a positive deep constraint of homology in the underlying generators, and convergence as the opposite sign of domination by external natural selection. The deep homologies in distantly related phyla revealed by the new and exciting field of developmental genetics, notably Hox genes, have signified the most important recent advance in evolutionary studies. Indeed, the population geneticists who have dominated the field for so long now risk being sidelined.

Chapter 11 is dominated by the subject of exaptation. For the study of the phyletic histories of complex lineages, exaptation is of fundamental importance, as it signifies a disconnection between historical origin and current utility. Thus bird feathers probably arose for a thermoregulatory function in dinosaur ancestors, and were later co-opted for flight. Who else but Gould would have discovered that this sort of disconnection was first clearly recognised by Nietzsche in his *Genealogy of Morals?* One of the criticisms that Darwin found most difficult to cope with was that of St. George Mivart, concerning the supposed inability of natural selection to explain incipient, and apparently useless, stages of adaptive structures. What use is 1/6 of a wing? But Darwin never went beyond the principle of original adaptive origin, whereas the ubiquity of "spandrels" (surely not a term requiring definition here) suggests that many non-adaptive features of organisms were simply co-opted.

The final chapter is concerned with historical contingencies, most notably catastrophic mass extinctions, which breaks the conventional Darwinian extrapolationist scenarios and must be factored into any comprehensive study of evolution. It closes with an epilogue about the enlargement and reformulation of Darwinism that will recapture for general theory the consignment of a large part of macroevolutionary patterns to the realm of historic contingency, or unpredictability. There was no historic inevitability about our own emergence on this planet.

The sum of £27.50 is a ridiculously low price to pay for a book of nearly 1,500 pages by someone who was designated in 2001, by the Library of Congress, as one of America's 83 Living Legends—people who embody the "quintessentially American ideal of individual creativity, conviction, dedication and exuberance." (I was told by the author that the low price is because the publishers are heavily subsidised by the financial proceeds of an oil well in Texas). Alas, Steve Gould is no longer living. The premature death of a person of such exceptional gifts is tragedy enough, but the tragedy would have been so much greater if he had died before completion of this magisterial work. No one seriously interested in evolution can afford to ignore it.

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The Structure of Evolutionary Theory

Stephen Jay Gould. 2002. Harvard University Press. 1,433 pp.
ISBN 0-674-00613-5. £27.50.

The English philosopher Bertrand Russell once remarked about his and Alfred North Whitehead's 2,000 page magnum opus of mathematical logic *Principia Mathematica* that 'I used to know of only six people who had read the later parts of the book, three of these were Poles, subsequently (I believe) liquidated by Hitler. The other three were Texans, subsequently successfully assimilated.' With publication of *The Structure of Evolutionary Theory*, Stephen Jay Gould has produced his own magnum opus that, like *Principia Mathematica*, sets out not to reformulate its parent topic fundamentally, but to rescue it from needless error while, at the same time, placing it on a more logical footing. While I doubt whether *The Structure of Evolutionary Theory* will manage to obtain the readership among his target audience of professional evolutionary biologists that Gould desired, this won't be for lack of effort on his part. The amount of material summarized between these two covers is indeed formidable; the product of a very productive lifetime's reading and thinking about evolutionary questions from a uniquely palaeontological point of view. Rather, the problems with this book—that will limit its readership—stem from (1) the virtually insurmountable stylistic barriers that Gould himself has erected around the book's messages and (2) his tendency to lapse into the advocacy-based rhetorical style that served him so well in his popular writings rather than grounding his arguments in the comprehensive and dispassionate presentation of hard evidence that professional scientists find most convincing.

The book's core messages are simple and familiar to those already acquainted with Gould's work. To Gould, Darwinism is constructed along three (somewhat confusingly named) themes: *agency* (which Gould characterizes as that part of the theory that addresses itself to an analysis of the targets of evolutionary processes), *efficacy* (which involves ideas about the factors that actuate and/or channel evolutionary processes), and *scope* (which encompasses the idea of how the actions of evolutionary processes operate within the different and hierarchically structured levels of biological organization). Gould characterizes Darwinism structurally as reductionist or unilevel (evolutionary processes target only individual organisms), externalist (only external environmental factors actuate evolutionary processes), and extrapolationist (all macroevolutionary patterns are produced through the actuation of microevolutionary processes). This he regards as an archaic formulation that was not even supportable in Darwin's own time, much less ours. Instead, Gould describes modern evolutionary theory as pluralist or multilevel (evolutionary processes operate at all levels of biology's organizational hierarchy; *e.g.*, genes, cell lineages, organisms, demes, species, clades), constrained and contingent (external selection pressures are mediated by structural, historical, and developmental constraints), and hierarchical (a unique class of macroevolutionary processes exist and are responsible for the patterns seen at the higher hierarchical levels). In support of these claims Gould offers a 486 page historical review of seemingly all major—and most minor—contributors to the development of evolutionary theory that recounts their contributions to these themes, followed by a 725 page discussion of empirical evidence. In the latter, Gould suggests that (1) the ontological concept of individuality supports his case for pluralism/multilevelism, (2) his model of punctuated equilibria, coupled with the concept of species selection, validates his concept of constraint and contingency, (3) recent work on the developmental aspects of morphological change supports his ideas about the evolutionary importance of formalist constraints that limit the nature of organisms' responses to selection, and (4) the 'theory of mass extinction' provides a mechanistic rational for his ideas about evolution's hierarchical scope.

Needless to say, any technical book of such intellectual scale is almost as daunting a task to read as it must have been to write. Unfortunately, this is made much more difficult than it should be by the author's uniquely prolix prose. Gould's endless indulgence in digressions within digressions from the main point often neither enlighten nor impress, but only serve to frustrate and, eventually, to irritate. Acclaim as a science writer, popularity, income from royalties, and awards notwithstanding, never have I seen a manuscript more in need of a good editing as this one. A single sentence will serve to make my point. Here, Gould describes the results of his search for an illustration from the classical literature he could use to make the simple and non-disputed point that 'Because primates are visual animals, complex points are best portrayed or epitomized in pictorial form.' (p. 15):

> "I claim no general significance whatsoever for my good fortune, but after a lifetime of failure in similar quirky quests, I was simply stunned to find a preexisting image—not altered one iota from its original form, I promise you, to suit my metaphorical purposes—that so stunningly embodied my needs, not only for a general form (and easy task), but down to the smallest details of placement and potential excision of branches (the feature that I had no right or expectation to discover and then to exapt from so different an original intent)." (p. 16)

Call me soulless or hyper-rational, but this sort of passage in a technical treatise represents the worst sort of authorial excess at the expense of the reader's time and patience.

And what of the arguments? Overall, I liked the historical chapters much better than the chapters devoted to Gould's defence of his view of evolutionary theory. Gould's popularity as a writer has always seemed to me to stem from his historical essays on the ideas of the people who developed evolutionary theory. After writing some 300 such essays you would think that he had already said all there was to say about this subject. Yet, the first 500 pages of this book are chock-full of new information, striking insights, and wonderful juxtapositions. Thus, we learn that far from being antagonists, Darwin actually owes a debt of gratitude to Lamarck for pioneering the concept of the external environment as the prime instigator of evolutionary change; that the supposedly staunch Darwinian August Weismann offered a theory of hierarchical selection regimes far more in accord with Gould's ideas on this topic than his mentor's; that the 1830 public debate between Cuvier and Geoffroy was not about evolution *per se*, but rather about their difference of opinion as to whether it is more appropriate to interpret morphology in a formalist or a functionalist context; and that Richard Owen—so often miscast as the 'Darth Vader' of 19th Century evolutionary controversies and an ardent special creationist—predated Darwin in accepting the principle of evolutionary change (at least within archetypes), but rejected the latter's commitment to strict morphological functionalism, that Gould also questions. All of these tales of evolutionary lore are delivered with Gould's characteristic verve, lucid explanation of context, and unparalleled attention to detail. Gould's penchant for digression is here, but somehow it doesn't seem as disruptive to the overall narrative as in the latter, more technical material. I would recommend, nay require, the first 500 pages of this book to anyone with a serious interest in the historical development of evolutionary theory; and especially to all nascent historians of science as the best modern example of why it is important to gain an absolute grasp of a discipline's technical detail before attempting to write its history either in whole or in part.

However, when Gould turns to his technical discussion, things go downhill rapidly; not so much because of what he says—though the deleterious effect of the uncontrolled digressions is more evident— but more because of what he neglects to say. Tellingly, Gould entitles this section 'Towards a Revised and Expanded Evolutionary Theory', as if it were merely a summary of work in progress or a prelude to some future synthesis planned as a separate project.

One of the best of his arguments in this section is the first, which deals with the implications of regarding species as ontological individuals. Gould notes that the seminal contribution to this literature was Michael Ghiselin's (1974) *Systematic Zoology* article entitled '*A Radical Solution to the Species Problem*'. In that work, Ghiselin formulates and defends the idea that many of biology's long-standing problems with the species concept could be eliminated by regarding them not as classes (= universal categories), but as a type of composite individual (= a particular thing made up of different parts) with unified and recognizable starting and ending points separated by an event-laden history. While Ghiselin was not interested primarily in the implications of his reconceptualization for the levels-of-selection, Hull (1976) pointed out that by accepting in principle the idea that individuation can exist at multiple levels, evolutionary biologists were opening the door to theories that described selection as operating at different levels. Gould seizes on this idea and attempts to extend it as a philosophical justification for the existence of macroevolutionary processes in general and species selection in particular. Readers must judge the success of this argument for themselves, but after a 150 page disquisition on the extension, including the tracing of its implications for each level of the systematic hierarchy along with a detailed (and highly critical) review of Richard Dawkins 'selfish gene' ideas, I was left with more a sense of gratitude for his having summarized all of this material in one place, than a feeling that the argument had been extended in any unique or profitably way.

Gould's 279 page treatment of punctuated equilibria suffers by comparison. Here he argues that "the clear predominance of an empirical pattern of abrupt geological appearance as the history of most fossil species … remains the standard testimony (as documented herein) of the best specialists in nearly every taxonomic group." (p. 75). One can only respond that the standards of acceptable testimony don't seem to be very high while his crack about 'best specialists' seems almost wilfully designed to inspire contempt in the very audience he should wish to reach.

Much of the testimony presented in this section involves little more than anecdotal statements by palaeontologists based on subjective impressions gained over long years of distinguished study of fossil morphologies, but study for purposes other than the documentation of morphological stasis or intermediacy. Such a research strategy could hardly be less scientific. Moreover, given the contemporary preponderance of concern for phylogenetic and high-resolution stratigraphic analyses, the fact that Gould accepts testimony from studies that so obviously fail to justify themselves on either of these grounds also seems problematic. Most damaging to the credibility of this section, though, is Gould's cavalier treatment of his theory's many critics. In some cases, morphometrically documented gradualism in large organismal groups (*e.g.*, foraminifera) is dismissed as being the result of peculiarities of genetic systems without making any attempt to explain just what these peculiarities might be. In others (*e.g.*, size changes in bacterial lineages), morphometric data for gradualism are reinterpreted as data for punctuationalism by superimposing a punctuated model over the data without making any attempt to prove that the punctuated model provides a better fit than the gradualistic model. In others, equivocal observations of morphological conservatism (*e.g.*, existing of so-called 'living fossils') are shoehorned into acting as props for the preferred theory. Finally, in a truly depressing realization, many of the most trenchant criticisms of the punctuated equilibrium model (*e.g.*, the stabilizing selection arguments of Lande 1982) are simply not mentioned.

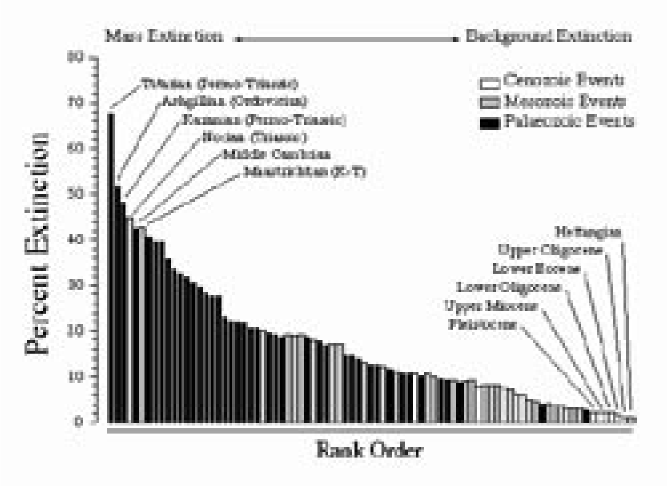
Lest the reader of this review get the wrong impression, understand that I too regard the evolutionary literature as containing many well-justified instances of evolutionary stasis. It also contains many well-justified examples of phyletic gradualism. My contention is that, contrary to Gould's review, the evidence for punctuated equilibrium is neither so strong, nor the evidence for gradualism so weak as he portrays. The entire subject is badly in need of less rhetorical heat and more empirical light.

Gould's penultimate section on the nature of constraints in morphological evolution is spread over two chapters (chapters 10 and 11) and totals 270 pages. This is, hands down, the best section in the technical part of the book, drawing as it does from Gould's long-standing interest in developmental issues (*e.g.*, Gould 1977). Gould is a central figure in the founding of the (ghastly named) 'evo-devo' research programme, a debt that most of this field's morphological practitioners acknowledge freely. Irrespective of the degree to which the simple existence of developmental constraints contributes to the justification of either punctuated equilibrium or macroevolution, they—along with structural and historical constraints—exist and must be taken into account in any modern theory of evolution. This section also contains a very nice discussion of the connection between the modern data in this area from the standpoint of the formalist/functionalist debates of over a century ago and that were so well described in this book's historical section.

Last, but certainly not least, Gould turns towards mass extinctions and their implications for his ideas about the scope of evolutionary processes. This is the shortest section of the book (a mere 47 pages) and, for me (many will say unsurprisingly), the most problematic. In terms of the quality of the presentation it marks a return to the unconvincing rhetoric of the punctuated equilibrium chapter, but this time without the benefit of any first-hand knowledge of the mass extinction research field.

Gould argues that mass extinctions 'change the rules' of natural selection by forming an evolutionary filter capable of sorting species into victim and survivor classes irrespective of previous adaptation levels. The logical problems with his model are (1) how, in an intrinsically varying environment, one knows that some environmental-change threshold has been passed such that different 'rule regimes' can be specified unambiguously and (2) whether such thresholds—assuming they exist—are unitary or are species specific, community-specific, regional, or some combination thereof.

The most straightforward way of demonstrating the existence of such thresholds in palaeontological data would be to demonstrate the existence of a discontinuity of extinction magnitudes such that a special class of intense (or 'mass') extinctions could be defined and objectively separated from a larger class of less intense (or 'background') extinction events. In a work cited favourably by Gould, Jablonski (1986) demonstrated that mollusc survivorship across the Cretaceous-Tertiary (K-T) boundary 'mass extinction' differed from 'background extinction' intervals. While this is an interesting and important dataset, its focus on a single 'mass extinction' event compromises its extrapolation as a general explanation of what happens during all 'mass extinction' events. Indeed, the entire concept of 'mass extinction' as a phenomenological category was first challenged by David Raup (1991) and can be appreciated easily by rearranging the Sepkoski extinction data by rank order of extinction intensity (see Figure).



Stage-level extinction-intensity estimates for Phanerozoic marine genera arranged in rank order. Data from Sepkoski (1994).

The lack of an obvious discontinuity in the resulting extinction-intensity spectrum underscores the reason why the concept of mass extinction has no precise definition and, by implication, no objective reality. Indeed, the fact that the term 'mass extinction' is applied routinely to some of the smallest extinction events (*e.g.*, the Pleistocene 'mass extinction') shows that the term refers effectively to any extinction event—or any aspect of any extinction event—one wishes to discuss at any particular time. The continuity of this distribution provides compelling evidence for an underlying continuity of extinction-related mechanisms. Needless to say, Gould neglects to discuss this alternative interpretation of mass extinctions.

Gould's favoured mass extinction mechanism is large-bolide impact because of its abruptness and intensity, but, as before, he fails to offer any detailed description of other, more progressive extinction mechanisms (*e.g.*, sea-level change, large igneous province eruptions); fails to discuss any of the many examples of progressive change across well-known mass-extinction horizons (see MacLeod *et al.* 1997 and references therein); fails to discuss any of the objections or describe any of the controversies surrounding the studies he cites as evidence supporting his interpretation of mass extinction dynamics (*e.g.*, see Hulbert and Archibald's 1995 critique of the statistical methods used by Sheehan *et al.* 1991 to support a catastrophic extinction of dinosaurs in the Hell Creek and related sections); offers incomplete and/or incorrect discussions of critical tests for progressive patterns of taxic change near or across extinction horizons (*e.g.*, contrast Gould's discussion of the Signor-Lipps effect with the discussion provided in the original

publication, see Signor and Lipps 1982); fails to cite any of the recent survey literature showing that palaeontologists overwhelmingly reject a single-cause mechanism for mass extinction (*e.g.*, Galvin 1998); and fails to cite any of the secondary literature in which these topics are discussed (*e.g.*, Hallam and Wignall 1997). Overall this discussion has a rushed, incomplete quality that only compounds the problems present in most of the other technical chapters.

Overall then, the book is a decidedly mixed bag. I think the material would have been better served if the book had been broken into separate historical and technical volumes with a greater emphasis on original and detailed analysis—as opposed to selective historical review—in the latter. Yes, the price is modest. However, of what use is a modest price if the arguments fail to reach (or convince) their intended audience simply because so much extraneous material has been included? While I can recommend the book unreservedly as the most complete summary of Gould's ideas on the many areas of evolutionary biology he contributed to, *The Structure of Evolutionary Theory* cannot be regarded as an adequate summary of that field. Too much is either missing entirely or misleadingly presented.

Perhaps Gould intended to fulfill the promise of his technical section's title and provide a genuine synthesis between his views and those of more mainstream evolutionary biologists at a later date. Unfortunately, his death—which followed this book's completion closely —foreclosed that option. Gould will be remembered for his iconoclastic views on the nature of evolutionary processes, and his perceptive historical essays, and his love of a good intellectual fight, with both of the latter being much in evidence here. Regardless, it will be for a future Gould to establish the place of his technical contributions within the context of his time and within the context of a fair and complete presentation of the full range of alternative ideas about the nature of evolutionary processes. To paraphrase Darwin, there is grandeur in Gould's view of evolutionary theory, with its multiple agents, complex efficacy, and expanded scope. But I suspect wide acceptance among the community of professional evolutionary biologists will be a long time in coming and probably achieved slowly, if at all.

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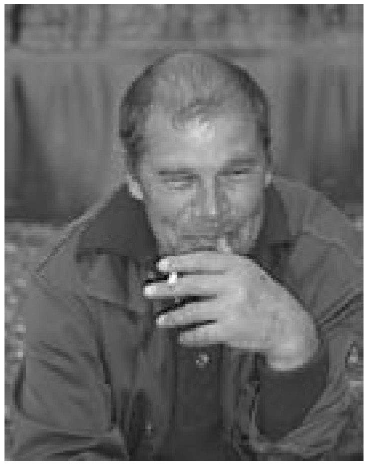
——OBITUARY——

V. V. Missarzhevsky (1934–2002)



Vladimir Vladimirovich Missarzhevsky died of cancer earlier this year in Moscow, the city where he was born 68 years earlier. A graduate of the Moscow Geological Exploration Institute, he spent a couple of years working on uranium-bearing shales in Ukraina before he was employed at the Geological Institute of the USSR Academy of Sciences, where he remained to his retirement. More than anyone else, he founded the study of the "small shelly fossils," the rich array of shells, sclerites, tubes and spicules initiating the Phanerozoic succession of animal fossils.

Volodya Missarzhevsky's last major work was published in 1989, the year the Berlin wall crumbled and fell. This was too late to make a difference for him. As many other Soviet scientists, he had been confined to working within the well-guarded mental and physical boundaries of that regime, and he did not have the political persuasion or the diplomatic finesse to render him a ticket to the international arena.

But the Soviet territories themselves, particularly Siberia and Kazakhstan, had enough challenges for his keen mind and power of observation. He was the main discoverer and explorer of the wonderfully rich faunas of skeletal fossils that herald the incoming Cambrian biotas on the Siberian Platform. In two major monographs of the late 1960s, he and A. Yu. Rozanov,

partly in cooperation with other Soviet and Polish palaeontologists, launched the concept of the Tommotian Stage as the initial Cambrian stage containing a succession of skeletal fossils predating the first trilobites. This concept inspired intensive research into Precambrian–Cambrian boundary beds all over the world, leading to much modification of the initial ideas and generally to a much more precise understanding of what went on when the Proterozoic biosphere was transformed into the Phanerozoic one. The real paydirt in these classical publications, however, was Missarzhevsky's systematic descriptions of the new fossil finds, demonstrating a previously unknown diversity of early skeletal fossils. This is now one of the cornerstones of our understanding of the Cambrian explosion.

Missarzhevsky published in Russian, and although a few of his works were translated into English, most were not readily accessible to the global community. Fortunately, in the early 1970s he was visited by another diamond in the rough, the Scottish geologist/palaeontologist Crosbie Matthews, then at Bristol University. Matthews had taken an interest in the Lower Cambrian succession at Comley and its non-trilobite fossils. He realized that there was a goldmine of comparative material in Missarzhevsky's office in Moscow, and went there to study it. Volodya and Crosbie found it easy to bridge the language barrier by non-lingual means, and went on to publish a review paper in English that became a citation classic for the "small shelly fossils", a term introduced in the title of that paper and thereafter impossible to stop (I know, because I tried).

Missarzhevsky then went on to work in Kazakhstan, publishing from there another seminal monograph (with A.M. Mambetov) on the Lower Cambrian "small shelly fossils". He gradually became convinced, on the basis of his own studies as well as those of other prominent Soviet biostratigraphers, such as V.E. Savitsky, A.K. Val'kov, and V.V. Khomentovsky, that there was a significant succession of "small shelly fossils" below the Tommotian. Highly controversial for a long time, these findings are now generally accepted, and the pre-Tommotian fossiliferous beds recognized under the names Nemakit-Daldynian or Manykaian (the term Missarzhevsky preferred) Stage. Missarzhevsky's 1989 monograph represents his legacy, presenting his interpretations of the Siberian stratigraphical sequences in a global context, as well as updating and complementing the systematic work on the "small shelly fossils".

It was easy both to like and to dislike Volodya Missarzhevsky. He had a friendly, playful nature, and was a great lover of cats. He was also opinionated and could be rudely dismissive of others' points of view. It was stimulating to draw on his considerable experience and understanding of the Lower Cambrian sequences in Siberia and Kazakhstan, and their contained fauna. His observations were many, and his ideas could be both novel and intriguing. At the same time, he had great faith in perceived regularities in evolutionary and stratigraphic successions, and this influenced his interpretations to a considerable extent. It could be frustrating to argue such points with him. I sometimes wondered whether his life and his scientific contribution would have turned out different had he been allowed to travel abroad freely. In the end I concluded that it was best not to know. For better or worse, Volodya Missarzhevsky was a lone ranger, and in a different world he may not have been able to make the substantial contributions to science that are now his legacy.

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SYLVESTER-BRADLEY AWARD REPORTS

The Lower Pliocene of West Coast, South Africa. Comparisons with the Upper Miocene of Kerassia, Greece.

The West Coast Fossil Park in Langebaanweg (South Africa) contains Upper Miocene–Lower Pliocene fossil localities. These localities are of world-wide significance because of the great number of recovered species, the sheer abundance of individuals and the exceptional preservation of the fossil material. The thousands of fossil bones indicate overwhelming palaeodiversity. Mammals represent the most diverse group: thirteen of the fourteen orders of mammals that now occur in Africa and the adjacent oceans are recorded here, with only Sirenia absent. In addition to the mammals there are thousands of birds, reptiles, frogs, fish, gastropods, a variety of other invertebrates and pollen. The stratigraphy and the palaeontology in these localities have been well studied. Different depositional environments are represented in the sedimentological succession, from near-shore marine, beach and mud flat to floodplain and river channel deposits.

According to Hendey (1982) the palaeogeographic setting would have been close to the estuary of the precursor of the present Berg River (its present estuary is found to the north). This explains the marine influence in the succession and the presence of marine fossils in the fluvial deposits, such as seal remains in river channels. Conversely, terrestrial fossil remains have been recovered from marine deposits. However, the great majority of the fossil bone material is found in fluvial floodplain and river channel deposits.

Kerassia is a new Upper Miocene (Turolian) mammal locality situated at the northern part of Euboea Island in Greece. The fossil material comes from seven different sites. Owing to the nature of the deposits, the complex faulting and covering vegetation, the correlation between the different layers and the different bone accumulations in time and space is difficult. Despite this, at least two fossiliferous horizons have been recognised. In each of these the bone accumulations are found as separate lenses within fluvial channels. The surrounding sediments are red-brown fluvial deposits and mainly red-brown silts and silty-muds, which represent a floodplain setting.

The Sylvester-Bradley award provided me with the opportunity to accept Dr Roger Smith's (South African Museum of Cape Town) invitation to participate in the excavation last June in Langebaanweg. The excavation was aimed at reconstructing the sequence of events that led to the accumulation and burial of this vertebrate fossil occurrence. Another aim was to leave the exposed bones *in situ* as an educational and tourist resource. An area of more than 30m^2 has been exposed, giving the opportunity to scientists and tourists to see this unique bone accumulation.

This summer's excavated material was found in river channel deposits near a very large phosphate deposit, which was thought to trap and concentrate river-borne carcasses. I had the fortune to study the exposed bone assemblage and its spatial arrangement, and this investigation indicated that a catastrophic event caused the death of the animals. The bulk of the bones from the dig site belong to a large, very robust, short-necked giraffe, *Sivatherium hendeyi*. A large number of the specimens represent juvenile individuals. Two more species of giraffes have been found in the deposits.

The Kerassia fauna consists mainly of Perissodactyla and Artiodactyla, but Carnivora and Proboscidea are also present. Hipparions and bovids are the most abundant elements in the fauna, with Giraffidae well represented by four species (mainly by the large Sivathere, Helladotherium) (Theodorou *et al*., in press). The presence of different taxa found together in the bone accumulations suggests an attritional mode of death in the assemblage. The scarcity of articulated elements indicates transportation of the bones within the fluvial channels. Bone modification due to scavenging by Hyaenas or other carnivores is also present. The Kerassia fauna is part of the Upper Miocene West Eurasian "Pikermian" fauna. Solounias *et al.* (1999) state that the majority of the Recent African land mammal species have their origins in the "Pikermian" biome.

The land mammal faunal content in the West Coast Fossil Park and Kerassia is quite similar at family and generic level. In Langebaanweg the palaeoenvironment is thought to represent deposition in river channels and floodplains, close to an estuary, whilst in Kerassia the deposits represent only a floodplain setting.

My PhD research at the Kerassia locality has involved aspects of Giraffidae systematics, stratigraphy and taphonomy. Thus working on the South African bone assemblage has been particularly beneficial and important for my project. Studying the different depositional settings provided me with a better understanding of taphonomic processes, which I will now apply to the Kerassia locality.

I would like to acknowledge the Palaeontological Association for providing me with the Sylvester-Bradley award, Dr Roger Smith from the South African Museum in Cape Town for his invitation, Pippa Haarhoff and the people in the West Coast Fossil Park for their hospitality.

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Fossil Plants of the Middle to Late Devonian of the Yangtze region, central China

The Middle to Late Devonian sediments from the Yangtze river area of China, part of a marine transgressive facies, are well known for containing abundant and well preserved fossil plants. So, in October 2001 I winged my way to China to search for unique and scientifically interesting specimens, the findings of which would form part of my PhD research on the origin of the seed.

Currently there is a controversy over exactly how the seed plants (Spermatophytes) evolved. The plant group Progymnospermopsida, established in 1960 by Charles Beck (Beck, 1960a) based on the organic connection of *Archaeopteris* and *Callixylon* (Beck, 1960b), are central to this debate. The progymnosperms are an advanced group of Devonian and Carboniferous pteridophytes (early Eifelian to Tournaisian) that evolved from within Devonian Trimerophytes (a primitive group of vascular plants that were extinct by the end Middle Devonian) and are reproductively primitive (fern-like) but anatomically advanced (with a gymnospermous anatomy). This combination of characteristics has led some to believe that progymnosperms are the most likely group from which at least some of the seed plants evolved (*e.g.* Beck, 1960a).

So far the only progymnosperm found in China is *Archaeopteris* (*e.g.* Cai, 1981; Wu *et al.* 1982). Therefore, fieldwork commenced with the main aim of discovering more progymnosperms; the collection of any other plants would be a bonus. Fieldwork was completed in three localities in the Hunan Province resulting in a large collection of specimens—cladoxylopsids, lycopods and some probable progymnosperms.

Permineralised cladoxylopsid remains were collected from a small quarry exposing Middle Devonian sediments in Hupinshan Natural Conservation Area, Shimen County, western Hunan. These specimens with well preserved anatomy are currently being studied at Cardiff University (Berry, pers. comm.). Additionally, sediments from a roadside quarry near Ningxiang yielded further lycopod remains—mainly coalified leaf compressions. These are also being studied at Cardiff as part of an ongoing project looking at stomatal densities of a variety of Devonian plants (Edwards, pers. comm.). After three days of hammering and chiselling (and much digging and by the locals for which we are truly grateful) it was time to move on with our large pile of new specimens.

Another three days were spent at an Upper Devonian (?Frasnian) locality near Liuyang, eastern Hunan. Fossil plants were abundant in loose blocks of pink sandstone from the banks of a large reservoir, so unfortunately no stratigraphy was preserved. A great variety and number of specimens were collected, including vegetative and fertile axes, large and small, showing many levels of complexity, ultimate divisions and some very well preserved sporangia. Most fragments preserved only morphology as compressions and impressions, but a few examples show anatomical preservation. Currently, based on the overall morphology, it is believed these fossils could be progymnosperms. However, many of these fragments also resemble early seed plants, especially in the nature of their fertile parts, so a detailed investigation will be made in due course. The anatomy is likely to have a key role in determination of the plants' affinity.

This final phase of fieldwork was a success. Another mountain of rocks was collected and sent back to Beijing to the happy sounds of beer glasses clinking. Whatever these plants do turn out

to be, they have the potential to be very important. The Upper Devonian was an important time in the evolution of land plants. Numerous important botanical innovations occurred, including the development of forest environments and the transition to the seed habit. Three major plant groups present at this time were 'ferns', progymnosperms and the seed plants, traditionally considered to be interrelated. The new specimens should provide fresh data on the relationships of these important plant groups. Additionally, where the Chinese specimens (*e.g. Archaeopteris*) have been studied, they are distinct from European and North American examples from contemporaneous sediments. The new specimens will help achieve a global perspective for this evolutionarily innovative period.

Unfortunately all specimens currently remain in Beijing due to unforeseen circumstances. It is hoped that in the near future I will be able to return to China with the remaining Sylvester-Bradley funds to collect the specimens, or pay for transportation to this country (in which case the difference will be returned to the Palaeontological Association).

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I would like to thank Professor Li Cheng-sen (IBCAS) for organisation of all the fieldwork and his support for the duration of my stay, Yen and Ti-Mei for their help in the field, Kou and everyone else at the Botanical Institute for making me so welcome in China. Finally thanks to the PalAss for granting me the Sylvester-Bradley award, without which this work would not have been possible.

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The biological affinity of the enigmatic ichnotaxon Beaconites *in association with a nonmarine ichnofauna from the Early Devonian of southwest Wales*

Structures assigned to *Beaconites* represent actively filled burrows (displaying a meniscate backfilled architecture) of uncertain biologic origin (see Bradshaw 1981 for a review of producers) generally associated with Upper Palaeozoic fluviatile sediments and more recently characterised within the *Scoyenia* ichnofacies (Buatois and Mangano 1998). Since the initial description (Vialov 1962) the ichnogenus has been widely described (although sometimes spuriously, *i.e.* differing views on morphology) with occurrences recorded particularly from the Palaeozoic of Antarctica, Europe and North America.

Previous studies have concentrated especially on the ichnotaxonomic assignment of *Beaconites* (see Pal. Ass. *Newsletter* **31** and **32**), although a clear consensus remains lacking. Analysis of *Beaconites* in this study focused on the probable producers, the mode of production, and the palaeoecological distribution. Data were obtained from the literature; either from sources where the name *Beaconites* was used, or additionally from sources recording unnamed meniscate burrows. A preliminary ichnotaxonomic review maintained both ichnospecies: *Beaconites antarcticus* and *Beaconites barretti*. Differentiation was based on burrow morphology (in particular burrow size and form of individual menisci), with neither ichnospecies possessing a wall lining. *B. antarcticus* with a maximum width of 30 mm and a burrow fill composed of thick arched sediment packets displaying moderate curvature, and *B. barretti* having a marked sinuosity and overall larger size (greater than 30 mm), with a fill comprising shuffled gently curving menisci (see Retallack 2001 for a recent ichnotaxonomic review of meniscate-filled burrows).

Fieldwork in Pembrokeshire (LORS, Lower Old Red Sandstone) revealed a suite of ichnotaxa (including *B. barretti*) of which certain elements remained previously unrecognised and unique to the Welsh record (see Morrissey and Braddy 2001).

***Beaconites* analysis**

Arthropleurid producer hypothesis: Various Upper Silurian to Lower Carboniferous terrestrial ichnofaunas record the presence of *Beaconites* burrows and *Diplichnites* trackways in the same facies associations (albeit at different levels), sometimes even on the same bedding surface (*e.g.* Woolfe 1990, Draganits *et al.* 2001, Morrissey 2001). Some workers have noted the particular association between *B. antarcticus* and *D. gouldi; e.g.* Gevers *et al.* (1971, p. 86) noted "narrow near surface burrows of *B. antarcticus* may occur with the narrow types of *Diplichnites*" and further recorded trackways that occasionally ended in small rounded terminations (interpreted as vertical components of horizontal burrows).

The size distribution of *Beaconites* burrow widths and *Diplichnites* external widths from different ichnofaunas spanning the Upper Silurian to Lower Carboniferous shows a positive correlation between the two trace forms. The range of burrow widths usually lies within that of the generally larger trackways. This evidence infers a strong arthropod (especially myriapod)–*Beaconites* association, with the inferred producer of *Diplichnites* trackways generally regarded as being a myriapodous arthropod (*e.g.* an arthropleurid).

The size distribution (width) of myriapod body fossils throughout the Palaeozoic, when compared with the distribution and size of *Beaconites* burrows, also shows a strong correlation. The age ranges and size distributions of both the eoarthropleurids and the arthropleurids reveal a persistent similarity with burrows assigned to *B. barretti*. The maximum recorded width of *B. barretti* correlates well with the occurrence of gigantic forms of *Arthropleura* in the Lower Carboniferous, represented additionally by large *Diplichnites* trackways. The *Arthropleura* body fossil record persists until the end of the Lower Permian, a similar distribution recorded for *B. barretti*. The size distribution of kampecarid myriapods suggests that they may be considered as candidates for the production of *B. antarcticus* and narrower *D. gouldi* trackways throughout the LORS facies.

Palaeoecological analysis: A summary of the occurrence of *Beaconites* in context of its hosting sedimentary facies indicates that it remains confined to terrestrial palaeoenvironments dominated by fluvial, and secondarily by lacustrine, processes. Sediments of both a sandy channel nature (point bar/channel margin) and muddy units of overbank origin (levee, floodplain, ponded facies) are consistently associated with both ichnospecies of *Beaconites*. This association with either ephemeral water systems and environments where discharge was seasonal followed by periods of desiccation, or where substrate exposure is evident at specific intervals, is recorded throughout the Upper Palaeozoic and Mesozoic (a strong signature conveyed by the ORS facies from both northern and southern continental landmasses, with the host lithologies often displaying deposition reactivation surfaces, red beds, desiccation cracks, and palaeosols with calcretization).

The development of a Euramerican *Beaconites* ichnocoenosis throughout the Laurasian ORS continent is confirmation of the widespread distribution of similar non-marine ephemeral systems and facies associations (morphological differences between Laurasian and Gondwanan *Beaconites* burrows remain absent suggesting the widespread range of the producing organism/s).

Producer analysis: The dominance of both ichnospecies of *Beaconites* burrows within similar Upper Palaeozoic red bed sediments of a semi-arid fluvial origin (*e.g.* Rat Island Mudstone, LORS southwest Wales) suggests a possibly amphibious arthropod capable of burrowing and withstanding relatively harsh seasonal environmental conditions. Animals colonising abandoned sites of subaqueous deposition in order to burrow would suggest an aquatic/amphibious animal in search of moisture in order to avoid desiccation. A process that is extremely common in this environment is aestivation, something adopted by both arthropods and amphibians. The aestivating/moulting habits of extant arthropods (*e.g.* myriapods) offers a suitable analogue to *Beaconites* burrow formation.

In summary, evidence from size distribution, trackway associations, and palaeoenvironmental analysis (especially animal/sediment interactions and mode of life) suggests that *B. barretti* can be produced by an arthropleurid.

Burrowing strategy: Given a myriapodous arthropod as the most likely producer of *Beaconites*, comparison with extant forms shows a variety of excavating techniques, but not backfilling. This absence of known infaunal backfilling in large extant terrestrial organisms (invertebrates/vertebrates) remains problematic, but it is likely that a variety of organisms were capable of producing such fill architectures.

The backfilling burrowing model (Morrissey 2001) describes the different ways in which a backfill may be produced. Burrows observed in the field reveal that the original heterogenity of the host lithology dictates the composition of the menisci. In homogenous sandstones menisci are variably defined by weathering acting on sediment segments showing differential compaction/cementation. The burrows were clearly unlined but often displayed scalloped/irregular wall architectures. The observed degree of vertical penetration by the burrowing organism was not size controlled; *i.e.* larger burrows do not penetrate further into the sediment than smaller individuals. This suggests that both juveniles and adults were adopting the same burrowing strategy in order to achieve an equal depth.

Welsh ichnofauna: A new ichnofauna from the LORS of southwest Wales was documented in this study. It is dominated by an extensive but low diversity *Beaconites* ichnocoenoses. Arthropod trackways characterise an active, gregarious arthropod epifauna of arachnids (*Paleohelcura*) and myriapods (*Diplichnites* and *Diplopodichnus*). Additional ichnotaxa include arthropod foraging and resting traces (bilobed trails, *Rusophycus*, 'scratch arrays' (*cf. Stiallia*), and *Selenichnites*), and worm burrows (*Cochlichnus*, and *Palaeophycus*). Trace preservation is clearly subaerial with all components representative of the *Scoyenia* ichnofacies. The description and application of this ichnofacies is becoming more refined (Buatois and Mangano 1998), but recognition of facies crossing ichnotaxa and generally low ichnodiversity in terrestrial environments remains problematic.

Analysis of subaqueously produced arthropod trackways (Smith *et al.* in press) and the recent discovery (by the author) of *Undichna*-like fish trails from the LORS of the Brecon area, in association with a more diverse subaqueous arthropod epifauna, will contribute towards an improved understanding of the LORS palaeoecology and wider palaeoecological distribution of early terrestrial organisms.

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A re-examination of the phylogenetic position of the unusual sauropodomorph, Anchisaurus

The small sauropodomorph, *Anchisaurus*, is known from several partial skeletons from the Pliensbachian-Toarcian (Early Jurassic) of the Newark Supergroup of Eastern North America. It has long been thought of as the archetypal 'small prosauropod' and at one time a family-level taxon based upon it, the Anchisauridae, held most of the known prosauropod genera. Nevertheless as our understanding of the anatomy of other prosauropods has increased it has become increasingly clear that *Anchisaurus* is quite distinct from all others. This is reflected in the lack of consensus as to its relationships amongst recent cladistic analyses. It has been found variously to be a primitive prosauropod near the base of the Plateosauria, a member of a novel clade containing *Melanorosaurus* and *Massospondylus,* and the sister taxon to the traditional Melanorosauridae. In my own analysis (in press) it was found to be so variable that it needed to be removed using reduced consensus techniques to achieve some resolution. To resolve this situation I spent a week examining the specimens of *Anchisaurus* held in the Yale Peabody Museum, New Haven, Connecticut. This was very fruitful as the only known near-complete skull has been re-prepared, making many features visible for the first time. I was particularly interested in the dentition. Although most of the teeth were badly damaged, one dentary tooth was in reasonable condition and a silicone rubber peel was made in order that a polyester cast could be examined with a SEM. A recent contention that the contemporary *Ammosaurus* was a synonym was supported. A number of autapomorphies are shared by both sets of specimens, while the differences are both slight and attributable to ontogeny.

A great number of derived similarities between *Anchisaurus* (including *Ammosaurus*) and sauropods were noticed, including characters of the dentition, skull roof, braincase, forelimb, pelvis and hindlimb. A new cladistic analysis incorporating this new data clearly resolves *Anchisaurus* as the most basal member of a clade that contains Eusauropoda and all taxa more closely related to it than to the Prosauropoda (which is resolved as a clade containing *Riojasaurus* and Plateosauria). As such it conforms to the accepted phylogenetic definition of the Sauropoda (all taxa more closely related to the eusauropod *Saltasaurus* than to *Plateosaurus*). The node that connects *Anchisaurus* with other sauropods is robust (with high bootstrap and decay values). In addition, a templeton test reveals that the hypothesis that *Anchisaurus* is a sauropod is a significantly better explanation of the data than placing it in the Prosauropoda or as a stem sauropodomorph. Thus *Anchisaurus* should be classified as a sauropod and becomes the smallest and most primitive member of the group. It reveals a great deal about the evolution of the Sauropoda. For example the very large body size, columnar limb posture and specialised herbivory once thought to be diagnostic of Sauropoda can be shown to have evolved long after the group diverged from the Prosauropoda. The results of this study are now being prepared for publication.

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Valanginian Palaeobiogeography and ammonite biostratigraphy of East Greenland

During the Early Cretaceous two faunal realms can be distinguished in the northern hemisphere, the Tethyan and the Boreal. The Boreal ammonite faunas are clearly distinct from Tethyan ones. Provincialism was so pronounced at the Jurassic–Cretaceous boundary and in the earliest Cretaceous that different stage names are used for the two realms. In the Valanginian, strong provincialism still prevails but biogeographical boundaries were opening, making it possible to correlate between the realms using areas with partial overlap of faunas. Definition and correlation of the Valanginian Stage has been a matter of debate since 1854 (see review in Rawson, 1983). The Valanginian of East Greenland contains a rich and diverse ammonite fauna, which so far has only been described by Donovan (1953). He recognised a dominance of typical boreal forms of the family Polyptychitidae, but also forms of strong Tethyan affinity represented by a significant number of specimens of *Phylloceras* and *Lytoceras*. The strong Tethyan affinity of the East Greenland fauna is not known anywhere else in the boreal region. It indicates long distance migration of ammonites, thousands of kilometres from the southern warm waters of the Mediterranean to the cold seaway of East Greenland in the boreal North Atlantic. An open seaway west of Great Britain connecting the Tethys with the northern Boreal Ocean was suggested by Donovan (in Callomon, Donovan & Trümpy, 1972) in order to explain the strong Tethyan affinity of the Valanginian assemblages in East Greenland. Ager (1971) proposed the presence of a warm ocean current to explain the migration of the typical Tethyan brachiopod *Pygope* represented in Greenland by a single specimen.

The Valanginian ammonites of East Greenland are now being studied in a Ph.D. project supervised by Professor Finn Surlyk, Geological Institute, University of Copenhagen. The aims of the study are 1) to make systematic descriptions of the ammonites, 2) to erect an ammonite zonation for East Greenland, 3) to correlate biostratigraphically to Arctic Canada, the Russian Platform, Siberia, Britain, NW Germany and if possible to the Tethys, 4) to focus on the palaeoceanographic implications indicated by biogeographical distributions.

The study is based on several collections of ammonites carried out by a number of workers in the Traill Ø and Wollaston Forland areas since the 1940s. It includes Donovan's collection from the 1950s. Unfortunately the majority of previous collections are from loose blocks. For instance all the material from Traill Ø is weathered out from muddy sediments, which are heavily affected by solifluction. This effectively excludes the possibility of detailed stratigraphical collection. Previous collections from the Wollaston Forland area also lack the desired sampling accuracy to be useful in detailed stratigraphical studies since they were carried out during mapping or helicopter reconnaissances. Further fieldwork with the aim of providing detailed information on the stratigraphic successions of ammonites was thus very much needed. Recent collections in 2001, supported by a **Sylvester-Bradley Award**, were carried out at a number of localities in the Wollaston Forland area. The Valanginian succession in this area is markedly better exposed compared to Traill Ø, making it possible to carry out bed by bed sampling of fossils in carefully measured sections.

The Lower Cretaceous succession in the Wollaston Forland area was deposited in a halfgraben system (Surlyk, 1978). The deepest parts of the grabens contain very thick successions of very coarse-grained submarine fan deposits. They gradually thin up the hanging wall and become fine-grained towards the submerged block crests, on which very condensed mudstones were deposited. The condensed succession comprises fine, sandy, grey and yellowish mudstones with calcareous concretions of the

Albrechts Bugt Member and claret coloured mudstones of the Rødryggen Member. These condensed units are rich in fossils, and fieldwork was therefore focused on outcrops of the two members. Two localities were studied at Stratum Bjerg in the western part of Wollaston Forland, three at the Rødryggen ridge and one at Brorson Halvø in the central and northeastern parts of Wollaston Forland. The quantity and quality of fossils differed a lot between localities and even at the most fossil-rich locality ammonites were few compared to Traill Ø. We succeeded, however, in collecting ammonites in a number of distinct horizons at most localities. For example, ammonites were recorded at eight horizons at locality 2 at Stratum Bjerg and at 13 horizons at locality 4 at Rødryggen. In addition, *Buchia*-bivalves, a few brachiopods and echinoderms, and numerous belemnites were sampled. Belemnites will be used in Strontium isotope analysis in order to develop a Sr-isotope stratigraphy for the interval, and they will also be used in Oxygen isotope analysis in order to develop a temperature/salinity curve for the interval. Rock samples were collected for lithological, geochemical, mineralogical and palynological analysis. The material is presently being analysed.

The ammonite fauna is highly diverse and includes boreal forms of the ammonite genera and subgenera *Surites*, *Menjaites*, *Tollia (Tollia)*, *T. (Neocraspedites)*, *Nikitinoceras (Russanovia)*, *Polyptychites (Polyptychites)*, *P. (Euryptychites)*, *P. (Astieriptychites?)* and *Delphinites*. Ammonites of the genera *Phylloceras*, *Lytoceras*, the heteromorph genus *Bochianites* and the nautiloid genus *Paracymatoceras* represent Tethyan forms.

Acknowledgements
I am grateful to the Palaeontological Association for granting me a Sylvester-Bradley Award, which made it possible to carry out fieldwork in northern East Greenland. I am greatly indebted to Morten Bjerager who assisted me during one month of fieldwork in Wollaston Forland.

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View across the Cardiocerasdal-valley towards Stratum Bjerg in western Wollaston Forland.

>>*Future* Meetings of Other Bodies

Third International Congress on Environmental Micropaleontology, Microbiology and Meiobenthology
Institute of Paleontology, Vienna, Austria *1 – 6 September 2002*

The conference will cover a wide range of topics, with special focus on: micro- and meioorganisms as indicators of past and recent environments; micro- and meioorganisms as indicators of pollution for ecological risk assessment; industrial application of micro- and meioorganisms; application of micro- and meioorganisms to archaeology and medicine. Dr. Irena Motnenko, Osorno Enterprices, Inc., Suite 301, 162-2025 Corydon Avenue, Winnipeg MB R3P 0N5, Canada, tel: +1 (204) 488-1538; fax: +1 (204) 488-1566; e-mail <**congress@isemmm.org**>.

50th Symposium of Vertebrate Palaeontology & Comparative Anatomy; Symposium of Palaeontological Preparators & Conservators
University of Cambridge, UK *9 – 15 September 2002*

SVPCA 50 will be held at the Sedgwick Museum & Department of Earth Sciences, Downing Street, University of Cambridge, CB2 3EQ, UK, with accommodation provided at Emmanuel College, Cambridge.

The organising committee is composed of David Norman <**dn102@esc.cam.ac.uk**>, Paul Upchurch <**pupc98@esc.cam.ac.uk**>, Leslie Noe <**lnoe01@esc.cam.ac.uk**>, Alison Allen <**alison@esc.cam.ac.uk**> (administrator), and Sarah Sangster <**ss348@esc.cam.ac.uk**> (postgraduate student contact).

For further information and initial contact, please contact Alison Allen via e-mail, by telephone (+44 (0) 1223 333459), or by fax (+44 (0) 1223 333450).

Exploration biostratigraphy
University College London *11 – 13 September 2002*

The American Association of Stratigraphic Palynologists (AASP), the Micropalaeontological Society (MS) and the North American Micropaleontology Section of SEPM (NAMS) are holding a joint meeting in September 2002 at University College London. The theme of this international meeting will be recent developments in applied biostratigraphy. Contributions are invited on four main themes: sequence biostratigraphy, reservoir/development studies, deep-water exploration, and outcrop analogues. There will also be an open session with emphasis on post-Palaeozoic palynology. The vision for the meeting is to encourage trans-Atlantic exchange of ideas, ultimately to seed new research initiatives. In particular, we aim to develop an integrated multidisciplinary approach in both academic and industrial realms. There will be no taxonomic, stratigraphical or geographical restriction on contributions. Posters are invited on any micropalaeontological, nannopalaeontological, palynological or biostratigraphical theme. A post-meeting excursion is planned to the Isle of Wight (Cretaceous–Paleogene) led by Statoil's Iain Prince and Bruce Tocher. The meeting is being convened by Jamie Powell (Dinosystems), Chris Denison (ChevronTexaco), Tom Dignes (ExxonMobil), Alan Lord (UCL), Rachel Preece (ChevronTexaco) and Jim Riding (British Geological Survey). Details can be found at the BMS website <**http://www.bmsoc.org/**> or by contacting MS Secretary Jamie Powell <**ajp@dinosystems.co.uk**>.

Jurassic Symposium 2002
Sicily *12 – 22 September 2002*

The First Circular for the 6th International Symposium on the Jurassic System has been circulated. The Symposium will be held in Sicily from 12th to 22nd September 2002. These dates include pre- and post-Symposium field trips. The Symposium Secretary is Dr Luca Martire (Torino), e-mail <**martire@dst.unito.it**>. You can get further information from the website at <**http://www.dst.unito.it/6thISJS/**>.

Evolution and Development 2002
University of Reading, UK *17 September 2002*

Organised by Seb Shimeld, Peter Holland and Marty Cohn. This is the third such meeting, and follows on from those held in Sunderland in 2000 and Cambridge in 2001. Talks will start at 11am to allow time for travel and, as in previous years, we have a relatively relaxed schedule to allow plenty of time for discussion. Buffet lunch and coffee will be provided.

The programme of speakers is: Peter Currie (Edinburgh), John Bishop (Plymouth), Hazel Smith (UCL), Chuck Cook (Cambridge), Phil Donoghue (Birmingham), Jukka Jernvall (Helsinki), Jean Deutsch (Paris), Marty Cohn (Reading). There is no formal pre-registration, but you must let the organising committee know by email if you intend to come. A registration fee of £10 (students, postdocs, academics etc) or £50 (non-academics) will be payable on arrival to cover coffee, lunch, *etc*. Cash or cheques only please. Receipts can be provided if necessary. A number of poster boards will be available for those wishing to present posters. These will be allocated on a first-come-first-served basis; please let me know if you would like to display a poster. As an incentive, Nature Publishing have kindly offered a year's subscription to *Nature Reviews Genetics* as a prize for the best poster. A poster board will be available for anyone wishing to advertise jobs or studentships. The meeting is sponsored by *BioEssays* and *Nature Reviews Genetics*. For full details on the various ways to get to Reading, please see the University website <**http://www.reading.ac.uk/Maps/whiteknights.htm**> and the School website <**http://www.ams.rdg.ac.uk/info/wherearewe.html**>. For further details contact Seb Shimeld <**s.m.shimeld@reading.ac.uk**>.

3rd European Meeting on the Paleontology and Stratigraphy of South America
Université P. Sabatier, Toulouse, France *19 – 20 September, 2002*

The objectives of the meeting are to gather geoscientists interested in fossil and sedimentary records, evolutionary processes, biostratigraphy, chronology or geological history. We specially encourage contributions addressing integrated stratigraphy, and correlations between Latin America and other parts of the world. Abstracts must be in English and not exceed two pages. Languages: English, Spanish and French. Registration fees: €155 ($US 150, £100); Students: €80 ($US 75, £55).

The 3rd European Meeting on the Paleontology and Stratigraphy of South America will immediately follow the 5th International Symposium on Andean Geodynamics—ISAG02, to be held on 16-18 September 2002.

Correspondence and enquiries: ISAG, IRD, 38 rue des 36 Ponts, 31000 Toulouse, France, e-mail <**ISAG@cict.fr**>. Etienne Jaillard <**Etienne.Jaillard@ujf-grenoble.fr**>, <**ejaillar@ecnet.ec**> and Peter Bengtson <**Peter.Bengtson@urz.Uni-Heidelberg.de**>.

Fresh- and brackish water (palaeo)ecosystems, European Palaeontological Association Workshop
Fribourg, Switzerland *23 – 25 September 2002*

The workshop consists of two parts. The first part will be a general introduction to Recent fresh- and brackish-water ecosystems (sedimentology, fauna and flora, geochemistry, stable isotopes). This part will provide the theoretical basis for the second part that deals with fossil examples from the Palaeozoic to the Tertiary. Keynote lectures by invited speakers will be supplemented by posters of other participants. The aim of the workshop is to improve our understanding of fossil fresh- and brackish-water ecosystems and to discuss the appropriate study methods. For further information contact Prof. Dr Jean-Pierre Berger, Institut de Géologie, Université de Fribourg, CH-1700 Fribourg, Switzerland; tel +41 26 3008975; fax: +41 26 3009742; e-mail: <**jean-pierre.berger@unifr.ch**>.

Morphology, molecules, evolution and phylogeny in the Polychaeta and related taxa
Haus Ohrbeck, near Osnabrück *23 – 27 September 2002*

For details check out the symposium website <**http://www.uni-bielefeld.de/symposium/**> or contact the meeting organisers Günter Purschke (Universität Osnabrück, FB Biologie, Spezielle Zoologie, D-49069 Osnabrück, Germany; tel: +49-541-9692857; e-mail: <**purschke@uni-osnabrueck**>) and T. Bartolomaeus (Universität Bielefeld, Fakultät für Biologie, D-33501 Bielefeld, Germany; tel: +49-541-1062721; e-mail: <**t.bartolomaeus@biologie.uni-bielefeld.de**>).

Twelfth Canadian Palaeontology Conference (CPC-2002)
28 – 30 September 2002

For full information visit <**http://iago.stfx.ca/people/paleodiv/CPC2002cir1.html**>.

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

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

Alisa Martek, Institute of Geology, Sachsova 2, 10000 Zagreb, Croatia, tel: +385 1 6160786, fax: +385 1 6144718, e-mail: <**amartek@igi.hr**>.

Cromarty International Conference to celebrate the bicentenary of Hugh Miller
Cromarty, Scotland *10 – 13 October 2002*

The Bicentenary of Hugh Miller, geologist and naturalist, writer and folklorist, falls on 10th October 2002. His birth will be celebrated in Cromarty, 20 miles northeast of Inverness, with an international conference arranged by the Cromarty Arts Trust, in association with the University of the Highlands & Islands and the University of Aberdeen, with the support of Scottish Natural Heritage.

The opening plenary session will begin at 3.30 p.m. on Thursday 10 October, with keynote papers from Prof. David Lowenthal of Berkeley, California, Prof. Christopher Harvie of Tübingen University, and Prof. Eric Richards of the Flinders University of Adelaide, S. Australia. On the morning of Friday 11th October an excursion will be made to the Eathie Foreshore, site of Hugh Miller's early Fossil discoveries. On Sunday 13th October there will also be an excursion to Morayshire to visit the outstanding Elgin Museum's collection, and other sites which were explored by Hugh Miller's contemporaries.

On Friday and Saturday, 11th and 12th October, the conference will divide into three subject themes: Geology & Natural History, Ethnography & Folklore, and Church & Society. Speakers in the Geology theme will include Dr Hugh Torrens of the University of Keele, Dr Simon Knell of the University of Leicester jointly with Dr Michael Taylor of the National Museums of Scotland, Prof. Michael Collie, Dr Ralph O'Connor of St John's College, Cambridge, Dr Nigel Trewin of Aberdeen University, Dr Philippe Janvier of the National Museum of Natural History, Paris, Prof. John Hudson of the University of Leicester, and Dr Alison Morrison-Low of the National Museums of Scotland.

At the full plenary session on Saturday 12th October, the main speaker will be Dr James Secord of the Department of the History and Philosophy of Science of the University of Cambridge. The conference will have a supporting social programme.

Details of registration may be obtained from Dr Lester Borley, Cromarty Arts Trust, 4 Belford Place, Edinburgh EH4 3DH.

2002 Geological Society of America Annual meeting
Denver, USA *27 – 30 October 2002*

Thematic symposia include:

"Three Billion Years of Reef Systems". The planned session also will be sponsored by the Paleontological Society. See topic T76 at <**http://www.geosociety.org/meetings/2002/t_topical.htm**>. It intentionally is planned to be broad and to address diverse topics related to reefs, reef-like features and carbonate buildups from the Precambrian through Phanerozoic time. As stated in the summary, reefs are enduring marine ecosystems. Their biotic and geologic history has been affected by changes in atmosphere, nutrients, seawater chemistry, sedimentation, and the evolution of new biotic groups. This session explores interdisciplinary approaches better to understand the history and sedimentology of reefs. Some of the topics of this session will be reef evolution, processes on reefs and how reef systems (both biotic and sedimentologic) have changed over geologic time. If you are interested in participating, please contact George Stanley (Department of Geology, University of Montana, 32 Campus Drive #1296, Missoula, MT 59812 USA; fax 406-243-4028; tel 406-243-5693; e-mail <**fossil@selway.umt.edu**>) with a possible title and a brief summary.

"The Fossil Record of Predation", a *Paleontological Society* short course, GSA Denver, Saturday 26th October 2002, 8:15 a.m.–5:30 p.m., and convened by M. Kowalewski and P.H. Kelley. This short course provides the first comprehensive overview of research on the fossil record of predation for non-specialists and specialists alike. The speakers represent a wide array of disciplines including micropalaeontology, marine invertebrate palaeontology, palaeoentomology, vertebrate palaeontology, and physical anthropology. The course is subdivided into three parts: (1) **Methods**, focused on analytical and sampling strategies used to acquire data on the fossil record of predation; (2) **Patterns**, providing comprehensive review of the current knowledge of the fossil record of predation from protists to tetrapods; and (3) **Processes**, offering up-to-date syntheses of the current understanding of the evolutionary history of predator-prey interactions, including its evolutionary, ecological, and behavioural aspects. Contributors: Richard K. Bambach (Harvard, USA), Tomasz K. Baumiller (Michigan, USA), Stefan Bengtson (SMNH, Sweden), Carlton E. Brett (Cincinnati, USA), Karen Chin (Colorado at Boulder, USA), Stephen J. Culver (East Carolina, USA), James O. Farlow (Indiana-Purdue at Fort Wayne, USA), Thomas R. Holtz (Maryland, USA), Gregory P. Dietl (North Carolina State, USA), Forest J. Gahn (Michigan, USA), Gary Haynes (Nevada, USA), Ian Jenkins (Bristol, UK), Patricia H. Kelley (North Carolina at Wilmington, USA), Michal Kowalewski (Virginia Tech, USA), Conrad C. Labandeira (Smithsonian Inst, USA), Jere H. Lipps (California at Berkeley, USA), Blaire Van Valkenburgh (California at Los Angeles, USA), Geerat J. Vermeij (California at Davis, USA), Sally

E. Walker (Georgia, USA). No fee or registration. Additional information: Michal Kowalewski, Department of Geological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, (tel +1 (540) 961-2244; fax +1 (540) 961-3386; e-mail <**michalk@vt.edu**>.

Website: <**http://www.geosociety.org/meetings/2002/**>

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

18–20 September: Sessions, Granada.

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

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

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

Ichnia 2004: First International Congress, on Ichnology
Trelew, Patagonia, Argentina *19 – 23 April 2004*

Aims and Scope: we have foreseen the necessity and convenience for convening a large, international meeting where researchers with a bewildering variety of backgrounds and interests gather to exchange their different views of Ichnology. It is expected that this exchange will strengthen our discipline and enhance its recognition from the scientific and technical community. We intend to trace, extend and fortify existing bridges between different fields of Ichnology, *e.g.* between palaeoichnology and neoichnology, vertebrate and invertebrate ichnologists, benthic ecologists and palaeoichnologists, soft and hard substrate ichnologists, *etc*. We strongly encourage the participation of a wide variety of non-ichnological scientists in the meeting. Should a soil scientist working on the micromorphology of modern earthworm burrows and its destruction by trampling attend this meeting? What about a biologist or palaeontologist that works on biomechanical interpretation of extant or fossil organisms? Will an anthropologist contribution on human faeces or footprints be welcomed? Could a zoologist working on bioerosion or benthic bioturbation contribute to this meeting? The answer to all these questions is YES and we wish further to extend the invitation to petroleum geologists/engineers, wildlife biologists, reef biologists, trackers, entomologists, and any other scientist working on Ichnology-related issues.

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

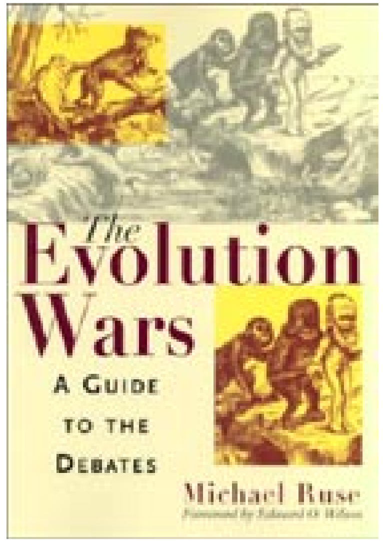
Visit the conference website for further details, at <**http://www.ichnia2004.com/**>.

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

Book Reviews

The Evolution Wars: A Guide to the Debates

Michael Ruse, 2001. Rutgers University Press, New Jersey and London. 325 pp. £21.95



This is definitely a first: a book on evolution that had me laughing out loud. Michael Ruse is well-known for his *Science Red in Tooth and Claw* and *Can a Darwinian be a Christian? The Darwinian Revolution* (1969) was for many people an essential and welcome introduction to the history and philosophy of the subject (followed closely by two other classics, Ospovat's *The Development of Darwin's Theory*, 1981, and Bowler's *Evolution: the Development of an Idea*). This new book, *Evolution Wars*, is definitely aimed at a popular audience. It is written in the first person and a very jaunty first person at that. For example, as a philosopher of science Ruse has a wonderfully jaundiced view of scientists who turn to the history and philosophy of science in their waning years (what John Maynard Smith called the "philosopause"): "when scientists turn to my subject for help … my heart sinks to my boots, for bitter experience has shown me that scientists turning to philosophy are up to no good. All too often, when scientists are a bit unsure of their ground they bolster the case with deep-sounding references to philosophy, preferably hard-to-follow German metaphysics with long words and the verbs at the end." Perhaps on the "walk before you learn to run principle," here Ruse sticks pretty closely to history while keeping that jaundiced eye firmly fixed on the scientists. Throughout, however, Ruse is always circling back to the position that "philosophical differences really count." This is no less true today than a hundred years ago.

Ruse presents a history of evolution in its modern (Buffon, Cuvier, Geoffroy, Lamarck, Erasmus Darwin, Charles Darwin, New Synthesis) and its post-modern (Wilson, Lewontin, Gould, Dawkins) phases. All at a cracking pace and all through the people involved as much as their ideas. His general approach is to give a good review, followed up with extensive notes on what to read next and why (sometimes a disconcerting number of those referenced are to his own works, but he very much approves of both Janet Browne and Adrian Desmond and James Moore on Darwin, and Bowler on evolution). His target audience is the person who knows a little about evolution and wants to know more—someone who will instantly be intrigued by the Prologue: "Darwin's detractors see a mishmash of ideas and suggestions and hypotheses and half thoughts—half-baked thoughts!—that were strung together without order or reason, not just in the *Origin* but also in a series of secondary writings of genuine Victorian length and tedium. And these were just the first editions. … They argue that Darwin's ideas are overblown, unsubstantiated, and little more than ideology—secular religion—masquerading as disinterested description and explanation. They think that Darwinians are deluded, arrogant, and mischievously influential..."

Having piqued the reader's interest, Ruse launches into a lively but not particularly original treatment of the usual suspects (Cuvier to Erasmus Darwin). It is not until we have been introduced to the saintly Charles himself and have moved on to Huxley and Spencer that the pace really picks up. From this point onwards I found the book irresistible. Ruse approves of Spencer and his treatment of Darwinism in America, which he sees as driven as much by Spencer as by the great man himself, which will probably be as much a surprise to British readers as it will be a pleasure to Americans.

It is easy to see who are Ruse's heroes and villains in the evolution wars as they ebbed, flowed, and changed direction. At the beginning we are regaled with the question of evolution as a rival to other theories. In the middle of the book the conflict is a shifting balance of internecine contests among Sewall Wright, Theodosius Dobzhansky, George Gaylord Simpson and Ernst Mayr, then E.O. Wilson and Stephen Jay Gould, not forgetting the wonderful Milford Wolpoff–Chris Springer, "multiregional" versus "out of Africa" debate over *Homo sapiens* (set in a good coverage of the history of human palaeontology), molecular biology, and Richard Dawkins' selfish genes. Only in the final chapter do we come to the Creation wars (which the person who picks up the book casually in the bookstore might have thought was the central theme).

The middle section, where Ruse picks off his targets one by one, is a fascinating account of a period which younger evolutionists will think of as ancient history; namely the building of the "New Synthetic Theory" largely on the basis of Dobzhansky's brilliant high-jacking of Sewall Wright's "Spencerian shifting balance theory," and the consequent triumph of an ultra-gradualistic paradigm based on the now faintly absurd notion that shifting gene frequencies within populations can account for the grand sweep of evolutionary history. That was the party line, and what fun it was to read the following: "A journal, *Evolution*, was started, with Mayr as the first editor. Firm guidelines were put in place. The obvious esoteric language was mathematics, and even though Dobzhansky and Mayr would not have known a symbol if their sister had married one, care was taken to see that their students were properly trained, and associates with mathematical skills were dragooned into co-authoring papers. Dobzhansky wrote a whole series of *Drosophila* articles with Sewall Wright: articles of which he understood the first lines and the last lines and absolutely nothing in between." (That was where my laughter disturbed a whole train-full of tired London-to-Oxford commuters.)

I was a graduate student at Harvard in the Mayr/Simpson days with Dobzhansky still down the road at Columbia and Julian Huxley (that "unabashed neo-Spencerian" and link to the broader world of intellectual respectability—namely literature) was a frequent visitor. Characters like J.L.B. Haldane were rather too dangerous to bring into the fold but just too eccentrically strong to be completely relegated to the sidelines; John Maynard Smith was always threatening from left field; other Brits like E.B. Ford were simply support staff. Ten years after the publication of *Genetics, Paleontology and Evolution* palaeontologists, except for Simpson and T.S. Westoll from Newcastle who always managed to pop up with the big boys, were still non-starters. The degree of toadying adherence to the New Synthesis in-group was spectacular, especially to a naïve Englishman who thought that such goings-on would be impossible at home! Ruse has done some nice homework here and produces from Simpson's files the following reviews: paper by one of the good guys, "first class in every respect"; paper by critic of the synthesis, "narrow-minded and shows consistent lack of thought into biological, as distinct from strictly mathematical aspects of the problems considered". It sounds familiar!

Something from this period that Ruse has somewhat glossed over is the question of enemies. In most fields, schools assemble in part according to what one has to believe and in part against someone or something else. In this case, Mayr gave every indication of trying always to counter Sewall Wright, and everyone was supposed to unite against two other personalised enemies and one philosophical (sorry about that) one. The two people were Tromfim Lysenko, in every respect the perfect villain from central casting in those Cold War years, and Richard Goldschmidt. Goldschmidt had been a hero of the early days of population genetics but after Dobzhansky there was only room for one hero. He was also the one remaining holdout for a non-gradual evolution so no seminar at Harvard in the early 60s was complete without the obligatory savaging of Goldschmidt (whose autobiographical memoir *Portraits from Memory*, 1956, ought to be compulsory reading in our field). Nor would it have been complete without a routine genuflection (more the waving of a garlic clove) against that ultimate horror—"typological thinking". Points could also be scored by making rude remarks against "bean-bag genetics," although no one seemed to be sure what precisely that meant, and sympatric speciation.

The New Synthesis wars had no sooner been "won" when the whole thing unravelled again with both factual and conceptual problems coming from new directions. Ruse neatly displays how the synthesis was first betrayed from within. Lewontin, who had been a hero with his revelation of the extent of variation in natural populations (well, *Drosophila*) turned into an arch-critic of the revered concept of adaptation. No matter that they didn't know a spandrel from a *pendentive*, or that others had made the point before, Lewontin and Gould pricked a massive hole into traditional evolutionism with their *San Marcos* paper. Then the Wilson versus Lewontin and Gould debates over Sociobiology (the age-old debate over nature or nurture), plus Eldredge and Gould versus all gradualists on punctuated equilibrium ushered in (as they say) a new rather unsteady phase of the theories and concepts of evolution (but not really any break-through in that bastion of palaeontology—macroevolution). The consequences of the molecular revolution for evolution (as opposed to systematics) have yet to be seen, but they will surely involve a solution (or an approach to a solution) of the one thing that Dozhansky and Mayr conveniently omitted from their theories—the developmental causes of variation (the place whence macroevolution may yet emerge).

Ruse is rather unkind about palaeontology. "In the eyes of the general public, this is what evolution is all about: fossils, dinosaurs, Lucy, and all of that. But … this is not at all the way that professional evolutionists see things. To them, palaeontology is just the thing that they have had to escape in order to raise the level of their science. To get out of museums and away from a quasi-religious system of hypothetical phylogeny building, they have had to turn to tight, mathematical, experimental, causal studies of fast-breeding organisms like fruitflies. I would hardly want to say that dinosaurs are an embarrassment, but …" We might reply "yes, and no", but many of us have just received a notice that the Museum fur Naturkunde in Berlin is to abolish its professorship of palaeontology on the grounds that "this subject has no scientific autonomy but derives from the objects it studies." And is to be replaced by "Systematics and Biogeography (including molecular aspects)"—which of course is totally different!

Ruse considers Gould a "terrific writer" but is less than enthusiastic about punctuated equilibrium: "I doubt that it is all-important, even if we discount the fact that since Stephen Jay Gould became *the* Stephen Jay Gould, he has been rather backtracking his earlier influences and enthusiasms … more pertinent to Gould's thinking, I suspect, is that whole approach to biology (which was, naturally, shared by Marx and Engels). It is the approach of the *Naturphilosoph*, who thinks that form takes precedence over function". The reader will have to wade through Gould's new *The Structure of Evolutionary Theory* (2002) to see if this criticism is true. Sadly, Gould died on the very day I was writing this review and is no longer able to defend his position.

The last chapter deals with Creationism and also pulls together a lot of what Ruse has slipped in to the rest of the book concerning the relationship between religious belief and science. He is very interesting on the question of whether Darwinism is a kind of religion, "a new myth, something replacing Christianity" which is where E.O. Wilson seems to be heading. He is crunchingly clear that Creationism, a late nineteenth century phenomenon arising out of American Protestant fundamentalism, is not science. Everything draws towards his last sentence: "The point is that just as being an evolutionist neither compels nor denies Christian belief, so also being an evolutionist neither forces one into nor, for that matter, prevents one from being a member of the Church of Darwin."

Evolutionary science has nothing to worry about from this kind of warts-and-all exposition, which deserves to be on the shelf of every student of the subject. Everyone who finds themselves philosophically (that word again) opposed to evolutionary science, and/or associated with the current debate over teaching Creationism in schools in Britain, will also find this a useful aid to sorting out what the fuss is about. Given the rather fuzzy state of the illustrations (and the curious placement of several) £21.95 may seem a little steep. But buy it, you won't be disappointed.

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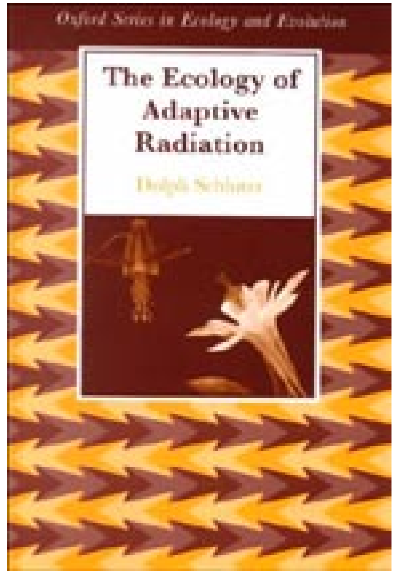
The ecology of adaptive radiation

Schulter, D. 2000. Oxford University Press, Oxford, 288p. ISBN 0 19 850523 X (hbk), 0 19 850522 1 (pbk), £39.50 (hbk), £24.95 (pbk).

The inherently interdisciplinary nature of palaeontology brings its practitioners many advantages. Among these I would include a diversity of audiences eager for information about the ancient earth, a diversity of research funding sources, and a diversity of employment opportunities. However, such advantages must be purchased at a price and that price is an extraordinary diversity of intellectual concepts to learn and relate to one another, coupled with a rather large number of research programmes to keep track of. Since no palaeontologist can hope to do this from casual perusal of the primary literature—especially in these times of ever increasing teaching, managerial, administrative, and even (thanks to the ongoing



communications revolution) technological demands—the publication of comprehensive review articles and books is really the only way for most of us to cope with this task. The Oxford Series in Ecology and Evolution (published by Oxford University Press and edited currently by Robert M. May and Paul H. Harvey) is one of a handful of series that are virtually made to order for helping palaeontologists keep abreast of important developments in biological fields related to many of their primary research interests. Over the years a number of classic titles have appeared in this series that I have found simply indispensable, not only from the standpoint of summaries of current thinking in these nominal disciplines, but also as a rich source of ideas for future palaeontological investigations (*e.g.*, Harvey and Pagel's *The comparative method in evolutionary biology;* Williams' *Natural selection: domains, levels, and challenges*). Consequently, I take particular pleasure in reporting the appearance of another classic in this series, and on this occasion, one that seems most especially relevant to the palaeontological audience: Dolph Schulter's *The ecology of adaptive radiation*.

Given the near ubiquity of reference to adaptive radiation in most discussions of evolutionary patterns, it may come as some small surprise to learn that this seemingly basic concept is a recent addendum to evolutionary theory. More surprising still (for some) may be the fact that it has something of a unique palaeontological pedigree. George Gaylord Simpson coined the modern definition of adaptive radiation in his 1953 book *The Major Features of Evolution* as the 'more or less simultaneous divergence of numerous lines from much the same adaptive type into different, also diverging adaptive zones.' (p. 223). Classic examples include Darwin's finches, West Indian *Anolis* lizards, the Hawaiian silversword alliance, and the cichlid fish faunas of Lake Malawi and Lake Tanganyika. Mechanistically, the modern evolutionary synthesis postulates that the phenotypic divergence, ecological specialization, and speciation characteristic of adaptive radiations stem from divergent natural selection on individuals operating against a background of differences between environments and resources with direct competition mediating the selection process. The purpose of Schulter's book is (1) to test the major elements of this explanation for adaptive radiation and (2) to evaluate the role of other mechanisms (*e.g.*, sexual selection, genetic drift) not included in Simpson's formulation. His stated hope is that, through this process, he will determine whether adaptive radiation remains a defensible evolutionary concept and (if so) establish the outlines of a new, more comprehensive, post-modern formulation.

At this point some may be wondering, "this historical link to Simpson is all well and good but what does adaptive radiation have to offer palaeontology other than a way of making a vague rhetorical link between fossil data and neontological evolutionary theory?" Actually, the careful consideration of adaptive radiation as a hypothesis has quite a lot to offer palaeontologists in both theoretical and practical terms, as Schulter takes pains (on occasion at least) to point out. The study of adaptive radiation is obviously about the origins of biodiversity, an aspect of natural history that is rather important to many contemporary palaeontological research programmes. Indeed, Simpson (1953) went so far as to claim that all of life's diversity could be traced to instances of adaptive radiation. Phylogeny also resides at the core of adaptive radiation (as contemporary systematists now appreciate, it does throughout their discipline). Because these ancestors almost invariably reside in the past, fossil data—recovered and assessed by palaeontologists—should play an important role in evaluating the subsidiary hypothesis of founder generalism. Phylogeny plays an especially important role in evaluating the topic of phenotype–environmental covariance which, in effect, makes (or breaks) the case for identifying diversification events as being 'adaptive' (see Gould and Vrba 1982; Coddington 1988; Harvey and Pagel 1991). To the extent that palaeontological data contribute to the specification of accurate phylogenies (see Donoghue *et al.* 1989 and Smith and Peterson 2002 for discussions), those data can and should play more important roles in current and future analyses of adaptive radiation than they have in the past. In addition, adaptive radiations have figured largely in providing examples of punctuated speciation events (*e.g.*, see Stanley's 1979 comments on the African Lake radiation of cichlid fish). Indeed, the entire question of speciation mechanisms is logically bound up in the investigation of this phenomenon. Finally, adaptive radiation events represent outstanding opportunities to examine aspects of macroevolutionary theory (*e.g.*, origins of long-term phenotypic trends, the role of contingency in evolutionary processes). For these and many other reasons, Schulter's book should matter to all palaeontologists interested in the evolutionary dimension of their data.

Each chapter considers a major aspect of the adaptive radiation phenomenon. Topics discussed in detail include the criteria whereby adaptive radiations can be distinguished from non-adaptive radiations (Chapter 2), the expected sequence of events in adaptive radiations (Chapter 3), the roles of competition and divergent natural selection—plus that of their alternatives—in the origin of both phenotypic and ecological species (Chapter 4), the empirical estimation and analysis of fitness surfaces (= adaptive landscapes) from morphological and environmental data (Chapter 5), the observational evidence for character displacement and the drivers of divergence (Chapter 6), the roles of ecological opportunity and key innovations (Chapter 7), the ecological context (or not) of divergent natural selection (Chapter 8), and the (potential) role of genetic canalization (Chapter 9). These discussions are bracketed by an introduction to the concept of adaptive radiation and a combined synthesis-prescription for future research (chapters 1 and 10 respectively).

Each chapter is relatively self-contained and organized into a tripartite presentation scheme. First the major principles—along with their alternatives—are discussed from purely descriptive and historical perspectives. This section also includes an analysis of the predictions these principles (and alternatives) make for patterns of variation that should be able to be observed in natural populations or assessed through experiment (*e.g.*, food web analyses, competition experiments, reciprocal transplant experiments). A summary of methods whereby these predictions may be tested quantitatively is then provided. Finally, these methods are used to analyze anywhere from four to thirty empirical datasets with the results and their implications

summarized. In this way the emphasis remains on formal hypothesis testing, along with the quality and quantity of evidence for (and against) particular propositions, all of which are presented in a consistent and satisfyingly empirical manner. At the end of the book you really feel that you've been presented with an accurate, comprehensive, and nuanced picture of the current state-of-the-art.

Scattered throughout the text the reader will also find highlight-box discussions of specific data analytic methods including: tests of trait–environment association (Chapter 2), detecting rapid speciation (Chapter 2), reconstructing ecological history (Chapter 3), estimating fitness functions (Chapter 5), estimating rates of phenotypic evolution from a phylogeny (Chapter 5). I found these a bit less satisfying in that they cover very large swaths of complicated material very briefly. For example, the principles of comparative method analysis are described in a mere five paragraphs. Few not already familiar with these topics will gain an appreciation of them here, and this may compromise the readers' understanding of the empirical results. Nevertheless, Schulter is diligent about citing up-to-date references in all of these highlight-box discussions so interested parties should be able to bring themselves fully up to speed in short order.

As a result of his argument structure Schulter is able to provide startling new and counter-intuitive insights throughout the text. In particular, evidence is marshalled to show that, contrary to many standard representations (1) adaptive radiations are most typically characterized by continuous expansion into new environments; (2) the initial stages of divergence tend to occur along lines of maximum genetic variance; (3) these radiations are 'self-similar' in the sense that there is a good deal of parallel evolution within the same radiation, but little morphological–ecological similarity between the adaptive radiations of distantly-related lineages; (4) after an initial (geologically instantaneous) divergence phase, moderate rates of morphological divergence are sustained for several million years during which time most of the morphological variation characteristic of the radiation is created; and (5) the founders of adaptive radiations are typically not morphological or ecological generalists and their descendants are not characterized by sustained trends toward increasing morphological–ecological specialization.

No book of this type would be complete without a detailed disquisition on future research topics. On this score Schulter predicts that the biological focus will now shift toward understanding the genetic mechanisms that underpin adaptive radiations. Since such a shift in focus is already underway, this prediction seems a pretty safe bet. However, more speculative—and more interesting to palaeontologists—are his predictions with respect to the morphological work remaining to be done. In this area he alludes to three research programmes that should have especially broad appeal within the palaeontological community. First, given Schulter's review on the criteria whereby adaptive radiation events may be distinguished from other radiation events, palaeontologists are now in a position to review their data with the eye of an evolutionary–ecological taxonomist. Which radiation events in the fossil record meet Schulter's criteria for adaptive radiation and which do not? Second, what is the role of extinction in the initiation and development of adaptive radiation? Classically, major extinction events were viewed as necessary precursors for adaptive radiations (*e.g.*, the non-avian dinosaur extinction at the end of the Cretaceous 'setting up' the Palaeogene mammalian adaptive radiation). However, more recent phylogenetic data have broken the tight time linkage that gave credence to these scenarios (*e.g.*, Penny *et al.* 1999). Third, what about Simpson's speculation that all biodiversity owes its origin to adaptive radiation events? Is this really the case or has biodiversity accumulated as the result of a larger process-delimited collage? In order to approach these questions successfully, paleontologists will need to make some new methodological contributions of their own (*e.g.*, when is a radiation event rapid (or slow) enough to be distinguished from other events such that its extreme rate implies the operation of novel evolutionary processes; see Schulter's Fig. 2.1), but these are well within our community's capabilities.

Schulter concludes his discussion by noting that, despite the need for some tweaking around the margins in the light of better data analysis methods and new evidence, the last 50 years' research has largely confirmed all of Simpson's most important claims for adaptive radiation. This seems a bit odd given the list of revisions to our understanding of this phenomenon that his book so nicely summarizes. Nevertheless, it can be said that the adaptive radiation concept has now withstood a very thorough empirical review of its major tenets and come through vindicated as a major evolutionary mechanism, grounded irrefutably in natural selection and ecological competition theory, and with a firm base of empirical support. The overall challenge now—to biologists of all types, but the palaeontologists in particular—is to use this well-corroborated theory, along with its modern alterations/extensions, as a finely-honed tool to test more refined hypotheses concerning the history of life. This book contains many excellent examples of exactly how this process may be carried forward. As researchers who work on the borders between disciplines, it behooves us to take these lessons to heart, combine them with our more detailed knowledge of ancient lineages, and work our data more firmly into the emerging synthesis that this book so eloquently describes. You simply will not be able to find a better summary of this field at any price.

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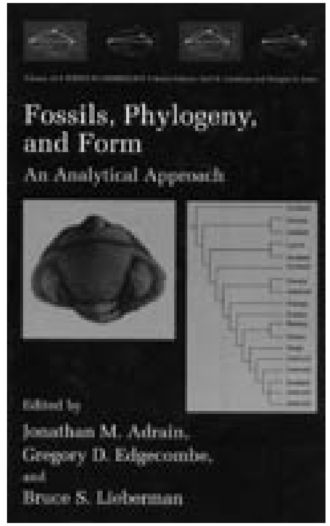
Fossils, Phylogeny, and form: an analytical approach

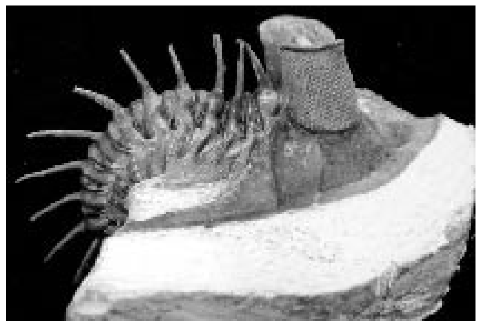
Adrain, J.M., Edgecomb, G.D. & Lieberman, B.S. 2001. 402 pp. New York: Kluwer Academic. ISBN 0-306-46721-6, £91.00.



Three trilobite workers have assembled a collection of essays designed to show the richness of morphology and analytical methods by which it can be described and used in phylogeny reconstruction. Studying trilobites they are in a good position, for these organisms are character-rich, with some species extending the limits of morphological variation to incredulity (see figure below). Trilobites also have the advantages of being both numerous and able to be stratigraphically well dated—perfect study material.

The book takes as its kernel the coding and use of morphological data in phylogeny reconstruction surrounded by a mixed flesh of palaeobiogeography, phylogenetic systematics, species sampling, speciation rates, cladogensis and databases.

So let's get to the kernel which is concerned with Morphometrics and Morphology, authored by Matt (Wills—Chapter 4), Miriam (Zelditch *et al.*—Chapter 5) and MacLeod (Chapter 6), supplemented by Hughes and Chapman (Chapter 3). Together these chapters occupy nearly one-third of the book and discuss the role that descriptors of morphology play in our attempts to recognise characters and how those characters can be used in phylogeny reconstruction and in measures of disparity. Wills' chapter occupies a full 90 pages but carries no signs of being laboured or repetitive. It is a magnificently clear and insightful commentary on a staggering amount of literature which has appeared over the last 20 years and which has attempted to quantify how the evolution of animals has occupied the theoretical and empirical morphospace available (sorry but plants do not seem to have figured in this). The primary literature out there contains some pretty dense concepts and mathematical tricks, but Wills cuts through all of this to relate the methods to real biological data. He makes a convincing case for utilising measures of disparity to say something meaningful about the early radiation of



A new and bizarre 5 cm trilobite from the Middle Devonian of Morocco which will even stretch the descriptive powers of Richard Fortey.

Picture courtesy of R.A. Fortey.

groups—this being that the early members of a clade occupy more divergent morphologies than the successors. I wonder if this is also true of molecular evolution? Anyone interested in getting to grips with morphometric literature should read this.

Zelditch *et al.* concentrate specifically on the use of morphometric characters in phylogenetic analysis. Their chapter is a good digest of many papers written in their various author combinations during the last decade. There has been considerable debate over which kinds of morphometric characters are allowable in phylogenetic analysis (see MacLeod & Forey 2002 for a similar volume—well, I'm entitled to get that one in!). They conclude that landmark data (shapes described in relation to specific comparable points on the form of a group of organisms) are admissible as long as the landmarks are already established as biological homologues. They are correct. They have been criticised on two counts: first that a reference shape (*e.g.* a specific taxon or specimen) is needed so that the deviations in shape, which are measured as warps, of the other taxa can be described relative to that form; and second, that the taxa have to be identified before analysis. Both are true, but they are stated up front. Let us not forget that standard cladistic analysis uses outgroups (the reference forms). And in most cladistic analyses the species taxa are more often than not established using—you guessed it—morphometric characters (length/breadth, numbers of legs/fin rays, ratios of parts *etc.*).

MacLeod is more wary about landmarks since, in pure morphometrics, these are infinitesimally small points, theoretically difficult to equate between species. Moreover he distinguishes three types of landmark data and questions whether any of them correspond to biological homology, thereby questioning their use in phylogenetic analysis. However, through the use of two data sets (cranidia of trilobites and complete tests of radiolarians) and landmarks he shows that various ways of warp analysis yield different species discrimination. He extends this through a modification of eigenshape analysis. For me, the strong message that comes through in MacLeod's chapter is that morphometrics is a powerful tool for shape description and has a place in character description just as does the use of a microscope.

Hughes and Chapman contribute a neat chapter on morphometrics and phylogeny in a group of Silurian trilobites. It provides an elegant case study of how morphometrics can be put to good use to say something about evolution. In this case the authors demonstrate by means of landmark analysis that some species are inherently more variable than others, and that the variation is located in different parts of the body in different species. Furthermore, by using a phylogeny, they demonstrate that stabilisation in the number of thoracic segments in the holaspid-stage (adult), acquired during the evolution of trilobites can secondarily break down, implying a relaxation of developmental constraint.

So what about the flesh surrounding this kernel? Well, this is very disparate in coverage and variable in quality. McLennan and Brooks' Chapter 2 deals with phylogenetic systematics methodology. It is pretentiously subtitled "five steps to enlightenment" but for me is anything but. It is phrased in old fashioned Hennigian argumentation with *a priori* polarity decisions and characters viewed as transformation theories. Their view that homology assessment is determined by time and financial constraints (p.16) defies belief, implying as it does that the veracity of phylogenetic trees can be assessed by the clock and cheque book!

In contrast Ebach & Edgcombe's chapter on biogeography is a very good summary of cladistic biogeography, and they tackle the nagging problems of widespread taxa, missing and redundant

areas. In cladistic biogeography the taxa at the tips of the phylogenetic tree are replaced by the areas that those particular taxa occupy. Area redundancy (where the same area appears more than once on the cladogram) has been likened to paralogy in molecular systematics. They suggest that paralogy may indicate that the original (repeated) area may actually signify two or more areas and that we may have been wrong in our assignment of areas of endemism in the first place. They also suggest a way in which vicariance and dispersal may be distinguished. Throughout they are much more aligned with Nelson's view of cladistic biogeography than that of Ronquist—that is, they are after patterns rather than ancestral–descendent processes. Good on yer!

I also enjoyed the next chapter where Adrain & Westrop take on stratocladistics and stratolikelihood, two methods of phylogeny reconstruction which are dedicated to reintroducing stratigraphic occurrence into tree building. They raise theoretical issues as to why time is inappropriately used here but their main gripe on this occasion is that, if we are going to use the stratigraphic occurrence as primary data, we had better be sure that the observed record is reasonably close to the (unknowable) true record. To evaluate this they examine nearly 1,900 sample horizons containing trilobites from the late Cambrian of Laurentia. They conclude that there are serious biases with respect to stratigraphic, geographic and environmental distribution. These biases are so extreme as seriously to question whether observed stratigraphic range comes anywhere near expressing the true time at which these trilobite species lived. If this is the case, the use of stratigraphy in tree building must be seriously questioned.

Niles Eldredge—self confessed "grizzled veteran at the Millenium" (p.369)—joins us in Chapter 10 carrying his 'sloshing bucket'. This is his analogy for the causes of adaptive evolutionary change which he identifies as ecological perturbations at ever higher intensities and spatiotemporal scales. He prescribes six levels of sloshing, ranging from seasonal fluctuations (no change) to mass extinctions. It is only at level 5 (permanent and dramatic ecological change) that the bucket is sloshed vigorously enough to stimulate real evolutionary change. And when this happens it follows, not surprisingly, the scenario of punctuated equilibrium. From this he sets out a series of predictions of patterns in the fossil record tested against trilobite examples. Good armwaving stuff this—but stimulating all the same.

Lieberman's Chapter 9 shows us several ways of measuring speciation (and extinction) rates, each of which have implications for inferences we have about the tempo and mode of evolution. The book is closed by a short Chapter 11 on database design by R. Kaesler, J. Krebs and D. Miller and is really based on their experience with *PaleoBank* and its relationship with the *Treatise on Invertebrate Paleontology* at the University of Kansas.

I rarely comment on the standard of editing—having a frailty in this area myself. But, a little more time should have been spent on this volume. There are quite a few typos, and some of the errors could cause confusion. For instance, in MacLennan and Brooks' chapter, the data matrix used for their exposition of phylogenetic systematics is presented in the reverse of what the text claims (the transformation series should be read as rows not columns). In Will's chapter something has gone wrong with the labels in figures 3 and 4 and the associated text and legends such that q = _ and F = _ making some difficulty in following the figs and formulae. And in MacLeod's chapter, the text citations to Figs 11 and 13 have been transposed making it difficult to follow future text.

This review is admittedly long and is due to the rather discrete subject areas. I found it difficult to follow through an integrated thread of argumentation that permeates every chapter and at just over £90 a reader would need to evaluate carefully how much would be of direct relevance to his or her own work before buying. That said, the pages are certainly worth turning.

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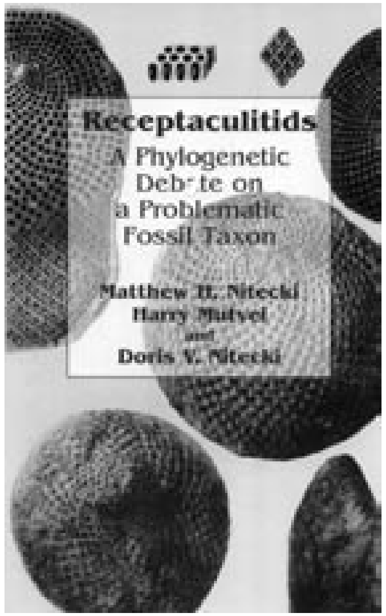
Receptaculitids: A Phylogenetic Debate on a Problematic Fossil Taxon

Nitecki, Matthew H., Mutvei, Harry, and Nitecki, Doris V. 1999. Kluwer Academic/Plenum Publishers, New York. 239 pp. ISBN 030646201X. £55.25.



Problematic fossils continue to grasp curiosity among both the public and professionals. The excitement grows while the progress of science continuously reduces the number of large enigmatic groupings of extinct organisms. After conodonts have found their place in the phylogenetic tree of chordates and the sponge nature of archaeocyaths and stromatoporoids becomes widely accepted, the receptaculitids remain probably the largest and longest living taxon of fossil organisms of still unknown affinities. No doubt that the very extensive and even pedantic review of existing evidence on the receptaculitids offered by Matthew Nitecki, Harry Mutvei and Doris Nitecki in their book is welcomed. They present data already published in journal papers and monographs interwoven with new results of their research on phosphatised receptaculitid skeletons from a fossil locality in Sweden (claimed to be, with some exaggeration, an extraordinary taphonomic window to the past, although such fossils seem to be widespread in the Ordovician and their influence on the authors' conclusions is hardly dramatic). The book is nicely illustrated, with numerous photographs of classic specimens of receptaculitids and cyclocrinitid algae. The extensive list of references will be of much help to researchers. Of special value is the chapter on phosphatization of mineral skeletons given as the addendum to the book.

The book's authors repeatedly declare that they want to clarify affinities of receptaculitids but do not specify on what methodologic basis this is to be achieved. What is implicit in their

discussion of the matter seems to be a rather static approach with interest restricted to the most derived members of the group, and with virtually no reference to evolution. This is a search for morphologic similarity which in some cases looks logically defective. If they conclude (Nitecki *et al.* 2002, p. 146) that "we have argued that no other group of the reference taxa contains all the receptaculitid features" one may comment that taxa with all the receptaculitid features are by definition already classified within receptaculitids. Arguments from skeletal anatomy are even more problematic, as if the authors did not distinguish between the skeleton and the soft tissue producing it (Nitecki *et al.* 2002, p. 139: *Mastopora* and *Cerionites* "could not have been algae; algae cannot have branches open to the exterior that would allow for the escape of the cytoplasmic content").

I would argue that if one wants to find a place for a clade of extinct enigmatic organisms, its possible ancestry should be searched for. That is, the phylogeny should be restored and the evolution extrapolated by retrodiction to meet something less enigmatic in geologically older strata. From this point of view the oldest representatives of a group are of the highest value. Among receptaculitids this would be *Calathium* (and *Soanites*, if truly distinct). Nitecki *et al.* (2002) refer to earlier works by other authors showing that the usually well preserved nuclear part of globular receptaculitids was their base, that meroms were added on the opposite upper end, that the oldest such receptaculitids were more or less conical in shape, grading into the cup-like *Calathium*. *Calathium* had an almost cylindrical, branching body and an extensive basal attachment area with a network of calcareous fibres around it and within the cup (too easily dismissed as epibionts). It is a pity that the authors did not attempt to show how the complex structure of meroms of the advanced receptaculitids originated from what is seen in *Calathium*, although they admit that "since the oldest receptaculitids were clavate, this shape may be a plesiomorphic character" and "since *Calathium* are the oldest receptaculitids, branching of their body may be a primitive character" (Nitecki *et al.* 2002, p.114). I am afraid that by ignoring this aspect of the fossil evidence the authors effectively prevented themselves from achieving their declared goal.

Perhaps the most interesting aspects of the receptaculitid research are those only barely mentioned in the book. Even after reading the book a reader may remain curious why at all receptaculitids were once considered algae and why the cyclocrinitids, so fundamentally different from receptaculitids in their skeletal organization, are at all mentioned in such context. In fact, both ideas originated as misunderstandings, a result of taking too literally what is seen in sectioned fossils.

The receptaculitids were made algae by Kesling & Graham (1962) who claimed identification of gametocysts beneath the outer wall plates of the Ordovician *Ischadites*. The idea of dasycladacean nature of receptaculitids was immediately grasped by Nitecki (1970, p. 7) who unified them with the early Palaeozoic cyclocrinitid algae, classifying the cyclocrintids as a lower rank taxon among receptaculitids and even placing some receptaculitid genera in it. It was already pointed out by Byrnes (1968, p. 369) that the supposed gametocysts of Kesling & Graham (1962) are actually cross sections of diagonal rays of meroms, whereas Rietschel (1969, p. 503) indicated that the mineral skeleton of algae (including cyclocrinitids) is in reverse relationship to that of receptaculitids: what is calcareous in algae corresponds to empty space in receptaculitids and *vice versa*. Apparently no rational argument was able to stop the wave. The algal interpretation of receptaculitids entered textbooks and dominated there for several decades.

This is a truly instructive case story showing how a basic misinterpretation of plain facts may influence the long term development of whole areas of research, and how difficult it is then to drop wrong ideas if the most influential people are personally linked with them. Unfortunately, the authors of the book did not attempt to analyse the problem, all their comments being restricted to a single sentence (Nitecki *et al.* 2002, p. 137: "reports on gametangia […] are either incorrect or unproven)". A popular explanation of such situations is that a theory may be true even if based on false arguments. Perhaps palaeontology is truly more a social activity than a search for the objective truth. If so, it would be more appropriate to replace numerous references to Karl R. Popper and his World 3 (of rather unclear connection with the subject) with citations of Thomas S. Kuhn works.

Anyway, the book seems to be worth reading for enthusiasts of problematic fossils and general palaeontology of the Palaeozoic—perhaps with the above comments in mind.

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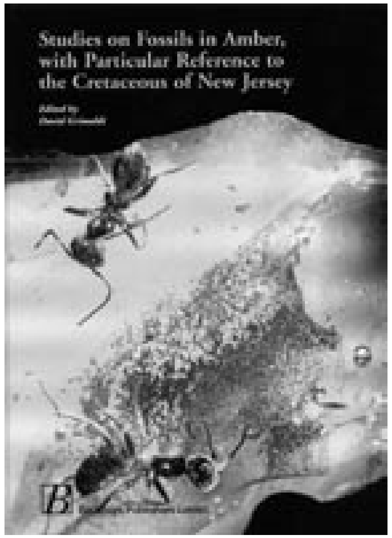
Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey

Grimaldi, D. (ed.) 2000. viii + 498 pp. Backhuys, Leiden.
ISBN 90-5782-060-9 €146.00

Amber is fossilised tree resin often preserving small fossils in exquisite detail. There have been a number of beautifully illustrated books on the subject in recent years. How does this one compare? Significantly, it is about Cretaceous ambers which have received much less attention



than Tertiary ones. One of the reasons for this relative neglect is that the older ambers are harder to fashion into necklaces and other gemmological artefacts. Another reason is that many Cretaceous deposits have only been investigated properly in recent years. One of these is New Jersey amber of Upper Cretaceous (Turonian; ca 92 Ma) age from the eastern U.S.A..

This is no simple 'look at' book. Following a substantial introduction, the analytical methodology is discussed, including CT scans and how to prepare such fragile amber for examination. The systematic part includes descriptions of a water bear (Tardigrada) and eight orders of insects (mayflies, termites, bugs, beetles, lacewings, wasps, caddisflies and true flies). There are some thirty authors of whom many are international taxon specialists. The editor contributes to no less than six papers. Even so, it is not possible to describe all the species present in New Jersey amber. This highlights one of the big challenges of palaeoentomology: the relatively high biodiversity in Cretaceous deposits.

Some of the entomological gems are on the cover: a pair of rare presumed social ants (metapleural gland present). It is hard to imagine terrestrial habitats without ants and, as I have suggested elsewhere, it is possible that ants only displaced small cockroaches ecologically during the Cretaceous. Another gem is the direct association of scale insects and a conifer leafy shoot (p. 64). A personal favourite is a mesoraphidiid snakefly (p. 282) as I had only previously seen these insects as rock fossils. A departure from New Jersey amber is a paper on biting midges from early Cretaceous Lebanese amber (a Gondwanan as opposed to Laurasian source). This paper provides the first cladogram (p. 445)! And if you are interested in ornithophily, then you will have to wait until p. 473.

There are few controversies in this volume. For example, the earliest bee (*Trigona prisca*) from New Jersey amber may be younger (latest Maastrichtian). New Jersey ambers actually span the whole of the Upper Cretaceous. Only time will tell if the preferred epoxy mounting of amber will outlast Canada balsam. If you are interested in fossil DNA or palaeoair, look elsewhere. Nevertheless, this is a highly focused key work of systematic amber science. If only there were more like it.

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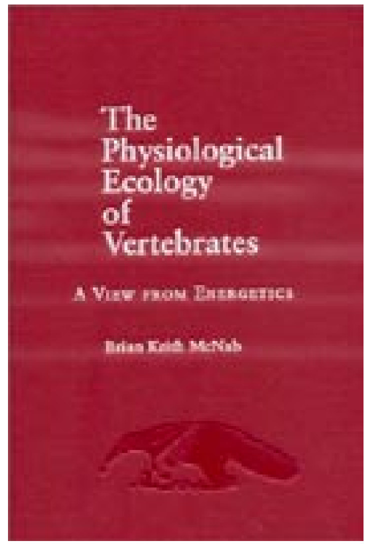
The Physiological Ecology of Vertebrates: a View from Energetics

Brian Keith McNab. 2002. Comstock Publishing Associates (Cornell University Press). 576 pp. Hardback. ISBN 0-8014-3913-2. £48.95.



Most palaeontologists have little background in physiology. Even vertebrate palaeontologists who came to the field via biology rather than geology usually have their expertise in anatomy, and perhaps also in ecology, but rarely in physiology. (I consider myself most fortunate that my undergraduate years at Cambridge exposed me to the teachings of the late Torkel Weis-Fogh, with his uniquely insightful understanding of how the interaction of the organism with the physical world determines many aspects of its biology.) Yet with the growing interest in extinct vertebrates as once-living, functional entities, attempts to understand their biology and lifestyle are increasingly dependent on an understanding of physiological processes.

When I was a student, the prevailing view towards this type of interpretation of extinct vertebrates was in the nature of: "They're all dead, so we can never know for sure what they did." Unfortunately, a prevailing view today echoes this under the rubric of "progressivism" in terms of phylogenetic reconstruction: namely that an extinct organism can only be placed in a cladogram, and interpreted in the context of its living relatives, and that their biology is otherwise unknowable (see Gee, 2000).

Both of these viewpoints display a profound ignorance of the various constants that relate to the physical nature of the environment, and the resultant physical constraints on organismal design. The mere body size of an animal can instantly tell you an immense amount about its biological capacities and limitations. It may be the case that goats can climb trees (or, at least, young goats can scramble up fallen tree trunks), or that golden retrievers can swim (albeit doing an inefficient dog-paddle) (see Gee, 1999, p. 187), but pigs cannot fly. This can be deduced not only from their anatomy (forelimbs not converted into wings) but by analysis of biomechanical/physical principles based on absolute body size and the demands of wing-loading, *etc*. (OK, perhaps *Quetzlecoatalus* raises some questions here, but the analogy remains sound.)

The issue of the physiology of extinct vertebrates has been highlighted in the past few decades by the debates about the metabolic status of dinosaurs ("hot-blooded" or not), but an understanding of physiology, in conjunction with anatomy, is actually essential to realistic (and potentially testable) palaeobiological reconstructions. With the increased demand for scientifically realistic reconstructions of the lifestyles of extinct animals (such as the various "Walking with —" series), an understanding of the physiology of living vertebrates becomes vital. McNab's book presents a dynamic approach to physiology in relation to environmental physical constraints, elucidating the principles that can be applicable to extinct organisms, even if they cannot be placed in a phylogenetic context. Thus this book is potentially a most useful resource for palaeontologists in amassing the current literature on living vertebrates.

The first section of the book, *Foundations*, highlights both the strengths and the weaknesses of the book. McNab is an unusual physiologist in that he considers animals in their phylogenetic context, rather than the more usual physiologist's approach of "the fish, the frog, the mammal", *etc*. Yet, unlike most of those physiologists who incorporate phylogeny into considerations (see, for example, Garland *et al*., 1992), he is sceptical of the current algorithm-driven phylogenetic approach. In Chapter 1 (*The Limits to Adaptation*) McNab takes a sly dig at Paul Harvey on p. 5, where he states: "What is unacceptable, however, is to argue that an evolutionary approach to the study of adaptation is required to account for phylogeny and then to maintain that ' … we see no reason why our analyses [of the impact of phylogeny on the basal rate of metabolism] should be systematically biased because they rest on unsatisfactory classifications' " (from Harvey *et al*., 1991). I find McNab's approach of pragmatic inclusion of phylogenetic principles, without becoming mired in polemical assertions of phylogenetic correctness, to be both appealing and refreshing.

In Chapter 2 (*Patterns of Physical Exchange in the Environment*) McNab shows that he is capable of providing clear discussion of principles and relevant examples, and of keeping these somewhat separate from his presentation of the mathematics and equations involved in their derivation (so that people like myself can just hum these bits if we feel so inclined). Other excellent features of the book as a whole, as first presented in this section, are the citations of a multitude of relevant studies, providing a great compilation of literature resources, plus a most useful synopsis at the start of each chapter and a point by point summary at its end.

Unfortunately, this first section also highlights some of the book's weaknesses. McNab is no palaeontologist, and although he evidently considers himself to be knowledgeable of the palaeobiological literature, the great majority of his citations throughout the book predate 1980. For example, in Chapter 1 he uses the outdated term "crossopterygian," and expresses the archaic notion that the marsupial mode of reproduction represents the primitive therian mammal condition.

Section II is the one most likely to appeal to the majority of palaeontologists, with the prevailing interest in the evolution of endothermy. Three chapters deal with *Thermal Exchange and the Environment;* one with the scaling of metabolism, one with the issue of poikilothermy/ectothermy, and one with homeothermy/endothermy. McNab does an excellent job of laying out the differences between ectothermy and endothermy, the advantages and disadvantages of both types of metabolic physiology, and the relationship between metabolic rate and body size. I found his discussion about the reality, and possible causes, of Bergmann's rule (increased size at higher latitude) to be particularly informative. While I was disappointed that there was little in the way of discussion about how the biochemistry of endothermy might differ between birds and mammals, I was intrigued to discover that birds lack mechanisms of non-shivering thermogenesis.

However, this chapter is less than satisfactory in its coverage of palaeobiological issues. Once again, the reliance on the older literature and the apparent lack of knowledge of many current debates is disappointing. For example, the only citation he provides for the notion that birds might be related to dinosaurs is from Ostrom (1969), that he then dismisses with a citation of Feduccia (1996). His only concession to the entire recent debate about the nature of dinosaur integument (which was certainly well-established enough by the late 1990s for some inclusion in this book) is a citation from Gibbons (1996), which is a *Science* staff writer comment rather than an original article. On page 128 he actually says "Little is known of the early evolution of birds." Despite a mention of "coelurosaurs", he falls into the typical neontologist's trap of imagining most, if not all, dinosaurs to be huge, outside of the body-size range of terrestrial mammals (this is in fact only true of the larger sauropods). This assumption leads him to favour ideas that dinosaurs could not have been endothermic because of problems with overheating.

McNab's discussion of the evolution of endothermy in the mammal lineage is equally confused. He (not surprisingly!) prefers his own explanation (McNab, 1978) as endothermy being related to the decrease in size from cynodonts to the first mammals; from a body mass of around 20 kg to around 20 g. However, he later reviews some of the anatomical evidence for elevated metabolic rate in cynodonts and other derived theraspids (such as the secondary palate or evidence for nasal turbinates), and somehow arrives at the conclusion that endothermy evolved several times convergently, each time in association with a decrease in body size. I was unable to follow the logic of this argument, except to realise that he must have been making the assumption that all earlier theraspids were the size of *Moschops* (about the size of a large cow).

Section III covers *Material Exchange with the Environment:* three chapters dealing with osmotic regulation, water and salt control, and gas exchange. The first chapter is informative to people interested in the origin of vertebrates, in the radiation of fishes into a variety of fresh-water and marine environments, and the origin of tetrapods. This chapter contains some very useful information on hagfishes, and argues that the production and excretion of urea by the ornithine cycle is a primitive gnathostome feature. The discussion on vertebrate origins is fairly good and up-to-date, but the discussion of the origin of tetrapods (or "labyrinthodont amphibians"—ouch) is less so. It is especially surprising that McNab appears to be completely unaware of the recent discoveries of *Acanthostega*, by Jenny Clack and her associates, and the impact that those findings have had on our thinking about tetrapod origins.

The second chapter covers useful reviews of topics such as uric acid and extra-renal salt excretion in amniotes (although I was disappointed that there was little discussion about the role and importance of the renal portal system). I was also delighted to see that there is apparently evidence of nasal salt glands in the ichthyosaur *Opthalmosaurus:* I recently set my comparative anatomy students an essay about why we had to infer the presence of salt glands in ichthyosaurs despite the lack of actual evidence!

The third chapter covers interesting topics such as the evolution of lunglessness in plethodontid salamanders, and I was intrigued to realise that the tetrameric (versus monomeric) form of the haemoglobin molecule is a gnathostome synapomorphy. While McNab covers a relatively recent argument (Daniels and Pratt, 1992) for the necessity of a bird-like flow-through lung in long-necked sauropods, he recycles old palaeontological chestnuts such as the presence of lungs in the placoderm *Bothriolepis*, and is apparently unaware of the important work of Colleen Farmer (*e.g.* Farmer, 1997) on the role of aerial breathing in fishes for levels of activity and the possible reasons for the evolution of lungs.

Section IV deals with Ecological Energetics, including two chapters on energy budgets and (of probable more relevance to palaeobiologists) one on locomotion and one on diet and nutrition.

The chapter on the energetics of locomotion deals with aquatic, aerial and terrestrial locomotion (including good coverage of limbless locomotion), with a final summary about the relative costs of different types of locomotion at different body sizes. The chapter includes some discussion on the differences between the energetics of ectotherms and endotherms, and p. 275 had a quote that I really liked: "Anaerobiosis in vertebrates is simply aerobiosis on the instalment plan." Unfortunately there is little discussion about extinct vertebrates in this chapter, apart from a consideration of pterosaurs (reasonably up-to-date) in comparison with birds and bats. There is little about the evolution of flight in birds—indeed there is rather more about the subsequent evolution of flightlessness, and the discussions of aquatic locomotion don't consider the evolution of secondarily marine tetrapods.

The chapter on diet and nutrition discusses gut morphology in all vertebrates, and the importance of food comminution in mammals (although McNab is unfortunately under the impression that sheep and pronghorn have ever-growing cheek teeth). A good portion of this chapter is spent in consideration of the special problems of herbivory, and he discusses a variety of interesting living animals such as turtles and pandas. He also covers such topics as the problem of herbivory at small body sizes, the correlation of social behaviour with nutritional ecology, and the different types of fermentation systems in various vertebrates (including interesting items such as the Hoatzin being the only foregut-fermenting bird).

McNab does consider more palaeobiological issues in this chapter in a section on the evolution of foregut versus hindgut fermentation. While it was nice to see my own work (Janis, 1976) well-cited, I wish that he'd incorporated later work by myself and others placing this evolutionary story more firmly in the context of changing Cenozoic environmental conditions (rather than some simple notion of competition). He includes a very brief discussion of the possibility of fermentation in dinosaurs, and it would have been nice if this had been elaborated upon a bit more.

The final section, *Consequences*, attempts to integrate the physiological ecology of individual organisms with the consequences for populations and their distribution in space and time. McNab takes a firmly anti-reductionist approach to ecology and biology in general, with an emphasis on emergent properties that appear at higher levels of organisation.

Chapter 13, *The Significance of Energetics for the Population Ecology of Vertebrates*, mainly examines the correlation between reproductive and growth rates with metabolic rates. Two very interesting ideas are promoted in this chapter. The first attempts to explain why it may be the case that some types of eutherians have apparently outcompeted marsupials (*e.g.*, carnivores in both Australia and South America), but other types of marsupials can live happily in conjunction with eutherians (*e.g.*, opossums in South America). Metabolic rate and diet are not coupled with reproductive rate in marsupials, whereas they are in some eutherians, namely those with certain diets (principally terrestrial carnivores and omnivores). Thus those types of eutherians can reproduce faster than their marsupial counterparts, and thus replace them over evolutionary time.

The second idea extends this notion of the coupling of reproductive rate with metabolic rate, and poses the hypothesis that high metabolic rates in general (*i.e.*, endothermy) may have been selected for precisely because of this very correlation. (See also the recent paper by Colleen Farmer (Farmer, 2000) where she also proposes a link between the evolution of endothermy and aspects of reproduction.)

In this chapter McNab takes another sideswipe at evolutionary biologists who regard that "phylogeny has priority over all other explanations" (p. 440). He comments: "At present, the tendency to 'blame' everything on ancestry is a statement that it is easier to classify an organism than it is to define its behavioural and ecological characters." And (I especially like this one): "If ancestry is so important in determining the quantitative characteristics of organisms, why should body mass retain its impact independent of phylogeny?" Way to go Brian—Blam, Kapow!

The final chapter, *Physiological Limits to the Geographic Distribution of Vertebrates*, examines various limitations (temperature, water and salt balance, gas exchange and food availability), and traces through various different extant vertebrate examples, how these might affect their distribution. McNab usually shows how distribution is limited by both physiological tolerance and historical biogeographical contingencies. For example, sea snakes are found only in tropical waters because of temperature tolerance, and are presumably absent from the Atlantic because of their origin in Southeast Asia, and their eastwards migration occurring after the closure of the Isthmus of Panama.

In a final summary, McNab considers how these distributions may be affected by climate change. He mainly considers the case of present-day problems, such as disappearing montane amphibians and the decline in the population of foraging seabirds off the California coast (the latter being fairly easily explicable by the decline in zooplankton related to the rise in sea surface temperatures). He briefly mentions the climatic changes at the end of the Pleistocene, and the change in the distribution of various extant taxa, but unfortunately does not take the opportunity to look at more profound changes in the history of vertebrates. For example, I wish that he'd even mentioned something unknown to most neontologists, that in the middle Eocene there were tropical-like forest habitats in the higher latitudes (although at least this topic was featured in *Walking with Beasts!*).

Interestingly enough his best example that relates to palaeobiology comes earlier in the chapter, under the subheading of osmotic limits. Here McNab notes that the sewellel or mountain beaver, the sole surviving member of the primitive rodent family Aplodontidae, is limited today to the northwest of America because of its need for high amounts of water intake. This is due to its kidney structure and its inability (unlike most rodents) to produce highly concentrated urine. However, aplodontids were common over much of the US in the Miocene and Pliocene, perhaps indicative of moister conditions.

In summary, as a palaeontologist with an interest in physiology, I found this book to be a terrific resource, both for a digest of information on living vertebrates, and as a source of literature references. Where McNab does less well, although it is by no means a worthless attempt, is where he ventures into discussion of physiological processes in a palaeobiological context. In some ways it's terrific that he even considers this to be a worthwhile enterprise, but it's disappointing that he's usually out of date in his examples, and misses opportunities for further (and relevant) discussions. Thus this book will be less useful for palaeontologists in this regard, and unfortunately rather misleading for neontologists if they consider these inclusions as a synthesis of present-day palaeobiology. What we really need is a book where someone pulls together the work done in recent years specifically on physiological aspects of vertebrate evolution, such as that by workers like Ruben, Farmer and Carrier. Perhaps after the laundry …

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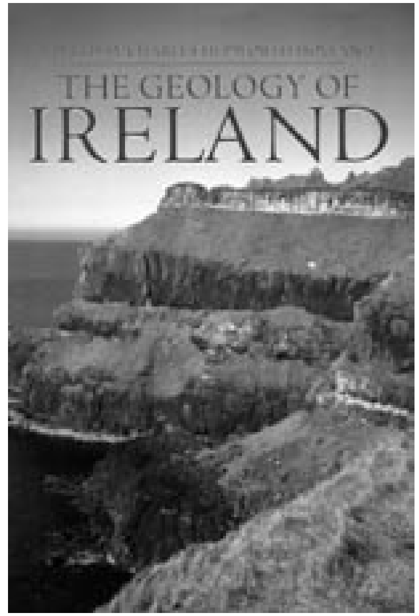
The Geology of Ireland

Charles H. Holland, ed., 2001. Dunedin Academic Press, 531 pp.
ISBN 1 903765 07 2 (paperback). £65.



Every country needs a book that provides a primary source for the description of the geology of its landmass. Such books provide the first portal to an understanding of the geology of a country. This type of book is a particularly important reference for those earth scientists who have only a slight knowledge of the area or who are completely unfamiliar with it. These books are also important for students and for those who have chosen geology as a leisure pursuit.

As someone who was once familiar with the geology of Ireland—at least as familiar as an undergraduate student gets—this book provides me with fresh insight to the advances made since the last time I needed to know the details, more than thirty years ago.

This book is reported to be a substantial revision of a book published by Scottish Academic Press in 1981 entitled *A Geology of Ireland*. After retrieving a copy of this earlier book from the library, I compared the two. The new book is larger both in format and content and is much more comprehensive. Virtually all the chapters are completely revised and some chapters from the old volume have been discarded and new ones generated, most notably the chapter on the offshore. Many of the authors of chapters are new and the content is completely different. The only chapter that is largely the same is that on the history of Irish geology by Gordon Herries Davies, but it remains a fascinating read and is now endowed (like the rest of the new book) with a more extensive list of references. In short, the new book is a major rewrite that bears only a passing resemblance to the earlier version, and it is therefore well worth buying.

The book's cover is a full colour illustration of Tertiary basalts along the coast of County Antrim. Unfortunately, there is no colour inside the book and this detracts from some of the illustrations, particularly the generalized geological map. Printing in colour still costs a lot of money, so the lack of colour contributes to the relatively reasonable price of £65. However, for a colonial with a value-challenged currency, the price is still very substantial.

The book opens with a brief introduction by the editor that provides some of the philosophy behind the book and points to other key references for understanding the geology of Ireland. Following the introduction, the book is arranged, as any geological story should be, in chapters that deal with successive periods of time. It starts with a chapter on the Precambrian, written by J.S. Daly, that describes how the Precambrian rocks have all been affected by that defining episode in Irish geological history, the Caledonian cycle of orogenic events. This chapter is a very fresh view and reflects a lot of recent advances; nearly 50% of the references cited were published in the last decade.

Ordovician orogenic events in northwest Ireland are highlighted in a separate chapter on the Grampian orogeny by W.E.A. Phillips. This is followed by separate chapters on the Cambrian, Ordovician and Silurian. The Cambrian chapter (by Holland) deals with the Cambrian of Leinster and highlights the difficulties inherent in recognizing and correlating Cambrian rocks in Ireland. It deals at some length with the Bray Group, from which the famous Cambrian fossil *Oldhamia* was described for the first time. A chapter by J.R. Graham deals with the Ordovician period, the rocks of which are much more extensively exposed than those of the Cambrian. This chapter highlights the recent advances in the understanding of Ordovician strata that have been made possible by the combination of palaeontological and structural studies. In Ireland, the rocks of the Silurian System have been extensively studied by Holland and his students, and the state of knowledge of Silurian rocks in Ireland has been vastly improved in the course of this work. The chapter (by Holland) provides a concise yet well detailed account of the broadly known Llandovery and Wenlock rocks of Ireland and includes illustrations of some of the fossils recovered. The upper part of the Silurian is not well represented in Ireland. A chapter each on Caledonian Igneous activity (by C.J. Stillman) and Caledonian deformation (by Philips) round out the treatment of the Early Paleozoic.

The Devonian in Ireland is dominated by deposits of the Old Red Sandstone that were shed from a large landmass. The distribution and nature of these rocks, and the modest amount of marine strata that were deposited during the Devonian, are ably described by J.R. Graham. The photographs are a highlight of this chapter, illustrating wonderful exposures of coarse clastic rocks and sedimentary features.

The Carboniferous Period, one of the areally dominant features of Irish geology, is treated in two chapters: the first on the Dinantian (by G.D. Sevastopulo and P.N. Wyse Jackson) and the second on the Silesian by Sevastopulo alone. These chapters provide a lot of detail through the portrayal of correlated measured sections from many regions of the country. Given that Carboniferous strata have been of great economic importance to Ireland, it is surprising that there is not more attention paid to the setting and economic contribution of mineral deposits hosted in Carboniferous rocks. A short chapter on Variscan structures (by Graham) completes the Carboniferous part of the story.

The areally restricted Permian and Mesozoic rocks of northeastern Ireland are the subject of a chapter by H.E. Wilson *et al*. I wish I had had this book when I was approached recently by a colleague in Calgary's oil patch about the Permo-Triassic rocks of Ireland. He assumed that someone who had grown up in Ireland should know, but I am afraid I had to plumb the depths of my ignorance, with the aid of only a highly dated book on stratigraphy of the British Isles. This chapter would have helped me, and consequently my colleague who was interested in a petroleum exploration proposal. This is exactly the value of this kind of book: a first reference for general information connected to more detailed references.

The Giant's Causeway is a World Heritage Site situated in northern Ireland that provides spectacular exposures of Tertiary basalts that cover a considerable area in northeastern Ireland. A chapter on Tertiary igneous activity (by J. Preston) describes the development of this large area and also the subsurface sills and dykes of Tertiary age.

A chapter entitled 'Geophysical Evidence' (by T. Murphy and A.W.B. Jacob) contains information on Ireland's history of earthquakes, especially the many recent events recorded by a seismic network established in 1978. It also provides information on the deep crustal structure of Ireland, mainly the results of the Celtic Onshore Offshore Lithospheric Experiment (COOLE), as well as interpretation of a Bouguer anomaly map.

The Tertiary and Quaternary history is dealt with in two chapters. The first deals with everything until 10,000 years before present (by P. Coxon), providing a brief assessment of the Tertiary landscape and vegetation, followed by significant details on Quaternary stratigraphy, biostratigraphy and palaeoenvironments. Highlights are some spectacular full-page photographs of Quaternary deposits. The second, shorter chapter (by R.H.W. Bradshaw) is on the Littletonian Warm Stage, dealing with the developing vegetation of the period, the history of the widespread peat deposits of this age and the effect of human development.

Perhaps the most exciting chapter in the book is that on the geology of the offshore by D. Naylor. It is in this area that so much of the recent development of understanding has taken place. The Mesozoic and Tertiary basins of the offshore were not understood at all until the commencement of offshore drilling that began in 1970. The developments in the understanding of stratigraphy, tectonics and palaeogeography of the offshore, that have resulted from increased exploration in the last twenty years, are excellently summarized in the chapter. Also included is brief reference to the history of oil and gas exploration.

The final chapter is the historical treatment of Irish geology by G. Herries Davies that is highly readable and extremely interesting. Missing from this chapter are illustrations of some of the early geological maps of Ireland, especially that of Richard Griffith, but perhaps they are not suitable for illustration in such a small format.

Overall, the book is well produced. One minor irritation is the fact that many figures lack any spatial reference and one is required to know a fair bit about the geography of Ireland in order to locate the illustrated places. This is not ideal, because the typical user of this book (someone from elsewhere) may not have this knowledge. A second small criticism is the general lack of information on the economic geology of Ireland. This is unfortunate because many of the users of this book might be like my colleague in Calgary, interested in investing in exploration in Ireland.

This book is an excellent introduction to the geology of Ireland. The chapters generally provide excellent summaries and a full suite of references gives the reader an excellent entry point into the details of Irish geology. In his introduction to the book, Charles Holland is at pains to point out that the book describes the geology of the whole island of Ireland, not just one or other of the political parts. He notes in his first sentence that "the geological sciences know no national frontiers" and it is refreshing to see how much more is now known about the geology of Ireland and how changed is the political climate in the country compared to thirty years ago.

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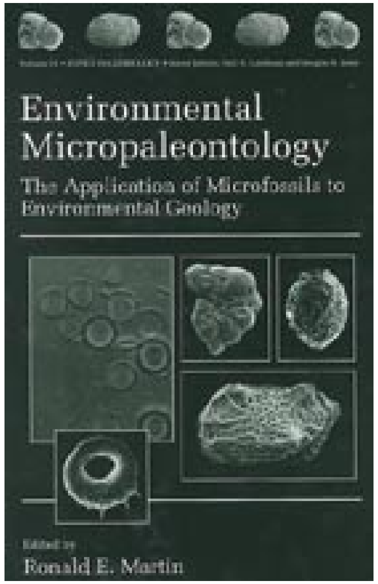
Environmental Micropaleontology

Martin, R.E. 2000. 500 pp. Kluwer Academic / Plenum Publishers.
ISBN: 030646232X. £90.



This book comprises nineteen chapters which together illustrate the changing role of micropalaeontology within the earth sciences over recent years. Many micropalaeontologists will have noticed the shift in research funding from hydrocarbon exploration and the understanding of Earth's geological history to investigations of 'recent' climate change, pollution and associated anthropogenic impacts. As such, this volume points the way forward for many (but not all) within our discipline. It is interesting to note that despite the focus on modern processes in this work the results of many of these studies may have implications for our understanding and interpretation of the fossil record.

The book is divided into five sections: *Baseline Studies of Foraminifera; Water Quality in Modern Marine, Marginal Marine and Freshwater ecosystems; Physiological Responses of Foraminifera to Pollution; Disturbance and Recovery Through Time;* and *Aquifers and Engineering*. These comprise a good mix of general papers and specific examples. The first paper (by John Murray), although using foraminifera as an example, provides an illuminating introduction to environmental change and the response of biological organisms to both physical and chemical variability.

The nineteen chapters vary in their scientific approach, geographical and environmental context and in the microfossil groups chosen for study. In this respect the book does not provide a balanced picture. The choice of subject matter is probably a reflection of the papers offered rather than the true scale and breadth of environmental micropalaeontology being undertaken today. This does not detract from the quality of the papers presented. The book is strongly focused on marine systems, and predominantly foraminiferal projects. Most studies are in some way related to anthropogenic impacts. Fifteen chapters are based on studies of marine and marginal marine ecosystems (twelve on the applications of foraminifera) while only four concentrate on non-marine environments. There is a wide range of research currently addressing the acidification and eutrophication of non-marine waters (especially through the use of diatoms and testate amoebae) which are only briefly covered here. In addition to the fifteen foraminiferal chapters, ostracods (three papers), thecamoebians (one paper), chrysophytes & diatoms (one paper), dinoflagellates (one paper) and pollen (one paper) are also dealt with. Geographically, the book mainly takes its examples from Europe and North America, with additional chapters covering work in the Pacific and the Middle East.

This book provides an important step between the geological and environmental sciences. However, it is not an all-encompassing review of current environmental micropalaeontology, but it does gives an indication of the direction in which the discipline is moving. As such it is an important resource. At £90 the book is very over-priced for a series of case studies and I imagine will only find its way on to a few private shelves. At such a high cost one would have also expected a higher quality of paper and image reproduction. Many of the grey-scale images are low contrast with the result that monotone areas often range from light to dark. Image resolution is also quite poor on some SEM and line drawings, detracting from the feel of the book. A useful index is provided at the end.

With subject matter ranging from the Chemical Ecology of Foraminifera to the Construction of the Thames Barrier and a range of pollution impact studies, the book should at least be browsed by those seeking an introduction to the use of microfossils in monitoring recent environmental change.

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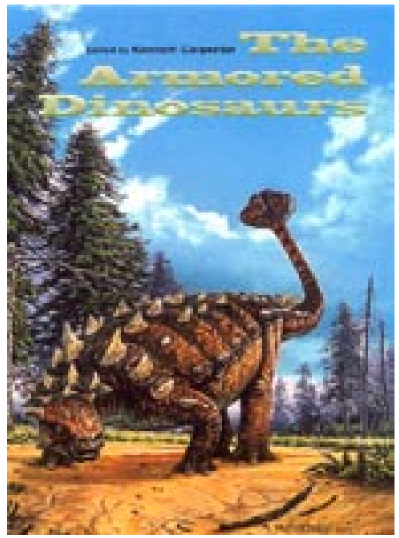
The Armored Dinosaurs

Kenneth Carpenter (ed.). 2001. 526 pp. Indiana University Press.
ISBN 0-253-33964-2 (hbk). $75/£49.95.

Indiana University Press has done it again with yet another impressive multi-authored academic volume, this time dedicated entirely to the thyreophorans (or thyreophores): the ankylosaurs, stegosaurs and their closest relatives. As such *The Armored* [sic] *Dinosaurs* is the first book ever to be devoted to this group alone, and its 21 chapters and 526 pages mean that more information on the armoured dinosaurs is gathered together in one publication than ever before. Needless to say, for those who have a special interest in this group it will be essential reading. Part of the book's wider appeal however might be the interesting questions posed about thyreophoran palaeobiology and evolution, and some of the approaches chosen to tackle these. Misconceptions that the Thyreophora encompassed little diversity or morphological innovation, that there are no new taxa to find, or that thyreophoran feeding styles were unsophisticated, are effectively refuted.



Included papers fall into the following major subject areas: the history of thyreophoran science (both European and American), functional morphology, documentation of morphology, thyreophoran systematics and phylogeny, and ankylosaur ichnology. The amount of new morphological information included in the book is impressive, with significant new descriptions of the brain of *Stegosaurus*, the skull of *Hylaeosaurus*, the armour of *Polacanthus* and kin and the first good description of the new *Shamosaurus*-like American ankylosaur *Cedarpelta*. The mysterious Australian ankylosaur *Minmi* is also subjected to a more thorough description than has been possible before though, unfortunately, the photographs of *Minmi*'s armour have reproduced poorly. In some of these the scale bar is missing or only just visible while in others it is present but not explained in the figure caption. Among other papers that caught my imagination are McWhinney *et al.*'s long-awaited contribution on stegosaur palaeopathology, Blows' new identification for some hitherto overlooked Wealden succession fossil, and Carpenter and Galton's review of Othniel Marsh's stegosaur finds.

One key taxon that could not be ignored in a volume like this, *Scelidosaurus*, forms the subject of a historical analysis by David Norman and a paper on tooth wear and jaw action by Paul Barrett. Norman's paper is admittedly somewhat familiar in view of one other of his recent papers (Norman 2000). It appears coincidental that new published work on *Scelidosaurus* is appearing at the same time as its phylogenetic position is becoming increasingly controversial. Several workers are now suggesting or arguing that *Scelidosaurus* is not a basal thyreophoran as proposed by Sereno (1986) but is instead more closely related to ankylosaurs than to other thyreophorans. In *The Armored Dinosaurs*, Carpenter states this view strongly in his chapter on ankylosaur phylogeny. However, though arguing that "*Scelidosaurus* has apomorphies that have traditionally been considered diagnostic of the Ankylosauria" (p. 463), he does not take the logical option of classifying *Scelidosaurus* as the most basal ankylosaur, proposing instead a new taxon (Ankylosauromorpha) for *Scelidosaurus* + Ankylosauria.

While Carpenter's chapter on ankylosaur phylogeny appears at first sight to be a much-needed review, closer inspection reveals that it is unsatisfactory in some aspects. In particular, Carpenter proposes phylogenetic definitions for a Polacanthidae anchored on *Gastonia* (rather than *Polacanthus*), an Ankylosauridae anchored on *Euoplocephalus* (rather than on *Ankylosaurus*) and a Nodosauridae anchored on *Edmontonia* (rather than on *Nodosaurus*). These decisions mean that, to those who adopt Carpenter's nomenclature, future phylogenetic studies could produce an Ankylosauridae that does not include *Ankylosaurus*, a Nodosauridae that does not include *Nodosaurus*, and a Polacanthidae that does not include *Polacanthus!* This situation is reminiscent of Sereno's (1998) unfortunate choice of *Coelophysis* (rather than *Ceratosaurus*) as the anchor for the theropod group Ceratosauria.

A not uncommon lamentation of those who work on ankylosaurs seems to be that armour is not described more thoroughly in historical monographs. Accordingly, it is fitting that several papers in *The Armored Dinosaurs* are devoted to armour, its morphological variability and its ontogenetic development. William Blows' new terminology for ankylosaur armour introduces a plethora of new terms for structures that have previously not been properly differentiated from others. While some of the new terms Blows has created, like caputegulum (for the small bones that cover ankylosaur skulls) and coronux (for the projecting posterior skull horns), are distinctive and might prove useful, his proposal to formalise terms like boss, plate, scute and spine seem more difficult because such terms are widely used for many (non-homologous) structures that occur outside of the Ankylosauria. Regardless, it will be interesting to see whether or not other thyreophoran workers adopt these terms in the future.

A little-known controversy in the study of armoured dinosaurs centres around the ontogenetic development of ankylosaur cranial armour: do superficial osteoderms fuse during growth with the skull's surface, or do the skull bones themselves grow an elaborate, rugose external texture? These questions are addressed admirably by Vickaryous, Russell and Currie through a combination of histological, phylogenetic, embryological and other techniques. Indeed, the focusing of several papers in the volume on controversial aspects of thyreophoran palaeobiology highlights the fact that arguments in dinosaur science are not exclusive to work on theropods, as those not well acquainted with the study of dinosaurs might think. How thyreophorans processed food orally has proved contentious and two important contributions, the first by Barrett on feeding mechanisms in all thyreophorans (concentrating in detail on *Scelidosaurus*) and the second by Rybczynski and Vickaryous on the jaw mechanics of some ankylosaurids, are included. Barrett's work compliments his previous papers on the feeding mechanisms of sauropodomorphs and other dinosaurs. Molnar and Clifford's description and discussion of a cololite discovered in one specimen of *Minmi* expands the brief description provided previously (Molnar and Clifford 2000) and, in suggesting the presence of substantial oral food processing in *Minmi*, augments the papers mentioned above.

As with the previous IUP dinosaur books, the standard of editing in *The Armored Dinosaurs* is high. While the volume is not cheap, I would say that you get your money's worth. The lack of a colour plate section is perhaps symptomatic of the fact that dinosaur artists spend most of their time painting theropods and the cover art is not as attractive as it could have been. While, from an academic point of view, colour paintings are arguably superfluous, they might have helped liven things up for the popular end of the market. The index is impressively thorough.

Despite the few problems alluded to in this review, Ken Carpenter and the team at IUP should be congratulated on producing another must-have volume that will soon be in the libraries of all dinosaur workers and aficionados. With future volumes destined to appear on sauropodomorphs, theropods, ceratopians and ornithopods, things are looking good.

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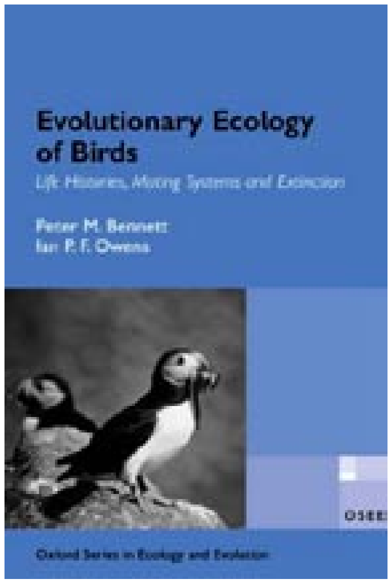
Evolutionary Ecology of Birds: Life Histories, Mating Systems and Extinctions

Bennett, Peter M. and Owens, Ian P. F. 2002. 278pp. Oxford University Press. ISBN 0-19-851088-8 (hbk) £49.50. ISBN 0-19-851089-6 (pbk) £24.95.

Why do life-histories and mating systems vary so extensively across bird species? This was the key issue that David Lack (1968) attempted to test in his book *Ecological Adaptations for Breeding in Birds*. Lack laid the foundation for much future work in avian ecology and despite many subsequent advances, there has been no comprehensive publication to bring the full range of issues of avian life-history up to date. J. David Ligon's (1999) tome *The Evolution of Avian Breeding Systems* covers much ground but is less quantitative than the current volume, and does not include, for example, consideration of extinction and speciation. *Evolutionary Ecology of Birds*, the latest addition to the Oxford Series in Ecology and Evolution, seeks to bridge the gap.

The central question of *Evolutionary Ecology of Birds* is identical to that addressed by Lack, but it is by no means merely a literature review of the work carried out in the intervening years. Peter Bennett and Ian Owens have produced a huge body of work that makes full use of modern phylogenetic comparative methods. Where Lack was reliant on observational and experimental methods, Bennett and Owens have the advantage of important methodological and theoretical developments to guide their investigations.

The most significant difference between these two books is the use of phylogenetic comparative methods. To put it simply, traditional comparative methods make direct cross species comparisons of the trait (or traits) in question. However, using species as data points is flawed because sister taxa have a shared phylogenetic history and are not strictly independent. This often leads to spurious correlations. Broadly speaking, phylogenetic comparative methods seek to account for shared ancestry. The most commonly used approach is 'independent contrasts' which compares the *differences* between sister taxa rather than the taxa themselves. Peter Bennett and Ian Owens present arguably the most extensive application of phylogenetic comparative methods yet in a single volume. Chapter 2, *Comparative methods*, is devoted to an introductory discussion of the principles, benefits, and limitations of the comparative approach. This forms the bulk of the first section of the book, *Comparative biology of birds*. As the authors acknowledge, accounts of phylogenetic comparative methods that are more complete are currently available; this is a book very much about the application of contemporary techniques to long-standing questions.



The book comprises 14 chapters which are split into five broad sections. Section 2, *Natural selection and diversity in life-history*, tests competing hypotheses on how natural selection has influenced life-history variation. It features detailed chapters on diversity (basic avian life-cycle, life-history diversity), patterns of co-variation between life-history traits, and the ecological basis of life-history diversity. This section is used first to establish a set of relationships among life-history traits. For example, measures of size, development, and survival are shown to be positively correlated, whereas a negative correlation between survival and fecundity is demonstrated. These relationships are then used to decouple the impact of allometry (the scaling of characters to body size) from the ecological basis of life-history diversity.

Section 3, *Sexual selection and diversity in mating systems*, covers a large spectrum of contemporary issues. It includes excellent chapters on variation in mating systems and sexual dimorphism, the ecological basis of mating system diversity, and the ecological basis of sexual dimorphism. Advances in these fields have been substantial in recent years, and it is not surprising that this is perhaps the most detailed and comprehensive section of the book. Ecological correlates are shown to be only small factors in determining mating systems, with entire lineages apparently predisposed to a particular mating system through their ancient phylogenetic history. Chapter 9, *Ecological basis of sexual dimorphism*, confirms that sexual size dimorphism is linked to social mating system and parental care.

In comparison, section 4, *Birth and death of bird species*, is rather brief. It deals with issues surrounding variation in extinction risk and species richness. The focus is primarily on conservation, but some discussion of extinction as told by the fossil and sub-fossil record is also included. Expected background extinction rates are compared to observed rates across different avian lineages, and results indicate that some lineages are predisposed to being more prone to extinction than others. A fifth section, *Conclusions*, provides a brief précis of the main themes and results.

I have only touched on a few of the major conclusions of Bennett and Owens. *Evolutionary Ecology of Birds* answers a multitude of questions but also raises many more. The chapters of further problems that conclude each of sections 2, 3 and 4 serve to highlight the array of avenues through which future research may pass. The fact that these paths are not explored in full should not be considered a limitation of this volume—rather they illustrate the multifarious potential of the comparative method and evolutionary studies in general. A further particularly useful feature of the book is inclusion of four data appendices. These provide the opportunity to reappraise much of the work as well as giving considerable scope for new analyses.

Overall, *Evolutionary Ecology of Birds* is an excellent book. Its presentation is functional rather than glossy (a feature of much of the Oxford Series in Ecology and Evolution). Nevertheless, it will have a broad appeal to those with an interest in avian evolution or comparative methods from final undergraduates upwards. Whilst fossils are not generally dealt with directly, this book may be of considerable value to many palaeontologists—phylogenetic comparative methods have even been referred to as "statistical palaeontology" (Pagel, 1998). Although only time will tell if this volume has the same impact as David Lack's seminal treatise, it certainly has the potential to act as a springboard for many exciting new studies in avian ecology and evolution.

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Rise of the Dragon: readings from *Nature* on the Chinese fossil record

Henry Gee (ed.) 2001. The University of Chicago Press, xiv+262 pp.
ISBN 0-226-28491-3 (pbk). £21.

The Chinese people have long held a pride in their heritage, extending beyond history and into palaeontology. In the early part of the 20th century Peking Man formed the focus of national esteem, but by the last few years of the century it was rather older fossils that came to hold centre stage. And the acclaim that these ancient finds have received is most definitely justified; recent palaeontological discoveries in China have been nothing short of remarkable. The papers and commentaries brought together here were originally published in *Nature* in 1997-2000, and the resulting volume fittingly captures the importance of this episode of discovery. The title of the compendium, *Rise of the Dragon*, of course alludes to the increasing significance of China's role in the advancement of palaeobiological science.

The collection includes original papers on the revelations that have already become legendary in the palaeontological community: the Neoproterozoic embryos of the Duoshantou phosphorites, the early vertebrates and putative chordates of the Chengjiang biota and, in particular, the 'feathered dinosaurs', birds and primitive mammals of the Jehol fauna. That so many of these finds were published in *Nature* is testimony to two things (at least). First, the enthusiasm and energy of Henry Gee, senior editor of *Nature* and aficionado of vertebrate palaeontology, who has encouraged authors to submit their papers to him for consideration and who solicited the valuable 'News and Views' commentaries that accompanied them and are reproduced here. Second, there is the Chinese system in which it is worth much more than a strand of filamentous integument in your cap to get a paper published in *Nature*—there are commonly financial as well as status rewards for those who succeed.

The strength of this compendium lies in its archival nature as a documentation of a dramatic period in Chinese palaeontology. There is no doubt that the excitement of the last few years is reflected here, and the papers record the basis for the continuing period of development that is sure to come in the next few. As noted by Luo Zhe-xi in his foreword to the volume, the timing of all the discoveries has fitted with remarkable coincidence into peaks of international scientific interest in questions of early metazoan phylogeny, the origin of vertebrates, the early evolution of mammals and angiosperms, and the relationships between dinosaurs and birds. So, it is certainly worthwhile to have these papers gathered together in a single set, especially as all the supplementary information in the form of character lists and analyses is also provided in a series of appendices. The weakness, though, lies in the selectivity. The restriction of the collection to papers that appeared in *Nature* means that the coverage is not comprehensive—although many of the key contributions were published in that illustrious magazine, not all were. An example would be the coverage of the early angiosperms of the Jehol biota, which may not be as dramatically important as first thought given the Barremian (rather than late Jurassic) age now assigned to the deposit, but still deserve more comment than they receive here.

So, given this constraint, where is the market for this volume? There is nothing new here, and most of us will already have acquired reprints or photocopies of many of these articles and probably have ready access to back copies of *Nature* if we need more. Moreover, the mode of production of the book means that the photographic figures are less clear than in the originals and it is often difficult to make out the stunning features of the fossils referred to in the text. With all this in mind, I tried a piece of very lazy and very limited market research to try to ascertain who might buy the book: I asked the opinions of three people, a retired geologist with a passion for palaeontology, a Chinese palaeontologist, and a UK university lecturer who teaches a module in vertebrate palaeontology.

I admit to being a little surprised by the results. My retired friend was positive; he might well buy the book, and would certainly have parted with his cash if it contained a brief, fully contextual overview of each of the main themes. My Chinese friend was also positive; he felt that the book would go down well in China, especially if there were a Chinese edition at a non-Western price. The only negative reaction came from the lecturer, who would not recommend students to buy it, although he refers them to many of the papers. But, overall, it looks as though a market does exist, so I can only wish the book every success. The way things are going in Chinese palaeontology, I guess we will be looking forward to the release of volume two in the very near future.

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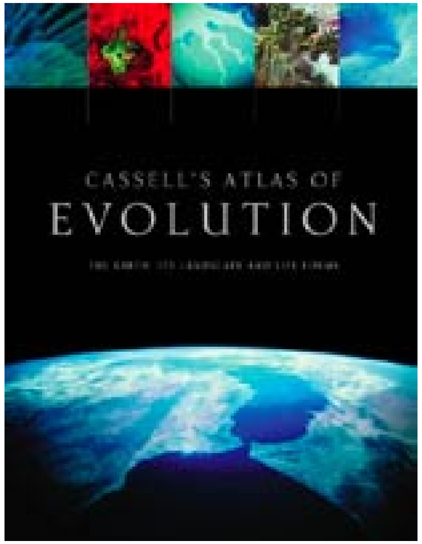
Cassell's Atlas of Evolution: The Earth, its landscape and life forms

Dixon, Dougal, Jenkins, Ian, Moody, Richard & Zhuravlev, Andrey. 2001.
368 pp. Cassell, London. ISBN 0-304-35511-9. £30.

At first glimpse this Atlas belongs to the category rather dismissively referred to as "coffee table" books, *i.e.* large format, with every page containing a large colour illustration, often of spectacular creatures that have formerly inhabited our planet. Though admittedly aimed at the general reader, with technical detail eschewed, such an assignation would be both unfair and unkind, because both the substantial text and illustrations are of high quality.

The *Atlas* is divided into six parts, corresponding to divisions of time. Part I, by Richard Moody, entitled *In the Beginning*, starts with a brief treatment of the Earth as a planet, followed by an equally short account of the origin and nature of Life, before dealing at greater length with the Earth's long Precambrian history. Part 2, by Andrey Zhuravlev, deals in more detail with the Early Palaeozoic, while Parts 3 and 4, by Dougal Dixon, are concerned successively with the Late Palaeozoic and Mesozoic; Parts 5 and 6, by Ian Jenkins, consider the Tertiary and Quaternary.



A wide range of topics is dealt with, from plate-tectonic models and continental reconstructions through time, to mass extinctions, the greenhouse effect and the deleterious influence of human beings on our environment. The treatment is up-to-date and is unlikely to mislead in important matters. Inevitably I found some points to cavil at on particular subjects about which I have some specialist knowledge. Thus the benthic environment of the Upper Jurassic Solnhofen Limestone was more probably inimical to life because of anoxia rather than, as Dixon states, because of high concentrations of lime and salt. The rise of sea level in the Jurassic is speculatively attributed to melting of polar ice, but there is no evidence whatever of ice in the Triassic.

A useful glossary follows the main text, after which there is a small quantity of recommended further reading, which could have been expanded and improved with only a small amount of effort. My main criticism, however, is the title, with the word Evolution printed in very large font, thereby giving a very misleading impression of the contents. This is a book dealing with Earth history and its biosphere. There is a modern cladistic treatment of major organic groups but no mention, let alone discussion, of evolutionary principles. "Cassell's Atlas of Earth History" would have been more accurate, and as such it can be recommended not just to the general reader but even to undergraduates not pursuing either palaeontology or stratigraphy as specialist subjects.

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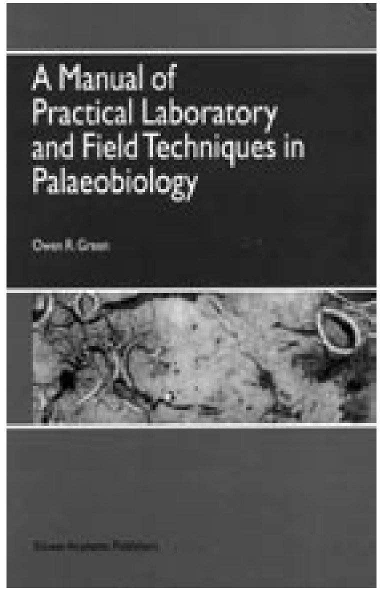
A manual of practical laboratory and field techniques in palaeobiology

Green, Owen R. Kluwer Academic Publishers. £85

A book of this type should prove of great value to all practical palaeobiologists, and fills a large void in the literature necessary for successful field work and for running an efficient and comprehensive fossil extraction and preparation laboratory. True, there are other practical geological manuals, but to the best of my knowledge, the best of them are now out of print and copies are hard to come by. These, it should be recorded, are the classic laboratory 'bibles' *Geological Laboratory Techniques* by Allman and Lawrence (Blandford, 1972) and the American *Handbook of Paleontological Techniques* by Kummel and Raup (Freeman, 1965). Where the Green volume scores of course is the very fact that it is current, and contains all (or, at the very least, most) of the advances in field procedures and fossil preparation techniques since



the two earlier books. It is nicely laid out and extremely comprehensive, whether you collect and extract large dinosaur bones or process for tiny palynomorphs, and while specialist preparators could maybe find a small omission or two in their particular fields (for example, I can nowhere find reference to the di-iodomethane method for the concentration of phosphatic microfossils), overall it is a tremendously impressive feat of data collection, improved by the author's own extensive laboratory experience. I particularly welcome the chapter on laboratory safety, and the frequent reminders about the safe use of dangerous chemicals which appear at all relevant points in the text. This aspect of laboratory procedure is at last receiving the attention which it so obviously merits. I also liked the easy to follow flow diagrams and step by step explanation of methods in the sections on laboratory procedure; the last thing a laboratory worker wants when learning new aspects of his 'art' is to be hamstrung by oblique methodology and the need to digest vast tracts of text. Numerous useful appendices on everything from describing sedimentary rocks and fossils in the field to the chemical resistance of laboratory gloves (an amusing typo sometimes renders this as 'gloove'), also add to the appeal of this volume.

But always one returns to the sheer magnitude of the data contained within the 538 pages of this excellent book. It is not just a field techniques and palaeobiology laboratory manual, but instead represents a most impressive gathering together of almost everything a successful practical palaeobiologist needs to be effective. At £85 it certainly ain't cheap, but when you consider that a routine order of hydrochloric acid from your local supplier costs about the same, I'd say it was very good value.

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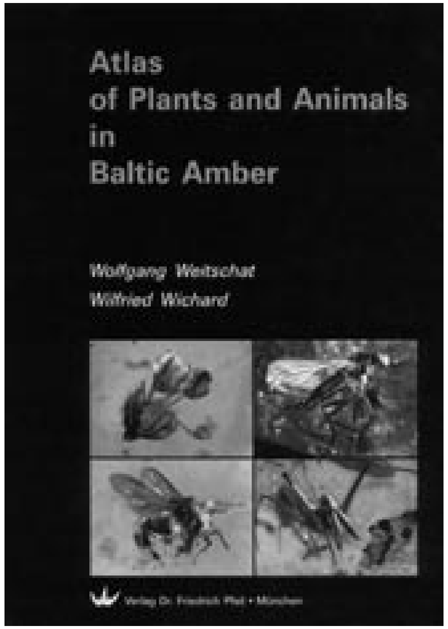
Atlas of plants and animals in Baltic amber

Weitschat, W. & Wichard, W. 2002. 256 pp. Dr Freidrich Pfeil, Munich. ISBN 3-931516-94-6. €75.

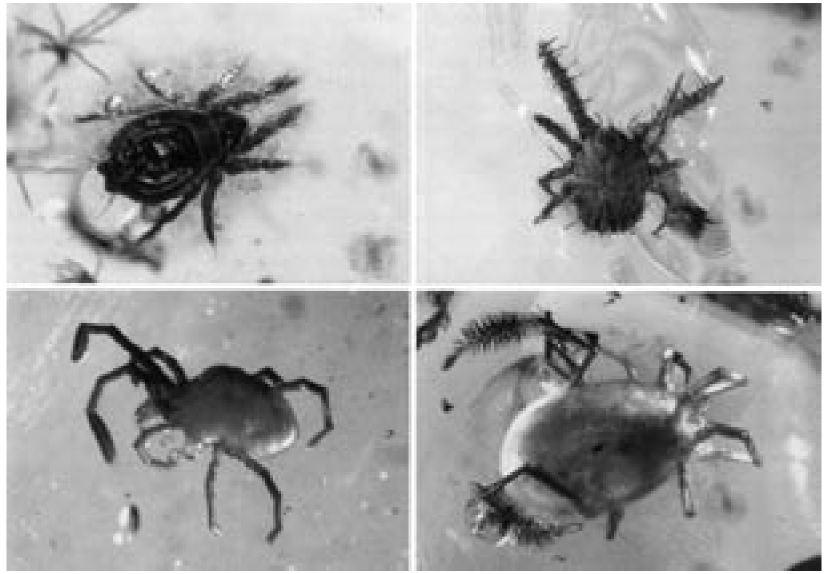
Baltic amber is the classical European amber known since prehistoric times. It also occurs further afield than the Baltic region from the east coast of the UK to the Ukraine. The authors recognise that a number of books on Baltic amber have been published and more are undoubtedly on the way. In fact, this is the English edition (translation) of a title originally published in German.



The book's strength is the breadth of treatment of the amber inclusions. It thus compares with Larsson's *Baltic Amber* (1978). The *Atlas* is, however, a quantum leap forward in the quality of the illustrations, with 92 four-colour photographic plates covering some 650 species. (Larsson's was a strictly two-colour work although I believe line drawings still have their uses.) Groups covered in the *Atlas* include plants ranging from bryophytes to angiosperms (mosses–flowering plants), nematodes (roundworms), annelids (segmented worms), molluscs (snails), reptiles (lizards), birds (feathers), mammals (hair) and arthropods. The latter are most numerous, including scorpions, pseudoscorpions, harvestmen, mites, spiders, crustaceans, myriapods and hexapods (insects *sensu lato*). Insects comprise the bulk of the inclusions, representing 28 orders ranging from springtails to bees.

A useful summary of each group present is given, covering taxonomic, biogeographical and ecological aspects. The main amber tree (whatever it was) clearly grew close to water as the fossil resin has indiscriminately trapped aquatic and terrestrial biota. For example, crustaceans found include ostracods and amphipods as well as woodlice. Even large insects such as dragonflies occasionally got stuck. The amber also provides unique vignettes of everyday life in the fossil record such as spider's webs, brood care, phoresy and nits (in mammalian hair). Exotic forms include the bizarre-looking fishflies (pl. 50).

The *Atlas* is necessarily selective in its inclusion of species. Space apart, there is a backlog of taxa awaiting detailed identification and description. Thus moths and butterflies are not named (pls. 78-9) and descriptions will have to be found elsewhere. Wherever possible, however, a checklist of species is given. It will be interesting to compare this and the family 'overviews' [lists] with new catalogues emanating from the extensive collections of Baltic amber in Poland. This is because the Baltic amber story is still unravelling. The predominant succinite with its distinctive IR spectrum is not the only Tertiary amber found in northern Europe. Does typical Baltic amber, found from the Eocene to the Holocene, represent one biome and epoch? The authors seem to think so. They consider that their Baltic Amber Forest dates from the Ypresian stage of the Lower Eocene (~54 Ma) and stretched from the Atlantic seaboard to the Urals. Marine transgression in the Middle–Upper Eocene flooded the Forest 10 Ma later. All post-Eocene amber occurrences are thought to represent secondary or even tertiary redeposition. I suspect that this view will not pass wholly unchallenged.



The literature on Baltic amber is diverse and extends back to Roman times. The *Atlas* is no history book, however, and the authors have drawn mainly from current, modern sources. Inevitably, the spread is imperfect with such a large biota, for example there is post-Ander work on the now relict cupedid beetles such as Neboiss' (*cf*. p. 152). These are challenges for future, more specialised works. In the meantime, Weitschat & Wichard have produced a lavishly illustrated guide to the exceptionally preserved inclusions turning up daily in Europe's classical amber. They are readily purchased at fossil fairs. This highly attractive, scientific introduction to Baltic amber deserves to be the basis of a travelling exhibition.

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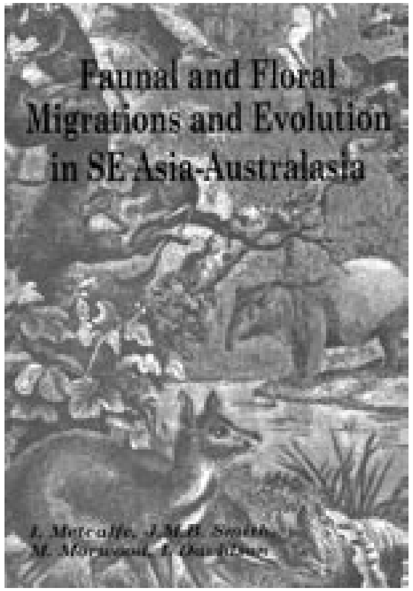
Palaeobiogeography of Australasian faunas and floras

Wright, A.J., Young, G.C., Talent, J.A. & Laurie, J.R. (eds). 2000. Memoir 23 of the Association of Australasian Palaeontologists, ISBN 0-949466-21-2 ISSN 0810-8889 (pbk)



Faunal and Floral Migrations and Evolution in SE Asia-Australasia

Metcalfe, I., Smith, J.M.B., Morwood, M. & Davidson, I. (eds). 2001.
Swets & Zeitlinger.
ISBN 90-5809-349-2 (hbk)

Like London buses, you wait ages for a volume on Australasian palaeobiogeography and then two come along at virtually the same time. However, there are distinct differences in scope and themes to these two volumes for them both to merit consideration for your own or institute's bookshelf.

Both volumes have arisen from conferences held in the past five years, the Metcalfe *et al.* (eds) from the "Where Worlds Collide: Faunal and floral migrations and evolution in SE Asia-Australasia" meeting held in New South Wales in late 1999, while the AAP tome emerges from the "Palaeobiogeography of Australasian Faunas and Floras" conference, Wollongong late 1997.

The AAP volume exists as a comprehensive data review arranged in stratigraphical order with each chapter discussing major taxonomic groups in turn, with a synthesis at the end of each epoch. Extensively referenced and with a list of authors that would make it easier to comment on who wasn't involved, it provides very much a first port of call for information on the temporal and stratigraphic distribution of Australasian fossil groups—certainly my review copy is now well thumbed and marked in the substantial Cambro-Ordovician sections, and it is rarely out of reach as a reference volume. Having said that, it would be unwise just to dismiss it as a source of data as many of the synthesis sections would be worthy of publication as relatively high-profile papers in their own right.

My only quibble with the volume is over the use of palaeogeographic base maps—much of the volume utilises those published by Li & Powell (2001), particularly in the Palaeozoic chapters, but somewhat curiously the base maps flip to Scotese & McKerrow (1990) for the Silurian. Without getting into the merits or demerits of one palaeogeographic reconstruction over another, one has to make the observation that it would have been preferable to follow one set of reconstructions throughout the volume.

Turning to the Metcalfe *et al.* book, it is clear from the outset that this is a very different beast. The emphasis here is very much focused on Wallace's Line, both in a modern biogeographic sense and in the recognition of palaeobiogeographic divisions with reference to the Australasian realm. Abbreviated Palaeogeographic Background and Palaeozoic and Mesozoic sections mean that the timelines covered are inevitably loaded towards the Cenozoic, with substantial discussions of Cenozoic terrestrial floras and vertebrate faunas (with particular emphasis on primates) in subsequent sections.

"Wallace's Line" and its place in modern biogeography is assessed in a section composed of six papers with the ultimate conclusion that Wallacea is still a key area for understanding biogeographic patterns on a number of different scales. Several papers elsewhere in the book should surely have come under this section (for example those of Kitching *et al.* and Keast), and this point is the main problem with the book—the volume as a whole appears to be the basis for three books: a collection on the Palaeozoic and Mesozoic geology and biogeography (much in the line of the AAP volume), an examination of Wallace's Line, and an overview of the modern biogeography of Australasia.

When presented with two volumes such as these, the ultimate role of a reviewer is to recommend purchase or not. The AAP volume must now be an essential reference for those with an interest in Australasian fossil faunas and floras. The Metcalfe *et al.* is a less coherent volume but worthy of consideration, particularly for those with a Cenozoic and Recent biogeographic research bias and an interest in the work of Wallace.

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Late Ordovician and Early Silurian pentamerid brachiopods from Anticosti Island, Québec, Canada

Jisuo, Jin & Copper, Paul 2000. Palaeontographica Canadiana 18. 140 pp., 31 pls. US$62.

The year 2000 was marked in style for brachiopod workers with publication of volumes 2 and 3 of the revised *Treatise*, while the Natural History Museum hosted the 'Millennium Brachiopod Congress', providing a lively forum for over 120 brachiopod researchers. Jin Jisuo and Paul Copper rounded off the year with the publication of another fine monographic work. The pentamerids form an important clade of early to mid Palaeozoic brachiopods. Nevertheless much is still to be understood about the ecology and evolution of the group at both regional and global levels. The late Ordovician and early Silurian pentamerid faunas from the Canadian island of Anticosti are some of the most abundant, diverse and well-preserved assemblages of this spectacular group outside the Ural Mountains. Jin Jisuo and Paul Copper have provided a magnificent, beautifully-illustrated monograph of the group from the Anticosti basin, documenting in detail the taxonomy together with the biostratigraphy and palaeoecology of nearly 30 species.

The core of the study is the systematic description of 27 pentamerid species assigned to 13 genera and simple bivariate plots of shell dimensions, and serial sections supplement subspecies descriptions and remarks. Particularly useful are the synonymies together with lists of species included or excluded from each genus.

Two pages of summary statistics are provided for over half of the species together with an appendix of detailed locality data. Arguably with such a wealth of data from well-preserved specimens much more might be gained from both intra- and inter-specific multivariate analyses.

Bearing in mind the difficulties associated with coating and photographing large specimens, the plates are generally excellent; very few shots are out of focus and a uniformity of brightness and contrast has been maintained across all 31 plates. Multiple external views are supplemented by occasional interiors and details of shell structures in the economically constructed montages.

This body of taxonomic data forms the basis for important and useful sections on the external and internal morphologies of the pentamerids. Here aspects of the shell shape and ornamentation are clarified and the internal structures, critical for the identification of many members of the group, are discussed and illustrated with a series of generalized peel sections. Pentamerid evolution during the early Silurian is explained in terms of four key lineages that lead directly on to the use of the group in the regional and global correlation of lower Silurian strata. A simple chart guides the reader through some of the key pentamerid brachiopod zones on Anticosti. The British chronostratigraphy is preferred to that of the American mid-continent, with the entire Ellis Bay Formation correlated with the Hirnantian. The community ecology of the group through the Anticosti succession is discussed in detail. The wealth of data allows considerable speculation on the ecological distribution of the group. Not all the community developments conform to Ziegler's classic onshore–offshore spectrum of five assemblages from the near-shore *Lingula* community to the off-shore *Clorinda* community. For example *Clorinda* occurs abundantly in shallow-water settings and both the *Pentamerus* and *Stricklandia* communities may have a much greater depth tolerance than previously assumed. This is hardly surprising since the range of Anticosti carbonate facies is quite different from that on the siliciclastic shelf of the Anglo-Welsh area. The monograph is completed by a useful taxonomic index.

This is a work of considerable scholarship and clearly a must for researchers intimately involved in the Lower Palaeozoic and its faunas. Nonetheless the methodology and wide scope of the volume make it an attractive addition to any palaeontologist's library.

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Studies in Palaeozoic palaeontology and biostratigraphy in honour of Charles Hepworth Holland

Special Papers in Palaeontology No. 67. 260 pp. ISBN 0901702773. £66 (£33 to members).

Edited by Patrick N. Wyse Jackson, Matthew A. Parkes and Rachel Wood

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Wyse-Jackson, P. N. and Parkes, M. A. Charles Hepworth Holland - palaeontologist and biostratigrapher.

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Clayton, G., Wicander, R. and Pereira, Z. Palynological evidence concerning the relative positions of Northern Gondwana and Southern Laurussia in latest Devonian and Mississippian times.

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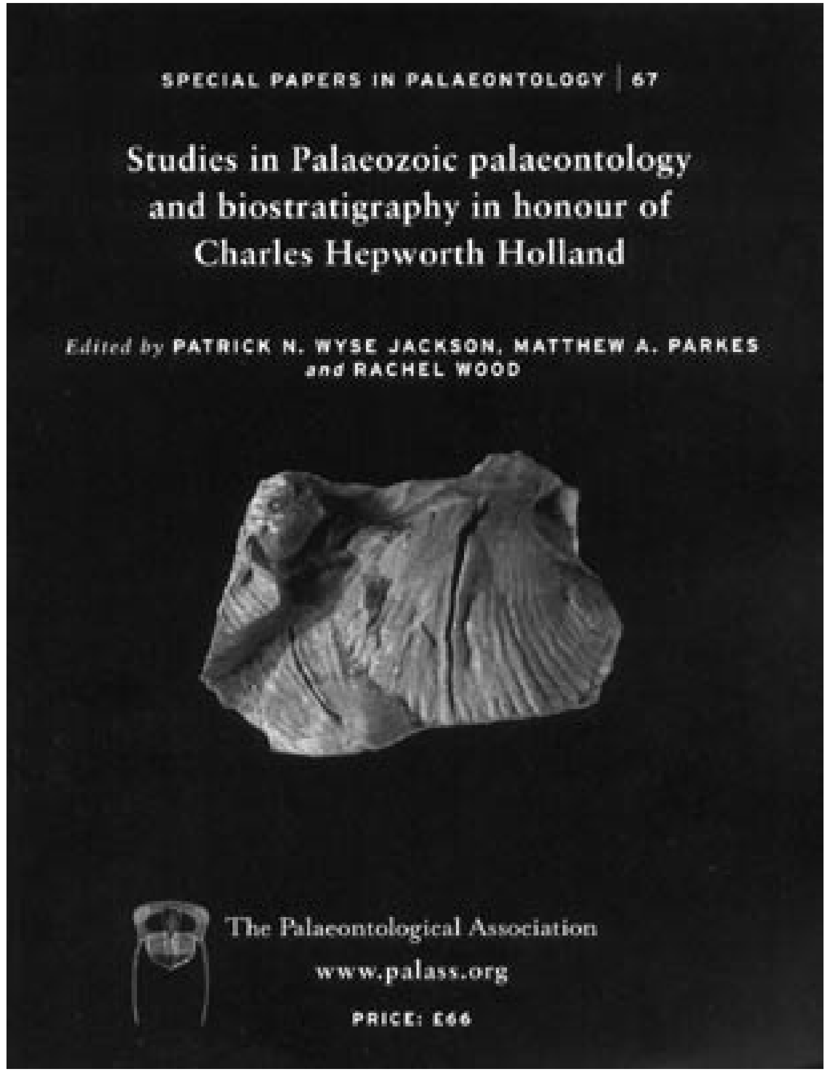

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