The Palaeontology Newsletter

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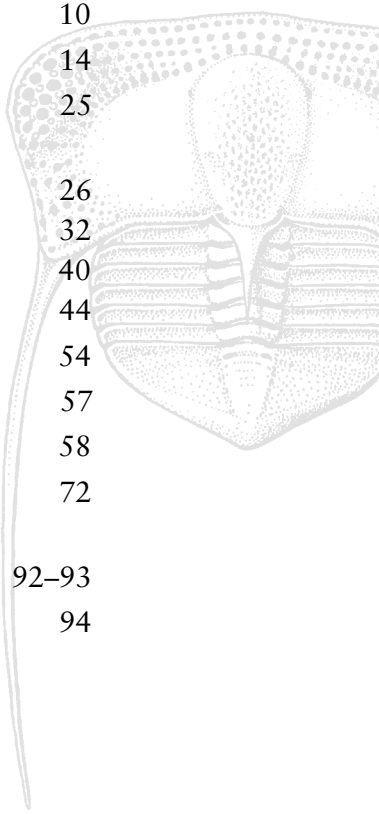


Reminder: The deadline for copy for Issue no 59 is 20th May 2005

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

Association Business

Nominations for Council

At the AGM in December 2005, the following vacancies will occur on Council:

Vice-President
Newsletter Editor
three handling editors
one Ordinary member

Nominations are now invited for these posts. Please note that each candidate must be proposed by at least two members of the Association and that any individual may not propose more than two candidates. Nominations must be accompanied by the candidates' 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 **Monday, 3rd October 2005**. They should be sent to the Secretary: Dr Howard A. Armstrong, Department of Earth Sciences, University of Durham, Durham DH1 3LE, email <**h.a.armstrong@durham.ac.uk**>.

Awards and Prizes

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

Hodson Fund

This award is conferred on a palaeontologist who is under the age of 35 and who has made a notable early contribution to the science. Candidates must be nominated by at least two members of the Association, and the application must be supported by an appropriate academic case. Closing date for nominations is **1st September 2005**. Nominations will be considered and a decision made at the October meeting of Council. The award will comprise a fund of £1,000, presented at the Annual Meeting.

Mary Anning Award

The award is open to all those who are not professionally employed within palaeontology but who have made an outstanding contribution to the subject. Such contributions may range from the compilation of fossil collections, and their care and conservation, to published studies in recognised journals. Nominations should comprise a short statement (up to one page of A4) outlining the candidate's principal achievements. Members putting forward candidates should also be prepared, if requested, to write an illustrated profile in support of their nominee. The deadline for nominations is **1st September 2005**. The award comprises a cash prize plus a framed scroll, and is usually presented at the Annual meeting.

Sylvester-Bradley Award

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

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

Electronic submission of applications, through the website, is preferred and will comprise a CV, an account of research aims and objectives (5,000 characters maximum), and a breakdown of the proposed expenditure. Each application should be accompanied by the names of a personal and a scientific referee. Successful candidates must produce a report for *Palaeontology Newsletter* and are asked to consider the Association's meetings and publications as media for conveying the research results. Deadline 1st November 2005.

Mary Anning Award 2004: Phil Bennett

Phil Bennett's interest in palaeontology began over ten years ago with the collection of graptolites from the Llandovery of mid Wales. He now specialises in fossils from the Old Red Sandstone.

Phil has donated, or made available for display, valuable material of vertebrates, arthropods and vascular plants at several Welsh institutions, including the Ludlow Museum, the Brecon Museum in Powys, and the National Museum in Cardiff.

Since 1999, he has collected an extremely well preserved assemblage from the Early Devonian near Brecon. Much of the vertebrate material is articulated, including the most complete specimen of the heterostracan *Protopteraspis* ever found. He has made this material available to a variety of specialists.

Since 2002 Phil has focused on a particular plant bed. A trigonotarbid arachnid, donated to the National Museum in Cardiff, is the oldest known arachnid from Wales (and the second oldest from anywhere) and is the subject of a paper just published in *Palaeontology* by Jason Dunlop and Paul Selden. Phil has also discovered other arthropods, including an undescribed myriapod, in the bed. Plant material from this locality is under investigation by Diane Edwards.

Phil Bennett has shown enormous dedication in compiling a scientifically important collection of fossil vertebrates, invertebrates and plants from the Silurian and Devonian of Wales and the Welsh Borders, which he has made available for expert investigation at every opportunity, resulting in a number of important publications.

Mary Anning Award 2004: Bjørn Funke

As a schoolboy Bjørn Funke was one of the initiators of a geology club, "Steinklubben," for young children living in the Oslo area. He regularly brought fossils to the University Palaeontology Museum to be identified and encouraged the staff there to help lead field trips for the club sponsored by the Museum, parents and the Esso company. This club is still active more than 40 years later and Bjørn Funke, although no longer leader, is still an active participant and regularly guides excursions.

In 1994 Bjørn set up what soon became known as PalVen (friends of the Palaeontological Museum, with himself as leader), an organization of amateur collectors who meet regularly at the Museum, organize lectures and excursions, exchange and identify fossils, and donate specimens for sale in the Museum shop. Income from these sales has exceeded well over €50,000, which the Museum has used to purchase top quality specimens, mainly for display purposes.

Many fine specimens found by Bjørn are also in the Oslo Museum's type or reference collections.

Bjørn Funke has done much to inspire young Norwegians and show them the rewards of collecting fossils, and has devoted his entire spare time to the service of both amateur and professional palaeontologists.

Hodson Award: Heather Wilson

Heather Wilson's interest in fossil arthropods started as an undergraduate at Mount Holyoke in Massachusetts where she did a senior thesis on the Rhynie Chert. Having taken her BA there, majoring in Biological Sciences, she moved to the University of Cambridge on a Marshall Scholarship to extend her training in Geology and Zoology, taking another BA in 1995!

Heather's PhD work with Paul Selden at the University of Manchester was fundamental in determining the affinities of the extinct arthropleurid myriapods. The giant Carboniferous forms, which reach lengths of up to 2 metres, had not provided definitive evidence of their phylogenetic position. Heather's description (with Bill Shear) of a new order, the tiny Microdecemplicida from Gilboa in the Devonian of New York State, showed that the arthropleurids lie within the Diplopoda, a group of millipedes with living representatives.

On completing her PhD in 1999 Heather moved to the University of Maryland to work with Jeff Shultz on the phylogeny of millipedes, funded by an NSF proposal that she generated herself. Her 2002 *Journal of Morphology* paper on the muscular anatomy of a spirostreptid diplopod is a landmark – a superbly illustrated, meticulous study of all the trunk muscles, requiring highly skilled dissection, comparative anatomy, and phylogenetic analysis. A study of the kinematics of feeding in the giant living millipede *Archispirostreptus* is in press.

Heather came to Yale in the Summer of 2002 to return to her primary focus, research on fossils. Earlier this year she published (in *Journal of Paleontology* with Lyall Anderson) the oldest definitive land dwelling myriapod, a new genus *Pneumodesmus* from the Silurian of Stonehaven, which preserves the earliest evidence of air breathing in any animal of any kind. She has published on myriapods from the Silurian to the Cretaceous, and has recently embarked on a field and laboratory investigation of early terrestrial arthropods, using hydrofluoric acid to dissolve mid-Paleozoic siliciclastics in pursuit of cuticle fragments.

Heather Wilson's contributions to myriapod biology and systematics exploit her remarkable range of technical and intellectual skills: she is one of those rare individuals who is just as comfortable working with living animals as she is with ancient ones; with molecular sequences as she is with morphological data; with trace fossils as she is with body fossils, with function as she is with phylogeny – and with teaching as she is with research.

Lapworth Medal: James W. Valentine

James W. Valentine, Member of the National Academy of Sciences, Paleontological Society medallist, former President of the Paleontological Society, is professor emeritus of integrative biology at the University of California, Berkeley, where he is affiliated with the Museum of Paleontology and the Center for Integrative Genomics. He has spent most of his career at the University of California – taking his PhD at UCLA in 1958, and spending time at Davis (1964–77), Santa Barbara (1977–90), and subsequently Berkeley.

Jim has researched the gamut of the history of life – in terms of both organisms and the time scale. He is a gentle giant: a quiet modest man, generous to his colleagues, contemptuous of rivalries within the discipline, excited by discovery, and a great enthusiast for science and scientists. But don't be taken in by the calm exterior. In the late 1990s Jim was working on some papers at the University of Chicago with Dave Jablonski and Doug Erwin. Their discussions became so animated that a delegation of graduate students appeared to ask them to keep the noise down!

Jim has made so many contributions to the fields of evolution and palaeontology that they are difficult to summarize, but four major areas stand out:

1. Pleistocene molluscs of California

Jim's work on Pleistocene molluscs, published mainly in the 1950s and 1960s, was concerned mainly with environmental controls on distribution. These papers provided a platform for his classic work in biogeography – in establishing the role of climatic gradients, geographic barriers, and organism adaptations in defining the boundaries between marine faunal provinces. Jim also used the Pleistocene faunas to consider preservation potential and the completeness of the fossil record.

2. Patterns of diversity of marine organisms through geological time
Jim was one of the first to develop a hierarchical approach to considering biodiversity. His 1969 paper on *Patterns of taxonomic and ecological structure of the shelf benthos during the Phanerozoic*, published in *Palaeontology*, predicts much of what Jack Sepkoski would refine and promote ten years later. Jim's 1970 *Nature* paper with Eldredge Moores led the way in understanding the relationship between diversity and plate movements, and the distribution of faunal provinces through time. This theme was developed in his very influential 1973 book *Evolutionary paleoecology of the marine biosphere*.

Jim taught a graduate seminar entitled *Paleocology* at UC Santa Barbara in the mid 1980s. The essence of graduate seminars, from the instructor's point of view at least, is in providing a forum for discussing just about anything that excites their scientific interest at that moment. When the students said one year that they would like the seminar actually to address palaeoecology, Jim thought for a time, rubbed his beard, and finally said "I don't know what that is anymore." The seminar covered the origin of molluscs.

3. Genetic variability, regulation and evolution
During the late 1960s and early 1970s Jim became interested in genetics, and in collaboration with Francisco Ayala and others he explored the genetic variability of marine animals with depth and latitude. He also contributed to an important textbook on *Evolution*, with Dobzhansky, Ayala and Stebbins, published in 1977.

Jim was one of the first palaeontologists to become familiar with molecular data. In 1976 he pointed out the potential for explaining the rapid development of major groups in terms of the evolution of gene regulation, an idea now supported by experimental evidence on the role of Hox genes and a lynchpin of the field of evolutionary development.

4. Origin and relationships of phyla
As early as 1973 Jim was publishing novel and provocative ideas on the relationships of phyla, but this has been a major focus in the last 20 years, culminating in his book *On the origin of phyla*. This landmark publication can be honestly described as a homage to the greatest biologist that has ever lived by one of the greatest palaeobiologists of the 20th century. But if any of you have ambitions to adapt to fill Jim's niche you'll have to bide your time. Since the beginning of the 21st century he has published on developmental macroevolution, the history of marine diversity, the Cambrian explosion, predator–prey in gastropods, gene activities, climate change, moulting in Ecdysozoans, and vendobionts.

It is difficult to better the comment in *Evolutionary Paleobiology* (1996) by Doug Erwin, Dave Jablonski and Jere Lipps: "Jim has so often been ahead of his time that workers are still rediscovering principles and evolutionary patterns in his publications from the late 1960s and early 1970s. Presumably the field will have caught up to his current work by the middle of the next century!"

Sylvester-Bradley Awards for 2005

M. Brazeau	*Vertebrate fauna from the Tournasian of New Brunswick*
R.J. Butler	*Ornithischian dinosaurs from China*
I. Corfe	*Phylogeny of the Tritylodontidae*
M. Friedman	*CT scanning of a Devonian near-Tetrapod jaw*
J.A. Gillis	*Tooth evolution in early sharks*
A. Page	*Graptolite extrathecal tissue and the nature of Dawsonia*
S. Sigurdsson	*Beak shape as a pointer to niche partitioning in extinct birds*
O. Vinn	*Ordovician cornulitids from China*
M. Vrazo	*Did eurypterids mass-moult and mate?*
V.J. Vuks	*Triassic/Jurassic forams of the western Precaucasus*
V. Weisbecker	*Carpal evolution in fossil wombats*
M.T. Wilkinson	*Experimental study of pterosaur aerodynamics*
T. Willatt	*Bone geochemistry of Miocene mammals from North Africa*

news

SYNTHESYS

SYNTHESYS Project funding is available to provide scientists based in European Member and Associated States to undertake short visits to utilize the infrastructure at one of the 20 partner institutions for the purposes of their research. The 20 partner institutions are organised into 11 national Taxonomic Facilities (TAFs).

The 11 TAF institutions represent an unparalleled resource for taxonomic research offering:

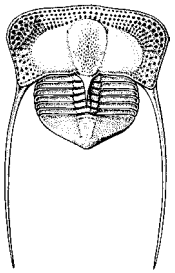
- Collections amounting to over 337 million natural history specimens, including 3.3 million type specimens.
- Internationally renowned taxonomic and systematic skill base.
- Chemical analysis.
- Molecular and imaging facilities.

SYNTHESYS is able to meet the users' costs for research costs, international travel, local accommodation, and a *per diem* to contribute towards living costs.

Forthcoming deadlines: 16th September 2005
17th March 2006
15th September 2006

For more information visit <**http://www.synthesys.info**> or contact <**synthesys@nhm.ac.uk**>.

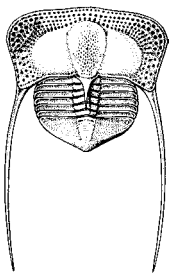
news

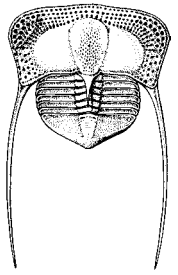


Palaeontology:
CALL FOR SHORT PAPERS!

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

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





ASSOCIATION MEETINGS

Rewriting the history of life: exceptionally well-preserved fossils and our understanding of evolution
BA Festival of Science, Trinity College Dublin, Ireland *5 – 9 September 2005*

Fossils are familiar objects to many people. The petrified remains of shells, bones and other rot-resistant hard-parts of organisms are the standard fare of museum displays and rock collections. But this view of fossils is misleading: looking only at hard parts gives a very distorted view of the history of life. This session will focus on recent discoveries of amazing fossils that preserve what normally rots away (dinosaurs with feathers, bizarre 500 million year old worms and other ancient oddities) and how they are reshaping our view of the evolution of life on Earth. Check out the BA website or contact the meeting organiser for further details: Dr Patrick Orr <**Patrick.Orr@ucd.ie**>, tel 00353 1 7162323, Department of Geology, University College Dublin.

49th Annual Meeting
Oxford, UK *18 – 21 December 2005*

The 49th Annual Meeting of the Palaeontological Association will be held in the Oxford University Museum of Natural History, under the auspices of the University Museum and the Department of Earth Sciences.

The meeting will begin with a reception in the University Museum on the evening of Sunday 18th December. The technical sessions will consist of two days of talks on 19th and 20th December in the lecture theatre of the University Museum, together with poster presentations situated adjacent to the lecture theatre. The talks and posters will be open to all aspects of palaeontology. The talks will be scheduled for 15 minutes inclusive of questions and there will not be any parallel sessions. Depending on submissions for oral presentations, some talks may have to be re-scheduled as posters. On Wednesday 21st December there will be a field excursion to the Mesozoic of Oxfordshire.

Venue and travel
Information about the city can be obtained from <**http://www.oxfordcity.co.uk/**>, and about the University at <**http://www.ox.ac.uk/**>. Oxford is easily reached from London airports, as well as those of Birmingham, Bristol and many other regional centres. It has frequent transport services from central London, from where it is reached in about an hour by train, and about one and a half hours by coach.

Accommodation
This will be in St Anne's College, which is situated about five minutes walk from the University Museum. There will be a range of accommodation with different facilities and prices.

Booking for accommodation, the field excursion and abstract submission must be received by **Friday 9th September 2005**. After this date abstracts will not be considered, and registration for the meeting will incur an extra administration cost of £15. The final deadline for registration and for booking accommodation is **Friday 25th November**. The maximum number of participants for the meeting is 300, and bookings will be taken on a strictly first come, first served basis.

Registration details and online registration

<**http://www.palass.org/forms/XannualRegistration.html**>

Registration, abstract submission and payment (by credit card) are by online forms at <**http://www.palass.org/**>.

Outline programme:

Sunday 18th December	**Evening reception**, Oxford University Museum of Natural History
Monday 19th December	**Scientific sessions**, Oxford University Museum of Natural History **Annual address**: *William Buckland and the dawning of palaeoecology*, by W.J. Kennedy (Oxford University Museum of Natural History) **Reception**, Blackwell's Bookshop, Oxford **Annual Dinner**, Christ Church College
Tuesday 20th December	**Scientific Sessions**, Oxford University Museum of Natural History **Presentation of awards**
Wednesday 21st December	Post-Conference field excursion to the Jurassic and Cretaceous of Oxfordshire

Travel grants to help student members (doctoral and earlier) to attend the Oxford meeting in order to present a talk or poster
The Palaeontological Association runs a programme of travel grants to assist student members presenting talks or posters at the Annual Meeting. For the Oxford meeting, grants of up to £100 (or the Euro equivalents) will be available to student presenters who are travelling from outside the UK. The amount payable is dependent on the number of applicants. Payment of these awards is given as a disbursement at the meeting, not as an advance payment. Students interested in applying for a Palass travel grant should contact the Executive Officer, Dr Tim Palmer, by e-mail at <**palass@palass.org**> once the organisers have confirmed that their presentation is accepted, and before 9th December 2005.

Annual Address

This year's annual address of the Palaeontological Association will be given by Prof. Jim Kennedy and will take place during the Association's Annual Meeting on Monday 19th December 2005, at the Oxford University Museum of Natural History.

Details overleaf…

William Buckland and the dawning of palaeoecology

Jim Kennedy
Oxford University Museum of Natural History)
<**jim.kennedy@oum.ox.ac.uk**>

William Buckland (1784–1858) was born at Axminster in Devon. He obtained a scholarship to Corpus Christi College in 1801, gained a BA in classics and theology in 1804, and was elected to a fellowship in 1808, in which year he was ordained.

A childhood interest in natural history led him to attend lectures by John Kidd, Reader in Mineralogy, and in 1813 he was appointed Kidd's successor. In 1818 he added the newly created Readership in Geology to his portfolio. Buckland's 1818 inaugural address on election to the geology post was an affirmation of the reconciliation of geology and theology (and was largely written by his friend and colleague William Daniel Conybeare (1787–1857)). It gave little indication of what was to come.

In 1816 he went on a grand geological tour of Europe, with Conybeare and George Bellas Greenough (1778–1855); this included visits to Goethe in Weimer, Werner in Freiberg, and the famous bear's bone cave at Gailenreuth. Hearing of a Yorkshire bone cave in 1821, he visited Kirkdale Cavern, and from a careful analysis of fauna and context, interpreted it not as the debris swept in by the waning waters of the biblical flood, but as a pre-diluvial Hyaena's Den. The results were published in the *Transactions of the Royal Society* in 1822, and in his *Reliquiae Diluvianae* (1823). There was not only interpretation, but also experiment: the bones from the cave were compared to those gnawed by a hyaena borrowed from a travelling menagerie, and found to be identical, as were fossil and recent faeces. Buckland was awarded the Copley Medal of the Royal Society for this work, and he has been claimed as the first palaeoecologist, taphonomist, and founder of cave science. In 1824, he provided the first scientific description of what Richard Owen (1804–1892) would subsequently include in his Dinosauria in 1842. Buckland had obtained the bones of the great lizard of Stonesfield already in 1814, and the delay in describing them remains a puzzle. In 1829 he published a brief note on ichthyosaur faeces, ink associated with fossil coleoids, and a pterosaur from Lyme Regis.

The coprolite work was published at length in Transactions of the Geological Society of London for 1835, and coprolites described from the Rhaetic Bone Bed to diluvial caves. In his conclusion he wrote that "the general law of Nature … bids all to be eaten in their turn … the Carnivoria in each period of the world's history fulfilling their destined office, to check excess in the progress of life, and maintain the balance of creation."

The coprolite study was expanded in the Bridgewater Treatise (1836), involving the casting of the gut of a range of sharks and rays, to produce analogues of fossil faeces.

Fossil footprints were an area of fascination for Buckland, notably those from the New Red Sandstone, and here too, experiment prevailed in the form of the artificial production of trackways (by the family tortoise on fresh pastry), an experiment repeated before his peers.

Functional morphology also received attention, and ranged from an interpretation of the adaptations of the giant sloth to the workings of the chambered shell of cephalopods.

Experimentation and comparison of living animals and plants with their fossil representatives led Buckland to advances in taphonomy, cave science, ichnology and functional morphology, and revealed him as an innovator at the dawning of palaeoecology.

And then, there were the toads …

Lyell Meeting 2006: Millennial-scale events
Burlington House, London, UK *15 February 2006*

This prestigious one-day meeting – the 2006 Geological Society of London Lyell Meeting, sponsored by the Joint Committee for Palaeontology, organised by the Geological Society and convened by Maurice Tucker and Howard Armstrong – is currently being planned for 15th February 2006.

Millennial-scale events and cycles are being increasingly recognised in the Quaternary stratigraphical record and in much older strata. Repetitions of beds, horizons, particular facies, fossil/microfossil occurrences *etc* on the scale of many hundreds to several thousand years record millennial-scale changes in the environment. In many cases these can be linked to changes in the climate, and in the Quaternary this is often related to changes in ice-cap volume or dynamics, which have knock-on effects on global temperature, wind regimes, oceanic circulation and sediment influx. Millennial-scale events are also recorded in strata deposited during greenhouse times, and here subtle changes in climate are again implicated.

This meeting is aimed at bringing together palaeoclimatologists, palaeontologists, Earth System scientists, modellers, sedimentologists, physical geographers, *etc*, to discuss the evidence, the mechanisms and the processes involved in the recording of short-term climatic events in the sedimentary succession.

Proposed titles and abstracts should be sent to Howard Armstrong by email to <**h.a.armstrong@durham.ac.uk**>, as soon as possible so that a scientific programme can be drawn up. Posters can be displayed during the meeting.

Further details will be posted on <**http://www.geolsoc.org.uk/**> and <**http://www.palass.org/**> once the scientific programme has been finalized.

Meeting REPORTS

48th Annual Meeting of the Palaeontological Association
Lille *17–20 December 2004*

From the tiny acorn of assumption does the mighty oak of madness grow. Having heard nothing from the esteemed editor of this newsletter, I assumed my report-writing skills were uncalled for this year. So I signed up to accompany five other Brummie earth scientists past and present on a road trip across Europe. Our intention was to traverse Belgium, the Netherlands and part of Germany before arriving in Lille on the Friday afternoon, hopefully in time for the Palaeobiogeography Seminar and Icebreaker. However, I was well aware these plans could go awry, and relaxed in the knowledge that I didn't have to produce a meeting review. I could take things easy.

Moreover, shorn of responsibilities I could take things silly. Excess consumption of Glühwein at Aachen Christmas market was perfectly reasonable, as was dressing up as Santa and wandering round the shops and bars of Maastricht. Even the in-car soundtrack of dreadful 1950s pop songs (most notably 'If I Knew You Were Coming I'd Have Baked A Cake') seemed to fit the bill.

Finally Friday came and it was time to head for France. The disappearance of a passport slowed us down, as did being battered by Belgian rainstorms, and any hope of attending the seminar soon had to be scrapped. But not to worry, the new reporter would be taking copious notes, and at least we'd be there for the Icebreaker.

It was dark and miserable as we exited the A25 into Lille and we were thankful our hotel was in the town centre and easy to find. Or at least it would have been if our maps hadn't been designed by someone eager to repel all foreign invaders from the city. Ninety minutes later, having been swept unwillingly along numerous one-way streets, crawled around much of the Rue Périphérique, and pleaded desperately to the Gods for some kind of informative landmark, we located our accommodation. The Icebreaker was long since over, so all that was left for us to do was seek the solace of a bar.

I fear we may have been too successful in this regard, for the following morning's alarm call was ignored. When we eventually surfaced there was still a trip to the gendarmerie to be made (to report the missing passport) and the talks were well underway by the time we materialized at Villeneuve d'Ascq. None of which would have been of great consequence if it weren't for the fact that, by now, a message had been relayed to me from Dr. Donoghue. Any chance I could write this year's meeting report?

So I apologize to all the speakers whose talks I missed: I was hoping to be able to watch the presentations retrospectively on the Lille website, but I can't seem to get an Internet connection. All of which means that my review does not begin at the beginning but some time just after coffee, with **Erik Tetlie** (Bristol) discussing the phylogeny of eurypterids and their position in relation to arachnids. Following Erik, **Rosie Dhanda** (Birmingham) examined the architecture of priniodinid conodonts. Their elements are very hard to distinguish and assembled apparatuses extremely rare, but an exceptional new specimen from North Dakota shows that there are no distinct element domains.

According to **Dave Bond** (Leeds), a Mass Extinction Olympics would see the Frasnian–Famennian event winning only the bronze medal. But what was its cause? Homoctenid and conodont distribution rule out sea level fall, so the most likely candidate is ocean anoxia. **Laura Braznell** (Birmingham) then uncovered complex mineralization patterns in her study of concretion fossils from the Coseley Lagerstätte. Early preservation of soft tissues was by kaolinite, with sulphides filling the voids later on, whilst siderite was encasing the lot, helping to prevent the tissues from compacting. However, it isn't clear whether the clay minerals were bacterial or colloidal. Completing the session, **Jesper Milàn** (Copenhagen) showed that some suspicious deformation structures were the first Danish dinosaur tracks, before **Tim Palmer** advised the audience on how best to smuggle weapons through UK customs. It appears that PalAss picnic knives are illegal in Britain.

The post-lunch segment began with **Graham Young** (Manitoba) and a fantastic Ordovician rocky shoreline preserved in Hudson Bay. Investigation of this ancient equatorial coral province is on a large scale (combining systematics, biostratigraphy, palaeoecology and stratigraphy), such that helicopters are an integral component, with hopes for some equally big conclusions. Remaining in the Ordovician, **Ben Fletcher** (Sheffield) examined whether liverwort spores could tell us much about atmospheric CO_2 at the time. Indeed they could, with isotopic analysis indicating that levels were between eight and 20 times as high as at the present day. Isotopes are versatile entities, which Chris Nicholas (Trinity College Dublin) revealed with a study of conodont feeding habits. By extracting the nitrogen and carbon from conodont elements it is possible to deduce what they were eating: Chris's results suggest a conservative pelagic diet, but with different species occupying different trophic levels.

Edouard Poty (Liège) then looked at coral distribution in the Panthalassic Ocean. Tournaisian sea-level rise saw them spread across the globe, only for a later fall to cause extinction and speciation. However, another rise resulted in a new abundance of taxa, so it was a tale with a happy ending. Alas, not so for the land snails of Tenerife, as introduced by **Claire Pannell** (Glasgow). They have been repeatedly incinerated by the island's pyroclastic events, a cooking too severe for even the most ardent *escargotier*, but they do retain some palaeontological value. Crush their shells, analyse the isotopes, and you might just obtain a proxy for local climate conditions at the time.

From the very hot we moved swiftly to the somewhat algid. **Jane Francis** (Leeds) has unearthed some Antarctic plant fossils that reveal palaeoclimate patterns during the Pliocene. *In situ* tundra vegetation, with old, small, slow-growing shrubs and mosses, indicates an environment much like modern Patagonia, and shows that the ice sheets aren't as fixed as we might imagine. Most people then scarpered to get some coffee, but anyone not needing to feed their caffeine dependency was invited to remain seated for an introduction to the Paleobiology Database <**http://www.paleodb.org/**>.

The final session of the day began with **Jenny Clack** (Cambridge) and a new Devonian tetrapod. I say new, although the fossil was found in 1947, which makes the Dead Sea Scrolls an equally recent acquisition and the music of Al Jolson cutting edge, but I digress. The taxon is another addition to an increasingly detailed fauna, with 17 Famennian genera now known. Next up, **Melise Harland** (Leeds) perused the polar conifers of the Cretaceous. Mixed evergreen and deciduous forests are fossilized in the Arctic, but it seems there were no obvious benefits to being deciduous at such latitudes, perhaps explaining why no such taxa have been found at the South Pole. Finally, the role of dispersal in diversity was studied by **Noel Heim** (Georgia), who wondered whether the Phanerozoic Marine Diversity curve reflects rates of migration.

For some, it was time to go and get changed ready for the annual dinner. For everyone else it was time for the AGM, incorporating the presentation of the Lapworth Medal to **Jim Valentine**, the Hodson Fund to **Heather Wilson**, and Mary Anning Awards to **Phil Bennett** and **Bjørn Funke**. This was swiftly followed by the handing over of the presidential reins; **Derek Briggs** (Yale) passing the onus of responsibility on to **Sir Peter Crane** (Kew Gardens). Peter's first task (if it should be described thus) was to introduce the Annual Address: '*Palaeontologia de profundis*' by **Stefan Bengtson** (Stockholm).

Stefan has been searching the depths of time and the farthest reaches of the globe for signs of early life, inevitably leading him Down Under. A sequence of metamorphosed tidal sediments between 1.2 and 2 billion years old have yielded strange double ridges that look suspiciously animalian. The problem then is convincing others that they are. The Early Worm Uncertainty Principle states that your peers will accept the age of the rock or the presence of fossils, but not both, with Stefan speculating that Bruce Runnegar shot down the idea as revenge for a mediocre

dinner he'd served him some years before. In south-western Australia, trace fossils are definitely present in a 1.7 Ga phyllite, but how did they burrow through metaquartzite? Did these early critters have teeth of diamond?

But still there is despair, as the eye of faith comes in. Ancient geodes find themselves being interpreted as small bilaterian animals, despite reviewers' concerns. Stare at clouds for long enough and you will see animals; Linnaeus found Christ in a banana. And then there's Mr. Okamura, whose fossil laboratory showed that all life began in miniature in a Japanese mountain. Stefan's moral: nurture your critical friends. Liam's footnote: and where better to do so than at the PalAss Annual Dinner?

Sunday morning, and I'm falling, as the Velvet Underground once declared. It's freezing cold, dark, and I'm miles away from Villeneuve d'Ascq, not quite feeling on top form. But at least the metro trains are quiet and I arrive at the conference centre in plenty of time to see **Dianne Edwards**' (Cardiff) Sunday confessional. Identifying and validating Palaeozoic bacteria is precarious work, with many morphologies misleading and not indicative of biogenic origin. Advocates of Martian life beware! **Lucy Wilson**'s (Cambridge) challenge was to make a Burgess Shale fossil; tough work with so many taphonomic variables. The organic carbon present was preserved by adsorption into 2:1 layer clays and Lucy's experiments show ragworms in kaolinite hold themselves together well, which is more than could be said of some members of the audience. **James Wheeley** (Cardiff) then showed that *Thalassinoides* from the Ordovician of Sweden represent the tunnels of infaunal trilobites. But what were they doing there? Protecting themselves? Oxygenating the substrate? Doing a bit of farming? An intriguing tale indeed.

In my notebook, the next speaker is described as an unshaven, scruffily dressed oik rambling about early molluscs. But before anyone takes offence, I should point out that the handwriting isn't mine and that the oik was **me**. I thought machaeridians were rather interesting, but one of my so-called friends obviously didn't agree. Cryptic planktonic forams and their use in testing molecular clocks were discussed by **Blair Steel** (Royal Holloway) before **Frank Wesselingh** (Leiden) brought the first session to a close. Flood prevention engineering between Rotterdam and Antwerp has provided boreholes for study, elucidating the palaeoecology of the North Sea. So far, the pattern revealed is one of a warm Miocene fauna, followed by a strange Pacific fauna, then an Arctic fauna, then a hiatus (with a major diversity drop between 4 and 2 Ma), and finally the modern fauna.

Fed up waiting for action? Just do it yourself! Or so said a jet-lagged **Guy Harrington** (Birmingham) as he began the post-coffee presentations with a piece on pollen. Hurlbert's PIE came into it somewhere, too, although my knowledge of botany and statistics is patchy, such that I'm not sure I quite grasped its significance. **Barry Lomax** (Sheffield) then examined whether sporopollenin could be used to reconstruct ancient UV-B light levels. Plants change their UV-B protection as levels fluctuate, and it might be possible to spot these screening compounds in the fossil record. Testing sea level curves at high palaeolatitudes was the aim of **Ian Troth** (Southampton) as he ventured to the Devonian of Bolivia. Acritarch evidence from these rocks seems to contradict the allegedly eustatic sea level curves derived from Europe and America, showing how precarious it can be to build a global picture from a regional record.

The wonderful British train service prevented Chris Berry from giving his talk on early seed plants, so **John Marshall** (Southampton) presented the findings instead. New material from the Devonian of Greenland appears to be the parent plant of previously orphaned megaspores, a sporangium containing both mega- and microspores showing that a two-part reproductive strategy was being employed. In warmer climes around the Dead Sea, **Hans Kerp** (Münster) found Upper Permian plants that grew in abandoned stream channels. The flora includes taxa known previously only from Euramerican parts of Gondwana. A mosaic of habitats was then described by **Bernard Gomez** (Rennes) from the Cretaceous of western France. From mangrove-type coastal forests with vertebrates in amber through to bioclastic limestones and shark nurseries, there was something for everyone. Bringing the morning to an end in a blaze of glory (© Herringshaw's Extraordinarily Obvious Puns, Inc.), **Claire Belcher** (Royal Holloway) showed that the K–T impact did not generate significant wildfires. Very little charcoal is found at the boundary, and although there is a reasonable quantity of soot, analysis indicates it was generated by the burning of oil or coal, not plants.

Before heading off for lunch, we were informed that Chris Scotese wished to show his movements to students, with DVDs available to interested parties. This sounded a little concerning, though I may have misunderstood the announcement.

The penultimate session commenced with **Rob Riding** (Cardiff) and his talk on the controls of calcification, masquerading as 'a few Summer holiday snaps'. Peaks of limestone accumulation correlate approximately with peaks in seawater saturation, but whereas the Palaeozoic fauna was largely biologically induced, post-Palaeozoic organisms have control over calcification.

It appears higher saturation favours induced taxa and lower levels the opposite, with three Phanerozoic phases of the former and two of the latter.

In flares and sparkly badges, **Colin Barras** (NHM/Birmingham) approached the podium like a young John Travolta. But, despite our pleas, he refused to present his talk using the medium of dance. Disaster! Or rather, *Disaster*!, since that taxon is vital to an understanding of echinoid evolution, connecting galeopygids to spatangoids. Next to take the stage was **Alex Page** (Leicester) who delivered a sermon of evangelical ferocity on the confusion over *Dawsonia* and some strange graptolite appendages. Tom Hanks' recent film *The Polar Express* has the disclaimer 'Contains scenes of mild peril' and I suddenly understood its meaning, sitting three rows from the front as Alex brandished his walking sticks like Samurai swords. Still, there was no danger of anyone nodding off.

Somewhat more sedately, **Lionel Cavin** (NHM) searched for the cause of the radiation of ray-finned fish, before **Ursula Göhlich** (München/Lyon) showed *Macelognathus* Marsh, 1884 to be a sphenosuchian. The Miocene climatic optimum was the final topic as **Loïc Costeur** (Lyon) looked at terrestrial ecosystems. A mean annual temperature of 20ºC sounds rather pleasant, although it did affect mammal morphology – not many medium-sized mammals were to be found in humid forests, apparently.

I confess to flagging a little by the final session and could perhaps have done with a dose of whatever it was Mr. Page was on (sugar, he tells me). **Andreas Braun** (Bonn) peered into diagenetic windows in the Cambrian of China; **Dennis Bates** (Oxford) found some dendroid graptolites with oval stolon nodes; **Gengo Tanaka** (Kanazawa) saw through the eyes of a podocopid ostracod, and **Rudy Lerosey-Aubril** (Montpellier) found trilobite larvae in the Devonian of Morocco and Germany and the Carboniferous of France.

Coral-encrusted brachiopods caught the attention of **Mikolaj Zapalski** (Warsaw). The auloporoid corals display preferential location close to the brachiopod feeding currents, with certain types of brachiopod shell sculpture being particularly tempting. **Willem Renema** (Leiden) then looked at the convergent evolution of chamberlets in Oligocene nummulitids, before **Christina Reimann** (Münster) brought the presentations to a close with a tale of trying to determine the ages of Pleistocene and Holocene mammal bones.

Another annual meeting was almost over, but **Peter Crane** was called back to don his presidential hat again and hand out some awards. The Poster Prize was awarded jointly, with **Lucy Muir** (NHM) and **Jessica Pollitt** (Bath) sharing the honours for their work on Ordovician sponges and trilobite systematics, respectively. **Claire Belcher**'s study of palaeo-wildfire proved popular with the judges, and deservedly won her the President's Prize for best talk. And that was your lot, at least in the conference arena. The next day saw two field excursions: one to the Mesozoic on the coast at Boulogne, the other heading to the Brabant Massif to peruse the Palaeozoic, and the weather was glorious, which is all you can hope for.

Congratulations to **Thomas Servais** and his organizing team for an incredibly well-managed programme of talks. I can't remember ever seeing a whole set go along so effortlessly, without technical problems or people running horribly over time. Sterling work! I am obliged to point out one or two problems with accommodation, not least the inaptly named Star Hotel, but

on the whole it was another top-notch PalAss. Lille was a very welcoming, friendly city and I thoroughly enjoyed myself. I look forward to December and the chance to do it all over again in Oxford.

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2005 Lyell Meeting: Applied Phylogenies
Burlington House, London *9 February 2005*

Wednesday 9th February saw the Geological Society and the Joint Committee for Palaeontology lay open the doors of Burlington House and admit the assembled brethren that was the Lyell Meeting 2005, being this year a symposium on 'Applied Phylogenies'. That there is no precise definition of what or who an applied phylogeneticist is did not hinder the meeting a jot. In fact, this ambiguity added to the variety of contributors on this cross-disciplinary occasion. With this in mind, it is now your chance, my readers, to put the Lyellian method of observation and empiricism into operation as you scan the following digest and deduce for yourselves just what exactly applied phylogeny is…

As ever, the convenors – **Haydon Bailey** (Network Stratigraphic Consulting) and **John Gregory** (Kronos Consultants/Natural History Museum) – had ensured that a full spread of refreshments was laid on for those who missed breakfast. Once the complimentary coffees were quaffed but before fellow conversationalists had fully managed to spray each other with several semi-masticated crumbs' worth of how-do-you-do, we were ushered into the Lecture Room. The meeting had begun. After a brief welcome from Haydon and an apology from John, who was in the Bahamas (there's money in the applied phylogeny business), the first of the stratigraphically ordered sessions began as we welcomed a keynote address from **Simon Conway Morris** (University of Cambridge). Simon argued against the presence of a deep-rooted fauna of complex Precambrian metazoans, and proposed that the blue touch paper for Cambrian explosion could only be found by a thorough examination of the fossils and strata of the Ediacaran Period. One particular slide in this entertaining talk illustrated a lavish diorama of the 'garden of Ediacara' as conceived by the London Rubber and Latex Company in the days before it was allowed to display their wares in its Soho shop-front window. Now without the extraction efforts of the oil industry we wouldn't be able to manufacture such marvellous PVC teaching aides, so with this in mind we moved to a nice paper by **Ken Dorning** (Pallab Research) on the evolution of the *Deunffia* lineage of process-bearing acritarchs and its application in the oil shales of the Qusaiba Shale, where he has collaborated with Saudi Aramco using acritarch biostratigraphy to constrain reservoir architecture. The session remained in the lower Palaeozoic plankton but moved from prey to predator as **Jan Zalasiewicz** (University of Leicester) suggested that the rapid evolution that makes graptolites an exemplary biostratigraphic taxon may be a consequence of their unique form of behaviourally mediated skeletal construction, whereby the individual zooids built the colonies exoskeleton in a form of animal architecture that may have

provided a form–function feedback and an extra gear for morphological change. So, having covered the first four and a bit billion years of Earth history in little less than ninety minutes, it was time for more coffee. Phew.

As any biostratigraphers worth their salt will tell you, one may be far more confident of defining a boundary on the first appearance of an animal if it occurs in sequence where its ancestors are also present. This is not the case with the GSSP for the Tournaisian-Visean boundary, which is currently marked by a foraminiferan foundling lying lonesome in the Carboniferous of Belgium. However, the morning's fourth talk allowed **Francois-Xavier Devuyst** (Trinity College, Dublin) eloquently to prove his biostratigraphic mettle by presenting a proposal for the Tournasian–Visean boundary GSSP to be moved to the Pengchong section of southern China, where it can be demarcated using the biometrically calibrated *Eoparastaffella 'ovalis'-E. simplex* (Foraminifera) lineage. Likewise, if one has a good fossil record and a stable taxonomy, phylogenetic analyses may be used to modify stratigraphic hypotheses, as was shown by the copiously named **Alberto Corrêa de Vasconcellos** (Universidade Federal de Sergipe, Brasil), who proposed, on the basis of an Hennigian phylogenetic analysis of Rugose corals from the Americas, that strata in the Merida region of Venezuela are of Pennsylvanian rather than Permian age. Rather than proceeding any further towards the Permian and tackling the death and disaster that is the Permo–Trias on an empty stomach, the meeting quite rightly paused for lunch. Those who had already presented drank an enjoyable luncheon upstairs, whilst those who had yet to speak found someone else to drink theirs.

Returning once more to oil geology and collaborative work with Saudi Aramco, the afternoon session began with the day's second keynote speaker, as **Peter Skelton** (Open University) talked on how Rudist bivalves may be used to refine reservoir models in the supergiant Shaybah Field of eastern Saudi Arabia. Taxonomic and palaeoecological determination of these exquisitely preserved assemblages allowed the precise identification of biofacies within a series of shallowing-up cycles, enabling engineers to maximise production and providing palaeontology with a mutual benefit. As Peter said, it really does appeal to one's 'sense of the baroque'. Though still in the Chalk the session moved closer to home, as **Malcolm Hart** (University of Plymouth) discussed the evolutionary lineages of benthonic Foraminifera and their diverse application in problem solving, with examples from the construction of the Thames Barrier and Channel Tunnel to the old chestnut that is the oil industry. However, as some agglutinating forms are able to tell sponge spicules from sand and biotite from muscovite, a more novel application to problem solving could involve struggling undergraduates culturing these beasts as an exam-busting ruse!

Now if Cretaceous Rudists are seen as baroque, the Chalk Sea is almost post modern: sedimentological models have been revised and rewritten, and the various lineages of the heart-urchin *Micraster* see shape and size going everywhere. Nevertheless, behind this apparent complexity is an underlying order. Having constructed a phylogeny based on changing plate pattern, **Andy Gale** (University of Greenwich) showed that beyond the series of shifting shapes there lies a subtle story of divergent speciation in a deepening environment. This sees a profound change in feeding habit as oral tube feet atrophy and mucus-string feeding becomes dominant in response to the decreasing supply of particulate foodstuff. To continue the

theme of eustatic variation and its impact on the evolution of benthic faunas, **Haydon Bailey** (Network Stratigraphic Consulting) addressed a topic he first considered thirty years ago, *viz*. the *Stensioeina granulata* (Foraminifera) lineage, which originated in Late Cenomanian and radiated across Europe in a series of transgressions. Previous work on this lineage suggested it went extinct due to a forced regression in the Middle Campanian; however Haydon suggested that the lineage may have just suffered a brief hiatus, related species surviving into the Palaeogene. With a view to the delegates surviving into the final session, the conference itself took a brief hiatus, allowing time for a quick caffeine fix and providing the chance to examine the collection of posters from the University of Leicester's PhD students and the British Geological Survey.

As the final drops of tea were carefully sipped and pinkies folded back into their rightful place (*when in Piccadilly, my dear boy*…), it was time to return to the Lecture Room once more. Introducing a theme that bracketed the final session, **Andrew Racey** (BG Group) discussed size increase in Palaeogene Larger Foraminifera, including the infamous *Nummulites*, which showed this general trend either side of an extinction event that hit k-strategists heavily at the end of the Oligocene. As these evolutionary trends tend to increase the porosity of reservoir rocks, the wily phylogenist can manage the real wheeze of studying macroevolutionary phenomena whilst keeping the wolf from the door. Similarly, if one can relate microfossil proxies to climate change there are big bucks about, and these big bucks can be spent drilling cores through variously interesting intervals of fossiliferous sediment. With a certain weaselly cunning, **Paul Pearson** (University of Cardiff), the day's final keynote speaker, had managed to do just this: whilst studying Eocene palaeoclimate using isotope proxies, a convenient choice of drill core sites had 'coincidentally' collected a representative sample of the entire *Hantkenina* lineage. The Hankeninids are a striking and distinctive group of planktonic forams, easily recognisable due to their hollow tubulospines, which originated from *Clavigerinella*, an unornamented progenitor, via a series of morphotypes bearing 'Noddy-cap' and 'wizard-hat' shaped processes. Using a stratophenetic approach to phylogeny to complement cladistic analyses, this excellent talk challenged the common assumptions of punctuated equilibrium and ghost lineages, showing that though 11 morphospecies with overlapping stratigraphic ranges may be identified, these do not necessarily correlate to biological species, but appear instead to represent a gradualistic progression in which a minimum of three cladogenic events is currently recognised. The isotopic analyses afforded by the palaeoclimatic origin of these collections suggest that early tubulospine-bearing forms may have originated as an adaptation to harvest food efficiently in deep, oxygen-poor waters. This data was the final piece of a fascinating jigsaw illustrating the gradual functional acquisition of a complex structure as seen in the geological record.

The next talk moved to a slightly finer scale: from forams to coccoliths and from macroevolution to microevolution, as **Jeremy Young** (Natural History Museum) reassessed the *Calcidiscus* lineage in light of cryptic speciation. As recent genetic and culture studies have shown, conventional species of modern plankton are typically composed of clusters of a few sibling species, though this means that conventional lineages may in fact be complex branched evolutionary networks, of tremendous biostratigraphic potential. When studied at high resolution (over a 10ka interval), the *Calcidiscus* lineage could be subdivided into five morphotypes, which exhibited complex evolutionary patterns within the two end-member morphocline that describes the lineage at the medium-resolution Middle Pliocene – Early Pleistocene interval found at ODP site 662. The

theme of size increase within Cenozoic forams returned to bracket neatly the day's final session, as **Norman Macleod** (Natural History Museum) applied a phylogenetic test to see if this patter was simply due to large offspring being the product of large ancestors (think fat American teenagers and their burger scoffing mothers). Though this work is only in its preliminary stage, with Norman admitting to having been scanning monograph images into his computer package at 7am that morning, it appeared that size increase was a genuine evolutionary signal: from where I sat at least, his graph showing the mean rate of size increase within lineages appeared to be the gradient of his mean test size data. And without further ado, a thoroughly enjoyable day concluded, as we retired for a wine reception in the Library. Several delegates commented that it was a fine vintage with a well rounded palate, while many more said they'd have another glass as it was free. So there it is, a day in the life of an applied phylogenist. It all seems rather pleasant really.

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Earth, Life and Climate: three billion years of interaction
Leicester Literary and Philosophical Society Geology Section Annual Symposium
Leicester University, UK *5 March 2005*

Founded in 1849, Section C of the Leicester Literary and Philosophical Society is one of the oldest geological societies in Britain, and as part of its wide programme of activities it holds an annual symposium. This year's event was privileged to have a host of distinguished speakers, coming from a diverse range of fields but all united under the burgeoning aegis of Earth Systems Science.

After welcome from the Section's chairman, Andrew Swift of Leicester University's Department of Geology, **Nick Butterfield** (University of Cambridge) started appropriately enough at the beginning of it all: he argued that Precambrian Earth was a truly fascinating place because nothing much happened. Lower biodiversity, smaller organisms, simpler and virtually "extinction-proof" ecosystems and slower evolution apparently characterised most of our planet's history, constituting a fundamentally different world to that of the Phanerozoic. A (probable) absence of animals in particular also contributed towards this comparatively sedate, stable biosphere.

Moving forward in time, **Professor Bob Spicer** (Director of CESPAR, The Open University) described how the spread of terrestrial plants early in the Palaeozoic shaped in large part the "Modern World" in which we now live; both with their physical presence (mitigating erosion, for example) and their influence on the climate, particularly through the hydrological cycle. Concurrently, a kind of physiological bootstrap process of floral evolution, with plants building on the ecosystems their evolutionary forebears formed, led to increasing stature and the first forests. He reminded us that even in death, these forests continued their shaping of the world indirectly: through their incarnation as coal, fuelling the Industrial Revolution. We can only

hope that, through our industrial mediation, they do not lead to the destruction of the Modern World they helped forge.

After these early years we of course reach middle age (the Mesozoic), and mid-life crises. Although perhaps not the best analogy for a Gaian paradigm, these were indeed crises on a planetary scale. **Peter Skelton** (Open University) led us through the convolutions and convulsions of the carbon cycle as it changed through time; including some equations formidable to anyone like myself whose GCSE chemistry is a little rusty (or should that be oxidised?). He argued that the changes were aided and abetted by biology, so that documentation of such variation provides a series of natural laboratory experiments that may indicate the fate of our world as we alter the carbon balance by increasing the levels of atmospheric CO_2.

Next, **Mike Benton** (University of Bristol) discussed his favourite mass extinction, the end-Permian, and his work in determining what happens when life is nearly extinguished; perhaps an overly pessimistic outcome of the current mass extinction, but it's always prudent to be aware of the worst-case scenario. Although geological maps were apparently a considerable national security concern in the USSR, their main value now is not to Russia's enemies, but in revealing fantastic terrestrial P–Tr sections, allowing a detailed analysis of what was transpiring and indeed expiring on land during this "unpleasant" event.

As **Gavin Foster** (University of Bristol) observed, mountain altitudes are liable to be a touch chilly, but more importantly they could perhaps make things much colder elsewhere. He discussed the possible effect of tectonics and the resulting geomorphology on global climate: specifically, orographic uplift along the western seaboard of North America and the onset of the northern hemisphere glaciation. His conclusion, that such changes were not the direct cause but a contributing factor in the glaciation, highlights the synergistic complexity of the Earth system and the holistic approach that is required to understand it.

To close, **Mark Williams** (British Antarctic Survey) – with videos and animations aplenty – based his talk around Hutton's updated motto: the past is the key to the future. Using GCMs based on palaeoclimate data is an effective way of realising this concept; in this case, information from the mid Pliocene, when there was an anomalous rise in temperatures within the general cooling trend of the past fifty million years. What could this tell us about the future fate of a warming Earth? Not too much; yet. More data is needed, he emphasised, a conclusion particularly applicable to any area of Earth Systems Science.

The day ended with a question and answer session, allowing the audience to grill (or rather lightly toast) the speakers. Andrew Swift closed the symposium, justifiably praising the speakers for a day of genuinely high-calibre talks in what has become an extremely topical area of science. Each talk necessarily focused on a very small part of a very large jigsaw but, as always with talks of this nature, I was left with an impression of just how daunting is the task that faces us: to understand the intricacies and capriciousness of our only home and, most importantly, learn how to ensure our own continued occupancy.

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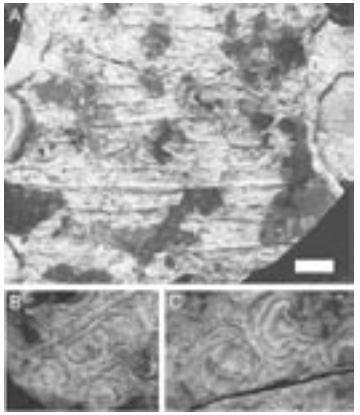
MYSTERIOUS FOSSILS

Good news! Mystery Fossil Number Two now has a name, although it turns out not to be a fossil at all. Simon Braddy at Bristol has identified it as the pseudofossil *Rhysonetron*. To quote the Treatise W 178, *Rhysonetron* was "originally regarded as Metazoa of unknown systematic position, compared with tubes of modern annelids; interpreted by Donaldson (1967) as originating through deformation of an algal mat; recently explained by Hofmann (1971) as diagenetic structure resulting from shrinkage crack filling …". Thank heavens for that! Undisturbed sleep beckons.



Mystery fossil 7

Mystery Fossil Seven was found recently by post-graduate students in a thin section of beach rock from the Bahamas in the Leeds University Earth Sciences teaching collection. The fossil appears to be formed of calcium carbonate and is round and cog-like with eleven "spokes". It is approximately 400 microns in diameter. The host beach rock sediment may only be a few hundreds of years old. Ideas as to its origin include calcareous green algae or holothurian plates.

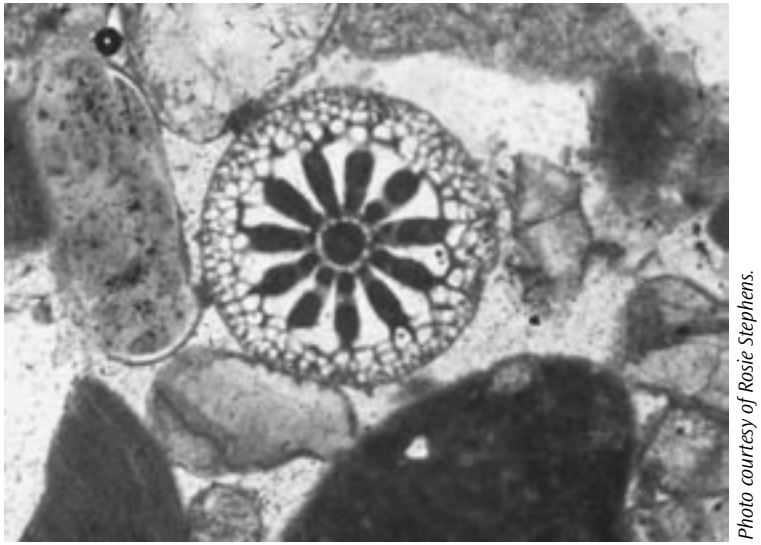


Photo courtesy of Rosie Stephens.

Answers in an email (or, if the traditionalists prefer: on a postcard, scanned and attached to an email) to Cris Little <**c.little@earth.leeds.ac.uk**>.

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From our Correspondents

Something Old, Something New: Inferring Developmental Mode from the Fossil Record

Continuing with our discussion of topics relevant both for developmental biologists and palaeontologists, this article addresses how mode of development can be interpreted from fossilized developmental stages of extinct metazoans, using knowledge from extant metazoans. We also present examples of how life history information from extant species can enhance our understanding of fossilized developmental stages, and discuss the importance of these fossils to modern biological research. Unlike living taxa, for which collection of embryos is at least possible (although admittedly, not always practical), among fossil forms such opportunities are extraordinarily limited at best. Where fortuitous taphonomic conditions preserve entire developmental series (*e.g.*, Dong *et al.*, 2004), such instances are the extreme exception to the rule, and cannot be expected for the majority of species. Fortunately, features of fossilized adult and juvenile skeletons, and traces and impressions of soft tissues, can provide clues to developmental mode.

Mode of development can be *direct*, when a miniature version of the adult form is born/hatched, or *indirect*, when one or more free-living larval stages undergo metamorphosis to attain the adult form. The presence of a larval stage is the defining characteristic of indirect development. Larvae are, by definition, morphologically distinct from the adult form, often possessing different structures and body plans from the adult, and typically make use of different ecological niches (see Hall and Wake, 1999 for further discussion of larvae). One of the most widely recognized examples of indirect development is the metamorphosis of a larval caterpillar into an adult butterfly. Along with developmental mode, growth rates, feeding strategies, age and size at maturity, death rates, and reproductive mode are collectively referred to as life history traits (Wake, 2003). Together, these traits determine how an organism interacts with its environment and the roles it plays within the ecosystem.

Life history information is useful in clarifying relationships between metazoan taxa that would otherwise be obscured by drastic differences between adult and larval morphologies. A classic example is the realization that ascidians are chordates, which was discovered by looking at the morphological features of their tadpole larvae (Hall, 2005). Mode of development is also helpful in differentiating cryptic species with similar adult forms (*e.g.*, the sea urchin genus *Heliocidaris,* in which adults of both species are morphologically identical, yet one species (*H. tuberculata*) has a feeding larval form while the other (*H. erythrogramma*) does not (Raff *et al.*, 1999). Comprehensive surveys can also elucidate the evolution of differential developmental modes within a particular taxon. For example, ten of the approximately thirty extant anuran families exhibit direct development; parsimony dictates that indirect development is the ancestral state (Hanken, 1999).

Similar information can be gleaned from fossil embryos of both direct and indirect developers. In the discussion that follows, we highlight diagnostic features of direct and indirect developers from a host of metazoan taxa, and briefly discuss the implications of the recognition of developmental modes and fossilized developmental stages.

INVERTEBRATES

Echinoderms

Echinoderms, such as sea urchins, exhibit both direct and indirect development. Due to their well-mineralized skeletons both adults and larvae are commonly recognized in the fossil record (Déflandre-Rigaud 1946; Sprinkle, 1987). Calcium carbonate skeletal rods, called spicules, are characteristic of planktonic feeding (planktotrophic) echinoderm larvae. Spicules may be present in direct developing species, lacking a “true” larval stage (such as brooded embryos), or lecithotrophic species (nonfeeding larvae with yolky eggs; Emlet, 1995), but they are typically not as elaborate or well organized as those of indirect developing species.

Larvae of extant sea urchins metamorphose into juveniles that grow in size to become adults. The juvenile develops as a cluster of cells within the larva, and the juvenile skeleton is deposited within this cluster as a series of calcium carbonate plates. Some of these plates develop in association with the proximal end of the spicules. Studies using polarized light have shown that the crystallographic axes of the calcium carbonate crystals that form the larval spicules determine the axes of these plates (Emlet, 1985). In general, if a juvenile plate has formed from a spicule, as it would in indirect developers, the plate will have a crystallographic axis that is nearly parallel to that of the spicule from which the plate originates. Alternatively, in direct developing species, the juvenile plates do not form from spicules and the crystallographic pattern of the affected plates would be expected to be nearly perpendicular to that of the plate surface (Jeffery and Emlet, 2003). Consequently, the developmental mode of a fossilized adult sea urchin can then be determined by placing the fossil under polarized light and observing the axes of the plates.

Molluscs

In molluscs that secrete an external, calcified shell, the shell forms early in development, and mode of development can be inferred from scanning electron microscopical studies of the shell at nearly any time during ontogeny (see review by Jablonski and Lutz, 1980). Among snails (Gastropoda), shells can be classified into three sections: protoconch-1, protoconch-2 and teleoconch, each secreted at a different stage in development (pre- and post-hatching, and post-metamorphosis, respectively). One can infer egg size and amount of yolk, which indicates larval type, from each segment. In general, a small, well-defined protoconch-1 indicates a small (<200µm) egg with a small amount of yolk, typical of planktotrophic larvae. A large protoconch-1, and protoconch 1-2 boundary that is not readily discernable indicates that the specimen was likely a product of a larger, more yolk-filled egg; this is typical of nonplanktotrophic developers (including lecithotrophic and brooded embryos).

A similar analysis can be applied to bivalves. The trochophore (first larval stage) and veliger (second larval stage) shells, formed prior to metamorphosis, are termed prodissoconchs 1 and 2, respectively; the dissoconch is formed post-metamorphosis. Again, shells that have distinct boundaries between sections, have a small (<150µm in length) prodissoconch-1

and a relatively smooth prodissoconch-2 surface suggests planktotrophic development (see also Moran, 2004), while a large (>135µm) prodissoconch-1 and a small or nonexistent prodissoconch-2 is indicative of lecithotrophic development. Shells of brooded embryos often have a very large (>>230µm) and rough prodissoconch-1. It may be difficult, however, to classify shells of a direct versus an indirect developer when sections fall in an intermediate size range (135–150 µm).

Bryozoans

Bryozoans are yet another marine invertebrate group exhibiting diverse modes of development and having mineralized elements which fossilize well. Although colonial bryozoans most often reproduce asexually, extant species are also known to produce both lecithotrophic and planktotrophic forms. Lecithotrophic bryozoan larvae are usually larger than planktotrophic larvae, and may exhibit brood chambers (McGinnis, 1997). The first larva to settle to the substrate, metamorphose and start a colony is called the ancestrula (Pechenik, 2000). Examining and measuring the size of fossil ancestrulae can therefore provide some insights into mode of development of particular taxa. This information must be used in combination with knowledge of the palaeogeographic and palaeogeologic distributions of the taxa in question further to corroborate mode of development (Pachut and Fisherkeller, 2005).

Many other invertebrate groups have also been found as fossils, and inferences have been made as to their development (see Raff, 1996; Morris, 1998; Budd, 2004; Dong *et al.*, 2004).

VERTEBRATES

Fish

Of course, indirect development is not limited to the invertebrates; a number of fossil fish larvae are now known. In fact, the oldest known vertebrate larva is a lungfish larva from the Middle Devonian (Thomson *et al.*, 2003). Some groups of fish have unique larval characteristics providing clues to their taxonomic affiliations and life histories. For example, the cranial adhesive glands common to larvae of substrate-brooding cichlids are reduced or entirely lacking in larvae of extant mouth-brooding cichlids (Richards and Leis, 1984; Meijide and Guerrero, 2000). Klett and Meyer (2002) show that substrate-brooding and larval cranial adhesive discs are primitive, and that mouth-brooding and larval regressed cranial adhesive discs are derived for African cichlids when these characters are mapped onto a molecular phylogeny. Knowledge of these life history strategies and larval characteristics in cichlids would enable palaeontologists to recognize the existence of fossil cichlid larvae should they be discovered.

Anuran amphibians

Indirect development is also common to many amphibians. Although rare, fossilized anuran tadpoles representing several species, including extant genera (*e.g.*, *Pelobates* from the Miocene of Turkey; Wassersug and Wake, 1995), are known. Larval forms resembling tadpoles and salamander larvae have been found dating back to the Carboniferous (Milner, 1982). Two recent studies (Chipman and Tchernov, 2002; Bàez and Pugener, 2003) reveal beautifully preserved ontogenetic series of anuran species – one from a large grouping of soft tissue imprints and skeletons from the Lower Cretaceous (the pipid *Shomronella jordanica*), and the other a soft tissue assemblage from the mid-Eocene to early Oligocene

(reportedly representing a new pipid taxon). The presence of tadpoles confirms that these species exhibited indirect development and corroborates an ancestral designation for indirect development in anurans.

Direct development in amphibians is not represented in the fossil record (Elinson, 2001). This is more likely a failure of fossilization of early developmental stages of amphibians than it is of their recognition, as direct- and indirect-developing amphibians can be readily distinguished based on discrepancies in skeletal development. For example, the elongation and ossification of jaw cartilage occur sequentially in anuran larvae, but simultaneously in the direct developer *Eleutherodactylus coqui* (Elinson, 2001).

Urodele amphibians

Early descriptions of various salamander-like taxa separated those forms with external gills (so-called Phyllospondyli) from those without external gills ('branchiosaurs'). More detailed studies have since amended this notion, and now several temnospondyl amphibian groups are known from partial ontogenetic series that include larvae.

A study of the temnospondyl *Micromelerpeton credneri* (Witzmann and Pfretzschner, 2003) identified a series of ontogenetic characteristics that suggest adaptation to a terrestrial habitat from an aquatic environment. These features include sequential ossification of the postcranium (in craniocaudal and proximodistal fashion), relative shortening of the external gills, relative increase in the diameter of the sclerotic ring (and consequently the eye) and formation of a palpebral bone (indicating the presence of an eyelid, a feature not seen in larval/neotenic salamanders; see Witzmann and Pfretzschner, 2003 and references therein).

Other putatively transitional characteristics, such as changes in dermal sculpturing, are now considered to be individually variable and not necessarily linked with the adoption of a terrestrial lifestyle (Witzmann and Pfretzschner, 2003; Schoch, 2004). In *Micromelerpeton*, ontogenetic growth of the skull appears to be gradual, and the appearance of 'adult' characters (such as eyelids) simultaneous with the ongoing loss of larval features (such as the presence of external gills) suggesting that in at least some forms the transformation from larval to adult was prolonged (see Albrech, 1989).

Analysis of fossil larvae is also useful in inferring the phylogeny and evolutionary origins of amphibians. For instance, Roček's (2003) comparison of larval development in *Palaeobatrachus* and *Xenopus laevis* suggests that the two taxa are closely related. Similarly, Carroll and colleagues (1999) have extrapolated patterns of ontogeny, specifically the ossification rates of vertebral elements, from fossilized Palaeozoic tetrapods and compared them with those in modern amphibians. They note that ossification of the centra is expedited in caecilians, urodeles and lepospondyls relative to anurans and labyrinthodonts, and suggest that the anuran lineage split from basal tetrapods earlier than urodeles and caecilians.

All of these examples underscore the utility of early developmental stages of all metazoans (fossil and extant) for elucidating the taxonomic affinities, ecology and evolution of both extant and extinct taxa. The potential applications for information gleaned from fossil developmental stages, however, are not limited to the realm of palaeobiology. For instance,

fossil larvae may provide information useful to the geologist interested in climate variation or palaeotectonism. We hope this paper will serve as a general introduction on how knowledge of life history information allows us to distinguish developmental modes within the fossil record, and how fossil developmental stages contribute to discussions of the evolution of developmental forms and metazoans.

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Foiling vertebrate inversion with the humble nemertean

I'm writing this on Valentine's Day. Over the last few weeks, Americans have shown to be exemplary consumers. Obedient to the commercial precepts of this great capitalist nation, American men purportedly spent on average about 120 US dollars on gifts, candy, greeting cards and flowers, which, today, they will enthusiastically present to their wives, girlfriends and mistresses in one of the largest synchronized acts of courtship behaviour known in the world of mammals. However, lest your musings on the origins of this largest celebration of love and commitment in the Western world summon images of innocent walks in the park, and hands held at sunset, remember that current function does not necessarily speak to historical origin.

Valentine's Day has its roots less in a celebration of the subtle and sophisticated emotions of love, than in the raw carnal pleasures of the flesh, less a veneration of the sanctity of commitment, more a feast of flirting and fertility. Valentine's Day can be traced back to the ancient Roman festival of Lupercalia, or the festival of sexual licence, a yearly-celebrated purification and fertility ritual. At the heart of this ritual was the fertility god Lupercus, patron saint of shepherds, and great protector of the herds and crops. On the 15th of February Roman priests, called Luperci, would sacrifice a goat and a dog, and pieces of flayed and bloody goatskin would then be used to touch both crops and women to ensure their purity and fertility. Closely associated with the Lupercalia festival was the worshipping of Juno Februata, the goddess of women, marriage, and the fever of love. This worshipping took the form of a ritual that consisted of collecting the names of young girls in a container, which would then be picked at random by bachelor boys. The couples so constructed would be sexual partners for the coming year.

Needless to say, the Church was less than thrilled with such heathen rituals, and at the end of the 5th century (around 498 AD) the resident pope Gelasius I stepped in to sanitize these tainted ceremonies. The result was the substitution of Lupercus with St. Valentine (it remains, however, somewhat unclear who Valentine was, since the Catholic church recognizes three martyred saints named Valentine), and the lottery of sexual partners was abolished. As a result, Valentine's Day as we celebrate it today is a chimerical construct of Christian and ancient pagan traditions, retaining vestiges of both.

Well, you may ask, what has this cute little tale about the origin of Valentine's Day to do with evolution, and deriving vertebrates from nemertean worms? To understand this we will take one further step back into history. The Romans had derived their god Lupercus from the ancient Greek god Pan, who is probably better known in contemporary culture. Pan was the leader of the woodland gods known as Satyrs, and he was the presiding divinity of the Arcadians, the primordial Greeks, who lived off the fruits of the forest, and the milk and meat of their goats. We all know Pan as the symbol of unrestrained procreation and inexhaustible libido, as well as an incorrigible prankster and party animal. A typical day in Pan's life likely involved copulation with goats, or anything else that came his way, pursuing and courting the nymphs of the woods, and dancing and playing his flute, the syrinx. His appearance and his magic music had the power to incite either pan-ic or pan-demonium in unsuspecting people travelling through the forest.

The interesting point about Pan is that this Ur-hedonist embodied the intimate union of humans and animals, men and nature, for Pan and his fellow Satyrs were half man, half beast, with a human torso supported on hairy goat legs with cloven hoofs, and a bearded head sprouting horns and pointy ears. In a surprising way, then, the bestiality that marks Arcadian mythology shows that Western culture did not have to await the birth of evolutionary theory in order to be comfortable with notions about the continuity of men and animals. Indeed, before the Christian church started to exert its long history of homogenizing influence across the globe, nature worship in one form or another was widespread, and Pan's hybrid body symbolized the fundamental unity of humans and nature. Judeo-Christian theology drove a blunt wedge into this intimate embrace, creating a gaping chasm between men and nature. We were not of it, we were above it. Not surprisingly, the image of Pan as the emblem of nature's boundless diversity and productivity was transmogrified into that of absolute evil, the Devil himself.

However, in converting people to the new faith, church fathers frequently adopted the shrewd strategy of grafting new beliefs onto old pagan traditions. This explains why elements of ancient pagan mythology can still be recognized in modern Judeo-Christian theology. The Christmas tree, for example, has its origins in the ancient festivals that celebrated the winter solstice and the burgeoning increase in daylight. These celebrations were often accompanied by the exchange of gifts, which were attached to boughs of greenery that were used to decorate houses during the festivities. The church's strategy of allowing the old icons of worship to be retained, while at the same time newly reconstituting their meaning by the careful detoxification of their idolatrous connotations, certainly engendered a far lesser risk of upsetting the masses than a wholesale eradication of ancient beliefs, icons and all. Yet, the unity of men and beasts as part of a seamless natural whole seemed to have been irreparably damaged.

As a result, it is not an exaggeration to claim that for a very long time the Bible has stifled any serious attempts to reunite humanity and nature, other than in the simplest consumer–producer relationship. The great intellectual struggles of some of the most brilliant minds in the history of biology to come to grips with the seemingly irreconcilable teachings of the Bible on the origins of the world, and the accumulating facts of nature, are telling examples that it was forbiddingly difficult to make the step from observing only the peripheral twigs of nature's diversity, to a more penetrating expedition into the dark and tangled undergrowth of the primordial tree of life. You will only have to study the works of some of the greatest students of life's living and fossil diversity in the 19th century to sense the tension between revelation and observation, and to be forcefully reminded of the impenetrable boundaries of Christian metaphysics. Karl Ernst von Baer, Louis Agassiz, Georges Cuvier and Richard Owen were the greatest comparative biologists prior to the publication of the *Origin of Species*, and they certainly inferred chains of continuity between diverse organisms, formulated laws of embryonic development, and discovered parallelisms between ontogeny, phylogeny, and the fossil record. However, their wide-ranging comparisons were always resolutely restrained

within independent "types," "archetypes," or "embranchements," and it was only with the embrace of Darwinism that a synthesis was accomplished that ranged over all of life, no exceptions allowed.

For many naturalists the publication of the *Origin of Species* was the official starting shot to dive head first into the depths of phylogenetic history to trace the threads of continuity from our exalted selves to the rest of creation. However, this time it was not pagan superstition that was called upon to consecrate the new marriage, but rather the cool and calculated scientific method. This was an ideal time for inspired imagination. Darwin's theory of common descent justified the search for deep ancestors, not just the insecure dabbling on the surface of observed diversity as had previously been often the case. Moreover, comparative zoologists had compiled sufficient evidence about the diversity of animal morphology and development to form a sound foundation for further studies under the guidance of evolution. Not surprisingly, in the last decades of the 19th century these building blocks were incorporated into a rich variety of theoretical edifices, documenting the genealogical links of animal life. Especially the initiation of the programmes of evolutionary comparative embryology and morphology in the laboratories of Francis Maitland Balfour in Cambridge, and Ernst Haeckel and Carl Gegenbaur in Jena, provided a huge impetus to phylogenetic research, the goal of which during this time was virtually identical with the search for, and reconstruction of, distant ancestors. And since at this time knowledge of metazoan phylogeny, especially invertebrate relationships, was rudimentary at best, bold speculation was able to breathe life into the smallest scraps of empirical evidence to create some fantastic phylogenetic theories that could with some fairness be labelled as "myths."

Expectedly, in the decades immediately following 1859, it was the origin of our own phylum that inspired a considerable literature. In the remainder of this essay I will trace one particular aspect of the history of attempts to pinpoint the ancestors of the chordates in general, and the vertebrates specifically. In particular, I will focus on a theory of chordate origins that is little known today, and that was mostly considered, ever since its original proposal in 1883, to be at the fringe of serious phylogenetic debate. Nevertheless, the theory was revived repeatedly over the last 122 years, and it received endorsement by an unlikely succession of proponents, starting with a Dutch comparative embryologist in the 1880s, through the intermediates of a Scottish emigrant botanist in the United States in 1918, an English cytologist in the 1970s, and finally to an American comparative psychologist who started his advocacy in 1960 and carried the torch for more than 40 years into the new millennium. What, then, was this phylogenetic theory, and why did it manage to gather such a diffuse but persistent following?

The theory in question was initially devised as a response to the two most popular views on the origin of the chordates and vertebrates in the late 19th century. The first theory was erected on the basis of studies on the embryology of the cephalochordate amphioxus and the urochordate ascidians performed by the great comparative zoologist Alexander Kowalevsky during the mid- and late-1860s. Kowalevsky demonstrated that the embryology of amphioxus showed striking resemblances to vertebrate development, including the formation of pharyngeal gill slits, ectodermal folds that would form a neural tube, and a notochord. Surprisingly, Kowalevsky also discovered such typical vertebrate features in the development

of the ascidian tadpole larva. This finally allowed the ascidians to be released from their imprisonment in Cuvier's molluscan embranchement, and to be classified together with amphioxus and the vertebrates. In 1880 this new union was christened by Balfour's coining of Chordata, housing the vertebrates, cephalochordates and urchordates. Importantly, these findings established the ascidian tadpole larva as the long hoped for "missing link" (Hubrecht, 1883: 349) between the vertebrate and invertebrate domains of the animal kingdom.

However, seeking the origins of the vertebrates in their more simple looking cousins did not convince everyone. In particular, there were mounting concerns that amphioxus, and especially the ascidians, were merely degenerate offshoots from the main stem of vertebrate phylogeny. In a very vertebrate-centred interpretation, the ascidians could be regarded as nothing more than "degenerate vertebrates" (Hubrecht, 1883: 349). In 1875 Anton Dohrn and Carl Semper independently circumvented the problem of a degenerate vertebrate precursor by tracing the vertebrates back to the segmented annelids. And although this idea might seem rather fanciful to some, the annelid theory was nonetheless endorsed by several ruling minds of the time, including Karl Ernst von Baer, Berthold Hatschek and Charles Sedwick Minot.

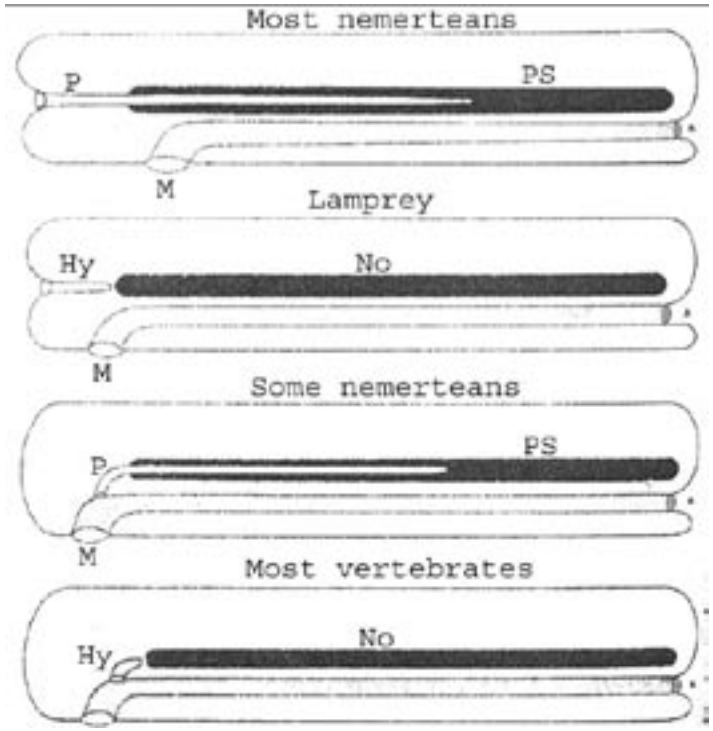
However, to some, these theories suffered from seriously debilitating defects. The ascidian theory of vertebrate origins appeared to dodge the issue of the origins of the striking chordate characteristics such as the dorsal nerve tube, and the notochord. Did we have to assume these complex structures just arose *ex nihilo*? The ascidian theory of vertebrate origins merely shifted the problem one step, rather than solving it. Surely a more penetrating expedition into invertebrate diversity was required to dig up the precursors of the chordate characteristics. Moreover, although the annelids theory appeared to do just that, it introduced another problem. Deriving vertebrates from annelid-like ancestors required the inversion of the back-to-belly axis, and the re-orientation of the anterior alimentary canal to allow the mouth to open on the proper side of the body. It seemed that all these problems could be solved at once by shifting the search image for ancestors to the unexplored realm of the lowly worms.

In 1883, as the community of comparative biologists was mourning the tragic death of Francis Balfour in a mountain climbing accident the previous year, the Dutch embryologist Ambrosius Hubrecht (1853–1915), former disciple of Gegenbaur, published his theory on the origin of the chordates from the nemerteans. The nemerteans, also known as ribbon or proboscis worms, are a group of mostly specialized benthic predators that were generally considered to be closely related to the flatworms, or platyhelminths. Incidentally, the Nemertea is the only phylum that I know of which received its name in reference to our pagan past. In 1817, George Cuvier named the first nemertean after the eponymous sea nymph *Nemertes*. In his search for a suitable chordate ancestor, Hubrecht (1883: 350) was guided by one central problem that he sought to resolve:

> "The great difficulty which is encountered in any attempt to point out a definite group amongst invertebrates most closely related to the primitive Vertebrata is the total absence of anything resembling so important and so early-formed an organ as the Vertebrate Chorda dorsalis"

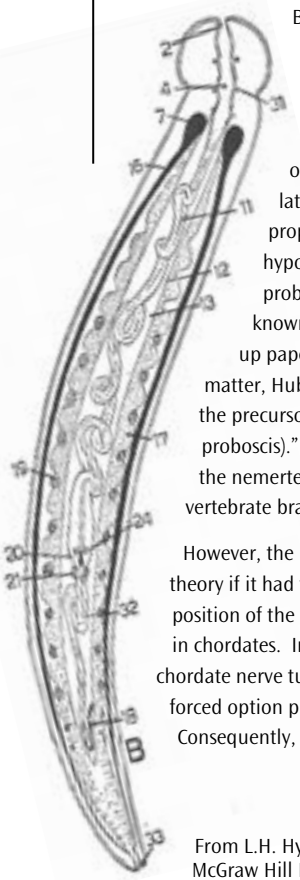
True, the ascidian tadpole larva and amphioxus possessed notochords, but these structures were fully formed, rather than merely incipient stages ready for later evolutionary elaboration. In contrast, annelids show no sign whatsoever of any structure that could reasonably function as an evolutionary precursor of the notochord.

Hubrecht solved this thorny problem with the nemertean's proboscis apparatus. The proboscis of nemerteans is an ectodermal invagination into the body, located dorsally of the digestive canal, and it can extend posteriorly for practically the entire length of the body. See the accompanying figure for schematic illustration (m = mouth; p = proboscis; ps = proboscis sheath or rhynchocoel; hy = hypophysis; no = notochord; figure modified from Hubrecht, 1883). The proboscis is invaginated into a mesodermally derived coelomic cavity, called the rhynchocoel. The proboscis can be rapidly everted through the contraction of the muscled walls of the rhynchocoel, and slung around an invertebrate prey.



At first sight, deriving the chordate notochord from the specialized nemertean proboscis apparatus might seem rather unpromising. However, as Hubrecht's schematic comparison indicates, some striking positional similarities are apparent between the nemerteans and vertebrates. In effect, Hubrecht proposed that the initially hollow proboscis sheath or rhynchocoel transformed into the vertebrate notochord by progressive filling up with cells. He adduced some evidence for this proposition by having observed that in older adults the posterior part of the rhynchocoel may have been filled with cellular material.

In addition, Hubrecht's excellent knowledge of comparative zoology allowed him to make an ingenious inference in trying to solve the origins of another, quite puzzling vertebrate peculiarity. Hubrecht noted that in vertebrates an enigmatic structure – called the hypophysis cerebri – typically develops at about the level to which the embryonic notochord extends. The hypophysis or pituitary gland was formed of two parts or lobes, with one part (posterior lobe or neurohypophysis) growing down from the developing brain, and with another part (anterior lobe or adenohypophysis) growing inwards from surface or stomodeal ectoderm. However, in the early 1880s virtually nothing was known about the important endocrinological function of the pituitary, and "the constant presence in all Vertebrates of an organ so rudimentary as the hypophysis, and about the significance of which no plausible explanation has as yet been offered" (Hubrecht, 1883: 352) was a puzzle screaming to be solved. However, since essentially nothing was known about the hypophysis' function, Hubrecht could only conclude that it was a vestige from past times, "a very ancient structure, which was once of great importance, and had a different and at the same time a more definite physiological function" (Hubrecht, 1883: 352).



From L.H. Hyman, 1951, *Platyhelminthes and Rhynchocoela*, McGraw Hill Book Company.

Because the hypophysis develops at the level of the anterior tip of the developing notochord, Hubrecht cast his eye on the anterior tip of nemertean proboscis sheath, his proposed notochord homologue. It is at this point that the proboscis meets the proboscis sheath, often at the level of the cerebral ganglion (see figure of longitudinal section of a nemertean, with the cerebral ganglia indicated as nr. 7, and main lateral nerve cords as nr. 16; from Hyman, 1951). As a result, Hubrecht proposed that the nemertean proboscis was the ancient precursor of the hypophysis. This interpretation was supported by the fact that both the proboscis and the hypophysis (at least the developing anterior lobe now known as Rathke's pouch) are ectodermal invaginations. In a later follow-up paper, and confidently confirming the old adage that sometimes size does matter, Hubrecht (1887: 644) expressed his satisfaction with his identification of the precursor of "the hypophysis cerebri as a massive and important organ (the proboscis)." At the same time, Hubrecht's theory implied homology of that part of the nemertean brain where the proboscis passed through it, with the region of the vertebrate brain where the hypophysis is located.

However, the nemertean theory would still fall into the same trap as the annelids theory if it had to rely on an inversion of the body axis to account for the different position of the lateroventral nerve cords in nemerteans, and the dorsal nerve tube in chordates. In his 1883 paper Hubrecht played with the idea of deriving the chordate nerve tube from dorsally coalesced nerve cords, but after further study, a less forced option presented itself in the dorsal nerve cords found in many nemerteans. Consequently, in 1887 Hubrecht adjusted his initial hypothesis to derive the unpaired

chordate dorsal nerve tube from the unpaired dorsal nerve cord in nemerteans. Hence, no need for vertebrate inversion, or any other "*fata morgana* that are so temptingly evoked before our eyes by the ingenious manipulations of the indefatigable founder of the first and foremost Zoological Station, when, following his lead, we find ourselves wandering in the barren deserts of that province of phylogeny in which he attempts to establish a close connection between Chordata and Annelida."

Well, you might say, "Hubrecht's theory strikes me as just as speculative, and potentially unfounded, as Anton Dohrn's day dreams. We all know that nemerteans possess the highly stereotypical spiral cleavage pattern, indicating that nemerteans are protostomes related to platyhelminths, annelids and molluscs, and without any affinities to the deuterostomes. It's not exactly good science to ignore such conflicting information…" Such an objection, however, cannot hold. Invertebrate phylogeny was still in its diapers, and it was not for another quarter century before Karl Grobben erected the theoretical fence separating Protostomia from Deuterostomia, as we basically know them today. In the 1870s and 80s it was not uncommon to find such prototypical protostomes as the polychaete annelids referred to as "Metazoa deuterostomata", as for example in the writings of Thomas Huxley. Moreover, it was only in 1892 that the famous cytologist and embryologist Edmund B. Wilson published his important paper laying out a system for labelling cells in spirally cleaving embryos that allowed cell lineage homologies to be traced between members of different phyla, thereby inaugurating the Woods Hole school of comparative cell lineage studies (Guralnick, 2002).

Hubrecht's theory, therefore, deserves to be regarded with respect and sympathy. In the 1880s it was an eminently sensible theory that took explicit issue with the tantalizingly difficult problem of the origin of evolutionary novelties, in a manner that, I think, does a better job than some of its contenders. The annelidan theory suffered from grave special pleading that had to accompany many of its imagined transformations, which were certainly more fanciful and far-fetched that those implied by the nemertean theory. Nevertheless, this didn't prevent the annelid theory from becoming more popular than the nemertean theory ever was. Although there is no space to explore this surprising finding in depth, it does reveal a very strong bias in phylogenetic thinking, that in certain contexts is still with us. The annelid theory gained a huge credence by explaining the segmentation shared between annelids and vertebrates as an homology (see also Jenner 2004). *A priori* assumptions about the homology of segmentation across the Metazoa have pressed a huge stamp on phylogenetic theorizing. Think only about the initial extreme reluctance of many to the Ecdysozoa hypothesis that tore apart the almost sacred union of annelids and arthropods that had been in place since Cuvier defined this embranchement (see Jenner & Scholtz, 2005).

However, the nemertean theory was not entirely orphaned in the 20th century. Three zealous advocates carried the theory to new highs and lows. In the sequel to this essay in the next newsletter I will discuss their ideas, and how they compare to the original formulations of Hubrecht. As we will see, what started out as a fertile and testable theory of chordate origins was gradually transformed into an *idee fixe* that was obstinately hauled against an increasing current of conflicting evidence. Stay tuned…

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PalaeoBioSuperstar

All the world's a stage, especially when gazed at widescreen. And the silver screen, complete with all-round surround sound and images that can scramble a passing retina at 500 paces, might just be the ideal medium to portray the drama of life's longest tapestry, and carry it on wings of celluloid to the widest possible audience.

That thought struck me when, long after the hype had passed, I finally got to see the striking ecostratigraphic predictions of *The Day after Tomorrow*. Now, here's where the long sweep of earth history collides with the short attention span of Hollywood, and most informed scientific input, one has been forewarned, has wound up on the cutting room floor.

Not that it's a dreadful film, by Hollywood standards. There's the brilliant lantern-jawed maverick hero scientist with work/family conflicts, the gawky brilliant adolescent offspring fighting off wolves to save his doe-eyed teenage sweetheart, the grizzled brilliant Scottish meteorologist meeting his fate with dram in hand, the clod-hoppingly stupid Vice-President denying the science until Los Angeles is trashed. All good stock characters. And maybe, on reflection, not so far-fetched at that.

What is striking in the film is the compression of climate change to meet contemporary narrative demands. Just a day or two of close-packed action and familial angst, and agroprairie and shopping malls alike are transformed into icy wastelands, flash-freezing a marine transgression in the process. Interestingly, surveys of the audience showed that they thought climate change was rather less likely than more to happen after seeing the film. Stands to reason, when you think about it. What could be scary, or serious, about *The Towering Refrigerator*?

Now the bits of science used here to buttress the case for an instant *terre gelée* was the idea of a Gulf Stream prone to switching off, which is respectable but debated, and then that hoary old bit of palaeontological near-mythology, the buttercups in the frozen mammoth stomachs. An indication of a climate instantly unhinged? Further evidence, if needed, that Hollywood understands tropical paradises far better than the mysteries of permafrost, active layers and the annual Arctic cycle, and so forgets just how productive and lush the brief Arctic Summer can be.

It's a shame that, somehow, no narrative device could be found to engineer a dinosaur or two into *The Day after Tomorrow*. The saurians have always been great cinematic crowd-pleasers. As a child I was deeply impressed by the shamelessly eclectic *One Million Years B.C.* (to which I have already paid stumbling *hommage*[1]) which didn't quite manage to mix dinosaurs and mammoths, but, in throwing in Stone Age people, giant spiders and Raquel Welch, could fairly be said to have touched all bases.

More up-to-date flim-flam came, of course, with *Jurassic Park*, which tried hard to be prescient about the science of fossilized DNA (helping fuel the debunking of dinosaur-cloning in serious journals for years afterwards) but showed a fine disregard for the geological timescale. If memory serves, six out of the eight terrible lizards pressed into service were

[1] **http://education.guardian.co.uk/higher/careers/story/0,1217084,00.html**

Cretaceous, not Jurassic. *Cretaceous Park*, of course, would not nearly have had the same sinister ring about it, so perhaps the producers simply went for poetic appeal rather than verisimilitude, perhaps loudly quoting Ralph Waldo Emerson ("petty inconsistencies are the hobgoblins of little minds!") along the way.

Is there no dinosaur epic that should not be put in the stocks and assailed with decaying vegetables by discerning movie-goers? One sixty-year old epic has, I think, worn rather well in general, and, serendipitously, perhaps even better since Walter Alvarez started playing with the geochemistry of the platinum group elements. In Walt Disney's *Fantasia*, you might recall there were two scary sections, among all the ice-sprites and winged ponies and tutu-clad hippopotami. One was the ghosts and devils of Walpurgis Night, to Mussorgky's *Night on the Bare Mountain*, which pulled few punches among the gravestones.

The other was Stravinsky's *Rite of Spring*, set to a picture of the evolution of the earth, from its beginnings to somewhere very close to 64.2 million years ago. Now *Fantasia* was seriously and ambitiously conceived, wore its educational heart very prominently on its sleeve, and obviously had benefited from some in-depth background reading. So the early solar system is not at all bad, and the Archaean is nicely phantasmagoric with its rhythmically belching volcanoes. The short subsequent clip of amoebae transmuting into fish into lizards was an ingenious way quickly to sketch in the notion of evolution, before it was time to slow down and linger on the saurians. (Enlightened days, those: some years earlier Woodrow Wilson – now I'm told an icon of contemporary US neo-Neanderthals – had said "Of course like every other man of intelligence and education I do believe in organic evolution. It surprises me that at this late date such questions should be raised.").

On to the dinosaurs. These – while not giving the impression that, given a door-handle they would instantly turn it and bound through, *Jurassic Park* velociraptor-style – were quite active enough to foreshadow Robert Bakker's interpretations (the urchin mini-dinosaur sliding playfully down a stegosaur's back; a nice touch, that). The subsequent fight between the stegosaur and the tyrannosaurus was a rare, and sobering, reminder in kids' films that the good guy doesn't always win. And then, the music reaching its umpteenth crescendo, exit all the dinosaurs for ever, amid searing air, shattered landscapes and onrushing waves. Extremely over-the-top, this bit, I used to think, smugly. Ha! The Yucatan fireball reaching half-way across the world, a calculated meteorite-generated seismic shaking of up to 13 on the Richter scale a thousand kilometres from the impact site, and the K/T tsunami deposits littering Haiti… Walt would have been amused. Stravinsky wasn't. Reputedly, on first seeing the film, and how his music had been used, he loudly termed it an abomination, or words to that effect, and stalked out. Igor was obviously a hard man to please.

Perhaps that's why, sixty years later, the Disney cartoonists tried again with Stravinsky, in *Fantasia 2000*. Now, unlike the studio-endangering, bankruptcy-threatening labour of love of the original, this was nobbut a fleabite in the contemporary Disney empire, with minimal resources trickled in, rather than poured. Even with serried ranks of computers to help the artists, the joins in the artwork show. Premiered with a fanfare? Not a chance. In the fair city of Nottingham, it had a single showing, on an obscure Saturday afternoon in an even more obscure back-street cinema.

Nonetheless, it's far better than anything else that the Disney empire has achieved in a couple of decades, possibly because the accountants knew that there would never be money in it and simply let the artists off the leash for a few days. It even achieved the near-impossibility of making me enjoy Gershwin's *Rhapsody in Blue* (alas… not quite jazz… not quite classical…) by its perfect fit with the bitter-sweet New Yorker-derived linework.

Stravinsky's music here is *The Firebird*. The theme, of course, is death followed by re-birth. The death in the film is of the landscape around a volcano, which is obviously Mount St. Helens, right down to the lateral blast. The spirit of the landscape is depicted as a benevolent sprite that conjures up the Springtime, and her sudden immolation in the onrushing wings of the firebird (alias a pyroclastic flow) caused audible gasps in the audience. In showing the post-blast devastation, and subsequent rebirth of both sprite and landscape, the cartoonists trod a fine line between mythology and ecology. Perhaps the shade of the touchy composer won't, in this case, be driven to pursue the producers with vengeful ostinati from beyond the grave.

Volcanoes are local bio-catastrophes. How can one, in these enlightened days, handle the bigger ones? Well, the K–T boundary, post-Alvarez, was depicted a few years back with zillions of dollars-worth of special effects in a film that, thankfully, I quite forget the title of. While the impact itself was impressively done, the talking, empathising, mutually affirming dinosaurs (it was a film for which the word 'anthropomorphic' could have been coined) were unspeakable.

What better? Well, if we bring extinction events closer to home, there is our very own omnipresent, continually unfolding, late Holocene (or early Anthropocene, according to some) extinction event. Here is all the drama of the clash between the short-term interests of humans and the rather longer-term interests, if that's the right word, of a functional biosphere. It's easy here to be heavily didactic, rather more difficult simply to sketch out the process. And, how on earth can a scriptwriter manage to conjure up a happy ending?

I've been impressed recently by *Princess Mononoke*, a film that Hayao Miyazake made before he carried off an Oscar with *Spirited Away*. Both films are cartoons, and possibly in the manga tradition – if I had the faintest idea what the manga tradition was, a little knowledge being often not so much dangerous as downright embarrassing. Whatever the mode of *oeuvre* these films might be in or not be in, they clearly violate the First Law of Hollywood. This, so eloquently outlined by that old celluloid hack Gore Vidal himself, states that the jaw-dropping special effects automatically get a trillion-dollar budget while the scriptwriter gets a dollar and forty cents a day plus extra cheeseburger vouchers on alternate Sundays.

Set in the Japan of a few centuries back, *Princess Mononoke*[2] could, in other hands, be a film of valiant eco-warriors battling against evil industrialists and despoilers of the landscape, and triumphing against impossible odds in the final reel: cue a fadeout of cute and/or noble forest creatures trooping back to Paradise reclaimed.

[2] Needs to be watched in the original. Neil Gaiman's subtitles aren't at all bad, and the Japanese voices are as atmospheric as one can wish for. On the other hand, new adjectives need to be thought up adequately to describe the dubbing into (and here one uses the word loosely) English.

With Miyazake at the helm, the narrative takes a quite different path. Here the despoilers are every bit as valiant as their adversaries, and their motives range from good old cynical self-interest to the preservation of a human community in times when life could only be made precious if, and only if, it became possible for it not to be taken away with such alarming ease. The forest creatures are noble in parts, but also wary, mutually suspicious and, in many cases, suicidally stupid. The eponymous princess herself, raised by wolves, is driven as much by hatred as by love of her wilderness. And the impossible odds finally prove to be, simply and inexorably, impossible. The film's a nicely tangential take on ecosystem collapse and the sixth Phanerozoic extinction, not, though, without humour (the jokes *are* good) or hope. There's always that next evolutionary re-radiation.

It's magnificent, but it's not quite, of course, palaeontology. What kind of spectacle might one wish for, or, if one was a benefactor rich beyond the dreams of Bill Gates, idly consider sponsoring? As regards humanity's current earth-scale geochemical experiment, the instant freeze of *The Day After Tomorrow* would be eschewed as counter-productive. How about, instead, a saga of a once-proud industrialist family fleeing, as generation succeeds generation, the encroaching incursion of the sea, from Baton Rouge to the Appalachian foothills, amidst increasing social disorder and sinister politics? The *Magnificent Ambersons* meets *Gone with the Wind* meets *Grapes of Wrath*. This might bring the global warming message home much more realistically.

More generally, the films about the past seem uniquely fixated upon cavemen and dinosaurs. That leaves a fair amount of geological time cinematically under-exploited. The wonderfully baroque Tertiary mammals could look very handsome on the big screen, just as they've trodden the boards lately on the small rectangular god in the left-hand corner of the living-room.

But let's go for broke. Picture the scene, then, with our rugged time-travelling hero swimming over a Silurian reef, idly stretching to pick a wriggling trilobite between thumb and forefinger. Then setting out to conquer some fiendish adversary in the deep, stagnant waters of that strangely still ocean. As he swims through the darkening waters he recoils from the poisonous stings of the graptolites circling around him. "So *that's* who ruled the seas for a hundred million years" he mutters *sotto voce* as more of the primeval, but highly organized colonies come in for the kill. The situation appears hopeless. But the lissom heroine in the clear waters high above sees his plight, and cleaves through the waters towards him like an arrow…

Bliss. Pass the popcorn. And consider the possibilities of that seriously big public outreach grant.

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Palaeo-math 101
Regression 4: Going Multivariate (Multiple Least-Squares Regression)

The analysis of relationships between two variables is highly useful, and very well understood. As we have seen, there are a plethora of models that can be applied in such instances. These emphasize different aspects of that relationship and provide us with the ability to test quite detailed and specific hypotheses. But the world is complex and, in most cases, we are interested in comparisons that can't be captured adequately using just two variables. Accordingly, analogues of the methods we've discussed so far have been developed to analyze relations between suites of variables. Because these suites are composed of multiple variables—as opposed to pairs of variables—the family of methods we're now going to discuss are useful for 'multiple variable' or 'multivariate' analysis (Fig. 1).

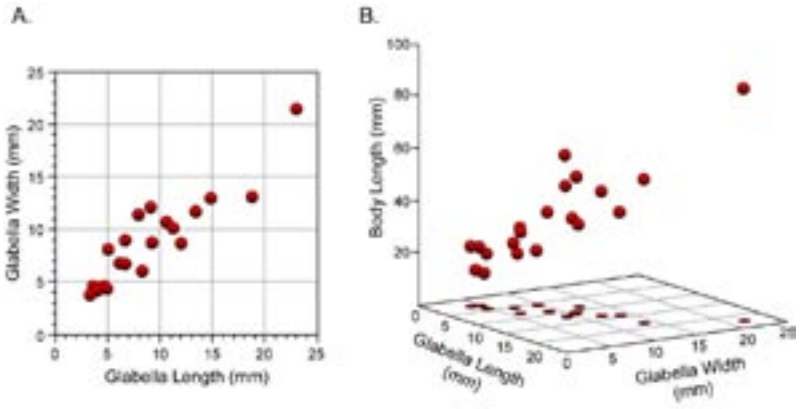

Figure 1. Geometric concepts of bivariate (A) and multivariate (B) datasets. In multivariate data analysis it is commonplace to synonymize variables in the analysis with dimensions in a coordinate system. However, this equation between variables and dimensions is implicit in bivariate analyses as well.

Multivariate methods represent a mathematical bestiary of different approaches, many of which have little in common with others. A natural taxonomy of such approaches that emphasizes underlying similarities would be useful for students and those new to the field. Conceptual differences among the various multivariate methods, however, are such that a formal taxonomy is difficult to justify objectively. Nevertheless, I've come to regard the most effective informal taxonomy as tripartite. For the purposes of this column then, we'll consider the universe of multivariate methods to be composed of 'the good', 'the bad', and 'the ugly'. This time out we're going to focus on 'the good'. Subsequent columns will take up 'the bad' (a series of columns) and 'the ugly' (also a series).

So, what do I include in 'the good' and what's so good about them? This category includes all multivariate methods based on the least-squares model. Least-squares methods are 'good' because they are grounded on well-established theory and support simple, yet powerful hypothesis tests that are often quite robust to deviations from model assumptions. You may recall we first discussed least-squares in the very first column in this series (Regression 1). Least-squares methods subdivide the variable suite into dependent and independent groupings and seek to express patterns in the former in terms of the latter according to the rule that the sum of the squared deviations of the dependent variable from the model must be minimized.

As always with least-squares methods, the distinction between the dependent variable (usually there's just one) and the independent variables is critical. Problems appropriate for least-squares analysis involve situations in which you're trying to estimate one parameter, but only have routine access to another, or a set of others. Since palaeontologists often need to perform just this sort of interpretive feat it's always been something of a mystery to me why one doesn't run across more examples of the application of multivariate least-squares methods in the palaeontological literature. This may be changing, however, in that geometric morphometrics has recently embraced the method we're going to be discussing today as part of its general-purpose, data-analysis toolkit.

Before we begin our discussion proper, let's set up a small dataset and a hypothetical problem we can use to illustrate the calculations. Our previous data are not well suited to the task of illustrating multivariate procedures in that they are bivariate data. We need more variables. So, let us add the overall length of the carapace to our glabellar measurements (Table 1, over the page). As for our problem, under many preservational conditions it is somewhat unusual to recover an entire trilobite. Isolated cephalons are much more common. There is a general relation between size of the cephalon and size of the carapace, but it would be useful to be able to estimate body size from measurements taken on the cephalon. It would also be useful to know which single cephalon measurement constitutes the best overall size proxy.

The questions I've just posed can be answered by using the multivariate extension of least-squares regression analysis. This method is usually referred to as multiple regression analysis, as if it were the only form of multivariate regression. As we have seen in our discussion of bivariate regression, such is not the case. We'll return to this nomenclatural issue in a subsequent essay. For now, we'll test also the statistical significance of the multiple linear regression using a multivariate extension of the analysis of variance (ANOVA) method we discussed last time (see Regression 3 essay in this series).

The basic equation for a multiple least-squares regression is as follows.

$$y_i = m_1 x_{1i} + m_2 x_{2i} + \ldots + m_k x_{ki} + b + \varepsilon_i \qquad (4.1)$$

In this expression y represents the dependent variable, m represents the set of partial regression slopes, x represents the set of independent variables (1 through k), b represents the y-intercept, and ε represents the error. In essence, this is the same equation we used for a linear regression, but one that has been expanded to encompass more than a single

Table 1. Trilobite Data[1]

Genus	Body Length (mm)	Glabellar Length (mm)	Glabellar Width (mm)
Acaste	23.14	3.50	3.77
Balizoma	14.32	3.97	4.08
Calymene	51.69	10.91	10.72
Ceraurus	21.15	4.90	4.69
Cheirurus	31.74	9.33	12.11
Cybantyx	36.81	11.35	10.10
Cybeloides	25.13	6.39	6.81
Dalmanites	32.93	8.46	6.08
Delphion	21.81	6.92	9.01
Ormathops	13.88	5.03	4.34
Phacopdina	21.43	7.03	6.79
Phacops	27.23	5.30	8.19
Placopoaria	38.15	9.40	8.71
Pricyclopyge	40.11	14.98	12.98
Ptychoparia	62.17	12.25	8.71
Rhenops	55.94	19.00	13.10
Sphaerexochus	23.31	3.84	4.60
Toxochasmops	46.12	8.15	11.42
Trimerus	89.43	23.18	21.52
Zacanthoides	47.89	13.56	11.78
Mean	36.22	9.37	8.98
Std. Deviation	18.63	5.23	4.27

independent variable. As with bivariate linear regression, the point of multiple regression is to find the set of partial regression slopes that minimize deviation from regression model. Once these have been determined the *y*-intercept and error terms are easily calculated.

It's always a good idea to keep in mind a geometric model of what the equations represent when performing numerical analyses. If you understand what the equations look like when graphed you can gain an important sense of intuition about both the analytic method and about the particular dataset under study. Many, if not most, mathematicians gain this sense from innate interest and long years of practice; so much so that the graphics are usually left out of most technical math articles. That's one of the things that makes them so difficult for non-mathematicians to understand. After all, the equation implies the graph so what's the point in showing the graph to an audience of professional mathematicians? The point, obviously, is that most researchers who would like to understand the math don't have the

[1] In order to include additional measurements this dataset differs from those used in previous essays.

facility of professional mathematicians for visualizing the geometric meaning of equations. This is especially important in multivariate studies that might contain large suites of variables. Fortunately, computer graphics packages are included with almost all numerical analysis packages. These tools take the drudgery, time and expense out of generating the necessary graphics. Learn to use them. They will help you.

It is not a big conceptual leap to see that the (now) familiar $y = mx + b$ linear regression equation represents a straight line usually inclined at some angle to the horizontal and vertical graph axes. Now, what does the $y = m_1x_1 + m_2x_2 + b$ multiple regression model equation look like? That model will have a dependent variable (*y*) and two independent variables (x_1,x_2). As we saw in Figure 1, these variables can be portrayed as axes in a three-dimensional coordinate system. The model has two linear slopes: one expresses variation in the x_1 vs *y* plane, and the other in the x_2 vs *y* plane. Combine these into a single three-dimensional coordinate system and (I hope) you can see the geometric model for a multiple regression analysis is a plane cutting through a cloud of points (Fig 2). This plane is oriented such that the deviation of the points is minimized along the *y*-axis. Of course, an infinity of planes with these slopes exist. You can visualize them as a stack of parallel planes above and below the one drawn in Figure 2. The particular plane that best corresponds to these data is located within this system of planes by the *y*-intercept. This is a single number because the slopes along both the x_1y and x_2y planes intersect the *y*-axis at the same point.

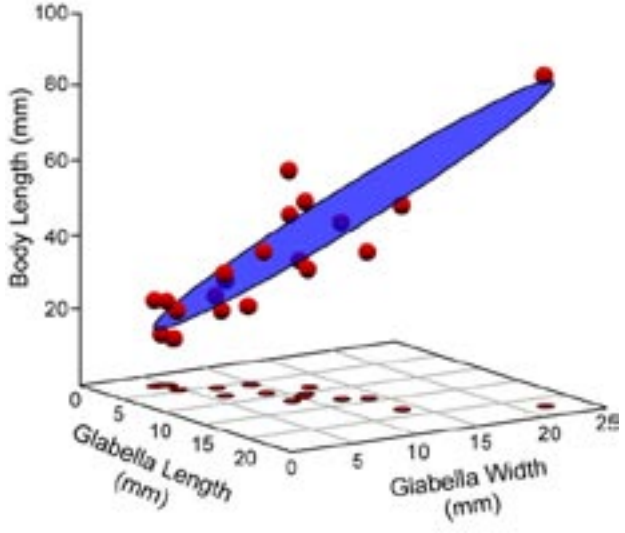

Figure 2. Because multiple linear regression includes more than a single independent variable, the result of an analysis is best visualized as a plane rather than as the line of a bivariate regression analysis. This plane (here shown in the three-dimensional space of a three-variable analysis) is defined by a series of slopes and a y-intercept value, and oriented such that deviations between the observed data points and the plane are minimized in the direction of the dependent variable (the vertical, or z-axis of this diagram).

Essentially what we need to do is solve a set of simultaneous equations, one equation for each set of observations or measurements in our system. How to do this? Say I wanted to find values of x_1 and x_2 such that the following relations were fulfilled.

$$2x_1 + 5x_2 = 19$$
$$5x_1 + 15x_2 = 55$$

The way most people would approach this problem would be to re-express these relations in their matrix form, as follows.

$$A\,X = B \tag{4.2}$$

In this expression A is the matrix of variable coefficients or weights, X is the matrix of unknown values, and B is the matrix of results. Expanding this symbolic form using our example values, Equation 4.2 becomes …

$$\begin{bmatrix} 2 & 5 \\ 5 & 15 \end{bmatrix} \mathrm{X} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} 19 \\ 55 \end{bmatrix} \tag{4.3}$$

To solve this equation we must use simple matrix algebra to isolate the unknowns on one side of the equals sign so they can be expressed in terms of known quantities. Thus, we must multiply both sides of the equation by the inverse of the A matrix.

$$A^{-1}\,A\,X = A^{-1}\,B \tag{4.4}$$

Since the product of $A^{-1}A$ is the identity matrix (I), and since the product of I with any matrix is that matrix, Equation 4.4 simplifies to …

$$X = A^{-1}\,B \tag{4.5}$$

Thus, pre-multiplying the matrix of resulting values with the inverse of the matrix of variable coefficients will give us the values of the coefficients that satisfy the expressions.

$$\begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} 3 & -1 \\ -1 & 0.4 \end{bmatrix} \mathrm{X} \begin{bmatrix} 19 \\ 55 \end{bmatrix}$$

$$\begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} 2 \\ 3 \end{bmatrix}$$

Matrix inversion and multiplication are labour-intensive processes if you try to do the arithmetic with a hand calculator, much less by hand. Fortunately, MS-Excel includes matrix inversion and matrix multiplication in its suite of functions (as MINVERSE and MMULT, respectively). One does need to be careful in that these operations can result in the generation of very large numbers that can be rendered inaccurate by truncation. Provided care is taken to transform inherently large numbers into 'normal sized' counterparts and not try to solve too large a system of equations, though, Excel should perform adequately. An example of these calculations is provided in this essay's *Palaeo-math 101* worksheet.

OK. So solving matrix equations in Excel is pretty neat. What does it have to do with multiple regression? Well, the equations that need to be solved in a multiple regression problem can be expressed—and solved—in exactly the same way. Take our trilobite data, for example: one dependent variable (Body Length) and two independent variables (Glabella Length and Glabella Width) all linked together by a set of constant values (slopes) representing the coefficient weights of the example problem above. The only real difference is that, whereas we only had two equations in the matrix-algebra example, our trilobite data are composed of twenty different simultaneous equations, one for each genus. Not only that, we know it is exceedingly unlikely all the equations will be able to be satisfied perfectly by a unique two-coefficient solution. The best we can do is estimate the general relation between our variables and use those to fit the best model we can, subject, of course, to the standard least-squares constraint.

Once we understand the logic of this basic approach we're almost there. The only piece of the puzzle we don't yet have is a way to estimate the general relation between variables. Actually, we discussed one way of approaching this estimation in the Regression 2 essay when I explained the concept of covariance. At that time, we needed a way of estimating the relation between glabellar width and length in order to calculate the major-axis regression. As you will recall from that essay, the covariance is a measure of the proportion of variance the two variables have in common. This time out we need a similar quantity, but it is computationally convenient not to base this estimate on the variables' raw values, but on their standardized equivalents (see Regression 2 for a discussion of data standardization).

The correlation coefficient is determined by normalizing the covariance calculated between two variables by the product of those variables' standard deviations.

$$r_{12} = COV_{12} \,/\, s_1\, s_2 \tag{4.6}$$

This is a dimensionless number that expresses the co-linearity of the variables irrespective of differences in their magnitude. Correlations of 1.0 signify perfect co-linearity (most often seen when a variable is correlated with itself). Correlations of -1.0 signify perfect negative co-linearity (rarely seen in observed data). Correlations of 0.0 signify perfect independence. Between these extremes lie a large range of values. The correlation coefficient is used to express the degree to which real observations approximate these end-member conditions.

Structural relations among the variables can be quantified in a correlation matrix that represents all pairwise comparisons between all variables. The correlation matrix for the three variables shown in Table 1 is shown as Table 2.

Table 2. Trilobite Measurement Correlation Matrix

	y(BL)	x_1 (GL)	x_2 (GW)
y (BL)	1.000	0.895	0.859
x_1 (GL)	0.895	1.000	0.909
x_2 (GW)	0.859	0.909	1.000

There are several things to note about this matrix. First, values along the left-right diagonal—also known as the 'trace'—are all 1.000 because these are positions within the matrix representing the correlation of a variable with itself. It should also be evident that the correlation matrix is 'square' in the sense that the upper-right triangle of values (above the diagonal trace of perfect correlations) is the mirror image of the lower-left triangle. Finally, note that, for our data, all the variables appear to have sub-equal, high correlations with one another. This is typical for correlations between morphometric measurements.

The correlation matrix embodies all the information we need to solve our multiple correlation problem. In this simple example, the simultaneous equations we need to solve are as follows.

$$1.000\, m_1 + 0.909\, m_2 = 0.895$$
$$0.909\, m_1 + 1.000\, m_2 = 0.859$$

As in the example above, these equations are in the form $AX = B$, and can be expressed in matrix form this way.

$$\begin{bmatrix} 1.000 & 0.909 \\ 0.909 & 1.000 \end{bmatrix} \mathrm{X} \begin{bmatrix} m_1 \\ m_2 \end{bmatrix} = \begin{bmatrix} 0.895 \\ 0.859 \end{bmatrix}$$

By taking the inverse of A matrix, and rearranging the matrix equation algebraically, we obtain the following relation.

$$\begin{bmatrix} m_1 \\ m_2 \end{bmatrix} = \begin{bmatrix} 5.767 & -5.244 \\ -5.244 & 5.767 \end{bmatrix} \mathrm{X} \begin{bmatrix} 0.895 \\ 0.859 \end{bmatrix}$$

Finally, carrying out the matrix multiplication we find …

$$\begin{bmatrix} m_1 \\ m_2 \end{bmatrix} = \begin{bmatrix} 0.658 \\ 0.262 \end{bmatrix}$$

These are the partial regression coefficients for the original data in their standardized form. Not only do they satisfy the equations above[2], they represent the slopes of the partial regression of x_1 on y and x_2 on y, respectively.

At this point let's be clear what we mean by *partial* regression. These values represent the average change (in standard deviation units) of the dependent variable (y) for a unit change in each of the independent variables (x) in isolation, the other being kept constant. Because these coefficients are set to the same (unitless) scale, they can be compared with one another directly. Thus, our analysis indicates Glabella Length is a stronger proxy for Body Length than Glabella Width.

[2] If you check you'll find the actual values are a little off, but this is due to the fact that I've only chosen to show you the answers to three significant figures.

Because the data in Table 1 are presented in units of millimetres, not standard deviations, we cannot use the standardized form of the partial regression coefficients to calculate the model values. Fortunately, the scalings needed to transform the values to their unstandardized, or conventional unit, equivalents are very simple, amounting to nothing more than multiplying them by the ratio of the standard deviations of the dependent and independent variables.

$$m_{\mathrm{Y}\bullet\mathrm{x_k}} = m'_{\mathrm{Y}\bullet\mathrm{x_k}} \left(s_{\mathrm{Y}}\, s_{\mathrm{x_k}} \right) \tag{4.7}$$

When these calculations are carried out for the trilobite data the m_1 and m_2 coefficients become 2.342 and 1.140 respectively. Once these have been obtained, the value of the y-intercept can be determined in the normal manner …

$$b = \bar{y} - \left(m_{y\bullet x_1}\, \bar{x}_1 \right) - \left(m_{y\bullet x_2}\, \bar{x}_2 \right) \tag{4.8}$$

… yielding the following multiple regression.

$$y_i = 2.342\, x_{1i} + 1.140\, x_{2i} + 4.029 + \varepsilon_i \tag{4.9}$$

This equation can be used as a general expression for estimating body length from glabellar length and width. The next obvious questions are: (1) how well does this regression perform and (2) is the regression statistically significant? The concepts and techniques used to answer these questions for simple linear regression were developed in the last essay (Regression 3). Fortunately, these have straight-forward analogues in multiple linear regression. The most useful single indicator of regression quality is, once again, the coefficient of determination, which, for a multiple regression, is termed the coefficient of multiple determination and calculated as follows.

$$R^2 = \sum_{k=1}^{K} r_{y\bullet k}\, m'_{y\bullet x_k} \tag{4.10}$$

In this expression K represents the number of independent variables. Thus, for our trilobite regression R^2 = ((0.895)(0.658))+((0.859)(0.262)), or R^2 = 0.814. This is quite a good result, indicating that the regression accounts for or explains over 80 per cent of the observed variation in the dependent variable. That's not a bad generalized estimator, especially insofar as glabellar length and width, on logical grounds, would seem to be somewhat independent of body length *per se*. Of course, this result only holds for this particular dataset. Inclusion of a greater variety of trilobite morphologies would, perhaps, yield a result closer to our intuition (or not?). Nevertheless, the principles and utility of the method are clearly demonstrated in this small example.

The statistical significance question is handled by the same ANOVA-based method described in detail last time. This time around, though, I'll show you a trick that will make the setting up of regression ANOVAs much simpler. Instead of calculating estimated values for the dependent variables and using these to summarize the residual variation about the regression

model, we can use the coefficient of multiple determination to calculate the necessary forms of these values directly. First, find the sum of squares of the original dependent variable observations. That value is 32,827.24 mm^2. The sum of squares of the estimated y-values and the residual y-values can be calculated directly using the following equations.

$$\sum \hat{y}_i = R^2 \sum y_i^2 \qquad (4.10)$$

$$\sum (y_i - \hat{y}_i)^2 = (1 - R^2) \sum y_i^2 \qquad (4.11)$$

Once these quantities are known, the following table can be completed and the relevant F-statistic calculated.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F-statistic
Total	32,827.24 mm^2	19	1,727.75 mm^2	
Regression	26,710.51 mm^2	2	13,335.26 mm^2	37.12
Error	6,116.72 mm^2	17	359.81 mm^2	

This is a statistically significant result. Remember, for multiple regression the degrees of freedom due to regression is equivalent to the number of independent variables and that due to the error is one less than the number of data points, less the number of independent variables. All other terms in the ANOVA are calculated as described in the Regression 3 essay.

Multiple regression is a vast topic. Many more tests and procedures exist for determining such things as whether there is a significant difference between partial regression coefficients, standard errors for various regression parameters, significance of individual variables, and so forth. Because multiple linear regression is one of 'the good' methods, there are also many sources of information about this technique. The references at the end of this essay will direct you to some useful standard presentations and summaries.

The *Paleo-math 101* worksheet that accompanies this essay provides complete Excel calculations for the example discussed above and for an additional example in which the distance between the eyes is included as a third variable in the multiple regression. Comparison of these examples is instructive, especially in terms of seeing how the answer is dependent on the number and character of the variables considered by the analysis.

One final word of caution regarding calculations. Because of the sizes of the numbers generated during a multiple regression analysis, and the complexity of the calculations, most multiple regression problems should be solved using a dedicated computer program or high-level generalized math package (*e.g.*, *Mathematica*, *MatLab*). The Excel spreadsheet supplied with this essay will solve small multiple regression problems, but its main purpose is to provide complete illustration of the calculations discussed in the text.

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Don't forget the *Palaeo-math 101* web page at

http://www.palass.org/pages/Palaeomath101.html

Norman MacLeod
Palaeontology Department
The Natural History Museum

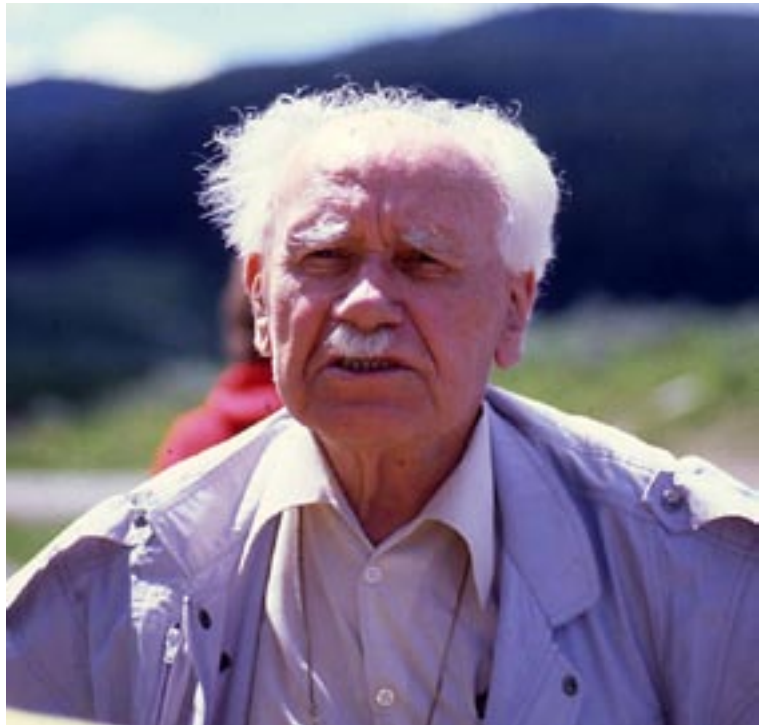
——OBITUARY——

Professor Ehrhard Voigt 1905 – 2004

The death of Professor Ehrhard Voigt (Universität Hamburg) on 22nd November 2004 brought to an end the career of a remarkable palaeontologist whose scientific publications span an incredible 80 years. Born on 28th July 1905 in Schönebeck/Elbe, Ehrhard Voigt published his first paper, on fossil bryozoans, as an 18 year-old (Voigt, 1923). Legend has it that the publisher was amazed when the schoolboy author arrived to collect his reprints. He was still working on papers when he died at the age of 99, the final one to appear while he was alive being published in 2002 (Ernst & Voigt, 2002). Ehrhard Voigt's extreme longevity as an active, publishing scientist was underscored when he once told me of how he had been visited as a young man in Germany by the American palaeontologist E.O. Ulrich. One of the famous Cincinnati palaeontologists, Ulrich is very much associated with palaeontology of the 19th Century.

Ehrhard Voigt received his schooling in Gießen and Dessau before studying geology, palaeontology, mineralogy and zoology at the universities in Halle and Munich. His mentor was Johannes Weigelt with whom he worked initially as an unpaid assistant in the Geologisch-Paläontologischen Institut of the Universität Halle. In 1929 he was awarded a doctorate for his work on the sediments of the Upper Cretaceous. Between 1930 and 1934 he led the geological excavations at the Geiseltal where Eocene lignites yielded some remarkable fossils, such as lizards with preserved red blood cells and beetles preserving striated muscles (see Voigt, 1988). His habilitation thesis, awarded in 1935, concerned the fossil fishes from the Geiseltal. In order to study the soft-bodied fossils from the Geiseltal he devised the 'Lackfilm' method for making surface peels. This was subsequently used for making pulls of soft sediment profiles, not only by geologists and archaeologists (see Voigt & Gittins, 1977) but also by artists impressed with its ability to generate 'natural canvases' of striking beauty, for example, iron-stained, multicoloured sands with pebbles and shells standing out from the background. Voigt's numerous early achievements were rewarded by his appointment as a lecturer at the Universität Halle in 1936.

From Halle he moved in 1939 to take up the chair of Geologie und Paläontologie in Hamburg. Any hopes of establishing a stable platform for his work were thwarted by the outbreak of World War 2. While serving as a geologist in the German army, his institute in Hamburg was destroyed by allied bombing and his collection of bryozoans and other fossils was lost. During the war he is rumoured to have rescued prize specimens from eastern European museums threatened with destruction by stitching them into the linings of his boots. He was captured on the eastern front and held prisoner by the Russians. That he harboured no resentment to his imprisonment is evident from his later friendships with Russian geologists which resulted in him publishing two large papers on Russian Cretaceous bryozoan faunas. In 1946 he returned to Hamburg to resume his academic career, rebuilding the institute and gradually accumulating a new and larger research collection. He was to spend the remainder of his life based in Hamburg, becoming Professor Emeritus in 1970 and continuing to undertake research until just before his death. Many scientists were welcomed by him to Parkallee 7, a large apartment which he



Professor Ehrhard Voigt photographed in the field in 1986

rented in order to be close to the University with the scanning electron microscope that became an essential tool in his research. His enormous fossil collections filled thousands of cavity slides, shoe boxes and trays distributed through almost every room of the apartment.

The scientific achievements of Ehrhard Voigt were numerous and varied. Bryozoans were his first (and indeed last) passion – he published more than 120 papers on bryozoans, the majority concerned with the immensely diverse Upper Cretaceous faunas of northern Europe. A particular focus of his research was the bryozoan fauna of the type Maastrichtian in The Netherlands. He spent many field seasons at Maastricht and amassed huge collections from the Tuff-Kreide which formed the basis for a series of systematic and palaeoecological papers. The latter included studies of the exquisitely preserved cryptic faunas encrusting the walls of pre-cementational burrows in hardgrounds. The Tuff-Kreide also provided him with a major source of bioimmured fossils (*e.g.*, Voigt, 1979a), many associated with seagrasses (Voigt, 1981a). He was the first palaeontologist to recognise the importance of bioimmuration for the preservation of soft-bodied and other delicate fossils, especially ctenostome bryozoans, hydroids and algae.

Ehrhard Voigt's contributions in other areas were similarly noteworthy. He wrote papers on synsedimentary tectonics (*e.g.*, Voigt, 1977a), the genesis of flint (*e.g.*, Voigt, 1979b), hardgrounds (*e.g.*, Voigt, 1959), Cretaceous-Paleocene stratigraphy (*e.g.*, Voigt, 1981b) and trace fossils (*e.g.*, Voigt, 1977b). His achievements were recognized by the honours bestowed upon him: he was

a fellow of the Academy of Nature Research, Leopoldina; the Academy of Science, Göttingen; the Royal Danish Academy of Science, Copenhagen; an honorary doctor of the University of Bordeaux; and a recipient of the Joachim Jungius Medal.

During later years he came to realise that he knew far more about Cretaceous bryozoans than he could ever hope to publish during his lifetime, however protracted. This caused him great anxiety, especially when old age and deteriorating eyesight hampered his ability to finish papers. Yet no matter how much knowledge has been lost with his death, Ehrhard Voigt has left us with a massive legacy in his publications and collections, the latter destined for the Senckenberg Museum in Frankfurt where they will be available for future generations to study.

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(For a more complete listing of Voigt's publications on bryozoans see **http://www.civgeo.rmit.edu.au/bryozoa/library/list/voigt.html**)

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15–16 JUNE 2005

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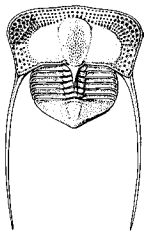


University of Leicester

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

10th Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics (CAVEPS)
Naracoorte Caves, South Australia *29 March – 2 April 2005*

The 10th CAVEPS will be held at the World Heritage listed Naracoorte Caves National Park and nearby Naracoorte township, approximately 360 km SE of Adelaide (capital city of South Australia), in the Limestone Coast region of South Australia. The Limestone Coast is well known for its Pleistocene vertebrate sites, with the most significant of these within the Naracoorte Caves World Heritage Area (serial nomination with Riversleigh, Queensland). The region is also famous for its high quality wine, wetlands and significant karst and geological features. CAVEPS is a biennial meeting of vertebrate palaeontologists from around Australia and overseas. CAVEPS 2005 will consist of three days of general sessions including papers on all aspects of vertebrate palaeontology, culminating in a two-day symposium which will focus on Quaternary extinctions and dating applications. Included in the general sessions will be a special session on cave palaeontology which will be held in the historic Blanche Cave. In addition to the main sessions, a student forum is proposed where students can present their project proposals or work in progress and benefit from professional input. The conference will be held during the AVCC (Australian Vice Chancellors Commission) common vacation week and will commence on Tuesday 29th March (Monday 28th is Easter Monday), and culminate on Saturday 2nd April.

For further details visit <**http://www.environment.sa.gov.au/parks/naracoorte/events.html**>, contact Liz Reed <**liz.reed@flinders.edu.au**> or Steven Bourne <**Bourne.Steven@saugov.sa.gov.au**>, or write to CAVEPS 2005 c/o Naracoorte Caves National Park, PO Box 134, Naracoorte South Australia 5271, Australia.

The Palms: an International Symposium
The Linnean Society and Royal Botanic Gardens, Kew *6 – 8 April 2005*

This international symposium aims to draw on recent advances by focusing on the current status of palm research both in evolutionary biology and in the environment. The symposium will take place at the Linnean Society and at the Royal Botanic Gardens, Kew. Invited papers will be given at the Linnean Society following the four main themes of:

Phylogeny & Evolution
Conservation & Sustainable Use
Structural Biology
Ecology

A poster session will be held at Kew, as well as a series of workshops, including one on bioinformatics. Tours of Kew's extensive living collections of palms and the Herbarium and Library will be available. All participants will be encouraged to present posters at the meeting.

The symposium is held in honour of Dr John Dransfield, Head of Palm Research at Kew, in recognition of his outstanding contribution to global knowledge of palms over the past four decades. John is well known as co-author with Natalie Uhl of *Genera Palmarum*, the benchmark monograph of the palm family.

To receive further information, contact <**janet@linnean.org**> (subject: **Palms 2005**) or write to the Linnean Society of London, Burlington House, Piccadilly, London W1J 0BF.

Applied Micropalaeontology: a short course
Department of Paleontology, University at Bonn *7 – 9 April 2005*

Organised by David Jutson, Gitte Laursen, Emma Sheldon and Martin Langer.

Applied micropalaeontology and biostratigraphy are integral tools in the exploration for oil and gas. Provided that the global population and economy will continue to grow at the current rate, the demand for fossil fuel energy resources will remain at a high level for at least another 60 to 80 years. This provides the economic incentive to sustain and reinvigorate training programmes in the university community to meet the future demand for stratigraphic (micro-)palaeontologists in the next several decades.

The course is designed to give the participants an introduction to, and an understanding of, the methods that have been developed to apply micropalaeontology to the requirements of the hydrocarbon industry. A full description of the various stages of drilling a well will be given with discussion of how these processes affect the sample material recovery and quality. The various techniques employed by industrial micropalaeontologists from collecting sample material to applying the analytical results will be discussed and demonstrated in practical exercises.

It is hoped that the course will give the participants an insight into applied micropalaeontological methods that will aid the understanding and application of analytical results when they are dealing with drilled material for academic or industrial purposes, and in this respect it should be particularly useful for academic researchers who undertake work for oil companies and students contemplating working in oil exploration and production. The course "Applied Micropalaeontology" is intended for geology/palaeontology students at advanced, undergraduate or early postgraduate level who have a keen interest, but little experience, in industrial and applied micropalaeontology.

Additional information and further programme details are available at <**http://www.Paleontology.uni-bonn.de/mitarbeiter/LANGER/INDEX.HTM**>

UK Meeting of IGCP Project No. 469: Variscan terrestrial Biotas and Palaeoenvironments
National Museums and Galleries of Wales, Cardiff *14 – 16 April 2005*

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

Schedule of Meeting:

14 April: Oral Presentations and Reports on Progress of Project
15 April: Morning – Oral Presentations. Afternoon – Workshops and Discussion Groups
16 April: Excursion to South Wales and Somerset (Radstock) Coalfields

Meeting Convenors:

Dr Christopher J. Cleal (<**chris.cleal@nmgw.ac.uk**>, Department of Biodiversity & Systematic Biology, National Museums & Galleries of Wales)

Prof. Barry A. Thomas (<**bat@aber.ac.uk**>, Institute of Rural Sciences, University of Wales Aberystwyth)

Meeting Administrator:
Helen Fraser (<**helen.fraser@nmgw.ac.uk**>, Department of Biodiversity & Systematic Biology, National Museums & Galleries of Wales)

Palaeobotany Specialist Group of the Linnean Society of London
Spring Meeting 2005
Linnean Society of London, Piccadilly, London *26 April 2005*

The Spring 2005 meeting of the Palaeobotany Specialist group is an open topic meeting including presentations on a variety of research areas that involve fossil plants. Time will be available for discussion on each talk. The full schedule with timings can be obtained from the Group Secretary (see below).

Talks include:

- *Progymnosperms and the Origin of the Seed* – Susan Hammond.
- *A Seed Megaspore plant from the Middle Devonian of East Greenland* – Christopher M. Berry, John E.A. Marshall, Alan R. Hemsley and Susan Hammond.

- *Two seed plant ancestors from the Middle and Upper Devonian of Belgium** – Phillippe Gerrienne and Cyrille Prestianni.
- *Molecular phylogenetics, molecular clocks and the age of the angiosperms** – Mark Chase.
- *Latest Middle Pennsylvanian tree-fern forests in lower delta-plain deposits, Sydney Mines Formation, Nova Scotia, Canada* – Howard J. Falcon-Lang.
- *"Rising from the ashes" – Fern colonisation of volcanic terrain and incipient soil development: experimental evidence and palaeoenvironmental inferences* – Jenny A. Cripps.
- *Can cuticles be used to identify conifer families?* – Tim Ewin.
- *Glacial cycles and atmospheric CO_2: evidence from Permo-Carboniferous megaspores* – Helen McGlashon.
- *Towards the development of a Palaeo UV-B proxy from fossil land plants* – Barry Lomax.

* Invited topic presentation.

The meeting rooms will be open from 9:30 with the first presentation starting at 10:00. **Please note that this meeting has been rescheduled** and now occurs the day before the one-day meeting of the Palynology Specialist Group. For further details, and to submit presentations, contact the Palaeobotany Specialist Group Secretary Jason Hilton at <**webmaster@palass.org**>.

Palynology Specialist Group of the Linnean Society of London:
Spring Meeting 2005
Linnean Society, Burlington House, Piccadilly, London *27 April 2005*

This meeting is to mark the retirement from the Royal Botanic Gardens, Kew, of former Palynology Specialist Group Secretary Madeline Harley. Speakers so far include: Peter Crane (Kew), Bill Chaloner and Margaret Collinson (Royal Holloway University of London), Hannah Banks (Kew), Raymond van der Ham (Leiden), Alan Hemsley (Cardiff), Michael Hesse (Vienna), Simon Owens (Kew). Offers of talks from people who know Madeline are welcome.

Please come along to wish Madeline well in her retirement (though I'm sure she won't be giving up palynology)!

For further details, or if you wish to attend the meeting, please contact Carol Furness, The Palynology Unit, RBG Kew, Richmond, Surrey TW9 3AE, U.K., tel: +44 (0)20 8332 5263, e-mail <**c.furness@rbgkew.org.uk**>.

Devonian vertebrates of the continental margins, IGCP 491 meeting
Yerevan, Armenia *22 – 27 May 2005*

The meeting will be dealing with all aspects of taxonomy, biostratigraphy, palaeoecology and biogeography of early vertebrates as listed in the scopes of IGCP 491: "Middle Palaeozoic Vertebrate Biogeography, Palaeogeography and Climate." Special focus will be on the neritic to hemipelagic vertebrate faunas of the Middle to Upper Devonian on the northern edge of Gondwana and their relationships to contemporaneous faunas of Laurasia and the rest of Gondwana. An IGCP 491 business meeting and a post-conference field trip to Armenian Devonian–Carboniferous sites are also planned. The meeting will be hosted by the Institute of Geological Sciences, National Academy of Sciences, Marshall Baghramian Ave., Yerevan, Armenia on 22–27 May 2005. The scientific sessions are planned for 23–25 May. A post-conference field trip of two days is proposed, on 26–27 May, to visit four Upper Devonian–Lower Carboniferous sections (Erdich and Noravank in the east of Armenia; Sevakavan and Khor Virap in the west). The approximate cost for the field trip is about US$70.

For further details, please contact the organisers, Dr Araik Grigoryan (Institute of Geological Sciences, Armenia), Dr Michal Ginter (University of Warsaw, Poland), e-mail <**fiszbit@uw.edu.pl**>, or Vachik Hairapetian (Islamic Azad University, Iran), e-mail <**vachik@khuisf.ac.ir**> or <**vh_hai@yahoo.com**>.

The Seventh International Congress on Rudists
Austin, Texas *5 – 11 June 2005*

The International Congress on Rudists calls together Cretaceous sedimentologists, palaeontologists, stratigraphers, and explorationists every three years to pursue research goals set forth in 1988 by the Cretaceous Resources, Events and Rhythms project of the Global Sedimentary Geology Programme. The 2005 Congress theme is "Cretaceous Rudists and Carbonate Platforms: Environmental Feedback." This theme will be developed in three sessions, "Depositional Environments of Cretaceous Carbonates," "Origins, Events, and Demise of Rudist Paleocommunities," and "Towards Rudist Taxonomy, Biogeography, and Phylogeny." Oral and poster sessions are planned.

Before the meeting participants will enjoy a one-day field trip to see the Texas Hill Country geology. Following the meeting a three-day excursion will give participants the opportunity to examine rudist-bearing outcrops and collect from classic middle Cretaceous carbonate buildups. The Texas Memorial Museum has developed a new exhibit of Cretaceous life, and the Museum will give access to its extensive and important collections of Cretaceous fossils for qualified specialists.

The University of Texas and the University of Tulsa will co-sponsor this seven-day conference and field trip. The John A. and Katherine G. Jackson School of Geosciences has made a very generous grant to the Congress, and the Department of Geosciences of Tulsa University is providing financial and logistical support.

To register and submit abstracts contact Debra Sue Trinque, Treasurer, 7th International Congress on Rudists, PO Box B, Austin TX 78713-8901, USA, or see the website at <**http://www.tmm.utexas.edu/npl/rudist2005/**>.

TAPHOS-05
Barcelona, Spain *16 – 18 June 2005*

The Facultat de Geologia of the Universitat de Barcelona and the Museu de la Ciència (Fundació La Caixa) are pleased to announce the celebration of the 4ª Reunión de Tafonomía y Fosilización / 2nd International Meeting TAPHOS-05 that will take place in Barcelona between 16th and 18th June 2005. The Reunión de Tafonomía y Fosilización will be celebrated for the fourth time, after the success of previous meetings in Madrid (1990), Zaragoza (1996) and Valencia (2002).

The growing number of participants in previous meetings and their variety of countries of origin show the increasing interest in this science and its utility in very different fields. The aim is to provide a periodically updated vision of the state of knowledge on the topic, which is achieved in two parallel ways: invited lectures by outstanding researchers, and poster/oral contributions by the rest of participants. In this meeting it is planned to give a great weight to participants' contributions through the organization of topic sessions coordinated by a specialist in the topic. Young researchers working in or having finished their Ph.D. concerning taphonomic aspects are particularly encouraged to participate. To register for circulars concerning this meeting send an e-mail to <**rosa.domenech@ub.edu**> with the message 'preinscription Taphos05' in the 'subject' field and including your name and complete postal address. Otherwise, further information on the meeting can be obtained by contacting the meeting secretary, Rosa Domènech, at <**rosa.domenech@ub.edu**>.

American Association of Petroleum Geologists Annual Convention
Calgary, Canada *19 – 22 June 2005*

At this meeting, the North American Micropaleontology Section of SEPM (NAMS) will sponsor a poster session on the 'Integration of Micropaleontology and Petroleum Exploration.' This session falls within AAPG Meeting Theme 5: 'Depositional Systems in Time and Space.' The NAMS session will be co-chaired by Dave McNeil (Geological Survey of Canada, Calgary) and Pete McLaughlin (Delaware Geological Survey/University of Delaware, NAMS President), who extend an open invitation to micropalaeontologists to submit an Abstract for consideration and come to Calgary to attend this major international conference. Our AAPG 2005 session topic was chosen so that virtually any aspect of micropalaeontology within any hydrocarbon basin from around the world could be included. The deadline for Abstract submission is 12th November 2004. We encourage you to present your data and interpretations, which we feel are important to understanding 'Depositional Systems in Time and Space.' Please note that last-day traffic for submissions is heavy and can cause 'gridlock.' If at all possible, don't procrastinate – submit before the last day!

Visit the meeting website for further details, at <**http://www.aapg.org/calgary/index.cfm**>.

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

The meeting will include field trips to Horton Bluff (Dev/Carb boundary: early tetrapod trackways), Wassen's Bluff (Tria/Jur: link fossil between dinosaurs and mammals), Joggins (Carboniferous: world heritage site), and Arisaig (a world class Silurian invertebrate site). Major field trips will include the Gaspé Peninsula (Quebec). The local organizer is David B. Scott (Centre for Environmental and Marine Geology, Dalhousie University, Halifax, Nova Scotia B3H3J5 Canada). The meeting website is at <**http://www.dal.ca/~es/staff/dbscott/scott.htm**>.

Sixth International Crustacean Congress
University of Glasgow, Scotland, UK *18 – 22 July 2005*

The conference is organised on behalf of the International Crustacean Council by The Institute of Biomedical and Life Sciences, University of Glasgow. The Meeting will also host the 5th European Crustacean Conference, the 4th Crustacean Larval Conference, and the 2005 Summer Meeting of the Crustacean Society. For more details see <**http://www.gla.ac.uk/icc6/**>.

The Fifth International Brachiopod Congress
Natural History Museum, Denmark; University of Copenhagen *4 – 8 July 2005*

The Copenhagen conference follows the successful meetings in Brest (1985), Dunedin (1990), Sudbury (1995) and London (2000). The main events, lectures and posters will be held in the Geological Museum of the University of Copenhagen. The Museum has a strong tradition in palaeontological research particularly in the Arctic and Baltic regions. The congress is being organised by David Harper (Chair), Lars Holmer, Sarah Long, Claus Nielsen and Nina Topp. There will be a pre-congress field excursion to Gotland and two post-congress field excursions, one to Jutland and one to Estonia. For more details see <**http://www.nathimus.ku.dk/geomus/**> or e-mail David Harper at <**dharper@savik.geomus.ku.dk**>.

II Latin American Congress of Vertebrate Paleontology (II CLPV)
Rio de Janeiro *10 – 12 August 2005*

The Museu Nacional/UFRJ will host the event. For further information, see <**http://acd.ufrj.br/mndgp/2clpv/en/**>.

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

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

Algorithmetic Approaches to the Identification problem in Systematics
Natural History Museum, Cromwell Road, London *19 August 2005*

Sponsors: The Systematics Association and The Natural History Museum, London.

The automated identification of biological objects (individuals) and/or groups (*e.g.*, species, guilds, characters) has been a dream among systematists for centuries. Despite much preliminary work in the 1950s and 60s, progress in designing and implementing practical systems for fully automated object identification has proven frustratingly slow. However, recent developments in computer architectures, and innovations in software design, have finally provided the tools needed to make the development of generalized, automated, specimen and/or group-identification systems a practical reality. In order to summarize the current state-of-the-art in automated group-recognition systems, and assess their potential to make practical contributions to systematics and taxonomy both now and into the future, the Systematics Association and The Natural History Museum, London have agreed to sponsor a free, one-day symposium, to he held in the Flett Theatre of The Natural History Museum, London on 19th August 2005.

The purpose of this symposium is to provide leaders of research groups, researchers, post-doctoral research assistants, and students working or studying in any area of systematics with an opportunity to (1) learn about current trends in quantitative approaches to the group-recognition problem, (2) become familiar with the capabilities of various software systems currently available for identifying systematic objects/groups and (3) evaluate various applications of this technology to present and future systematic problems. Special attention will be paid to showing how different approaches to automated identification can be applied to various organismal groups and in various applied research contexts (*e.g.*, biodiversity studies, biostratigraphy, conservation, agriculture, curation). Ample programme time will also be provided for discussions of issues relating to how these approaches and technologies can play a larger role in meeting the needs of current and future systematists.

This free symposium is being held in association with the Biennial Meeting of The Systematics Association which begins on Monday 22nd August 2005 at the University of Cardiff. Attendees of the Systematics Association meeting are encouraged to include attendance at this symposium in their Biennial Meeting plans.

If you would like to attend this symposium, provide a demonstration or contribute a chapter to a book of collected technical articles, please send your contact details to Norman MacLeod, Palaeontology Department, The Natural History Museum, Cromwell Road, London SW7 5BD (tel: +44 (0)207 942-5204/5295, fax: +44 (0)207 942-5546, e-mail: <**N.MacLeod@nhm.ac.uk**>. A symposium website is also available at <**http://www.nhm.ac.uk/hosted_sites/paleonet/aaips_symposium/**>.

6th Baltic Stratigraphic Conference
St. Petersburg, Russia *22 – 26 August 2005*

The Conference will be held at the A.P.Karpinsky All-Russian Geological Research Institute (Sredniy prospect 74) and St. Petersburg University (Universitetskaya nab. 7/9 and 16 Liniya 29). The scientific sessions and workshops are planned on 23–25 August. Pre-conference field trips (Lower Paleozoic and Carboniferous) will take place on 19–21 August, post-conference field trip (Devonian) on 26–28 August. In parallel with the scientific session, a business meeting of the IGCP 491 Project 'Middle Palaeozoic Vertebrate Biogeography, Palaeogeography' will be held. The main issue of the Conference will be every kind of problem relating to the sedimentary basin stratigraphy of Baltic and neighbouring regions. The number of sessions and topics of symposia could be specified according to the preferences of registered participants. Participants are invited to submit abstracts of both oral and poster presentations that will be published in a special issue. For further details please contact Andrey Zhuravlev, e-mail <**stratigr@mail.wplus.net**>, or Alexander Ivanov, e-mail <**aoi@AI1205.spb.edu**>.

IGCP 491 meeting: Middle Palaeozoic vertebrates of Laurussia; relationships with Siberia, Kazakhstan, Asia and Gondwana
St. Petersburg University, Russia *22 – 26 August 2005*

In conjunction with the 6th Baltic Stratigraphical Conference.

The meeting will deal with any aspect of research on Middle Palaeozoic vertebrates (taxonomy, morphology, palaeogeography, palaeoecology, biostratigraphy), with a focus on the vertebrate fauna of Laurussia and its relationship to the faunas of other palaeogeographic provinces. Participants are invited to submit abstracts for both oral and poster presentations (details below). An abstract volume will be published as a Special Publication of *Ichthyolith Issues*.

The IGCP meeting is organised by the Department of Palaeontology, St. Petersburg University. For further details, contact Dr. Alexander Ivanov Department of Palaeontology, St. Petersburg University, e-mail <**aoi@ai1205.spb.edu**>.

7th International Symposium on the Cretaceous
Neuchâtel, Switzerland *5 – 9 September 2005*

The meeting will be held in the University of Neuchâtel.

For more details see <**http://www.unine.ch/geologie/isc7/**>.

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

The First Circular can be downloaded from the Symposium website. We will offer a number of field trips with various contents (stratigraphically and ecologically), each also including an extensive touristic and cultural programme. Please have a look at our website at regular intervals, at <**http://www.palaeo.de/iso15/**>. We are perpetually updating and extending these pages, in order to inform you about congress, programme, excursions, accommodation possibilities *etc*., to be as complete and up-to-date as possible.

Seventh International Workshop on Agglutinated Foraminifera
University of Urbino, Italy *2 – 8 October 2005*

This Workshop will be held at the Scientific Campus of the University of Urbino. For further information please contact Rodolfo Coccioni <**cron@info-net.it**>.

IGCP 469 Late Westphalian terrestrial biotas and palaeoenvironments of the Variscan foreland and adjacent intramontane basins
Bucharest, Romania *7 – 13 October 2005*

In October 2005, for two days, the IGCP 469 meeting will be held in Bucharest, hosted by the Faculty of Geology and Geophysics, University of Bucharest. The meeting will include presentations, collection surveys and a practical workshop attended by Romanian students in Geology. A field trip in the South Carpathians, organized for visiting Upper Palaeozoic formations of the Resita, Sirinia and Presacina Basins, is scheduled after the talks in Bucharest.

For further information, see University of Bucharest at <**http://www.unibuc.ro/en/home/**> or the Faculty of Geology and Geophysics at <**http://www.gg.unibuc.ro/index_main.html**>.

Paleontological Society Annual Short Courses at GSA 2005
Salt Lake City, USA *16 – 19 October 2005*

Organiser: Bruce Lieberman.
Palaeobiogeography: Generating New Insights into the Coevolution of the Earth and its Biota
For more details see <**http://www.paleosoc.org/futureprograms.html**>.

65th Annual Meeting of the Society of Vertebrate Paleontology
Phoenix Marriott, Mesa, Arizona, USA *19 – 22 October 2005*

Further information is available at <**http://www.vertpaleo.org/meetings/**>.

Submit abstracts at <**http://www.vertpaleo.org/abstracts/**>.

Palaeobotany Specialist Group of the Linnean Society of London
Autumn Meeting 2005: New discoveries in old collections
Linnean Society, Burlington House, Piccadilly, London *26 October 2005*

This one-day meeting will focus on the continuing nature of discovery in historically collected fossil plant collections. Potential speakers are asked to contact the meeting organiser, Dr Chris Cleal, directly, by e-mail to <**chris.cleal@nmgw.ac.uk**> (National Museums and Galleries of Wales).

9th Symposium on Mesozoic Terrestrial Ecosystems
Manchester, UK *27 – 29 June 2006*

The 9th Symposium on Mesozoic Terrestrial Ecosystems and Biota (sponsored by the Palaeontological Association) will take place at the University of Manchester, England, from 27th to 29th June 2006, with optional field trips before and after the scientific meeting. Full details, key dates, contacts, and a pre-registration form can be found on the MTE website at <**http://homepage.mac.com/paulselden/MTE/**>.

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

Following the successful meeting at Oxford in April 2001 it was thought a good idea to spread the sequence of these gatherings to the Southern Hemisphere. Accordingly you are now invited to the Fourth International Meeting on Trilobites and their Relatives to be hosted in the Queensland Museum, Brisbane, Australia. The Queensland Museum dates from the 1860s.

Although it had an emphasis on vertebrate palaeontology until the 1970s it has recently become home to the large earth sciences collections of the University of Queensland and the Geological Survey of Queensland. Most significant among its holdings is the very large amount of Cambrian trilobite material collected by Frederick William Whitehouse during the 1920s to 1940s.

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

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

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

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

Organising Committee :

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

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

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

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

Palaeobotany Specialist Group of the Linnean Society of London, Spring Meeting 2006: A life of ferns and seed ferns
Montpellier, France *July 2006*

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

7th European Palaeobotany–Palynology Conference (EPPC)
Prague, Czech republic *6 – 11 September 2006*

For further information, see <**http://www.natur.cuni.cz/eppc2006/circular.pdf**>.

The International Symposium on Foraminifera (FORAMS 2006)
Piramide Palace Hotel, Natal *10 – 15 September 2006*

Technical sessions will consist of four days of talks and posters (11–12, 14–15 September), supplemented by social events. For further information, see <**http://www.labgis.uerj.br/forams2006/general.htm**>.

66th Annual Meeting of The Society of Vertebrate Paleontology
Ottawa, Canada ***18 – 21 October 2006***

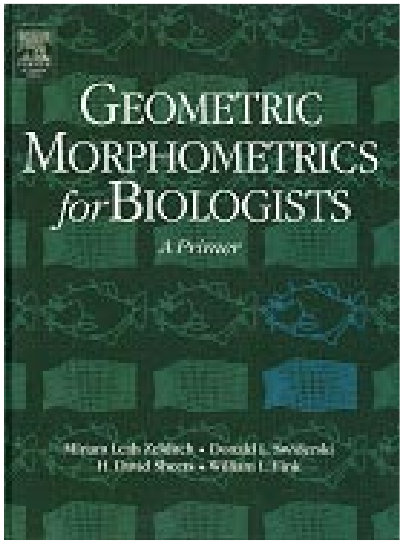
Location: Marriott Ottawa (Headquarters Hotel) and Crowne Plaza Ottawa. For further information, see <**http://www.vertpaleo.org/meetings/future_meetings.html**>.

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

Book Reviews

Geometric Morphometrics for Biologists: A Primer

Miriam L. Zelditch, Donald L. Swiderski, H. David Sheets, and William L. Fink (2004). Elsevier Academic Press, New York and London. ISBN 0-12-77846-08, £36.61/$69.95 (hardback).



Morphometrics is a seductive mistress. Despite its current popularity, and despite concerted attempts to explain the revolution that occurred in its practice during the 1980s and 90s, it still lulls nascent practitioners down the garden path of apparent mathematical sophistication. In return they are often left bereft and bewildered, having squandered their time carrying out simplistic analysis without engaging with the mathematics on which the discipline is grounded (limiting their ability to address novel future data-analysis challenges) and without gaining much insight into the biological processes that are supposed to be the focus of morphometric investigation. This, along with morphometrics' historical link to phenetics, leaves morphometrics often resembling an academic ghetto that graduate students and advanced undergraduates are sometimes encouraged to visit – to pick up some street smarts and a bit of local colour – but cautioned not to linger in; especially after dark.

The current book, by three prominent practitioner-systematists and a physicist-software/methods developer, seeks to present an overview of geometric morphometrics in primer mode. Primers are supposed to keep detailed exposition to a minimum while conveying a sense of what can be done using particular methods. They are, in an important sense, written to be the first word in the presentation of a topic, not the last. These authors set out to write such a book for the audience best positioned to appreciate a primer: those with no more than undergraduate mathematical training who want an emphasis on applications rather than theory. Certainly there is a need for such a treatment, as was originally noted by Bookstein (1996). The canonical modern morphometric texts (*e.g.*, Bookstein 1991; Small 1996; Dryden and Mardia 1998, Costa and Cesar 2000) are too technical and abstract to be fully understood by those not interested in making a commitment to the mathematics. At the same time, collections of generalized applications articles (*e.g.*, Rohlf and Bookstein 1990; Marcus *et al*. 1993, Marcus *et al*. 1996; Elewa 2004) are too eclectic and lack the unified focus necessary to be used as comprehensive introductions, while the special-topics collections (*e.g.*, Adrain *et al.* 2001; Zelditch 2001, MacLeod and Forey 2002) are too focused and contain too much non-morphometric material. But is this the primer we've all been waiting for?

At best, the authors' purpose has been only partially realized by the product of their labours. Many years ago Wilson and Bossert (1971) managed to write a brilliant primer of population biology in a scant 192 pages. More recently, Bryan F.J. Manley (1994) produced a highly useful primer of multivariate statistics in a mere 215 pages. Tipping the scales at 437 pages, *Geometric Morphometrics for Biologists* can hardly be called concise.

Part of the problem here may be that these authors intend their book to be used as a primary course text. This is not the traditional purpose of a primer. Nor is it a realistic course option in the biology or palaeontology programmes of most universities, pressed as these are to integrate topics from a large number of specialist fields. This desire to be a textbook – instead of a genuine primer – also explains the curious weight given to mathematics (the text contains over 200 equations, many of them complex matrix-algebra expressions, but neglects to include any description of elementary matrix algebraic operations) and theory (encompassing 261 of the 407 text pages *sensu stricto*) in what the authors describe as a non-mathematical, applications-based treatment.

Topically, *Geometric Morphometrics for Biologists* is divided into three parts: (1) basics of shape data, (2) analyzing shape variables, and (3) applications of morphometric methods to complex hypotheses. A final, small section discusses the analyses of coordinates located in three dimensions (usually a trivial mathematical extension of the 2D case) and the analysis of outlines (an enormous subject in its own right that is barely touched upon in this book; see Lestrell 1997). In keeping with the exclusivist philosophy that has done so much to mar the intellectual reputation of morphometrics, the book is actually about landmark-based morphometrics, which the authors treat both as if this school encompasses all morphometrics and as if it is one school of thought among many. A similarly biased text appeared a few years ago from the outline school (Lestrell 2000). Geometric morphometrics is unified at a very basic level by the theoretical implications of Procrustes superposition. But neither this unity, nor the manner in which other approaches to morphometrics are related to geometric methods, is ever made clear here.

Part 1 encompasses a discussion of landmarks (Chapter 1), shape variables (Chapter 2), shape theory (Chapter 3), superimposition methods (Chapter 4) and thin-plate splines (Chapter 6). The treatment of landmarks as a concept follows the more-or-less standard line that landmarks are both biological and topological homologues. Recent arguments disputing this stance (*e.g.*, MacLeod 1999, Humphries 2002) are not considered other than to assert "if discrete and recognizable structures are [biologically] homologous as structures, the discrete and recognizable locations on them are arguably [biologically] homologous as points" (p. 26). Such arguments from analogy confuse the ends of an analysis with the means by which these ends are accomplished. In the vast majority of cases it really doesn't matter whether topologically corresponding landmark locations are formal homologues or not, insofar as the landmarks need only be regarded as mathematical conveniences used to compare the relative positions of structures, which will always have a far less ambiguous claim to being actual homologues than do infinitely small point locations on structures. The simple fact that small random displacements of landmark locations have little effect on the overall analytic result is sufficient

to demonstrate how 'beside the point' the assertion of 'point homologies' really are. Of course, it is also a simple matter to envision datasets composed of landmark locations collected from functionally equivalent structures (*e.g.*, bird wing, bat wing, pterodactyl wing; porpoise body, shark body, ichthyosaur body) that could be subjected to landmark-based morphometric analysis, but which would specify demonstrably non-homologous comparisons. The authors seem to acknowledge this implicitly on the same page when they state, somewhat awkwardly "For a deformation to make mathematical sense, the points on one form must correspond to the points on another." Suffice it to say that topological correspondence is not necessary and sufficient evidence to infer homology, and that the point of a morphometric analysis is not to understand deformations mathematically, but biologically. The difference is subtle and not widely appreciated, but important.

In this chapter we also learn that a collection of shapes too distinct to be represented by numerous landmarks is not suitable for 'morphometric analysis' (p. 27). That outline-based methods have been used profitably to summarize precisely such complex patterns of morphological variation for many years, even within the context of geometric morphometrics *sensu stricto* (*e.g.*, Bookstein 1996a, 1996b) is not mentioned. The fact that these authors also discuss non-Procrustes-based outline-analysis methods later in their book (see p. 395) as though they represent alternative, geometric morphometric approaches simply adds to the reader's confusion. This section closes with a lengthy digression into the optics of cameras and digital image processing that, while related to the general topic of morphometric data collection, has little to do with landmark theory *per se*.

The same type of organizational anarchy finds expression throughout Part 1; indeed throughout the entire book. For example, the section on the 'statistics of shape coordinates' (p. 57–58) refers to multivariate analysis of variance (MANOVA) and Hotelling's T^2 test without explaining what either of these concepts are, or even cross-referencing them to (in this case) a chapter-long discussion provided later in the text (Chapter 9). At the end of the main methods chapters the smooth flow of the narrative is repeatedly broken by sections constituting an internally serialized user's guide for David Sheets' MathLab-based Integrated Morphometrics Programs (IMP) package. Few practising landmark morphometricians use the IMP package, and the decision to feature it over the simpler, more widely used, and more regularly updated public-domain software produced by F. James Rohlf (see **http://life.bio.sunysb.edu/morph/**) seems ill-advised, at least for the standard Procrustes-based methods.

On the positive side, the chapters on shape theory, superimposition methods, and the thin-plate spline are all quite good overall, with the shape-theory chapter being truly outstanding since much of this material has only been accessible to date in highly mathematical dissertations or (curiously) as part of the Help system in the Rohlf software packages. The thin-plate spline chapter also uses many useful analogies and examples that will greatly help students gain familiarity with the concept, and confidence with the interpretation of principal/partial warps. However, since this chapter is so successful in terms of the qualitative presentation, it seems more than a bit odd that the authors chose to drop a 37-expression-long algebraic derivation of partial warps into the middle of an otherwise excellent qualitative presentation. Such technical detail is unwarranted in a primer; superior mathematical discussions are available elsewhere, and, most

seriously, the abrupt shift in presentation style will likely put many prospective readers off the entire chapter, much to their loss. Curious also is the authors' failure to provide any but the most rudimentary discussion of relative warps, which most practitioners find at least as useful as partial warps for achieving ordinations of objects in a linear shape space (but see Zelditch *et al.* 1995 and Rohlf 1998 for clues as to why the expected discussion of relative warps is virtually absent).

Part 2 provides an overview of multivariate ordination methods (Chapter 7), computer-based statistical methods (Chapter 8), multivariate analysis of variance (Chapter 9), regression (Chapter 10) and partial least-squares analysis (Chapter 11). Despite its title, Chapter 7 treats only principal components analysis (PCA) and canonical variates analysis (CVA). Inclusion of PCA is an obvious choice since so many of the 'warp' procedures are based on this numerical analysis method. The authors' presentation is basic, but good. Canonical variates analysis is a somewhat more unusual choice insofar as it is not the basis for any warp-based method and indeed violates one of the basic tenets of the shape theory on which geometric morphometrics is grounded.

As the authors discuss in Chapter 3, a – perhaps *the* – basic aspect of the morphometric synthesis that is geometric morphometrics was the realization that the correct basis of shape comparison was not the set of 'individual variables' as they would be construed in classic multivariate data analysis (see Manley 1994), but the abstracted shape itself as represented by n different landmarks. Thus, for the purposes of geometric shape comparison, a triangle of landmarks (Fig. 1A) is not a collection of three scalar distances (d_1, d_2, d_3) or six coordinate locations (x_1,y_1; x_2,y_2; x_3,y_3). It is a single variable that exists in a non-linear space or 'shape manifold'. This manifold quantifies the relative positions of all possible combinations of shapes that can be formed from three landmarks (Fig. 1B). In order to ordinate a set of triangular shapes correctly

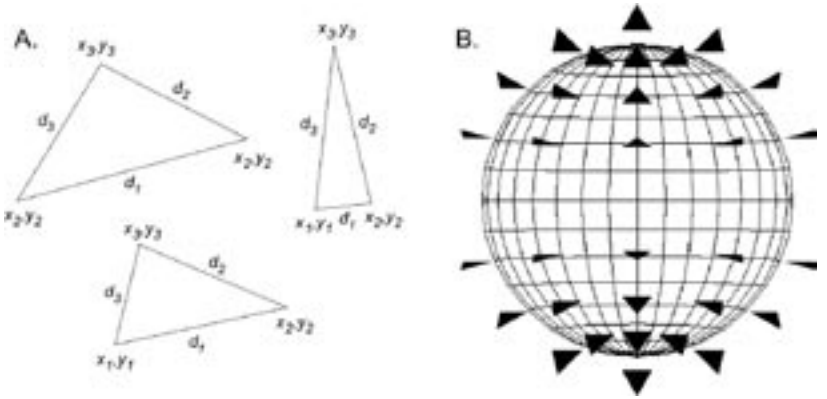


Figure 1. Alternative concepts of morphometric variables. A. traditional multivariate morphometric view of variables as either three inter-landmark distances (d_1, d_2, d_3) or six coordinate locations. This representation confounds size and shape variation. B. Geometric morphometric concept of shape variation in which shapes themselves are regarded as the variables. Here, a representation of the shape manifold for all Procrustes registered triangles can be visualized as a sphere. On the surface of the sphere all possible combinations of triangles may be arranged such that distances from each other are scaled to the deviation from the mean shape in any direction summed over all three coordinates (= the Procrustes distance).

one must locate them on the shape manifold (an operation accomplished by Procrustes superposition), and project the positions of the observed triangles on to a linear plane oriented such that it is tangent to the three-landmark shape manifold at some position that makes sense with respect to the analysis (*e.g.*, the mean shape). Operationally, this is accomplished in much the same way that three-dimensional coordinate positions on the Earth's surface are projected on to a piece of paper to construct a flat map. By taking advantage of this mathematical formalism, the resultant linear ordinations have the very desirable property[1] of allowing one to 'see through' their structure and 'sense' the geometry of shapes on the surface of the underlying shape manifold. However, the non-isotropic transformations used in canonical variates analysis to represent correctly distinctions between the within-groups and between-groups covariance matrices distort scaling relations within the shape tangent plane. Because of this it becomes impossible to make geometric interpretations of shape distributions within that plane that are accurate pictures of the underlying shape manifold. It's as if the canonical variates tangent plane had turned from a pool of clear water (the PCA-case that forms the analytic basis for principal, partial, and relative warps) into a funhouse-mirror-like lens that stretches this space in one region and compresses it in another, giving a wholly inaccurate picture of the underlying – and already complex – non-Euclidean spatial relations. The authors fail to point out this problem. Readers might be left with the impression that there is less difference between PCA and CVA with respect to the way each handles landmark data than is actually the case.[2]

Chapter 8 is really about resampling methods (*e.g.*, bootstrapping, jacknifing, Monte-Carlo simulation) that can be used to create probability density distributions for use with generalized shape-based hypothesis testing. Once again, these are basic but competent reviews. The obvious omission here is the lack of even a mention, much less a discussion, of the Mardia-Dryden shape similarity test (Mardia and Dryden 1989), which was the first such test formulated under the rubric of geometric morphometrics, and which is a far more simple and direct method of assessing shape similarity than any of the techniques they discuss. Much the same can be said of the chapters on multivariate analysis of variance (MANOVA, Chapter 9) and regression analysis (Chapter 10, which includes sections on bivariate and multivariate regression). These are, again, competent reviews with well-chosen examples that show how these methods can be used to evaluate morphometric hypotheses. It does seem unusual, though, to see a more advanced topic like MANOVA presented before regression analysis; especially insofar as ANOVA and MANOVA are routinely used to evaluate the results of bivariate and multivariate regression analyses respectively (see my PalaeoMath columns for an example of a more traditional presentation). This section concludes with a discussion of partial least-squares analysis, another – albeit an even more esoteric – technique that can be used to assess the covariance between shape variation and variation in a variety of external variables (*e.g.*, ontogeny, ecology, geography). This advanced numerical analysis method has huge potential, but its really adequate presentation – of which this is not, as it lacks the background material necessary for true understanding – is well beyond the scope of what's needed in a primer.

[1] For objects that may be represented by the same number of corresponding landmarks and are all basically similar in shape.

[2] See Klingenberg and Montiero in press for an attempt to address the problem of landmark-based CVA analysis within the context of geometric shape theory.

The third section reviews example applications of morphometric analysis to the issues of morphological disparity (Chapter 12), evolution and development (Chapter 13) and systematics (by which the authors mean species and character recognition, Chapter 14). Instead of using examples from the technical literature, the authors have opted for the presentation of example analysis. While this has the advantage of allowing the authors to go into more depth with the specific examples selected for presentation, to do this they have sacrificed much consideration of the breadth of studies that are undertaken in these areas; a deficiency that could have been mitigated by adding either introductory or concluding sections that reference other studies in these fields. Of these three chapters, all of which will repay a close reading, I think the chapter on ontogeny and evolution – the long-standing interest of Fink and Zelditch – holds up best. The text is rounded off by a short glossary of technical terms, a bibliography, and an index.

As I hope I've made clear, I have mixed views about the authors' success in achieving their stated aims. I'm quite sure *Geometric Morphometrics for Biologists: A Primer* will be popular among those who are predisposed to morphometric approaches to data analysis. This, of course, should include a fair number of palaeontologists. For those who plan to make a career in this field it should be regarded as required reading, as much for its failures as its successes. The danger here, of course, is that some may regard the methods descriptions and example analyses as standard exemplars of good morphometric practice. Suffice it to say that, in many cases, the advice and examples provided are controversial among other experienced practitioners.

Should members of the Palaeontological Association buy a copy? Probably not, at least not just now. Make sure your library orders a copy so you have access to one. Competition in this market will likely hot up in 2005 or 2006 when a much anticipated and more comprehensive text, currently being written by F. James Rohlf, is published. Unless you are already committed to the field, I'd put off making a decision regarding the best general morphometrics reference book – for *Geometric Morphometrics for Biologists* is not a primer – to buy until a comparison can be made with the Rohlf book. If the latter turns out to be a specialist mathematical treatise, *Geometric Morphometrics for Biologists* will have to do for the moment. On the other hand, if the Rohlf book turns out to be written and organized along the lines of Sokal and Rohlf's (1995) highly respected *Biometry*, it will surely give *Geometric Morphometrics for Biologists* more than a run for your money. Still, both will probably be overkill in terms of what the causal practitioner really needs, which is that short, simple, low-cost primer Bookstein alluded to back in '96.

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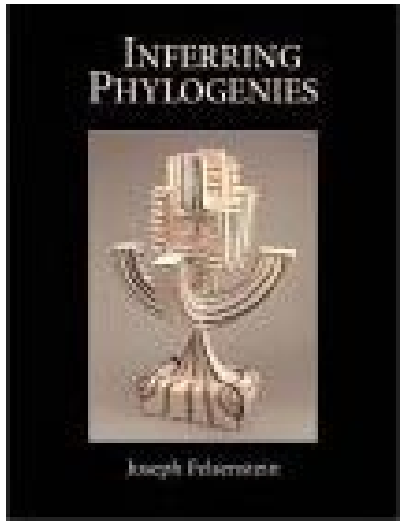
Inferring phylogenies

Joseph Felsenstein (2004). Sinauer Associates, Inc., Sunderland, MA. 0-87893-177-5, £33.99 (paperback)



I first became aware that there were rigorous methods that could be applied to build trees when I was a graduate student back in the late 70s. The philosophical turmoil that had erupted between cladists, pheneticists and evolutionary biologists was in full swing and the implications were slowly filtering through into palaeontology. Although parsimony, likelihood and distance computer programs were all available by that time they were certainly not mainstream, and in palaeontology, trees were almost always hand-crafted, based on consideration of a few 'key' characters.

How very different it all is now. The inordinate growth in computer power and availability of desk-top machines in the 80s spawned the first off-the-shelf software that made searching for the 'best' tree (by whatever criterion) a simple exercise in number crunching. First on the scene was Felsenstein's PHYLIP, followed shortly afterwards by PAUP and HENNIG, and most recently MrBAYES. These were quickly adopted by the systematic community and have led to a transformation in how we approach phylogentic reconstruction. Along with the basic tree searching programs came a burgeoning series of complementary computer programs to test tree support, measure tree asymmetry, reconstruct ancestral nodes, compare the compatibility of two or more trees, test for coevolutionary patterns, estimate divergence times, align genome sequences, and so on. All of these combine to provide a formidable array of statistical tools for analysing character evolution and thereby infer phylogenetic relationships.

A textbook that summarizes the advances made in this fast-moving field has been surprisingly lacking and is very welcome. What we have in this book is an overview written clearly and simply by one of the leading exponents. Many view Felsenstein as the father of statistical phylogenetics, and indeed he has initiated or been involved in many of the critical developments in this field. The book is intended for graduate-level courses, and assumes some knowledge of statistics, mathematics (calculus and fundamental matrix algebra), and molecular and quantitative genetics. So if you have ever wondered what phylogenetic ratchets, priors, Markov chains, LogDet distances, cliques and star decomposition are, these – and a great many more terms that litter the phylogenetic literature – are all elegantly explained here.

The book starts off simply with a description of the statistical basis for parsimony. There is no discussion here about the rights and wrongs of the underpinning philosophy (though a brief overview is given later) – focus is on explaining the statistical rationales and properties of the

methods applied. Here you will find descriptions of the cladistic methods and algorithms widely applied to palaeontological data very clearly laid out. Emphasis is always on the broad principles rather than the details of the algorithms and their proof.

Parsimony, however, is only the starting point for this book, where statistical principles can most clearly be explained. Felsenstein moves on to cover tree building based on distance methods and quartet puzzling with equal clarity. More advanced methods require predetermined models of evolution, and in two chapters Felsenstein reviews the statistical approaches that can be applied to model the evolution of discrete and continuous variables. This then opens the door for a discussion on the use of likelihood, bayesian, and hardeman techniques. Felsenstein uses equations where he has to, but always backs these up with very clear and simple examples for those (like me) who don't feel comfortable with long strings of Greek symbols and figures.

The second half of the book turns to statistical methods employed on trees once constructed. Here we get descriptions of the tests of compatibility, descriptions of approaches used to estimate divergence time with or without clock assumptions, bootstrap, jackknife and permutation tests of data robustness, and a whole string of techniques applicable to molecular data, including alignment. The book ends with a discussion of tree-drawing programs and a list of software sources.

From a palaeontological perspective there is plenty of interest to be gleaned from this book. There is even one chapter devoted specifically to 'phylogenies and paleontology'. Here we find brief descriptions of stratophenetics and stratocladistics, both of which Felsenstein notes require a dense and high-fidelity fossil record to provide reliable answers. The statistical basis for stratolikelihood is more thoroughly dealt with, both Wagner's approach ("a not-quite-likelihood method" which Felsenstein classes as a statistically inspired variant of stratocladistics) and the true maximum likelihood approach of Huelsenbeck and Rannala. However, stratigraphic data gets rather short shrift, since the statistical basis for these approaches is comparatively primitive, and stratigraphy has played little part in the modern revival of interest in phylogenetic reconstruction.

Parsimony analysis remains the primary tool we have for analysing fossil relationships and integrating palaeontological data into phylogenies constructed from combined morphological and molecular data. However, the parsimony method does have its potential limitations, notably that character change has to be relatively rare for the method to be accurate. For molecular data, where the system is simpler and we have a better understanding of how character states evolve, phylogeneticists have moved largely over to using maximum likelihood or Bayesian methods for reconstructing phylogeny. These assess the probability of a phylogenetic tree given the observed data and a model of evolution. A few attempts to apply maximum likelihood and bayesian approaches to morphological data have now begun to appear, based on Brownian motion models and Markov chains. Unlike parsimony, branch length now becomes a parameter not an incidental, and the Achilles' heel of these approaches is that their accuracy depends upon first having a reasonably accurate model of character evolution. Just how we do this is still under development, but some success is being claimed, at least for analyses of extant taxa (*e.g.* Nylander *et al.* 2004).

However, attempts to develop a more general model that accommodates palaeontological data are a long way off. This is because working with taxa from different time planes adds a whole level of complexity onto an already enormously difficult problem. Remember that both maximum likelihood and Bayesian analysis include branch length as a parameter in their test model as well as an estimate of the rate of character evolution. In analyses of living organisms all taxa are contemporary and thus separated from the basal node by path lengths that represent identical chunks of time, so the topology of the true tree is constrained. A tree that identifies a basal taxon with a long branch and relatively low rate of observed character change is likely to be assigned a lower probability. However, in fossil data the basal taxon may actually represent a short branch sampled at a much earlier time, and therefore displaying a more typical rate of character change. Having to consider trees where all tips are not contemporary greatly increases the field of tree topologies that must be searched. What is more, some model of fossil preservation potential through time should also probably be included as part of the model. As Felsenstein observes – a full maximum likelihood [or Bayesian] approach to palaeontological data lies well in the future.

Of course the philosophical question of whether we want to keep stratigraphic data independent as some sort of ground truthing of our phylogenetic methods is not even mentioned. There is very much a chicken and egg problem here – if we know the phylogeny then we can assess the quality of the fossil record accurately, but alternatively if we knew the quality of the fossil record we would be able to develop accurate methods of tree reconstruction. I am sure that model-based approaches will be important in palaeontology eventually, but they are going to take a great deal of work.

Felsenstein's book is a welcome addition and a rich source of data and ideas on rigorous approaches to phylogenetic reconstruction. It represents an outstanding achievement of synthesis and review, which makes a difficult field very accessible. Indeed it now forms one of the core text-books to the Imperial College–Natural History Museum M.Sc. in taxonomy, and I would recommend it to all interested in understanding the modern approaches to phylogeny reconstruction. Given the growth in this field over the last few years, it seems most unlikely that the spread of topics covered here will ever be squeezed into a single volume, and certainly never so ably.

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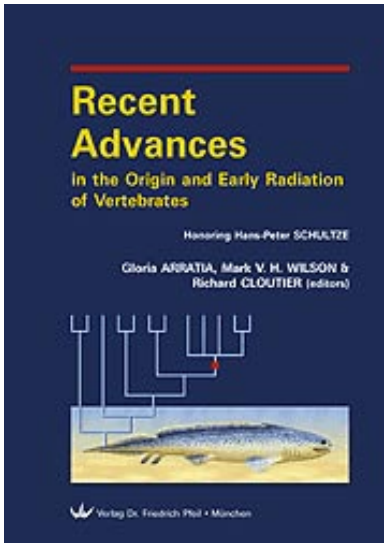
Recent Advances in the Origin and Early Radiation of Vertebrates Honoring Hans-Peter Schultze

Gloria Arratia, Mark V.H. Wilson and Richard Cloutier (editors) (2004). Verlag Dr. Friedrich Pfeil, München. ISBN 3-89937-052-X, €240 (hardback).



The size and scope of this 700+ page volume is impressive: divided into two parts, taxonomic coverage extends from microfossil remains of agnathans through to diversity and phylogeny in early amniotes. In its breadth, it is a fitting tribute to an individual whose impact on studies of early vertebrates has been considerable in terms of publications, meetings, fieldwork, and supervision of a series of talented students. Moreover, much of this was achieved, to Hans-Peter's great credit, in the US, where the bias towards mammalian and dinosaurian vertebrate palaeontology often defies belief.

Returning to the volume itself, the book is well turned-out, and resembles a 'Palaeozoic' addition to the *Mesozoic Fishes* series. Of the two parts, the first section, 'Recent Advances in Early Vertebrates,' ascends from 'agnathans' via placoderms, chondrichthyans, acanthodians, actinopterygians, and non-tetrapod sarcopterygians, to amniotes (and several points in between). The second section, 'Recent Advances in Fishes,' cuts the agnathans and tetrapods. Several of the thirty-three contributions are reviews, although most papers contain either new data or novel interpretations, with a total of fourteen new taxa described (two 'agnathans,' one placoderm, seven chondrichthyans, two actinopterygians and two tetrapods). For those who want further details of volume contents, abstracts for each contribution can be found at the publisher's website at <**http://www.pfeil-verlag.de/**>.

So, is it any good? Unfortunately, the short answer is that this is a proverbial curate's egg of a volume, the contents of which vary wildly in quality. In fact, the book starts out well with Janvier's wide-ranging review of stem gnathostome gill architecture. This mine of useful data should be of interest to both palaeontologists and neontologists alike. As with all good reviews, it presents the kind of synthesis one craves for advanced students: a discriminate and readable summary of materials, issues, and the current state of play. Other choice cuts include Maisey's chapter on chondrichthyan braincases, which is noteworthy as one of the few delivering a large body of detailed, new, morphological data, edging the chondrichthyan dataset closer to levels of anatomical detail more generally associated with their bony relatives. Schoch and Milner's pithy summary of the lissamphibian problem succeeds in unravelling the arguments behind (and between) hotly disputed trees and datasets. But these authors don't sit on the fence: a preferred set of solutions is identified, along with an agenda specifying likely avenues to progress. The relevance of albanerpetonitids has rarely been better explained. Elsewhere, a couple of chapters take a welcome look at tail morphology: Little and Bemis on elasmobranchs', and Hilton on chondrostean examples. Both articles highlight the importance of tails as an under-examined source of morphological diversity (see classic earlier works such as Nybelin (1963), and, appropriately enough, Schultze and Arratia (1986)), delivering the raw materials for new characters in future analyses. It is also refreshing to find two contributions on the Early Devonian sarcopterygians of China (Zhu and Yu, Chang), which, despite their vital importance in exposing deep splits in sarcopterygian phylogeny, remain incompletely described. And, last but by no means least in this (admittedly incomplete) run through the book's highlights, Arratia and colleagues' chapter on Cretaceous percomorphs deserves mention, because it sheds new light on the origins of the bulk of Recent teleost biodiversity. The Mesozoic record of perciforms is pitiful, so the discovery and description of whole bodies from where, beforehand, we had little more than scraps, provides at the very least important stratigraphic and geographic markers.

However, many of the contributions in *Recent Advances* confine themselves to fragmentary remains, likely to be of specialist-only interest. For better or worse, festschriften are becoming the venues of choice for such bits and pieces, while reports on better preserved specimens are reserved for destinations with some sort of identifiable impact factor. Thus, entire articles are devoted to items such as a Carboniferous tetrapod jaw fragment (Clack and Ahlberg), an arthrodire suborbital and skull roof (Mark-Kurik), and the incomplete dermal bones of a Cretaceous coelacanth (Gottfried *et al.*). All of these deliver useful new morphological data and, in some cases, broader implications also get a mention, but each is of limited appeal. Here, too, are chapters on isolated scales and teeth, with Karatajute-Talimaa and Meredith Smith describing a new form from the Ordovician–Silurian of Siberia, and a series of offerings from Turner, Ginter, and Hampe and colleagues, each concerning xenacanth teeth, or forms that more or less resemble xenacanth teeth. Once again, there are lots of useful data here, such as the detailed depiction of *Doliodus* teeth, now known to originate from a chondrichthyan body (Turner). But, after forty-two images of *Doliodus* teeth, the inclusion of only the briefest mention of *Doliodus* scale morphology exemplifies what is a central issue with ichthyoliths: the desperate need for more context.

Inevitably, consideration of *Recent Advances* draws comparisons with other multi-authored symposium volumes dedicated to 'lower' vertebrates, such as *Major Events in Vertebrate Evolution* (Ahlberg 2001), or even the first incarnation of *Interrelationships of Fishes* (Greenwood *et al.* 1973). A run through the contents table shows that *Recent Advances* is a different beast than either of these previous works. Whereas *Major Events* highlights the synthesis of neontological pursuits with the study of 'lower' vertebrates, accompanied by contributions on molecular systematics and developmental biology, *Recent Advances* largely glosses over the role of these fields in palaeontology. Where development and genetics do enter the fray in *Recent Advances*, they usually appear as haphazardly inserted buzzwords in concluding paragraphs. Janvier's closing discussion is the noteworthy exception: circumspect and deftly avoiding wobbly constructions of homologies and Hox genes. Comparisons between reconstructed ontogenies are attempted (*e.g.* Carroll *et al.* on labyrinthodonts), but the difficulty here lies in the incompleteness of taxonomic coverage. In this regard, Soler-Gijón's description of xenacanth growth-series represents a notable first for the chondrichthyan Palaeozoic record.

Recent Advances is better seen as a volume of morphologies and phylogenies. In this sense, it is a closer match to *Interrelationships of Fishes*, which – as its title suggests – primarily concerns

itself with systematic issues. *Interrelationships of Fishes* affirmed the role of phylogenetic systematics in the study of early vertebrates, an approach that found one of its earliest advocates in Hans-Peter Schultze. Cladistics gave contributors to *Interrelationships* the toolkit needed to tackle long-standing controversies in palaeoichthyology, and the response was a series of seminal works on subjects ranging from acanthodians to euteleosts. It is never easy to gauge how papers might weather the coming decades, but it is difficult to single out contributions in *Recent Advances* that seem to approach the impact of works in *Interrelationships*. Perhaps this is because of the great strides that have been made in the past three decades – maybe the "big questions" have all been answered. But this simply isn't the case: take, for example, the status of placoderms, acanthodians, and thelodonts. The monophyly of each has been questioned recently (Johanson 2002, Miller *et al*. 2003, Donoghue *et al*. 2000), but contributions to *Recent Advances* fail really to get to grips with these larger subjects.

Another basic shift between *Interrelationships* and *Recent Advances* concerns methods of phylogenetic inference; although the spirit remains the same, the execution differs. All of the cladograms in *Interrelationships* are hand-built affairs, with focus placed on a few critical and thoroughly reviewed characters. Since then, computerized algorithms for phylogeny reconstruction have allowed degrees of morphological sampling unheard of at the time of publication of *Interrelationships*. However, while such programs have democratized systematic biology, and allowed ever larger analyses, problems of basic character formulation remain as vital today as ever (Rieppel & Kearney, 2002). Predictably, characters sampled from various chapters in *Recent Advances* suffer from all of the usual diseases: fuzzy definitions, vague references to trends, lack of precision and repeatability, and scores for taxa in which relevant features are simply unknown (leaving the reader to guess at what scholarly sleight-of-hand achieved the desired result). Taxon coverage suffers similarly, and readers should take care to consider whether the phylogeny before them concerns the selective view of a favoured fossil assemblage, rather than serious analysis of a larger clade.

At the risk of picking an argument, we single-out Cloutier and Arratia's large analysis of basal actinopterygians because it illustrates many of the problems listed above. Although presented as an exploratory study, the extraordinary result of their work is just about undiscussed. They seem to have discovered that most if not all Palaeozoic actinopts belong on the stem-group of the ray-finned fishes – a novel hypothesis (to say the least) that conflicts with just about every previous solution offered to this problem. The authors then produce a rash of arbitrary data manipulations, but the meanings of the various output tree shapes are still not properly addressed. The problem here is that while their primary result will be cited, the possibility that this is spurious noise is ignored. To quote the author of PAUP: "And if you only get one tree, but you cannot explain it biologically – start all over again!" (Swofford, in – appropriately enough – Schultze and Marshall 1993). Mistakes invariably creep in to analyses, but readers need to be forewarned that problems are not limited to accidental miscodings (enough said, as the review authors slink away into hiding, clutching their own mucky matrices).

Recent Advances might, quite *reasonably*, be searched out as representative of the cutting edge, but what does this volume really say about the state of the art for studies of early vertebrates? Perhaps the pendulum has swung too far, and it is time to place renewed focus on the anatomy of the organisms at the expense of matrix size. For each taxon monographed exhaustively in

Jarvikian detail, there are dozens more that are described in only the most cursory fashion. This is the natural expectation for a field with so few researchers but such a vast taxonomic scope. It is no surprise that neontologists, typically a methodological step or two ahead of us palaeontologists, have already gone through similar systematic convulsions (Jenner 2001). For a better treatment of large-scale phylogenetic analysis and results, see Müller's contribution on diapsid reptiles. Arguments will no doubt continue about the correct location for turtles and their ilk, but here the consequences of a postulated branching sequence are investigated and laid bare to inspection. Furthermore, the author recognizes that solutions to persistent problems in the field are likely to be discovered through new interpretations based on solid morphological description: "the primary key to a well-resolved phylogeny still is the organism."

What, then, is our verdict on this volume? This is a necessary purchase for libraries, but we cannot recommend it for cash-strapped students. To paraphrase a recent review by Mike Benton [in *Pal. Ass. Newsletter* **56**], this is the usual multi-authored volume presenting a mish-mash of papers with no coherent theme or message, whose only connection is that many were delivered in the same meeting, and the unevenness in quality falls squarely at the feet of the editors. If researchers from outside of the discipline see the price tag and the authoritative title of *Recent Advances*, they might, with reason, expect a good deal more.

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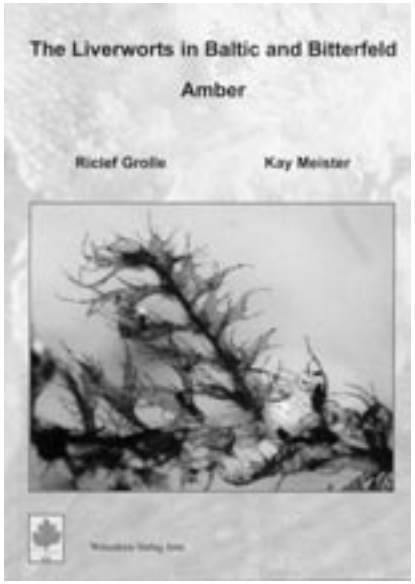
The liverworts in Baltic and Bitterfeld amber

Riclef Grolle and Kay Meister. 2004. Weissdorn-Verlag, Jena.
ISBN 3-936055-04-1 (paperback), €19.50



Bryophytes are very rare as fossils, and embedding in resin may have been the best chance to preserve enough characters for detailed taxonomic studies. In contrast to fossils of arthropods and higher plants, however, these cryptogams are rarely found in resins and the literature is sparse.

There are few specialists in taxonomy of recent liverworts, and maybe the most distinguished worker on extant and fossil ones was Riclef Grolle (1934–2004). He already studied liverwort inclusions in Dominican, Mexican and European fossil resins in the 1980s (for a detailed list of publications see Gradstein 1999). About twenty years of Grolle's preoccupation with liverwort inclusions from Baltic and Bitterfeld amber are now summarized in this monograph. The book was published rapidly by Weissdorn-Verlag in Jena only a few months after Grolle's death. Kay Meister, who collaborated intensively with Grolle during the last couple of years, finished his concluding palaeontological study.

Short but precise was the style of Riclef Grolle, so he needed less than 100 pages for his main palaeontological work. A short introduction is followed by a key to the genera. The main part of the book comprises species treated in alphabetical order. This chapter contains detailed species descriptions, synonyms, details of all specimens examined, citations of all previous illustrations, and remarks about extant relatives. Keys to the species of Frullania and Radula which are recorded by more than one species are also provided. A table gives an overview of all liverwort species in both fossil resins. Apart from taxonomical remarks, a main emphasis of the discussion is on taphonomy and palaeoecology. An alphabetical index of all scientific names ever used for liverworts in Baltic and Bitterfeld amber makes it easy to find the valid names. 23 plates with detailed drawings showing taxonomically relevant features and largely excellent photomicrographs of all recorded species are placed at the end of the book.

The monograph reviews all previous finds of liverworts from both famous European Tertiary amber deposits. Based on more than 200 identifiable inclusions, 26 species of liverworts are recorded from Baltic and Bitterfeld amber. All these species belong to extant genera of leafy liverworts (Jungermanniales). The recorded families and genera of the Jungermanniales still occur in the northern hemisphere. Taxa that are today restricted to the southern hemisphere are absent in the amber. Six of the 17 genera are today extinct in Europe. Three species,

Nipponolejeunea subalpina, *Notoscyphus lutescens* and *Ptilidium pulcherrimum*, exist today. Based on the ecology of the extant relatives of the fossils, the authors conclude that the liverworts recorded in amber represent members of communities from higher mountain altitudes within the amber forests.

The authors distinguish between inclusions of Baltic and Bitterfeld amber. This is important since modern studies (*e.g.* Knuth *et al.* 2002, Fuhrmann 2004) confirm an independent origin for the Bitterfeld amber and exclude the possibility it represents redeposition of Baltic amber. The central German Bitterfeld amber originates from the Oligocene–Miocene boundary and is, most probably, uppermost Chattian in age, whereas the Baltic amber forests grew in the Eocene.

There are only a few criticisms of the English, which is a bit halting in places, and the layout of the plates has too much empty space between the figures. The discussion is too short for a monograph such as this. At the very least, general comments about the present knowledge of the evolutionary history of liverworts including other finds, especially New World amber inclusions, should have been included.

That said, this first treatise on fossil liverworts in Baltic and Bitterfeld amber will doubtless be essential literature for a long time for bryologists, palaeontologists and amber collectors.

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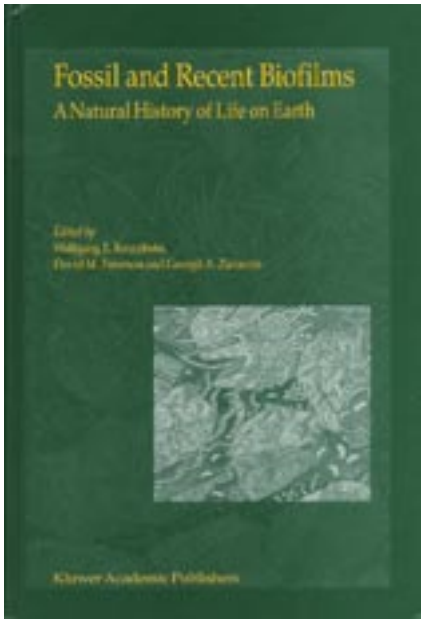
Fossil and Recent Biofilms, A Natural History of Life on Earth

Wolfgang E. Krumbein, David M. Paterson and Georgii A. Zavarzin (editors) (2003). Kluwer Academic Publishers, Dordrecht. ISBN 1402015976, £103/$164/€149 (hardback)

Many bacteria spend their lives attached to a firm substrate bathed by an aqueous solution. They do this not alone, but in close proximity to neighbours and relatives within a gelatinous matrix. The overall environment may be the sea floor, the inside of a garden hosepipe, cracks in rock, or the surface of someone's canine tooth. As Costerton & Stoodley point out in the Preface to this book, these bacterial biofilm communities were generally overlooked so long as microbiologists paid more attention to life in the water column than to the surfaces bathed by that water. With recognition – in the past thirty years – of the ubiquity of biofilms in aquatic Earth surface environments has come appreciation of the benefits to bacteria of anchored



community living. For a start it stabilizes their environment and facilitates interaction between trophically different bacteria – a microbial give and take. The key to anchorage is glue. This comes in the form of extracellular polmeric substances (EPS): a wide variety of polysaccharides, proteins and nucleic acids that are produced by algae and fungi as well as bacteria. These polymers facilitate not only adhesion and protection but also act as adsorbents and diffusion barriers that assist nutrition and metabolism. Large claims made concerning the benefits of EPS to biofilm bacteria include architectural structuring of the community, mutual recognition between bacteria, food storage, transfer of genetic material, and regulation of enzyme reactions. Like humans, most bacteria it seems also do not want to be rolling stones; they prefer to gather moss (or EPS), settle down, potter in the garden and party with the neighbours.

Interest in biofilm is wonderfully interdisciplinary; it concerns almost anybody wanting to get to the nitty-gritty of figuring out exactly what is going on at the microscopic level on substrates bathed by aqueous fluids at or near the Earth's surface. For geobiologists this ranges from the formation of stromatolites, which are constituted by biofilms, processes of sediment stabilization, larval settlement in competition or cooperation with microbes, synsedimentary microbially-mediated mineral precipitation, and fossilization of soft tissue, to recognition of bacterial fossils on early Earth and other planets. All these topics are here; crammed into 33 compact and diverse articles.

This is a wonderfully idiosyncratic compendium; evidently a labour of love (and dare I say, obsession) by the editors. Everything – quite possibly more than – you might wish to know about biofilms is let loose here. What this book lacks in discipline it repays twice over in breathtaking breadth and fully repays close reading, not least for some quotable quotes. Example: "Tininess is normal; we are anomalous" (p. 345).

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The Jehol Biota: The emergence of feathered dinosaurs, beaked birds and flowering plants

Mee-mann Chang (Chief Editor), Pei-ji Chen, Yuan-qing Wang, Yuan Wang (Co-editors), De-sui Miao (English editor). (2003) Shanghai Scientific and Technical Publishers. Review copy supplied by China Scientific Book Services. ISBN 7532373185. Price: $130 (Hardback)

Exceptionally preserved biotas are rightly celebrated as they provide palaeontologists with a more inclusive documentation of life at a given time than is normally captured in the fossil record after scavenging and decay processes have occurred. A number of excellent books have concentrated on the description of exceptionally preserved biotas. Some include an examination of several deposits containing exceptionally well-preserved fossils (Bottjer *et al.* 2002; Selden and Nudds, 2004, and see relevant chapters in Briggs and Crowther, 1990, 2001). Others concentrate on a particular fauna and as such are invaluable aids to those studying aspects of these deposits. Books focused on particular Lagerstätten include those by Hou *et al.* (2004), Briggs *et al.* (1994), Bartels *et al.* (1990, 1998) and Martill (1993). As well as being an excellent source of information for the academic, these books also provide the more general reader with a glimpse of the spectacular life that once was.

The Mesozoic Jehol biota (from Liaoning Province, China) reveals the rich biodiversity that thrived around Early Cretaceous lakeshores in northern China. It is most renowned for the discovery in the late 1980s and the 1990s of birds and feathered dinosaurs, and the Jehol biota is now recognised as an important world-class Lagerstätte. It has a roll call of several fossil 'firsts' – such as the first beaked birds, first plants with flowers and fruits, and it also preserves spectacular furry pterosaurs, an array of amphibians and invertebrates. The beautifully preserved creatures in this biota may shed light on bird, amphibian and angiosperm origins, and the co-evolution of pollinating insects and flowering plants. This book has handily pieced together the information on the Jehol deposit and its fossils that is otherwise scattered in many hard-to-get technical journals (often written in Chinese).

Aesthetically the book is splendid, and has a 'coffee-table' book appeal, although this may not suit all tastes. I enjoyed flicking through the glossy pages with large colour photographs, vibrant dioramas, and spotting the small iconic *Sinosauropterix prima* theropod – a rooster-sized theropod with its tail erect, head thrown back – as though strutting its stuff – used to draw attention to pagination throughout the book. After all when fossils are this beautiful why not endow pages with them? A few pages in, after two title pages, is a dynamic reconstructed scene of the Jehol biota by Xiao-lian Zeng, and this sets the tenor for the rest of the book – breathing

life back into the fossils. Here Cretaceous creatures glide, flap and buzz through the air, lumber, patter, hop and sprawl over the land, and paddle, splash and slice through the waters.

The contributors to the book are many (names, affiliations and addresses are listed at the front of the book) and constitute the teams of palaeontologists who have investigated, and published works on this biota. Many of the papers describing elements of this fauna are in Chinese so this book is very welcome to English speakers. It is also worth noting that the Jehol biota is not covered by those books already published on various Lagerstätten listed at the beginning of this review.

The introduction by Mee-mann Chang tells us that 'Jehol' is the transliteration of two Chinese characters. The literal meaning of these characters is 'hot river', derived from the many hot springs in the area. The fossils come from a large area where, during mountain building, fault basins developed and were filled with thick volcanic and fluvial-lacustrine deposits. The earliest material described was of small fish in 1880. The introduction then documents in a general way the importance of the fauna, placing special emphasis on the feathered dinosaurs and angiosperms. Interestingly, the age of the Jehol biota is still a matter of some controversy – being either Late Jurassic (*ca.* 145Ma) or Early Cretaceous (*ca.* 125Ma). Clearly, given the importance of evolutionary relationships and the many 'first' records in the Jehol, an agreed-upon date should be a priority for future investigations.

Chapter 2 outlines the environmental setting of the Jehol biota (be that Late Jurassic or Early Cretaceous). The picture painted is detailed in description, but it left me asking 'how did they know that it was like that?' A Mesozoic Pompeii is used as an analogy where volcanic eruptions, and their gases, may have caused mass mortalities, and where creatures caught in the lacustrine sediments were covered by layers of volcanic ash. In the sediments containing the Jehol creatures, articulated skeletons are the norm and soft tissue imprints abound. The chapter includes a geological map showing major basins and the locations of vertebrate fossil sites and the description (including a sedimentary log) of the stratigraphy and sedimentology/volcanology of the Jehol Group. (References to original works are absent and may have been useful). There are many fossil-bearing areas and in this chapter there are 20 colour photographs showing the exposure and topography of these localities; these really help in building up a picture of what fossil collecting would be like, and can be matched up with the geological map of the area. There are varying degrees of detail provided for each locality and a brief overview of the fossil taxa commonly found, with a description of their enclosing sediments. This chapter ends with an in-depth discussion of the various putative ages of the Jehol biota and their methods of determination.

The book is then divided into chapters based on the wide diversity of taxa found, including: gastropods, bivalves, conchostracans, ostracods, shrimps, insects and spiders, fishes, amphibians, turtles, Choristoderes, squamates, pterosaurs, dinosaurs, birds, mammals, charophytes, land plants, angiosperms, and spores and pollen. With so many contributing authors there are some differences in the format of treatment for each fossil group, but throughout there are numerous and beautiful colour photographs. Generally each group is treated to a brief introduction followed by a detailed look at the genera or species described. Where appropriate, cladograms show where Jehol fossils may fit in with their phylogenetic relatives.

The references occur at the back of the book but are divided into chapters, usefully stating if the work is in Chinese and whether the abstract is in English *etc*. There is a useful list of taxa

at the back but adding the page numbers where they occur may have been helpful – although navigating around this book is easy and fossil eye-candy.

I enjoyed this book, and as I read further it became easier to imagine myself exploring this world as though I were really there. The clarity of writing is generally very good. Yes, occasionally there is a small mistake in English such as "is extremely abundant but completely lack of diversity" – but the meaning is clear enough, and the occasional error does not detract from the book: after all I wouldn't understand *any* of it if I had to refer to original Chinese papers. However, there are a few places where it was a little difficult to understand meaning. For example, on page 14 there is a random sentence "contrariwise, clever augmentation and religious war are bound to be detrimental to the progress in science".

This book can be read by the academic interested in, or working on, the Jehol biota and by interested non-academics – although at $130 it is beyond most undergraduate student book budgets. I am going to order a couple of copies for our library, and now as I have this book I will find it much easier to include the Jehol biota in an undergraduate module on the importance of Lagerstätten. As a matter of interest I gave the book to a non-geologist friend for a quick read – they found the photographs and dioramas beautiful and intriguing but said that the text was definitely written for a scientist. An undergraduate said that they would definitely browse through such a book – especially as the dinosaurs and birds were "so cool".

I highly recommend this book for two principal reasons. Firstly, it is the only (English) collation of years of investigation on the palaeontologically important Jehol biota; and secondly, anyone who likes to journey in their minds to vistas of past life will thoroughly enjoy the narrative, reconstructions and photographs in this book.

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