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The Palaeontology Newsletter

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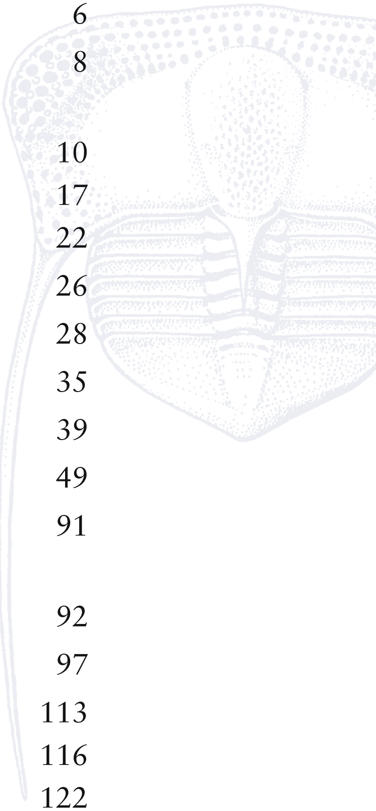
From our correspondents

Palaeontology



Reminder: The deadline for copy for Issue no 55 is 10th February 2004

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

Association Business

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 28th November 2003**.

Notification of the reorganisation of the Association year

E.G.M. to be held on Monday 15th December, at 4pm, at the University of Leicester

Over the last few years there has been a steady decrease in the number of members attending the Annual General Meeting of the Association in May. This has coincided with a decision by Council to move more of our formal events to the Annual Meeting at Christmas. Council is seriously concerned that the membership has been disenfranchised by these changes and this could have implications for our charitable status.

Council has fully considered the issues and proposes that the A.G.M. should become part of the Annual Meeting, likely to precede the Annual address. The Charity Commissioners have been consulted as an interim measure and have agreed to a rescheduled December AGM in 2004.

This reorganisation will have little impact on the rest of the Association year and has a number of advantages apart from allowing members a greater stake in Association business. The Executive Officer and the Auditor will not have to spend many days preparing the figures over Christmas and the New Year, at the time when there is maximum activity from membership renewals. It will no longer be necessary to make provision in the accounts for as many items still going through the system. Council will be able to approve the figures at the March meeting (or later) rather than the hectic February Meeting, when Sylvester-Bradley Awards are decided. Accounts and the Annual Report will be published in the Summer Newsletter without danger of this not getting to the membership with the statutory four weeks notice before the A.G.M..

It is necessary to put the proposed changes to a vote of the membership, and therefore Council proposes to hold an E.G.M. at the Leicester Annual meeting. Overseas members will be notified by post.

Proposed changes to the constitution

1) **Clause 5 para. 2**. The President shall serve for two years. Periods of service for other Officers shall be flexible but should normally not exceed two years for Vice-Presidents, and five years for Secretary, Editors, and Treasurers. Total consecutive service as an Officer (excluding service as President) shall not exceed ten years. Other members of the Council shall be elected for a period of three years. All members of Council are Trustees of the Association in accordance with charity law.

Proposed change:
Periods of service for other Officers shall be flexible but should normally not exceed two years for President and Vice-Presidents, and five years for Secretary, Editors, and Treasurers. Total consecutive service as an Officer (excluding service as President) shall not exceed ten years. Other members of the Council shall be elected for a period of three years. All members of Council are Trustees of the Association in accordance with charity law.

2) **Clause 6.** The Annual General Meeting shall be held on a date in the first six months in every year. Other meetings shall be held as determined by Council.

Proposed change:

Clause 6. The Annual General Meeting shall be held *within 12 months of the end of the Association year*. Other meetings shall be held as determined by Council.

3) **Council also seeks** the agreement of the membership that the President (Prof. Briggs) and senior Vice President (Prof. Harper) remain on Council until the December A.G.M. 2004.

Howard A. Armstrong
Palaeontological Association Secretary
<secretary@palass.org>

news

IGCP Project No. 491 – Middle Palaeozoic Vertebrate Biogeography, Palaeogeography and Climate

The project aims to enhance the exchange of ideas and data among scientists globally, through a series of web-based forums, workshops and field trips. The main focus is to compile a complex and highly organized global data set on the distributions in space and time of Early/Lower vertebrates. This in turn will provide more rigorous controls on the timing of connections and barriers implied by competing palaeogeographic hypotheses that incorporate extensive equatorial oceans during the Middle Palaeozoic. It will also provide a framework for understanding the global diversification of terrestrial ecosystems during the ‘Age of Fishes’ and its interaction with atmosphere composition, climate change, and extinction events.

The scope is primarily Devonian, but at a recent meeting in Riga, Latvia, the “Middle Palaeozoic” was stretched to include a presentation on the distribution of Ordovician microvertebrates. The project is a successor to IGCP projects 328, 406 and will extend the results of 411 and 421 with a link to the IUGS Sub-commissions on the Silurian, Devonian and Carboniferous.

The meeting next year will be held in conjunction with the 10th International Symposium on Early/Lower vertebrates to be held in Gramada, Brazil on 24–28 May 2004. Funding towards attendance at IGCP activities will be available with precedence given to students who are presenting their work. British workers should contact the National Representative, Giles Miller, at the address below for further details of these funds and for details about the project. Those seeking funding from outside Britain will need to contact their own national representative. Future meetings will be advertised in the Newsletter of Palaeontology.

Giles Miller
Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD
<G.Miller@nhm.ac.uk>

Palaeontographica Canadiana – Discounts to Association Members

The inventory on some early Palaeontographica Canadiana volumes is getting low (less than 100 copies), thus it shortly will be impossible to buy a complete, unused set.

The Geological Association of Canada is now offering a limited time, 20% discount on a set of Palaeontographica Canadiana No. 1–12 to Members of the Palaeontological Association (and their institutional libraries). The advertised selling price of $406.50 has now been reduced to $325.00 ($CDN for orders shipped to Canadian addresses; $US for orders shipped outside of Canada), until 29th February 2004. This price includes postage and handling via surface mail.

Please note the following:

- this offer is not available through the GAC website;
- you must be a PA Member (state this on your order) or a member’s institutional library (give member’s name);
- since the inventory of some of the volumes is low, the offer will only be available until the above date, or until supplies last, whichever comes first;
- GAC requires prepayment (Visa, MasterCard, American Express);
- Orders can be faxed to Arlene Power at 709-737-2532, or mailed to Geological Association of Canada, c/o Dept. of Earth Sciences, Memorial University of Newfoundland, St. John’s, NL A1B 3X5;
- GAC offers standing orders for this series, and if your university library would like to continue to receive these volumes as they are published Arlene can arrange to set up a standing order.
- No. 22 by Chatterton and Ludvigsen (Early Silurian trilobites from Anticosti Island) will be published by the end of 2003.

Do not hesitate to contact Arlene Power, Publications Manager if you require any further information. You can see the full Palaeontographica Canadiana listing at the GAC website (<**www.gac.ca**>).

Sandy McCracken
Chair, Joint Committee on Paleontological Monographs
<samccrac@NRCan.gc.ca>

Progressive Palaeontology 2004

CARDIFF
9th and 10th June 2004

School of Earth, Ocean and Planetary Sciences, Cardiff University

Progressive Palaeontology is a conference for postgraduate research students who wish to present their results at any stage of their research.

All aspects of palaeontology welcome.

One day of oral and poster presentations.

Free fieldtrip to the Glamorgan Heritage Coast.

Exciting social events including a reception at the National Museum and Gallery, Cardiff.

Convenors: James Wheeley, Susannah Moore, Susan Hammond and Christian Baars.

For further information please visit <**http://www.earth.cardiff.ac.uk/news/conferences.shtml**>

Or contact James <**WheeleyJR@cardiff.ac.uk**> or Susannah <**MooreS@cardiff.ac.uk**>

School of Earth, Ocean and Planetary Sciences
Cardiff University
Main Building
Park Place
Cardiff
CF10 3YE

Joint meeting between The Geological Society of London, the Palaeontological Association, the Palaeontographical Society, The Micropalaeontological Society and The Linnean Society of London

DINOSAUR PALAEOBIOLOGY

Wednesday 11th February 2004, Burlington House, London

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

10:30	**Registration and coffee**
11.00	David Norman (University of Cambridge, UK): Evolution of the dinosaurs
11:30	Paul Upchurch (University College London, UK): Biogeographic history of the dinosaurs
12.00	Angela Milner (Natural History Museum, UK): The dinosaurian origin of birds – a state-of-the-art review
12:30	**Lunch**
14:00	Paul Barrett (Natural History Museum, UK): Dinosaur herbivory: from functional morphology to macroevolution
14:30	Emily Rayfield (University of Cambridge, UK): Biomechanical approaches to feeding, skull form and function in carnivorous dinosaurs
15:00	Donald Henderson (University of Calgary, Canada): Stability and agility in dinosaurs
15:30	**Tea**
16:00	Kristi Curry-Rogers (Science Museum of Minnesota, USA): Dinosaur growth and physiology
16:30	Eric Buffetaut (CNRS, Paris, France): Dinosaur eggs and babies: facts versus fiction
17:00	Mike Benton (University of Bristol, UK): Extinction of the dinosaurs
17:30	**Reception** (until 19:00)

Technical Convenors

Professor Michael J. Benton (University of Bristol) <**mike.benton@bris.ac.uk**>
Dr Paul Barrett (Natural History Museum, London) <**p.barrett@nhm.ac.uk**>

Registration is free for members of the above named organisations. Please contact the conference office for a registration form.

For further details contact:

Jessica Canfor, Conference Co-ordinator
Address: Burlington House, Piccadilly, London W1J 0BG
Tel: +44 (0)20 7434 9944
Fax: +44 (0)20 7494 0579
Email: <**jessica.canfor@geolsoc.org.uk**>

Association Diary

2003 November 5-6 Review Seminar: **British Dinosaurs**
Organisers: David Martill (Portsmouth, UK) and
Martin Munt (Dinosaur Isle
Location: Dinosaur Isle (Sandown) & Quay Arts Centre (Newport),
Isle of Wight, UK.
Contact: <**martin.munt@iow.gov.uk**> tel: +44(0)1983 404344

26 **Sylvester-Bradley Awards** deadline for applications
<**www.palass.org**>

December 14-17 **2003 Annual Meeting**
Organiser: Mark Purnell (Leicester, UK)
Location: University of Leicester, UK.
Contact: <**leicester2003@palass.org**>

15 **2003 Annual Address** by Prof Mike Benton (Bristol, UK)
'Palaeontology and the future of life on Earth'.
Organiser: Mark Purnell (Leicester, UK)
Location: University of Leicester, UK.
Contact: <**map2@le.ac.uk**>

2004 February 10 **Copy deadline** for Newsletter 55

11 **Lyell Meeting 2004**: Dinosaur Palaeobiology
Organisers: Mike Benton (Bristol, UK) & Paul Barrett (NHM, UK)
Location: The Geological Society, Burlington House, Piccadilly,
London, UK.
Full programme: <**http://www.geolsoc.org.uk/**>
Registration: free to Association members, but must pre-register on
form available from <**jessica.canfor@geolsoc.org.uk**>
Contact: <**mike.benton@bristol.ac.uk**> <**p.barrett@nhm.ac.uk**>

June **Progressive Palaeontology 2004**
Organisers: James Wheeley, Susannah Moore
Location: School of Earth Sciences, University of Cardiff, UK.
Contact: <**WheeleyJR@cardiff.ac.uk**>, <**MooreS@cardiff.ac.uk**>

25 **Copy deadline** for Newsletter 56

August **Stem groups and the establishment of vertebrate bodyplans**
(PA symposium)
Organisers: Philip Donoghue (Bristol, UK) and
Mark Purnell (Leicester, UK)
Location: 7th International Congress on Vertebrate Morphology,
Florida State University, Boca Raton, Florida, USA.
Contact: <**p.c.j.donoghue@bham.ac.uk**>, <**map2@le.ac.uk**>

October 8 **Copy deadline** for Newsletter 57

December 17-20 **2004 Annual Meeting and AGM**
Organisers: Thomas Servais (Lille, France)
Location: University of Lille, France.
Contact: <**lille2004@palass.org**>

2005 February 9 **Lyell Meeting 2005: Applied Phylogeny**
Organisers: Haydon Bailey & John Gregory
Location: The Geological Society, Burlington House, Piccadilly,
London, UK.
Contact: <**haydonbailey@btconnect.com**>

December 18-21 **2005 Annual Meeting**
Organiser: Derek Siveter (Oxford, UK)
Location: University of Oxford, UK.
Contact: <**oxford2005@palass.org**>

From our Correspondents

Darwin’s cirripedology meets modern phylogenetics

Charles Darwin was no dunce when it came to invertebrate morphology. Darwin’s field of expertise in this respect was cirripedology, or the study of barnacles. In October 1845 Darwin was anxious to start his cirripede work as was obvious from a letter he wrote to his friend and confidant, the botanist Joseph Dalton Hooker, with whom he had started a lifelong correspondence two years previously. Darwin (in Newman, 1993: 355) wrote: “I hope this next summer to finish my S. American geology, then to get out a little zoology.” This doesn’t reveal any clear intent of spending a considerable amount of time on cirripedes. A year later in another letter to Hooker, Darwin wrote: “I am going to begin some papers on lower marine animals, which will last me some months, perhaps a year” (Newman, 1993: 355). However, we all know that Darwin’s estimate of the time he would spend on ‘a little zoology’ was a bit too conservative.

In December 1846 Darwin wrote to Hooker: “I have been nearly 3 months on Cirripedia and have done only 3 genera!!!” (Newman, 1993: 356), and in February 1847 Darwin started to wonder whether the cirripedes were worth the expenditure of so much time. In a letter to the great comparative anatomist Richard Owen Darwin wrote: “I hope to heaven I am right in spending so much time over one subject” (Browne, 1995: 476). Gradually, signs of desperation over the cirripede project began to surface in Darwin’s voluminous correspondence. In June 1848 Darwin wrote to John Edward Gray of the British Museum: “In truth never will a mountain of labour have brought forth such a mouse as my book on the Cirripedia: it is ridiculous the time each species takes me” (Newman, 1993: 358). Desmond (1994: 42) describes Gray as “a closet taxonomist who twinkled at the sight of pickled invertebrates,” and if it wasn’t for Gray, Darwin might have concluded his barnacle work years earlier that he actually did. Gray persuaded the British Museum to lend Darwin its entire Cirripedia collection, and he even gave up his own unfinished cirripede work so that Darwin could work on the group! In 1850 Darwin wrote to Hooker: “I can see no end to my work” (Newman, 1993: 358), and in October 1852 Darwin wrote to his cousin and good friend William Darwin Fox: “I am at work on the second vol. of the Cirripedia (LC2), of which I am wonderfully tired: I hate a Barnacle as no man ever did before, not even a Sailor in a slow-sailing ship” (Newman, 1993: 358). In the end, what was originally intended as ‘a little zoology’ dedicated to resolving the affinities of the peculiar burrowing cirripede *Cryptophialus minutus* turned out as eight years of almost full-time work on all the cirripedes, culminating in his famous series of four monographs on living and fossil cirripedes.

His cirripede work made Darwin a leading expert on the morphology, life history, classification, evolution, and biogeography of the cirripedes worldwide. However, even Darwin makes mistakes, and for the most part these were quickly identified and corrected by other workers. For example, in the autobiographical sketch (Darwin, 1995) that Darwin wrote for the benefit of his children, he noted in a section humbly titled “My several Publications” that he “blundered dreadfully about the cement glands” (Darwin, 1995: 39). How did Darwin err here? Darwin considered the sessility of barnacles as a unique characteristic among non-parasitic crustaceans, and he was therefore naturally interested in how barnacles attached themselves to the substrate. Based on his careful studies Darwin drew a curious conclusion. He observed that the cement glands are connected to the ovarian tubules, and that there was no separate opening for the ovaries to the outside world. In pedunculate cirripedes the cement gland is located in the stalk, and connected through a duct to an opening in the base of the stalk. Darwin thought that the ovarian tubules were connected to the cement gland in the stalk, and that an oviduct connected the tubules with the ovaries, which were located adjacent to the stomach. Because no opening from the ovarian system to the outside was seen, Darwin thought that this would imply that the eggs could only leave the parent’s body through the moulting process. By forming a new cuticle between the ovarian tubules and the old skin the ova could thereby be segregated from inside to outside the body. Darwin also noted that he was “well aware how extremely improbable it must appear, that part of an ovarian tube should be converted into a gland, in which cellular material is modified, so that instead of aiding in the development of new beings, it forms itself into a tissue or substance, which leaves the body in order to fasten it to a foreign support” (Newman, 1993: 368). Nevertheless, the idea of a connection between the cement glands and the ovarian tubules was the result of the best of Darwin’s dissecting and observational skills, and was not merely an unsupported fantasy.

Yet, although Darwin was convinced he had made out the internal anatomy of the barnacles correctly, doubts apparently kept gnawing at his mind, and in 1854 he asked the brilliant comparative anatomist Thomas Henry Huxley to look into this problem. To Darwin’s great surprise Huxley could not confirm his findings. Yet it was the Russian born anatomist August Krohn who in 1859 published a paper claiming that Darwin was wrong (Newman, 1993). Although the cement gland and the ovarian tubules were located very close to each other in the stalk, Krohn claimed that there was no connection between them. Moreover, Krohn concluded that Darwin confused the salivary glands, which are closely associated with the stomach, for the ovaries, and that the oviduct that Darwin traced from the ovarian tubules to the ovaries, actually opened to the outside at the base of the first cirri. In contrast, Darwin erroneously thought that these little apertures were acoustic organs! Already sensitised by Huxley’s failure to confirm his conclusions, Darwin reluctantly conceded that Krohn might be right, as he indeed turned out to be. Interestingly, although Huxley properly cites the work of Krohn on the reproductive system in cirripedes in his *A manual of the anatomy of invertebrates animals* (1888), Huxley nevertheless appears to accept Darwin’s rather than Krohn’s view! Figure 67 in Huxley (1888) still shows the oviducts connecting to the so-called gut-formed glands of Darwin, rather than the correct connection to the genital apertures at the base of the first pair of cirri. Although I haven’t read all available literature on Darwin and the cirripedes, it remains a mystery to me why Huxley chose to present Darwin’s incorrect views in a figure alongside the correct views of Krohn in the text, which had been published almost 30 years before.

It is nice enough for us mere mortals now and then to see proof that even the greatest minds can make mistakes, but I selected this example for another reason as well. It may seem very odd that Darwin would accept the physical connection of two structures with such different functions as the cement gland and ovarian tubules. However, in view of Darwin's ideas about the importance of functional shifts in the origin of evolutionary novelties, the idea of a connection between two seemingly unrelated organs may seem less fanciful. Just as the origin of feathers may have been associated with a role in thermo-regulation, later to be co-opted for a role in flying, so too may the cement glands of cirripedes originally have had a role in the cementing of the eggs to a substrate, and only later became functional in cementing the parent animal to the substratum. Indeed, this is effectively what Darwin suggested in his third cirripede monograph published in 1854. With respect to the closest, as yet undiscovered, relatives of the cirripedes, Darwin wrote: "I imagine they would prove to be Crustaceans, of not very low rank, with their oviducts opening at or near their second pair of antennae, and that their ova escaped, at a period of exuviation, invested with an adhesive substance or tissue, which served to cement them, together, probably, with the exuviae of the parent, to a supporting surface. In Cirripedes, we may suppose the cementing apparatus to have been retained; the parent herself, instead of the exuviae, being cemented down, whereas the ova have come to escape by a new and anomalous course" (Newman, 1993: 368).

The infusion of such functional, adaptive arguments into evolutionary reasoning marks Darwin's comparative morphology as something fundamentally different from previous efforts to keep the study of structure and function separate, and to study comparative morphology in a formal, atemporal manner, which mostly ignored the close correlation between morphology and habitat. Darwin did not only apply adaptive reasoning to explain a phylogeny constructed by other means, but functional considerations were an integral part of Darwin's phylogenizing. Ghiselin (1996: 51) writes: "the use of functional criteria for establishing homologies which are in turn evidence for relationships, is commonplace in Darwin's work." Accordingly, Darwin's barnacle monographs with their integration of function and evolution were read by many contemporaries as "straight-forward phylogenetics" (Ghiselin, 1996: 50). Indeed, a functional morphological approach, especially when the possibility of functional change is taken into account, can be a very powerful evolutionary tool. This is perhaps nowhere clearer than in the work of the comparative morphologist Anton Dohrn who became notorious for his theory of the annelid origins of the vertebrates. When seemingly extremely different organs can evolve from each other by a shift in function, then there is nothing to stop one from proposing that vertebrate gills slits are derived from annelid segmental organs, and that the vertebrate penis is derived from annelid gills, with both of these hypotheses being endorsed by Dohrn (Bowler, 1996).

Darwin also used functional reasoning in his attempt to answer other questions brought up by his cirripedes. Cirripedes figured especially prominently in Darwin's efforts to construct a comprehensive theory of sexual biology for both animals and plants, and he was concerned with such fundamental questions as whether hermaphrodites generally cross-fertilize (which he affirmed with his studies on barnacles and experimental studies on plants), whether the habits of an organism are correlated to its reproductive mode (as suggested by the evolutionary association of hermaphroditism and sessility in barnacles), and what the direction of evolutionary change was in taxa with diverse reproductive strategies (Ghiselin, 1984). When Darwin started working on barnacles, they were generally thought to be exclusively hermaphroditic, and primitive hermaphroditism is an exceptional situation among the crustaceans. However, one of Darwin's great accomplishments in cirripedology was his discovery of separate dwarf males in distantly related cirripede species that live in close association with the bigger hermaphrodites or females. After showing that the cirripedes show different strategies of reproduction, Darwin asked whether hermaphroditism or gonochorism (separate sexes) is primitive for the group. "Evidently Darwin answered the question of which came first through the analysis of the possible ways in which the change might occur" (Ghiselin, 1984: 116). In other words: "the direction of change was derived by considering the kinds of selection pressures that must have existed under the prevailing conditions of life" (Ghiselin, 1984: 117). The minute size of the male cirripedes, and the histological similarities of the males to larvae, led Darwin to conclude that they were derived from more fully developed hermaphrodites by truncation of development. He posited progenesis, or precocious sexual maturation, to be the process responsible for the evolution of males from hermaphrodites within the cirripedes. Darwin apparently thought that the alternative scenario, in which the diminutive males were the starting point for the evolution of a much more complicated creature, was a lot less likely (Ghiselin, 1984, 1996).

Today the situation has changed completely, both with regards to phylogenetic reasoning and the specific answers to some of Darwin's questions. If we look at cladistic analysis as the most commonly employed modern method of phylogenetic analysis, then we see that functional arguments to infer the direction of evolutionary change, and to establish homologies for phylogenetic analysis, are no longer an essential (or even desired) part of the central toolkit of phylogenetics. To be sure, there are still biologists who give serious attention to evolutionary process considerations in the reconstruction of phylogenies, but this seems to be more and more a minority position within a field dominated by a pattern approach, which eschews all assumptions about the evolutionary process. It becomes interesting when the process and pattern approaches clash with each other. A paper by Lee and Doughty (1997) presents several examples from vertebrate evolutionary biology, but here I want to point to some examples from the invertebrates, beginning with Darwin's cirripedes.

Darwin's work on the evolution of cirripede sexual systems has influenced views for a very long time, and the view that the cirripede ancestor was hermaphroditic was consequently generally accepted until very recently. According to Høeg (1995) two factors are responsible for accepting this view in recent times: first, the majority of cirripede species are hermaphroditic, and second, the thoracican cirripedes (the familiar barnacles we find on the rocks of our coast) have long been seen as the core group from which the parasitic rhizocephalans and burrowing acrothoracicans evolved. Consequently, the Urcirripede became the Urthoracican, which was assumed to be hermaphroditic. To address the first point first, we all tell our students that 'common is primitive' should not be used as an explicit rule of thumb, but most of the time we cannot help ourselves, and this useless guideline therefore keeps raising its ugly head in the literature. For example, some of the recent claims that Urbilateria was an impressively complex organism with a biphasic life cycle, in which microscopic ciliated larvae transform into macroscopic adults with fully fledged coelomic cavities, can simply be defused by exposing their foundation as the flawed common = primitive principle. It becomes quite ironic when this principle is applied to phylogenies from which all directly developing (lacking ciliated larvae) taxa that lack coeloms are excluded (see Jenner, 2000). As regards Høeg's second point, recent phylogenetic analyses of the cirripedes suggest that the acrothoracicans and rhizocephalans may not be ingroups of the thoracicans, but their nearest outgroups. It then becomes significant to note that both rhizocephalans and acrothoracicans primitively have separate sexes, as do the next nearest outgroups of Acrothoracica + Rhizocephala + Thoracica. This pattern approach thus leads to the conclusion that the Urcirripede had separate sexes, and that hermaphroditism evolved within the cirripedes as an autapomorphy of Thoracica. This conclusion conflicts with Darwin's hypothesis of a hermaphroditic Urcirripede that was heavily influenced by evolutionary process reasoning, and that was widely accepted for more than a century. Clearly, one can be misled if functional evolutionary reasoning is unconstrained by a phylogeny. However, parts of Darwin's functional arguments may still hold because the separate sexes of the rhizocephalans and acrothoracicans include dwarf males, which may have evolved through progenesis from more complex precursors. However, Høeg's phylogenetic perspective shows that functional arguments about the evolutionary process should not take place in a phylogenetic vacuum, but should instead be integrated. In this respect it is noteworthy that Lee and Doughty (1997) argue that process and pattern approaches should initially be kept separate, so that their consilience can later be examined.

However, it is not always that simple. For example, Westheide *et al.* (1999) review different recent approaches to reconstructing the phylogeny of the Annelida, ranging from a hardcore morphological cladistic approach (*e.g.* Rouse and Fauchald, 1995), to a phylogenetic approach that explicitly incorporates functional considerations of the relation between form and the environment (*e.g.* Westheide, 1997; Purschke, 1999). When a cladistic approach is employed without recourse to functional considerations, the polychaetes and clitellates may be resolved as sister taxa (Rouse and Fauchald, 1995). In that case one may define the polychaetes on the basis of possessing parapodia used in locomotion, and nuchal organs, which are thought to be chemoreceptors (Ax, 1999). Both of these features are not found in clitellates. However, the reason that the clitellates lack these structures may be due to secondary character loss, rather than primary absence. Purschke (1999), for example, argues for a terrestrial origin of the clitellates (from marine polychaete precursors) in connection with a burrowing lifestyle. If that is true, than parapodia and nuchal organs (which only function in water) would be less useful, and clitellates may thus have lost these features. To corroborate these ideas, Purschke noted that secondarily terrestrial polychaetes tend to reduce or completely lose their parapodia and nuchal organs, and to converge to a more clitellate-like habitus. This would additionally suggest the possibility that polychaetes are paraphyletic with respect to clitellates, and this appears indeed to be supported by molecular evidence. In this case, a purely formal translation of comparative morphology into cladistic 0s and 1s may actually be misleading, while a functional morphological interpretation may be more valuable. At the very least we cannot simply dismiss all process oriented approaches, or functional scenario-based approaches to reconstructing evolution as conceptual fossils from a time when pattern-based cladistics was not yet developed. However, given the widespread dislike of functional adaptive reasoning in cladistic analysis, this viewpoint may not be accepted by many.

To conclude, I want to mention one last interesting case of a clash between pattern and process approaches, this time involving molecular phylogenetics. The interpretation of metazoan body cavities can be regarded as one of the most controversial, yet influential, subjects of comparative zoology that is perhaps only rivalled in scope and intensity by discussions on the evolutionary significance of larval forms. In my column in the last issue of the *Newsletter* I already introduced the important concept of a division between acoelomate, pseudocoelomate, and coelomate bilaterians. Zoologists have argued endlessly about which of these body organizations is primitive for the Bilateria, and whether convergent evolution has been important in producing seemingly similar morphologies. To provide some independent perspective on this vexing problem, Winnepenninckx *et al.* (1995) published the first molecular phylogenetic analysis of 18S rRNA sequences of a broad sample of pseudocoelomates. They write (p. 1136) "The most fundamental evolutionary implication of multiple origins of pseudocoelomates is that the body cavity type is of less phylogenetic significance than previously considered…and implies that body cavities that appear to be pseudocoeloms could easily be derived by the modifications of existing eucoeloms." This is particularly revealing since both cladograms in Winnepenninckx *et al*. (1995) favour the alternative interpretation, with basal pseudocoelomates, and therefore the primitive lack of a coelom and the independent evolution of coeloms in the protostomes and deuterostomes! How can this conflict be explained? The solution lies in the morphological papers that Winnepenninckx *et al.* (1995) cite. These papers draw an analogy between the evolution of interstitial annelids and pseudocoelomates. For several interstitial polychaetes it has been found that they have reduced their coeloms to become functionally non-coelomate, although anatomical signs of a coelomate ancestry often remain visible. In analogy it is argued that the non-coelomate phyla such as the nematodes, gastrotrichs and priapulids could also have lost their coeloms. However, for these phyla there is no independent anatomical evidence that supports this evolutionary scenario, and this clearly illustrates the limitations of extending an analogy from closely related species to distantly related phyla. This shows that a phylogenetic pattern in plain sight can be obscured by ingrained assumptions about the evolutionary process, and that this is not unique to Winnepenninckx *et al.* (1995) is shown by a paper by Aguinaldo and Lake (1998), which adopts the same fallacious reasoning.

There seems to be no easy answer to the question of whether functional considerations should be kept out of cladistic analyses at all costs. As much as it is true that failure to consider morphology in its relation to the environment and natural selection may mislead our reconstructions of evolutionary history, so too can largely unconscious and unsupported assumptions about the direction of evolutionary change lead us to false interpretations of pattern. In the last *Newsletter* I also posed the question of what has been a shared impediment to understanding the evolution of turtle and molluscan body plans. The answer to this question will have to wait until next time, but the German poet and polymath Johan Wolfgang von Goethe is a cryptic hint to the answer.

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Inside and Outside Skeletons

We are all familiar with the terms exo- and endoskeleton, for – literally – skeletons on the outside and on the inside of organisms. Classifying skeletons is, however, rather more complex than segregating them into outside and inside.

Patterson (1977) viewed the vertebrate skeleton as two distinct systems with different developmental and phylogenetic histories. The *endoskeleton*, which is composed of vertebrae and associated axial structures, limbs, brain case and various components of the skull, and the dermal or *exoskeleton*, composed of teeth, scales, fin spines and dermal bones. This skeletal dichotomy has since been widely adopted (Smith and Hall, 1990, 1993; Francillon-Viellot *et al.* 1990; Huyseunne 2000, and others).

Rigid skeletons also exist within the invertebrates. Mineralization of these skeletons allows for their fossilization. Invertebrates have both endoskeletal and exoskeletal elements and although poorly studied, it is commonly accepted that the endoskeletal elements are mesodermal whereas the exoskeleton derives from the ectoderm (Brusca and Brusca, 2003). Exoskeletons are present within many different invertebrate taxa and range in hardness from the thin skeletal lamina of rotifers to the thick calcareous shells of some gastropods (the latter being one of the more commonly known invertebrate skeletons from fossil literature), and other mollusks (*e.g.* ammonites), brachiopods, and arthropods (*e.g.* trilobite). The chitinous exoskeleton of arthropods is well known to anyone who has sat down to a lobster dinner with dinner tools reminiscent of the hammers and vices one would find in a carpenter's toolbox. Among arthropods, one of the most speciose extant groups of animals, the exoskeleton is complemented internally by endoskeletal elements that in many cases are similar histologically to the vertebrate tissue fibrocartilage. These elements serve to attach the musculature to the exoskeleton.

Many other invertebrates have extensive endoskeletal elements, with the calcified endoskeleton of echinoderms likely the best known among palaeontologists and beachcombers alike. Other mineralized endoskeletons include spicules in sponges and tunicates. Furthermore, unmineralized invertebrate cartilaginous endoskeletons also exist. We have already mentioned the fibrocartilaginous connectives within the arthropods, but connective support tissue that is cartilage-like can be found within the mesoglea of cniderians and the lophophores of brachiopods. Collagenous skeletal elements support the gills of hemichordates and mollusks, and cellular cartilaginous elements can be found in arthropods, annelids and mollusks. Thus, endo- and exoskeleton are readily distinguishable in invertebrates. This is apparently not the case for vertebrate skeletons, for we now have a proposal for three not two skeletal systems in vertebrates. This is the theme of this column.

In response to a previous column (*Palass Newsletter* **51**:27–30), Smith (*Palass Newsletter* **52**: 34–37) states that the viscero-somatic animal (*sensu* Romer, 1972; see Figure 1 in this column) provides us with the basis for a three-fold division of the vertebrate skeleton:

1) the visceral skeleton situated around the pharynx and including cranial neural crest derived teeth with endodermal induction;

2) the 'true endoskeleton' of neurocranium, axial and appendicular skeletons, derived from somatic mesoderm with notochordal induction); and
3) the dermal skeleton as the externally ornamented skeleton, which is neural crest derived with ectodermal induction.

We question Smith's proposal for several reasons – discussed previously in *Palass Newsletter* **53**: 48–51 and detailed below – and discuss some alternative and more classical views of the subdivision of the vertebrate skeleton. We then discuss Smith's proposal, with some emphasis on the placement of teeth within the visceral skeleton.

Donoghue (2002) points out that in recent literature, scientists have used the terms dermal skeleton and exoskeleton interchangeably, with the term exoskeleton used merely as an antonym for endoskeleton. He further highlights that the majority of the exoskeleton develops within the dermis and therefore should be assigned to dermoskeleton or dermal skeleton, and that the term exoskeleton should be restricted to keratinous elements like horns, nails, claws, hairs and feathers. However, as Donoghue observes, separating dermal and exoskeletons may be entirely inaccurate from a historical perspective and merely semantic. Developmentally, however, these two terms may be useful, especially when considering the epithelial sources of dermal skeletal elements (*e.g.* scales), and teeth (and oral scales), which are argued to have been distinct since early in vertebrate phylogeny (Smith and Coates 1998, and 2001) although they are now considered homologous.

In summary, most authors agree on a dermal skeleton (which may or may not be synonymous with the exoskeleton) and an endoskeleton. To this Smith (*Palass Newsletter* **52**:34–37) adds the visceral skeleton, which includes teeth, a neural crest derivative. Significantly, she considers teeth to form via endodermal induction (discussed below). The visceral skeleton as proposed by Romer (1972, our Figure) is of ectodermal origin and neural crest derived. Nowadays, and using topographical criteria, most regard the internal skeleton as the endoskeleton, without considering its embryological origin.

In the recent past, teeth have been viewed as modified scales (*e.g.* Reif, 1982) and considered to be homologous with skin denticles, which being patterned by ectoderm were later co-opted for margins of the mouth. In a recent article in *Nature,* Miller *et al.* (2003) describe the articulated skeleton of a chondrichthyan from the Early Devonian and report teeth that resemble modified dermal scales, without any associated dental membranes. Smith and Coates (1998, 2001) take exception with this origin for teeth and propose a new model "pharyngeal patterning mechanisms existed independently from those of skin and that these were co-opted for dentitions". Thus, pharyngeal denticles are phylogenetically distinct from skin denticles (Smith 2003) and reside in endoderm. Smith and colleagues thus propose a tooth developmental model based on homology with pharyngeal denticle sets and endodermal induction.

So where does this leave us? Should teeth be considered part of the endoskeleton since they can (sometimes) be induced by endoderm, or should they be considered part of the dermal skeleton as they are induced by ectoderm and borne by dermal bones? The presence of a dental lamina is regarded as one of five synapomorphies of chondricthyans, acanthodians and osteichthyans (Smith and Johanson 2003) and the dental lamina is derived from the stomodeum (lined with ectoderm). Alternatively, should they be considered part of a visceral skeleton as proposed by Smith (*Palass Newsletter* **52**:34–37) based on their proposed homology with pharyngeal denticles?

The issue of three rather than two skeletons started with conodont elements, so let's briefly return to these enigmatic structures. Conodonts lack a mineralised dermal covering but do demonstrate a mineralised feeding apparatus, which is internally (buccopharyngeally) located. However, as conodonts lie outside the gnathastome lineage, their mineralised biting elements appear to have arisen independently of gnathostome teeth. Therefore, in order to resolve the issue of where teeth fit in the palaeo-closet, conodonts are no help.

We need to take a closer look at the induction and origin of teeth. In humans, the mouth develops partly from the stomodeum, which is lined by ectoderm, and partly from the floor of the anterior portion of the foregut (Gray 1994; Sperber 2001). The stomodeum is separated from the anterior end of the foregut by the buccopharyngeal membrane, which is formed by apposition of the stomodeal ectoderm and foregut endoderm. The lips, teeth and gums are formed from the walls of the stomodeum and are therefore ectodermal.

Early researchers showed that oral endoderm and stomodeal ectoderm are both (independent) inductors of teeth (Sellman 1946; Wilde 1955). Graveson *et al.* (1997) combined these two tissues with neural crest cells from both cranial and trunk regions to show that the potential to make teeth extends into the trunk region. The neural crest derived mesenchyme cells become dentine-secreting odontoblasts, while the jaw epithelium (ectoderm and/or endoderm depending on the taxon) differentiates into enamel-secreting ameloblasts.
The neural crest derived mesenchymal cells (or ectomesenchymal cells) are by definition mesenchymal cells produced from the ectoderm. In mice, rostral trunk neural crest cells when combined with mandibular epithelium in culture also produce teeth (Lumsden 1988). Lumsden (1984) also showed that neither migration nor contact with pharangeal endoderm is a requirement for tooth formation. The evidence for ectodermal induction of teeth is strong and although teeth can be induced by endoderm (in some cases), this characteristic of endoderm may be secondary. There is no phylogenetic evidence for teeth to be considered endodermal in origin. We therefore do not accept Smith's argument that endoderm and not ectoderm induce tooth formation. Secondly, Smith's statement (*Palass Newsletter* **52**: 34–37) that the endoskeleton is composed of neurocranium, axial and appendicular skeleton and forms from somatic mesoderm with notochordal induction is incorrect. Neither the neurocranium nor the appendicular skeleton is induced by the notochord. The notochord is located medially within the chondrocranial basioccipital, and typically continues rostrally as far as the basicranial fenestra. Also, the exoccipital is considered to be homologous to several (fused) neural arches (ancestrally part of the axial skeleton). This may be where some of the notion of the endoskeleton including (parts) of the neurocranium comes from. It would be difficult to remove the notochord to determine if the basioccipital and exoccipital would still form, so the notochordal induction may be somewhat difficult to confirm.

In conclusion we support the view that the vertebrate skeleton comprises two skeletons: the endoskeleton and the dermo/exoskeleton (see *Palass Newsletter* **51**:27–30). This division is congruent with the views of Patterson (1977) and others:

The dermo/exoskeleton is neural crest derived and develops in contact with epithelium, either ectoderm or with endoderm. Examples of exoskeletal elements are dermal bone, scales, and fin rays and teeth. The bony elements of the dermo/exoskeleton develop intramembranously without a cartilage precursor. Teeth are part of the exoskeleton.

In contrast, the endoskeleton, which is derived from neural crest or mesoderm, does not form in contact with ectoderm or endoderm and develops endochondrally. Examples are long bones in mammals. Teeth are not part of the endoskeleton.

We welcome your views or comments.

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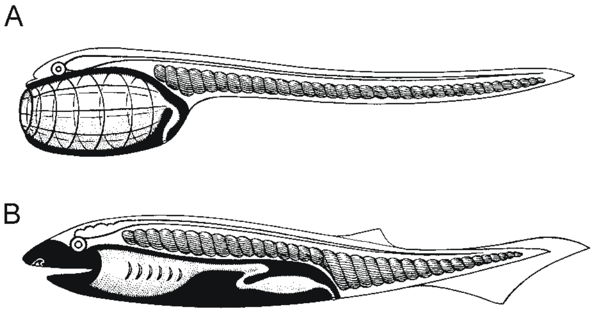

Figure 1:
The somatic and visceral animal modified from Romer (1977). (A) a tadpole larva and (B) a fish. The "visceral" area is shaded black whereas the "somatic" area is shaded grey.

Interesting times

Plus ça change, plus ce n'est pas, these days perhaps, la même chose. Interpreting the past, as we all know, is treacherous. Divining the future is even more so. The present is always a hopeless mess, though to make any sense of it, the context provided by imperfect past and hoped-for future can come in handy. In individuals, to make it even worse, past, present and future are linked by caprice: I'm writing this column, for instance, because a house-martin chirped out of turn, thirty-odd years ago, and propelled me into a life in palaeontology. On a large scale, things might work differently, as I'll get on to. But the house-martin might need some explaining first.

As a child, I had the usual rash of enthusiasms: stamps, football, conkers, ping-pong. These were patiently supported, or more often endured, by my parents. An enthusiasm came for old things: coins, old bottles, bits of pot and clay pipe, flint scrapers, fossils. I jumbled these up innocently, little dreaming that I was not being simply ignorant, but prematurely interdisciplinary. I'd persuaded my parents to go to Whitby, and we hunted for ammonites. This was very fine, but then ambition grew. Ammonites were no longer enough: I needed to possess the exotic, enigmatic, infinitely mysterious carapace of a trilobite to make my collection complete. The pictures I pored over in books, of wondrous specimens from the Wenlock Limestone, ratcheted up my avarice to stratospheric levels.

Hell hath no mitherer quite like a thirteen-year-old collector unfulfilled. So off to Wenlock Edge we drove, my long-suffering parents and I. Corals we found, and brachiopods, and gastropods. But of trilobites, not a trace. This was my first encounter with biofacies variability, and it hurt. Disillusioned, we drove to Ludlow for a cup of tea, before the long drive home.

We went into the teashop, my parents, me, and the house-martin. Here, a little background might be necessary. My mother, then, had created, and ran, a wild bird hospital. A labour of love, it was a 24-hour a day, seven day a week occupation, something I remember whenever I'm tempted to think that lecturing is a difficult job. Some of the birds could not be left, even for a few hours. Such was the house-martin: it was a cripple, its balance organs smashed after a blow to its head, perpetually staggering as if drunk on a teaspoon of brandy.

We always carried it in a cage which was covered in cloth, in an attempt to disguise it as a handbag of Lancastrian proportions, so as to avoid curiosity and long rounds of explanations. This ploy usually worked. Not this time. The bird began to chirp. It chirped. And chirped. And chirped. Our usual response (to pretend that nothing was happening, or if something was, it was nothing at all to do with us) hadn't a prayer of working. A couple at the next table with excellent stereophonic hearing leaned over and enquired. We explained. Why were we in Ludlow? We explained. Were we successful? We explained. In that case, they said, sympathising with my inconsolable chagrin, why not visit Ludlow Museum? There was a man there called John Norton who might be able to help.

We hurried across. The sign at the museum door said closing time was 5 o'clock. It was then 5 o'clock exactly. The man at the door said that John Norton was about to get his bus home. But, perhaps he would see us… He did. He missed his bus. He told us where trilobites could be found (the sunken lane at Burrington, if you're a Ludlow aficionado), and how to get there. He showed us examples of the kinds of fossils which we might find. And he did this in a way which did not suggest that he was tired at the end of the day and simply coping with a klepto-palaeomaniac kid of the worst stripe, but rather that he was one enthusiast talking to another. Later I realised that he treated everybody quite equally, whether it was some snotty-nosed five-year-old bringing him a couple of dead dandelions in a jar, or a professor wanting to use the museum collections. But then it simply struck me as an entirely novel form of adult-child discourse.

Some months later we went to Burrington, found a small hoard of gleaming trilobites as predicted, and proudly took them to show him. He labelled them for us, in a beautiful hand which I tried for years, but always failed, to copy, introduced us to the rest of the museum staff, showed us fossil fish from the Clee Hills, dinosaur bones from India, Murchison's hand-drawn geological cross-section. I was entranced by this Aladdin's cave, with wonders neatly packed in stack upon stack of shirt-boxes, and by the humour and tolerance of the people who worked at the museum.

That tolerance must have been severely strained over the next few years, and the sense of humour indispensible. For I started to go across in the summers to 'help' at the museum. My help translated as taking out neatly packed specimens, scattering them all over the floor, and attacking them with needles and electric engravers in muttonfisted and wildly unsuccessful attempts to develop them further out of their rock matrix. I would carry on savaging the specimens until it was time to leave, when I would depart, atomized fossils and rock chippings strewn behind me across the floor. And each time John Norton would thank me, with utter sincerity and a blind eye to the ruin I'd created, for the help I'd given.

After that I knew I had to become a palaeontologist, working on fossil fish (for the cephalaspids of the Clee Hills had long eclipsed the trilobites). Well, I eventually became a palaeontologist working on graptolites, so I was only out by half a notochord. I didn't think much, then, about why one should study fossils, let alone get paid for it. It was self-evident that these objects were fascinating, and it was also somehow self-evident that these things should be kept safe, and studied, and displayed, as one would, say, catalogue and analyse the paintings of Vermeer and Titian. It was an activity that not only had no relevance to the problems of the real world, but was also an escape from them. The real world was then overshadowed by noisy sabre-rattling between superpowers. If only, I often thought then, people would stop brandishing nuclear bombs at each other, all would be well, life would go on its endless cycle, and one could go on quietly cataloguing the strange beasts that lived long ago.

Well, it's no longer thought to be a minute to midnight, or at least not in quite the same way. Nuclear bunkers in suburban back gardens everywhere have been converted into potting sheds and wine cellars. The world has moved on, and global angst has mutated variously. I'll take just one strand of this. There are perhaps ten times more cars driving around the world now, for instance, than when I started out as a teenage fossil-collector. A few more billion people have come into the world. Levels of carbon dioxide in the atmosphere have gone up from 320 to 360 ppm, and global temperatures have gone up by about half a degree centigrade. A good proportion of the world's rainforests have been cut down. The world's oceans have seen population crashes in those few decades of not just commercial fish stocks such as the cod, but also of, say, most shark species, caught in the crossfire between humankind and edible fishkind.

All that in one fraction of a human lifespan. These trends have moved quite inexorably and with few hints of caprice. The brute numbers are simply adding up. Now add them up and continue that gradient (currently exponential) into the near future. This century will now very likely see, for example, another three billion or so people added. They will all need feeding. So pretty well all productive land on the planet will need to be put to use, and thus – short of anything Micawberish turning up – only miniscule amounts of those rain forests can remain. Every one of the nine billion humans will, quite understandably, strive for a slice of the good life, so the levels of Carbon Dioxide in the atmosphere will inexorably double, and the world will warm by four degrees or so, to take a rough average of IPCC estimates. It feels, even now, like science fiction, even surreal, but that's the likelihood. This will mean that the chances for those other oases of species richness, the coral reefs, don't look good. Now, the competition of various human societies (increasing) for planetary resources (holding steady or dwindling) seems to be the root cause for symptoms such as, say, the currently fashionable global preoccupation of terrorism and the making of war on it. So levels of rational discussion and compromise between societies might not improve.

We *are* living in interesting times, to quote that double-edged Chinese proverb. Those increasingly interesting times will likely form an increasingly intrusive subtext to all our endeavours. And, in this, palaeontology will tend to be something less of an escape and more something imbued with an extra, and very contemporary, frisson; for our global predicament is, unavoidably, the leading edge of the three-billion-year-plus history of the evolution of life. By some coincidence, at about the time that we are all about to enter what might well promise to be one of the most interesting and extraordinary phases in the history of life since the Cambrian explosion or the K-T boundary event, the science of palaeontology is just about becoming able to interpret bits of the past in enough detail to be able to draw sensible, and perhaps even useful, comparisons between past and present.

I'm struck by the way the view of the past has evolved. As a student, I remember interpretations of the past as essentially static tableaux, those painted interpretations of Silurian seascapes and the dinosaur-haunted swamps of the Jurassic. The fossils were put into evolutionary successions, to be sure, and used for correlation, but I got little sense of how past environments could be linked together and made to work. The joins between adjoining tableaux – say at the K-T boundary – were such a field for unconfined speculation that it was almost not worth bothering with them, except to jeer at the most outlandish (dinosaurs dying out from mass constipation? Outrageous!).

Compare that with what is being done today: the reconstruction of successive biotas, as patterns of diversity and global biomass, within the multiple contexts of climate, palaeoceanography, tectonics and the perturbations caused by meteorites and hypervolcanic outbursts, all within near-real time-scales constrained by single zircon crystals and Milankovitch patterns. Earth history is no longer a series of giant murals, but a multi-dimensional movie, getting less jerky with each year's new crop of publications.

That movie might provide some useful alternative plots for the way of the world, to be sure. What might be a better guide is not plot but mode: the ever-clearer picture that change, when it happens, can be quite sudden. Again, since my days of helpfully-intentioned vandalism, past extinctions have sharpened from fuzzy events which might well have taken a good few million years, to changes that are about as abrupt as Messrs Signor and Lipps can allow. And it's not just the great events. The synchronized changes of carbon dioxide, methane, temperature and biota at the end, say, of the last glacial phase should be enough to convince even the most presidential intellect that greenhouse warming has all the appearance of a tried and tested planetary formula.

Even more fascinating is the contrast between the earth as a jumpy, nervous creature, skittering up or down five degrees globally in the course of a few decades: yet the earth as a planet has constrained this febrility within a narrow set of conditions. The oceans have never boiled away, and Snowball Earth never froze completely. Can Gaia (in whatever interpretation) really be at work?

Plus ça change? It's never been an aphorism of universal applicability. In the realm of mass extinctions, the more things changed, the more they were never the same again. It'll be fascinating to see how the new anthropogenic trends fit into old patterns shown by old fossils. Interesting times, indeed. The capriciously-propelled palaeontologists of the future should have plenty to go at, and plenty to say. I'm not sure I wholly envy them.

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The Mystery Fossil

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

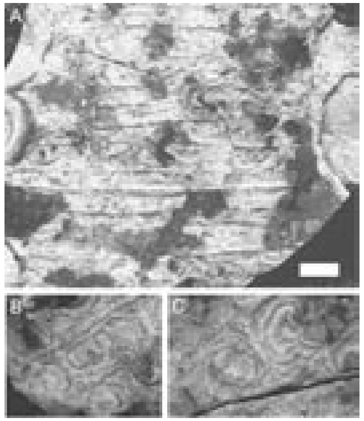
Mystery Fossil Number Two remains a mystery so far with zero suggestions as to its identity. Marc Philipe at the Université Claude Bernard Lyon 1 says he has found an amazingly similar structure in the basal Cretaceous of Byers Peninsula, Livingston Island, South Shetland Islands, but is also stumped (possible pun?) as to what it might be.

Mystery Fossil Three comes to us from Ivan Sansom and Paul Smith (Birmingham, UK), and it is unusual in that it already has a name (*Dictyorhabdus priscus* Walcott 1892) and a history. *Dictyorhabdus* comes from the Harding Sandstone Formation (Caradoc, Ordovician) of Colorado, and occurs in great abundance on certain bedding planes. Originally described as the notochordal sheath of a chimeroid fish by Walcott, it has had something of a nomadic existence since, having been assigned to the cephalopods and glass sponges before residing very much within the incertae sedis. The overall structure appears to be one of a flexible phosphatic tubular sheath with a series of notches on one aspect opposed by a hinge – many specimens have opened up along this hinge but was this possible in vivo or is it a post-mortem feature? Additionally, some opened specimens have what looks superficially like a bivalved termination. We're not even clear if it's a body fossil or a mineralised trace.

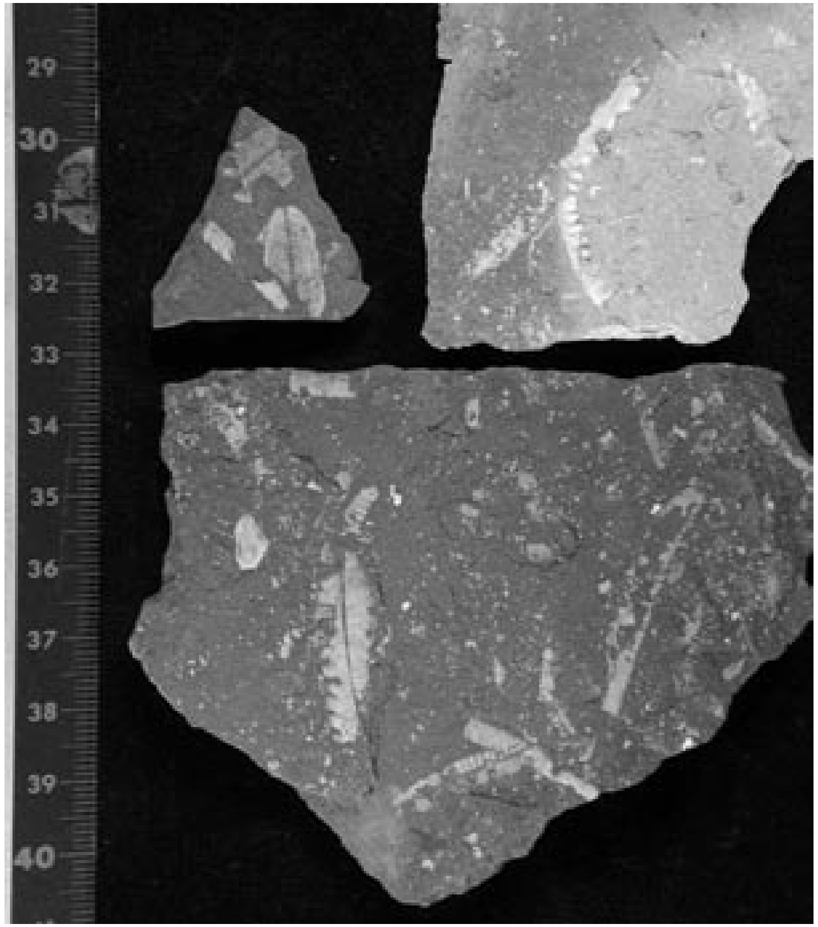
Have you got the faintest idea what *Dictyorhabdus* is? As ever, answers in an email to Cris Little <**c.little@leeds.ac.uk**>. The most convincing answer will win you a Pal Ass field guide of your choosing.

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

Cris Little
Department of Earth Sciences, University of Leeds, UK
<**c.little@leeds.ac.uk**>



(Mystery Fossil no. 2)



>>*Future* Meetings of Other Bodies

The Measurement and Origin of Biodiversity
Dunedin, New Zealand *5 December 2003*

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

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

PhytoPal workshop 2003
Department of Geology, University of Leicester, UK *12 December 2003*

In 2003 the Leverhulme Trust awarded a Research Interchange grant to Dick Aldridge (University of Leicester) to enable closer links to be formed between scientists interested in Palaeozoic acritarchs and prasinophyte algae. The name phytoPal was, therefore, coined. The free exchange of ideas lies at the heart of phytoPal. This exchange takes place via regular workshop meetings, through discussion on an email distribution list and through exchange visits. The first workshop of the phytoPal project will be hosted by Dick Aldridge and Gary Mullins at the Department of Geology, University of Leicester on Friday 12th December 2003. This workshop is timed to occur just prior to the 47th annual meeting of the Palaeontological Association at Leicester on 14th–17th December <**http://www.palass.org/**>.

The workshop is an informal day long meeting for all Palaeozoic palynologists to present talks and posters on aspects of their on-going research projects. Financial assistance to cover part of the cost of travel to the meeting and/or accommodation may be available for participants who intend to present talks on acritarch and prasinophyte algal research topics (contact Gary Mullins at <**glm2@le.ac.uk**>). The deadline for registration, which is free, and abstract submission is 31st October 2003. Refreshments and a buffet lunch will be provided on the day.

Further information is available from <**http://www.le.ac.uk/geology/glm2/phytopal_workshop_2003.htm**>.

26th Nordic Geological Winter Meeting
Uppsala, Sweden *6 – 9 January 2004*

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

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

Seventh International Organization of Paleobotany Conference
Bariloche, Argentina *21 – 26 March 2004*

This conference takes place at the Llao Llao Hotel and Resort on the Andean Range. The VII IOPC is open to all those interested in fossil plants as well as scientists linked to plant biology and geology disciplines. For additional information, please check the meeting Web page at <**http://www.iopc2004.org/**> or contact the organizer by e-mail to <**info@iopc2004.org**>.

International field seminar
Kerman, Iran *14 – 18 April 2004*

Iran has a rich and varied geology, but much of it remains little-known outside the country. In Kerman Province (east-central Iran) there are especially well exposed and extensive sequences of Cambrian-Ordovician-Silurian-Devonian rocks, Jurassic-Cretaceous sediments, and Cenozoic rocks including sediments, metamorphic complexes and extensive volcanics. This notice is the first announcement of plans to hold a field-based seminar programme centred at the University of Shahid Bahonar, Kerman City. Estimated costs are US $950 to include registration, accommodation, all meals and field transportation (students US $600). Day 1: Introductory lectures on the geology of Iran. Days 2,3,4,5: Fieldwork covering four separate themes (Lower Palaeozoic-Devonian stratigraphy and faunas; Jurassic-Cretaceous geology and faunas; Cenozoic sediments, volcanics and structure; Economic geology including ore mineralogy and regional metamorphism). Each theme will run separately over the full four days of fieldwork, with co-ordination and guidance by local experts. For further details contact either Assoc. Prof. Mohammad Dastanpour (Department of Geology, Shahid Bahonar University, P O Box 76169-

133, Kerman, Iran, Fax: [+] 98 341 2267 681, <**dastanpour@mailuk.ac.ir**>), or Prof. Michael G. Bassett (Department of Geology, National Museum of Wales, Cardiff, CF10 3NP, Wales, U.K. Fax: [+] 44 2920 667 332, e-mail <**Mike.Bassett@nmgw.ac.uk**>).

Ichnia 2004: First International Congress on Ichnology

Trelew, Patagonia, Argentina *19 – 23 April 2004*

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

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

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

10th International Symposium on Early Vertebrates/Lower Vertebrates

Gramado, RS, Brazil *24 – 28th May 2004*

Subjects covered will include intercontinental and interhemispherical stratigraphic correlations based on lower/early vertebrates (Palaeozoic); palaeoenvironments/geochronological dating based on early vertebrate faunas, correlations of marine/non-marine fish-bearing strata, systematics and evolution of fossil and extant agnathans and fishes and basal tetrapods, IGCP business meetings, oral presentations and posters. There will be a post-Meeting field trip to Devonian, Carboniferous, Permian and Triassic vertebrate localities of the Paraná Basin. An abstracts volume and a special volume of selected papers will be prepared for the Meeting.

For further information visit <**http://www.ufrgs.br/geociencias/evento.html**>.

XI International Palynological Congress (IPC2004)

Conference and Exhibition Centre, Granada, Spain *4 – 9 July 2004*

This international conference will bring together all those people actively involved or interested in the study of pollen from a wide variety of standpoints (botany, biology, environmental sciences, medicine, palaeontology, sedimentology, archaeology). Symposia include: Pollen biology, Pollen and spore morphology, Aerobiology, Pollen and allergy, Entomopalynology and melissopalynology, Forensic palynology, Palaeopalynology and evolution, Quaternary palynology and World pollen databases. The meeting includes a number of pre- and post-congress fieldtrips to Andalusia, south-eastern Spain, Morocco, central Spain, Camino de Santiago-Picos de Europa, Canary Islands, Balearic Islands.

Further details can be obtained from the Technical Secretary (tel +34 958 208650, fax +34 958 209400, e-mail <**eurocongres@eurocongres.es**>), and on the Congress website at <**http://www.11ipc.org/**>.

Computer techniques in the modelling and analysis of biological form, growth and evolution

Firenze, Italy *22 – 28 August 2004*

The 32nd International Geological Congress will take place in Firenze, Italy, in August 2004. The first circular is available on-line on the Congress website, at <**http://www.32igc.org/home.htm**>. The first of the general symposia planned in section G17 (Palaeontology) is entitled “Computer techniques in the modelling and analysis of biological form, growth and evolution”. Organisers are Enrico Savazzi (Uppsala University <**enrico.savazzi@pal.uu.se**>) and Richard A. Reyment (Swedish Museum of Natural History <**richard.reyment@pal.uu.se**>). The symposium will encompass the following five topics:

- Theoretical morphology of biological skeletons: This topic includes all techniques for generating and displaying models of biological skeletons. Different approaches will aim at modelling morphology alone, or at modelling the growth and constructional processes that govern skeletal morphology.
- Morphogenesis of colour, relief and structural patterns: Unlike the foregoing topic, which has long been the domain of palaeobiologists, this aspect has been largely studied by biologists. It deals with smaller-scale patterns on or within skeletal parts. Of special interest to palaeobiologists are the modelling of morphogenetic programmes producing surficial patterns

on shells that grow by marginal accretion, and the modelling of the genesis of microstructures in these shells.

- Modelling of evolutionary processes: This is a little developed area of computerized modelling but one that has a high potential. It embraces all aspects of the modelling of evolution, and contributions integrating evolutionary and morphological modelling will be especially welcome.
- Computer-assisted statistical and morphometric techniques: This topic is concerned with applications of geometric morphometrics to problems in the analysis of shape-variation in organisms, though with particular emphasis on advances in Geometric Morphometrics in the spirit of Bookstein, Dryden, Kendall, Kent and Mardia.
- Computer-assisted imaging techniques applied to palaeobiology: This topic will embrace applications of results accruing from image-analytical aspects of morphometrics. Although connected to the foregoing topic, this field involves a different area of expertise.

The symposium will take place over half a day, and will consist of approximately six to eight oral contributions, some from invited speakers. A poster session in connection with the symposium is possible, and can be used to host contributions that cannot be accommodated in the oral part of the symposium. We encourage the submission of volunteered abstracts and expressions of interest in participating by other scientists. Submission of abstracts by invited and volunteering speakers and/or poster proposers should meet the deadline in **late November, 2003**.

Since the International Geological Congress is very large, funds will not be available to subsidise symposium organisers and invited speakers. However, a Geohost program will be available, mainly to help individual scientists from developing countries to help cover their attendance costs. Information on this will be available on the Congress website. Contact the organizers (Savazzi and Reyment) for more information.

Chemosynthetic communities through time (32nd IGC)

Firenze, Italy *22 – 28 August 2004*

This is session T-18.4 at the 32nd International Geological Congress, Florence, 2004. The aim of the session is to gather together researchers interested in the evolution of chemosynthetic faunas, both microbial and macrofaunal. The convenors are Crispin Little <**c.little@earth.leeds.ac.uk**>, Roberto Barbieri <**barbieri@geomin.unibo.it**> and Kathy Campbell <**ka.campbell@auckland.ac.nz**>.

The session will have a half-day duration, and will include up to ten standard oral presentations (including invited presentations). Standard oral presentations have a 15 minute duration, including time for questions. Invited speakers include Crispin Little (Leeds University), Jack Farmer (Arizona State University), Lisa Levin (Scripps Institution of Oceanography), Antje Boetius (Alfred Wegener Institute for Polar and Marine Research) and Marco Taviani (Consiglio Nazionale delle Ricerche). Deadline for submission of abstracts and initial registration is 10th January 2004.

Through the generous sponsorship of NASA Astrobiology Institute the registration cost (€430) will be covered for up to six individuals whose submitted abstracts are selected by the convenors to give oral presentations. Costs will be reimbursed after the conference.

The second circular for the 32nd IGC is now available on the Web at <**http://www.32igc.org/home.htm**>. This lists registration details and deadlines for submission of abstracts and various payments for the Congress. The circular also has details of a post-congress fieldtrip P 07 – Fluid expulsion and authigenic carbonates in Miocene foredeep and satellite basins (northern Apennines) that may be of interest (see <**http://www.32igc.org/circularN-field05_1.asp**>). The Organizing Committee will help individual scientists mainly from developing and East-European Countries to attend the Congress by partially subsidizing their expenses via the GeoHost Program <**http://www.32igc.org/circular-gen07.htm**>.

Paleobiodiversity and major biotic changes in Earth History

Session G-17.3, International Geological Congress *20 – 28 August 2004*

Palaeontological research on biodiversity has concentrated on global-scale patterns of diversity of taxa and of broad ecological groups, especially with respect to mass extinctions. However, biodiversity was originally defined to include all biological levels from genetics to ecosystems and landscapes. Here we invite papers that address any biodiversity level, or relationships between levels, with an emphasis on radiations and background trends through time.

Palaeontology provides historical perspectives from long-term patterns, and therefore complements studies of living biodiversity. After several decades of research however, there is still no satisfactory universal model for taxonomic biodiversity that integrates ongoing ('maintenance') and historical processes. Therefore we particularly encourage papers that identify problems which currently hinder our progress towards an integrated theory of biodiversity and suggest ways forward.

Papers may be based on any group(s) of organisms. Possible subjects include: measurement and analysis of biodiversity; development of open-access databases; sampling controls; phylogenetic constraints, including molecular *vs* palaeontological patterns; modelling (*e.g.* causal links between earth system processes and life processes); methods for investigating controlling factors; problems of scale (*e.g.* relative importance of ecological, regional and global factors); roles and relative importance of tectonic, eustatic, climatic, oceanographic and biogeochemical factors; proxies for, and possible roles of, nutrients; Adaptive innovations, including role of symbioses.

The **deadline** for abstract submission (oral or poster presentation) is **10th January 2004**. Please follow the guidelines available at <**http://www.32igc.org/**>. For further information feel free to contact the conveners: Francesca Bosellini <**frabos@unimore.it**>, Gian Luigi Pillola <**pillolag@unica.it**>, or Brian Rosen <**B.Rosen@nhm.ac.uk**>.

4th International Bioerosion Workshop (IBW-4)

Prague (Czech Republic) *30 August – 2 September 2004*

The aim of the workshop series is to combine the knowledge of biologists (working mainly in reef ecosystems) with the experience of palaeontologists interested in bioerosion of all types of substrates (reefs and other calcareous matters, wood, bone, *etc.*). All participants should communicate their results or problems as talks, posters or presentations of specimens. The workshop will be held at the Czech National Museum in Prague. Several additional days of field trips are planned during and prior to the meeting (*e.g.*, Devonian and Jurassic reef facies, Cretaceous and Miocene rockgrounds and hardgrounds, Miocene bored mollusc deposits, recent wood borings). For information please contact: Dr Radek Mikulá, Institute of Geology, Czech Academy of Sciences, Rozvojová 135, CZ–165 00 Praha 6; e-mail <**mikulas@gli.cas.cz**>.

North American Paleontological Convention

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). More information will soon be appearing at <**http://www.dal.ca/~es/staff/dbscott/scott.htm**>.

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

Meeting REPORTS

Second Symposium on Mesozoic and Cainozoic Decapod Crustaceans

Oertijdmuseum de Groene Poort, Boxtel and Natuurhistorisch Museum
Maastricht, The Netherlands *3 – 6 September 2003*

I missed the first such decapod crustacean meeting, held in Italy, but with the second almost on my doorstep I had every reason to be there. The latest symposium was organised by René Fraaije, John Jagt and their very capable team. Registration and the ice breaker party were on the afternoon and evening of 3rd September. Although a select group, the 25–30 delegates came from at least nine countries including Japan, Mexico and the USA. A feature of registration was the abstract volume. Extended abstracts of oral and poster presentations had been solicited by the organisers, and these were published in volume 72, nos 2–3 of *Contributions to Zoology*. This ensured that the abstract/conference volume reached a much larger audience than just those who actually attended the meeting, and we were all able to leave Boxtel without the pressure of having unwritten papers for the conference volume hanging over our heads. Communication was also served by an unusually lively exchange of offprints between delegates; by the end of the meeting I had accumulated a pile of papers and monographs over 4 cm thick!

The real business of the meeting started the next morning, following a welcoming address from the deputy mayor of Boxtel. The meeting was very informal, with lively discussion within sessions that spilled over into coffee breaks, lunch and dinner. Because posters outnumbered oral presentations, speakers were allowed up to 45 minutes or more to make their presentations. This resulted in all papers being given in considerable depth, which made for an unusually informative meeting, particularly for this 'crab dabbler.' It also meant that there was no artificial cut-off as the discussion became more involved. This seems to have been generally appreciated, particularly when quieter members of the audience have become involved.

Gérard Breton *et al.* began the proceedings with a discussion of Kimmeridgian decapods of Bure in France, produced from wells several metres in diameter that are being dug by the French nuclear waste management agency ANDRA. These excavations are yielding a large and diverse fossil biota. The four species of decapod crustaceans from this site, although fragmentary, exhibit features such as colour patterns and, possibly, sexual dimorphism. The latter feature was demonstrated in the thalassinoidean *Etallonia isochela* (Woodward); 50% of the dactyli of this species show a tubercle at the mid length, a feature missing in the other half.

After a coffee break (and Dutch coffee is always worth breaking for), **Donovan *et al.*** gave an appraisement of the development and current state of knowledge of the Cretaceous and Cenozoic decapods of Jamaica. Apart from three papers by T.H. Withers in the 1920s, based on specimens collected by D. Woolacott and C.T. Trechmann, Jamaican decapod crustaceans have only been the subject of a sustained research programme for the past ten years. The eight species recognised before 1993 have now swollen to 85 taxa and counting. However, there are still obvious gaps in the record, such as in the Eocene and Oligocene.

Carrie Schweitzer gave a particularly focused account of the systematic problems associated with the xanthoid brachyurans. Features commonly used in classifying extant species, such as juveniles and sperm, just don't get fossilized. Extant taxa may have very different carapace morphologies, yet are determined to be closely related on features of the male claw; what chance is there of making such a determination based on the typically fragmentary fossil material? An approach to the critical assessment of fossil material using measurable characters such as ratios and angles of carapace features works for many examples, a result that would have intrigued D'Arcy Thompson.

In the afternoon, **Francisco Vega Vera *et al.*** gave a broad introduction to the Upper Cretaceous fossil arthropods of Chiapas in southern Mexico, not just decapod crustaceans, but also terrestrial groups such as cockroaches, dragonflies and spiders. This was a fine advertisement for a geologically fascinating area and was instrumental in a narrow victory for Chiapas when delegates voted for the venue for the next (2006) meeting; southern Germany will host the 4th symposium three years later.

René Fraaije then presented a fascinating discussion of the fossil occurrence of lobsters and ammonites in an Upper Liassic oil shale in Germany. The ammonites are preserved in this deposit as the periostracum only, just 1 mm thick! Over 50% of the ammonites are damaged at the base of the living chamber, suggesting predation or perhaps scavenging. Complete lobsters and fishes are preserved in the body chambers of what must have been dead ammonites, which were apparently used as refuges. That some lobsters were eaten is indicated by their occurrence as food balls within some ammonite body chambers, showing a distribution that suggests the position of the gut.

Afternoon coffee was followed by posters and further discussions. Posters were on display throughout the meeting and, on the afternoon of the second day (5th), their authors were invited to give short oral presentations in front of their displays and to make themselves available for questions. All 18 posters were produced to a very high standard, and examined subjects as diverse as preparation and photographic techniques (**Sten Jakobsen**), systematics (*e.g.*, **Barry van Bakel *et al.***), microstructure of the exoskeleton (**David Waugh & Rodney Feldmann**) and faunistics/biogeography (*e.g.*, **Pedro Artal *et al.***). Dinner on the 4th was followed by a group discussion on progress and publishing strategy of the revised decapod crustacean volume of the *Treatise on Invertebrate Paleontology*.

First up on the second morning, after the presentation of a birthday present to one of the delegates, were **Anja Mourik & Tsjitske Visser**, discussing the detailed biometrics of *Protocallianassa faujasi* from the Campanian and Maastrichtian. Their biometric analysis recognised claws of males, females and juveniles based on multiple characteristics. Exceptionally, burrows from the Campanian of the Dülmen area of Germany include multiple specimens of shrimps, which may represent some sort of death or post-mortem accumulation.

Rodney Feldmann then gave a lively and far-ranging review of the interpretation of palaeoecology and palaeophysiology of fossil decapod crustaceans. This paper probably touched on aspects of the research programmes of everyone present. The fossil record of decapods is biased by diverse taphonomic influences and their multi-element skeletons show varied

modes of preservation. Groups that are relatively weakly mineralised such as the shrimps are undoubtedly under-represented in the fossil record. Anachronous patterns abound, such as that shown by stridulation mechanisms; the oldest fossil evidence is Miocene or Oligocene, yet on phylogenetic grounds they are predicted from the Jurassic.

Fred Schram & Christopher Dixon discussed "Fossils and decapod phylogeny." They have produced a robust cladistic analysis of the crustaceans using 70 morphological characters, 50–55 with multiple character states. The structure of this tree, originally based on a database derived from extant crustaceans only, was maintained when palaeontological data were incorporated, an encouraging result.

After lunch **René Fraaije** gave a talk entitled "Evolution of reef-associated decapod crustaceans through time, with particular reference to the Maastrichtian type area." He introduced the geology and palaeontology of the Maastrichtian of Zuid Limburg, the most southerly province of The Netherlands, which was to be the area of the field excursion on Saturday. As one of the leading exponents of the decapod crustaceans of this area, Fraaije was able to exhibit taxa in their stratigraphic context, and discuss aspects of their palaeoecology and taphonomy. However, as we were to discover, even forearmed with this information and an informative field guide, very careful observation and collecting were necessary to find and tease out the rare fossil crustaceans from these deposits.

The last talk, by **Günter Schweigert & Alessandro Garassino**, examined progress in the study of decapods from the Upper Jurassic lithographic limestones of southern Germany. Numerous taxa were discussed from these deposits, probably the best known rock sequence for fossil shrimps. Most specimens are moults that have been squashed flat, but rare dead animals are preserved in three dimensions and infilled with phosphate. The study of morphological detail is aided using ultraviolet illumination.

Carcinologists and coffee at the Oertijdmuseum de Groene Poort in Boxtel, The Netherlands. Left to right: Roger Portell (Florida Museum of Natural History, Gainesville), Joe Collins (scientific associate of The Natural History Museum, London) and Sten Jakobsen (Geological Museum, University of Copenhagen).

After two days of fine weather, Saturday dawned overcast with some gentle drizzle. Most delegates of the meeting attended the field excursion, led by **John Jagt**, and, as our coach travelled south, the weather improved, at least for the morning. The excursion was comprised of three distinct parts. Having spent the formal session of the conference in the Oertijdmuseum de Groene Poort, where we could examine the many fossils from Zuid Limburg on display, we spent Saturday morning at the Natuurhistorisch Museum Maastricht which boasts the largest fossil collection from the type Maastrichtian. From here it was a short coach ride to the ENCI quarry in St. Pietersburg, which includes the type section of the Maastrichtian stage, and where we spent a pleasant afternoon collecting from the two highest units of the Maastricht Formation, the Nekum and Meersen members. By now the sky had clouded over, which made it easier to see fossils in the pale coloured limestones, and most delegates had some success, albeit limited, the commonest finds being claws of *Protocallianassa faujasi*. From here we travelled to Geulhemmerberg, and went underground in the limestone mine system to examine the Cretaceous-Tertiary boundary section, its nine boundary clays and associated fossiliferous deposits. This was followed by a conference dinner in a nearby hotel. The only 'disaster' of the meeting occurred on the way home; the coach broke down just after we left the car park and we didn't get home until after midnight. However, with animated conversation on decapods continuing by the roadside while we waited for a replacement vehicle, it seemed that many delegates almost welcomed this extension to the meeting's discussion time.

Stephen K. Donovan
Nationaal Natuurhistorisch Museum, Leiden, The Netherlands
<**Donovan@naturalis.nnm.nl**>

Post-graduate opportunities in Palaeontology

This is our third digest of career opportunities in palaeontology. Careers advice is available from the Palaeontological Association website <**www.palass.org**> and includes a series of biographies from Palaeo-MSc students through to Professors of Palaeontology, Museum Curators, Science Publishers, and workers in both Show- and Oil-business, all of whom have made their way through a career path in palaeontology. Descriptions of palaeontology, and palaeontology-related, MSc courses are listed below, followed by a digest of all PhD projects currently open for applications to begin in October 2004.

M.Sc. in Palaeobiology: University of Bristol, Department of Earth Sciences

The M.Sc. in Palaeobiology offers a broad-based overview of modern approaches in palaeobiology. Students study nine out of 16 possible options, and topics range from taphonomy and palaeoecology to mammalian palaeobiology, dinosaurs to trace fossils, systematic methods to macroevolution. Then there is a six-month independent project, and students are offered a wide range of topics. The programme is designed for students with a BSc in either a biological or earth sciences subject, and conversion courses in evolution, basic palaeontology, and sedimentology are offered. Students also receive training in writing scientific papers, creating websites, applying for Ph.D.s and jobs (both in Britain and overseas).

So far, 60 students have graduated, and many have gone on to rewarding careers in palaeontology and related scientific areas. Full details of the programme, of former students, and how to apply are available on the website <**http://palaeo.gly.bris.ac.uk/opportunities/MSc.html**>. Application forms may be downloaded from the website, or they can be provided by <**shirley.sparks@bris.ac.uk**>.

M.Sc. Micropalaeontology: University College London

The science of Micropalaeontology studies the microscopic remains of animals, plants and protists belonging to biological groups mostly of simple organisation and less than 1mm in size. These organisms were extraordinarily abundant and diverse in the past and continue to be so in modern environments, in many cases forming the primary elements in marine, lacustrine and terrestrial organic productivity cycles and food chains. The production of these organisms is a basic component of the global biogeochemical system, intimately linked to present and past environmental change. In this way microfossils are keys to palaeoceanography and palaeoclimatology and to understanding the evolution of the biosphere. Our ability to use the pattern of evolution of microfossil groups during the last 400 million years as a means of ascribing relative ages to sedimentary rocks and reconstructing their environmental histories is of great value for understanding global sedimentary geology, and has especially important applications, for example, in the hydrocarbon industry.

The M.Sc. and Diploma course in Micropalaeontology was founded in 1959, was the first of its kind in Britain and was specifically designed to train professional micropalaeontologists. The importance of the subject for biostratigraphy and palaeoenvironmental interpretation is firmly established through its application to hydrocarbon exploration, and also as a key to understanding the history of the continental shelf and oceanic basins. A high proportion of graduates have entered the oil industry, either following the M.Sc. course or after further research. Close links are maintained with the hydrocarbon industry.

The course is broadly based and covers calcareous, organic-walled and siliceous microfossils. Great emphasis is placed on the biostratigraphy and spatial distribution of the organisms and their application to problems of zonation and correlation and to environmental analysis. All major post-Palaeozoic microfossil groups are covered in the M.Sc. curriculum. Individual and team project work forms an important part of the course.

The entry qualifications for the M.Sc. in Micropalaeontology are: at least a Lower Second Class Honours degree in Geology, although joint combinations with Geography, Biology and Oceanography may be acceptable. We welcome enquiries from graduates with experience in oil companies who wish to obtain further qualifications.

Further details and application forms are available from:

Professor A.R. Lord
Department of Geological Sciences, University College London, Gower Street, London WC1E 6BT, UK. Tel: (44) 020 7679 7131; Fax: (44) 020 7388 7614
<micropal@ucl.ac.uk>

M.Sc. Advanced methods in taxonomy and biodiversity: Imperial College London

Imperial College of Science, Technology and Medicine and The Natural History Museum are jointly offering a Masters degree course in Advanced Methods in Taxonomy and Biodiversity.

The one-year full-time M.Sc. course provides essential skills for all concerned with taxonomy and biodiversity. The course is composed of ten taught modules followed by a four-month research project. The series of modules seeks to provide as wide as possible an overview of the theory and practice of modern taxonomy and systematics, with associated biodiversity studies. During their four-month research project, students can specialise in their chosen area.

The course is based at The Natural History Museum, London, one of the world's premier institutions for research on the diversity of the natural world. The collections include over 68 million specimens, 800,000 of which are type specimens, and the Museum houses a world class library covering all areas of taxonomy and systematics. The Museum is situated next to the main South Kensington campus of Imperial College, and there are close research and teaching links between the two establishments. Students will therefore be situated in the heart of London, and are able to make full use of the facilities at both institutions.

Students are trained to a high level of competence in systematics and a detailed understanding of the various uses and problems involved. The course provides methodological background, including quantitative skills, computer applications and practical skills in morphological and molecular techniques of taxonomy and systematics. The most up-to-date ideas and research in taxonomy and biodiversity are taught, to a large extent from primary literature. Hands-on training in conducting research in this area will be provided by project supervisors, with specialisation in the student's field of choice. After completing the course, students will be able to:

- apply a wide range of techniques to the study of systematics, including collections management, identification, key construction, taxonomic revision, phylogeny reconstruction and comparative methodologies;
- understand the diversity of living organisms in space and time, and be familiar with methods for measuring this diversity and monitoring changes due to both anthropogenic and natural factors, and in Earth history;
- select appropriate methods to solve taxonomic and biodiversity problems, and be able to acquire and analyze taxonomic data, including both traditional and molecular data;
- understand fully the conceptual basis of taxonomy and phylogenetics and in particular, cladistics, and to understand "biodiversity" within this framework;
- apply these concepts to issues of biodiversity and conservation management and research, to set priorities for sustainable development, environmental assessment and inventories; apply these concepts to other areas of biology such as parasitology and epidemiology.

Who is this course aimed at?

The course is aimed at anyone concerned with taxonomy and biodiversity. It is relevant to those involved with biodiversity assessments, conservation and sustainable development, from biomedical sciences to agriculture and fisheries, as well as to those intending to pursue academic careers in systematics and related fields.

Entry requirements

Applicants should normally either have or expect to gain at least a lower second class honours degree (or equivalent) in a biological or environmental subject (*e.g.* zoology, botany, microbiology, agriculture and veterinary science). Exceptionally students with different backgrounds or with related work experience will be considered.

Further details are available from:

Ms Amoret Brandt
Department of Entomology, Natural History Museum, London SW7 5BD, UK tel: +44 (0)20 7942 5036; fax:+44 (0)20 7942 5229
<a.brandt@nhm.ac.uk>

Royal Holloway, University of London: Department of Geology

MSc Geology by Research

This programme is offered to prospective students who wish to pursue research in a selected field of the Geological Sciences for a period of one calendar year full time or two calendar years part time and be awarded a Masters degree. Students will receive training in research skills, including data collection, data handling and analytical techniques as well as transferable and presentation skills. Students will take a course in a subject area closely related to the chosen field of research, selected from a menu of masters level courses offered by the department. The main outcome of the programme is a piece of independent research presented in the form of a dissertation. Upon completion of the programme students will have gained experience of research and presentation of material in the geological sciences which equips them to publish work in international scientific journals.

Prospective students should contact individual members of staff in the department in the first instance to discuss potential research projects. The research interests of staff are available on the department website <**http://www.gl.rhul.ac.uk/staff/acad.html**>.

Ph.D. Palaeo projects for 2003

The following is a digest of the PhD projects courses offered to commence in October 2004. This is by no means an exhaustive list and the institutions listed, plus others that are not listed, may well extend this list over the next few months. Further details for many of these projects are already available on institutional websites (url supplied); details for all will be available shortly. An email address is included for first point of contact for expressions of interest in any of the titles and it is advisable to make your interest known as soon as possible. Application deadlines can be as early as January 2004, and interviews usually take place during the period January–April. Funding for subsistence and tuition fees is usually awarded on a competitive basis.

University of Birmingham: School of Geography, Earth & Environmental Sciences

The latitudinal distribution and diversity of pollen morphology in North America

Supervisor: Guy Harrington
Contact Guy Harrington for further details <**g.j.harrington@bham.ac.uk**>

Palaeofloristics of a Lower Carboniferous terrestrial lagerstätte: evolutionary significance, palaeoecology and ecosystem dynamics

Supervisors: Jason Hilton and Richard M. Bateman (NHM, London).
Contact Jason Hilton for further details <**j.m.hilton@bham.ac.uk**>

Separating similarities: the role of ancestry and parallel evolution in seed fern evolution

Supervisor: Jason Hilton
Contact Jason Hilton for further details <**j.m.hilton@bham.ac.uk**>

The architecture and development of Silurian reefs

Supervisors: Alan Thomas, Paul Smith, Don Mikulic (Illinois State Survey) & Joanne Kluessendorf (University of Wisconsin)
Contact Alan Thomas for further details <**a.t.Thomas@bham.ac.uk**>

Further information can be obtained from <**http://www.gees.bham.ac.uk/**>.

University of Bristol: Department of Earth Sciences

Character acquisition through geological time

Supervisors: Mike J. Benton and Philip C.J. Donoghue
Contact Mike Benton for further details <**mike.benton@bristol.ac.uk**>

The end-Triassic mass extinction: fine-scale palaeontological and geochemical resolution

Supervisors: Mike J. Benton and Richard J. Twitchett (University of Plymouth).
Contact Mike Benton for further details <**mike.benton@bristol.ac.uk**>.

Gigantism in Palaeozoic arthropods: palaeobiological and phylogenetic perspectives

CASE award with the Natural History Museum, London.
Supervisors: Simon Braddy and Richard Fortey (NHM).
Contact Simon Braddy for further details <**s.j.braddy@bristol.ac.uk**>.

Palaeobiology of primitive armoured vertebrates

CASE award with the Natural History Museum, London.
Supervisors: Philip Donoghue, Philippe Janvier (Museum national d'Histoire naturelle, Paris) and Peter Forey (NHM, London).
Contact Philip Donoghue for further details <**phil.donoghue@bristol.ac.uk**>.

Further information can be obtained from <**http://www.gly.bris.ac.uk/**>.

University of Cambridge: Department of Earth Sciences

Early zooplankton and the Cambrian Explosion

Supervisor: Nicholas J. Butterfield.
Contact Nic Butterfield for further details <**njb1005@esc.cam.ac.uk**>.

Siliclastic- and carbonate-hosted Ediacaran faunas in Russia

Supervisors: Dmitri Grazhdankin and Nicholas J. Butterfield.
Contact Nic Butterfield for further details <**njb1005@esc.cam.ac.uk**>.

Analysis of cranial form and function using Finite Element analytic techniques

Supervisors: Emily Rayfield and David Norman.
Contact David Norman for further details <**dn102@esc.cam.ac.uk**>.

Ecological restructuring of hard substrate communities across the K-T boundary

Supervisors: Dr E.M. Harper (Cambridge) and Dr P.D. Taylor (Natural History Museum, London).
Contact Dr Harper for further details <**emh21@cus.cam.ac.uk**>.

Further information can be obtained from <**http://www.esc.cam.ac.uk/**>.

University of Cambridge: Museum of Zoology

Students interested in pursuing projects concerning early tetrapods, sarcopterygian fishes, aspects of the fish–tetrapod transition or related topics should contact Jenny Clack directly to discuss possibilities.

Contact Jenny Clack for further details <**Jac18@hermes.cam.ac.uk**>.

Further information can be obtained from <**http://www.zoo.cam.ac.uk/museum/jenny.htm**>.

Cardiff University:
School of Earth, Ocean and Planetary Sciences

Ocean climate and ecology in the middle Eocene at 55°S, New Zealand

Supervisors: Paul Pearson, Jenny Pike and Caroline Lear.
Contact Paul Pearson for further details <**PearsonP@cf.ac.uk**>.

Integrated approaches to the reconstruction of early land vegetation

Supervisors: Dianne Edwards, Paul Wright and John Richardson (NHM, London).
Contact Dianne Edwards for further details <**edwardsd2@cardiff.ac.uk**>.

Reassessment of biodiversity among Jurassic Shelf communities

Supervisors: Lesley Churns and Paul Wright.
Contact Lesley Churns for further details <**churns@cardiff.ac.uk**>.

Further information can be obtained from <**http://www.earth.cardiff.ac.uk/**>.

University of Durham: Department of Geological Sciences

Biosphere and geosphere dynamics during end Ordovician climate change

BGS Case Award
Supervisors: Howard Armstrong, Alan Owen (University of Glasgow) and Mark Williams (BGS, Keyworth).
Contact Howard Armstrong for further details <**Howard.Armstrong@durham.ac.uk**>.

Further information can be obtained from <**http://www.dur.ac.uk/h.a.armstrong/**>.

University of Leeds: School of Earth Sciences

Chemosynthetic communities from Devonian barite deposits in Nevada, USA and Mexico

Supervisors: Crispin Little, Kathleen Campbell (University of Auckland, NZ), Sarah Long (NHM, London).
Contact Cris Little for further details <**c.little@earth.leeds.ac.uk**>.

Silurian and Devonian cold seep communities from Morocco: palaeoecology and palaeoenvironments

Supervisors: Crispin Little, Jörn Peckmann (Research Center for Ocean Margins, University of Bremen, Germany), Jon Todd and Sarah Long (NHM, London).
Contact Cris Little for further details <**c.little@earth.leeds.ac.uk**>.

Further information can be obtained from <**http://earth.leeds.ac.uk/**>.

University of Leicester: Department of Geology

Late Ordovician extinction and Early Silurian recovery: the phytoplankton record

Supervisors: Richard J. Aldridge & Gary L. Mullins.
Contact Dick Aldridge for further details <**ra12@le.ac.uk**>.

Taphonomic, environmental and stratigraphic biases in the fossil record of early vertebrates

Supervisors: Mark Purnell, Sarah Davies and Alain Blieck (Université des Sciences et Technologies de Lille).
Contact Mark Purnell for further details <**map2@le.ac.uk**>.

Major ecological transitions in early vertebrate evolution

Supervisors: Mark Purnell, Jan Zalasiewicz and Jane Evans (NGL).
Contact Mark Purnell for further details <**map2@le.ac.uk**>.

Further information can be obtained from <**http://www.le.ac.uk/geology/**>.

University College London: Department of Anatomy and Developmental Biology

The group has broad interests in the evolution, radiation, systematics, and functional morphology of small reptiles and amphibians, living and extinct. Project options can be discussed with individual candidates. The Department operates a common selection procedure for studentships whereby all applications are scrutinised by a postgraduate committee and then selected qualified candidates are short-listed for interview. Please note that any prospective candidate must have, or expect to achieve, a good 2:1 or First in a relevant discipline. This applies both to BSc and MSc/M.Phil applicants.

Contact Susan E. Evans for further details <**ucgasue@ucl.ac.uk**>.

Further information can be obtained from <**http://evolution.anat.ucl.ac.uk/people/evans/evanmain.htm**>

University of Liverpool: Department of Earth Sciences

The evolution of dispersal strategies in Cretaceous spatangoid sea urchins

Supervisors: Charlotte Jeffery and Jim Marshall
Contact Charlotte Jefferies for further details <**chj@liv.ac.uk**>.

Further information can be obtained from <**http://pcwww.liv.ac.uk/earth/web/Phd.htm**>.

University of Manchester: Department of Earth Sciences

Mesozoic palaeoecology: the Jehol fauna of Liaoning, China

Supervisors: John Nudds and Paul Selden
Contact John Nudds for further details <**john.nudds@man.ac.uk**>.

Computer 3D reconstruction of fossils in nodules by serial sectioning

Supervisors: Paul Selden and Derek Siveter
Contact Paul Selden for further details <**paul.selden@man.ac.uk**>.

Further information can be obtained from <**http://www.earth.man.ac.uk/**>.

University of Plymouth: School of Earth, Ocean and Environmental Sciences

Micropalaeontological changes across the K/T boundary in Denmark

Supervisors: Malcolm Hart and C. Smart
Contact Malcolm Hart for further details <**mhart@plymouth.ac.uk**>.

Micropalaeontological extinctions at the Triassic/Jurassic boundary

Supervisors: Malcolm Hart, G. Price and Richard Twitchett
Contact Malcolm Hart for further details <**mhart@plymouth.ac.uk**>.

Further information can be obtained from <**http://www.plym.ac.uk/**>.

Royal Holloway, University of London: Department of Geology

Ephemeral continental environments, pedogenesis and ichnofacies

Supervisor: Gary Nichols
Contact Gary Nichols for further details <**g.nichols@gl.rhul.ac.uk**>.

Chemical oxidation in snowpacks: removing palaeoclimate signals and processing of environmental pollutants

Supervisor: Martin King
Contact Martin King for further details <**m.king@gl.rhul.ac.uk**>.

Unlocking the information potential of modern and ancient charcoal assemblages

Supervisors: Andrew Scott and Margaret Collinson
Contact Andrew Scott for further details <**a.scott@gl.rhul.ac.uk**>.

Further information can be obtained from <**http://www.gl.rhul.ac.uk/research/resops/**>.

University of Southampton: School of Earth and Ocean Science

Global sea-level and the Red Sea during the last 70,000 years

Supervisors: David Smeed and Eelco Rohling.
Contact David Smeed for further details <**ejr@soc.soton.ac.uk**>.

Extreme climates in the late Cretaceous and early Cenozoic

Supervisors: Paul Wilson and C.R. German.
Contact Paul Wilson for further details <**paw1@soc.soton.ac.uk**>.

Centennial scale palaeoceanography of the Gulf of Oman since the last deglaciation

Supervisors: E.J. Rohling and P.P.E. Weaver.
Contact Eelco Rohling for further details <**ejr@soc.soton.ac.uk**>.

The Mid Palaeozoic glacial record in West Gondwana

Supervisor: John E.A. Marshall.
Contact John Marshall for further details <**jeam@soc.soton.ac.uk**>.

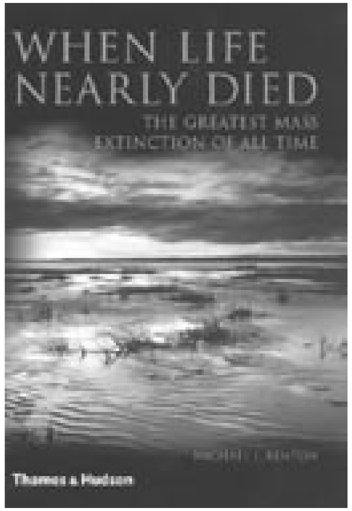
Further information can be obtained from <**http://www.soc.soton.ac.uk/soes/graduate/**>.

Book Reviews

The Extinction of All Life and the Sublime Attraction of Neocatastrophism

When Life Nearly Died: The Greatest Mass Extinction of All Time

Benton, M.J. (2003) Thames and Hudson, 336 pp; ISBN: 050005116X (hbk), £16.95



Mike Benton has just published a book on geology and extinctions. The title is *When Life Nearly Died: The Greatest Mass Extinction of All Time*. Based on this you might expect the book would be about the Permo-Triassic extinctions. You might expect all the new information about these extinctions that has come out since Doug Erwin's (1993) *The Great Paleozoic Crisis: Life & Death in the Permian* to be reviewed, compared, and summarized in an authoritative yet engaging manner. You might expect this information to be set in a novel context that would make it clear why the study of geological extinctions is important enough to have held the interest of researchers across the scientific spectrum for almost 30 years now. You might even expect a few new insights from a researcher who has been active in the front lines of work on this particular watershed. If you read the book you'll get all these things … and, curiously, less.

What makes a good popular science book by a scientist author? No doubt there are as many answers to this question as there are readers, and no doubt the answer will differ for palaeontological novices as opposed to members of the Palaeontological Association. Yet some generalized principles – call them standards if you will – do seem relevant. For me, the first of these is completeness. While no book can cover all possible sides of any large research programme in depth, all major arguments, both pro and con, involved in the topics the author chooses to discuss need to be aired. Failure to do so suggests an author is stacking the rhetorical deck in favour of their preferred hypothesis, a stance as unscientific as it is dishonest. Deviations from this principle are often justified *post hoc* in the name of either brevity or simplification for an anticipated non-technical audience. I am unmoved by such rationalizations. If a story is not worth telling completely and well, or if an author has such little regard for their audience's ability to grasp technical concepts, why tell it at all?

The second principle is originality. Readers expect scientist authors who have participated in the research programme to do more than merely write reviews of other people's work. Non-scientist authors often fall afoul of this principle because they don't feel comfortable making original linkages and forming their own opinions. This in turn leads them simply to regurgitate the arguments of others without stopping to consider whether those arguments are reasonable; in some cases, even logical. This trap should be able to be avoided by scientist authors who, owing to their intimate familiarity with the subject, should be able to bring greater insight to their work. Deviations from this principle are made typically on the grounds that the author is simply 'reporting' what others have said. This rationalization coming from a scientist author strikes me as either an abdication of responsibility or an admission of plagiarism; probably both. The third principle is consistency. It bothers me when I come across statements in one part of a book that contradict statements in another part. I suspect failure in this area is as much the editor's fault as that of the author. Regardless, readers have a justified expectation that the narrative will remain as consistent between chapters as it should between sentences and paragraphs.

With these expectations and principles in mind, let us now take a look at *When Life Nearly Died*. The title refers to Dave Raup's (1979) rarefaction study of the size of the Permo-Triassic bottleneck, which yielded a maximum estimated 96 per cent species extinction. Of course, since Raup's study only applied to marine invertebrate taxa with a body-fossil record, the claim that this figure applies to 'all life' is grossly exaggerated. [Note: most living biomass and diversity in marine and terrestrial settings is concentrated in the microbiota and meiobiota, both of which are notoriously under-represented in palaeontological datasets.] Nevertheless, if the purpose of a title is to grab the attention of prospective book-buyers, this one succeeds.

The book is divided conceptually into four sections. The first of these (chapters 1 and 2) represents an eclectic collection of short essays on a variety of topics, including: Sir Richard Owen's recognition of new amphibian and reptile species in Murchison's collections of fossils from Russia, Benton's involvement with the somewhat oddly titled television documentary *When Pigs Ruled the Earth*, what lystrosaurs looked like and did with their time, the nature of fossils, Cuvier's arguments about the reality of extinction, and the discovery of dinosaurs (Chapter 1), followed by an extended recounting of the early history of Russian geology with emphasis on Murchison's two expeditions there and the vertebrate fossils he collected (Chapter 2). The purpose of this material appears to be one of establishing the reality of extinction and relating this – at least in some sense – to Murchison's discovery of Permian vertebrate faunas. It's all a rather low-key beginning, almost as though Benton is testing the audience's staying power. 'Get through this and you'll find the rest easy!'. All the topics mentioned above (except the bit about the TV documentary and Murchison's personal experiences during the Russian expeditions) have been better covered in other books and Benton's discussion adds nothing really new so far as I can tell.

The one thing I did find intriguing in this material was Benton's short piece on how John Phillips' 1860 diagram of the Phanerozoic fossil record bears just a superficial resemblance to Sepkoski's diversity charts (Fig. 1). Benton argues that the point of Phillips' diagram was only to show that Palaeozoic, Mesozoic, and Cenozoic biotas were all different from one another. Having now read Phillips' description myself, this is true. Nevertheless, it strikes me as a highly unusual diagram to use in making this point. The suggestion of diversity differences between these eras is not needed to demonstrate the uniqueness of their constituent biotas, especially in the wake of Darwin's species book. In addition, the diagram seems suggestively close to our modern picture of Phanerozoic biodiversity; perhaps too close to be mere coincidence. We are, I trust, all familiar with the practice of using diagrams constructed for one purpose to serve another. It will be for others to determine whether this might be the case for the Phillips diagram. Still, I can't help but suspect there's more to this diagram's story than has been told to date.

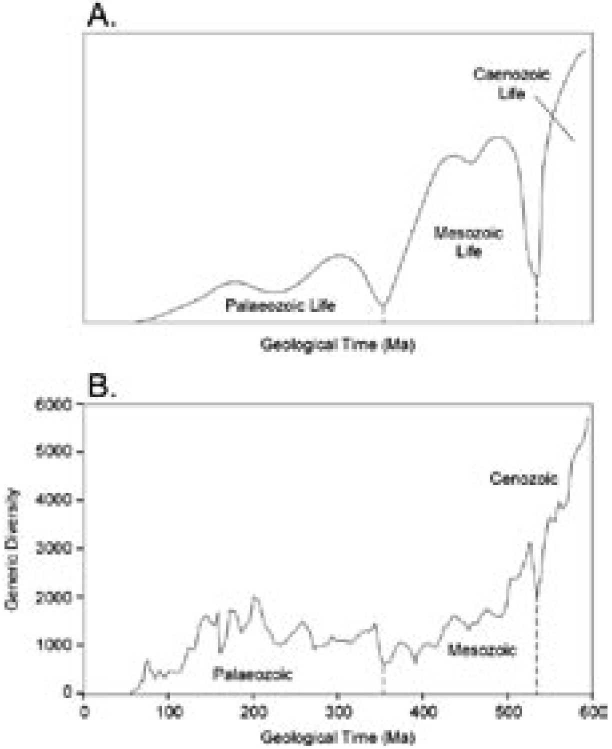


Figure 1.
Comparison between John Phillips' (1860) estimate of Phanerozoic marine biodiversity patterns (A) and those of Sepkoski (2002) (B). Note lack of a vertical axis label on the Phillips diagram. This seems meant to convey information about diversity, not – as Benton implies – only the unique nature of the Palaeozoic, Mesozoic, and Cenozoic biotas. See text for discussion. A. Redrafted and rescaled.

The second section (chapters 3 to 6) gets down to real extinction business with a 100 page extended discussion of … another eclectic group of topics. This group seems loosely based around the general issue of 'neocatastrophism'. What is neocatastrophism? Like the term post-modernism, neocatastrophism refers to a concept that is well established on historical grounds and then implies some sort of updating or transcendence. In Chapter 4 Benton laments the fact that catastrophism is dead and blames Lyell for its murder. This is presented as a bad thing because, in Benton's words '… the catastrophists were right about [mass] extinctions.' (p. 57). Benton does not attempt a definition of catastrophism, but characterizes it as a doctrine that explains geological history in terms of 'explosions, meteorite impacts, sudden extinctions, and miraculous events' (p. 58). Uniformitarianism, on the other hand, is characterized as 'an attempt to explain the former changes of the Earth's surface, by reference to causes now in operation' (ibid, this appears to be a direct, but unreferenced, quote from Lyell 1830–33). Note the difference in tone and specificity between these two definitions. Benton then goes on to associate catastrophism with Cuvier's 'revolutionary' interpretation of the alternating marine and terrestrial deposits in the Cenozoic strata of the Paris Basin, and uniformitarianism with Lyell who thought Cuvier's 'revolutions, evolutions, and catastrophes' (p. 61) were 'dangerous' (p. 62). While no one seriously disputes that Lyell's books had an enormous influence on geologists, I think Benton, along with many others, goes too far when he suggests (1) that post-Lyellian geological theory was strictly uniformitarian (in the Huttonian or Lyellian senses) and (2) that the current crop of impact-related hypotheses seeking to account for a wide variety of geological, and some evolutionary, phenomena represent any credible challenge to what has passed for a 'uniformitarian' approach to geological theorizing since the late 1800s.

Before we can judge the correctness of either Benton's or my claims, it's worthwhile reminding ourselves what terms like catastrophism and uniformitarianism meant in the early and middle 1800s. As we all know, uniformitarianism was developed by James Hutton – a name missing from Benton's book – and first presented at a meeting of the Royal Society of Scotland in 1785. Such diverse authorities as Adams (1938), Rudwick (1972) and Gould (1987) have shown that Hutton's theory of the Earth focuses not so much on mechanisms as on the cyclic nature of geological processes. To Hutton, uniformitarianism meant that the land was elevated (and deformed by that elevation), eroded, buried beneath sediments, heated by compaction from overlying sediments, and elevated again in an unceasing or uniform cycle, with 'no vestige of a beginning, no prospect of an end'. Hutton thought of the Earth as a machine that, by cycling endlessly through uplift, erosional, and depositional phases, *had no objectively verifiable history*. This was the point of Hutton's interpretations of angular unconformities such as the ones exposed at Jedburgh and Siccar Point in Scotland.

Hutton argued forcefully that this cycling implied the existence of what we now call 'deep-time' though Rudwick (1972, p. 130) mischievously noted that Hutton only mentions the doctrine of gradual causation in reference to the erosional part of this cycle. Cuvier, along with his contemporaries (*e.g.*, Buffon, Brongniart, Elie de Beaumont, d'Orbigny, Agassiz), argued contrawise (1) that the marine-terrestrial couplets seen in the Paris basin were produced by the sudden elevation of the land – an idea compatible with Huttonian uniformitarianism on technical grounds, and (2) that the quasi-cyclic nature of the resulting rock record is only apparent due to short-term pseudo-elevations (with structural complications) created by the unidirectional contraction of the Earth as it cooled from its initially molten, nebular state (Gould 1987). The important points (for me) of the new scholarship that has emerged concerning this debate are that uniformitarians and catastrophists agreed on far more than has usually been acknowledged, that both groups were committed to using field observations as tests of theoretical propositions, and that – contrary to Benton's allusions – scientific catastrophism had no truck with the theological rationalizations for 'shallow time' that were being circulated during this period in the forums of popular opinion. Enter Lyell.

Charles Lyell initially accepted the cyclical or uniformitarian idea as the fundamental component of uniformitarian theory; so much so he believed that in both previous and subsequent cycles, exactly the same organisms would be created. As a consequence, Lyell held the extreme (even in the early 1800s) opinion that extinctions – not just mass extinctions – were an epiphenomenon. Hence, Henry De La Beche's caricature of Lyell as 'Professor Ichthyosaurus' lecturing on the lower orders of ancient mammals as evidenced by a fossilized human skull. Benton recounts the De La Beche story accurately (pp. 66–68), but misrepresents the strict Huttonian-Lyellian line on extinction.

Lyell's preference for Hutton's theory seems somewhat odd given the former's reputation for field work and the clear message on extinction coming from field observations made by UK and continental geologists, but appears to relate to Newton's success in identifying the mechanism that causes heavenly bodies to move in cycles. Both Rudwick (1972) and Gould (1987) have deconstructed Lyell's several mechanistic uniformitarianisms and Benton draws heavily on those studies. These include the uniformities of law, process, rate, and state. As Benton correctly notes, the first two of these are subsumed under the rubric of actualism and were agreed by uniformitarians and catastrophists alike. On the uniformity of state the two groups were divided. To Lyell, this meant the state of nonprogression and, to the catastrophists, this meant that the Earth had a history and that this history was deducible from geological observations. With respect to the uniformity of rate though, I think any reasonable reading of the historical record argues, once again, for much overlap between the groups. We know, for instance, that the catastrophists explicitly accepted that geological changes could be wrought by processes operating at modern rates. We also know that at this time there were several dramatic demonstrations of catastrophic processes that changed the face of the Earth over reasonably short time scales, both modern (*e.g.*, the eruption of Krakatoa in 1883) and geological (*e.g.*, Agassiz's discovery of Pleistocene continental glaciations in 1840).

Given these facts, the questions we must ask ourselves to judge whether we can accept Benton's thesis include 'After 1833 did geologists live in a world philosophically dominated by a strictly cyclic, ahistorical, Huttonian-Lyellian uniformitarianism against which no one dared speak? Did geologists believe that studying historical geology was a futile activity? Was Phillips committing an outrage by suggesting that differences between Palaeozoic, Mesozoic, and Cenozoic biotas were real? Did geologists betray uniformitarianism when they accepted Agassiz's catastrophist hypothesis of continental glaciation? Were the best geological minds of the late 1800s to the middle 1900s so blinkered by Lyell that they could not imagine the idea of larger volcanoes, bigger floods, stronger earthquakes, and even the occasional meteorite falling from the sky?' Of course the answer to these questions is 'No'. We know this because such mechanisms have been proposed repeatedly by trained geologists, many in the technical, peer-reviewed geological literature. Benton's is a nice story, that as a science we've been held back by an inappropriate allegiance to a Lyellian uniformitarian ideal that's now past its sell-by date. But it's a straw-man argument. Important aspects of the strict Huttonian-Lyellian line on uniformitarianism were past their sell-by date – and known to be so – by the 1850s. This is not to say that neither Hutton's nor Lyell's ideas were influential at the time. Of course, they were. But the ideas that drew the most allegiance to their 'uniformitarian' cause were also being espoused by the scientific catastrophists in addition to the latter's consistent and successful support of such non-uniformitarian ideas as the realities of both earth history and extinction.

That modern 'uniformitarianism' (neouniformitarianism?) owes as much to the position of Cuvier and the catastrophists as it does to Hutton and Lyell seems now beyond question historically. Specifically, modern 'uniformitarianism' combines the actualistic aspects of natural history inference that were accepted by both groups, with the progressionist stance and commitment to field geology of the scientific catastrophists (an anti-Lyellian component in terms of his uniformity of state). Modern uniformitarianism also retains sufficient flexibility to accommodate an expanding range of processes and rates, many of which cannot be observed directly by modern humans, but can be assessed through careful study and logical inference. Indeed, it is this dual commitment to evaluative rigour and mechanistic flexibility that has allowed uniformitarian theory to progress successfully and adapt to new insights, ideas, data, and technologies over the past 100 years. The initial rejection of Wegener's continental drift on mechanistic grounds, and its eventual acceptance once a reasonably detailed mechanism had been discovered, is perhaps the classic example of the modern theory's rigorous-yet-flexible aspect. This adaptability, in turn, leaves us with an interesting and important question: 'At what point do phenomena once rejected by uniformitarian theory become subsumed into its structure?'. Put another way one might ask 'how long does it take before a process that cannot be observed, but is known to have existed in the past (*e.g.*, continental drift, large igneous province eruptions, major sea-level regressions, large bolide impacts), is admitted into the corpus of uniformitarian theory? To claim that a natural process is 'nonuniformitarian' after it has been accepted as plausible and consistent with available geological evidence is to confuse historical precedent with operational reality.

Benton is correct that extinction studies have emerged as an intellectually respectable research programme only in the last 20 years. I think he is wrong though, to excuse this based on a historically (mis)informed allegiance to strict Huttonian-Lyellian uniformitarianism. Extinction studies have, until recently, failed to evoke much confidence among geologists because, frankly, most of the hypotheses advanced were so patently untestable as to have left the realm of science altogether (see Benton 1990 for many excellent examples). The 1980 Alvarez *et al.* model for an impact at the Cretaceous-Tertiary boundary – like Vine and Mathews' seminal plate tectonics paper on magnetic striping of the ocean crust – fell strictly within this modern uniformitarian mode because (1) it was based on empirical geological observations, (2) it predicted a pattern of other geological observations that could be used to verify its claims, and (3) the process of crater-forming bolide impacts having occurred during Phanerozoic time had been demonstrated in the 1950s and 60s through the pioneering work of Eugene Shoemaker and others. In other words, it was good science. True, the idea that a Phanerozoic bolide causing widespread extinctions had certain historical resonances that can be traced back to Lyell's (1830) dismissal of William Whiston's scenario involving cometary influences over physical earth processes. Nevertheless, it is a mistake to read more into this resonance than is there. Whiston's model has more in common with the discredited ideas of Velikovsky (1956), than with the Alvarez *et al.* end-Cretaceous impact hypothesis.

In Chapter Four we move on to the subject of extinctions proper. Here the water gets even muddier as Benton confuses uniformitarian theory (involving the cyclic reprocessing of Earth materials that denies the possibility of a recognizable Earth history) with the mechanistic uniformitarianisms of state and rate. Thus, Darwin's preference for a uniform and gradual rate of evolutionary change, which Julian Huxley later pointed out was a logical corollary of natural extinction, is seen as evidence for the malign hand of Lyellian uniformitarianism. In point of fact, Darwin's theory of evolution provided such strong evidence against Lyell's uniformitarian theory that it forced him eventually to abandon this central tenet of Hutton's theory. Lyell himself could not get his uniformity of rate hypothesis to work correctly for the quantitative zonation of Secondary strata as he (thought he) had for the Tertiary. Similarly, Pleistocene glaciation is discussed in terms that would lead one to think that uniformitarianism was a theory of tempos rather than modes. Benton's claim that Boucher de Perthes derived his deluge-centred theory of Pleistocene extinctions from Cuvier tries to forge a link between scientific catastrophism and theology. In the mind of de Perthes and his followers this was indeed the case. But Cuvier and the scientific catastrophists entertained no such theological aspirations (see Rudwick 1972; Gould 1977, 1987). Benton ends this review of extinction history by reiterating that the catastrophists have won the debate because 'The Earth was hit by a giant asteroid 65 million years ago, and that impact did kill off the dinosaurs' (p. 95).

Chapter Five is about the K-T boundary extinctions. [Note: we are now a third of the way into a book ostensibly about the Permo-Triassic extinction.] This is a standard retelling of the Alvarez *et al.* (1980) Ir anomaly, the postulation of the extinction mechanism as a dust cloud that 'blacked out the sun for a year or more, thus preventing normal photosynthesis in plants and hence cutting off the base of food chains on sea and land.' (p. 100, recently challenged by Kevin Pope 2002 based on the size distribution of K-T dust deposits) and the discovery of the Chixculub crater which, for most, settled the question of whether an impact occurred, with brief excursions into crater hunting, the physical signatures of impact structures, and into the politics and public relations of this most public of scientific controversies. All good stuff, well told. At the end of this chapter though there is a very curious statement in the summing up section entitled *Where are we today?* In seeming defiance of his earlier statements on the primacy of catastrophism in modern extinction studies (p. 57) and the causal role asteroid impact played in the demise of the dinosaurs (p. 95, both cited above), Benton writes the following.

> 'The K-T event is not completely resolved. … some criticisms offered by palaeontologists in 1980 are still valid today. Many groups of organisms [presumably including dinosaurs (see Archibald 1996)] were indeed in decline before the impact and these declines may relate to deteriorations in climate or changes in sea level. It is important also to recall that many plants and animals were seemingly unaffected by the impact, so the killing model has to take account of that. Ever more detailed studies of fossil occurrences up to the K-T boundary may shed further light on what was going on.' (p. 121).

The sentiment in this chapter – the only one that discusses the evidence for a mass extinction at the K-T boundary – is clearly that things are not so certain after all and much more research is needed.

Chapter Six continues the extinction theme in a discussion of the mass extinction phenomenon. [Note: at the end of this chapter we will be half way through a book apparently about the Permo-Triassic extinction.] Mass extinctions are definitionally a bit like the US Supreme Court's idea of obscenity, the first test of which involves determination of whether the average person, applying contemporary community standards, would find that a work, taken as a whole, appeals to prurient interest. In other words there really is no definition of obscenity other than what most people would understand to be dirty pictures, words, or thoughts. Similarly, there is no operational definition of a mass extinction other than what most qualified palaeontologists would understand to be a big extinction (see Ward 1995 for an alternative court-based metaphor and MacLeod 1996 for a rebuttal). Benton struggles manfully to make more out of this anti-climatic definition by appealing to such exotica as statistics and biogeography, but in the end it's no good. A mass extinction is just a big extinction. Benton plumps for five big extinctions (Late Ordovician, Late Devonian, end-Permian, end-Triassic, K-T), but admits this choice is arbitrary. What he doesn't mention is that membership and relative order in this 'big five' changes depending on which extinction metric is employed. [Note: using the generic dataset of Sepkoski 1998 the rank order of the K-T extinction varies between 1 and 13 (between 1 and 23 if the high-extinction Cambrian stages are included) depending on the metric employed.] Come to think of it, Benton even neglects to mention that there are different extinction metrics, though his diagrams jump between these metrics without calling readers' attention to these changes. Caveat emptor.

After a quick tour through the designated five Benton next considers the case for extinction periodicity (unproven), estimation of species-level extinction rates (subject to certain statistical estimation constraints, modest levels of extinction among higher taxa probably indicate very large numbers of species-level extinctions), sampling issues, the quality of the fossil record, and extinction selectivity. While one can quibble with Benton's presentation of all these areas[1], it is nice to see them discussed. Benton is also to be commended for including a section on phylogenetic strategies for assessing the quality of the fossil record, as this is often overlooked in extinction books. There is one embarrassing mistake in this material, though. In the section entitled 'Seeing what you want to see' the figure of the K-T transition at El Kef, Tunisia is included with a caption containing the following passage, '…sediments show a species loss of 65% at the K-T boundary.' (p. 142, reproduced here as Fig. 2). By my count a total of 32 species encounter or cross the K-T boundary in this diagram, but only 11 (34%) terminate at the boundary itself. A further 13 disappear from the record below the boundary. If, due to sampling problems discussed by Benton, these 13 taxa are regarded as having reached the boundary (but not a mm higher), the extinction rate could conceivably be extended to 53 per cent. This, however, would beg the question of why these 13 taxa should be allowed to rise to the boundary while the 11 taxa going 'extinct' at the boundary might be required to hold their positions in order to achieve the higher figure? [Note: Benton uses a similar scenario to try to collapse the extended P-Tr faunal turnover to a single horizon later in the book.] The point is, I have no idea where the 65 per cent figure comes from and neither the figure caption (which doesn't even cite where these data came from) or the text passages are enlightening. One does indeed see what one wants to see when dealing with a 'catastrophic' extinction.

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[1] For example, Benton cites the Jablonski and Raup (1995) study of K-T extinction selectivity in bivalves and correctly reports their results. He fails to mention, however, that this study specifically excluded rudistid bivalves from consideration. As noted by the authors themselves, had the rudistid data been included, the results would show strong latitudinal selectivity. Jablonski and Raup's reasons for excluding the rudistid data could have been discussed and evaluated. Regardless, Benton's statement that K-T bivalves show no latitudinal differences in extinction intensities (p. 153) is incorrect, as Jablonski and Raup (1993) acknowledge (see also Morris in MacLeod *et al.* 1997).

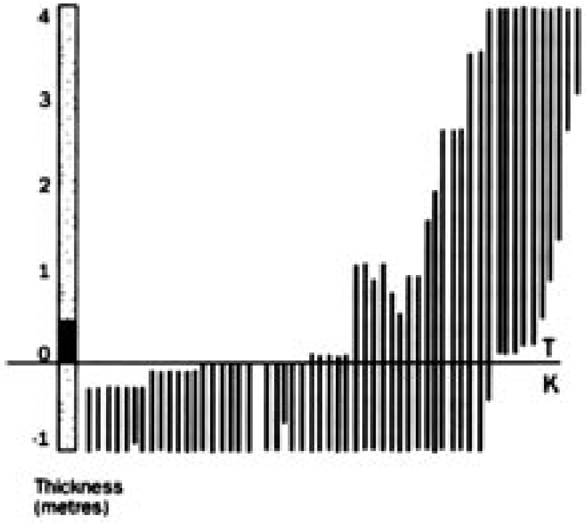

Figure 2.
Benton's Figure 20 illustrating a catastrophic extinction of planktonic foraminifera at the K-T boundary in the El Kef section, Tunisia. Data from the figure are not credited. Benton's caption suggest these data record a 65% species extinction at the boundary, but as can be plainly seen only 11 of the 32 species encountering the boundary record their last appearances at that horizon. See text for additional discussion.

The penultimate book section (chapters 7 to 11) finally arrives at the Permo-Triassic. The question under consideration is 'was the mass extinction at the end of the Permian so different from the *geologically instantaneous* KT event?' (p. 156, emphasis mine). Chapter 7 sets the stratigraphic and geographic scene, discussing events leading to establishment of the Lower Triassic GSSP in the Southern Chinese Meishan Section at the *Hindeodus parvus* first appearance datum. Although Benton's Figure 27 (reproduced as Fig. 3, overleaf) suggests turnover to be a complex of extinction events spanning over one million years, Benton's text qualitatively summarizes an article by Jin *et al.* (2000) that proposed the three separate horizons were sampling artefacts *à la* the Signor-Lipps effect. There have, however, been several challenges (not mentioned by Benton) to the use of this sort of argument to construct extinction patterns (*e.g.*, MacLeod 1996; MacLeod *et al.* 1997), including explicit warnings against this usage in the nominal article (Signor and Lipps 1982). More recent modelling work (*e.g.*, Solow and Smith 2000; Payne 2003) has confirmed that, 'There will always be a range of gradual extinction scenarios [that are] statistically indistinguishable from simultaneous extinction.'. (Payne 2003, p. 50). Benton also draws attention to the d^{13}C shift that coincides with the largest extinction pulse (see Fig. 3). It is interesting to note that aspects of the form of this isotopic shift are similar to that found in K-T boundary sections (*e.g.*, Abramovich *et al.* 1998).

Chapters 8 and 9 provide group-by-group overviews of the extinction event for marine and terrestrial taxa respectively. The section on the marine extinction seems rather thin (only 17

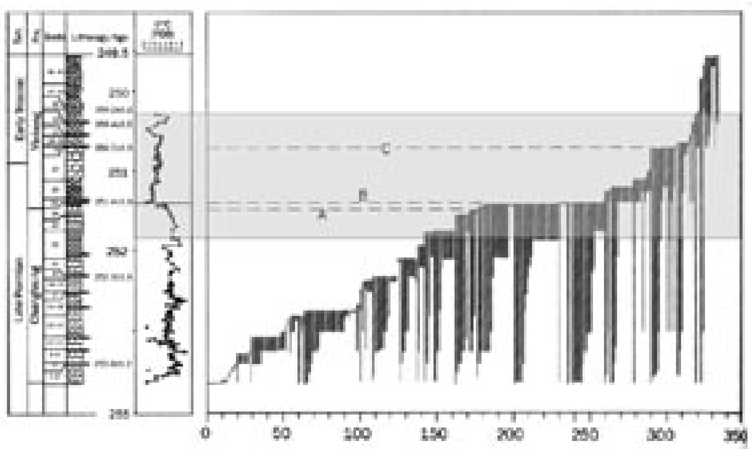

Figure 3.
Benton's Figure 27 illustrating the extent and timing of species extinctions in the end-Permian Meishan section in South China. One of the problems with studying mass extinction events lies in defining their boundaries. Benton's text describes the end-Permian event variously as taking place instantaneously at extinction horizon B (p. 173) and as having a duration of 800,000 years. Based on the importance he accords to the d^{13}C record, the event might also be regarded as having a duration similar to that shown by the shaded region. Note also the fact that the d^{13}C curve maintains a much lower average value for a considerable time after the most prominent extinction pulse. The duration of this low phase is similar to the d^{13}C record across the K-T boundary and suggests – as does Benton's description – that a collapse in marine primary productivity was not the sole case of this isotopic change (see Abramovich *et al.* 1998).

pages or so) and, on the whole, is less detailed that the comparable sections in Erwin (1993) and Hallam and Wignall (1997). I was particularly struck, though, by the lack of any information whatsoever on phytoplankton. This has been a particular bugbear of mine for some time now. What groups composed the late Permian phytoplankton flora? No one seems to know (for a tangential review see Rigby and Milsom 2000). The diversity of filter feeding organisms implies that a diverse phytoplankton flora of some sort must have existed. This flora is often discussed in absentia since a productivity crash is assumed to have caused the extinction of these filter feeders. But who were they? This question is important because it has been suggested that the Mesozoic-Cenozoic rise of the modern phytoplankton flora has been an important factor in damping marine extinction intensities (see Wignall 2001; MacLeod 2003, in press).

Chapter 9 extends this theme to dry land where we meet a rather limited group of players, including *Lystrosaurs*, *Thrinaxodon*, *Pareiasaurus*, *Dicynodon*, *Procynosuchus*, and the gorgonopsians. Benton also returns here to the heavily historical narrative style of the book's first section in the form of an interweaving of information on the discoverers of these beasts. I view the addition of these human-interest stories as an essential component of any popular science writing and one that is too often ignored. Science is hard work often done by people whose dedication often seems eccentric, sometimes stepping over into the psychotic. We tell stories about colleagues' trials and tribulations to one another routinely. They serve as a 'tribal lore' and are used to attract and acculturate newcomers in all scientific disciplines. Telling stories of science without telling the stories of scientists is to present only half the tale, and often the more uninteresting half at that. Benton has made the right choice in this area and his historical passages are among the most compelling parts of his book. He commits a minor error, though, in this section in his curious mixing of lithostratigraphic and biostratigraphic units (*e.g.*, his reference to the '*Dicynodon* Zone' of the Beaufort Group on p. 216) and treating both as units of chronostratigraphy. This oversight only confuses people and serves as a poor example for students. More serious still – though not technically an error – is Benton's astonishing claim that the end-Permian extinctions affected terrestrial faunas more than marine. This turns out to be a 'fun with numbers' argument arrived at using data forced to a constant sum (percentages). Thus, the extinction of 38 amphibian and reptile families in the last five million years of the Permian translates into a 75 per cent loss, whereas the loss of 141 marine families over the same interval translates into a seemingly much less impressive 45 per cent loss. Of course, the fact that almost four marine families were lost for every extinct terrestrial family is obscured if one only reports the percentage values.

The purpose of Chapter 10 is to establish the global nature of the end-Permian extinction by showing that the same sedimentological and faunal turnover patterns that characterize the Karoo Basin in South Africa also characterize the Russian Tikhvinsk sections. This story is told in the form of an anecdote-laden recounting of Benton and Glenn Storrs' two Tikhvinsk expeditions (1993 and 1995). The point is made and the anecdotes told, but I found this section to be too much of a break from the main narrative for my taste.

The final chapter of this section (Chapter 11) considers evidence for the cause of the end-Permian event. This is by far the best chapter in the book and comes to a perfectly reasonable conclusion. I won't steal Benton's thunder by giving the proposed cause away. I will say, however, that, after reading this chapter, I had to go back and re-read some of the previous statements in the book and, after doing so, was left wondering why those previous statements were made and why such a balanced approach never seems to be applied to interpretation of the K-T event, even by Benton himself. If you don't buy the book, get a hold of a copy and read Chapter 11.

The book's final chapter is really a post-script on modern extinctions, whether they constitute a mass extinction of geological proportions, and whether the end-Permian extinction scenario developed in Chapter 11 contains any lessons that might be applied usefully to conservation biology. Much is made of the fact that we don't know how many species exist today and so cannot calculate extinction rates accurately. In this sense, geological extinction events are known in much more detail than the modern extinction event. For me, this was the worst chapter simply because it falls back on tired platitudes and fails to engage with any of the contemporary arguments over the issue (*e.g.*, the role of development and technology, the idea that conservation is a rich society's concern, the pressures of human population expansion, the politics of limits). To be fair, these issues deserve – and have received preliminary – book-length treatments of their own and are well outside most palaeontologists' areas of expertise. Nevertheless, this book would have been better without its last 'social relevance' chapter, though could also have been improved greatly by including one that adopted as hard-hitting an approach to this topic as it has to some of the more scientific material.

The only major question left unanswered after reading *When Life Nearly Died* for me was why, after all this time, do extinction events from the past still obsess us so? We must acknowledge their attraction to scientists. Understanding the process of extinction is crucial to understanding evolution and reconstructing the history of life correctly. But these are esoteric topics not well understood by the general public. What is it about extinctions that cuts across educational, occupational, geographic, cultural, employment, and seemingly all other societal subdivisions and rivets the attention of public audiences?

For the answer to this question – which is not raised in Benton's book – I believe we must return to the time just before Benton's book starts in Chapter 1, to the scientific enlightenment of the middle and late 1700s. One of the principal intellectual touchstones of that era, Edmund Burke's 1757 treatise *A Philosophical Enquiry into the Origin of Our Ideas About the Sublime and Beautiful,* has been long neglected by students and historians of natural history. In it, the horrific but, at the same time, pleasing emotional response experienced by those who encounter uncontrollable 'terrible objects' (*e.g.*, rushing cataracts, violent storms, cliff edges, waterfalls) was first analyzed for the nascent modern audience. This 'sublime' response, as Burke called it, was regarded as the 'strongest emotion which the mind is capable of feeling.' (p. 36). The sublime can be seen as the necessary antithesis to the emotional responses evoked by being in the presence of safe, small, delicate, lightly coloured, smooth objects that are 'beautiful' (*e.g.*, man-made objects), but do not possess the frisson that comes from an awareness of almost infinite size, power, scope, or age. In a sense, Burke recognized, as had classical scholars before him, that there was something about our common humanity that makes us like being scared, so long as the danger does not press too close. To put it another way, 'If there is a precipice, a cataract, a mountain of snow, *etc.* in one part of the scene, the nascent ideas of fear and horror magnify and enliven all the other ideas, and by degrees pass into pleasures, by suggesting the security from pain' (Hartley 1749).

The sublime response has long been a favoured aesthetic subject inspiring its own literature and many schools of visual art. For example, the ever-popular British painter William Turner was strongly influenced by the early 19th Century sublime movement that was prefigured by parts of the romantic school (*e.g.*, Caspar David Friedrich) and included Phillipe Jacques de Loutherbourg, Thomas Cole, Frederic Edwin Church (Fig. 4), and Albert Bierstadt, among many others. What has not been given due attention, however, is the role an appreciation of this sublime/beautiful duality – so well captured by the institutional dualities of natural history museums and museums of art – has played in the development of modernity in general (see Johnson 1991 for many examples) and of modern science in particular. The long-standing popular obsession with dinosaurs dates from the same early modern time in cultural history in which sublime art flourished, and linkages between these cultural phenomena are just beginning to be explored (*e.g.*, Mitchell 1998).

In a similar vein, I believe the unexpected, and unexpectedly long-lasting, popular obsession with major extinction events of the past stems from this same source. Consideration of the sublime aesthetic's role within the natural sciences might also help explain why it took such a long time for the scientific study of extinction to be taken seriously. On seeing the imprecise, almost artistic manifestos offered as 'explanations' of 'mass extinction' events, hard-nosed scientists – most of whom deny any knowledge of, or interest in, aesthetics – didn't know how to react, other than to shun the entire business. As with dinosaur studies, the link between so-called catastrophist extinction scenarios (as well as natural history itself) and the sublime aesthetic movement of the 1800s has become lost as other artistic/intellectual movements have replaced a concern with the sublime and as uniformitarianism broadened to encompass both cyclical and directional views of Earth history. The Alvarez *et al.* (1980) paper proved to be a watershed not only because it offered a different type of extinction theory – one that was rigorously scientific – but because it also provided release from the pent up frustrations among scientists at living alongside this attractive aesthetic construct, but not being able to address it in ways deemed respectable by their peers. Benton's passage on the penultimate page of his book, that he now feels free to 'preach asteroids and mass extinctions to [his] students' is much more understandable when seen as a homily to the attractions of the sublime, as are his lyrical descriptions of post-apocalyptic Triassic world, his clear preference for scenarios that emphasize sublime implications of extinction studies (often in the face of much hard scientific and logical evidence to the contrary). This latter conflict in Benton's text is most obviously symbolized by the inconsistency of his statements regarding the nature of the mass extinction events. As Burke noted two and half centuries before, the attractions of the sublime are indeed powerful.

Figure 4.
Painting of the eruption of Cotopaxi in Mexico (1862) by F.E. Chruch. Church was part of the Hudson River School of American landscape painters who specialized in sublime topics and did much to popularize the terrible majesty of natural processes in the middle and late 1800s. The discovery of dinosaurs, uniformitarian/catastrophist debates, and the initial work on geological extinctions occurred coincident with the sublime cultural movement in western European societies. This type of artistic style is also followed by many modern illustrators of extinction-related topics, though not with such originality and skill.

What we have here, then, is an uneven treatise on geology and extinctions. Benton's first message, that the catastrophists were right all along, is based on an oversimplification of scientific uniformitarianist and catastrophist theory. Asteroids from space do not require a new, neocatastrophist approach to the study of geology simply because all the important tenets of scientific catastrophism – especially the fact of extinction and the directional nature of time's arrow – have been part of the modern or neouniformitarian approach to geological theory for over a century (though admittedly, the true nature of Huttonian-Lyellian uniformitarianism has been clarified only recently). Modern uniformitarianism can absorb the very slight changes in emphasis required by a heightened appreciation for the frequency of bolide impacts in the same way modern evolutionary theory absorbed a heightened appreciation for the frequency of morphological stasis that resulted from the punctuated equilibrium debates. Benton's review of mass extinction studies is competent, but marred by many errors of commission and omission. His discussion of the end-Permian extinction – which occupies less than half the book – is good, especially his emphasis on the terrestrial components of that record and his discussion of causation. Finally, his post-script on the modern extinction event provides an adequate summary of the problems associated with the study of these data, but neglects to come to terms with the real issues raised by coexistence between large, economically developed human societies and natural populations.

I regard *When Life Nearly Died* as a timely successor to Doug Erwin's *The Great Paleozoic Crisis*. Much has been learned about the end-Permian event in the last ten years and it's nice to see so much of this material summarized in a readily accessible form. Benton's character sketches of the people who have contributed to this topic through the last 150 years are also both charming and informative. The book is well produced by Thames and Hudson and remarkably free of printing, editing, and graphic errors. The book's failures will, no doubt, go largely unnoticed by the majority of its non-specialist readership. For the more knowledgeable audience of the Palaeontological Association I can recommend the book's purchase to anyone needing a quick and convenient summary of the topics included, but must extend a caution about taking much on the material presented in sections 1, 2, and 4 at face value. The book that will define both the scientific importance and aesthetic allure of extinction studies, both past and present, for the contemporary popular audience remains to be written.

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Acknowledgments

Somewhat unusually an initial version of this review was shown to Mike Benton who forwarded a series of comments on its content to me. I have used those comments in preparing this version of the review and would like to acknowledge his contribution. Of course, Mike will not agree with everything I have said and I accept full responsibility for any errors of fact or interpretation within.

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Darwin's Cathedral: Evolution, Religion, and the Nature of Society

David Sloan Wilson, 2002. University of Chicago Press, Chicago and London.
vii + 268 pp; ISBN 0 226 90134 3 (hbk). £17.50.

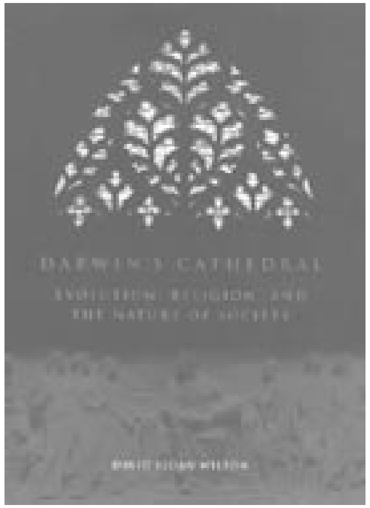
When you see a colleague carefully counting the number of ribs on a brachiopod or setting out eagerly into the field in search of more "Medals of Creation" (to use Gideon Mantell's evocative phrase) it would defy belief that such harmless enterprises were, at least according to some, the exact reverse. Yet the hum-drum of palaeontology is not so far removed from the continuing "evolution wars" where the cardinals of science (Dawkins, Dennett, Ridley, *etc.*) are set as shining lights against the howling mob of obscurantists and flat-earthers. So too, the readings of the more lurid biographies of Darwin and Huxley are as often as not accompanied by the authors' intense satisfaction at seeing a religious system crumble into dust, or at least apparently so. How fond, for example, is the writer Adrian Desmond of the word "smash".

Now we are so cocksure that the world is as we wish it to be, that the notion of scientific knowledge actually imperilling our souls seems simply risible. Yet it was Mantell's near contemporary John Ruskin who complained of "the sound of those dreadful hammers", as geologists prised open the once closed book of Earth history, to reveal an abyss of almost infinite time. So too Ruskin's fellow enthusiast for the Lake District, Adam Sedgwick, was implacable in his opposition to the concepts of Darwinian evolution because of what he saw as the clear implications for the place of humans, not least as moral agents. Sedgwick (and in a different way, Ruskin) lost the argument comprehensively, and we have inherited a fractured world marked by the atheistical rantings of Dawkins, the oily evasions of Gould with his fictional magisteria, and the inanities of creation "scientists". One doesn't know whether to laugh or cry: the arguments are so tendentious; it is as if the entire world has been taken over by lawyers.

It is, therefore, with apparent relief that readers of this *Newsletter* may turn to David Sloan Wilson's book on the relation between evolutionary theory and religious beliefs and practices. Here seemingly is a model of clear and dispassionate writing, where lofty sentiments from a leading member of the Academy illuminate the strengths of human tradition and its past mistakes in that yellowish light that streams from pragmatic scientism. Yet the light comes from a strange source, a sun that can be stared at directly, sheds no heat, and equally oddly casts no shadows.

Before beginning to explore this odd one-dimensional world, where everything is sensible, evil a regrettable consequence of failed potty-training, and metaphysics a comfortable delusion of the idle, it is only fair to delimit Wilson's thesis. His arguments centre on three propositions, one of which is entirely uncontroversial, one of which is probably true on occasion (but possibly not otherwise), and one that may be mad. They are in this in order: the reality of evolutionary adaptation, the possibility that selection at the group level can really work, and the claim that human religions (and attached moral systems) are a result of the first two propositions so that any such system confers a survival benefit even if some of the individual members are dysfunctional. This is a bald summary and it is important to point out this thesis is hedged in with a series of major assumptions, including the proposal that emergence of religion qualifies as a "major evolutionary transition" in the sense of John Maynard Smith and Eors Szathmary.

Darwin's Cathedral presents, therefore, an over-arching synthesis that at first sight seems not only compelling, but so reasonable, in fact so nice: just the sort of thing everyday folk could happily adopt. Yet, just as with E.O. Wilson's *Consilience*, even a cursory second inspection reveals a much more ramshackle and debatable series of propositions held together with the fraying string of special pleading, the elastic bands of imprecise definitions and the sellotape of unwarranted assumptions. As with *Consilience* the thesis only holds by repeated dodging and weaving: again and again we are told matters can only be understood on a "case-by-case basis" (p. 17) and in terms of special conditions, both of which are usually only sketched out in the most tentative fashion. With this imprecision you can argue almost anything.



In fact, the overall thesis turns out to be banal, and hinges on both a profound misunderstanding of religion, and a relativism that ultimately leads to a path where you can encounter some very ugly customers. To take the second difficulty first it is simply facile to claim, for example, "rational thought is itself a Darwin machine, rapidly generating and selecting symbolic representations inside the head" (p. 31). If that were true we would never know anything. Wilson, however, subscribes to the fashionable relativism, and to continue the quotation writes "Confront many human groups with the same novel problem and they will come up with different solutions, some much better than others. If the groups are isolated from each other, they may never converge on the best solution; evolution is not such a deterministic process" (p. 31). This is questionable on all counts. Convergence, which I address elsewhere, shows evolution to be far more deterministic than generally realized. More importantly, even in the restricted sense of Wilson there is evidence for convergences in terms of political organization and agriculture, and in the context of this review notably in the parallel and growing sense of monotheism in the centuries spanning the beginning of the Common Era. And what in Wilson's context does the word "better" mean? The reality is that such relativism is both evasive as to its ground-truths (as John Greene has clearly demonstrated it depends on a wholesale and unacknowledged hijacking of Judaeo-Christian precepts), and more importantly it is helpless to prevent the repeated descent to the killing fields. Similarly, it is equally misleading for Wilson to claim that "people in all cultures – even the most 'primitive' – possess the foundation of scientific thought: a sophisticated factual understanding of their world and the ability to reason on the basis of evidence" (p. 41). First, it does not explain why science only arose once, in medieval Christian Europe, a religion against which, as we will see, Wilson has a distinct animus. Second, even if rightly science is a property of all mankind, it also fails to explain why although technologies are easy to transfer (we're all allowed to kill the innocent by atomic bombs, anthrax or sarin, now), in reality the scientific method is quite a rare skill and in some cultures remains strangely stagnant.

Such politically incorrect views are one of the quickest ways of goading the relativist to foaming anger, yet these arguments are important. Despite its gentle rhetoric this book is simply an attempt to wrest power and impose a scientistic programme on societies and their muddled attempts to find a moral system that actually works on at least two cylinders. Thus Wilson writes "I have tried to emphasize both the power of the scientific method and also the many factors that impede it for a subject such as religion. The organismic concept of religious groups can be stated as a hypothesis and tested against alternative hypotheses … religion has been studied for over a century by scholars earnestly trying to employ the scientific method, *without this clarity of outcome*" (p. 132, my emphasis). Behind this statement, and its false modesty, is a thinly veiled social Darwinism that uneasily resurfaces where the adaptive framework leads to such remarks as "There can be little doubt that size itself can be a group-level adaptation. Larger societies tend to replace smaller societies unless their larger size is offset by problems of coordination and internal conflicts of interest" (p. 36). Either way that reads to me like a recipe for totalitarianism.

Well even if I, and Professor Wilson, would be rightly horrified by the suggestion maybe that is the way it is: science often presents us with what are (or more usually what we are told are) unpalatable facts and the sooner we come to terms with them, the better. Such a view, in the context of *Darwin's Cathedral*, presupposes, however, that the concepts of group selection are valid and Wilson's concepts of religion have any practicality. Again, to take the second point first, it is simply the case that his employment of the term religion is so broad-based as to be effectively useless: as adaptive groups with self-imposed moralities set in a social context you can prove almost anything. Thus, Wilson's key example of Calvinism based in Geneva is treated as a distinct religion, and its connections to Christianity are almost incidental. Even so, and as also already noted, it is Christianity that irks Wilson the most: such a tiresome religion! Here

there is a curious echo across two millennia, from the contempt of the Romans Pliny, Suetonius and Tacitus for those "odious atheists", to the continuing exasperation by the proponents of relentless consumerism and media manipulation that for some the world (and its tarnished glory) is not enough. In any event, Wilson's view of this religion's origins and dynamic are woefully simplistic. It is the almost unavoidable curse of specialization that leads intelligent and thoughtful scholars to facile conclusions, which in any other context would fail to satisfy a GCSE examiner. Thus in the case of the astonishing rise of Christianity, and incidentally the more we learn of its history the odder it is, Wilson might have been better advised to spend a bit more time reading works by such writers as Martin Hengel, Raymond Brown and Tom Wright. Or would he, I wonder? After all, the gnostic clap-trap of the second century AD has plenty of echoes in the huggy-fuggy, my soul is a cosmic flower, new-ageism that is the entirely predictable outcome of a rudderless world. Somewhere, and amusingly nobody can find exactly where, G.K. Chesterton reminded us that "When people stop believing in God, they don't believe in nothing, they believe in anything".

As seriously, despite the thesis that religious groups are adaptive units, no explanation is given as to why some succeed, yet others fail, apart from the lame observation that tautologically they are adapted to particular "circumstances" that allow "subversion" to be controlled. That there might be an element of truth in this is not to be doubted, but as an over-arching explanation it falls flat. So too, given humans are intensely curious, active imitators and inveterate travellers it is far from clear why the manifest "advantages" of particular systems do not win supremacy. Here too it is perfectly easy to cobble together *ad hoc* explanations, but the matter is surely far more complex than such scientistic sentiment allows. So in this way the arguments of group selection are at best unconvincing, and as often simply tendentious. Wilson makes great play on the evolution of guppies and social insects, especially bees, as adaptive analogies to religion. The similarities are, of course, worth discussion because as a product of evolution it is more than likely that animal behaviours, and especially their mentalities (even in bees), will be a rich source of insights into the origins of our own complexities. So, incidentally, they might open *our* eyes as to how we choose to treat animals as anything more than utilitarian objects. But to imagine that there is a simple translation from beast to man entirely misses the point. Wilson is far from revolutionary, indeed he is embedded in the *Zeitgeist* of naturalistic naivety that remains perpetually puzzled that there are dimensions to this world that science will never fathom. Somebody (and who could it have been?) reminded us that if we use the tools of science to understand our world all will be well, but if we use them as tools in themselves, then we are on the royal road to destruction. However, for a society that has swallowed without protest the concept of selfish genes, and now opens its arms to a wonderful future of eugenics, *Darwin's Cathedral* will no doubt be a smash hit.

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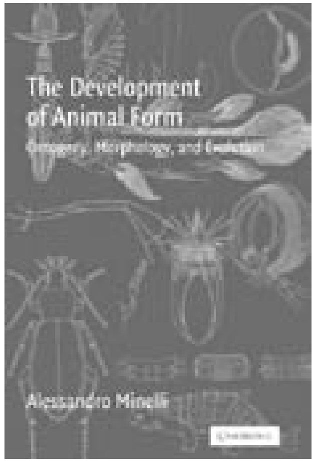
The development of animal form. Ontogeny, morphology, and evolution

Alessandro Minelli. 2003. Cambridge University Press. xviii + 323 pp. Hardcover. ISBN 0 521 80851 0. £55.00.



Do you have to be a Renaissance man or woman if you want to digest fully all that is dished up in Minelli's wonderful *The Development of Animal Form*? Two recent experiences I had might suggest so. One of my colleagues in Cambridge recently finished a review paper on germ cells for *Development*, which is the prime journal of her trade. The referee's comments came back accompanied by a note from the editor that specified the need for a glossary for the paper. Among the terms suggested to be included in the glossary were such arcana as "derived," "phylum," "clade," and "Diptera." Perhaps such terms are indeed necessary for some biologists who skipped a few classes during their undergraduate courses in systematics and evolution, and perhaps it is a bit too demanding to expect a modern developmental biologist to be able to classify *Drosophila* as anything more specific than just an insect. However, I found it amusing that the editor of *Development* apparently found it necessary even to include "gonoduct" as a term in the glossary, as the gonoduct is usually the last part of the parent's internal anatomy that the gametes or embryo will pass before they enter the outside world or the embryologist's object slide. If a glossary can be interpreted as demarcating the essential vocabulary of a specialist in a professional discipline from the seemingly unwieldy terminology necessary for being a Renaissance man or woman, then Minelli's book is not going to be a bedtime read for the general readership of *Development*.

The pages of *The Development of Animal Form* are strewn with crustacean pleons, priapulan caudal appendages, phoronid actinotrochs, arthropod eosegments, and kinorhynch zonites, as well as a plethora of gene names and developmental processes. These topics are integrated into an impressively broad panoramic overview of animal development and evolution. Indeed, one of the overarching goals of Minelli's book is to "inject from these traditional branches of biology [such as comparative morphology and the study of postembryonic development] into the lively arena of evo-devo biology a number of facts, concepts, and problems, which have failed, until now, to find the place they deserve in today's debates and research agenda" (p. xv). Minelli sees developmental genetics as the major impetus for the modern integration of evolutionary and developmental biology. However, this focus on developmental genetics appears to be almost exclusive, creating a conspicuous imbalance between the contributions of developmental and evolutionary biology to the new synthesis of evo-devo. This important point has recently also been emphasized by Love (2003: 315) who writes that "the problem lies in taking the exclusion of embryology [from the Modern Synthesis] and rise of developmental genetics as the *whole* story for understanding the need to rejoin evolution and development" (italics in original). In line with Minelli's book, Love (2003: 332) therefore argues that "more attention needs to be given to disciplines such as morphology and paleontology," not only to forge a modern evo-devo synthesis, but also properly to understand the history of contemporary evo-devo.

However, Minelli's book should not only be seen as a means to remedy the passive deficit of knowledge that almost automatically accretes during professional ultra-specialization. It is certainly useful to learn about kinorhynch zonites, but perhaps a more fundamental hurdle to the full integration of developmental and evolutionary biology may be rooted in details of, and I don't know how else to put this, personal attitudes towards learning. Let me illustrate my concern. When I was working on my PhD research at the University of Amsterdam, I met Prof. Rudolf Nieuwenhuys, an emeritus professor in comparative vertebrate neuroanatomy who was keenly interested in exploring the wonderful details of the development and evolution of the invertebrates. We decided that the appropriate format for indulging our interests would be to get together one afternoon per two weeks to discuss various topics in an informal way. The bonus of our gatherings would be their location: the Artis library of Amsterdam, which houses one of the most important natural history collections in the Netherlands, including a superb Linnaeus collection. To complement our own evolutionary expertise with some developmental perspective, we decided to send a letter to the Hubrecht Laboratory, the Netherlands Institute for Developmental Biology, asking whether any resident developmental biologist would be interested in exploring these issues with us. To our surprise, the response letter claimed that not a single person was interested in doing this.

This experience shows that in this time of extreme professional specialisation we too often become so immersed in the microcosm of our immediate research, that we lose sight of the beauty and importance of a broader outlook. An unfortunate corollary of extreme focus, professional or otherwise, is that what lies beyond the edge of our field of vision becomes blurry or invisible. In the worst case this results in our inability to talk to specialists from a different discipline, as we are unable to mesh together our individual windows into a single panoramic outlook that is essential for a full integration of evolution and development. For me this comprehensive focus on both molecules and morphology is the key to the significance of Minelli's book. It reminds me again why I became so interested in developmental and evolutionary biology in the first place. Therefore we should try hard actively to recapture that sense of fascination that made us students of Nature in the first place, and that made many of us read so widely in many different topics early in our careers, before the strictures of professionalism pulled the blinds on our panoramas to the point where we could only look out of a single window. Of course, constraints of energy and time may be largely responsible for our choices to read a paper on *Drosophila* development, but not one on phoronid embryology, to attend a lecture on arthropod *Hox* genes, but not one on population variation in the number of centipede segments. But we should realize that such myopic perspectives are a major stumbling block to a satisfactory integration of evo-devo, across all that is its subject matter. Minelli's book shows the value of such a broad outlook, and I hope that for those readers for whom the expression patterns of *engrailed* and *Brachyury* in *Drosophila* and the mouse represent the outer reaches of their world-view (alternatively, for non-developmental biologists who don't know what a promoter or a homeobox is) this book will provide the motivation to break free from professional myopia. If *Development* and *Development, Genes and Evolution* comprise the core of your literary diet, than please also look at the table of contents of *Palaeontology* and *Zoological Journal of the Linnean Society* once in a while, or vice versa.

So what then is Minelli's book about? In Minelli's own words (p. xvi) "to redress the balance between the metaphysics of evolutionary biology and the metaphysics of developmental biology. The latter, in my view, is still heavily biased by a finalism whose equivalent in evolutionary biology has been long since removed by Darwinian revolution." Minelli (p. xvi) tries to adopt a "more sober approach to evo-devo biology," "in which there is little space for many old questions which are, in my view, a simple byproduct of an unnecessarily complex holistic view of the organism and its development" (p. 252). Key to understanding Minelli's perspective is that he is uncomfortable with a finalistic, adultocentric, goal-directed view of development, in which the embryo is just a means to generate a new adult through steps dictated by a genetic program hardwired in the DNA.

The philosopher Daniel Dennett (1995: 114) offered an interesting metaphor for development: "Compare genomes to musical scores. Does a written score of Beethoven's Fifth Symphony *specify* that piece of music? Not to Martians, it wouldn't, because it presupposes the existence of violins, violas, clarinets, trumpets" (original italics). In his book Minelli wants to draw more attention to the importance of violins and trumpets, rather than the musical score, a bit more epigenetics and a bit less genetics. Consequently, a good proportion of the ten chapters that make up Minelli's book are about the "generic" rather than the genetic aspects of development, such as segments, cell layers, the cuticle, cilia, and mineralised skeletons. Minelli argues that "genetic" and "epigenetic" shouldn't simply be seen as "program" and "data" respectively. He tells us not to dichotomise "developmental" and "housekeeping" genes, and he considers the existence of "master control genes" as "questionable." In short, Minelli emphasizes the physico-chemical properties of cells and tissues as very important for development and its evolution. Some of this writing is distinctly reminiscent of aspects of the work of Brian Goodwin, whose popular 1994 book *How the leopard changed its spots* brought several of the ideas about the importance of generic mechanisms in development and evolution to the attention of a broader audience. Central to both Minelli's and Goodwin's perspectives is that developmental genetics is not the whole story of morphogenesis, but in other respects their views diverge in important ways.

Furthermore, Minelli suggests that developmental features should be explained not with strict reference to the adult state, but with respect to the developmental process itself. For example, Minelli argues that the cuticle of ecdysozoans may not have originated as an adult adaptation (for example as a protection against predators), but as a specific adaptation to help control the patterning of development. Throughout his book he illustrates his points with many fascinating examples that betray his wide-ranging knowledge. For example, Minelli presents an amusing comparison of some of the recent views of Urbilateria as a morphologically very complex animal with Johann Wolfgang von Goethe's Urpflanze (archetypal plant). This hypothetical archetype featured virtually all imaginable variations of plant morphology, and could therefore serve as a model from which all existing variants could easily be derived, however, without it becoming any clearer how all these features originated in the first place.

Minelli's wide-ranging discussions of body regions, axes and symmetry, size factors, pattern formation, homology, and much more are intended to serve one overarching goal: to do away with the adultocentric perspective on development. In the end (p. 252) Minelli want his readers to come away with three main ideas. First, the evo-devo "urgently needs a bulky injection of facts and concepts from disciplines such as comparative morphology, descriptive embryology and the study of postembryonic development." Second, we should very carefully qualify concepts such as segments or larvae as they may mean different things in different contexts. Third, we should adopt a comprehensive comparative outlook that goes beyond the few model organisms that are now studied in detail if we are to make any meaningful generalisations about development and evolution.

However, although I like many things in his book, in places I think Minelli takes things a bit too far. For example, in noting the existence of checkerboard-like patterns from the arrangement of earthworm chaetae, to arthropod setae, to dorsal bumps in arthropods, to colour patterns in leeches, to the armoured plating of a Cretaceous ankylosaur, Minelli conjectures they may represent a generic form. He is similarly impressed by the prevalence of the number five or something close to five in noting the number of body regions in certain animals, different elements in plants, wing veins in insects, digits in tetrapods, developmental phases during an animal's life cycle, and even the number of "mental boxes" used in classification and the subdivision of time. Ironically, Minelli doesn't mention Quinarianism here. Perhaps all these things have something to do with each other? Minelli thinks so. He attempts to explain these disparate phenomena strictly by invoking constraints. He writes that a greater degree of differentiation (forming many more than about five units for example) is not possible even under strong "adaptive selection" because "as the number of those parts and the richness of interactions among the parts increase, there will also be a rapid increase in the number of conflicting constraints of design among the parts" (p. 87). Surprisingly, he doesn't seem to entertain any functional arguments at all. Perhaps having three body regions may be just right for a brachiopod? Perhaps having much more than four or five different life cycle stages, each of which is adapted to its own different ecology, is simply not necessary or even practical in order to reach sexual maturity? Minelli appears to have an exclusive preference for structuralist explanations. About "all these hard-wired points of animal anatomy" he concludes that they "have perhaps a developmental, rather than an adaptive, explanation" (p. 156). Paucity of evidence clearly allows one to have different preferences here.

Nevertheless, there are many pearls of wisdom in this book: "Complexity is not a feature of the external world, but strictly depends on the way we ask questions about the world" (p. 93); "Statements to the contrary notwithstanding, the role of genes in morphogenesis is likely *always* to be an indirect one" (p. 24, original italics); "In the absence of specific arguments to the contrary, shared patterns of gene expression should not lead us, per se, to homologise organs that a comparative morphologist would never try to compare" (p. 23); "I do not see any need to subscribe to the widespread belief that developmental processes exhibit specific adaptations to the putative function of creating a complete organism" (p. 19). Minelli's general approach is to look at familiar things from a new perspective, at times more successfully than at others. Whether you agree with these statements or not may not be the most important thing. After all, as Minelli amply exemplifies in his delightful book, science is not only about finding the right answers, it is about asking the right questions.

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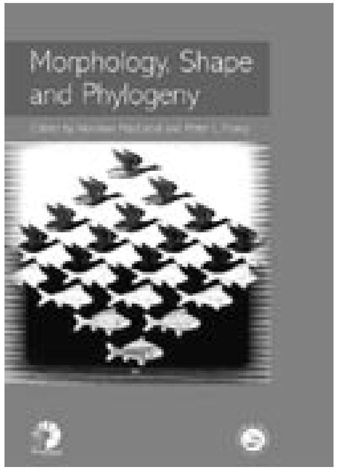
Morphology, Shape and Phylogeny

Macleod, N. and P. Forey, (Eds). 2002. Systematics Association Special Volume Series 64. Taylor and Francis, London and New York, 308 p.
ISBN 0-415-24074-3. £70.00.

The fields of morphometrics and phylogenetics are not intrinsically or necessarily opposed to each other. At worst, the two fields have existed in benign neglect of each another, without much fruitful interaction among the advocates and practitioners of each discipline. Norman Macleod and Peter Forey, in convening a symposium and editing the resulting volume *Morphology, Shape and Phylogeny*, have sought something of a rapprochement between these historically disjoint fields. The editors are to be congratulated on their success. They have solicited contributions from leading figures in phylogenetics, morphometrics, palaeontology and comparative biology, and the result is an edited volume that includes useful summary papers, thoughtful conceptual pieces and, most importantly, innovative original research.

In the Introduction to the volume, Macleod and Forey provide a brief overview of phylogeny and morphometrics, and then outline four fundamental questions that motivated the symposium and book. These four can be reduced to two even more fundamental questions: (1) How should quantitatively measured traits be used in the inference of phylogeny? (2) How may morphometric data be combined with independently-derived phylogenetic information?



In considering how to use quantitative characters to infer phylogeny, the first issue that arises is whether or not quantitative traits are even appropriate for the task. Some workers in the past have suggested that measured traits are *a priori* unacceptable for phylogenetic analysis. In the current volume, no author takes such an extreme view, and many cite Thiele's (1993) lucid exploration and defence of quantitative characters. The chapter by Humphries considers the nature of homology and characters in cladistic analysis, and while doubtful of some uses of quantitative traits, concludes that "all data should be scrutinized for potential analysis." This general conclusion seems to be the consensus among those that address the issue in this volume.

Once one has decided that it is acceptable to consider quantitatively measured traits for phylogenetic inference, how should such traits be quantified? This question is the subject of the contributions by Macleod and Swiderski, Zelditch and Fink. Both chapters seek to explore what morphometric techniques produce variables acceptable for phylogenetic analysis. Although their conclusions can be summarized like a scorecard with checks next to approved techniques (*e.g.*, Swiderski *et al.* favour partial warps and discredit outline approaches and principal component scores, while Macleod prefers relative warps over partial warps and does not object to principal components or outline methods), it is more informative to consider the reasons behind the distinctions that are being made. For example, Swiderski *et al*. argue that it is inappropriate to use techniques such as principal components analysis because the variables that are produced are sensitive to the choice of taxa in the analysis. Macleod disagrees, suggesting that systematists implicitly incorporate such information when considering qualitative characters so it need not be excluded from the evaluation of quantitative characters. At heart of much of the wrangling in these two chapters is a concern for homology of descriptors: the more that a morphometric variable reflects a complex amalgam of shape from different parts of the organism, the less secure one feels about judging similar values of that variable to be homologous. I am not sure that the distinction between a meaningful and a meaningless morphometric variable is a property of the technique that produced that variable. Instead, I suspect that nearly all approaches are capable of producing morphometric variables that range from homologous to meaningless. The biology of the organism and the intuition of the systematist will likely be the most useful guides for recognizing where on this continuum a particular descriptor falls.

It is interesting that at the end of these long chapters, both Macleod and Swiderski *et al.* conclude their contributions with examples of how morphometric analysis may be fruitfully applied in a targeted manner to those features that a systematist perceives to vary informatively among taxa. This approach lessens homology concerns, and I believe it also better represents how systematists actually use (or should use) quantitative traits in phylogenetic analysis. It would not be very productive to perform a morphometric analysis of, for example, a set of landmarks scattered over the organism of interest and then try to mine the resulting variables (partial warps, Procrustes coordinates, PC scores, or whatever) for characters that happen to be phylogenetically informative. In my own work (and I suspect this is true of many phylogeneticists that employ quantitative characters), the order of these actions is reversed: first I observe morphological variation in a feature that, although seemingly informative, may be difficult to score qualitatively with confidence. Then, I measure that feature in whatever way proves to be accurate and expedient in order to test if the original observation withstands closer scrutiny.

Once one has a continuously-varying morphometric variable (produced by whatever technique judged to be acceptable), the next decision is how to use this variable to infer phylogeny. There are two choices: filter this continuous variable into discrete states and include the resulting variable in a standard cladistic analysis, or leave the variable continuous and use a clustering algorithm or a model-based approach to infer phylogeny. There is a small cottage industry of algorithms for creating discretely coded variables from continuously-varying ones, several of which are reviewed in the chapter by Reid and Sidwell devoted to this subject. These authors express concern about the arbitrariness of all available techniques, a sentiment that is echoed by other authors in the volume, including Humphries and Rae. I think this arbitrariness is unavoidable because there is no reason to think that evolution will necessarily produce nicely clustered values of continuous traits. Arbitrariness therefore may be the wrong standard to apply to methods that recode continuous variables into discrete ones, because all will fail by this criterion. Instead, perhaps we should focus on whether a technique produces phylogenetically informative codes, and the extent to which these codes distort the original similarities among taxa.

Of course, if the algorithms that convert continuous variables to discrete codes are suspect, why not use the original continuous variables to infer phylogeny? Clustering algorithms can do just that, but lack a real evolutionary basis. The other approach is to use a model-based approach to infer evolutionary relatedness. To date, the only model that has been much considered is that of diffusion, as would be expected if populations were evolving by neutral genetic drift. The chapter by Felsenstein takes this one step further, considering the model of genetic drift plus an added component of multivariate natural selection. He then goes on to other more complex models, but is pessimistic about phenotypic data being sufficient to infer the necessary parameters without help from molecules.

The chapter by Bookstein offers an alternative approach to recognizing discrete characters from landmark configurations. This method recognizes qualitative differences between pairs of landmark configurations, termed creases, by looking for particular features while extrapolating the mapping of one configuration to another. Although some of the mathematics of this technique were beyond my comprehension, its purpose is clear: to discover qualitative differences (creases) that may underlie apparently continuous deformations. As such, this approach has potential to uncover features of shape that lend themselves easily to discrete coding and therefore phylogenetic analysis using standard software and algorithms. Time will tell if the mathematical formidability of this approach prevents its wide scale adoption by practising systematists.

The second big question posed by this volume concerns how to analyze morphometric data in the context of a phylogeny. This is the domain of comparative methods, and in one sense, morphometrics variables are no different from any other quantitative description of a taxon. Procedures exist for reconstructing ancestral states, tracing evolution and accounting for phylogenetic dependence for any kind of quantitative characteristic. One aspect that may differ is how these results are visualized. The chapter by Rohlf covers both the inference of ancestral morphologies and a nifty way of displaying these inferred forms from the manipulation of digital images. The chapter by Cole, Lele and Richtsmeier evaluates the presence of phylogenetic signal in morphometric data by comparing a phenogram based on morphometric data to a cladogram derived from independent data. Although the method is well-explained and quite general, I was unclear as to the advantage of comparing branching diagrams instead of directly comparing morphometric and phylogenetic distances.

The last three chapters all consider mathematical models of morphological evolution, and each makes use of fossil data to consider questions of particular interest to palaeontologists. In the first of these, Polly considers the pace of evolutionary divergence of viverravid mammals using Gingerich's (1993) log-rate log-interval (LRI) approach. Polly emphasizes the importance of using calibrated phylogenies (including possible ancestor-descendant pairs), and not merely cladograms to estimate divergence times and evolutionary rates among taxa. The second contribution, by Webster and Purvis, starts with a clear description of the different algorithms and software for reconstructing ancestral states on a phylogeny. These authors then compare the predicted ancestral states to morphologies observed in fossil taxa thought to be ancestral in two empirical studies. Somewhat surprisingly, they find that simple linear parsimony tended to perform best, and that more complex models did not do any better than simpler models. As these authors acknowledge, it is possible that the fossil taxa in question were not truly ancestral or that the tree topologies were incorrect, but regardless, this study demonstrates how palaeontological data can and should be used to inform and evaluate comparative methods.

In the final chapter of this volume, Pagel uses mathematical models to analyze the evolution of cranial capacity in hominids. This is a model study for how to test hypotheses about evolution using explicit statistical models. To date, most modelling work has assumed a diffusion (= unbiased random walk) model of evolution. Although many have expressed scepticism about this model, there have been very few studies that have rigorously compared it to other models of morphological change. Using generalized least squares, Pagel compares the diffusion model to one that allows secular trend in the trait of interest. In addition, he also varies scaling parameters that reflect rates of change relative to branch lengths and a parameter that reflects punctuated versus gradual change. He finds that the best-fitting model is one that allows a secular increase in cranial volume, and also that brain size has evolved gradually and at an accelerating rate over the history of hominids. In my view, the approach used in this chapter will prove to be a very fruitful one in future palaeontological research. Rather than argue about, for example, whether the visual impression of a set of samples suggests gradualistic or punctuated change, model-fitting approaches allow researchers to evaluate explanations on well-established statistical grounds. Palaeontologists, with their unique temporal view, are well-positioned to employ such approaches.

Aside from content, *Morphology, Shape and Phylogeny* is a well-assembled volume. The layout is attractive, the figures look good, and the index seems thorough. I did notice some typographic/editing errors, but they are not very numerous and generally quite minor. The book itself seems to be of solid construction; my copy has withstood reading and re-reading without much sign of wear.

So, who will find this volume worth its not so insignificant cost? Palaeontologists interested in both phylogenetics and statistical modelling of morphological evolution will be hard-pressed to find a volume with more to offer than this one – there are simply too many strong contributions from leading figures in these fields to ignore. Even palaeontologists with strong interest in one but not the other of these topics will likely find the volume worth their consideration. Palaeontologists with only casual interest in these subjects will likely pass, as will hard-core morphometricians as there is only one chapter that is purely morphometric in nature. In recent years, both phylogenetic systematics and statistical hypothesis testing have grown to be increasingly important components of palaeontological research. For those interested in these fields, *Morphology, Shape and Phylogeny* will be a source of ideas, new directions and active debate for years to come.

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Tangled Trees

Page, R.D.M., 2003. 350pp. University of Chicago Press.
ISBN 0-226-64467-7 (pbk). £20.

Interest in tree comparison has steadily grown over the last few years, with an increasingly large body of papers being published on the subject. This collection of twelve papers (and an introductory section by the editor, Roderic Page), therefore, is a welcome and timely attempt at an overview of the state of play in co-evolutionary studies.

In his introduction, Page presents a background description of co-evolution that merges nicely with his brief succeeding review of the book's contents. In all, the section provides an excellent and accessible springboard into the diversity of topics that are addressed afterwards.

The remainder of the volume is dividable into two sections. The first, which makes up a good third of the entire book, is devoted to theory and methodology. The second section is a collection of practical studies on a modest variety of organism groups.

Fredrik Ronquist gets the ball rolling with his paper on parsimony-based approaches to tree comparison, a subject he has very much promoted in recent years. He presents a detailed 'tree-fitting' method that facilitates the comparison of co-evolving trees, using various (two, three and four event) models. Of particular interest is his mapping out of the optimisation surfaces that serves to emphasise the fact that most co-evolutionary methods are simply trying to find a 'low' or a 'high' point (an optimum) in the solution space of whichever model they adopt. Ronquist also includes a useful discussion on algorithm speeds, an issue that is rarely discussed, but is relevant to both theoretical and practical systematists. In all, his paper is a general defence of his own methodological stance and I think he is successful in this aim. I get the impression that he is somewhat averted to the other approaches being taken towards solving co-evolutionary problems, and

it would appear that he sees the other currently available methods as all being reducible to "special-cases" of his own system. This latter assertion is certainly interesting, although I doubt that, from this paper alone, he will convince most workers of its validity.

The method discussed by Mike Charleston and Susan Perkins represents one of these 'other approaches', specifically, a method called 'Jungles'. Without going into details (of which there are many), Jungles accounts for the differences in two co-evolving trees using a model whose solutions specifically allow for horizontal transfer of parasite lineages. The mainstay of the paper is about the application of Jungles to *Anolis* lizards and their malaria in the Caribbean, and as a result, I think it would be better placed in the applied section of the book. The lizards have two varieties of malaria and they do not show similar solutions upon analysis. The apparent horizontal transfers of the malaria do, however, accord with the wind vectors in the region, which makes for an interesting dispersal scenario. The model used by Jungles (and, indeed, those used in Ronquist's schemes), require costs to be set for the various explanatory processes before the analysis, and for me this is the biggest weakness of these methods: if we cannot know meaningful values for the costs *a priori*, surely it is the job of theoretical science to come up with techniques that can handle the costs as genuine 'unknowns' and then infer them *a posteriori*? Despite this worry, without a doubt, Jungles is a valuable and powerful addition to the co-evolutionist's armoury.

Next, John Huelsenbeck, Bruce Rannala and Bret Larget treat us to what in my opinion may be the most robust paper in this publication. They describe the application of Bayesian analysis to the problem of co-evolution. Essentially, they take a statistical approach to answering the questions: (1) are the histories of hosts and parasites phylogenetically independent? (2) are the histories of hosts and parasites identical? (3) how can we infer the history of co-speciation, host switching and lineage sorting? After briefly examining a maximum likelihood approach to addressing these questions, the authors then go into a full exposition of a Bayesian approach that is both thorough and informative. In particular, they point out how problems such as those encountered in co-evolution studies are highly amenable to Bayesian analysis because for any number of taxa, there exists a knowable distribution of possible sets of relationships (trees) for them. This is important because being able to sample a distribution is required in order for Bayesian methods to be successful. In all, I think the authors outline a fruitful new avenue of exploration, so this paper is a must for all the co-evolutionary methodologists out there.

The next paper is by Bruce Rannala and Yannis Michalakis, and it truly is one for the theoretician. In this work, they attempt to relate the ideas of population genetics to patterns of co-speciation, providing some rather formidable mathematics along the way. From their analysis, which considers both within- and between-population associations, Rannala and Michalakis conclude that demographic factors are principally responsible for host-parasite congruence. These conclusions rely quite heavily upon arguments derived from the coalescent process, particularly in the modelling of lineage sorting. The paper is certainly for the more mathematical reader, but I believe it would be possible for any reader to extract the essential ideas without paying too much attention to the equations.

So much for the theory. J.-P. Hugot kicks off the practical section of the volume by using knowledge of rodent pinworm phylogeny to support the monophyly of hystricognath rodents.

In a well-rounded discussion, the program TreeMap is used to compare quantitatively the evolutionary histories of the hosts and their parasites. Hugot's conclusions challenge the idea that caviomorph rodents arrived in the Americas in a single immigration event.

Joanne Martin, Peter Kabat and Michael Tristem then examine the phylogenies of vertebrates and their viruses in order to understand events of horizontal transfer. As the authors point out, work such as this is of particular relevance because it may have important implications for epidemiology. Using TreeMap to analyse their data, they focus upon murine leukaemia viruses (MLVs), which are associated with certain kinds of blood cancer. Their analysis reveals a high level of intraclass transmission of MLVs in mammals, although the actual timings of these transmissions cannot be pinned down accurately. An obvious and interesting future direction for the work in this paper is to analyse the presented data set using Jungles, given that it is specifically geared towards studies of associate horizontal transfer.

The succeeding paper is by Mark Hafner (a stalwart of co-evolutionary studies), James Demastes, Theresa Spradling and David Reed. The work is a general overview of Hafner's group's research throughout the years, including the now archetypal gopher-lice study. This paper is easily the best in this book for someone who is looking to get a handle on the most important recent developments in co-evolutionary studies, and is essential reading for any serious worker. For the beginner, it is a perfect primer; for the more seasoned campaigner, it is simply interesting to read a historical account of the developments written by one of the pioneers of the modern subject. Mention of the most recent work includes the efforts that are being made to consider the bacteria that live on the lice of mammal hosts. Whilst simple, I find this idea to be an elegant conceptual expansion in the subject. Tantalisingly, results up until now seem to show co-phylogeny between the lice and these bacteria.

James Demastes, Theresa Spradling and Mark Hafner then proceed to explore co-phylogeny from the perspectives of different temporal and spatial scales. They find that a study of *Thomomys* does not corroborate earlier studies that have demonstrated disparate rates of evolution between hosts and their lice. From brief theoretical considerations, and with recourse to this and other studies, the authors discuss how varying temporal and spatial scales can affect the results of an analysis. In particular, they can affect the chances of detecting certain co-evolutionary events because characteristics of a group's population dynamics may introduce complexities such as incomplete lineage sorting and heterogeneity in the rate of evolution. The authors conclude that these characteristics may make, for the purposes of co-evolutionary studies, some hosts and their parasites incommensurable.

Jason Taylor and Andy Purvis, in another study of mammals and their lice, then consider the largest data set to be presented in this volume (404 mammal hosts and 234 lice – impressive!). Using TreeMap, the two trees are compared (although not all at once – TreeMap is not able to deal with so many taxa at once), and it is found that around a half of all possible co-speciation events occurred. The degree of host-parasite co-speciation is also found to vary quite highly amongst different mammal clades. When Taylor and Purvis perform the statistical analyses of these results, however, they are found to be insignificant. Instead, it appears that host switching is the dominant associate event (another use for Jungles?). The authors conclude, therefore, that co-speciation is the exception, not the rule, amongst mammals, and that Hafner's classic gopher-lice study is likely to be a special case, and not an indicator of the presence of a fundamental co-evolutionary relationship. Quite a disappointing conclusion, to be sure, but I thoroughly enjoyed this dose of counter-results.

Next, Kevin Johnson and Dale Clayton investigate the evolutionary patterns of two parasitic lice (wing lice and body lice), which occupy the same avian (Columbiforme) host. Through the use of a TreeMap analysis, they detect host-associate co-phylogeny for both kinds of lice, but the events of co-speciation for the lice are not congruent. Johnson and Clayton therefore conclude that the two kinds of lice are evolving independently with respect to each other, and are responding to different host dynamics. Although they originally reason that lice with the same ecological connections to the host should correlate in their evolution, they also point out that the result obtained in this study may be a function of deficiencies in the currently available tree comparison algorithms: that they do not explicitly incorporate an associate's failure to speciate. An interesting idea, and one that will no doubt get the methodologists thinking.

In the penultimate paper in this book, Adrian Paterson, Ricardo Palma and Russel Gray shrewdly investigate the 'reality' of the processes that are built into current co-evolutionary algorithms. For me, this paper represents the 'sharpest' science in the volume: the processes built into such algorithms are hypotheses, and it is one job of applied science to test the fidelity of these hypotheses reciprocally, given that they constitute the basis of the algorithm in question. That is, I find the spirit adopted by the authors to be more important (and far wider reaching) than the actual results that they present here. Considering seabirds and their lice, they conclude that a 'missing the boat' encapsulation of a sorting event (parasites not present on the host) is more important than a 'drowning on arrival' encapsulation (parasite going extinct in the host lineage) for co-evolutionary models of these animals.

Last, but not least, Dale Clayton, Sarah Al-Tamimi and Kevin Johnson attempt to synthesise ecological and phylogenetic considerations in order to understand co-speciation. Examples of 'ecological factors' are abundance and distribution, *e.g.*, chimp lice have less chance of going extinct than human lice because they are more abundant and their microhabitat (hair) is more extensive. Using arguments based on theoretical reasoning and empirical studies, they conclude that it should be possible to discern the ecological basis of co-evolution. This is because lice that have more congruent phylogenies with their hosts have fewer factors in their ecology that promote non-co-evolutionary processes (missing the boat, failing to speciate, duplication events *etc*).

In all, I recommend this book to any worker who wishes to get a broad view of state of the art co-evolutionary methodology and practice. The papers are all of a high quality, and the questions they address are relevant. I am pleased that a substantial portion of the book was devoted to theory/methodology because in today's science, where results, results, results gets a lot of the limelight, it is sometimes easy to forget that good results rely upon sound and rigorous methods. Roderic Page should be congratulated for ensuring that the three main methodological 'philosophies' (for want of a better term), broadly represented here by the perspectives of Ronquist (first paper), Charleston (second paper) and Huelsenbeck and Rannala (third and fourth papers), each get a fair airing. This makes the important emphasis that the jury is out on which methods are the 'best' (it's probably more accurate to say that the jury hasn't even got as far as leaving). The editing in the book is of the highest quality, to Page's credit, and there is barely a typo to be seen throughout. The diagrams, which are numerous, are also clear and of sufficient size. I do, however (and rather inevitably for those who know me), have a few complaints. Firstly, and a point I will quickly pass over because Page acknowledges it in his Introduction, the practical studies in the volume only look at a rather limited diversity of organisms, and are very much focused on chewing lice. Of course, this is very much a function of the data available to workers, but the practical aspect of the book would have came across as more rounded if more studies had been made of, say, bacteria and viruses (as associates) and amphibians, fishes and plants (as hosts). Slightly more serious is my note to biogeographers. For some time now, it has been the general wisdom to group the biogeographical system in with the other more classical co-evolutionary systems, those of species and genes, and hosts and parasites. Recent developments in the understanding of the biogeographical system, however, suggest that it has some properties that are not applicable to the other two 'host-associate systems' (the most obvious is that the host lineages have equal predispositions to converge and diverge – which implies that algorithms would need to consider convergent host patterns in their solutions). For me, this sheds some doubt on the purported universal applicability of the host-associate system as it is currently understood because it questions the notion that the species-area system is the same as the host-parasite system at a theoretical (and hence methodological) level. For those interested, I refer to work done by, for example, the likes of Lieberman (2000) and Legendre and Makarenkov (2002). So, whilst species and area trees are indeed 'tangled trees', they represent a system where the hosts have subtly different growth dynamics to those considered by the papers in this book, and this should be born in mind as you read.

This biogeographical gripe aside, 'Tangled Trees' is probably the most authoritative and up-to-date text available on co-evolution/tree comparison so I heartily recommend it to all serious students of the subject. It is packed full of good science and interesting findings, and it also opens up several intriguing paths of future research. For a mere £20, it's a sterling purchase.

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Invertebrates

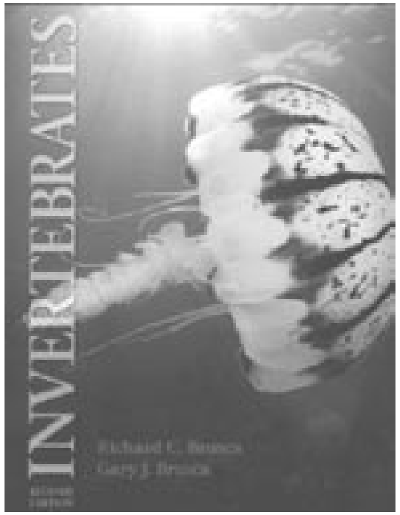
Richard C. Brusca and Gary J. Brusca. 2003. Sinauer Associates, Inc., Publishers. xx+936 pp. Hardcover. ISBN 0-87893-097-3. £34.99.

The essential section

Richard and Gary Brusca can be congratulated for producing this second edition of their popular textbook on invertebrate biology. The book looks less massive than its predecessor, but this is only appearance as the authors have included much new information that became available since the first edition was published in 1990. It is doubly impressive because Gary Brusca passed away during the revision process, so that Richard had to complete the project alone. I cannot begin to compare this new book with the first edition because I was raised on *Invertebrate Zoology* by Ruppert and Barnes (1994) (a new edition of this book hit the shelves a few weeks before writing this review), and attempting to read just one textbook to completion was already enough of a challenge!

In 24 chapters *Invertebrates* provides an overview of invertebrate diversity, phylogeny, structure, development, and life history. All major animal phyla are discussed either separately in a chapter, or grouped together with closely related taxa. One chapter is devoted to the protists. Several chapters deal with more general topics across the invertebrates, such as what the fossil record tells us about their origins, and where they live (chapter one), what tools are used to classify their diversity and reconstruct their phylogenies (chapter two), how invertebrates are built in terms of their major organ systems and their functions (chapter three), and what their general patterns of embryonic development are (chapter four). Chapter 24 concludes the book with a discussion of invertebrate phylogeny.

This book offers everything that a textbook for undergraduate students should offer. It presents a comprehensive introduction to invertebrate structure, development, function, and evolution. The authors have attempted to write around two fundamental themes: unity and diversity. A consideration of functional body architecture (what they call the Bauplan concept) provides unity, while phylogenetics provides a framework for understanding diversity. And last but not least, the book is attractively presented, lavishly illustrated with many clear schematic drawings as well as black and white and colour photos, and with coloured boxes that summarize the major characteristics of the taxa under discussion. At the end of chapters a helpful list of selected references is given.



Of course, in a work that tries to encapsulate such a magnitude of information between its covers a lot can be forgiven, or can it? Textbooks are not famous for the speed with which they incorporate new information. Invertebrate biology has been a very active field during the last decade, not least because of the renewed interest in metazoan phylogeny. Since phylogeny functions as a guiding principle in the book, and because my own area of least ignorance happens to be invertebrate phylogeny and body plan evolution, perhaps I can gauge the degree to which this textbook presents up-to-date information by focusing on those sections in the book in particular. At this point, however, the glass of wine at my lips is not simply to celebrate.

The optional section

If you don't want to read the rest of this quite bulky review, just go out and buy the book. It will be money well spent. However, if your lunch break isn't over yet, and you appreciate a rough guide to the soft spots of this book, please hang on. To save space I do not quote the references upon which my claims are based. Interested readers can e-mail me.

Species diversity

First, let us have a look at the data that are without exception the most ambiguous and most rapidly obsolete information in zoology textbooks: estimations of species numbers within higher taxa. The continual description of new species makes it virtually impossible to report a reliable species number that is not immediately obsolete, especially for highly speciose taxa such as the Arthropoda. Nevertheless, at the time the book went to press, Brusca & Brusca managed to tabulate exactly 1,097,631 known species of extant arthropods, which is remarkably precise for such a challenging estimate. However, if we expect even more precise estimates for the less diverse taxa, we are wrong. For example, 16 extant species of priapulids are mentioned. However, at the time the book went to press 18 extant species had been described, while it is known that several new undescribed species await description. It is unfortunate that Brusca & Brusca did not include *Halicryptus higginsi* in their book, which was described in 1999, and which represents the largest priapulid known, dwarfing all hitherto known extant and fossil species. With almost 40 centimetres length, this Alaskan species even exceeds in length the large Middle Cambrian priapulids, such as *Ottoia prolifica*, and *Louisella pedunculata*. But at the moment the grand total of described extant species of priapulid is 19, with the description of a new meiofaunal species from a submarine cave in Italy. Similarly, 23 species of extant cephalochordates are tabulated, while a 1996 comprehensive survey indicated at least 29 valid species. Perhaps today the writing of an up-to-date textbook on the invertebrates is too much for a single person to cope with?

The fossil record

More serious problems surface when information from the fossil record is considered. For example, in the introductory chapter (p. 5) we learn that the Precambrian Ediacara fauna "contains the first evidence of many modern phyla." These include *Dickinsonia*, which is "probably a polychaete annelid," and "numerous soft-bodied trilobites" (p. 6). Additionally, the Lower and Middle Cambrian are known for its different marine onychophorans (p. 7 and p. 463), primitive crustaceans such as the different species of anomalocaridids, and malacostracan crustaceans such as *Canadaspis*. These statements betray the absence of any familiarity with the recent literature on the evolutionary and phylogenetic significance of the fossils in question. The nature and affinities of many Ediacaran forms remains hotly debated, and although several diploblasts may be present, I think that on the basis of available evidence very few would count *Dickinsonia* as a polychaete annelid, or assign several highly problematic soft-bodied arthropod-like fossils unambiguously to the trilobites. The origin of trilobites is generally considered to be in the Cambrian, and not even quite at the base either. Moreover, just to call the Cambrian lobopodians "onychophorans," anomalocaridids and *Canadaspis* "crustaceans" would sooner confuse than enlighten a student unfamiliar with these animals. Here Brusca & Brusca forego a precious opportunity to introduce the phylogenetic concepts of crown and stem-groups, which could have provided some rigorous clarity to the narrative. In a book for which one of its main themes is phylogenetics, this is particularly regrettable.

Not surprisingly, in other parts of the book fossil information fares equally badly. For example, in the chapter on ctenophores "only two questionable records" of fossil ctenophores are mentioned. This glosses over the convincing description of three species of Middle Cambrian ctenophores in 1996, which allowed some unique insights into the early history of this group (showing, for example, that these forms possessed more than the eight comb rows that characterize extant species, but probably still in multiples of eight). In stating that since the Cambrian no phylum of animals has gone extinct (p. 16), the reader is then left to guess what exactly has gone extinct with the disappearance of animals like *Odontogriphus*, and *Nectocaris*. In those rare instances when Brusca & Brusca comment upon data from the fossil record that are not taxon specific, such as the dynamics of diversity patterns throughout geological time, the situation is not much more encouraging. For example, in remarking that species diversity has increased "perhaps exponentially" (p. 16) since the end of the Proterozoic, they give no attention to an important new study published in early 2001 that throws serious doubt upon an exponential increase in diversity in the Phanerozoic. In conclusion, the inclusion of data from the fossil record scarcely goes beyond a courtesy gesture, and what is included is not reflective of critical study. Of course, this book is specifically concerned with the extant invertebrates, but I think it would be nice for students to see the inclusion of some of the most notable recent discoveries from the fossil record as these would add a unique dimension to understanding the origins and evolution of various taxa. The book could benefit from a dash of *Pikaia* here, a sprinkle of *Yunnanozoon* and vetulicolian there, even if that necessitates removing a picture of a purple sea star or a Colorado beetle. The discussion of some of the Upper Cambrian Orsten arthropods in the arthropod chapters, and fossil echinoderms in the echinoderm chapter, are exemplary in this respect.

Invertebrate structure and development

But there is more. With respect to presenting the basic facts of invertebrate morphology and development, the Bruscas generally succeed. However, in certain places they are simply not as up-to-date as they could have been. Here follows a selection. In the description of tardigrade structure and development, they are unambiguously presented as coelomate animals with enterocoelic (outpouchings from the archenteron) formation of the coelom. However, this ignores the only modern publication on tardigrade development, published in 1996, that could not confirm the enterocoelic coelomate nature of the tardigrades, while adult ultrastructural anatomy also does not indicate the presence of coeloms. With respect to the embryology of hexactinellid sponges (glass sponges) they note the existence of only one study from the early 20th century. This ignores a new detailed study published in 1999. In discussing the phoronids, the trimeric organization of the actinotroch larva is cited to support a deuterostome affinity of the Phoronida. This ignores an important ultrastructural study from 2001 that threw considerable doubt on the trimeric organization of phoronids, principally by showing that the anterior-most region of the larva does not contain a coelom (protocoel) as is required in a trimeric organization. A number of other omissions are also notable. First, the higher-level taxon Micrognathozoa (*Limnognathia maerski*), which was described in 2000, was not included in the book, but the Cycliophora, which were described in 1995, are. In several instances Brusca & Brusca describe complex patterns of development and morphology, however, without providing any illustrative material. Such is the case for ctenophore cleavage patterns and the external morphology of the vestimentiferan tubeworms. In both cases an explanatory drawing would make things much clearer. In addition, to support the possible triploblastic organization of the ctenophores Brusca & Brusca cite a paper from 1885 for a fate map of the ctenophore embryo, and a review paper from 1985. Remarkably, a modern fate mapping study from 1999, which provided much more reliable support for the presence of mesodermal structures in ctenophores, is not even mentioned. And the intracellular or tissue parasites the myxozoans are all but invisble. Myxozoa is not listed in the index, and only two short paragraphs are dedicated to these remarkable animals that have only recently been moved from the protists to the more stately mansion of the Metazoa.

Chapter three of the book provides a general overview of animal architecture, introducing the structure, function, and diversity of the major organ systems in the Metazoa. This is a very important chapter for students to study, because variations upon the themes of nephridial systems, body cavities, and cerebral ganglia recur throughout the book. Yet, I do not like this chapter. The general reason for this is visible throughout the book: the relative lack of information derived from ultrastructural studies of morphology. Most of the recent studies on invertebrate morphology today use electron microscopy, in particular transmission electron microscopy, to reveal the intricacies of internal anatomy. However, disregarding the nine transmission electron micrographs that are presented in the chapter on protists, only an additional two are present in the rest of the book. Although many of the drawings and photos are typically of a high quality, and a number of schematic drawings are based upon electron micrographs, many of the drawings are based upon older light microscopy, such as the work of Libbie Hyman. In these instances much relevant information is missed, notable the nature and orientation of epithelia, which is essential to understand the lining of coeloms, the structure of muscles, the organization of nephridia, and the structure of blood vessels. A case in point is the schematic cross-sectional drawing of the placozoan *Trichoplax adhaerens* in figure 7.1, which can only be labelled as pitiful.

I was therefore disappointed by the general presentation of the nature and function of coeloms, nephridia, and blood vessels in particular. For example, only a very schematised drawing of three different types of internal body organizations in bilaterians (called acoelomate, blasto- or pseudocoelomate, and coelomate) is presented (Fig. 3.5). It is concluded that these represent three “major grades of construction.” Yet, this does not make it clear that acoelomate and pseudocoelomate organizations are histologically extremely similar, principally only different in the relative amounts of interstitial space and fluid between the internal organs, and that within a single animal different body regions can be designated as acoelomate or compactly organized, pseudocoelomate or more loosely organized, and coelomate. A coelom is properly defined as a cavity formed within the mesoderm, and thus lined with a mesodermal lining. However, the coelom is said to be lined by a peritoneum, which is defined as a “squamous epithelial layer.” Although Brusca & Brusca are not alone in defining a peritoneum like this, recent ultrastructural studies have led to the refinement of this term only to mean a non-contractile epithelial layer, to distinguish it from the contractile myoepithelial cells that are part of the epithelial lining of all coeloms. Therefore the coelomic lining can be termed mesothelium irrespective of its ultrastructure. In many coelomate animals the myoepithelial cells of the coelomic linings are at the same time the body wall muscles. In other cases the simple coelomic epithelium is differentiated into different layers, so that in extreme cases a non-contractile peritoneum faces the coelomic lumen, and overlies myoepithelial cells and/or non-epithelial myocytes. A real peritoneum is thus much more restricted in distribution than a mesothelium, and does not occur in all coelomate animals. From the textbook, this structural and functional connection between coeloms and muscle systems remains obscure.

I found the discussion of blood vessels equally unsatisfactory. Open and closed blood systems are distinguished, but nowhere is it made clear where in the body the vessels are exactly located, and that the difference between the two is chiefly the distance of the basal laminas that form the boundaries of the systems. So-called closed blood vessels are bordered by relatively closely opposed basal laminas or basement membranes, such as those of coelomic and gut epithelia in the gut wall, epidermis and coelomic epithelia in the body wall, and between adjacent coelomic epithelia in mesenteries and coelomic septa. More open circulatory systems are also bordered by the extracellular matrix (connective tissue) compartment of the body, but the absence of closely opposed epithelia provides for a more spacious, open system. In this respect open circulatory systems are histologically equivalent to pseudocoels and intercellular fluids. All this is not clearly explained in Brusca & Brusca. Instead it misleadingly stated that “the blood itself is physically separated from the intercellular fluids,” and that “capillaries typically have membranous walls that are only a single cell layer thick” (p. 71, 72). In contrast, the connective tissue compartment is continuous from the smallest intercellular spaces to the lumen of the blood vessel system, although the precise composition of the extracellular matrix may vary from place to place. And capillaries in invertebrates are certainly not lined by a single cell layer. This situation is restricted to endothelium-lined blood vessels in vertebrates, and cephalopods. It is furthermore stated that “muscles of the blood vessel walls” (p. 72) help propel the blood through the vessels, without making it clear that these muscles, like body wall muscles, are specialized regions of the coelomic epithelium.

When describing filtration nephridia, the book states that in protonephridia filtration occurs “across the thin cell membranes” (p. 69). However, the filtration weir is not composed of the cell membranes of nephridial cells, but the semipermeable extracellular filter made up of the cell’s basement membrane. In describing the function of metanephridia it is nowhere stated that filtration actually occurs across the basement membranes of blood vessels lined by specialized cells called podocytes, and that these may be located some distance away from the site of the metanephridial funnels that collect the primary urine. A greater attention to ultrastructural data would allow a much more accurate and clear introduction to these topics, as is done, for example, in chapters five in Ruppert & Barnes (1994) and Westheide & Rieger (1996). Even after reading more than 900 pages of textbook, I do not think that a student who is only using Brusca & Brusca can give a clear overview of what a coelomic lining is, how it relates to body wall muscles, how a filtration nephridium functions, what the differences and similarities between proto- and metanephridia are, and how blood vessels relate to the intercellular connective tissue compartment of animals.

Molecular biology

And when it comes to introducing some of the data and concepts from molecular biology and the blossoming field of evolutionary developmental biology, other problems arise. First, it is inappropriately suggested (p. 4, 17) that homeobox genes are equal to Hox genes, leading to the conclusion that Hox genes are present in all phyla that have been examined. However, no unambiguous Hox genes are yet known from poriferans. Then two functions of Hox genes (p. 17) are distinguished: "(1) they encode short regulatory proteins that bind to a particular sequences [sic] of bases in DNA and either enhance or repress gene expression, and (2) they encode proteins that are expressed in complex patterns that determine the basic geometry of the organism." However, these "different" functions are simply the result of looking at different levels in the organizational hierarchy, and in terms of the development of an organism, function two is achieved through function one. It seems to me unnecessary to separate these functions, lest we want to specify the function of each molecule at all levels of organization, but this may be a matter of taste.

Furthermore, in writing that chelicerates lack a deutocerebrum (p. 492), no mention is made at all of important recent molecular developmental papers that argue that a deutocerebral segment is present in the chelicerates. It is argued that poriferans "share as many similarities with protists than they do with the higher Metazoa" (p. 203, 204). Here would be a good place to introduce some of the findings of molecular biology that show that on the one hand sponges are firmly linked with the remaining Metazoa, and on the other hand suggest a close relationship between the choanoflagellates and the Metazoa. In mentioning the standard textbook ingredient that only molluscs and arthropods possess hemocyanin as a respiratory pigment, it could have been pointed out that molecular phylogenetics shows that these proteins are unrelated in these two phyla, and that additionally hemocyanin has now been identified in an insect as well. In discussing the phylogenetic placement of the problematic mesozoans, no mention is made of the accumulating evidence from 18S rDNA sequences and Hox genes that at least dicyemid rhombozoans are probably lophotrochozoan bilaterians, a phylogenetic placement that would at least be compatible with the equally unmentioned spiralian nature of the first cleavage divisions in dicyemids. In these instances some strategic mention of modern insights from molecular biology would encourage students to appreciate the increasing integration of comparative biology.

Phylogenetics

For a book that is organized around phylogenies and phylogenetic concepts, I found several passages where the didactic value seemed doubtful. For example, on page 32 it is stated that cladograms "are constructed to depict only genealogy, or ancestor-descendant relationships." This is precisely *not* what cladograms do; they represent atemporal patterns of sister-group relationships only. They may form the basis for *inferring* hypotheses of ancestor-descendant relationships in their promotion to an evolutionary tree or scenario, but a cladogram contains no such information. An autapomorphy is strictly defined as a feature present only in one species, although autapomorphies can of course also be assigned to monophyletic multi-species higher taxa, if that is the level of phylogenetic analysis. Primitive and derived character states are first defined as "relatively old" and "relatively recent" respectively. This suggests an unnecessary degree of ambiguity that is easily circumvented by introducing these notions as being strictly related to a certain level on a phylogeny, which is only done much later in the section. To strip definitions such as these of all unnecessary ambiguity is very important as this may be a student's first contact with such material, and from my experience in teaching these concepts I know that confusion comes all too easy.

Finally, Brusca & Brusca have chosen to discuss animal evolution using a combination of rigorous phylogenetic reasoning (cladograms), and narrative discussion. This creates a highly readable product, but with a strange flavour because the narrative discussions may contain logic that is in direct conflict with rigorous phylogenetic arguments. For example, the text is pervaded with many evolutionary assumptions that are neither substantiated by logic nor by data, and may therefore be confusing to students. It is, for example, assumed that the two clades of protostomes and deuterostomes are coelomate clades (p. 261), thus implying that animals such as the pseudocoelomates are secondarily non-coelomates (p. 338, 381), a hypothesis unconstrained by a phylogeny. I believe that the book does not emphasize enough that phylogenies function in constraining the number of possible evolutionary scenarios. For example, the hypothesis that platyhelminths have directly descended from the ctenophores is not supported by any recent phylogenetic evidence and therefore no longer tenable. Instead of presenting the issue thus, Brusca & Brusca chose to write much more ambiguously that this hypothesis "no longer has much popular support" (p. 313). Then, in further discussing the phylogenetic placement of the platyhelminths, they write that "we are left today with at least two very different ideas on the origin of the phylum Platyhelminthes" (p. 315). One hypothesis derives the non-coelomate flatworms from the non-coelomate diploblasts, "making Platyhelminthes the first descendant group" of the triploblastic spiralians (p. 315). However, this is inappropriately arguing for a basal phylogenetic position on the basis of a plesiomorphic character state. A second scenario that is presented derives the platyhelminths from a common coelomate protostome ancestor as the sister taxon to all coelomate protostomes. Although the discussion of these hypotheses is interesting from a historical perspective, neither of the two has been seriously entertained for at least the last two decades. None of the recently published morphological or molecular computer-assisted phylogenetic analyses is considered in the discussion. None of these analyses provide support for either of the two discussed alternatives. I will refrain here from discussing chapter 24 on metazoan phylogeny. Interested readers may consult Jenner (in press).

In being critical I do not intend to dissuade people from using this book, quite the contrary. I merely pay a tribute to a primary intention of this book: to be critical. In the preface Richard Brusca (p. xvii-xviii) writes that "we always knew that some of you, professors and students both, would disagree with our methods and ideas to various degrees – at least we hoped you would. Never placidly accept what you see in a textbook." And this book contains enough frayed ends for students to sink their teeth into. After all, understanding the invertebrates requires "the dedication of a career, not just dabbling" (p. xviii).

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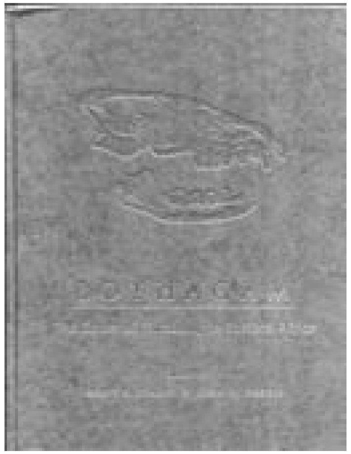
Lothagam. The dawn of humanity in eastern Africa.

Leakey, M.G. & Harris, J.M. (eds.). 2003. Columbia University Press, New York. ISBN 0-231-11870-8. £134.50

Lothagam is described almosty romantically in this impressive monograph as "an island of sediments surrounded by sandy, windswept plains of the Turkana desert", but it is one of the most important fossil sites in Africa. Situated to the west of Lake Turkana in northern Kenya, Lothagam is an upfolded fault block 10 km by 6 km, which contains a rich and diverse assemblage of mostly vertebrate fossils. Its sediments span the period 4–8 million years ago in the late Miocene and its fossils reveal what happened to the East African mammal fauna as equatorial forests shrank and were replaced by modern C_4 savanna vegetation. Because of this, Lothagam is one of the most important fossil sites in Africa, although the first excavations occurred only in 1967. Since then more than 2,000 vertebrate fossils and 7,000 fish elements have been discovered, catalogued and studied. This multi-authored volume represents the results from five field seasons from 1989 to 1993.



After an introductory chapter about the location and its palaeontological history, the next three chapters deal with geological aspects of the area, including its stratigraphy and depositional history, its palaeosols, and the dating of its strata. The bulk of the book is taken up with specialist chapters on the systematics of crabs, fish, turtles, crocodilians, birds and the mammalian orders that comprise the majority of terrestrial vertebrate fossils that have been found at Lothagam, including the descriptions of many new species and genera. Included is some discussion of the Lothagam hominids, which appear to be identified tentatively, but uncertainly, as being most similar to *Australopithecus anamensis* and *A.* c.f. *afarensis*. The final chapters deal with how stable isotope analysis from the tooth enamel of herbivorous mammals can be used to reconstruct the palaeoecology of the area around Lothagam. A final chapter summarises the many findings of this momentous monograph and places them in the context of findings from sites elsewhere in the world.

Illustrated throughout by excellent photos and line drawings, an added dimension is given to the chapters by Mauricio Anton's detailed reconstructions. *Lothagam* presents us with an excellent and unrivalled insight in to the far-reaching ecological changes and their impact on the vertebrate fauna that occurred in the late Miocene as today's east African savanna grasslands first began to appear.

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Ordovician Fossils of Argentina

J.L. Benedetto *(editor)* 2003. Universidad Nacional de Cordoba. Secretaria de Ciencia y Tecnologia. ISBN 987-453910-2. 560 pages, 66 text-figures, 109 plates. Price: US$100, € 90. (website with ordering information **<www.ordovician.com.ar>**: e-mail **<info@ordovician.com.ar>**)

The Ordovician system is well represented in northwestern Argentina, and the body and trace fossils are frequently very well-preserved. Many classic studies have been undertaken on this material, such as Harrington and Leanza's renowned monograph (1957) *Ordovician Trilobites of Argentina*. Yet much of the voluminous literature which has accumulated in recent years remains scattered, and sometimes difficult of access. Accordingly, and just after the 8th International Symposium on the Ordovician (ISOS) in Prague in 1999, Luis Benedetto and his colleagues conceived this new and major work, intended to be a comprehensive synthesis of all available information on the Ordovician palaeontology of Argentina. A formidably strong team was assembled, centred on Cordoba but with experts from other Argentine universities and institutes, and as a result of their hard work and dedication this magnificent publication was ready for the 9th ISOS in San Juan in August 2003. It is a tribute to all the contributors and the editor that all this information could be put together in less than four years, and assembled in so attractive a form.

Ordovician Fossils of Argentina has an appealing green cover, illustrating a ring of different invertebrate fossils set against a south polar projection of Gondwanaland, so enticing the prospective reader to enquire within. And the contents do not disappoint. Within this book one finds twelve chapters, of which the first five provide the sedimentary, tectonic, palaeogeographical and ecological setting for our understanding of the faunas; the remainder are essentially systematic treatments of particular fossil groups. There is such a wealth of information here that it would be hard to single out specific points. Ch. 1, by R. Astini, *The Ordovician Proto-Andean Basins* (74pp, 40 figures) details the history of the various Ordovician depocentres and integrates them into the larger picture of the evolution of western Gondwanaland. Ch. 2, by E.D. Brussa *et al.*, *Biostratigraphy* (16 pp, 4 figures) provides an essential chrono- and biostratigraphic framework for the Argentine Ordovician. Ch. 3, by J.L. Benedetto, *Palaeobiogeography* (38pp, 7 figures) gives an overall framework and sets out the case for a Laurentian origin for the Precordilleran terrane. In Ch. 4, by T.M. Sanchez *et al.*, *Palaeoecology and global events* (18pp, 8 figures) there are presented attractive palaeocommunity reconstructions. Some of these are in colour. Ch 5, by F.L. Cañas & M.G. Carrera (12pp, 5 plates) describes *Precordilleran reefs*, with particular reference to sponge-microbial associations. There follows the systematic section. Ch. 6, by M.G. Carrera, *Sponges and bryozoans* (30pp incl. 9 plates); Ch. 7 by J.L. Benedetto, *Brachiopods* (102pp, incl. 24 plates); Ch. 8 by T.M. Sanchez, *Bivalves and rostroconchs* (20pp, incl. 3 figures and 4 plates); Ch 9 by B.G. Waisfeld and N.E. Vaccari, *Trilobites* (144pp incl. 34 plates); Ch.10 by M.J. Salas, *Ostracods* (28pp incl. 8 plates); Ch. 11 by B.A. Toro and E.D. Brusca, *Graptolites* (64pp, incl. 16 plates, both photographs and drawings), and Ch. 12 by M.G. Mangano and L.A. Buatois, *Trace fossils* (49pp incl. 9 plates). The length of the chapters on brachiopods and trilobites reflects the diversity and abundance of these groups, but also the fact that they have been extensively treated systematically. A brief appendix includes references to other groups such as cephalopods, which are otherwise not covered here, and which points the way for future research. There is a useful systematic index.

The standards of production are exceptionally high. All the papers without exception are easy to read, and well written in good English, the text figures are clear and explicative. Each chapter has an extensive and comprehensive bibliography. But perhaps the most excellent thing about this book is the exceptionally high quality of the 109 plates. Each photograph has been carefully scanned in to an appropriate size, and the tones match perfectly. The result is that each plate is a pleasure to look at and a work of art in itself, quite apart from its scientific value. This must have been a major undertaking, considering that there are 1,885 separate photographs, if I have counted correctly.

In all respects this book is quite outstanding, and will surely become an essential reference for all Ordovician workers, and not just those who specialise on Gondwanan faunas. The editor and his team have given us a work of great appeal and enduring usefulness, and one which no one interested in the Ordovician should be without. Let us hope that it receives the global attention which it so clearly deserves.

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ABSTRACTS

On the track of French Cretaceous dinosaurs – in the field and in Museums

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Dinosaur remains are known from many Cretaceous formations in France, but the quality of the record is variable.

Early Cretaceous dinosaurs are known mainly from shallow marine deposits. Curiously enough, very few dinosaur specimens have been reported from the Wealden facies of NW France. Some of the best Early Cretaceous material comes from the Hauterivian, Barremian, Aptian and Albian of the eastern Paris Basin. Many of the quarries which have yielded that material are no longer accessible, and recent discoveries have often been made in museum collections. Good examples are an *Iguanodon* jaw from the Hauterivian *Toxaster* Limestone of Aube, recently found at the Natural History Museum in Troyes, and a set of theropod, sauropod and ankylosaur remains from the Albian Greensand of the Argonne region (collected during the late 19th century "phosphate rush") found at the Zoological Museum in Nancy. The scanty Early Cretaceous dinosaur remains from southern France are mainly from marine deposits, too. Comparisons with the better known British assemblages from the Wealden and the Cambridge Greensand suggest significant resemblances.

Very little is known about French dinosaurs from the beginning of the Late Cretaceous, although a few fragmentary specimens have been found in coastal deposits of Cenomanian age in central-western France.

The record is much better for the last stages of the Cretaceous (Campanian and Maastrichtian), which are represented by extensive non-marine formations in southern France, from Provence to the Pyrenees. Although the occurrence of dinosaurs in these formations has been known since the mid-nineteenth century, systematic excavations were started at a relatively recent date. Field work carried out in the last 15 years has resulted in the discovery and exploitation of several important and productive localities. Many of them (such as Fox-Amphoux, Cruzy and Campagne-sur-Aude) are Late Campanian / Early Maastrichtian in age and yield a diverse dinosaur assemblage including dromaeosaurids (*Variraptor*), possible abelisaurids, titanosaurids (*Ampelosaurus*), ornithopods (*Rhabdodon*) and ankylosaurs (*Struthiosaurus*), as well as birds. Although bones and teeth are often abundant at these localities, articulated specimens are rare. The recent discovery of a nearly complete titanosaurid skeleton at Campagne-sur-Aude is therefore worth mentioning. Dinosaur eggs belonging to different types are also found in abundance in the Late Cretaceous of southern France.

The last French dinosaurs are from Late Maastrichtian deposits in the Corbières and the foothills of the Pyrenees in Ariège and Haute-Garonne. This assemblage contains titanosaurid sauropods and ankylosaurs, as well as theropods, but lacks *Rhabdodon*. Instead, hadrosaurs, which are unknown from older deposits, are abundant. This indicates an episode of faunal change during the Maastrichtian, the causes of which are poorly understood, as the geographical origin of those hadrosaurs is uncertain.

The return of the *Cetiosaurus*: taxonomy, nomenclature and relationships of a historic British sauropod genus

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The sauropod genus *Cetiosaurus*, erected by Richard Owen in that first, famous manifestation of dinosaur mania in 1841 (Owen, 1841; Owen, 1842), was not even, to begin with, a dinosaur. As Hugh Torrens describes in another paper at this symposium, Owen named *Iguanodon*, *Megalosaurus* and *Hylaeosaurus* as the Dinosauria – and later had them immortalised in concrete at the Crystal Palace. But he had *Cetiosaurus* as a huge, sea-going crocodile. Nevertheless, Owen included several species in the genus, and started *Cetiosaurus* on its way to becoming the wastebasket taxon that it has been for over 160 years.

The 1968 discovery of a partial sauropod skeleton at Great Casterton, Rutland, its preparation, description and assignment to *Cetiosaurus* over the following years (Jones, 1970; Martin, 1987; Upchurch and Martin, 2002) paved the way for a review of all material referred to the genus.

The genus included at least 14 species at the last count. Owen erected seven, but other authors have compounded the problems; some species are, or include, indeterminate dinosaurs, unidentifiable or unrelated sauropods, or iguanodontids. Some material is in more than one species; some taxa are effectively *nomina nuda*, while another started life in the genus *Cetiosaurus* but now appears, surreptitiously re-described, in an unrelated taxon.

Most of Owen's type material, together with parts of perhaps three individuals of *Cetiosaurus oxoniensis* Phillips 1871, are in the Oxford University Museum. A review of these skeletons, other referred specimens in the Natural History Museum, London, and elsewhere, and of the Rutland skeleton has provided the first detailed description of the genus and led almost to emptying of the wastebasket. We propose retention of the historic name *Cetiosaurus* but establishment of *C. oxoniensis* as the new, lectotype species based on valid material in Oxford. The Rutland specimen, indistinguishable from the type, provides useful information on elements not preserved in Oxford. *Cetiosaurus* displays characters that appear to place it as the sister taxon to all advanced neosauropods, as described by Paul Upchurch at this meeting (and see Upchurch, 2003), and the first sauropod establishes its legitimate place in current dinosaur palaeontology.

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The history of the English invention of Dinosaurs

Hugh Torrens

Dinosaurs were invented on April Fool's Day 1842. Before this there were no such things, and they can properly have no history (only a long pre-history). From 1790 on, a series of wondrous fossils had been discovered throughout Europe, like the marine and flying reptiles found in Dorset by the Anning family (perhaps the first to make a good living here from selling fossils). Fossils of two enormous, and now entirely English, terrestrial, animals were also soon discovered. They were publicised by the cleric Rev. William Buckland from Oxfordshire and the surgeon Gideon Mantell from Sussex. These opened up unknown worlds to a fascinated public.

The absence of any competent comparative anatomist in Britain before the 1820s meant that much of the expertise in first deciphering these fossils had to come from France. But Georges Cuvier died in 1832 (after the Reform Bill of 1831) and a political struggle started to take over his science here. Battle lines were drawn between Mantell, provincial amateur; Richard Grant, badly-paid London professor, and Richard Owen, well-placed London professional anatomist, and nearly a generation younger than the others. Dinosaurs-to-be became weapons in the personal battles between them and in the ideological warfare between theories of evolution against creation which also developed in the highly politicized world of science in 1830s England. The British Association for the Advancement of Science supported the metropolitan Owen against the provincial Mantell. In a strikingly original assessment of the relationship between the, by now, three different genera, all very fragmentary, of these English fossil reptiles, Richard Owen invented Dinosaurs. This was in his published report to the BAAS. But he had found none of the fossil evidence himself…

Owen's dinosaurs were very large (but soon shrank), some clearly fierce, and all were extinct. The critical specimen, which Owen saw demanded the creation of his new Order of fossil Reptiles, had come from the Isle of Wight. It was in the collection of a radical socialist who believed in educating the working classes. Politics and science were never closer.

A review of British ornithischian dinosaurs

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The British record of ornithischian ('bird-hipped') dinosaurs spans the basal Jurassic (Hettangian) to the early Late Cretaceous (Cenomanian) and therefore offers a valuable window on to the evolutionary history of the clade. This window was open for much of the Mesozoic, although the temporal distribution and abundance of the British material is patchy, ranging from the species-rich dinosaur communities of the Lower Cretaceous Wealden Group to sporadic occurrences in the marine facies of the Late Cretaceous. Some British ornithischians are known from multiple complete, or near-complete, specimens (*e.g. Scelidosaurus*, *Hypsilophodon*, *Iguanodon*) whereas others have been erected on the basis of meagre material, often comprising isolated, unique elements (*e.g.* '*Sarcolestes*', '*Trachodon cantabrigiensis*').

All major ornithischian clades are represented in the British record, with the sole exception of the Ceratopsia, or horned dinosaurs. Approximately 50 different taxa have been based on the British material, but many of these have subsequently been sunk into synonymy or have proved to be *nomina dubia*. Currently, 13 genera (including 18 species) are recognised as valid, though these statistics are likely to change following further taxonomic work.

Thyreophoran ('armoured') dinosaurs are well represented, with several ankylosaurs and stegosaurs present. Excellent material of *Scelidosaurus* represents the earliest-known ankylosaur and fragmentary records from the Middle and Late Jurassic ('*Sarcolestes*', '*Cryptosaurus*', '*Priodontognathus*') provide useful data for a poorly sampled interval of the global ankylosaur record. Early Cretaceous ankylosaurs include the nodosaurids *Hylaeosaurus* and *Anoplosaurus* and the polacanthid *Polacanthus*, while material of '*Acanthopholis*' extends the range of the UK ankylosaurs into the Late Cretaceous. Stegosaur material is present in Middle and Late Jurassic deposits, and several partial skeletons and much isolated material have been recovered (*Lexovisaurus*, *Dacentrurus*). Stegosaur remains include one of the earliest known records of the group (early Bathonian) and also rare Early Cretaceous occurrences (*Craterosaurus*, '*Regnosaurus*').

The majority of UK ornithischians (in terms of both abundance and diversity) are ornithopods. By the far the most abundant are iguanodontian-grade animals: *Iguanodon*, *Valdosaurus* and *Camptosaurus*. Material of these taxa comes largely from Wealden sediments, but occurrences of *Camptosaurus* span the Late Jurassic to basal Cretaceous. Iguanodontians formed the bulk of UK dinosaur biomass during the Early Cretaceous interval. Hadrosaurs ('duck-billed dinosaurs') are present in two late Early/early Late Cretaceous localities: though the material is poor, these specimens plausibly represent some of the earliest known records of this important clade ('*Trachodon cantabrigiensis*', '*Iguanodon hilli*'). The basal euornithopod *Hypsilophodon* is a common component of Isle of Wight Wealden faunas, but otherwise small ornithopods are relatively rare in the UK. *Echinodon*, from the basal Cretaceous Purbeck Limestone Formation, may represent a late surviving lineage of heterodontosaurid ornithopod, significantly extending the temporal and geographical range of this otherwise Early Jurassic, largely African, group.

A single fragmentary skull roof forms the hypodigm of *Yaverlandia*, the only Lower Cretaceous pachycephalosaur and the only member of this group to be described from Europe.

British ornithischians are important for a variety of reasons. In historical terms, they include the first ornithischians to be described scientifically (*Iguanodon* in 1825; *Hylaeosaurus* in 1833): both of these animals were also part of the triumvirate upon which the Dinosauria itself was founded. The UK record covers several time intervals (notably the Early and Middle Jurassic and Early Cretaceous) in which ornithischian remains, or dinosaur localities, are rare globally, and thus contribute much needed data to overviews of dinosaur evolution in particular and of Mesozoic terrestrial palaeoecology and palaeobiogeography in general. Also, although some of the material is fragmentary, British ornithischians significantly extend the temporal and geographical ranges of many dinosaur groups. Finally, many UK taxa occupy central positions in systematic and taxonomic studies of the different ornithischian sub-clades. Consequently, although the British record is in some ways less spectacular than those of other regions, and is sometimes unjustly overlooked, it is still of major significance to those interested in dinosaur evolutionary history and palaeobiology.

Iguanodon – a focus for palaeobiological research

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Discoveries attributable to *Iguanodon* are among the earliest records of the dinosaurian fossil fauna of the Isle of Wight and involve such luminaries as Gideon Mantell and William Buckland. However, the value of the Isle of Wight in this respect was not fully appreciated until the late 19th and early 20th centuries through the work of J.W. Hulke and R.W. Hooley. In 1870 John Hulke discovered the partial skeleton of a very large and robust species of *Iguanodon* just West of the foot of Brook Chine. He named it *Iguanodon seelyi* in 1882, just a year after P.J. van Beneden had established the robust species *I. bernissartensis* on the basis of several remarkably well-preserved skeletons from Bernissart (Belgium). In the 2nd decade of the 20th century Reginald Hooley discovered an articulated and well-preserved *Iguanodon* skeleton in a cliff fall at Atherfield Point. The specimen was described (posthumously) in 1925 and was named *Iguanodon atherfieldensis* in honour of its place of discovery. This publication also has the honour of being the first detailed anatomy of this dinosaur to be published (in spite of the unusually long and rich history associated with this dinosaur); and it, very fittingly, marked the centenary of the publication by Gideon Mantell that first established the name *Iguanodon*. Articulated and well-preserved remains of *Iguanodon* are comparative rarities in the cliffs of the Isle of Wight, though two notable and important discoveries have been made since the mid-1980s.

During the 1980s, detailed anatomies of *Iguanodon* were published and marked the commencement of a new phase of interest in this historically and geologically ancient dinosaur. These new works promoted work on a variety of aspects of the anatomy, taxonomy, biology and evolutionary history of *Iguanodon* and closely related taxa. Detailed anatomical analysis resulted in an alteration to the general understanding of the posture and mode of life of this dinosaur. Careful examination of the skull resulted in a number of discoveries that provided insights into more detailed aspects of the biology of the once living animal. This work included the discovery of the structure of the brain, its cranial nerves, blood supply and even the structure of the inner ear. Consideration of jaw mechanics and tooth function, in these quintessentially herbivorous dinosaurs, led to the discovery of an entirely new and unexpected mode of feeding. This, in turn, had repercussions on our general appreciation of the problems encountered by 'reptiles' that are herbivorous, and also to a consideration of the impact that large numbers of herbivorous dinosaurs may have had on floral communities during the period when dinosaurs were most abundant on Earth. This type of approach also leads, quite naturally, to a consideration of the feeding mechanisms in carnivores of the time.

Dinosaurs, such as *Iguanodon*, also have an evolutionary past and future that can be partially traced through the Fossil Record. Understanding the stratigraphic and geographic distribution of *Iguanodon* has led to investigations that attempt to incorporate its evolutionary history into plate tectonic models through the patterns of distribution of this dinosaur and its close relatives during the Cretaceous Period – investigations that have led from Europe across Asia into North America.

Far from being old and exhausted, there seems to be a bit of life in the old beast yet!

Coelurosaurian theropods of Britain

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Coelurosauria is the youngest and most diverse of theropod clades and includes Tyrannosauroidea, Ornithomimosauria and Maniraptora (including Aves). While most non-avian coelurosaur taxa are Asian or North American, and most British coelurosaur fossils are scrappy and incomplete, Britain is home to several taxa of particular historical or phylogenetic significance, and to a hitherto unsuspected diversity. Compsognathids, tyrannosauroids, oviraptorosaurs, dromaeosaurids and basal birds are all present in British strata.

The Middle Jurassic taxon *Proceratosaurus bradleyi*, described by Woodward in 1910 as a megalosaur and known only from an incomplete, well-preserved skull discovered at Minchinhampton (Gloucestershire), has recently been shown to be a basal coelurosaur (Holtz, 2000; Rauhut, 2003*a*). A dorsal projection on the nasals of *P. bradleyi* has conventionally been interpreted as the base of a *Ceratosaurus*-like horn, but may instead be part of a sagittal crest like that seen in the Middle Jurassic Chinese carnosaur *Monolophosaurus*. In combining a basal position in Coelurosauria with an unusual cranial morphology, *P. bradleyi* is a significant taxon that warrants further study.

Compsognathids are represented in the British fossil record by *Aristosuchus pusillus* from the Wessex Formation of the Isle of Wight. *A. pusillus* was originally described as a crocodile, was later employed by Seeley as a member of a hypothetical group intermediate between crocodilians and birds, and was long confused with a second probable Wessex Formation coelurosaur, *Calamospondylus oweni*. Correspondence between Owen and William Fox, the discoverer of both *A. pusillus* and *C. oweni*, shows that the two were named for different specimens but the present whereabouts of the *C. oweni* holotype is unknown (Naish, 2002). A third Wessex Formation taxon, *Calamosaurus foxi*, is based on two opisthocoelous cervical vertebrae that exhibit some similarities to the cervical vertebrae of compsognathids (Naish *et al*., 2001).

Eotyrannus lengi, also from the Wessex Formation, exhibits several characteristic features of tyrannosauroids (Hutt *et al*., 2001). It lacks tyrannosaurid synapomorphies however, and is interpreted as a basal tyrannosauroid. While other basal tyrannosauroids were small dinosaurs, *E. lengi* was large, raising the possibility that *E. lengi* may be the sister-taxon to other large-bodied tyrannosauroids. While the discovery of a Cretaceous tyrannosauroid in Britain is exciting, Rauhut (2003*b*) has suggested that *Iliosuchus incognitus* from the Middle Jurassic Taynton Limestone Formation may also be a tyrannosauroid and thus the oldest known representative of this clade.

Because *Baryonyx* and other dinosaur taxa found in Lower Cretaceous England are present in the Barremian Calizas de la Huérguina Formation of Las Hoyas, Spain, it is likely that the Las Hoyas ornithomimosaur *Pelecanimimus*, or a closely related taxon, awaits discovery in the English Wealden Supergroup. Possible British ornithomimosaur material has been reported from the Upper Jurassic Kimmeridge Clay Formation.

Thecocoelurus daviesi is based only on an incomplete cervical vertebra from the Wessex Formation. It exhibits several characters unique to Oviraptorosauria and is strikingly similar to cervical vertebrae of North American caenagnathids (Naish & Martill, 2002), though more material is needed to confirm this assignment.

Both dromaeosaurine and velociraptorine dromaeosaurids are known from Lower Cretaceous Europe. Recent work has shown that velociraptorines are present in both the Purbeck Limestone Formation (Milner, 2002) and the Wessex Formation (S. Sweetman, submitted), and several postcranial elements from the Wessex Formation, including the holotype sacrum of *Ornithodesmus cluniculus*, also appear to belong to dromaeosaurids. Dromaeosaurid- and troodontid-like teeth have been reported from Middle Jurassic localities in Britain and represent significant early records of these groups if properly identified.

Alleged Mesozoic birds were reported from Britain as early as 1824 but these records have proved erroneous. *Wyleyia valdensis*, based on a humerus from the Weald Clay and identified as avian by Harrison and Walker (1973), has been excluded from Aves by a number of authors but probably is a basal bird. *Enaliornis*, a basal hesperornithiform from the Cenomanian Cambridge Greensand, has recently been reviewed and redescribed in a series of papers by Galton and colleagues.

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Baryonyx, a fish-eating dinosaur (Theropoda: Spinosauridae) from southern England and the palaeobiology and palaeogeography of the spinosaurids.

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The spinosaurs are a group of highly derived long-snouted Cretaceous theropods that show jaw and tooth characters convergent with those of crocodiles. They occur from the Barremian to Cenomanian in Europe, North Africa and northeastern South America. The earliest known spinosaur, *Baryonyx,* comes from the Wealden of southern England and has proved to be a key taxon in the understanding of the morphology, palaeobiology and palaeogeography of the group.

Spinosaurs are characterized by long and low skulls with the nares set well back from the end of the snout. They exhibit a suite of unusual characters, especially in the elongate prenarial region of the jaws. These include a terminal 'spoon-shaped' expansion or 'rosette' in both upper and lower jaws; an 'S'-shaped upper tooth row and a high tooth count in the lower jaws. The dentition is also highly unusual compared to the typical theropod tooth form with conical often-straight tooth crowns that are very finely serrated or lack serrations entirely. Those features, together with the possession of powerfully built forelimbs ending in huge curved claws, have been interpreted, in *Baryonyx*, as adaptations to piscivory and perhaps specialist scavenging.

Recent cladistic analyses place spinosaurs as basal tetanurans within the Theropoda. *Baryonyx* from the Barremian of England and Spain, and the Aptian of Niger, shares a suite of characters in common with *Spinosaurus* from the Cenomanian of Egypt, with recently discovered skull and postcranial elements from Morocco and with *Irritator* from the Albian of Brazil. The Cenomanian material exhibits more derived character states, associated, like *Baryonyx*, with specialised feeding mechanisms suggesting piscivory and perhaps scavenging.

The palaeogeographical distribution of spinosaurs in Europe, North Africa and South America suggests that they may have originated in Laurasia but are predominantly Gondwanan in distribution. Fragmentary spinosaur remains are recorded right across North Africa from Morocco to Egypt, and as far south as Cameroon and Kenya. All of the spinosaur occurrences are associated with flood plain, lake or near shore marine sediments together with abundant fish fossils. They may represent a clade of specialised large piscivores that characterised river, lake and coastal margin habitats.

New dinosaur sites in Catalonia and Valencia (J/K Boundary and Upper Cretaceous) and a short overview of Mesozoic sites of Spain

Àngel Galobart, with Rodrigo Gaete, Andrés Santos-Cubedo, Maite Suñer and **Bernat Vila**

Although the study of dinosaurs is a relatively recent discipline in Spain, some spectacular recent discoveries, and the widespread area of Mesozoic outcrops, has resulted in the Iberian Peninsula becoming one of the most important places for dinosaur palaeontology in Europe. Here we describe some of the more recent discoveries in Catalonia and Valencia, and outline the possibilities for finding new material and new sites. Classic dinosaur sites in Spain are known from the J/K boundary, from the Lower Cretaceous and from the final stages of the Cretaceous (Campanian and Maastrichtian).

The most important sites with ichnites come from the uppermost Jurassic of the Tereñes and Latres formations (Asturias), the Lower Cretaceous of La Rioja and Sierra de Cameros, and from the Upper Cretaceous of Fumanya (Barcelona).

The best known fossil sites with skeletal remains come from the J/K boundary of Galve (Teruel) and Los Serranos (València). In the Lower Cretaceous there are two Konservat-Lagersätte: Las Hoyas (Cuenca) and Montsec quarry (Lleida), and other important sites as at Peñarroya de Tastavins (Teruel), Els Ports (Castelló), Cuenca and Burgos. The Upper Cretaceous is well represented in Laño (Alava), Carlet (València), Arén (Huesca) and Tremp/Isona (Lleida).

Some of these sites were excavated during the 1980s and early 90s (Los Serranos, Els Ports, Tremp/Isona) with many new sites and specimens being discovered. Two years ago, a new research team from Palaeontological Institute "M. Crusafont", Geological Dept. of Valencia University and Stratigraphic Dept. of Universitat Autònoma de Barcelona, joined together with small museums (Isona Museum, Coal-Mines Museum of Cercs) and local associations (Grup Guix) close to the sites, to begin a new project to find, dig, prepare and study dinosaur and other Mesozoic reptiles from these sites.

Presently this team works in three different areas. In chronological order, the oldest corresponds to the J/K Boundary from Los Serranos (València) with at least three sites with partially articulated sauropod remains, and the presence of stegosaurs and theropods. Also, two well preserved sites with ichnites allowed us to identify the presence of two different ornithopods and a theropod. All the material is now under preparation in Alpuente, a little village close to the sites.

In the Lower Cretaceous of Els Ports (Castelló), the most classical site corresponds to that at Morella, but with the beginning of a new excavation in the "Ana" site (close to the locality of Cinctorres), one of us (S-C., A.) prospected around the Lower Cretaceous outcrops and found 25 new sites with evidence of dinosaur bones. On the other hand, digging campaigns in the "Ana" site provided new material of *Iguanodon*, theropods and sauropods.

At the Upper Cretaceous sites (Campanian and Maastrichtian) the main work corresponds to Catalonian Pre-Pyrenees area. We work at three different groups of sites. One of them, Fumanya, has a great vertical surface with 3,500 ichnites and about 60 tracks, and also some places with dinosaur eggs and nest. The second one, Coll de Nargó, is a classic dinosaur nesting site, with a great number of new prints. The third site corresponds to the "classical" "Tremp Basin" that historically yielded dinosaur bones (*Pararhabdodon isonenis*), nesting sites (Basturs, suterranya) and, although less important, some sites with ichnites. Our work in this area began with detailed prospecting work that produced 60 new sites with evidence of bone; ten of them are potentially important sites. The first excavations in Basturs Poble, Serrat del Corb and other sites yielded large numbers of complete bones, mainly from hadrosaurs.

The joint study in the Pre-Pyrenees area will hopefully provide a more detailed picture of Iberian dinosaur faunas, as documented from bones, eggs and tracks.

England at the Crossroads: Early Cretaceous Dinosaurs from Utah indicates the Last Mesozoic Pan-Laurasian Fauna predates Alaska

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The Neocomian was an interval of tectonic quiescence and erosion over most of North America leading to an erosional surface representing the 25 million years at the base of the Cretaceous. During the Barremian (~125 mya), local salt tectonics in eastern Utah led to the local deposition of the basal Yellow Cat Member of the Cedar Mountain Formation in the area around Arches National Park, and is dated using charophytes and dinosaurs (Kirkland *et al*., 1997, 1999). The dinosaurs include abundant polacanthine ankylosaurids, *Gastonia burgei*, the large ornithopods *Iguanodon ottingeri*, a sail-backed iguanodontid (= *I. ottingeri* ?), brachiosaurid *Cedarosaurus* (Tidwell *et al*,. 1999) and undescribed titanosaurid sauropods, a small coelurosaurian theropod, *Nedcolbertia justinhofmanni*, and the giant dromaeosaurid, *Utahraptor ostrommaysorum* (Kirkland, 1993, this volume; Kirkland *et al*. 1997; Kirkland, 1998a; Britt and Stadtman, 1997). The polacanthine ankylosaurs, iguanodontids, some theropods, and titanosaurid sauropods indicate close temporal and geographic ties to the Barremian of Europe (Blows, 1993; Benton, 1995; Kirkland *et al*., 1997, 1999), predating the Albian origins of Alaska and the diversification of flowering plants.

The overlying Poison Strip Sandstone Member has begun to yield a dinosaur fauna that includes the titanosauromorph sauropod *Venenosaurus*, the iguanodont *Planicoxa*, and the polacanthid ankylosaur *Gastonia* (Tidwell, 2001; Dicroce and Carpenter, 2001) suggesting continued ties to Europe.

The Ruby Ranch Member of the Cedar Mountain Formation across eastern Utah preserves an extensive dinosaur fauna that is as yet only partially studied (Kirkland *et al*., 1997, 1999). Dinosaurs include a large nodosaurid close to *Sauropelta*, the primitive iguanodontian *Tenontosaurus*, sauropods assigned to *Pleurocoelus (= Astrodon),* dromaeosaurid teeth identified as *Deinonychus*, a large carnosaurid with coarsely serrated teeth, and the giant high-spined theropod *Acrocanthosaurus* characterized by finely serrated teeth (DeCourten, 1991; Kirkland, *et al*. 1997). Dinosaur faunas of this general composition are widely distributed across North America where early neoceratopsians and oviraptosauroids are known, suggesting that these taxa entered North America from Asia through Europe, as Alaska was still not in place. Slender toothed brachiosaurids ("*Astrodon*") and *Tenontosaurus* appear to be endemic to North America, suggesting isolation of North America with the flooding of Europe. The uppermost Ruby Ranch Member on the north end of the San Rafael Swell has recently yielded the remains of several shamosaurine ankylosaurids, *Cedarpelta bilbyhallorum* representing a group of animals only known from Asia (Carpenter and Kirkland, 1998; Carpenter *et al*., 2001), a giant undescribed nodosaurid, the primitive iguanodontian *Tenontosaurus*, abundant brachiosaurid sauropods assigned to *Pleurocoelus (= Astrodon)*, dromaeosaurid teeth identified as *Deinonychus*, and the theropod *Acrocanthosaurus.*

Along the western side of the San Rafael Swell in east-central Utah, the Mussentuchit Member of the Cedar Mountain Formation spans the Albian/Cenomanian boundary based on radiometric dates and preserves a diverse terrestrial fauna known from both microvertebrate sites and skeletal remains (Cifelli *et al*. 1997b, 1999; Kirkland *et al*., 1997). This dinosaur fauna is dominated by the derived "*Probactrosaurus*" grade iguanodontian *Eolambia caroljonesa* and also includes a small ornithopod, the small nodosaurid *Anamantarx ramaljonesi*, ceratopsian teeth, pachycephalosaur teeth, tiny sauropod teeth, a dromaeosaurid, possible troodontid teeth, cf. *Richardoestesia* teeth, cf. *Paronychodon* teeth, and an early tyrannosaurid (Cifelli, *et al* 1997, 1999; Kirkland *et al*., 1997; Kirkland, 1998; Carpenter and Kirkland, 1998; Chinnery *et al*., 1998). The Mussentuchit dinosaur fauna indicates that there is a dramatic faunal shift near the Albian–Cenomanian boundary with replacement of dinosaurs typical of the Aptian–Albian by those characteristics of the Late Cretaceous (Cifelli *et al*., 1997, 1999; Kirkland *et al*, 1997, 1999). This dinosaur fauna is remarkably similar to those of the Campanian and Maastrichtian of western North America for which only the toothless theropods have not been recorded in the Mussentuchit fauna as yet. As the most likely ancestors of the tyrannosaurid, *Eolambia* and pachycephalosaur are from the Early Cretaceous of Asia, the dramatic shift to faunas typical of the North American Late Cretaceous is interpreted to result from the opening of migration corridors to and from Asia through Alaska at the end of the Early Cretaceous, when migration to eastern North America was still possible (Kirkland, 1996, Cifelli *et al*., 1997; Kirkland *et al*. 1997, 1999). However, flowering plants were coming into dominance during this same interval and may account for some of this faunal turnover.

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British Triassic dinosaurs

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The record of dinosaurs in the British Triassic is sparse, but potentially important. The geologically oldest records in the literature are based on footprints from the Lower and Middle Triassic, but a careful examination of these (King and Benton, 1996) showed that they were all misidentified. Next comes *Saltopus elginensis* from the Lossiemouth Sandstone Formation of NE Scotland (Carnian), a putative dinosaur, represented by a single skeleton, but as yet not identified confidently as either dinosaurian or non-dinosaurian.

The Norian record of dinosaurs in Britain is richer, with the remarkable basal sauropodomorph *Thecodontosaurus* from the Bristol region (Benton *et al*., 2000), and convincingly dinosaurian footprints from South Wales. Isolated dinosaur bones in the Rhaetic suggest that diversity was increasing.

Late Triassic faunas from elsewhere in Europe show that Britain lacked the large basal sauropodomorph *Plateosaurus* and a small theropod like *Halticosaurus*, although these taxa may have been responsible for the footprint faunules.

The British record contributes in a small way to a larger-scale debate over the origin of the dinosaurs. The traditional view was that the dinosaurs rose gradually to prominence, over a time interval of perhaps ten or twenty million years, and that they prevailed because of their supposed warm-bloodedness or because of their upright (erect) posture and gait (Charig, 1984).

Some years ago (Benton, 1983), I proposed a radically different idea, that the dinosaurs had radiated relatively rapidly after the previously dominant terrestrial herbivores (mammal-like reptiles, rhynchosaurs) had died out. This opportunistic model for the origin of dinosaurs does not demand any special new adaptation of dinosaurs that allowed them to compete head-on with other reptiles. The opportunistic radiation model does, however, make very different predictions about the pattern of reptilian radiations during the Triassic, and its macroevolutionary implications are strikingly different also from the long-term competition model. The proposed model was slow to gain support, but new data and many current reviews support it now (*e.g.* Fastovsky and Weishampel, 1996; Sereno, 1999; Hallam and Wignall, 1997).

At least five lines of evidence suggest that the dinosaurs radiated relatively rapidly and opportunistically, and not gradually and competitively (Benton, 1983, 1986, 1993, 1994):

(1) The pattern of the fossil record (Fig. 1b) indicates the opportunistic model.

(2) The 'superior adaptations' of dinosaurs were probably not particularly profound.

(3) There is good evidence for other extinctions at the end of the Carnian.

(4) Many critical adaptations of the three dinosaur lineages were already established *before* the dinosaurs emerged as the common large-bodied fauna (Sereno, 1999).

The previous view of a long-term competitive replacement of mammal-like reptiles and basal archosaurs by the dinosaurs is part of an outmoded and simplistic view of macroevolution

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The Palaeontological Association

47th Annual Meeting
14th–17th December 2003

University of Leicester

ABSTRACTS

Annual Meeting of The Palaeontological Association

Department of Geology, University of Leicester

14 – 17 December 2003

On the following pages you will find the abstracts, outline programme and schedule of events for the 47th Annual Meeting of The Palaeontological Association. You will see that this year, at the suggestion of members, we have introduced some shorter 10 minute slots in addition to the usual 15 minute talks. There are **no parallel sessions**. At the time of going to press more than 220 people are registered for the meeting, many from outside the UK; further evidence that our Annual Meeting is now the largest annual meeting dedicated to palaeontology in Europe (the world?).

Confirmation of registration

We are currently in the process of preparing booking confirmation letters and receipts for registration (which should have been sent out by the time you read this), but if you have not heard from us and wish to confirm your registration, a list of registered participants has been posted to the website (accessible from <**www.palass.org**>, or go direct to <**http://www.palass.org/pages/annual2003/participants2003.html**>).

If you wish to attend but have not yet registered, the booking form is at <**www.palass.org**>. There are only a few rooms remaining in the Conference accommodation. Registered participants should note that it may not be possible to refund registration and accommodation fees for bookings cancelled close to the date of the meeting.

Venue, Accommodation and Travel

Leicester is centrally located in England and is easily accessible by road or rail, with good links to international airports. Maps and details of routes to Leicester are available online at <**http://www.le.ac.uk/maps/maps.html**>. All registered participants will be sent a map and details of routes nearer to the date of the meeting. For overseas participants, Birmingham and East Midlands airports are within an hour of Leicester. There are direct trains from Stansted Airport (many budget flights from European countries fly into Stansted), and London (St Pancras Station; a little over one hour). For online train times, prices and booking, visit <**www.thetrainline.com**>.

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

Accommodation is in Beaumont Hall, situated in landscaped grounds in Oadby, 3.5 km from the University Campus. Buses will be provided to transport participants to and from the University Campus at the beginning and end of each day; a scheduled bus service (no. 80) runs throughout the day (online timetables and routes at <**http://www.arriva.co.uk/real/web/arriva/internet/bustimes.nsf/pgaFrameset?OpenPage&Leicester**>).

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

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

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

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

For programme, speakers and abstracts see subsequent pages.

See you in Leicester!

Mark Purnell
on behalf of the organising and scientific committees (Dick Aldridge, Roy Clements, Sarah Gabbott, John Hudson, Gary Mullins, Mark Purnell (Chair), David Siveter, Andrew Swift (field excursion co-ordinator), Jan Zalasiewicz).

Travel grants

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

Schedule of events and timetable for oral presentations

Speakers marked with an asterisk are being considered for the President's Prize (best oral presentation by a member of the Association under the age of thirty). For details of contenders for the Council Poster Prize, see the Poster Abstracts.

SUNDAY 14th December

Registration for those attending the Seminar from 12:00 in Bennett Foyer. Otherwise at Beaumont Hall from 4:00 pm onwards.

Oral presentations in Bennett Lecture Theatre 1

1:30 to 5:00 Seminar: Stem Groups – *Fossils, Origins and the Evolution of Body Plans*

Stem groups and crown groups in relation to the early radiation of the deuterostomes
R.P.S. Jefferies

Stem groups, the fossil record and molecular dates for the origins of major clades
Philip C.J. Donoghue

The search for stem groups in the Cambrian and the origin of the phyla
Graham Budd

Land plant origins: body-building from scratch
Paul Kenrick

Assembling a tetrapod body-plan: definition, slippage, and stems
Michael I. Coates

Stem groups and angiosperm origin
Else Marie Friis

The origin of birds, feathers and flight: have palaeontologists solved the problem?
David Unwin

5:00 Buses from Bennett Building to Halls and Bar

6:00 Dinner and Ice Breaker (Beaumont Hall Bar)

MONDAY 15th December

Oral presentations in Rattray Lecture Theatre, Posters in Bennett Foyer

8:45 Welcome

9:00 Arms with feet: An exceptionally preserved starfish from the Silurian Herefordshire Lagerstätte
Mark D. Sutton, Derek E.G. Briggs, David J. Siveter and Derek J. Siveter

9:15 Insights into Neoproterozoic embryology
James W. Hagadorn and Shuhai Xiao

9:30 Vertebrate trackways: indicators of terrestrial community development?
*Lauren Tucker**

9:45 What have geochemists done for us (lately)? Recent advances in geochemical investigations of ancient vertebrate tissues
*Clive N. Trueman**

10:00 Do tree-rings in fossil woods give a palaeoclimatic signal?
*Howard J. Falcon-Lang**

10:15 You've all just been made redundant!?! Understanding (and coming to terms with) automated object recognition in palaeontology
N. MacLeod, Mark O'Neill, and Stig Walsh

10:30 Break and posters

11:00 Four hundred and ninety million year record of bacteriogenic iron oxide precipitation at deep-sea hydrothermal vents
Crispin T.S. Little

11:10 Enigmatic Lower Ordovician Fe-stromatolites in the Prague Basin (Czech Republic)
Oliver Lehnert, Oldrich Fatka and Pavel Cerny

11:20 Morphometric analysis of the Ediacaran frond *Charniodiscus* from the Mistaken Point Formation, Newfoundland
Marc Laflamme and Guy M. Narbonne*

11:30 Borings in *Phanerotrema* (Gastropoda): a cautionary tale from the Silurian of Québec, Canada
Jan Ove R. Ebbestad and Leif Tapanila

11:40 The influence of non-masticatory functional complexes on lipotyphlan glenoid morphology
Stefan N. Gabriel and P. David Polly

11:50 Exceptional preservation of amphibians from the Miocene of NE Spain
Maria McNamara*, Patrick J. Orr, Luis Alcalà, Pere Anadon and Enrique Peñalver Mollà

12:00 Resistance of spiders to Cretaceous–Tertiary extinction events
David Penney, C. Philip Wheater and Paul A. Selden

12:10 First Permian spider and the diversity of late Palaeozoic mesotheles
Kirill Eskov and Paul Selden^{spkr}

12:20 New arachnids from Baltic amber: the first opilioacariform mite and the first Baltic camel spider
Jason A. Dunlop and Jörg Wunderlich

12:30 The origin of a living fossil: the earliest synziphosurines from the Silurian of the USA
R.A. Moore, D.E.G. Briggs and S.J. Braddy*

12:40 Stem groups, the fossil record and molecular dates for the origins of major clades . . . of HIV
Una R. Smith

12:50 Thylacocephalan arthropods: their Early Cambrian origin and evolutionary significance
Jean Vannier, Jun-Yuan Chen, Di-Ying Huang, Xiu-Qiang Wang, Shigetaka Yamaguchi, and Kazuyoshi Endo

1:00 Break and posters

2:00 An early Neoproterozic problematic fossil and the animal-fungal divergence
Nicolas J. Butterfield

2:15 Charophyte Algae from the Early Devonian Rhynie chert, Aberdeenshire, Scotland
Ruth Kelman, Monique Feist and Nigel H. Trewin

2:30 On the stem lineage of Arthropoda
Andreas Maas, Dieter Waloszek and Jun-Yuan Chen

2:45 Silurian sex and evolutionary stasis: An ostracod with soft parts from the Herefordshire Lagerstätte
David J. Siveter, Mark D. Sutton, Derek E.G. Briggs, and Derek J. Siveter

3:00 The affinities of sinacanthid fishes
Ivan J. Sansom, Nian-Zhong Wang and Moya M. Smith

3:15 The position of rugose corals in the Anthozoa
Alberto Corrêa de Vasconcellos

3:30 Gastropod evolution at the Palaeozoic-Mesozoic transition
Alexander Nützel

3:45 Mismatch between taxonomic and morphologic recovery from the Permo-Triassic extinction in ammonoids
Alistair J. McGowan

4:00 E.G.M., followed by break and posters

5:00 Annual Address: Palaeontology and the future of life on Earth
Mike Benton

6:00 Members Reception (sponsored by Blackwell Publishing)

7:00 Buses to Beaumont Hall and Bar

7:45 Annual Dinner, Beaumont Hall
followed by late bar (the bar area will remain open after the bar has closed)

Tuesday 16th December

Oral presentations in Bennett Lecture Theatre 1, Posters in Bennett Foyer

9:00 Oceanic anoxic events (OAEs) and plankton evolution: a case study from mid-Cretaceous Radiolaria
Taniel Danelian, Caroline Ricordel and Benjamin Musavu-Moussavou

9:15 Ostracods cross the rubicon: colonising non-marine habitats during the early Carboniferous
Mark Williams, Ian P. Wilkinson, Melanie Leng, Mike Stephenson, Maxine C. Akhurst, David J. Horne and David J. Siveter

9:30 Ordovician biodiversity trends in Girvan, SW Scotland
Sarah E. Stewart

9:45 Summer temperatures of Late Eocene to Early Oligocene freshwaters
Stephen T. Grimes, Jerry J. Hooker, Margaret E. Collinson^{spkr}*, David P. Mattey*

10:00 Who wants to eat a brachiopod?
E.M. Harper, L.S. Peck and K. Hendry

10:15 The systematic position of the Lower Cambrian brachiopod *Heliomedusa* Sun and Hou
Lars E. Holmer, Guo-Xiang Li, and Mao-Yan Zhu

10:30 Break and posters

11:00 Early Silurian armoured polychaetes?
Philip R. Wilby, Mark Williams, Antoni E. Milodowski, Maxine C. Akhurst, Jan A. Zalasiewicz and Mark A. Purnell

11:10 An exceptionally preserved biota from Upper Silurian submarine channel deposits, Welsh Borderland, UK
*David J. Gladwell**

11:20 Exceptionally preserved conodonts from the Silurian Eramosa Lagerstätte of Ontario, Canada
Mark A. Purnell, Peter H. von Bitter and Denis K. Tetreault

11:30 Taphofacies of the Burgess Shale
Jean-Bernard Caron and Kevin Gostlin*

11:40 Rediscovery of the Gutterford Burn 'Eurypterid Bed' Pentland Hills, Midlothian, Scotland
Lyall I. Anderson

11:50 Phylogenetic systematics of early (Tremadoc-Arenig) hollinoidean ostracods
Tõnu Meidla, Oive Tinn, Roger Schallreuter, and Ingelore Hinz-Schallreuter

12:00 The genealogy of the aberrant Devonian brachiopod *Tropidoleptus:* resolving morphological and ultrastructural data
David A.T. Harper, Fernando Alvarez, Arthur J. Boucot, Rémy Gourvennec, Alwyn Williams and Anthony D. Wright

12:10 Variability of setal arrangements in the early evolution of brachiopods
Uwe Balthasar

12:20 Chitinozoan biostratigraphy in the type area of the Ashgill Series, Cautley district, Cumbria, UK
Thijs Vandenbroucke, R. Barrie Rickards and Jacques Verniers

12:30 Geographic variation in growth of the Bathonian (Middle Jurassic) oyster *Praeexogyra hebridica* and its cause
Andrew L.A. Johnson, Mark N. Liquorish and Jingeng Sha

12:40 The relationship between ammonite distributions and sea-level changes in the Sarcheshmeh and Sanganeh Formations (Upper Barremian–Lower Albian) in the Kopet Dagh Basin in north east Iran
Seyed Naser Raisossadat

12:50 Arenig ostracod assemblages and biofacies in the Baltoscandian Palaeobasin
Oive Tinn and Tõnu Meidla

1:00 Break and posters

1:30 Break and posters and workshop on digital publication

2:00 The preservation of Lower Cambrian animals of the Chengjiang biota
Sarah E. Gabbott, Xian-Guang Hou, Mike J. Norry and David J. Siveter

2:15 The taphonomy of the Bear Gulch Lagerstätte
*Natalie Thomas**

2:30 A new enteropneust-like hemichordate from the Middle Cambrian Burgess Shale
*Elizabeth Boulter**

2:45 Arthropod terrestrialization: new ichnological data from the Late Silurian Clam Bank Formation, Newfoundland
Bjørn-Gustaf J. Brooks, Lance B. Morrissey and Simon J. Braddy*

3:00 Biologically-induced changes in the brachiopod *Heteralosia slocomi* during the middle Pennsylvanian
*Alberto Perez-Huerta**

3:15 Inferring evolutionary patterns from the fossil record using Bayesian inversion: an application to synthetic stratophenetic data
*Bjarte Hannisdal**

3:30 Palaeophylogeography: phylogenetic and geographic analysis at and below the species level
P. David Polly, Jason J. Head, Tamsin M. Burland, and Steven C. Le Comber

3:45 Tertiary cold seeps in the Caribbean region
F.L. Gill, C.T.S. Little and I.C. Harding*

4:00 Break and posters

4:30 The millipede fossil record, friend or foe for resolving phylogeny?
Heather M. Wilson

4:45 Sex and brainstorming in mitrates
Bertrand Lefebvre

5:00 Fossil floras of the Late Carboniferous and Early Permian of North China: implications on extinction patterns and phytogeographic realms
Jason Hilton and Christopher J. Cleal

5:15 Cambrian Brachiopoda of the Rift Valley, Jordan and Israel
Michael G. Bassett, Lars E. Holmer and Leonid E. Popov

5:30 Ediacaran microbial colonies
Dima Grazhdankin

5:45 Announcement of prize winners and close

Wednesday 17th December

Field Excursion, The Precambrian Biota of Charnwood Forest.

Leaders: Helen Boynton, John Carney and Dima Grazhdankin

Depart Beaumont Hall 9:00 am, return 5:00 pm approx.

Abstracts of oral presentations

Rediscovery of the Gutterford Burn 'Eurypterid Bed' Pentland Hills, Midlothian, Scotland

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A programme of field excavation undertaken by National Museums of Scotland staff, volunteers and other interested parties during early July 2003 had three main aims. Firstly to relocate the exact position of the 'Eurypterid Bed', a fossiliferous sediment which in the late 1880s yielded the world's most diverse assemblage of Silurian chelicerate arthropods; secondly to characterise the likely sedimentary depositional setting and preservational mechanics of this Fossil Konservat-Lagerstätte; and thirdly to investigate the wider relevance of this fossiliferous unit to the more fully known sequences lying stratigraphically higher in the inlier as detailed by the work of Clarkson *et al.* (2001).

After extensive excavation, the 'Eurypterid Bed' lithology was located *in situ* on the banks of the Gutterford Burn stream section. Detailed sedimentary logging and sampling indicated that volcaniclastic sediments played a major role in the formation of the bed; both discrete ashfall bands and ash-rich sediment were discovered in the metre-thick unit along with monograptids. Overlying the 'eurypterid bed' occur sporadic horizons yielding dendroid graptolites and numerous (at least 12) thin, discontinuous bands of decalcified marine limestone, rich in invertebrate remains. The fauna within these bands shows a degree of similarity with that identified in the overlying Deerhope Formation.

Variability of setal arrangements in the early evolution of brachiopods

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The setae of extant brachiopods are secreted in inner epithelial follicles at the outer mantle margin. Together with muscles attached to the follicle and a connection to the nervous system, this setal apparatus forms a functional unit. The similarity of modern setal apparatuses between extant groups and evidence of setal muscles in Lower Cambrian organophosphatic brachiopods indicates that the modern type setal apparatus was acquired by the basal crown group or earlier.

The presence of setae protruding the sclerites of the stem group brachiopod *Micrina*, the pseudointerarea of *Mickwitzia*? cf. *occidens* and the shell of *Mickwitzia*? *muralensis* indicates significant differences in the respective setal apparatuses and their functionality. A detailed study of the microstructure of *Mickwitzia*? *muralensis* demonstrates that its shell perforating setae were secreted in a follicle. Based on functional grounds it appears unlikely that this apparatus was acquired underneath the shell, but represents an inner epithelial follicle that became incorporated into shell secreting outer epithelium. The apparatus of the shell protruding setae of *Micrina* and *Mickwitzia*? cf. *occidens* did not include a follicle and represents a more basic design.

These results show that shell or sclerite perforating setae evolved at least twice during the early evolution of brachiopods.

Cambrian Brachiopoda of the Rift Valley, Jordan and Israel

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The middle Numayri Dolomite member of the Burj Formation, exposed extensively in the Safi area to the east of the southern Dead Sea coast, comprises mostly very shallow water, transgressive sequences of dolomites (including sabkhas) and dolomitic limestones with a number of discrete horizons containing linguloid, obolellid, acrotretoid, matutelloid, protorthoid, kutorginoid and nisusioid brachiopods. Some of the assemblages are preserved in life position, but they are mostly found in storm generated, silicified coquinas of disarticulated valves. The age is late Lower Cambrian (Toyonian).

Kutorgina, *Psiloria* and *Trematobolus* form distinct assemblages at some levels, whilst other beds contain discretely scattered valves of *Trematosia*, *Trematobolus*, *Eoobolus*, *Psiloria* and *Vandalotreta*. Associated fauna includes the problematic sclerite *Stobostromus* together with hyoliths, hexactinellid sponge spicules, and *Chancelloria*. Very small carbonate build-ups appear to be bound by calcareous algae.

Approximately co-eval beds in the Timna National Park of the southern Negev, Israel, contain a less abundant assemblage of *Chile*, *Kutorgina*, *Trematosia*, *Israelaria*, *Glyptoria* and *Leioria*, accompanied by hyoliths and helcionellid molluscs.

Biogeographically, protorthides are distinctive components of peri-Gondwanan terranes. *Glyptoria* and *Chile* are known otherwise only from Kyrgyzstan. As a whole, the faunas demonstrate a compositional structure precursory to the Palaeozoic Evolutionary Faunas, with *Leioria*, for example, being a likely ancestor of the pentameride clade.

ANNUAL ADDRESS: Palaeontology and the future of life on Earth

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

A new enteropneust-like hemichordate from the Middle Cambrian Burgess Shale

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The early fossil record of soft-bodied hemichordates is meagre (though various Cambrian fossils have been interpreted as hemichordates). This is unfortunate, as hemichordates are likely to have an important role in understanding the evolutionary relationships of the morphologically disparate deuterostomes.

A previously undescribed enteropneust hemichordate is one of the most common taxa found in the Burgess Shale of British Columbia. The specimens have the typical enteropneust tripartite body-plan of proboscis, collar and trunk. The internal collagenous skeletal rods (of the dorsal branchial region) that would have supported the gill slit apparatus are well preserved, as are several other internal features of interest. The morphology of these specimens suggests that the major characters of the enteropneust body-plan have remained in a remarkable degree of stasis since the Middle Cambrian.

The transport and subsequent preservation of the material (including the influence of decay and rotting prior to fossilization) will be considered in light of the soft-bodied nature of enteropneust hemichordates and the currently prevailing models of transport and deposition of the Burgess Shale fauna. In addition, the non-cuticular nature of modern enteropneusts poses a few, puzzling taphonomic questions for current models of Burgess Shale preservation. Here it is proposed that secreted mucus and organo-bromides may have played a part in the preservation of these soft-bodied hemichordate fossils.

Arthropod terrestrialization: new ichnological data from the Late Silurian Clam Bank Formation, Newfoundland

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Late Silurian arthropod trackways, back-filled burrows and unusual foraging traces, from the Clam Bank Formation in Newfoundland, eastern Canada, bolster evidence suggesting that arthropods were already exploiting terrestrial environments by the Late Silurian. Among these trace fossils are three *Diplichnites* trackways, which were produced by myriapods. Based on biomechanical formulae of arthropod locomotion and theoretical *bauplans* based on computational and functional analyses, probable producers (*e.g.* eoarthropleurid and kampecarid myriapods) are assigned to these trackways.

Additionally, the Clam Bank Formation has recently produced a *Beaconites* burrow, demonstrating an adaptive burrowing/aestivation strategy amongst these arthropods to cope with the strenuous terrestrial landscape. Furthermore, a distinct array of scratch-bundles, which resembles *Striatichnium* (known previously only from the Rotliengendes of Germany), extends the stratigraphic range of this rare ichnogenus, and provides convincing evidence for foraging behaviour in a myriapod or euthycarcinoid producer.

The search for stem groups in the Cambrian and the origin of the phyla

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The origin of the bilaterian animals has long been one of the most controversial topics in palaeontology and zoology. The particular problems involved include a continuing extremely poor understanding of basal bilaterian relationships in the modern fauna, a shortcoming that has hampered recognition of putative basal members of clades in the fossil record. Another problem has been a consistent failure to apply stem- and crown-group distinctions to Cambrian fossils, leading researchers to stumble into a series of predictable snares. As the subject matures, however, Cambrian fossils are increasingly being regarded as being pivotal in our understanding of the origins of major modern groups, and a surprisingly large number of (albeit controversial) examples where this is the case are now emerging. Several extremely fruitful areas of research stand out in particular. The first is that the stem-/crown-group distinction can be used to probe the timing of the origins of groups, a point of considerable controversy between palaeontologists and molecular biologists. The second is the reconstruction of functional routes of evolution of the major body plans, providing a framework and a constraint around which currently popular “evolution of development” hypotheses must be fitted. Finally, stem-group reconstruction at this level potentially allows a greater understanding of the relationships of the living “minor phyla”, providing an important point of cross-fertilization between the fossil record and the extra information available from extant taxa.

Despite the great potential of Cambrian taxa, many problems remain in their interpretation. Not least of these is recognising the subtle stem-/crown-group boundary itself, which has proved to be highly problematic in several Cambrian cases, and may be a more general problem worth a wider investigation. Even with the recognition that not all phylum-level crown groups have definitively emerged by the Middle Cambrian, this bare fact should not necessarily be interpreted as meaning that all important body-plan evolution took place after this time: the distinction involved may in some cases be a semantic one.

An early Neoproterozoic problematic fossil and the animal-fungal divergence

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As the putative sister group of metazoans, fungi are expected from the Proterozoic record, though a convincing case for pre-Ordovician fossils has yet to be made. Analysis of a large exceptionally preserved population of the acanthomorphic acritarch *Tappania*, from the ca. 850 Ma Wynniatt Formation, arctic Canada, shows it not to be the reproductive cyst of a planktic unicellular autotroph – the default assignment for acritarchs – but rather a metabolically active, multicellular, benthic, (probable) heterotroph. In particular, the ability of its cellular processes to branch and undergo self-fusion is directly comparable to the hyphal fusion of filamentous fungi; the resulting system of irregularly distributed closed loops shows marked similarity to the predatory traps of living nematophagous ascomycetes. Other features of *Tappania* appear to be unique, but do not rule out a fungal affiliation. The presence of a branching hyphal system in *Ichthyophonus*, a parasitic mesomycetozoan protist from the animal-fungal divergence, emphasizes the likelihood that *Tappania* represents a stem-group, possibly of the fungi, but alternatively of the choanozoa and/or metazoa. The fossil record of *Tappania* extends from 850 Ma to at least ca. 1450 Ma.

Taphofacies of the Burgess Shale

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Evaluation of post-mortem effects, biostratinomy and diagenesis, is crucial in assessing the quality of any fossil deposit. For the Burgess Shale, most taphonomic studies have focused on the diagenetic conditions necessary for soft tissue preservation, and biostratinomic analysis has attracted relatively little attention. In this study, the biostratinomy of the sponge *Eiffelia*, the brachiopod *Micromitra*, the hyolith *Haplophrentis*, the scleritome-bearing animal *Wiwaxia*, and the arthropods *Marrella*, *Olenoides*, *Sidneyia*, and *Waptia*, is compared in 36 individual fossil assemblages from the “Greater Phyllopod Bed.”

Fossils range in preservation from fully articulated individuals, sometimes showing soft parts, to isolated skeletal elements within individual fossil assemblages. Organisms that are fully articulated are thought to have been alive at the time of burial. Most disarticulated specimens were animals that were dead and had started to decay prior to their final burial. The presence of both a “live” and a “dead” assemblage at the same site of deposition indicates that most individuals have not been transported out of their original life habitat. Variations in the relative frequency of articulated specimens across species and assemblages demonstrate the presence of different taphofacies, and provide clues for the reconstruction of temporal and spatial dynamics of the Burgess Shale community.

Assembling a tetrapod body-plan: definition, slippage, and stems

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Stem groups precede crown groups: their definition and significance have been summarized elegantly in several articles (*e.g.* Budd 2001). Body-plans and bauplans are hypotheses of general and specialized shared conditions abstracted from crown group memberships. Thus, body-plans and last common ancestors of living groups have tended to blur one into the other, and stem groups have emerged as a unique means of investigating the evolutionary sequence (and possible significance) of body-plan assembly. However, the most basal fossil taxon matching a crown-based body-plan is likely to branch from below the crown-node. So the generally accepted definition of, in this case, Tetrapoda, will probably include the crown group plus a chunk of the stem. But fossils are incomplete, thus raising issues about assumed conditions of unknown parts. Moreover, this problem increases towards the stem base, where membership was probably less diverse, fewer characters unite taxa with the crown, fossils are rare and fragmentary, and hypotheses of stem-membership are more controversial. Theories of bauplan assembly suffer accordingly.

Stem groups should not be interpreted as ancestor-descendent sequences, and neither should their body-parts (*i.e.* character states). The pectoral fins of *Eusthenopteron* did not transform into the polydactylous forelimbs of *Acanthostega* (Coates *et al.* 2002). Conjectured homologies between these structures are based upon morphological similarity, but explanations consist of hypothesized shared developmental conditions. Therefore, anatomical markers in stem taxa (such as paired fins, digits or feathers) deliver minimum hypotheses of developmental evolution. Finally, stem groups are often used to explore the sources of classic evolutionary innovations, such as ‘the tetrapod limb’. Such innovations are often presented as causal to functional and ecological change. Here, a summary of stem group tetrapod fins and limbs will be used to consider the detailed pattern of changes, and the extent to which these support standard textbook scenarios of the fish-tetrapod transition and vertebrate terrestrialization.

BUDD, G. 2001. Climbing life’s tree. *Nature* **412**: 487.

COATES, M.I., JEFFERY, J.E. and RUTA, M. 2002. Fins to limbs: what the fossils say. *Evolution & Development* **4**, 390–401

Oceanic anoxic events (OAEs) and plankton evolution: a case study from mid-Cretaceous Radiolaria

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The impact of OAEs on the marine biosphere is of interest to palaeobiology because OAEs represent major environmental perturbations of the ocean-climate system. As a siliceous group with a long evolutionary history, Radiolaria constitute an interesting proxy to gauge the biotic response of zooplankton. Previous studies suggest that Radiolaria experienced important faunal turnovers during the mid-Cretaceous OAEs. We have focused on the members of family Archaeodictyomitridae (Early Jurassic-Palaeocene) for which we have first analysed the phylogenetic relationships of its various Cretaceous morphospecies. Our analysis was based on literature review, collection of new material with a high resolution sampling and phenetic analyses performed with the help of PAST software.

We find that some previously thought extinctions of Archaeodictyomitrid species during OAE1b (late Aptian – early Albian) are in fact pseudoextinctions. Indeed, our material from Albania suggests that a major diversification took place at the base of this OAE.

A high-resolution study across the Bonarelli level (OAE2) confirms the step-by-step pattern of numerous real extinctions (end of lineages), some of which started in the late Cenomanian, long before the C/T boundary. This might suggest that extinctions were not driven by abrupt environmental changes, but by the *ca*. 2 Ma environmental deteriorations which began with the mid-Cenomanian event.

Stem groups, the fossil record and molecular dates for the origins of major clades

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The veracity of the fossil record as a repository of the evolutionary history of life on Earth, and in terms of its ability to inform on the timing of origin of major clades, is now in question more than at any time in the past. This situation has been arrived at, in particular, from the development of so-called molecular clocks. At their simplest, molecular clocks estimate the time of origin of clades by calibrating molecular phylogenetic hypotheses to time, using palaeontological dates to correlate one or more branches to time, and using this quantitative relationship to constrain the time of origin of all the other branches. Although some molecular clock and palaeontological estimates show close approximation there are many infamous examples of disagreement and, in almost all instances, dates derived from molecular data are considerably older than those based on palaeontological data. This is attributed either to systematic biases in molecular clocks, or the vagaries of the fossil record.

Despite the fact that molecular biologists generally couch their taxonomic concepts solely within the framework of living taxa, *i.e.*, the crown-groups of clades, molecular clock estimates pertain to the time of divergence of clades from their nearest living sister-groups, *i.e.*, the origin of total groups. This can lead, and has led, to confusion, both between molecular biologists and palaeontologists, and amongst molecular biologists themselves, over precisely which taxon putatively competing analyses are aimed at. The discrepancy in time estimates can be very considerable.

Finally, the distinction between the time of origin of total- and crown-groups has been used as a possible rapprochement for the consistent pattern of disparity between molecular clock and palaeontological estimates. This is based on the idea that lineages diverge long before they acquire morphological apomorphies and, thus, lineage divergence is likely to be invisible to the palaeontological record until each of the lineages diversify (so molecular clocks estimate the origin of the total group while palaeontological estimates better reflect the origin of the crown-group). However, this fails to take account of the hierarchical nature of total- and crown-groups, wherein the time of origin of one crown-group is also the time of origin of its constituent total groups – and there is no evidence that molecular clocks and palaeontological estimates are proportionally any better at lower taxonomic rank.

New arachnids from Baltic amber: the first opilioacariform mite and the first Baltic camel spider

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Opilioacariform mites (Arachnida: Acari) are a very rare group (only 20 extant species) whose biology is poorly known. Some authors have raised them to a separate arachnid order (Opilioacariformes) and they are widely perceived as one of the most primitive clades among the mites. The first fossil opilioacariform mite is presented here, a beautifully-preserved inclusion from Tertiary Baltic amber. With this amber mite all arachnid orders now have a fossil record and the specimen can be assigned to an extant genus restricted today to Central Asia. A second well-preserved amber fossil is also described: the first camel spider (Arachnida: Solifugae) from Baltic amber. It is only the second record of this group from amber (the other is Dominican) and this small camel spider can be assigned to the extant family Daesiidae. Similar forms occur in Southern Europe today. Both these new fossils extend the geographic range of their respective groups and support the idea that the Baltic amber forest had a warm palaeoclimate. Interestingly, both taxa are also indicative of arid conditions; especially camel spiders which are almost exclusively found in dry habitats today.

Borings in *Phanerotrema* (Gastropoda): a cautionary tale from the Silurian of Québec, Canada

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Borings in shells are evident throughout the fossil record, and are commonly used as evidence of predation. Modern predatory borings are site-specific, often leaving a circular *Oichnus* boring – similar forms are known as early as the Ordovician. Here, drilled holes in *Phanerotrema* (Gastropoda) from the Silurian Jupiter Formation on Anticosti Island, Québec, are documented. Holes occur in 4 of 19 specimens (21%), with a total of 12 completed holes (diameter 0.3–3 mm). They are stout and narrowing conically with depth, and multiple borings within the same shell mostly cluster along the selenizone of the conch (67%). The angle of penetration relative to the surface is variable, but two holes cut into the sediment infilling the shell. The borings in *Phanerotrema* are interpreted as *Trypanites* dwelling cavities excavated within a sediment-filled shell. *Trypanites* is common in skeletal material and hardgrounds from Anticosti, where site-specific distributions occur, especially favouring high-profile substrates. Large shells of *Phanerotrema* likely resisted complete burial, and were exposed longer to the water column and settling larvae of bioeroders. The highly sculptured selenizone was the preferred target, as it was the highest point on the recumbent conch. The rugosity of the site also may have favoured settling and initiation of boring larvae. Viewed individually, some of the borings could convincingly be interpreted as resulting from predation, but they provide a cautionary example against hasty interpretation.

First Permian spider and the diversity of late Palaeozoic mesotheles

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The arachnid fossil record is characterized by long periods of absence punctuated by peaks of relative abundance (Fossil-Lagerstätten), or single occurrences, which dramatically affect knowledge of the evolution of the group. By far the longest interval without spider fossils within the record of Arachnida lies between late Carboniferous and late Triassic times, a gap of some 70 Ma, which includes the whole of the Permian period and extends across the Permo-Triassic extinction event. We report here on a fossil spider from beds of Permian (Cisuralian: c. 275 Ma) age from the type Permian area of the Ural Mountains, Russia, which thus narrows this significant gap in the record. The fossil shows clear evidence of belonging to Mesothelae (the spider suborder showing most plesiomorphic character states) but differs from all other mesotheles in having elongate, pseudosegmented spinnerets. These indicate that it was probably a weaver of funnel webs, a new life-mode for Mesothelae, and is evidence for a greater diversity of Mesothelae in late Palaeozoic times than today.

Do tree-rings in fossil woods give a palaeoclimatic signal?

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Tree-rings in pre-Quaternary fossil woods have long been used as important quantitative indicators of palaeoclimate. In this paper, a global analysis of the relationship between climate and tree-ring parameters is presented that appears to invalidate the use of fossil woods in this way. Three parameters, specifically, mean ring width, mean sensitivity, and percentage latewood, were analyzed from 1,000 sites worldwide using data reprocessed from the International Tree-Ring Data Bank. Results reveal that variability in modern trees related to taxonomy, ontogeny and ecology tends to obscure the palaeoclimatic signal except where sample size is very large, and sample taxonomy and ontogenetic age are constrained. As it is unlikely that such conditions can ever be met in fossil studies, the validity of using quantitative tree-ring parameters as indicators of Pre-Quaternary climates would seem questionable.

Stem groups and angiosperm origin

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Considerable progress has been made over the past few years towards a better understanding of phylogenetic relationships among angiosperms, and phylogenetic analyses based on molecular data have begun to produce consistent ingroup topology. The recognition of Amborellaceae, Nymphaeales, Illiciales, Trimeniaceae, and Austrobaileyaceae as the earliest diverging lineages at the base of the angiosperm tree has been an important step towards the formulation of a new concept of early angiosperms diversification. The new model conflicts with previous phylogenetic reconstructions, but it has received support from the fossil record as well as morphological and developmental studies, and it appears to clarify character patterns that have otherwise been difficult to explain, *e.g.* patterns of carpel closure, one of the most critical features (papers in Zimmer *et al.* 2000). There are, however, a number of major, unresolved problems that have to be solved before a robust model for angiosperm origin and early evolution will be in place. One of these problems is to establish the position of angiosperms in relation to other seed plant groups and to root the angiosperm tree precisely. Phylogenetic models based on morphological data strongly supported an anthophyte clade with angiosperms nested within the seed plants together with Gnetales and Bennettitales. Molecular analyses have indicated alternative positions, including a strongly supported model that resolves angiosperms as sister to all other seed plants and nests Gnetales within the conifers (*e.g.*, Chaw *et al.* 2000). Currently, however, molecular studies do not appear to be sufficient for the unambiguous identification of relationships among seed plants (Rydin 2002) and information from the fossil record therefore appears crucial in the reconstruction of phylogenetic patterns leading to the crown group angiosperms. So far no stem group angiosperms have been recognised. This could partly be explained by the lack of fossils with key reproductive features preserved, but difficulties are exacerbated by the lack of a solid phylogenetic framework for seed plants as a whole.

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The preservation of Early Cambrian animals of the Chengjiang biota

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The diversification of animal life in the Cambrian is one of the most significant events in the history of life and continues to source controversy. Investigation of this event utilizes the fossilized remains of mineralised and non- and lightly-mineralised Cambrian animals, study of the latter being vital in providing a more inclusive representation of Cambrian life. The Early Cambrian Chengjiang biota of Yunnan Province, China, is of prime importance in this respect, because it contains the earliest known diverse metazoan record.

Gauging preservational bias is crucial in providing a potential assessment of the completeness of this fauna and whether it represents a true depiction of early Cambrian life. We present a new model to explain the exceptional preservation and details of the decay process. Pyrite replaced mineralised, lightly-mineralised and non-mineralised tissues. The geochemistry of the sediment provides an insight into the bottom and pore water conditions which were important in preservational processes. This study provides a foundation for interpretation of Chengjiang fossils by revealing bias in the preservation processes.

The influence of non-masticatory functional complexes on lipotyphlan glenoid morphology

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The shape of the mammalian glenoid varies widely. It ranges from the tight transverse hinge of some carnivorans, through the mildly concave surface found in humans, to the longitudinal slot of hystricomorph rodents. These variations in morphology are normally explained in terms of

allowing particular styles of mastication to be performed. Nevertheless it is probable that other aspects of cranial morphology influence the form and position of the temporo-mandibular joint.

The relationship of the glenoid to the pharyngeal region and braincase in extant Lipotyphla was examined using geometric morphometrics. It was found that: 1) the shape of the glenoid varies with the anteroposterior length of the auditory region; 2) the position of the glenoid moves posteromedially as basicranial flexure decreases (as indicated by pharyngeal narrowing and the foramen magnum becoming more posteriorly directed), with this rotation seeming to conserve the length of the vector of the lateral pterygoid muscle; and 3) the position of the lateral margin of the glenoid changes with basicranial flexure and braincase width.

In order to broaden this work to encompass glenoid morphologies not present today, this analysis is being extended to fossil lipotyphlans including *Apternodus*, *Oligoryctes* and *Domnina*.

Tertiary cold seeps in the Caribbean region

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Cold seeps are unusual environments populated by low-diversity animal communities in which the dominant mode of nutrition is chemosymbiosis. The primary producers in this ecosystem are bacteria, which metabolise reduced chemical compounds in the seep fluid in order to fix carbon and produce organic molecules. This process – chemosynthesis – is closely linked to the formation of distinctive carbonate deposits, which allow cold seep sites to be recognized in the fossil record. Modern cold seep communities occur in varied geographical settings and are relatively well known in terms of ecology and animal physiology. However the biogeographic distribution of cold seep fauna, as presently known, is poorly understood. The reasons for the high degree of endemism among cold seep species; disparities between the Atlantic and Pacific seep faunas and the links between cold seep taxa on a regional to global scale are as yet undiscovered. Answers to some of these problems may lie within the fossil record of cold seeps.

This study concerns Tertiary cold seeps in the Caribbean region – an area of unique palaeobiogeographical significance since the Caribbean Sea previously provided a direct, open water connection between the Atlantic and Pacific Oceans. Cold seep deposits are described from Barbados, Trinidad and the northern coast of Venezuela. Biodiversity of the seep fauna is documented. Comparisons are made between this fauna and published data on modern Caribbean seep communities, and fossil Tertiary seep communities in Eastern Pacific, Western Pacific and Mediterranean regions. Implications for the origin and distribution of modern seep faunas are discussed.

An exceptionally preserved biota from Upper Silurian submarine channel deposits, Welsh Borderland, UK

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An exceptionally preserved biota of Upper Silurian (Ludlow Series) age is found in submarine channel fill deposits around Leintwardine in the central Welsh Borderland. The deposits are of importance as they represent a rare example of exceptional preservation in organisms of Silurian age; they also provide a unique palaeoenvironmental setting.

The channel biota comprises a range of Upper Silurian marine animals; approximately 50 species of invertebrates have been recorded. Along with typical Silurian forms such as brachiopods, graptolites and trilobites, there are also more unusual taxa such as abundant and diverse echinoderms (ophiuroid and asteroid sea stars, echinoids, crinoids and ophiocistioids), eurypterid and xiphosurid chelicerates, phyllocarids and worms. The asterozoans are one of the most interesting and diverse groups of the fauna. The ophiuroids are by far the most abundant of the echinoderms; the asteroids are rare in comparison. The degree of disarticulation varies throughout the invertebrate fauna; the echinoderms are mostly complete, whilst the majority of the arthropod material consists of disarticulated components. Asterozoan specimens are almost always preserved intact, revealing the finest morphological detail. Almost all of the fossils are preserved as 'hard-parts'; occasional soft-body preservation of palaeoscolecid worms may occur. The unusual channel fauna generally occurs in concentrated horizons through the channel fill; much of the remainder of the fill is relatively barren. The starfish fauna appears to occur exclusively within these horizons, although some of the other unusual fauna such as eurypterids and phyllocarids also occurs at other levels.

Ediacaran microbial colonies

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Discoidal impressions are the most abundant, as well as stratigraphically and geographically the most widely distributed element of the late Neoproterozoic Ediacaran fossil assemblage, however their relation to the evolutionary history of the Metazoa is obscure and controversial. They were originally assigned to fossilised jellyfish, but have subsequently been reinterpreted as holdfast structure of frondose benthic organisms. In fact, taphonomic features, organisational patterns (such as concentric rings, radial structures, central dome or crater), and growth-related morphogenesis suggest a microbial origin of the discoidal fossils *Ediacaria*, *Paliella* and *Cyclomedusa*. The coherent ring pattern in the discoidal fossils is similar to the concentric zonation seen in bacterial and fungal colonies. Pyritized preservation of *Ediacaria* reveals a fine filamental structure of the discoidal body and suggests that the concentric zonation is a manifestation of a microscopic rhythmicity in filament production. Some of the Ediacaran discoidal fossils are compared to so-called "fairy rings", the concentric ring-shaped surface structures formed in modern microbial mats as a reaction to diurnal chemical cycles. Discoidal fossils from pre-Ediacaran sequences have attracted some attention as representing possibly the oldest metazoan fossils. Their relevance to metazoan evolution, however, is questionable, and the alternative interpretation as microbial colonies seems reasonable.

Summer temperatures of Late Eocene to Early Oligocene freshwaters

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The first major glaciation of the Cenozoic (Oi-1) affected Antarctica in the Early Oligocene. Recent published work attributes ~1‰ of the 1.2‰ +$\delta^{18}O$ isotope shift in marine benthic foraminifera to increased ice volume rather than to temperature decrease. Expanding upon new techniques (Grimes *et al.* 2003 GCA, In Press) we report the first oxygen isotope derived freshwater palaeotemperatures from the Late Eocene to the Early Oligocene. Three absolute Summer season palaeotemperatures for southern England (values unaffected by changes in ice volume) were derived from multiple palaeoproxies (rodent tooth enamel combined with three different freshwater biotic carbonates) at each of six horizons. Each of these independent palaeotemperatures displays similar trends and indicates a variable warm subtropical climate throughout the Late Eocene to early Oligocene. We also calculated time-averaged Mean Annual Temperatures (MAT), which, like temperatures derived from $\delta^{18}O$ in the marine realm, are affected by changes in ice volume. At the Oi-1 glaciation our trend in MATs decouples from the trend in summer temperatures, which is consistent with a change in global ice volume. Published work on marine fish otoliths and molluscs indicates that temperature decrease in low latitudes at the Eocene–Oligocene transition selectively affected the Winter season. Combined results suggest that the climate at low and mid-northern latitudes was not strongly affected by the southern hemisphere Oi-1 glaciation. Our technique provides a new method of independently testing climate trends and of obtaining absolute palaeotemperatures for the continental realm.

Insights into Neoproterozoic embryology

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Phosphatized Neoproterozoic animal embryos, algae, and problematic fossils from the Doushantuo Formation of the Weng'an region of China were analyzed using microfocus x-ray computed tomography. X-ray attenuation variations within cells and cell packets correspond to mineralogic and density variations in these fossils, and may represent reproducible biological characteristics which can be used to assess the fossils' taxonomic affinity. Isocontouring and volume rendering of x-ray variations allows visualization of the morphology of individual cells, the three-dimensional arrangement of cells, and the nature of possible organelle-like structures. For example, cells that are not exposed on the surface of 16-celled *Parapandorina rhaphospissa* appear to be 15-sided polyhedrons characterized by flat irregular pentagonal faces. Many cells within 4-celled *P. rhaphospissa* contain paired kidney-shaped structures which do not overlap one another and which do not abut cell walls. These techniques offer insights into taphonomy as well, allowing us to distinguish inorganic structures such as fractures, pyrite tunnels, or diagenetic voids from putative organelles or borings. With further work, this data can be used to test hypotheses about the number of cells in each embryo, the geometry of individual cells, the orientation of cleavage in embryos and algae, and the nature of organelle-like structures.

Inferring evolutionary patterns from the fossil record using Bayesian inversion: an application to synthetic stratophenetic data

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This project formulates the inference of species-level evolutionary patterns from fossil data as an inverse problem: given morphological and stratigraphic data, how can we estimate the parameter values of models of evolution, ecophenotypy and preservation? A forward simulation, linking a high-resolution basin-fill model (SedFlux) to simple palaeobiological models, is used to discover the statistical relationships that, for given values of the model parameters, allow predictions of values on observable parameters (simulated data). Probabilistic (Bayesian) inverse theory offers a framework for incorporating uncertainty in both observed data and model, as well as information on their relationship obtained from the forward simulation. For high-dimensional nonlinear inverse problems where no analytical expression for the forward relation is available, the general solution requires Monte Carlo methods of sampling and optimization in the space of feasible solutions, providing measures of resolution and uncertainty of the parameter estimates. The Miocene sequences of the U.S. mid-Atlantic margin are well constrained in terms of sequence-, bio- and isotope stratigraphy, sedimentary facies, bathymetry and age, and available cores and outcrop contain abundant benthic microfossils. Sedimentological and stratigraphic information will be combined with morphometric measurements on microfossils to document stratophenetic series in two co-occurring taxa at multiple locations within the basin. As a means of demonstrating the method, an application of the Bayesian inversion procedure to synthetic data is presented.

The genealogy of the aberrant Devonian brachiopod *Tropidoleptus:* resolving morphological and ultrastructural data

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The distinctive, short-lived but widespread Devonian brachiopod *Tropidoleptus* Hall contains an anomalous assembly of morphological and ultrastructural characters. Not surprisingly *Tropidoleptus* has been variously linked to the orthides, strophomenides and terebratulides and despite much active research on the phylum, related to the revised *Treatise*, its systematic position remains in doubt. A new, multidisciplinary reinvestigation of the genus has emphasized its strophic, concavoconvex shape, a fibrous, endopunctate shell structure, cyrtomatodont dentition together with the development of a brachidium and median septum. Together these features merit superfamilial status, but association with the orthide, strophomenide and terebratulide clades is unlikely. The origin of the group is unclear although certainly located within the cyrtomatodont, endopunctate rhynchonelliformeans. Phylogenetic analysis suggests a relationship with the spire-bearing clades, where the superfamily may serve as a focus for several other aberrant groups of cyrtomatodonts.

Who wants to eat a brachiopod?

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It is often argued that rising predation pressure from the beginning of the Mesozoic had a profound effect on the course of bivalve evolution. In principle, the same arguments ought to apply to articulated brachiopods. There is, however, a marked conflict between those who claim that post-Palaeozoic brachiopods have been restricted to refugia by predation pressure and those who suggest that they are virtually immune to predation pressure. Despite the vigour of these assertions there are few records of predation on modern brachiopods. It is very difficult to establish whether this is because there really is little predation pressure, even where they occur in shallow water communities or, as suggested by Donovan and Gale (1990), because so few studies have specifically looked for evidence.

This talk will present a comparison of predation levels and patterns from surveys of living brachiopods from South Georgia and the Antarctic Peninsula, as well as of the giant Pliocene *Apletosia maxima* from the Coralline Crag. The South Georgian and Pliocene brachiopods lived in communities alongside a full range of predatory taxa whereas the fauna of the Antarctic Peninsula is well known to lack major fish and crustacean groups.

Fossil floras of the Late Carboniferous and Early Permian of North China: implications on extinction patterns and phytogeographic realms

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Late Carboniferous and Early Permian fossil floras from northern China are critically assessed in order to determine their compositions and systematic affinities of the plants encountered, providing base data for comparisons with other Late Palaeozoic floras. This highlights the significance of the Late Carboniferous (Westphalian) Benxi Formation and the Early Permian (Asselian-early Sakmarian) Taiyuan Formation, both of which contain plants previously considered distinctive and diagnostic of the Late Palaeozoic wetland plant communities of Europe and North America. Many of the plants present, and also the compositions of the floras, challenge previous concepts that considered the demise of wetland terrestrial ecosystems towards the end of the Carboniferous in North American and northern Europe to represent an extinction event. Rather, the occurrence of the same plants in northern China shows that the disappearance of these ecosystems represents geographical changes in plant distribution. Palaeoclimatic and palaeoenvironmental implications of these findings are discussed. These data also support the presence of an Ameriosinian phytogeographical realm, and show that many of the plants and floral assemblages in the lowland basins of the Late Palaeozoic of China are not as unique or geographically isolated as previously thought.

The systematic position of the Lower Cambrian brachiopod *Heliomedusa* Sun and Hou

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The systematic position of the Lower Cambrian *Heliomedusa* Sun and Hou from the Chengjiang lagerstätten (Yu´anshan Formation), Yunnan, is re-evaluated in the light of new material. *Heliomedusa* was most recently assigned provisionally to the craniopsid group of brachiopods (Subphylum Craniiformea, Class Craniata, Order Craniopsida). The new specimens demonstrate that *Heliomedusa* has a punctate shell that was perforated by tubes, some of which contain chitinous seate at the surface. The ontogeny includes a differentiated juvenile shell (about 1 mm wide), and both the juvenile and mature have a distinctive pustulose ornamentation, with pustules arranged in radiating rows. The presence of these characters casts doubt on the craniopsid affinity of *Heliomedusa* and indicates that it belongs to the Family Mickwitziidae, proposed recently as a stem group of the Brachiopoda.

Stem groups and crown groups in relation to the early radiation of the deuterostomes

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For a monophyletic group with still extant members, Hennig distinguished between the total group (Gesamtgruppe), the crown group (*Gruppe) and the stem group (Stammgruppe). The total group comprises all forms, extant or extinct, which are more closely related to the extant members of the group than to anything else still extant. The crown group comprises the latest common stem species of the extant members of the group, plus all its descendants extant or extinct. And the stem group comprises all members of the total group which are not members of the crown group. Passing through every stem group is the stem lineage, all members of which are direct ancestors of the crown group. Every fossil belongs to one and only one stem group, in a less or more crownward position.

The monophyly of the Deuterostomia has been confirmed on DNA evidence, with the probable parenthetic structure (Chordata ((Echinodermata + Hemichordata) Xenoturbella)). Among recent animals, only the echinoderms retain a skeleton with each plate a single crystal of calcite. Parsimony based on extant animals might therefore suggest that all such fossils are more closely related to extant echinoderms than to any other extant group. The anatomically complex "carpoids", however, comprising fossils with such a calcite skeleton but no radial symmetry, probably include the stem groups of the echinoderms, ambulacrarians (= hemichordates +

echinoderms), hemichordates, craniates, tunicates, acraniates and chordates, implying that the calcite skeleton has several times been lost. Among primitive deuterostomes, therefore, the distinction between stem groups and crown groups is capital.

Geographic variation in growth of the Bathonian (Middle Jurassic) oyster *Praeexogyra hebridica* and its cause

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Marine bivalves of the Bathonian in north-west Europe are smaller than earlier and later forms. To test a proposed explanation for this – reduced salinity – extensional growth-rate and shell thickness of a euryhaline oyster, *Praeexogyra hebridica* Forbes, was investigated at sites in England representative of differing salinities. Contrary to expectation, values for extensional growth-rate (determined through use of ligamental growth bands to age shells) and shell thickness are greater from a low-salinity location (Ketton, Rutland) than a site of higher salinity (Langton Herring, Dorset). These results imply the over-riding influence of another factor. Possibilities such as the density of individuals, temperature, emergence, water agitation, turbidity and frequency of attempted predation can all effectively be ruled out, leaving general food availability as the likeliest control. Higher levels of suspended organic particles are typical near sites of freshwater influx (and lower salinity), mainly due to elevated nutrient supply and phytoplankton productivity. The low *absolute* growth-rate of *P. hebridica* in Rutland shows, however, that availability of suspended food was only *relatively* great compared to Dorset. That supplies were very meagre indeed in Dorset is supported by the morphology of *P. hebridica* there, as well as aspects of the associated fauna and sediments. How primary productivity could have been so low within the context of presumed high fluvial input of nutrients is not yet clear.

Charophyte algae from the Early Devonian Rhynie chert, Aberdeenshire, Scotland

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Charophytes, a non-marine green algae, are the ancestor of higher land plants and have been around at least since the Ordovician. However, the fossil record of charophytes is relatively sparse, with typically only the calcified female gametangia, or gyrogonite, being preserved. One of the oldest known charophytes is *Palaeonitella cranii* (Kidston and Lang) Pia, found in the Early Devonian Rhynie chert, Aberdeenshire, Scotland. P. cranii has been silicified enabling the preservation of the thalli, antheridia and non-calcified gyrogonite and providing a unique opportunity to compare the structure of a Palaeozoic charophyte with that of the extant family Characeae.

Palaeonitella cranii is a relatively small charophyte with long thin stems that give rise to whorls of multicellular branchlets; the male reproductive organs (antheridia), preserved in life position, are attached to these branchlets by a short stalk. The structure of the thalli and the position of the antheridia are remarkably similar to those of species belonging to the extant Nitelleae tribe. However, the gyrogonite of *P. cranii*, which is composed of six sinistrally spiralling cells and has six coronula cells arranged in one single tier, is more reminiscent of the Chareae tribe. This suggests that *P. cranii*, although retaining some of the characteristics of the Nitelleae, is an ancestor of the Chareae, supporting existing molecular studies which indicate that the Nitelleae are basal to the Chareae within the Characeae.

Land plant origins: body-building from scratch

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The usefulness of stem groups is dependant on our ability to recognise their members and to compare them with crown groups. This works well in complex organisms with durable parts, but such comparisons are generally less informative among microscopic organisms and those that are composed predominantly of soft tissues. This is unfortunate, because certain aspects of body plan evolution – such as the development of multicellularity – involve just these things. Land plants evolved all or nearly all of their morphology during or following the transition to the land. One consequence of this is that part of the stem group is missing from the fossil record. Also, the recognition of stem group members becomes problematic the further back we go because the characteristics of the land plant total group are based on aspects of soft tissue morphology, subcellular structures, or metabolism, which are not commonly preserved in fossils. One weakness of the plant fossil record therefore is that it is uninformative with respect to the very early stages in the development of multicellular plant life, and it is likely to remain so. Despite these limitations, the land plant stem group is highly informative with respect to the assembly of other key elements of the plant body, but it only captures those durable aspects that appeared following terrestrialisation.

Morphometric analysis of the Ediacaran frond *Charniodiscus* from the Mistaken Point Formation, Newfoundland

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Charniodiscus is one of the most widespread and best-known representatives of the Ediacara biota (terminal Neoproterozoic; 575-543 Ma). This soft-bodied, leaf-shaped organism consists of an ornamented frond attached to a stem that was anchored to the seafloor by a basal attachment disc. The scarcity of complete specimens has previously hindered the evaluation of the taxonomy and biology of *Charniodiscus*. The presence of literally hundreds of complete specimens from the Avalon Zone of Newfoundland has allowed for detailed morphometric analyses and construction of growth series, which permits the recognition of features that vary with growth (*e.g.* stem length, frond width, and disc diameter) versus those that reflect taxonomic differences (*e.g.* number of primary branches, presence of a distal spine, frond shape ratios). Ratio plots and principal components analyses (PCA) distinguish two feeding strategies within the *Charniodiscus* population at Mistaken Point Newfoundland. The first strategy consisted of building a large, wide frond with a short stem, thereby maximizing food gathering from the lower tiers. The second form sacrificed frond area in order to construct a longer stem that elevated the feeding structure above the lower tiers, permitting feeding up to 50 cm above the sea floor. The competition for resources in this deep water community resulted in the sympatric speciation of *Charniodiscus* into two, morphologically distinct species unique to the Mistaken Point Formation. By feeding from different tiers, the adult forms of both species effectively reduced the competition for resources and represent two similar, yet ecologically distinct forms of stalked filter feeders.

Sex and brainstorming in mitrates

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Stylophorans (cornutes, mitrates) are bizarre-looking calcite-plated Palaeozoic fossils, whose anatomy and phyletic position (echinoderms or primitive chordates) are still warmly disputed. A pair of finger-like structures has been recently redescribed in the Upper Carboniferous mitrate *Jaekelocarpus oklahomaensis*. These structures correspond to tubular extensions of an internal calcitic layer borne by each of the two anterior-most plates (“adorals”) of the convex thecal surface. They have been presented as evidence supporting the existence of internal gill slits in *Jaekelocarpus*, and thus the interpretation of this mitrate as a stem-tunicate. However, very similar structures (*i.e.* finger-like extensions of internal calcitic layer of adorals) are known in several other mitrates (*e.g. Mitrocystella*), and frequently interpreted as evidence supporting the existence of a complex nervous system. Comparison of finger-like structures in *Jaekelocarpus* and *Mitrocystella* thus raises the question of their proposed interpretations: gill slits or nerves? Probably none of them, as suggested by careful examination of the internal anatomy of various mitrates: these ramified structures are the imprints of canals connecting paired organs to the external medium either through specialized pores, or through the anal opening. These organs are here interpreted as gonads and the finger-like structures of *Jaekelocarpus* and other mitrates as the imprints of gonoducts.

Enigmatic Lower Ordovician Fe-stromatolites in the Prague Basin (Czech Republic)

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Stromatolites represent a dominant feature of Precambrian and Cambrian warm and shallow-water environments. After the evolution of organisms that graze on these (mainly) cyanobacterial mats, stromatolites were relegated to a relatively minor role for most of the Phanerozoic and are described mainly from restricted environments. The situation in the western part of the Prague Basin near Holoubkov represents an unique record from an apparently restricted environment where stromatolites are preserved as iron-ores around volcanic centers. Polished slabs reveal a variety of different morphologies from biolaminites to stacked hemispheroids.

No macrofossils are known from these successions, which supports the idea of unfavourable life conditions. This poses the problem of no direct biostratigraphic information for determining the age of the sedimentary ore unit. A Lower Ordovician age (Tremadocian to Arenigian) is given by the regional lithostratigraphic framework. Recently published models demonstrate the possibility that the ferric iron in the Precambrian BIFs may have been generated by microbial activity. We propose a major role for microorganisms, rather than chemical precipitation, in the formation of Fe-stromatolites and Fe-laminites from Holoubkov.

Four hundred and ninety million year record of bacteriogenic iron oxide precipitation at deep-sea hydrothermal vents

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Fe-oxide deposits are commonly found at deep-sea hydrothermal vent sites at mid-ocean ridge and back-arc sea floor spreading centres, seamounts associated with these spreading centres, and intra-plate seamounts, and can cover extensive areas of the seafloor. These deposits are direct precipitates from low temperature vents and commonly contain filamentous textures. Filaments are usually between 1 and 5 µm in diameter, and 10s to 100s µm long. Some are cylindrical casts of Fe-oxyhydroxides formed around bacterial cells, and are thus unquestionably biogenic. The filaments have distinctive morphologies very like structures formed by neutrophilic Fe-oxidizing bacteria. It is becoming increasingly apparent that Fe oxidizing bacteria have a significant role in the formation of Fe oxide deposits at deep-sea hydrothermal vents. The presence of Fe-oxide filaments in Fe-oxides is thus of great potential as a biomarker for Fe-oxidizing bacteria in modern and ancient deep-sea hydrothermal vent deposits. The ancient analogues of modern deep-sea hydrothermal Fe-oxide deposits are jaspers. These are stratiform beds of hematitic chert within volcanic rock sequences, commonly associated with massive sulphide deposits. A number of jaspers ranging in age from the early Ordovician to Eocene contain abundant Fe oxide filamentous textures, which have been tentatively linked to Fe oxidizing bacteria. This presentation reviews these occurrences, presents new data on five filament-rich jaspers, and discusses the evidence for biogenicity. I will show that there is direct evidence for bacteriogenic Fe-oxide precipitation at deep-sea hydrothermal vent sites for the last 490 Ma of the Phanerozoic.

On the stem lineage of Arthropoda

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We report on a new arthropod from the Lower Cambrian Maotianshan-Shale fauna of China and discuss its bearing on the early phylogeny of Arthropoda. Its head comprises the eye segment and one limb-bearing segment. The trunk is elongated, dorsoventrally flattened and bears one pair of rod-shaped, finely annulated appendages with flap-shaped exopods per segment until its tail piece. The second body, or head, segment bears one pair of short, 15-segmented and uniramous appendages regarded as the antenn(ul)ae. The tergite of this segment is drawn out into a voluminous "head shield" extending some distance laterally and caudally, loosely covering the short and narrow first six trunk segments. Comparisons with another Maotianshan-Shale animal, *Fuxianhuia protensa* Hou, 1987, showed that the two resemble each other in several aspects, but also that several features of *Fuxianhuia* have to be re-interpreted in the light of the evidence brought up by the new form. Character composition of the new species and *Fuxianhuia* suggests that both are basal arthropods in the sense of being stem lineage derivatives of the Euarthropoda. On the other hand, they clearly share also features with Euarthropoda. This excludes other stem lineage arthropods like Onychophora, Tardigrada, Pentastomida and the Cambrian lobopodians from a taxon embracing *Fuxianhuia protensa*, the new species and the Euarthropoda.

You've all just been made redundant!?!: Understanding (and coming to terms with) automated object recognition in palaeontology

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The automated recognition of systematic objects has long been a goal of morphometric analysis. The need for such systems is manifest in many contexts, from the poor reproducibility of taxonomic identifications to the looming taxonomic impediment. A number of previous attempts have been made to design computer-vision systems capable of identifying fossil morphologies. While progress has been made, none has achieved accuracy levels comparable to those of measurement-based multivariate analysis. This latter approach is not viable as a generalized automated-identification system strategy because of the broad diversity of fossil morphologies and the limited number of common landmark points available for morphological characterization. The PalaeoDAISY system takes a scene-based approach to this problem by using data-compression algorithms to boost the signal-to-noise ratio of training sets, treating compressed files as sets of object-characterization variables, and partitioning the scene space into group-specific domains. Current PalaeoDAISY implementations work well as generalized fossil identification systems, routinely achieving over 90% accuracy for datasets consisting of crudely oriented specimens. Unoriented specimens are handled by adding examples of specimens photographed in multiple orientations to training sets. PalaeoDAISY has the capability – at least in principle – of using all the visual information available to experienced systematic palaeontologists. PalaeoDAISY makes identifications much more consistently than humans and is limited itself only by the availability of adequate training sets. The advent of systems like PalaeoDAISY will free palaeontologists from the burden of routine identifications, and, in so doing, force a practical rethinking of what it means to be a palaeontologist.

Mismatch between taxonomic and morphologic recovery from the Permo-Triassic extinction in ammonoids

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Studies of taxonomic and morphologic diversity indicate that the two need not be closely linked. Mass extinctions, and their associated recovery periods, can be viewed as natural experiments for testing the linkage. After the Permo-Triassic mass extinction ammonoid taxonomic diversity rapidly recovers to pre-extinction levels. However, taxonomic diversity is only one possible metric for measuring diversity. Morphologic diversity, measured as variance, was used to study the recovery of Triassic ammonoids after the Permo-Triassic. Morphologic diversity decreases between the Griesbachian and Dienerian, despite an approximately three-fold increase in taxonomic diversity, then rebounds to a Griesbachian level during the Smithian. The final loss of the survivors of two morphologically distinctive lineages during the Griesbachian, followed by the evolution of a number of morphologically convergent forms during the Dienerian, explains this pattern. Ammonoid cephalopods suffered another severe taxonomic diversity crisis during the Triassic-Jurassic extinction. No mismatch was detected in the Early Jurassic between taxonomic and morphologic diversity. This mismatch questions whether taxonomic metrics alone adequately characterize biotic recovery, and suggests that our understanding of extinction and recovery could be improved through use of both taxonomic and morphologic indices of biodiversity.

Exceptional preservation of amphibians from the Miocene of NE Spain

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The Libros, Ribesalbes and Rubielos de Mora lacustrine basins of NE Spain host exceptional faunas ranging from Early to early Late Miocene in age. The exceptionally preserved faunas and floras include amphibians, insects, birds, snakes and leaves, hosted within the deep-water laminated mudstone facies in each basin. SEM investigation of frogs from the Libros basin reveals that layers of lithified microorganisms and EPS (Extracellular Polymeric Substances) define the soft tissues from the thigh and thorax regions. On the basis of size, shape, habit and mineralogy the microorganisms are differentiated into at least two distinct categories. Both carbonaceous and phosphatic microorganisms are present, and are partitioned into a number of size-specific layers within the fossilised soft tissues. In addition, but to a lesser extent, soft tissues are directly replicated in aggregates of calcium phosphate crystallites. Replication of bacteria in authigenic minerals is restricted to limited phosphatisation at, and towards, the external surfaces of the specimens; unlike superficially similar early Cenozoic lacustrine faunas, *e.g.* Grube Messel, there is no evidence of extensive authigenesis of bacteria.

Phylogenetic systematics of early (Tremadoc-Arenig) hollinoidean ostracods

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The study is aimed at resolving the phylogenetic systematics and evolution pattern of early (Tremadoc-Arenig) hollinoidean (Palaeocopa) ostracods, an important component in the fossil assemblages, lacking, however, any modern representatives.

Baltoscandia, showing the greatest record of the studied taxa, seemingly served as the centre of radiation for most important families, both towards the low latitudes (to Laurentia and also to Siberia) and towards the Perigondwanan area. Another important centre of radiation was Siberia.

50 ostracod genera were analysed cladistically, using the PAUP programme. The 27 selected characters were mostly non-ornamental, being more stable in generic taxa and having higher systematic value. The characters coded valve contact features, general valve sculpture, details of sulcation and lobation, cristal sculpture, admarginal sculptures and type of dimorphism, peculiarities of adventral sculpture in heteromorphs and in tecnomorphs.

The results of the analysis prove that the Palaeocopa of Tremadoc-Arenig from Baltoscandia, Siberia and Australia form a monophyletic clade. The ancestral palaeocopes show affinity to the monophyletic Siberian Soanellide clade, but the Siberian Cherskiellids form a distinct monophyletic clade. Distinction between Tetradellidae, Ctenonotellidae and Tvaerenellidae needs further study and perhaps a revision in future.

The origin of a living fossil: the earliest synziphosurines from the Silurian of the USA

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Synziphosurines are an extinct paraphyletic group of primitive Xiphosura, a Class represented today by only four species within three genera (*e.g.* the well-known 'living fossil' *Limulus polyphemus*). New synziphosurine material from the Lower Silurian of Wisconsin and the Middle Silurian of Iowa, USA, represents at least two new taxa, significantly increasing our understanding of the morphological diversity of this poorly known group. Along with *Bembicosoma pomphicus* from the Pentland Hills of Scotland, they are also among the earliest-known representatives of this group.

The new material bears most resemblance to the family Weinberginidae (a higher taxon in some need of revision), which currently contains the monospecific genera *Weinbergina opitzi*, *Legrandella lombardii* and *Willwerathia laticeps*. The preservation of six pairs of prosomal appendages in the exceptionally preserved Wisconsin material is in contrast to the seven pairs seen in *W. opitzi*, from the Lower Devonian Hunsrück Slate. This suggests this taxon occupied a more derived position than *W. opitzi* despite its older age. A preliminary cladistic analysis of synziphosurines, including the new taxa, will be presented.

Gastropod evolution at the Palaeozoic-Mesozoic transition

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Gastropod diversity has increased relatively steadily throughout the Phanerozoic. However, the great mass extinctions produced or accelerated considerable changes in the taxonomic composition of the Gastropoda. Especially the end-Permian mass extinction triggered a fundamental turnover. Excellently preserved gastropod faunas from the Late Permian of South

China and the Olenekian Moenkopi Formation (USA) have been studied in order to recognize real extinction and survivorship and eliminate wrong signals by improving taxonomic data. The highly diverse Caenogastropoda show an almost complete turnover on the genus-level even in the Early Triassic. The first unequivocal opisthobranchs are numerous in the Early Triassic but lack in the Late Palaeozoic. However, vetigastropods and neritaemorphs behave more conservatively: similar forms are present in the Late Palaeozoic as well as in the Triassic. The subsequent recovery period (or better replacement period) is characterized by a strong increase of reported taxa which peaks in the Carnian. Most species-rich Early and Late Triassic faunas are compared according to their diversity and taxonomic composition. Rarefaction analyses show that the richest Early Triassic gastropod fauna (Moenkopi) is far less diverse than the richest Late Triassic faunas. Comparison of the most diverse faunas of different stages suggests that the published fossil record reflects the evolution of biodiversity to some degree, *i.e.* the absence of highly diverse gastropod faunas in the Early Triassic represents no preservational artefact.

Resistance of spiders to Cretaceous–Tertiary extinction events

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Throughout Earth history a small number of global catastrophic events leading to biotic crises have caused mass extinctions. Here, using a technique that combines neontological and palaeontological data in the form of a phylogenetic tree and also using independent numerical data derived from relative abundance of amber spider inclusions, we consider the effects of the Cenomanian – Turonian and Cretaceous – Tertiary mass extinctions on the terrestrial spider fauna. We provide the first evidence that spiders suffered no decline at the family level during these mass extinction events. On the contrary, a weighted regression analysis shows that they increased in relative numbers through the Cretaceous and beyond the K/T extinction event. This trend for spiders is similar to that observed for insects. However, the increase in insect palaeodiversity over time masks underlying extinction and origination events. This is not true for spiders. Extinction resistance in spiders may be facilitated by their generalist predatory strategy.

Biologically-induced changes in the brachiopod *Heteralosia slocomi* during the middle Pennsylvanian

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Brachiopod faunas may represent an important source of information about the response of the biosphere to palaeogeographic and climatic change during the Carboniferous Period. However, little is known about how those changes modified brachiopod assemblages. To address this question, studies on Pennsylvanian brachiopods from the eastern Great Basin, Nevada (USA), have been conducted. These brachiopods were selected because of their stratigraphic context within cyclic depositional sequences, the origin of which may be related to eustatic sea-level change linked to fluctuations in ice volume on Gondwana.

Rapid fluctuations in sea-level changed the structure of benthic communities, affecting the populations of brachiopod faunas. A chaetetid-like colonial coral is found in association with the brachiopod species *Heteralosia slocomi*, but only in the shallowest facies of the sedimentary cycles. The size of the populations of this brachiopod species increases when this coral is present, as does the morphological variation shown during the ontogeny of the brachiopod. The presence of this coral seems to be beneficial for the brachiopod. A symbiotic relationship is suggested in which the brachiopod would provide nutrients and the coral, shelter against predation. Analyses of these data suggest that rapid sea-level changes linked to climatic change alter the ecology of benthic organisms. These studies, therefore, may provide a better understanding of the effects of climatic change in the development of benthic communities.

Palaeophylogeography: phylogenetic and geographic analysis at and below the species level

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Phylogeography, the study of intraspecific evolution using molecular markers, has revolutionized research on living species because speciation, divergence and migration leave their imprint on gene sequences. Phylogeography is possible because molecules evolve quickly, allowing reconstruction of intraspecific relationships. Except in cases where DNA has been recovered from fossils, phylogeography has bypassed palaeontology because morphological data, as traditionally analyzed, do not offer such fine resolution. We have studied quantitative morphological traits of the type typically preserved in the vertebrate fossil record to assess their suitability for phylogeographic analysis.

We find that morphology evolves at rates that differ trait to trait and group to group. A particular trait is suitable only if it evolves quickly enough for measurable divergence to have accumulated, but slowly enough not to be unduly 'saturated' by evolutionary reversals. Multivariate traits, such as geometric morphometrics, are often superior for palaeophylogeographic work because, *ceteris paribus*, the probability of exact evolutionary convergence decreases with dimensionality, although univariate traits diverge more quickly. Maximum-likelihood phylogenetic analysis is particularly suited to multivariate morphometric data. Tree support can be assessed by bootstrap in which the members of each population are resampled, population means recalculated, and reordination and tree construction iteratively performed.

Exceptionally preserved conodonts from the Silurian Eramosa Lagerstätte of Ontario, Canada

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Very few Silurian conodont taxa are known from complete skeletons, and only one preserves traces of soft tissues, so the recent discovery of abundant articulated assemblages and fused clusters of elements in the Wenlock age Eramosa Member of the Guelph Formation from the Bruce Peninsula, Ontario, Canada, is of particular significance. These strata form part of a shallow marine sequence, and nodular limestones with bituminous shales, and laminated organic-rich dolostones have yielded scores of bedding plane assemblages and fused clusters. These natural assemblages are remarkably well-preserved, the best known from the Silurian, but the fauna is limited in diversity, probably because of environmental restriction. Most assemblages are *Ozarkodina excavata* (Branson and Mehl), several represent a new species of *Ozarkodina*, and a few assemblages are assigned to the more enigmatic *Ctenognathodus*. A single assemblage of *Panderodus* has been recovered.

Apart from the breathtaking quality of the preservation, the significance of this material lies in the information it holds concerning the skeletal composition and three-dimensional architecture of species that are relatively plesiomorphic within the clade of complex conodonts. Excitingly, traces of conodont soft tissues are also preserved.

The relationship between ammonite distributions and sea-level changes in the Sarcheshmeh and Sanganeh Formations (Upper Barremian–Lower Albian) in the Kopet Dagh Basin in north east Iran

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The Lower Cretaceous sequence of the Kopet Dagh basin includes the Shurijeh, Tirgan, Sarcheshmeh and Sanganeh formations. The sequence starts with red sandstones and conglomerates of the Shurijeh Formations. The change from the thick-bedded limestones of the Tirgan Formation to the marly and shaly limestone beds of the Sarcheshmeh Formation marks a significant sea-level rise, during which Late Barremian heteromorphs such as *Martelites* and *Heteroceras* and planispiral forms such as *Turkmeniceras* invaded the basin. During the Early Aptian sea-level fluctuations the most important genus is *Deshayesites*.

When deposition of the shales and siltstones of the Sanganeh Formation commenced in the western part of the basin during Early Aptian times, smooth-shelled genera such as *Aconeceras*, *Melchiorites* and *Pseudosaynella* entered the area. These forms failed to penetrate further east, where the Sarcheshmeh Formation was still being deposited. The Late Aptian sea-level rise introduced some ribbed forms such as *Hypacanthoplites* and *Parahoplites*.

In most cases the first appearance of new taxa happens in transgressive and highstand systems tracts. The most abundant ammonite faunas also often coincide with these tracts. Although sea-level changes appeared to influence the first appearance of particular taxa, ecological and local bathymetric conditions also influenced the distribution of ammonites within the basin.

The affinities of sinacanthid fishes

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On the basis of well preserved specimens from the Lower Silurian of the Tarim Basin, Xinjiang uygur autonomous region and Shiqian, Guizhou Province, China, we describe in detail the histological structure of sinacanthid spines, the only known remains of a group of fish common in Siluro-Devonian strata from China. Sinacanthid spines are something of an enigma and have previously been assigned either to the acanthodians or to the chondrichthyans. However, the histological structure of the spine is sufficiently distinctive to be able to diagnose sinacanthids and also helps to resolve their phylogenetic position. The spine structure is comprised of an outer layer of atubular dentine and an inner layer of globular calcified cartilage, and the nature, distribution and style of growth of these tissues strongly argues in favour of a position within the total group chondrichthyes. Further evidence is required both on the general anatomy of sinacanthids and on the nature of chondrichthyan apomorphies before they can be firmly placed as part of the crown-group or as a crownward component of the stem group.

Silurian sex and evolutionary stasis: an ostracod with soft parts from the Herefordshire Lagerstätte

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An exceptionally preserved ostracod from the Silurian of Herefordshire, UK, pushes back the earliest described evidence for the soft-part anatomy of this important group of living crustaceans by nearly 200 million years. It is the first unequivocal evidence for the occurrence of Ostracoda in the Palaeozoic. The fossil has striking similarity to the extant myodocopid ostracod family Cylindroleberididae, to which it is assigned, and demonstrates remarkable evolutionary stasis over 425 Ma years. It also provides the earliest unequivocal testimony for the male sex in animals.

Stem groups, the fossil record and molecular dates for the origins of major clades … of HIV

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HIV, the AIDS virus, is a human tragedy and medical challenge of global proportions. HIV is also a phenomenal model system for research in molecular palaeontology. Most of this research is being done now by researchers with no training in nor even awareness of the field of palaeontology; there are significant challenges and opportunities here for palaeontologists who dare to enter the world of molecular systematics. Open problems include the nature and origin (in both time and space) of major crown groups, which have the HIV-specific taxonomic rank of subtype. Do HIV-1 M subtypes represent (a) separate transmissions from chimpanzee to human hosts, or (b) recombinations between distantly related strains, or (c) major epidemic outbreaks, or (d) some other phenomenon?

We support the global HIV research community by building and curating public databases (<**http://hiv-web.lanl.gov**>), providing analysis tools (online and/or downloadable), publishing annual compendia, and conducting research both independently and in collaboration with laboratory research groups. Our research is strictly computational, and the focus of my own research is on estimating the time of origin of major clades of HIV.

Ordovician biodiversity trends in Girvan, SW Scotland

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Arguably the greatest sustained rise in diversity in the Phanerozoic took place in the Ordovician. Some groups, including molluscs and the more problematic taxa, have often been neglected in the study of many shelly faunas, hence their contribution to the Great Ordovician Biodiversification Event may be far from completely understood. The richly fossiliferous Ordovician succession from Girvan, SW Scotland, provides a variety of environments, close to the Laurentian margin, in which the diversity of these taxa, and of whole faunas, can be assessed.

Recent sampling and study of museum collections show that gastropods are ubiquitous throughout most of the Llanvirn to Ashgill at Girvan. The problematic bellerophonts diversified through the Caradoc and into the following Ashgill, particularly in siliciclastic facies, with some species being selective in substrate type. Unequivocal bivalves appear in the Caradoc and are mainly small infaunal nuculoids and ctenodontids in siliciclastic facies. Following the global pattern, epibyssate forms occur in the upper Caradoc faunas, and most modes of life had appeared by the Ashgill. Of the more neglected molluscs, polyplacophorans occur throughout the succession, albeit at low diversity, and in most instances low abundance. However at one locality they are extremely abundant and occur with a diverse but highly unusual shelly fauna in which other molluscs are very rare.

Arms with feet: an exceptionally preserved starfish from the Silurian Herefordshire Lagerstätte

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Bdellacoma is an asteroid hitherto known only from the Ludlow of Leintwardine. New specimens from the Wenlock Herefordshire Lagerstätte are fully articulated and preserved in three-dimensions. Computer reconstructions have been prepared from coarse-scale serial-sawing data to reconstruct gross morphology, and from fine-scale serial-grinding data to reconstruct detailed anatomy. The latter reveal details of elongate tube feet, which are collapsed medially, but preserve flared tips that may represent suckers. They are expanded into ampullae at their bases, confirming the long-held assumption that these structures were housed in the open podial basins of Palaeozoic asteroids. Fine-scale reconstructions also reveal details of a delicate aboral plating structure on the arms, and a complex arrangement of spines. A set of short sub-cylindrical spines adorn the aboral surface, while long curvi-planar spines flank the ambulacral groove, forming a complex overlapping mesh from which the tube feet emerge. Additionally, *Bdellacoma* arms bear large articulated pedicellariae of the *Bursulella* type, previously thought to belong to an echinoid rather than an asteroid.

The taphonomy of the Bear Gulch Lagerstätte

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The Bear Gulch Beds (late Mississippian) of central Montana, USA, are well known because they contain one of the most diverse fossil fish assemblages in the world, and a broad range of excellently preserved invertebrate organisms. For the first time a detailed examination of the taphonomic history of fossils from the Bear Gulch Beds has been undertaken. Biomineralised and non-biomineralised tissues are represented. Traditional (Energy Dispersive X-Ray Analysis on a Scanning Electron Microscope) and novel (Raman Spectroscopy) analytical techniques have revealed that soft tissues are variously mineralised by either apatite or calcite. Some soft tissues remain organic in composition, whilst others are preserved as moulds. Biominerals show differential dissolution; aragonite has been lost whereas apatite survives. Secondary dolomitization has occurred throughout the beds and has affected much of the morphological integrity of fossilized soft tissue. The sediment is dominated by calcite and quartz, and geochemical analyses suggest that both minerals are of biogenic origin. Rapid burial of carcasses in a reducing sediment that was inimical to macroscavengers were important factors in the process of preservation.

Arenig ostracod assemblages and biofacies in the Baltoscandian palaeobasin

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Fairly well preserved ostracods of the Baltoscandian Middle Ordovician carbonate shelf succession provide an exceptional opportunity to explore early ostracod assemblages and biofacies in detail. 260 ostracod samples from twelve sections of the Baltoscandian area have been analysed using multivariate statistical methods.

Although the number of documented ostracod species reaches 50, the ten most abundant species form up to 95 percent of the total fauna. The generally low-diversity ostracod fauna is dominated by palaeocopes *O. bocki*, *B. palmata* and *R. mitis*. However, two eridostracan species – *C. socialis* and *I. ventroincisurata* – belong to the most abundant species of the studied fauna, the former showing also wide distribution over the whole study area and throughout the entire study interval.

Different cluster analyses reveal about 10 ostracod assemblages, of which the high-diversity *C. socialis* and *I. ventroincisurata* assemblages are spatially and stratigraphically widespread, the low-diversity *T. primaria*, *B. palmata* and *O. bocki* assemblages, on the contrary, restricted to certain stratigraphic levels or facies regions.

At least three ostracod biofacies can be distinguished in the study area, representing different depth zones of the epicontinental sea. However, the analysis also reveals the alternation of the shallow-water ostracod faunas with ostracod faunas associated with deeper water conditions, reflecting sea level fluctuations of the basin.

What have geochemists done for us (lately)? Recent advances in geochemical investigations of ancient vertebrate tissues

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Vertebrate palaeontology lags well behind scientific archaeology when it comes to the awareness, application and development of geochemical methods to extract information from ancient bones. This despite the fact that most equipment used to study ancient bone is housed in geology and/or biology departments. Such a relative ignorance of chemical applications is partly explained by the difficulty of dealing with substantially older materials. The severe alteration of bone during diagenesis (fossilisation) has meant that many techniques that could be applied to relatively recent bone remains could not be applied to ancient fossils. Recent conceptual advances in the study of bone diagenesis, however, warrant re-evaluation of geochemical techniques and their potential for vertebrate palaeontology.

In this presentation, I will outline the current state of knowledge regarding mechanisms and rates of bone diagenesis, and will briefly discuss three geochemical techniques with reference to recent case studies:

- Survival and analysis of ancient bone proteins
- Direct and relative dating of bone mineral
- Stable and heavy isotope composition of ancient bone mineral.

These techniques are still under development, but have great potential to advance many fields of vertebrate palaeontology.

Vertebrate trackways: indicators of terrestrial community development?

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Vertebrate trackways have long been known to yield palaeobiological information not yielded by body fossils, and traditionally have been used to examine aspects of trackmaker biomechanics and behaviour. However, it is feasible that vertebrate traces may also be used, in conjunction with body fossil data, as indicators of terrestrial community development, thereby allowing insights into patterns of faunal turnover, adaptive radiation, and taxon displacement. This is tested using a synthesis of Permo-Carboniferous trackway data from Europe and North America. The Late Carboniferous and Early Permian represent a key stage in the development of terrestrial tetrapod communities, as the 'temnospondyl' assemblages of the Carboniferous declined with the rising dominance of the amniotes during the Permian. Trackway data reflect this change in community structure, and support the body fossil evidence for a tetrapod extinction event during the Late Permian, as identified by Benton (1989a, b). However, trackway data indicate a different community structure than that implied by estimates of taxonomic richness from skeletal material, and enable Late Palaeozoic tetrapod faunal turnover to be investigated from a new perspective.

BENTON, M.J. 1989a. Mass extinctions among tetrapods and the quality of the fossil record. *Philosophical Transactions of the Royal Society of London, B*, **325**: 369–386.

BENTON, M.J. 1989b. Patterns of evolution and extinction in vertebrates. 218–241. In ALLEN, K.C. and BRIGGS, D.E.G. (eds). *Evolution and the Fossil Record*. Belhaven Press, London. 265 pp.

The origin of birds, feathers and flight: have palaeontologists solved the problem?

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Deconstructing and understanding major evolutionary transitions such as the origin of birds and flight and then communicating this understanding to other scientific (and non-scientific) disciplines is one of the key tasks of palaeontology. In the case of birds, palaeontologists have made many significant and spectacular contributions, not least the discovery of their nearest relatives, feathered, non-avian dinosaurs, but recent developments have also shown that a broad collaboration with neontological studies (notably embryology and biomechanics) is vital if incisive understanding is to be gained. The central achievement of palaeontology, so far, has been to demonstrate that non-avian theropod dinosaurs form a sequence of successively closer stem groups to birds, of which *Archaeopteryx* is still the most basal known taxon. Arguably as significant as the phylogenetic results has been the discovery of feathers and feather-like structures in a variety of non-avian theropods, cementing the 'theropod-bird' link, and throwing some light on the origins and original function (possibly thermoregulation, but almost certainly not flight) of these extraordinary structures. The discovery that 'vertical climbing' may have been an important step in the origin of avian flight has at least moved the debate on from the over simplistic dichotomy of 'trees down' or 'ground up', but this work stems from biomechanical studies of living taxa. Palaeontologists, by contrast, have reached no real consensus regarding the likely locomotory abilities, behaviour or ecology of key taxa such as *Archaeopteryx*, although recent developments in computer-based quantitative approaches show promise.

Chitinozoan biostratigraphy in the type area of the Ashgill Series, Cautley district, Cumbria, UK

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Fifty-nine samples, collected from the upper Onnian to the lower Silurian strata of the Westerdale, Taythes and Murthwaite Inliers within the type area of the Ashgill in the Cautley District, Northern England, were studied for chitinozoans. Interestingly, the stratigraphy in the area is being revised, as Rickards (2002) has recently shown that the Rawtheyan Stage of the type Ashgill Series belongs to the *linearis* graptolite Biozone, implying that the base of the Ashgill, in terms of graptolites, begins earlier than previously believed. Both samples taken from the graptolite slabs and collected in the field were used in this study. They yielded diverse assemblages of moderately well preserved chitinozoans, allowing us to distinguish at least six chitinozoan biozones, from bottom to top: the *Fungochitina fungiformis*, *Tanuchitina bergstroemi*, *Conochitina rugata* (three Baltoscandian biozones), *Spinachitina fossensis*, *Bursachitina* sp. 1 n. sp. (two typical Avalonian biozones) and the *Belonechitina postrobusta* Zones (one global lower Silurian biozone). Within Ingham's (1966) shelly fauna zone six (in the Rawtheyan part of the Cautley Mudstone Formation), a distinctive *Ancyrochitina merga* level can be observed, typical of the upper Rawtheyan of Northern Gondwana. Thus, a new consistent chitinozoan biozonation, easily correlated with several palaeocontinents and tied to the graptolite and shelly fauna biozonations in this stratigraphically important area, will be presented.

INGHAM, J.K. 1966. The Ordovician Rocks in the Cautley and Dent Districts of Westmoreland and Yorkshire. *Proceedings of the Yorkshire Geological Society*, **35**, 455–504.

RICKARDS, R.B. 2002. The graptolitic age of the type Ashgill Series (Ordovician) Cumbria. *Proceedings of the Yorkshire Geological Society*, **54**: 1–16.

Thylacocephalan arthropods: their Early Cambrian origin and evolutionary significance

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The Thylacocephala are bivalved arthropods with a long fossil record (Lower Silurian to Upper Cretaceous), a worldwide distribution (Europe, North America, Australia, China and South America) and a most peculiar morphology exemplified by a rostrum-bearing bivalved carapace, hypertrophied visual organs and, in some species, long raptorial appendages. Despite key-information obtained over the years from several Lagerstätten (Solnhofen, Germany; Mazon Creek, Illinois and La Voulte-sur-Rhône, France), the Thylacocephala has long remained an odd group of animals with unknown origin and uncertain affinities within the Arthropoda (*e.g.* crustaceans). The discovery of thylacocephalans in the Maotianshan Shale Lagerstätte of South China opens new evolutionary perpectives and reveals the importance of the group.

1) Thylacocephalans have Early Cambrian ancestors (*Zhenghecaris shankouensis*).
2) the myodocopids (Upper Ordovician-Recent), abundantly represented in present-day marine environments, may originate from the thylacocephalan stock and may no longer be considered as ostracods. This new evolutionary scenario is supported by morphological, ontogenetical and molecular evidence from 18S ribosomal DNA sequences that all indicate an important gap between the myodocopids and the ostracod lineages. It contradicts the classical view of Ostracoda as a monophyletic taxon and leads to a redefinition of this major group of extant crustaceans.
3) Enigmatic Cambrian globally-distributed taxa such as *Isoxys*, *Tuzoia* and other bivalved arthropods probably belong to Thylacocephala, making the group a new important component of the Early marine communities.

The position of rugose corals in the Anthozoa

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This study presents the first attempts at ordinal level revision of the Rugosa based on the results of phylogenetic analysis. It aims to: (1) test monophyly of the Rugosa; (2) assess at which hierarchical taxonomic level the characters commonly used in rugose systematics are informative, and (3) formulate a hypothesis of the position of the Rugosa among Metazoa.

To accomplish these goals a revision of two Orders of the Rugosa, Cystiphyllida and Stauriida *sensu* Hill (1981), was performed. The phylogenetic analysis used these two orders as the ingroup, and a combination of fossil corals and extant Anthozoa as the outgroup (126 characters; 90 biomineralised, 36 "soft tissue"). Two phylogenetic analyses were performed. The first analysis used Alcyonaria as the prime outgroup yielding six trees that were merged into a single tree after optimisation. The second analysis used *Tabulaconus*, a Cambrian fossil coral, and yielded six trees. These trees were combined into a single tree after optimisation, to produce the most informative tree for the problem at hand.

The analysis supports monophyly of Rugosa, but eight of the sixteen sub-orders of the Stauriida are rejected. The Rugosa is the adelphotaxon of a group formed by fossil corals and the Scleractinia with cyclic septal insertion. The major implications for the Anthozoa are: (1) the subclass Zoantharia is rejected and replaced by the subclass Hexacorallia; (2) the Alcyonaria is rejected as a subclass, becoming a family within the Hexacorallia; (3) the time of origin of the Anthozoa is accepted as Early Cambrian. A new classification for the Anthozoa is provided.

An early Silurian armoured polychaete?

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The Polychaeta are a successful and diverse marine class but their body fossil record, with the exception of jaw elements (scolecodonts), is sparse. Even chaetae, which are produced in vast numbers by most species, are extremely rare. We report abundant disarticulated associations and articulated arrays of chaetae from a widely occurring, but enigmatic, Lower Silurian organism. Its chaetae share a number of characteristics with the setae of polychaetes but are substantially more robust, and appear to differ in their arrangement.

The restriction of the chaetae to graptolitic black mudstones is curious. Whilst some modern polychaetes can withstand dysoxia or short bouts of anoxia, the absence of any associated trace fossils or shelly benthos with the fossils appears to preclude them having had a benthic ecology. Similarly, there is no evidence to suggest that they had been transported in from more shallow marine settings, and they appear to have been too heavily armoured to have formed part of the plankton.

Ostracods cross the Rubicon: colonising non-marine habitats during the early Carboniferous

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Jurassic freshwater ostracods have their origins in those Namurian and early Permian species that survived the end-Permian Extinction Event. By the Cretaceous, diverse non-marine ostracod fauna had evolved, some surviving the 65Ma Extinction Event to develop into modern taxa. But a fundamental question remains, *when did ostracods originally become non-marine?* Most Early Palaeozoic to Devonian species colonised marine-shelf habitats, although some leperditiids inhabited more marginal marine settings. But, unequivocal 'freshwater' taxa were unknown until the Namurian.

In central Scotland the Ballagan Formation (early Carboniferous, Tournaisian) occupies the transition between the Old Red Sandstone lithofacies and the more marine-influenced later Viséan succession. Deposition occurred in quasi-marine and non-marine (lacustrine, coastal floodplain and fluviatile) environments, which supported paraparchitacean, platycope and podocope ostracods. Although these groups are generally considered to be marine, all provide firm evidence of colonising non-marine habitats. The stable isotope ratios of ostracod carapaces (13C/12C and 18O/16O), macrofaunas and host sediments provide consistent non-marine signatures. Some platycopes associate with algal palynomorphs including *Botryococcus*, suggesting low salinity (freshwater?). Some paraparchitaceans and certain podocopes associate with *Modiolus* (Bivalvia), thought to signal brackish water. Other paraparchitaceans occur in sediments interpreted as alluvial fan deposits. Thus, ostracods had made their most fundamental ecological shift by the early Carboniferous, colonising a range of non-marine aquatic habitats.

The millipede fossil record, friend or foe for resolving phylogeny?

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Millipedes are one of the most diverse groups of terrestrial arthropods (60,000 species estimated) and have been important components of terrestrial ecosystems for over 400 myrs. In order to resolve millipede interordinal relationships, phylogenetic analyses were conducted: maximum-parsimony (MP) and Bayesian analyses of combined sequences from three nuclear protein-encoding genes (EF-1 , EF-2, Pol II) and MP analysis of skeletomuscular characters. Palaeozoic millipede taxa were revised and included in morphological MP analyses. In the molecular analyses, some clades received strong bootstrap support while other clades that are widely believed to be monophyletic based on strong morphological evidence were not recovered. The MP analysis of skeletomuscular characters provided greater resolution. Fossil taxa were not helpful in resolving phylogeny as millipede morphology has been remarkably conservative through time. Palaeozoic millipedes can either be assigned to an extant clade (e.g. Oniscomorpha, Colobognatha, Juliformia) or to an exinct clade (*e.g.* Arthropleuridea, Archipolypoda) possessing character combinations that are not helpful in establishing character polarity in extant taxa. Construction of a stratocladogram suggests that large amounts of cladogenesis occurred in the Ordovician and Silurian, an interval for which we have almost no myriapod body fossils. The stratocladogram also suggests that many extant orders were present in the Palaeozoic for which no representative fossils have been found. All known Palaeozoic millipedes, with the exception of the Microdecemplicida, are large, robust forms while the vast majority of extant millipedes are relatively smaller, suggesting that many of the "missing" orders comprised smaller forms with low preservation potential.

Poster presentations

Posters will be displayed in the foyer of the Bennett Building, where tea, coffee and buffet lunches will be served. Poster presenters are asked to attend their posters during the session after the E.G.M. on Monday (4:00 – 5:00 pm). Authors marked with an asterisk are being considered for the Council's Poster Prize (best poster by a member of the Association under the age of thirty).

Abstracts of poster presentations

A phylogenetic analysis of the British Jurassic irregular echinoids

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The irregular echinoids originated early in the Jurassic, and diversified to such an extent that today they account for approximately 50% of all echinoid species. Much of this diversification occurred early in the history of the group. By the late Early Jurassic to Middle Jurassic, two clades, the spatangoid-holasteroid and the clypeasteroid-cassiduloid, had been initiated. This important period during the evolutionary history of echinoids remains poorly understood. In order to resolve the order of events during this critical period, it has been necessary to re-examine, and taxonomically revise, the British Jurassic fauna (with representative species in the genera *Clypeus*, *Pygurus*, *Nucleolites*, *Galeropygus*, *Collyrites*, *Pygomalus*, *Pygorhytes*, and *Disaster*). Cladistic analysis on each of these major groups has been undertaken, and the various preferred phylogenies combined into a single tree containing all of the British fossil taxa, comprising over 30 taxa. This will provide a robust framework for analysing the order of character acquisition and the comparative rates of evolution in the two lineages.

A taxonomist's nightmare: Builth Inlier ostracods, and the Ordovician Radiation

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Pre-Llandeilo Ordovician ostracods are rare in Avalonia, and only five species in total are currently recorded from the Builth Inlier, from the Llandeilo and Caradoc. New localities in the uppermost *murchisoni* and upper *artus* biozones (Llanvirn) have yielded diverse mouldic faunas of binodicopes and lesser palaeocopes. Although several genera can be recognised, many of the specimens are morphologically intermediate. In particular, the binodicope genera *Bullaeferum*, *Laterophores* and *Klimphores* form a continuous group, with few consistent species. Some early specimens of *Bullaeferum* show a velum, and an additional posterior node, suggesting a relationship to the tetralobate palaeocopes; in this case, *Laterophores*, *Klimphores* and perhaps some other binodicopes must also be re-examined. Since very few certain binodicopes are known prior to the Llanvirn, this genus group may be relevant to their derivation from palaeocopes.

Several additional localities are being investigated, and a biostratigraphic succession of ostracod taxa in the inlier is being prepared. In outline, diversity and disparity increase rapidly during the early stages of volcanism (upper *artus* Zone), and remain high, with indistinct species boundaries until the lower *teretiusculus* Zone, when volcaniclastic sedimentation decreases. Thereafter, a few species dominate, and by the *gracilis* Zone, only *Conspicillum bipunctatum* and smooth taxa are recorded. Although the record is complicated by environmental and taphonomic variations, this is consistent with models of genetic heterogeneity encouraged by volcanic disturbance.

Heteractinids and hexactinellids: unravelling basal sponge relationships

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The relationships of the sponge classes are highly controversial. A compilation of molecular, zoological and palaeontological data suggests that demosponges and hexactinellids are sister groups, with Calcarea more primitive; it is normally assumed that mineralization was independent between Calcarea and siliceous sponges. However, a new specimen of the heteractinid calcarean *Eiffellia globosa* Walcott, and a re-examination of the type specimens, has revealed the presence of diagnostic hexactinellid spicules as a substantial component of the skeletal mesh. The arrangement of these spicules in *Eiffellia* is shown to be precisely equivalent to that of various protospongiid hexactinellids, and growth occurred through an identical pattern. Contrary to established views, on morphological grounds, the Eiffelliidae and Protospongiidae cannot be clearly separated. The only significant distinction is the presumed compositional difference, although spicules of early representatives of each group are invariably completely recrystallised. Nevertheless, features of the taphonomy of *Eiffellia* can be used to provide a speculative account of the mineralogical transition. The heteractinid Calcarea are thus suggested to be paraphyletic with respect to the Silicespongea.

Dealing with didymograptids: biostratigraphic problems in the Llanvirn (Ordovician)

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Pendent didymograptids have been used historically to subdivide the British Llanvirn into the biozones of *Didymograptus artus* and *D. murchisoni*. A plethora of similar pendent didymograptid species have been defined, on the basis of quantitative features of the rhabdosome, such as thecal spacing, stipe expansion rate and divergent angles. Quantitative studies of a population of pendent didymograptids from a new section in the *murchisoni* Biozone of the Builth Inlier, Mid Wales, have revealed a spectrum of variation encompassing many previously published species. These studies allow statistical distinction of two variable morphs; one corresponding approximately to the *artus–murchisoni* plexus, and a larger form similar to the debated *D. amplus*. Each of these includes variation exceeding that of typical specific definitions. *Didymograptus artus* and *D. murchisoni* are index fossils for their eponymous biozones, but it is becoming increasingly clear that forms similar to both species occur throughout most of the Llanvirn. The intra-population variability of at least some faunas, such as those of the present study, implies that the present use of pendent didymograptids for stratigraphic division is unreliable. Diplograptids may provide a better basis for stratigraphy; work in progress suggests that the appearance of *Diplograptus foliaceus s. l.* may be an appropriate marker for the base of the *murchisoni* Biozone.

Palaeoenvironments and taphonomy of the Upper Carboniferous Coseley Lagerstätte

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The Late Carboniferous Coseley Lagerstätte from the West Midlands, UK, contains exceptionally preserved plant and animal fossils found within siderite nodules that occur within Westphalian B mudstones of the Coal Measure Group. The interbedded sandstones, mudstones and coals represent a freshwater lacustrine environment that formed within a typical coal measure swamp forest. The biota includes a diverse assemblage of plant and animal fossils that show soft tissue preservation. The plant specimens include lycopsids, sphenopsids, ferns and pteridosperms represented by a wide selection of plant organs including stems, leaves, cones and seeds. The animal specimens are dominated by a diverse arthropod and fish assemblage that includes xiphosurans, arachnids, millipedes, winged insects, crustaceans, cartilaginous jawed fishes and bony fishes.

The soft tissues have been replicated by clay minerals, notably kaolinite, and very fine detail is preserved, such as colour banding on insect wings. This very early clay mineralisation is closely followed by sulphide and carbonate precipitation where void filling sphalerite, pyrite and galena have formed within the siderite nodules. The Coseley Lagerstätte is closely comparable with the more famous Mazon Creek Lagerstätte of Illinois, USA, and is closely comparable with the fresh to brackish water Braidwood biota of the latter, but there is no equivalent of the marine Essex fauna. Taphonomically, the Coseley Lagerstätte differs from the Mazon Creek in being preserved by a more complex range of mineral phases.

A landmark-based morphometric approach to bryozoan systematics: preliminary results from the Miocene–Recent cheilostome *Microporella*

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Landmark-based morphometric methods have previously been employed successfully to explore shape variation in a variety of unitary organisms. However, their application to modular, colonial animals has been limited and there are no published examples utilising these techniques in bryozoans. The most suitable bryozoans for this technique are cheilostomes because their taxonomy is based on skeletal characters of individual zooids visible on the colony surface that are readily landmarked. For this pilot study, we chose the cheilostome *Microporella*, a cosmopolitan Miocene-Recent genus comprising over 90 nominal species. Differences between species can be subtle, with the relative positions of the orifice, ascopore and avicularia being important. Twelve homologous landmarks were initially selected to represent these relationships as well as other major features of zooidal morphology. The aim was to establish whether landmark-based analysis could discriminate between two Recent species of *Microporella*, *M. ciliata* and *M. hyadesi*. A total of 61 zooids of *M. ciliata* and 75 of *M. hyadesi* were digitally landmarked from scanning electron micrographs. A Procrustes superimposition (GPA) was conducted, and then relative warp scores were calculated, using the tpsRelw package (version 1.33, Rohlf, 08/08/2003). Subsequent analyses omitted aberrant zooids associated with row bifurcations. Results showed a clear clustering of zooids according to species. Further analyses considering only five key landmarks yielded similarly promising results. This study indicates that these bryozoan species can be discriminated successfully using this technique.

Growth increments and REE geochemistry of *Leedsichthys* fin-ray spines and gill rakers: taphonomic and environmental implications

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Comparison of growth increments in fin-ray spines and gill rakers allows determination of relative development of these two structures within *Leedsichthys problematicus*. Geochemical data throughout transects of these two types of bone provides information on the environment of bone diagenesis throughout the decaying carcass and of element partitioning between pore water, sediment and bone.

Barium and manganese have been reported previously as being anomalously depleted in the Oxford Clay; they are found here to be enriched in bone material of *Leedsichthys* to levels exceeding 100ppm. The rare earth element (REE) signature pattern across growth increments in a fin-ray spine element is relatively constant though becomes depleted by approximately 87.5% in the innermost growth increments. The REE depletion gradient within the gill raker element is much greater than for the fin-ray element. The internal growth increments of the fin-ray element are characterised by an enrichment in MREE relative to the peripheral growth increments, a pattern that cannot be explained by passive diffusion of REE alone. These differences may be explained by perturbations in crystallinity between the two elements and throughout each element. This study provides the first geochemical taphonomical study on material of *Leedsichthys problematicus* and demonstrates differential REE uptake in separate bone elements of the same animal. Growth increments in *Leedsichthys* bone do not appear to present a record of *in vivo* REE fluctuation.

Ichthyostega: the makeover

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The Devonian tetrapod genus *Ichthyostega* has stood in popular and scientific imagination as an icon for the 'fish-tetrapod transition' for almost 70 years. Renewed study of the material has shown that not only is *Ichthyostega* different from the popular image, and that earlier presented by Jarvik, but that it also possesses some extreme and bizarre specialisations that are unexpected in so early a tetrapod. We have described a uniquely modified ear region unlike that of any other known fish or tetrapod, that was apparently aquatically adapted. This is combined with the first report of gill bars in *Ichthyostega*. We have discovered that the vertebral column shows the earliest evidence of regional differentiation along its length, and that some of its modifications resemble those of mammals rather than any early tetrapod. The previously described 7-digited pes with its unprecedented arrangement of digits is incompatible with a walking gait, but resembles a paddle. The digits of the manus are still unknown, but study of new forearm specimens suggests that the forelimb likewise did not perform a conventional walking gait. We present a summary of recent work and a new reconstruction of this exceptional animal, which shows radical differences from previous accounts.

IGCP Project 469: Late Westphalian terrestrial biotas and palaeoenvironments of the Variscan Foreland and adjacent intramontane basins

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The earliest known tropical rain forests covered large areas of wetlands across Europe and North America during the Westphalian Epoch (Late Carboniferous). They acted as a significant carbon sink and were probably responsible for a significant lowering of global temperatures. Towards the end of the Westphalian, the area of forestation contracted dramatically as tectonic activity caused changes to the habitats, making them unsuitable for the dominant plant-types (arborescent lycophytes). IGCP Project 469 is examining in detail the distribution of terrestrial floras and faunas, and of key physical environmental indicators (*e.g.* coals, red-beds) across the Variscan Foreland and in the adjacent intramontane basins during this time of critical environmental change. By integrating these different data-sets, it is hoped to get a better understanding of how and why there was this catastrophic collapse in these tropical wetland habitats. The poster gives further background to this project.

Billingsella associations from Iran (Cambrian Brachiopoda)

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Shallow marine biotopes on the inner shelf of most palaeocontinental margins in the late Cambrian contain a distinctive, recurrent assemblage of rhynchonelliformean brachiopods dominated by the genus *Billingsella* (Bassett *et al.* 2002). Whilst the *Billingsella* association is part of the Cambrian Evolutionary Fauna, it has a precursory ecological structure heralding those of the Palaeozoic Evolutionary Fauna, including components that can be traced phylogenetically into Ordovician descendants.

Cambrian rocks are fairly widespread through Iran, and the *Billingsella* association is well developed in three regions: 1) Tabas, in Yazd Province, where the eponymous genus is abundant in storm-generated coquinas of the Derenjal Formation, accompanied by other brachiopods such as *Archeorthis* and *Palaeostrophia*; trilobites and echinoderms are present in thin limestone units; 2) Zardeh-kuh in Isfahan Province in shale and siltstone sequences with dominant *Billingsella* accompanied mostly by related orthoideans; 3) At Kuh-i-Nanak in the Zagros Mountains of south-west Iran, where *Billingsella* accompanied by echinoderm plates occurs in limestone blocks incorporated within salt-plugs of probable Permian age. In this region the presence of redlichiid trilobites suggests that the allochthonous blocks are also partly of late Lower Cambrian age.

BASSETT, M.G., POPOV, L.E. and HOLMER, L.E. 2002. *Brachiopods: Cambrian-Tremadoc precursors to Ordovician radiation events*. In CRAME, J.A. and OWEN, A.W. (eds) 2002. Palaeobiogeography and biodiversity change: the Ordovician and Mesozoic-Cenozoic radiations. *Special Publications Geological Society of London*, **194**, 13–23.

Observations on the acritarch microflora

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The acritarch microflora and prasinophycean algae provide a proxy record of primary phytoplankton productivity in the Palaeozoic oceans. Together with the organic-walled dinoflagellate cysts, they form a significant element of phytoplankton productivity in the Mesozoic and Cenozoic. Excellent preservation of the organic wall ultrastructure together with the diverse spectrum of overall morphology allows the recognition of groupings of acritarchs that are of particular value in palaeoenvironmental, palaeoecological and palaeoclimatic interpretation. Utilising quantitative palynological analyses, the abundant, continuous fossil record of the marine phytoplankton and terrestrial flora preserved through many marine shelf sequences provides the potential to estimate the preserved phytoplankton productivity at a high resolution, together with giving indications of long-term changes in the terrestrial productivity. Acritarch diversity patterns in marine shelf depositional environments show remarkable similarities to shelly macrofossil associations.

Protein control over calcium carbonate biomineralisation

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Biominerals are inorganic-organic composite materials in which the organic component exerts control over mineral development. The organic fraction consists of proteins, glycoproteins and carbohydrates, and varies in both concentration and composition between taxa. The proteins present within the biomineral control mineral nucleation, morphology and polymorph type. Proteins from the calcium carbonate skeletons of three marine invertebrates and an avian eggshell have been extracted and characterised in relation to molecular weight and isoelectric point by polyacrylamide gel electrophoresis (SDS-PAGE) and isoelectric focusing (IEF) respectively. The four systems provide a range of ultrastructures and two calcium carbonate polymorphs. The bivalve *Mytilus edulis* has an outer prismatic calcite layer and an inner layer of aragonite. The articulated brachiopod *Terebratulina retusa* has a primary layer composed of acicular calcite and a fibrous secondary layer, while the inarticulated brachiopod *Novocrania anomala* has an acicular calcite primary layer and a secondary layer of calcite semi-nacre. The calcite eggshell of the domestic fowl (*Gallus gallus*) differs in that it is precipitated rapidly within a distinct environment. By characterising the protein component we can identify the proteins that control polymorph type and the formation of these four calcium carbonate biomineral systems.

The Endocerida – a divided order?

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Traditionally, the nautiloid order Endocerida has been regarded as a coherent taxonomic grouping, despite the difficulties in assessing the relationships between constituent members of the group. Put simply, the presence of endoconic endosiphuncular deposits has been seen to unite this group. Endocerid remains are notorious for their poor preservation and a significant part of their taxonomy has been based upon the structure of the endosiphuncular deposits – often the only surviving part of the phragmocone. The key to resolving this problem lies in understanding the form and structure of the endosiphuncular deposits, paying particular attention to the taxonomic distribution of the conchiolin crests. This, combined with a survey of the gross morphology of these organisms, as well as a review of their stratigraphical distribution, suggests that Endocerida are a polyphyletic grouping originating from at least two separate lineages within the 'Ellesmerocerida'. The order Pilocerida is proposed for those taxa removed from a much-reduced Endocerida, and the uncertainties with regard to the relationships between the constituent taxa are more resolved.

An intriguing new plesiosaur from the Pliensbachian of England

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A plesiosaur skeleton recently collected from Blockley, Gloucestershire (*luridum* subzone, *ibex* zone, Lower Pleinsbachian, Lower Lias) represents a previously undescribed taxon. The specimen is a relatively small adult (approximately three metres in length), and is remarkably robust in overall morphology.

The material shows a mosaic of characters, and does not at first sight appear to fall neatly into an existing plesiosaur family. Twenty-three cervical vertebrae are preserved, and initial analysis shows that the neck may have had in the region of 27 vertebrae. The cervical neural spines are inclined and expanded which, along with the comparatively short neck, suggests pliosauroid affinities. Unfortunately, the length of the rostrum and lower jaw symphysis are unknown. However, in the skull the frontals are large and form the anterior border of the pineal foramen, the premaxillary facial process is short, and the teeth are long and slender. These are all plesiosauroid characters. The clavicular arch is large and forms a significant part of the pectoral girdle structure, which is the plesiomorphic state for plesiosaurs. However the humerus has a significant preaxial expansion and the epipodials are short and broad, both of which are derived characters.

Initial phylogenetic analyses using existing datasets have so far proved inconconclusive. The taxon moves between major branches of the cladogram depending on the subset of characters (*e.g.*, cranial or postcranial) analysed.

A hexapod from the Early Devonian Windyfield chert, Rhynie, Scotland

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New diagnostic morphological features discovered following further preparation and re-examination of the holotype of the myriapodous arthropod *Leverhulmia mariae* Anderson and Trewin, 2003 from the Windyfield chert are discussed. Leg appendages have been discovered with attached pretarsi comprising a pair of lateral claws, a fixed median claw and possible unguitractor plate, suggesting affinities with non-ellipuran Hexapoda. We interpret the holotype as part of an abdomen bearing at least five pairs of segmented cercal leglets. The condition of the pretarsi is strongly reminiscent of Diplura, Archaeognatha and Zygentoma (= Thysanura s. *str*.), and the presence of segmented cercal leglets on the abdomen show similarities with fossil representatives of these clades known from the Carboniferous.

Leverhulmia is the second hexapod species found in the cherts at Rhynie, the only other form being the collembolan *Rhyniella praecursor* Hirst and Maulik, 1926. Showing closer affinities with the Diplura, Archaeognatha and Zygentoma, *Leverhulmia* may well represent the earliest fossil apterous insect known to date.

School is where it all begins

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Promoting interest among school children in science is difficult, perhaps because of negative associations promoted through the media and peer group associations. The study of fossils however holds many fascinations for the young mind and can be an initial catalyst in awakening the principles of scientific discovery. Resource constraints and lack of professional assistance result in some would-be palaeontologists failing to acquire the help needed to gain access to the discipline. A case study of a student highly motivated to study palaeontology revealed a negative response from his peers and a lack of facilities for study.

We suggest ways in which the Association could assist in the further popularisation of the discipline and raise public awareness of the importance of the science.

The first occurrence of the mitrate, *Promitrocystites Barrandei* (Jaekel, 1918), in Great Britain and some questions that it raises

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The Ordovician fossil fauna of the Shelve Inlier of Shropshire has been studied for over two centuries but continues to provide new species and palaeoenvironmental evidence to this day. The richly diverse fossils of the lower Ordovician strata contain a variety of carpoids that have received very little attention. The first occurrence of the mitrate, *Promitrocystites Barrandei* (Jaekel, 1918), in Great Britain is reported from the Llanvirn (*Didymograptus bifidus* zone) where it is found in association with an undescribed solute. The specimens are preserved in a soft shale and are moldic. This gives access to some of the anatomical features first discussed by Jefferies.

Partial specimens of *P. barrandei* together with the partial remains of the same undescribed solute are known from Bohemia in the Czech Republic. They were thought to represent the disarticulated remains of a single species by Jaekel. These fossils are rare and limited in range; it seems unlikely that this is an entirely coincidental association. Discussion of the similarities in the echinoderm and trilobite faunas leads to the conclusion that material from Great Britain and the Czech Republic may need to be compared and revised.

Sclerochronology and stable isotopic records of "*Lithiotis*" facies bivalves: rapid growth rates not longevity

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The Early Jurassic "*Lithiotis*" facies bivalves radiated rapidly and dominated tropical nearshore ecosystems. Much confusion has surrounded these bivalves, which have been compared to rudists because of their large size (≤ 1 m) and unusual morphologies. However, previous research had assigned these bivalves to estuarine environments with very low growth rates, unlike rudists. This study combines growth band increment data with stable isotopes to quantify growth rates.

Stable isotope analyses were performed on *Cochlearites loppianus* and *Lithioperna scutata*. Two younger bivalves were sampled for comparison. A *Crassostrea titan* (Miocene) was selected as its large size and prominent growth bands enabled easy and consistent sampling. *Isognomon janus* (modern) was selected because of its proposed phylogenetic affiliation. Peaks and troughs in the $\delta^{18}O$ isotopes correspond to internal and external growth bands in both *Lithioperna* and *Cochlearites* specimens. These growth bands are interpreted as representing annual growth bands. Proposed growth rates were calculated for *Lithioperna* (17.6 mm/year), *Cochlearites* (11.2 mm/year). If the assumption of an annual growth rate is extended to *Lithiotis problematica* specimens, then Lithiotis had rates between 10.8–34.1 mm/year, depending on the region. The upper range is similar to published values of two late Cretaceous rudists, *Gorjanovicia* cf. *costata* and *Vaccinites ultimus*.

Conservation of process for vertebrate dentitions of their own design

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Recent palaeontological data have challenged long-standing assumptions that all vertebrate dentitions are homologous; instead it has been proposed that basal taxa of crown group gnathostomes each have a unique pattern for tooth addition. Because studies investigating the genetic regulation of odontogenesis have used principally the murine model, those that regulate odontogenesis for continuous tooth addition and replacement, in particular in fish, are unknown. Control of dentition patterning through a dental lamina is proposed as a synapomorphy for crown group gnathostomes. However, tooth initiation in the rainbow trout (*Oncorhynchus mykiss*) may not depend on a dental lamina. Our studies compare three sites of tooth production in the rainbow trout, marginal teeth, tongue teeth and pharyngeal teeth with gene expression data for these regions. A number of genes identified as homologous to the murine genetic cascade, responsible for tooth initiation, have been isolated using RT-PCR and are expressed during the patterning and replacement of trout teeth. Expression data of key genes *Shh* and *Pitx2*, identified as early markers of odontogenic initiation, relates to sites of tooth formation. This confirms the conservation of developmental controls at one stage, between trout and mouse, both in initiation of the dentition and its replacement. These genetic and morphological studies on the rainbow trout attempt to unravel questions of developmental conservation and the evolution of vertebrate dentitions.

A reconstruction of the humeral myology of the basal sauropodomorph *Saturnalia tupiniquim*

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Saturnalia tupiniquim from the Carnian of Brazil is one of the earliest dinosaurs known. As the most basal sauropodomorph discovered so far, the forelimb myology of *Saturnalia* was probably close to the plesiomorphic condition for both Sauropodomorpha, and Saurischia as a whole.

The muscles of the forelimb and pectoral girdle were reconstructed using the extant phylogenetic bracket method (Bryant and Russell, 1992; Witmer, 1995). This approach allowed the humeral attachment sites for the coracobrachialis, deltoides, pectoralis, scapulohumeralis, subscapularis, supracoracoideus, extensor and flexor muscles, to be determined. In addition the method suggests that certain other muscles (*e.g.* the brachialis) were probably present in *Saturnalia*, as they are found in all extant reptile groups. However as their attachment sites vary in extant taxa, their locations in *Saturnalia* are uncertain and they have not been reconstructed.

BRYANT, H.N. and RUSSELL, A.P. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Philosophical Transactions of the Royal Society of London*, **B 337**, 405–418.

WITMER, L.M. 1995. The Extant Phylogenetic Bracket and the importance of reconstructing soft tissues in fossils. Pp. 19–33. In THOMASON, J.J. (ed.). *Functional morphology in vertebrate palaeontology*. Cambridge, Cambridge University Press.

Neoproterozoic microbiota from the Banded Iron Formation (BIF), Eastern Desert, Egypt

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The BIF is widely exposed in the Eastern Desert of Egypt. Different workers regard the origin of these iron dreposits as being either magmatic-related or sedimentary. In the present work well-preserved microbiota were observed using maceration techniques and thin sections. Mat-forming and stalked cyanobacteria and several types of diversed colonial unicellular forms dominate this microbiota. These microfossils were mainly extracted, for the first time, from the intercalating chert mesobands. Small coccoids and thin filaments prevailed over large coccoids and thicker filaments. The taxa include *Obruchevella*, *Eosynechococcus amadeus*, *Navifusa majensis*, *Trachyhystrichosphaera vidalii*, *Cymatiosphaeroides kullingii* and others. The assemblage correlates well with those described from the Neoproterozoic BIF worldwide and, therefore, supports a Neoproterozoic age assessment for the Egyptian BIF. From a palaeoecological point of view, these microbiota were thought to have thrived during an anoxygenic to an oxygenic atmosphere under calm, below the photic zone and wave base, warm, and alkaline conditions, during the BIF deposition. The role of this microbiota in the precipitation of the BIF is discussed.

A Scottish Lower Carboniferous macrofossil Assemblage

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New material from a disused East Lothian quarry in the uppermost Lower Carboniferous (Dinantian, Brigantian, P2b) Skateraw Limestone represents a very significantly more diverse, varied and rich macrofossil fauna than that previously noted from the locality. Numerous forms of bryozoa, brachiopoda and cephalopoda (mainly orthocerid and nautilid nautiloidea, but with a few goniatitid ammonoidea too) dominate the fauna. Bivalvia and gastropoda are also present in considerable numbers, as are fewer porifera, rugosid cnidaria, annelida, amphineura, crinoidea, echinoidea, dendroid graptolithina, trilobita and problematica. Pisces, algae and plant fragments also occur. Some components of the macrofossil assemblage are illustrated and discussed in the context of the biofacies (Wilson 1989) of the Blackhall Limestone (of which the Skateraw Limestone forms the south-eastern geographical part). It is concluded that the assemblage is atypical, and cannot reasonably be assigned to any of the particular biofacies previously described. The implications of this conclusion are briefly considered.

WILSON, R.B. 1979. A study of the Dinantian marine macrofossils of central Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **80**, 91–126

Deciphering the evergreen/deciduous signal in high-latitude Cretaceous woods

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For most of the geological past high latitude regions were covered by dark dense forests. These forests would have significantly modified both the polar and global climate due to their low albedo and their effect on the land-surface heat budget and hydrological cycle. The leaf life span of conifers and their deciduous or evergreen habit would have played a significant part in this feedback. However, in the past this habit has been difficult to assess in fossil floras. A new technique that characterises the cell patterns within growth rings in conifer wood, developed by Falcon-Lang, can be used to determine whether fossil conifers were deciduous or retained their leaves for several years. This technique has now been refined to assess evergreen or deciduousness of extant conifer species and apply it to fossil wood samples. The technique has now been applied to Early Cretaceous conifer wood from Svalbard. Analysis of tree taxa and tree rings of the Svalbard samples indicates that the conifers, including for example *Piceoxylon* and *Juniperoxylon*, grew under strongly seasonal and often variable climates. The conifers had a predominantly evergreen habit, even though they lived at palaeolatitudes of ~70°N.

Brachiopod, arthropod and echinoderm faunas from the Seroe Domi Formation, Curaçao: cryptic and mobile elements of the Plio-Pleistocene ecosystem of the southern Caribbean basin

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Abundant and diverse coral and mollusc faunas characterize the Plio-Pleistocene carbonate successions of the Netherlands Antilles. The Seroe Domi Formation on Curaçao, however, contains important brachiopod, arthropod and echinoid associations in an ecosystem that marked the southern margin of the late Cenozoic Caribbean basin. The micromorphic brachiopod *Thecidellina* is abundant, disarticulated and rarely found cemented to the substrate. The valves are well preserved and show variable degrees of asymmetry, probably forming cryptic communities, cemented within cavities in the coral buildups. This biofacies contrasts with coeval deeper-water assemblages dominated by the pedunculate *Argyrotheca*, *Terebratulina* and *Tichosina* elsewhere in the basin. Common crustaceans include the coral-inhabiting barnacle *Ceratoconcha* occurring in association with their coral hosts and as isolated shells. Six species of decapods occur, the most plentiful being the frog crab *Ranilia* commonly found as complete carapaces. Next in abundance is a box crab found as chelipeds and isolated fingers. The formation has now yielded *c.* 12 echinoid taxa, making this the most diverse echinoid fauna within the Antilles. Taxa range in size from pea-like regular echinoids to *Clypeaster rosaceus* Linné up to 200 mm in length. Marginal ossicles provide the first evidence for fossil asteroids from Curaçao.

Contribution to the Middle Jurassic Rhynchonellida (Brachiopoda) from Gebel El-Maghara, Northern Sinai, Egypt

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The stratigraphic sequence of the Jurassic rocks in Gebel El-Maghara of northern Sinai has attracted the attention of many workers in the world. The measured stratigraphic sequence is part of El-Maghara massif. El-Maghara represents the first salient massif about fifty kilometers south of the Sinai Mediterranean coast and is situated between longitude 33° 10’ and 33° 40’ E and latitude 30° 35’ and 30° 50’ N incorporating an area of about 1,300 Km^2. The aim of the present work is to study the rhynchonellid Brachiopoda from the coralline limestone of Mahl Member (Bajocian age) as well as the calcareous shales (Bathonian-Callovian ?) from Gebel El-Maghara. These rocks have yielded *Burmirhynchia gutta* Buckman, *Torquirhynchia roueriana* (d’Orbigny) and new genus and species *Septirhynchella hassi* respectively. These fossils are serially sectioned at different intervals in order to study their internal characteristics. The analysis of internal structure of the latter new genus has revealed that it is characterized with a well developed septalium, septalial plates and canalifer type of crura in addition to ventral umbonal septa.

Macroevolutionary effects of competition on zooid size in cheilostome and cyclostome bryozoans

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Feeding efficiency is an important factor in determining the level of competition between two organisms sharing a similar ecological niche. Certain morphological characters of bryozoans, such as zooid size, are ideally suited as proxies for feeding efficiency as the size of the lophophore feeding apparatus is directly related to skeletal morphology. Zooid size and feeding behaviour have been shown to vary between living members of two major clades of bryozoans, the cyclostomes (Ordovician-Recent) and cheilostomes (Upper Jurassic-Recent). Today, cheilostomes are more efficient than the cyclostomes as a result of different morphologies. Here, zooid size will be recorded for the two clades from fossil specimens ranging from Jurassic to Recent.

What can machaeridian microstructure tell us?

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The fact that little is known about the microstructure of machaeridian sclerites makes it difficult to understand several aspects of this problematic taxon. Now well preserved sclerites of *Plumulites* sp. from the Lower Ordovician Kanash Shale of the Great Basin (Utah, USA) together with sclerites of especially *Turrilepas* from the Silurian of Gotland promises to increase our knowledge and to shed light on the affinity of the group.

Machaeridian sclerites possess at least two calcite layers where the thin outer layer is produced by lamellar deposition along a growing margin and a thicker inner layer consisting of calcite elements radiating from the umbo, clearly visible in the Kanash material. This inner layer seemingly grew by addition and incorporation of new elements as the sclerite widened. The distinct granulation universally seen on the inner surfaces of the sclerites is a feature of the inner layer as well, and in well preserved material the granulation appears closely aligned with the radiating elements. Marginal spines when present may be a third component enveloping the margin and producing the doublure especially evident on the inner surface of turrilepadid sclerites.

Although morphologically very different the problematic Multiplacophora is one of the few taxa with sclerites that appear to possess two calcite layers roughly similar to those found in machaeridian sclerites. The inner layer displays radiating elements and the outer layer is produced by marginal accretion.

Eocene-Oligocene mammalian faunal turnover and other biotic events in the Hampshire Basin, UK: calibration to the global timescale and the major cooling event

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As a result of a long-term field and collecting programme, a new high-resolution mammalian record is documented across the Eocene-Oligocene transition in the Hampshire Basin. This charts diversity changes and faunal turnovers from the Bembridge Limestone Formation to the Hamstead Member of the Bouldnor Formation. It also narrows down the span and position in the Solent Group succession of the Grande Coupure, a major Europe-wide faunal turnover when incoming Asian taxa replaced or displaced much of the endemic fauna. This coincides in time with the first major Cenozoic glaciation of Antarctica. To eliminate pseudo-extinctions and pseudo-originations, only species with autapomorphies are distinguished when establishing turnover. In interpreting these faunal changes, potential biases such as the Signor-Lipps Effect and range truncation are addressed. The first is tested using rarefaction analysis. The second is investigated through correlation to the Paris and Belgian Basins by means of a range of biostratigraphic indicators and the sedimentary record. A morphometric analysis of charophyte gyrogonite assemblages (*Harrisichara*) and records of higher plant fossils, combined with the mammalian evidence, demonstrate the existence of three biotic events, of which the youngest is the Grande Coupure. Through this multi-taxonomic approach, a complex pattern of environmental changes, including both climate and dispersal events, across Eocene-Oligocene transition are beginning to emerge.

Coniacian ammonites from the Eastern Desert and Sinai, Egypt: Macropalaeontology, biostratigraphy, and inter-regional correlation

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In Egypt, the Coniacian sequence is generally composed of mixed siliciclastic and carbonate successions of terrestrial to shallow marine origin, showing a remarkable variation in facies and thickness as well as condensation in certain localities. The present study aims to establish an ammonite biozonation for a refined age determination and a precise definition of the Coniacian Stage in Egypt. It is based on detailed palaeontological and stratigraphical analyses of several columnar sections exposed at the Eastern Desert and Sinai.

Based on vertical distribution of the index ammonites, the Coniacian Sequence of Egypt has been subdivided into: the *Barroisiceras onilahyense – Forresteria brancoi*, *Metatissotia fourneli*, and *Subtissotia africana* biostratigraphic zones. The established ammonite zones are calibrated with foraminiferal as well as other macrofaunal zones for the purpose of regional stratigraphy and inter-regional correlation.

The basal Coniacian is marked by FOD of the faunal assemblage of the ammonite *Barroisiceras onilahyense – Forresteria brancoi* Zone, as well as by LOD of the Turonian ammonites of *Coilopoceras* spp. The Coniacian/Santonian boundary is delineated by FOD of the basal Santonian *Texanites texanus* and/or *Tissotia semmamensis* and LOD of the Late Coniacian *Subtissotia african*a and other Coniacian ammonites.

The biostratigraphic character of the fauna, chronostratigraphic correlation of the proposed zones, and lithological framework show that the sedimentation in the Egyptian lands was interrupted by several minor breaks, probably diastems, during the Coniacian time. Besides the intra-Coniacian minor breaks, the Coniacian succession is bounded by two unconformity surfaces coeval with the Turonian-Coniacian and Coniacian-Santonian boundaries in several localities.

The influence of sea-level change on the evolution of *Cahabagnathus* Bergström (Conodonta)

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The evolution of *Cahabagnathus* Bergström and its palaeogeographic distribution was strongly influenced by sea-level fluctuations. Species of *Cahabagnathus* range from the early *Pygodus serra* Zone through the *Baltoniodus gerdae* Subzone of the *Amorphognathus tvaerensis* Zone (Upper Darriwilian through Lower Caradocian). We recognize two lineages in the cahabagnathids that evolved from a yet unknown common ancestor during the Lower-Middle Darriwilian. Lineage 1 includes *C. friendsvillensis*, *C. chazyensis*, *C. sweeti*, and *C. carnesi*. The wide distributions of *C. friendsvillensis* and *C. sweeti* correspond to two large transgressions, and the more narrow distribution of *C. chazyensis* and *C. carnesi* relates to regression events. Lineage 2 consists of *C.* n. sp. *1, C. directus*, *C.* n. sp. *2*, and *C.* n. sp. *3*. A similar relationship exists between sea-level change and the distribution of species in this lineage.

In general, the evolution of the cahabagnathids is influenced by the rise of sea level, which widely distributed taxa, and the fall of sea level which isolated taxa. We propose that it was from these peripheral isolates that endemic *Cahabagnathus* taxa (*C.* n. sp. *1*, *C.* n. sp. *2*, *C.* n. sp. *3, C. chazyensis*, and *C. carnesi)* evolved.

Biotic pre-curserresponse to OAE1b precursor event from at Blake Nose, North. Atlantic

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Oceanic anoxic events (OAEs) are exceptional episodes in Earth history; the research involved in their investigation has significant relevance for understanding dramatic and abrupt fluctuations in climate, such as those seen in the modern world today. ODP Site 1049 at the Blake Nose in the North Atlantic hosts a near-continuous and exquisitely preserved sequence of mid-Cretaceous sediments, including those deposited during the early Albian OAE 1b event. OAE 1b is represented by a single black shale horizon and associated ∂C13 excursion. Approximately two metres below the black shale an equivalent negative ∂C13 excursion is recorded (Gröcke *et al,* 2002) associated to significant colour and lithology change. Here, we present pPlanktonic and benthonic foraminiferal population counts, and matrics over this interval are presented. Relative planktonic species counts and correspondence analysis (CA) show distinctive pre-, syn- and post-∂C13-excursion assemblages, accompanied by a major decline in pelagic abundances and diversities. Increased benthonic foraminiferal accumulation rates and a major decline in planktonic/benthonic ratios suggest elevated palaeoproductivity, whilst a decrease in benthonic foraminiferal oxygen index values record lower bottom water oxygenation at this time. It appears that a significant disruption of oceanic circulation and/or productivity affecting ecosystems in entire water column occurred. Data presented is concluded as indicative of a notable anoxic event prior to the main black shale event, suggesting onset of OAE1b may have taken place preceding black shale deposition in the north Atlantic. We compare the event in the north Atlantic with that of the Niveau Kilian black shales of the Vocontian Basin, south-east France, and suggest an associated regional event to have occurred at Blake Nose which did not result in sapropelic deposition.

Palynology of the Sabaya Formation (Late Aptian to Early Cenomanian) from the Ezab El-Qasr-3 and Ismant-1 wells, central Egypt

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The basal part of the Sabaya Formation (Ezab El-Qasr-3 well, core depth 560–566 m) encounters the columellate *Afropollis operculatus/zonatus* group. Other significant pollen such as *Tucanopollis annulatus* and *Tucanopollis* cf. *crisopolensis* occur. These taxa favour an Aptian age, but the stratigraphic position above the well-dated Abu Ballas Formation (Lower

Aptian) suggests an Upper Aptian age. Consequently, the previous assumption that the Sabaya Formation could range down into the Aptian is acceptable. A fairly humid palaeoclimate is supported by the presence of abundant araucariacean pollen, ferns (e.g. *Deltoidospora*), water ferns (*Crybelosporites*) and freshwater algae (*Botryococcus* and *Ovoidites*). Humidity is thought to have existed during deposition of the upper part of the formation (Ismant-1, core depth 301–307 m). In this interval the non-columellate *Afropollis jardinus* appeared. *A. jardinus* (an Albian-Cenomanian angiosperm) is associated with *Integritetradites porosus* and *Crybelosporites pannuceus*. *I. porosus*, when erected by Schrank and Mahmoud, 2000, is regarded as Cenomanian pollen. Therefore, an Albian-Lower Cenomanian age is suggested. However, the nexinal body in *A. jardinus* is sometimes being divided into two parts. Based on this and on the morphological similarities, size ranges and the patterning of the reticulate exines in all members of the species, a dimorphism might be suggested.

Drenching the Mammoths: a new view on the woolly mammoth ecosystem?

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Remains of ice age mammals have long been found throughout Siberia and Europe. Despite the overwhelming amount of fossil material, the interpretation of the material regarding the Late Pleistocene ecosystem, leading from the earliest idea of an ice world to the most recent idea of the 'mammoth steppe', has still not yielded a clear and unambiguous idea. Here, a coherent faunal list is presented, based on fossil material from the late Pleistocene, collected at a wet sandpit nearby Losser, the Netherlands. The faunal list consists of 41 species (4 fish species, 19 bird species and 18 mammal species) of which some are new in the Netherlands. This faunal list is combined with a floral reconstruction of palaeobotanical remains from Orvelte (Nld.), where remains of a woolly mammoth have been found *in situ*, to be able to reconstruct a late Pleistocene ecosystem. The picture that arose is that of a waterbody surrounded by rather dry grassy plains with a diverse flora and fauna.

A scolopendromorph centipede from the Cretaceous Crato Formation of Brazil

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Preliminary morphological interpretation of a new, exceptionally preserved Mesozoic fossil scolopendromorph chilopod from the Crato Formation of the Araripe Basin, N. E. Brazil is presented. The centipede is preserved in right lateral view and shows features, including a tracheal spiracle, not seen in previously described fossil scolopendromorphs from this locality. All four known fossil centipedes from this Formation are morphologically indistinguishable from modern forms while extant genera from other terrestrial invertebrate orders are known from Cretaceous fossils. Therefore, the new specimen cannot be placed in a fossil taxon on the basis of age alone. Rigorous morphological comparison with extant specimens is required before the correct taxonomic status of the specimen can be determined.

Micropalaeontology of Oligomiocene deposition, southwest of Tehran, Iran

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Saveh is located in central Iran, 120 km southwest of Tehran. Most of the area is covered by plutonic and volcanic masses of Eocene to Miocene age, and Quaternary fluvial and lacustrine deposits, but lesser outcrops of limestone and marble also occur. The thickness and percent of marble increase from east to west, and 120 samples from limestone beds were taken from north and northwest of Saveh for palaeontological and stratigraphical investigations. Thin sections were studied for microbiostratigraphic aims.

This study has recognized important species of foraminifera, such as *Neoalveolina melocurdica*, *Peneroplis evolutus*, *Dendritina rangi*, and *Meandropsina iranica*. This fauna indicates a Burdigalian (Lower Miocene) age, and microfossils such as *Miogypsina irregularia*, *Miogypsinoides complanata*, *Operculina complanata* and *Amphistegina lessoni*, which range from Aquitanian to Burdigalian, indicate equivalence to members C4, E and F in the stratotype. This indicates that during the latest Aquitanian and Burdigalian The Qum sea north and northwest of Saveh covered the Tertiary volcanic masses, depositing coral limestone and marble. The Qum sea was a continental and warm sea with coral reefs which have low dip in this area.

Fish trails from the Lower Old Red Sandstone (Early Devonian) of South Wales

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Undichna, trails produced by swimming fish, are relatively uncommon within the fossil record. Alluvial deposits of the St. Maughans Group (Lower Old Red Sandstone, Early Devonian) of Tredomen Quarry, near Brecon, South Wales, have yielded the oldest known trails of swimming fish as well as body fossils of heterostracan and osteostracan vertebrates. *Undichna unisulca* comprises a single sinusoidal wave (of varying amplitude and wavelength) and is attributed to the caudal lobe or fin of a swimming agnathan (probably a heterostracan or osteostracan). Variation in the dimensions of *U. unisulca* trails (together with functional analysis of the probable producers) suggests different fish sizes and swimming speeds. *Undichna* cf. *simplicitas* shows a more complex arrangement of intertwined waves and is interpreted as being produced by a combination of the caudal fin, anal spine and paired pelvic spines of an acanthodian. A new ichnotaxon comprises three isolated furrows arranged in parallel with associated paddle imprints, and is interpreted as the trail left by a "cruising" cephalaspid, intermittently pushing off the substrate with its pectoral fins. The presence of *Undichna* within these relatively proximal fluvial sediments (displaying no evidence of marine influence) is indicative of an *in situ* vertebrate freshwater community. Taphonomic constraints on *Undichna* preservation, in combination with sedimentological analysis, suggests weak bottom currents and rapid burial, post trace formation.

phytoPal: a database of Palaeozoic phytoplankton

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The Palaeozoic phytoplankton fossil record is composed principally of the cysts of acritarchs and the phycomata of prasinophyte algae, with very rare zygotes of zygnematalean algae. From the perspective of the fossil record it appears as if these groups of phytoplankton formed the basis of the marine food web. We intend to document, via a relational database, the global and stratigraphical distribution of Palaeozoic phytoplankton at species and generic level. This database will be achieved through the collaboration of an international team of phytoplankton workers. One of our principal aims is to document the diversity of Palaeozoic phytoplankton through the construction of a Sepkoski-type curve. The distribution of the phytoplankton can then be related to changing patterns in global climate, macrofaunal diversity and the end Ordovician, Late Devonian and Permo-Triassic extinction events.

The synonymy of the osteolepid fish *Thursius*

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In 1888 Ramsey Traquair created the genus *Thursius* to accommodate *Dipterus macrolepidotus* and a new species *Thursius pholidotus*. Later, in 1948, Erik Jarvik created a new species *Thursius moythomasi* based on scale row counts and differences in the proportions of the plates of the head. The two authors whilst conducting fieldwork in Scotland have found it difficult to distinguish between *T. macrolepidotus* and *T. moythomasi*. On examining Jarvik's description and specimens used, we have discovered that the two species actually represent the two end ranges of a very variable species. We have also collected many new specimens that fit between these ranges, so *T. moythomasi* must be regarded as a synonym of *T. macrolepidotus*. In the course of this study, it has also been found that *T. pholidotus* is so different from *T. macrolepidotus* that it cannot belong in the same genus (a view also suggested but not acted on by Jarvik), and we propose the new genus name *Andrewsia* to accommodate this species. We have also found that the various worldwide species referred to *Thursius*, where generically diagnostic, belong in *Andrewsia*.

Upper Carboniferous syncarid crustaceans from the Montceau Lagerstätte (France)

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Syncarid crustaceans were extremely abundant in the Montceau biota (Upper Carboniferous; France) although represented by a single species, namely *Palaeocaris secretanae*. The remarkable 3D-preservation of the material (sideritic nodules) allows very detailed comparisons with modern syncarids (*e.g. Anaspides*) and accurate reconstruction of the anatomy and autecology of the animal. Three different locomotion modes were used by *P. secretanae:* crawling (thoracic endopods), swimming (thoracic exopods + pleopods) and escape reaction (uropodial fan + telson). The small size of its maxillipeds exclude predatorial habits. Instead, the mandible design, almost identical to that of *Anaspides*, suggests a non-selective feeding mode. Well-developed stalked eyes provided the animal with a wide angle of lateral vision. A series of sensory pores along the trunk segments indicate that *P. secretanae* possessed a dense network of mechano-possibly-velocity receptors. Clustered eggs preserved *in situ* along the ventral side of females indicate brood care as in some modern crustaceans (*e.g.* phyllocarids). Congeneric species of *Palaeocaris* occur in other assumed freshwater communities of comparable age, elsewhere in Europe (England, Ireland) and in North America (Mazon Creek Lagerstätte). In the Montceau biota, *P. secretanae* is associated with other crustaceans (*e.g.* conchostracans, freshwater ostracods), chelicerates (limulids, scorpions), insects, myriapods, euthycarcinoids, annelids (fireworms) and vertebrates (amphibians, fish).

On the palaeoecology of dolichosaurs (Squamata)

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This study provides an analysis of the palaeoecology of dolichosaurs. A detailed description of the stratigraphy/depositional setting of dolichosaur fossil remains demonstrates that these marine lizards were geographically wide spread, inhabited the vast epicontinental seas of the Upper Cretaceous, and were generalist occupying a broad range of environmental parameters. In addition, fossil evidence indicates that dolichosaurs originated in the Tethys Seaway in the Lower-Middle Cenomanian, migrating west into the Western Interior Basin in the Upper Cenomanian, and going extinct in the Upper Turonian. Furthermore, a palaeobiological examination reveals that dolichosaurs developed a number of anatomical features associated with an amphibious lifestyle including a streamlined body, reduced fore and hind limbs, and pachyostotic vertebrae. Their body proportions suggest they were anguilliform swimmers that utilized both their elongate bodies and paddle-like limbs to generate propulsive forces. Both body proportions and tooth structure lead to the conclusion that dolichosaurs were predatory animals feeding on a variety of relatively small marine vertebrates and invertebrates. They were not pursuit predators, but rather ambush predators that may have foraged within small crevices and/or utilized a predatory strike. Overall, the palaeoecological evidence shows that dolichosaurs share similarities with the Upper Cretaceous limbed snake *Pachyrhachis*.

Simulating evolution of shape over palaeontological timescales

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Evolution of morphology can be simulated using the covariance matrix of geometric morphometric variables. This method automatically incorporates correlations from functional integration or developmental constraints, because these are embedded in the matrix. The matrix is first rotated to its principal components and a time-series simulation is applied to each individually. The collective results of the simulations are rotated back to the original shape space to produce the end morphology. The simulation can incorporate different evolutionary models, from completely random to highly constrained.

This method can be used to study the relationship between microevolution and macroevolution. When the matrix is based on a single species, the simulation can be run for millions of iterations (representing the number of generations elapsed over palaeontological time scales), and the results compared to real morphological differences between taxa. Any disparity indicates that the model or rate is not realistic. Application to mammalian molar shape suggests that either strong stabilizing selection, small rates of evolution, or low heritability have been the case because unconstrained evolution, even at moderate rates, produces results that are too disparate.

The conodont *Distomodus kentuckensis:* alternative reconstructions, a bedding plane assemblage, and the implications for apparatus evolution

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Almost all aspects of modern conodont palaeontology, including systematics, taxonomy, palaeoecology and palaeobiology, rely on an understanding of conodonts as skeletal apparatuses, not just as isolated elements. Unfortunately, the conodont fossil record consists almost entirely of disarticulated remains, and for the vast majority of taxa the skeletal apparatus must be reconstructed using indirect methods. The confidence that can be placed in these reconstructions varies, but even the best are nothing more than hypotheses, the ultimate test of which is the discovery of the constituent elements as an articulated skeleton.

Among conodonts with morphologically complex apparatuses, taxa currently assigned to the order Prioniodontida are particularly problematic because articulated skeletons have been described from only two species, and there is uncertainty concerning the number of elements in prioniodontid apparatuses. This is frustrating, because the prioniodontids are important in understanding the evolutionary history of complex conodonts. The discovery of a partial skeleton of *Distomodus kentuckyensis* Branson and Branson, only the third prioniodontid to be described from a natural assemblage, has a direct bearing on these uncertainties.

Species or sexes? Dimorphism in the aquatic sphenodontid *Pleurosaurus*

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The elongate sphenodontid *Pleurosaurus* currently contains two species. *Pleurosaurus goldfussi* is known from the Solnhofen Formation of Germany while *P. ginsburgi* is described from the Canjuers Formation, of France. The latter species has been hypothesised to represent a more advanced stage in aquatic adaptation, with a greater reduction in forelimb length and increase in body length. Recent discoveries have cast doubt upon this distinction. The species are now thought to coexist spatially and temporally. Furthermore, the presence of intermediately proportioned forms from Solnhofen questions their morphological separation. The present study incorporates data from over fifty pleurosaur specimens. Multivariate and bivariate statistics have been used on numerical data such as humerus length, skull length and presacral length. The results support the presence of two adult morphologies, varying in limb proportions.

The current investigation reveals no other metric or qualitative anatomical differences that support the division made by limb proportions. Because of the spatial and temporal co-occurrence of these morphologies, as well as the small degree of difference between them, I do not consider them separate species but prefer their interpretation as sexual morphs of *P. goldfussi*.

Palaeobiogeographical implications of an echinoderm fauna from the Mississippian of southern France

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Preliminary study of an echinoderm fauna from the late Viséan of the Montagne Noire, southern France, suggests that it is more similar to faunas of comparable age in Britain and Ireland than to those in north Africa. Late Viséan crinoid faunas from the former areas contain few camerates, whereas coeval faunas from the Béchar Basin, Algeria, are characterised by a diverse assemblage of camerates. The fauna under study contains the following taxa which also support affinities with faunas from Britain and Ireland: the codiacrinids *Cydonocrinus* and *Lageniocrinus;* a new genus of allagecrinid, known previously only in northwest Europe; and a new species of *Litocrinus* known previously only in Ireland. The suggested faunal affinity will be further strengthened if it can be confirmed that the aberrant blastoid *Astrocrinus*, tentatively identified from a fragment on the basis of its distinctive ornament, is really a part of the fauna from the Montagne Noire. An unexpected component of the crinoid fauna is the codiacrinid *Clistocrinus*, reported previously only from the Pennsylvanian of Alaska.

Palaeogeographical reconstructions of Tethys during the Mississippian generally show the ocean closing to the west so that the Montagne Noire on the Euramerican Plate and the Béchar basin on the advancing Gondwana Plate were in close proximity. The evidence from the echinoderm faunas suggests that the western end of Tethys closed later than late Mississippian. Analysis of the palaeobiogeographical affinities of the rich faunas of brachiopods, bryozoans and corals from the Montagne Noire is required to substantiate this suggestion.

Phosphatized embryos from the Lower Cambrian of Kuanchuanpu, China

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Insoluble residues of the Kuanchuanpu Lagerstätte contain abundant phosphatized globular bodies. Among these, two types of unambiguous microfossils can be distinguished besides numerous globules with a polygonal surface pattern of equivocal biotic origin.

One of these microfossils is *Olivooides* Qian 1977, for which a developmental series including presumed postembryonic, *i.e.* hatched, stages has been described recently (Yue and Bengtson 1999). The morphology of the postembryonic stages, which are rare, suggests the presence of more than one species. One of such specimens exhibits a pentaradial symmetry on the whole body, as it is present in the embryonic stages but differing from the postembryonic stages described by Yue and Bengtson (1999; they show pentaradial symmetry only at their apex).

The second kind of globular microfossil so far undescribed can be readily distinguished from *Olivooides* by its considerably smaller size and different topography. Here, too, a developmental series can be recognized, although the available range of stages is far narrower. Postembryonic stages are absent, which makes determination of the direction of development difficult. On one pole of the globe, the presumed embryo bears an array of plate-like compartments. The fossil displays biradial symmetry, therefore it is not possible to determine an anterior-posterior orientation. Structures on the opposite pole of the fossil are less prominent, but a smooth region delimited by furrows can be discerned. Because of the limited insight in the developmental series, with the absence of postembryonic stages, attempts towards a phylogenetic placement were not successful so far. Our foremost aim at this point of investigation is the adequate documentation of this microfossil.

YUE, Z, and BENGTSON, S. 1999: Embryonic and post-embryonic development of the Early Cambrian cnidarian Olivooides. *Lethaia*, Vol. **32**, 181–195.

Does the phytoplankton distribution correlate with the big isotope excursion of the Ludlow of Gotland (Sweden)?

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The stratigraphical succession of the Silurian sediments of Gotland, Sweden, is characterised by limestone-marl alternations, in which C/O stable isotopes have been measured and show one of the largest C-isotope excursions of the Phanerozoic. The isotope excursions in the Silurian have been attributed to climate changes between humid and arid periods. The palynological content of the sediments around the Ludlow isotope excursion has been observed in detail in order to understand the phytoplankton (acritarch) distribution in this critical interval. Our results indicate a generic content with distinguished patterns of temporal distribution. Some genera are restricted to the time interval situated before the isotope excursion (humid period), while other genera show higher abundances during the isotope excursion of the upper Ludfordian. The infrageneric composition of the abundant acritarch genus *Micrhystridium* Deflandre 1937 is also analysed and shows similar results with high abundances of complex morphologies in the humid time interval and less ornamentated morphotypes in the upper Ludfordian arid period. Additionally, the phytoplankton distribution of an isochrone proximal-distal transect from the lower Gorstian humid period has been analysed. Our results indicate that the phytoplankton distribution can be related to different ocean circulation models, and possibly to climate changes.

A new cheloniellid arthropod from the Ordovician of Morocco

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Cheloniellids are rare and poorly-known Palaeozoic arachnomorph arthropods characterized by a procurved posterior margin of the carapace and by radially arranged opisthosomal pleurae. A site probably belonging to the Upper Fezouata shale formation (Lower Ordovician, Arenig) northeast of Zagora (southeastern Morocco) has yielded fossils of a new cheloniellid. Specimens are rather small and elongated, and show long spines surrounding the entire dorsal exoskeleton. In one specimen, a pair of antennae can be seen to protrude in front of the carapace, and there are indications for the presence of at least three, and possibly four, other pairs of prosomal appendages. The opisthosoma consists of ten tergites with pleurae, followed by a cylindrical somite to which a pair of short furcae attach dorsally, and terminates in a small, rounded telson. Their Lower Ordovician age makes these fossils the oldest cheloniellids known. The presence of a spine fringe is a feature allying the new fossils with the Upper Ordovician *Duslia*. Because cheloniellid appendages were so far only known from the Lower Devonian *Cheloniellon calmani*, the preserved head appendages of the new material add to the knowledge of the cheloniellid head. The current fossils also support the presence of a cylindrical somite without pleurae in front of the telson, a feature tentatively identified in *Cheloniellon*.

Middle and Upper Ordovician chitinozoans from the Shelve Inlier, Welsh Borderland, UK: preliminary results

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Thirty-one samples were collected from the Meadowtown, Rorrington Shale, Spy Wood Sandstone and Aldress Shales formations in the Lower Wood Brook and Spy Wood Brook sections of the Shelve Inlier, across the base of the Upper Ordovician Series. The graptolites from the *H. teretiusculus*, *N. gracilis* and *D. foliaceus* zones of these sections have recently been restudied by Bettley *et al.* (2001), resulting in a proposal for a stratotype for the base of the *N. gracilis* zone in the Lower Wood Brook section. Subsamples from these graptolite collections have been used in this study to assure a good correlation between the graptolite and chitinozoan biozonations. The studied samples yielded rich but, unfortunately, not very diverse chitinozoan assemblages. Biostratigraphically important species include, amongst others, *Linochitina pissotensis* and *Euconochitina tanvillensis*. However, some problems with respect to the interpretation of the ranges of these species will need further attention. Future work in addition to this preliminary study will include correlations with the nearby Caradoc Type area (South Shropshire), and a comparison with the chitinozoan collections from Jenkins (1967).

BETTLEY, R.M., FORTEY, R.A. and SIVETER, D. J. 2001. High resolution correlation of Anglo-Welsh Middle to Upper Ordovician sequences and its relevance to international chronostratigraphy. *Journal of the Geological Society*, London, **158**, 937–952.

JENKINS, W.A.M. 1967. Ordovician Chitinozoa from Shropshire. *Palaeontology* **10**, 436–488.

Missing molluscs: captured in the Carboniferous!

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The molluscan fossil record is generally accepted to be very good. However, recently investigated silicified Silurian and Jurassic shelly lagerstätten have shown that, in carbonate faunas at least, the molluscan record is significantly taphonomically biased in favour of calcite bearing taxa. The wholly aragonitic component is lost through early large-scale aragonite dissolution and only 'captured' in early lithified scenarios. Here we present another mollusc-rich lagerstätte (part of the Cliff Salter collection), this time from the Lower Carboniferous (Asbian/ Brigantian) Hotwells Limestone of Compton Martin, Somerset, UK. Carboniferous limestone faunas are characteristically composed of calcitic taxa. However, this fauna is not silicified as in the previous cases, yet still contains a major formerly aragonitic molluscan component including shallow infaunal bivalves (*e.g Edmondia*, *Parallelodon*, *Sanguinolites*), the rostroconch *Conocardium*, gastropods and chitons. Epifaunal bivalves with calcite in their shells are present with typical Carboniferous calcitic taxa. Limestone lithification must have been extraordinarily early as colour banding is preserved on some gastropods and brachiopods, and the bivalves demonstrate exquisite detail. The reddish clay-rich matrix associated with this fauna is being investigated. This unusual, mollusc-rich Carboniferous fauna provides a further case supporting the proposal that taphonomic bias has radically skewed the fossil record.

Three dimensional phosphatic preservation of hyolith guts from the Montagne Noire: insights into hyolith ontogeny and phylogeny

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The occurrence of three-dimensionally preserved digestive tracts of hyoliths from the Lower Cambrian of the Montagne Noire, France, presents a unique opportunity to study their behavioural ecology. The guts are preserved by phosphate within orthothecid conchs and have a simple U-shaped morphology, which differs markedly from other known orthothecid guts found in Australia, France and Antarctica which are much longer and sinuously coiled.

There appears to be a correlation between conch size and gut preservation potential in that only very small conchs (<3mm) contain the preserved guts. This may be related to the presence of a detached operculum in the juvenile which could be withdrawn into the shell creating a sealed microenvironment in which preservation of the soft-parts was possible. If so, it is possible that juvenile orthothecids possessed fairly simple digestive tracts which lengthened and coiled when reaching adulthood, presumably as a result of a change in diet and/or gut to body volume ratio. Occurrences of well preserved guts in hyolithids shows them to have a simple U-shaped morphology, although this is in an adult form, raising the possibility that the hyolithids and orthothecids may be linked by heterochronous evolution.