The Palaeontology Newsletter

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Reminder: The deadline for copy for Issue no 61 is 20th February 2006.

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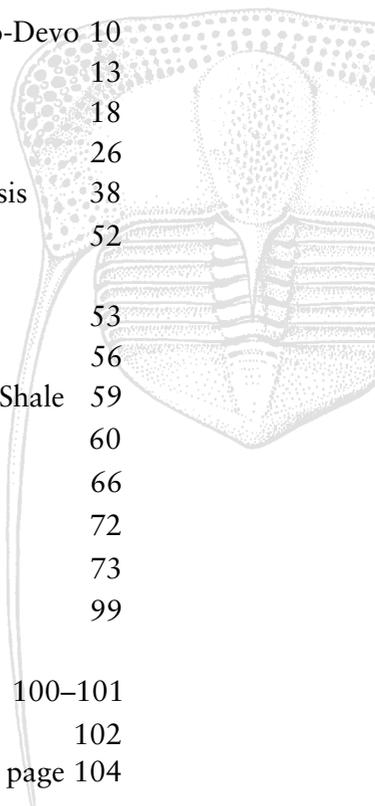
Association Business

Reviving the Annual Association field meeting?

This item comes under the disguise of market research. A number of members have expressed concern that the Association field meeting has disappeared from our calendar of events. In the past this meeting provided a forum for members to discuss our science, in the best place, by the outcrop. I am therefore seeking:

a)   your views on re-establishing this meeting,

b)   volunteers who might offer a weekend field excursion in 2006.

Please send responses to <**secretary@palass.org**>.

Reminder about web awards

The number of websites nominated for the "Golden Trilobite Award" was disappointing this year. There were no professional sites nominated and all the amateur sites were focused on trilobites. This is a reminder that nominations can be submitted at any time during the year; decisions are made in September. (See <**http://www.palass.org/**> for rubric.)

Howard Armstrong
Secretary
<**secretary@palass.org**>

Grants in aid for IPC 2006, Beijing

The Palaeontological Association wishes to show its support for the International Palaeontological Congress to be held in Beijing on 17–21 June 2006, by making a number of travel grants available to students.

The awards will be up to £500 (pounds sterling) each and will be made payable to the student's Department, specifically for the support of his or her attendance at the meeting. The awards will be made to students who are members of the Palaeontological Association, about which more can be found at <**http://www.palass.org/**>

The on-line Membership site is at <**https://www.palass.org/catalog**>.

Awards will only be made to those who are making a presentation at the Conference, and the selection of the award recipients will be made on the basis of the Abstract for the presentation, as well as on such other criteria as the selection panel may think important.

Application for the awards should be made by e-mail. The application should arrive by 1st December 2005 in the first instance. It cannot be guaranteed that the application period will be extended if a sufficient number of applications are received by this date.

If you wish to apply, please send the following information, in an e-mail entitled 'IPC 2006 grant application', to <**palass@palass.org**>:

1.   Your name, institutional address, phone number, and e-mail.

2.   A brief statement (not more than 50 words) saying what you are researching into, the research degree that you are hoping to obtain, when you expect to obtain it, and the name of your research supervisor(s) / advisor(s).

3.   A copy of the Abstract for your presentation at the IPC Beijing conference.

4.   A brief statement of your estimated travel costs.

5.   The name, address, phone number and e-mail of the financial administrator at your institution with whom we can communicate if the application is successful.

Tim Palmer
Executive Officer
<**palass@palass.org**>

SYNTHESYS

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

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

- Collections amounting to over 337 million natural history specimens, including 3.3 million type specimens.

- Internationally renowned taxonomic and systematic skill base.

- Chemical analysis.

- Molecular and imaging facilities.

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

Forthcoming deadlines: 17th March 2006
   15th September 2006

For more information visit <**http://www.synthesys.info/**> or contact <**synthesys@nhm.ac.uk**>.
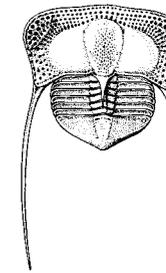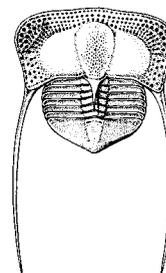
Palaeontology:
CALL FOR SHORT PAPERS!

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

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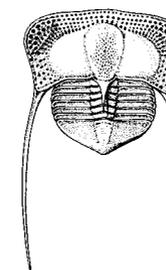
ASSOCIATION MEETINGS

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

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

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

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

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

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

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

Outline programme

Sunday 18th December

Seminar: Ediacaran biotas, Oxford University Museum of Natural History. Talks will be given by:

Doug Erwin (Smithsonian Institution, Washington): *The origin and relationships of early animals*.

Guy Narbonne (Queen's University, Kingston): *Earth's earliest Ediacarans*.

Mary Droser (Riverside University, California): *Palaeoecology of the Ediacaran biota*.

Shuhai Xiao (Virginia Polytechnic Institute, Virginia): *Palaeobiology of the Doushantuo Formation: the first 80 million years of the Ediacaran Period*.

Martin Brasier (University of Oxford, UK): *Decoding the Ediacaran enigma*.

Evening reception: Oxford University Museum of Natural History

Monday 19th December

Scientific sessions, Oxford University Museum of Natural History

Annual address: *William Buckland and the dawning of palaeoecology*, by W.J. Kennedy (Oxford University, Museum of Natural History)

Reception, Blackwell's Bookshop, Oxford

Annual Dinner, Christ Church College

Tuesday 20th December

Scientific Sessions, Oxford University Museum of Natural History

Presentation of awards

Wednesday 21st December

Post-Conference field excursion to the Jurassic and Cretaceous of Oxfordshire

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

Annual Address

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

William Buckland and the dawning of palaeoecology

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

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

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

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

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

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

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

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

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

And then, there were the toads …

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

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

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

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

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

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

From our Correspondents

A module on modularity in Evo-Devo: Subunit 1. Introduction to modularity

Introduction

Modularity is a central concept of evolutionary developmental biology, facilitating the comparison and discussion of the evolution of parts of organisms and the recognition of homologies. Modules are important biologic units upon which natural selection can act to produce different phenotypes. The power of modularity comes in its ability to integrate information from all areas of biological study, *e.g.*, genetics, biochemistry, cytology, ecology, developmental biology, morphology, *etc*. In this column, we review definitions of modularity and discuss how modules evolve to provide a background for a future column discussing some examples of the application of the modularity concept in evo-devo and palaeontological research.

Defining Modularity

Defining modularity and identifying modules is not an easy task. Like homology and species, modularity is conceptually flexible, allowing for the construction of various operational/ functional and theoretical definitions (Rieppel, 2005). Each definition consists of criteria facilitating the recognition of a module. Definitions of modularity constructed by evolutionary biologists generally focus on deconstructing *adult* phenotypes into discrete parts or subunits (such as the limb module, eye module, *etc*.), whereas definitions of modularity created by developmental biologists tend to focus on recognizing parts of *developing* organisms that give rise to phenotype(s) (such as a limb bud, or an imaginal disc), each of which has an intrinsic set of patterning mechanisms with predictable cell populations, cell fates and genetic networks. Modules are hierarchical with other modules, and/or may have sub-modules nested within them (Franz-Odendaal and Hall, in press). Individuals that are part of colonial organisms can be considered evolutionary units (modules) with the application of the modularity concept.

Bolker (2000) noticed that most definitions of modularity have several characteristics in common, including: a greater internal than external integration of parts and processes, a unique functionality reflective of the integration, and a fate distinguishing it from other modules. Furthermore, it is widely agreed that a definition of modularity should be applicable to all levels of the biological hierarchy. Although there are many discussions on various aspects of the concept of modularity – for example, are modules 'individuals' or 'kinds' (Winther, 2001; Rieppel, 2005) – most definitions simply vary in their presentation of the qualities mentioned by Bolker (2000) (compare Raff, 1996; Bolker, 2000; Winther, 2001; Mabee *et al*., 2002; Gass and Bolker, 2003; Rieppel, 2005).

Testing for Modularity

Despite the tendency to identify modules *a priori*, one can test for modularity with experimentation and comparative analyses against hypotheses of function and properties of a module. For example we can test if a forelimb bud is the module necessary to produce the forelimb *experimentally* by removing the limb bud from the embryo and culturing it *in vitro*. A forelimb should still grow if the limb bud is the critical module for the development of the forelimb. We can also *compare* the development of the forelimb bud and hindlimb buds to test for their existence as serial homologues.

Types of Modules

Winther (2001) identified three types of modules:

1. *A structural* module is a part of an organism at a single time in ontogeny, *e.g.*, a single bony element or organ. A single structural module can result from several developmental modules.

2. A *developmental* module is a part/unit/component that changes over ontogeny, *e.g.*, endoderm or limb bud.

3. A *physiological* module is recognized by its function, *e.g.*, eyes, optic nerve.

Winther (2001) noted that the concept of homology, as defined traditionally, only applies to structural and developmental modules.

How Modules Evolve

Raff (1996) discussed three processes leading to the evolution of new modules: dissociation, duplication and divergence, and co-option (Fig. 1):
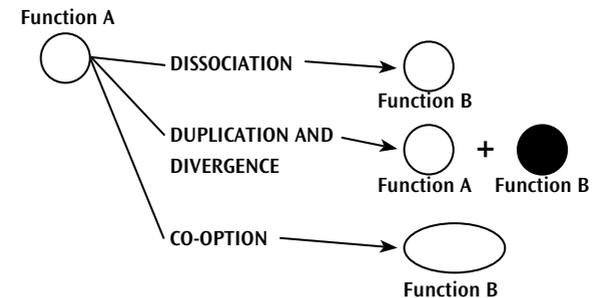

Figure 1: The three evolutionary processes dissociation, duplication and divergence, and co-option are figured as acting on a single module represented by a circle and with a given function. The end results may or may not result in a change in function (from A to B), or structure (from circle to infilled circle or oval). A change in structure can refer to morphology, chemical structure, etc.

Dissociation occurs when a module assuming one function dissociates from the system it is currently functioning in to perform another function, or perform the same function in another system. Dissociations can be of time, space, or of relationships between modules. Heterochrony – dissociation of timing – is the best known process behind modular dissociation. Edgecombe and Chatterton (1987) suggested that the dissociation of the developmental regulation of the pygidial and cephalic regions of encrinurine trilobites may have produced the peramorphic features observed in the pygidium and paedomorphic features observed in the cephalic region.

The shifting of genes functioning on one cell group to another, and homeotic mutations, are examples of spatial dissociations of modules. Modules whose effects on another module change over time could dissociate for another purpose and would be an example of dissociation due to interactions between modules. Raff (1996) makes sure to note that dissociation doesn't involve the creation of anything new; dissociation results in modules being shifted in function or space without the loss or gain of anything substantially new.

Duplication and divergence occurs when a module duplicates and then changes to take on a new form or function. Meristic counts usually focus on elements resulting from what are inferred to be duplication and divergence events. Serial homologues, like teeth, feathers, ribs, pharyngeal arches and their derivatives, are examples of duplication and divergence of modules. The maintenance of duplicated genes is the basis for divergence events.

Co-option events result in the incorporation of one module into another, or a change in functionality of a module. Raff (1996) discussed how the concept of co-optive events replaces the necessity for the terms "preadaptation" or "exaptation". The evolution of wings in vertebrates by co-opting the bony structure of load-bearing limbs and the evolution of limbs from fins are two examples of co-option events. Regulatory genes are largely responsible for the prevalence of co-options that we see in nature.

Summary

In this column we introduced the concept of modularity. How is the concept of modularity useful to palaeontologists? In our next column we will present examples of how evolutionary developmental biologists and palaeontologists apply the concept of modularity to their research.

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Museum as Muse

Art reflects life. Or does it? Now here's a point to think on, as the evenings draw in. Perhaps more precisely, and a little more parochially, art reflects the artist. And artists being human, that vision is personal: a reflection more of their own spirit than of the fragment of the universe that they portray. That painted sunset is a Monet or a Turner, not simply the refraction of the light of our nearest star through a planetary atmosphere at just *such* an angle and with just *such* an interaction of humidity, wind speed and turbulence.

So, take this antique science of ours and look for its reflection in the culture of the day, and what might we find? Today, the answer is, mostly, depressingly banal. A million plastic dinosaurs in supermarkets up and down the land, and yet more pluggly saurians computer-generated on that multiplex screen somewhere near you.

But this is now, when the prehistoric has become familiar, and lost much of its power to shock. What about that time when the idea of the unimaginably ancient was new? When an earth without human dominion saltated from a brief biblical prologue to being almost all that there is, and was? Did the art of the time reflect this, when seen – to pursue a theme against all wiser counsel of taste and discretion – through a musical prism?

One can look among the works of the great Romantic composers and their successors. They do, for sure, reflect the political tumult of those times, as in Beethoven's more promethean works and, nearer the bone, Verdi's frequent tussles with the censor prior to the unification of Italy. There are constant allusions to historical and mythological times: think of Verdi's destiny-freighted kings, the Norse gods of Wagner, Stravinsky's firebird. But did they stretch farther back into those gargantuan, new-found abysses of pre-human time?

There's not much that comes to mind. There's only one work that I can think of, offhand, that overtly puts the fossil world on to centre stage. No deep knowledge need be pretended here, as the title itself is a giveaway: *Fossils*, the antepenultimate piece in Camille Saint-Saens' *Carnival of the Animals*, sandwiched neatly between *Pianists* (well, some of those particular animals would find a place in any bestiary) and the lovely *Swan*. Now, what did Saint-Saens have in mind when he composed the piece? There is a clue: he did not allow any public performance of the *Carnival* until after his death. As a successful, serious (even daunting, to the awe-struck young pretenders), long-lived (no Mozart, he) and much-lauded pillar of the French musical establishment, he thought such frivolous stuff would damage his reputation. The Conservetoire then, obviously, had little truck with public outreach programmes.

To be fair, *Carnival* was composed in 1886 while Saint-Saens was on holiday, for the diversion of friends, or in aid of a real-life carnival (sources here differ). Either way, it was written to amuse, not exalt. In keeping with this, *Fossils* is a sprightly piece, with xylophone prominent (those dancing bones, you see), borrowing a little from Saint-Saens' own *Danse Macabre*, and interleaving bits of other tunes: a snatch of an aria from Rossini's *Barber of Seville*, a couple of oft-sung French nursery tunes.

Now, according to musicologists, the prehistoric past doesn't serve here as the main focus of a musical vision: rather it's a metaphor. The target here is melodies so well-worn – old themes

by dead composers – that they had even then become museum pieces. It's Saint-Saens poking a little fun about music that he thought outmoded and so fair game for some delicate satire. Subtle stuff, this, and put in those terms it maybe wouldn't play so well to the gallery.

Time marches on, though, and music can acquire a different, and in this case more direct, evocation. For performances (once Saint-Saens had ascended to his pantheon in the sky), each piece in the Carnival was often accompanied by verses from the pen of Ogden Nash. In the words to accompany *Fossils*, palaeontology was put firmly back into central focus, albeit in the brightest of fairground colours:

> Last night in the museum hall
> The fossils gathered for a ball
> There were no drums or saxophones
> But just the clatter of their bones
> A rolling rattling and carefree circus
> Of mammoth polkas and mazurkas
> Pterodactyls and brontosauruses
> Sang ghostly prehistoric choruses
> Amid the mastodonic wassail
> I caught the eye of one small fossil
> Cheer up, sad world, he said and winked
> It's kind of fun to be extinct

It's workaday stuff, this, for Nash, though the talent for a well-worked epigram comes roaring back in the last couple of lines. Yet, in mooting this holiday piece by a composer who did not belong, perhaps, quite among the immortals, we are stretching a point: that squeaky noise you hear is of a barrel being vigorously scraped. The late nineteenth century view of our place in the world may have been transformed by the works of Hutton, Darwin and Lyell, but to hear more than a distant echo of this revolution in the serious music of the time needs a keener ear than mine.

If this near-eternal take on the past wasn't sung of in the concert halls, it could, though, in other hands, raise the roof in a Scottish inn of a Saturday night. Lacking inspiration from the god-like talent of the greats, we need take the long downslope glide to the homely praise of the averagely gifted mortal. Take a fragment of Robert Dick's *Song of a Geologist*, a favourite, it was said, of Roderick Impey Murchison's (the whole is reprinted in issue 43 of *The Edinburgh Geologist*):

> Hammers an' chisels an a',
> Chisels an' fossils an' a';
> Resurrection's our trade; by raising the dead
> We've grandeur an' honour an a'.

Celebratory stuff, indeed. A little while on, though, the tone becomes sharper, and might, incidentally, have been of use in Kansas courtrooms both old and new:

> Here's freedom to dig and to learn–
> Here's freedom to think an' to speak;
> There's nane ever grumbled to look at a stone,
> Aye but creatures 'baith stupid and weak.

There are a good deal of other songs in the same vein, both old and new, often composed on the wing when geologists met and ambrosial liquors flowed. The Quaternarists of the University of Wisconsin seem to have developed a fine tradition of this kind of stuff. I couldn't resist, roots being what they are, tracking down the lyrics to their immortal *Bring Back My Polish Drumlin*, the words carefully engineered to intermesh with the tune of *You've Lost that Loving Feeling*. The chorus gives some flavour of the entire *oeuvre*:

> You've lost that streamlined profile
> Oh that streamlined profile
> You've lost that streamlined profile
> Now it's banana, banana, banana oh

Hats off, gentlemen, a masterpiece! (as someone once said in another context which quite escapes me). It has an enviably careless grace, perhaps partly attributable to the vodka alluded to in one of the verses. One should point out, though, in the interests of formal correctness, that bananas feature only rarely in pollen diagrams.

We are still left with the observation that, in the realm of music, visions of timelessness and eternity remain mostly human abstractions, internalised, little modified by the hard-won understanding of our science. So, with the mountain keeping its distance from Mahomet, Mahomet must perforce venture into the hills yet again. If the art doesn't plumb the temporal depths, the fossils, perhaps, can sing a song of their own. A song, moreover, that can be used as a means to some genuine taxonomy, the heart of the art, the real M'Coy.

Far-fetched? Well, it's been done. Palaeontological sonification, it's been termed, a creation of Allan (aka Tony) Ekdale and Alan Tripp of the University of Utah (Ekdale and Tripp, 2005). Their logic is indisputable, and the point that's made is perfectly apt. With five senses at our disposal, palaeontologists generally persist, most unambitiously, in only using one, that of sight. It is perfectly possible to use others, and the considerable case of Geerat Vermeij was quoted: blind since very early childhood but, in his work on mollusc assemblages, performing miracles of analysis through the use of touch alone (and, incidentally, performing further miracles in writing about them with an unsurpassed grace and clarity, not least in the marvellous *A Natural History of Shells*).

So why not, they say, consider using sound? We humans, after all, have a fine capacity for distinguishing different sounds, and have used it unconsciously for taxonomy since childhood, in discriminating the bark of a dog from the meow of a cat and the moo of a cow (and in the case of our species, of course, intraspecific discrimination allows us to recognise individuals by voice alone). But how to extend this to fossils? Ekdale and Tripp have taken fossil patterns such as ammonite sutures, drawn in standard technical fashion on paper, scanned into a computer, and then subjected to a program that renders patterns into series of tones, the timbre and pitch and rhythm of which reflect the visual pattern. Thus, a goniatite suture can produce a simple rhythmic repetitive tune, while one of the more florid Cretaceous ammonites can give rise to an exquisitely complex cadenza. Alternatively, they say, one can dispense with the computer and simply improvise using musical instruments or even, at the risk of starting something that can get alarmingly out of control, get students literally to sing a song of suture…

It's a brilliant idea, and something, for good measure, that can be perfected in the pub of a Friday night, thus mixing business and pleasure, even if threatening the youthful wholesomeness of one's constitution in the process. There's certainly something to be said for anything that can make a student think creatively about the fine details of fossil morphology, a topic that has, alas, a reputation in some quarters – entirely undeserved, naturally – for being just a mite tedious.

This idea can be taken further, if we want our human capacity for sensitivity and discrimination to be fully employed. For there are still two senses left out in the cold: taste and smell. Taste, of course, may be quite the primary sense to be deployed when faced with, say, a recently defrosted mammoth in a part of Siberia to which the McDonald's franchise has not yet penetrated. To take a more familiar example, it's well known that geology influences the character of wine-growing areas, and hence that of the wines themselves, and also that limestones provide a particularly good substrate for vines. One can take this logic just a little further, and start a programme to reconstruct the constituent fossil assemblages from the taste of the wines grown on them. This might, of course, take quite a little practice to provide really sensitive taxonomic discrimination. Still, palaeontologists are renowned for their patience and dedication to their art: they do not shirk a challenge.

As for smell, we are, as humans, woefully under-endowed, compared with say, a bloodhound or a truffle pig. Our noses are but mere appendages, whose bulk more accords with the function of pre-warming the chilly autumnal air than in interpreting the olfactory landscape.

So how to combine a human sense of history and scientific methodology, and a bloodhound's sense of smell? There is one ideal combination. It is, of course, the werewolf. For such a distinctively-endowed individual is likely to have, in addition to the hair, claws and aggressively competitive academic instincts, a schnozzle sensitive enough to detect not only the subtle olfactory patterns produced by its prey – normally the obligatory heroine in the long nightshirt who, for reasons best known to herself and the scriptwriter, ventures out into the castle grounds at midnight – but those generated by different fossils.

Which fossils, though? Some are bound to be better than others. The standard calcium carbonate shell, is likely to smell of, well, calcium carbonate. And microfossils of any type will demand delicate micro-sampling of exhalative gases for which, alas, the claws and notoriously short temper of a werewolf are – while being assets in most committee work – a little maladaptive.

It is the organic-walled fossils that represent the most promising target: plant remains and, of course, graptolites. All those complex organic molecules and their breakdown products, the phantasmagoria of an organic geochemist, would surely give information on phylogenetic affinity, and, as a bonus, on post-mortem diagenetic pathways as well. A breakthrough in palaeontological methodology obviously beckons, if only you choose your PhD candidates carefully enough (while the departmental rugby team may benefit, too).

The upshot of all this, of course, is that it is possible to make palaeontology a fully rounded sensual experience, capable of bringing the drama of the earth's prehistoric past to life as never before. In these difficult times, the temptation to exploit this realization for barrowloads of gold is quite overwhelming. Such an experience would not, regretfully, be for everyone. The marketing will be targeted only at the super-rich, those jaded multibillionaire sybarites who have already tired of every idyllic tropical island, who have discarded their expensively assembled

football team, who have been to outer space and back, and whose yacht lies unused in the harbour at Cannes.

For them, one can – for a price – conjure up the mystery of the past. Picture the scene. A restaurant, its walls lined with prints (one of the senses has to be conventional, at least) taken from, say, Owen's monograph of dinosaurs, or that of Darwin on barnacles. The originals, naturally.

Seated on a chair hand-crafted from sections of the petrified skin of one of the more select dinosaurs – a unique tactile experience – our very special guest would examine the delights on the menu, itself woven from the flexible eopapyrus recovered from a remarkable, and top secret, Tertiary lagerstätten. What to choose? For the main course, perhaps *Fricassée de mammouth bien sauté avec croutons d'ambre*, served, of course by a suitably Raquelesque cavewoman or hirsute caveman (depending on gender or inclination), dressed appropriately – or perhaps inappropriately – for the occasion.

This dish might be washed down by wine from a secluded vineyard sited on – what else? – the Solnhofen Limestone. For an extra fee – a considerable extra fee – the wine would be from a vine guaranteed to be rooted in the impossibly perfect skeleton of a genuine archaeopteryx, located by a team of the most skilled and unscrupulous fossil-rustlers in the business. Playing in the background would be subtle, digestion-enhancing harmonies from a computer-generated aural synthesis of the legendary starfish bed of Astrakhan, while the air would be heavy with the scent of ancestral cycad and auracaria.

Perfection, absolute perfection. When the word gets out, the hyper-rich would beat a path to the door. One would have to fight them off with a club; made, naturally, from the thighbone of a giant sloth. A few weeks fleecing the high-rollers, and one would have enough money to buy a university department or two, liberate the ragged internees from the iron yoke of whichever research assessment exercise happens to be doing the rounds, and re-ignite the poor waif scholarship in that blighted wasteland.

What to study? There is so much to do. But, as a priority, the Holy Grail of palaeontology surely beckons: the deciphering of that sixth sense so often used in taxonomy when all rational means have failed: when ecophenotypes vary beyond all reasonable measure, when sibling species surreptitiously sidle on to your bedding plane assemblage, when that irreplaceable holotype has crumbled into a small mound of rotted pyrite, as if touched by some evil magician's wand, when all cladograms are equally parsimonious.

The shades of Darwin and Linnaeus, Arkell and J de C Sowerby, if they could only hear of this project from their castle in the sky, could only approve. Music, it would be, surely, to their celestial ears.

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Scotoma of systematics, or Herschel's headaches and Darwin's metaphysics

On scotoma

In 1974, one of my favourite authors, Oliver Sacks, was climbing in a remote part of Norway. In an unfortunate accident Sacks severely injured the nerves and muscles of his left leg. During his recuperation period in the hospital his leg was without any sensation or movement for several weeks. This created the extremely uncomfortable feeling as if Sacks' leg was no longer a real part of his body, merely an inconveniently attached lifeless prosthesis. Neurologists have a general term to describe such a phenomenon: scotoma. Scotoma "denotes a disconnection or hiatus in perception, essentially a gap in consciousness produced by a neurological lesion" (Sacks, 1995: 150).

Sacks writes that scotoma is literally unimaginable to those who have not experienced it, and to attain some appreciation of this bizarre phenomenon he recommends those curious enough to read his book *A leg to stand on*, in which he relates his experience, while under spinal anaesthesia. I think there is a less intrusive way to get a superficial or visceral sense of scotoma by trying to sleep tonight on your back with your arms folded behind your head. Whenever I do this, I often wake up with either one or both my hands completely senseless and unable to move, perhaps due to a combination of restricted blood flow and constant pressure on the nerves of my lower arms. It may then take up to a minute or so to regain sensation and movement in my hands. I can only imagine what an extreme form of this must feel like for an entire leg over an extended period of time!

No matter the interest of the physical manifestation of scotoma, the specific purpose of Sacks' (1995) insightful essay, however, was to point out that the concept of scotoma can be transplanted with surprising ease to the realm of culture, history, or science. In this context it refers to a loss of knowledge, a disappearance of insight, a deletion from memory. Sometimes certain facts or ideas enter into the written record or the communal consciousness of a discipline or culture, whereupon they simply fall off the radar.

Sacks noticed that this applied to his scotomal symptoms. His surgeon considered his predicament to be unique. Sacks was puzzled by this assessment, and decided to search the scientific literature to find out more about the symptoms he was suffering from. Three years in the library resulted in nothing. It wasn't until Sacks bumped into a circular from 1864 by American neurologist Weir Mitchell that he found ample documentation of similar symptoms, mainly from victims of the American Civil War 1861–65. However, after a period of brief interest, Mitchell's observations disappeared into the great dustbin of history, until World War I secured a rich stream of fresh cases for documentation. But again, history repeated itself, and the documentation was scotomized, only to re-emerge during World War II, when large numbers of injured people provided a rich substrate for documentation. Interestingly, these instances appear to have been genuinely independent, for no acknowledgments of previous work were recorded in the successive studies.

Sacks uncovered another interesting instance of disciplinary scotoma when he studied migraines in the mid-1960s. Himself suffering migraines since he was a little child, and starting work in a

headache clinic, Sacks was drawn into an in-depth study of migraine. As a doctor charged with recording crisp diagnoses of the symptoms afflicting his patients, he was puzzled that often this seemed impossible. His patients would report perceiving complex geometrical patterns during migraine attacks, symptoms that had apparently been left entirely unrecorded in the literature of the time. It wasn't until Sacks hit upon an 1860 volume of the Victorian physician Edward Liveing in the rare book section of his college library that he found the first brief reference to the geometrical patterns reported by his patients.

His attention was especially attracted by a reference to a paper by the astronomer John Frederick Herschel who gave comprehensive descriptions of exactly the symptoms described by Sacks' patients. This paper was doubly remarkable because it was autobiographical. Herschel essentially described his own visual migraines. Sacks writes: "I felt I had struck paydirt at last." For about a century between Herschel's report and Sacks' work in the headache clinic, no other reports of these particular migraine symptoms seemed to have been recorded, even though Sacks estimated that about five percent of his migraine patients experienced them occasionally. Consequently, this finding was one of the decisive triggers that motivated Sacks to cure this case of scotoma by recording the symptoms of his own patients and going off into a writing frenzy in which he composed the complete first draft of his book *Migraine* in a mere nine days!

A personal scotoma revealed

I read this story several years ago, and it was certainly not on my mind when I passed 19 New King Street in Bath a few weeks ago. I recently moved to the University of Bath to start work on a large integrative project to elucidate the phylogeny of crustaceans, and while I walked home after work, my head swimming with images of the creatures I had to collect and all the lab equipment that I needed to order, I suddenly noticed two plaques framing a white door on a house just a block from my home. One read "The William Herschel Museum," while the other read "Here lived William Herschel A.D. 1781." The name Herschel rang a faint bell. Somehow it reminded me of Charles Darwin, but I didn't know why. As I started to trace the source of my indistinct memories, it became clear that I was about to discover the extent of a personal scotoma that I had incurred over several years. As I bared several layers of my intellectual scotoma a nice story about the connections between Charles Darwin and the Herschels started to take shape. It turned out that migraines were not John Herschel's only headache, and identifying the other headache revealed a scotoma of truly momentous proportions.

On intellectual scotoma

Barring an unfailing photographic memory of unlimited capacity, it is inevitable to sustain intellectual scotoma. This explains why many of us can read a book for the second time with as much enjoyment as the first time, and why even our own writings, which we consciously committed to paper at some time, may strike us as fresh insights when read several years later. One way to counteract the entropic force of time, that ineluctably reduces our memories to formless heaps, is to structure the information we take in as much as possible. It is easier to remember information when it consists of a cluster of bits of data that are logically connected to each other, than it is to remember a jumbled mess of unrelated bits. This is probably the reason why I couldn't quite place the name Herschel, although it sounded familiar. It turned out that over the years I had encountered John F. Herschel a number of times while reading about the history of science. Especially biographical works are studded with countless names, and unless

they are immediately fastened by ties of logic to thematic anchors in the banks of memory, they will start a life as the tumbleweeds of the mind. For years John Frederick Herschel lacked a permanent memory address in my head. This essay has provided me with the framework to cement him more securely in my memory, which he certainly deserves.

The beginning of Herschel fame

It turns out that I live practically next door to the very spot where in March 1781 William Herschel (1738–1822), father of John F. Herschel, discovered the planet Uranus. William was born as Friedrich Wilhelm Herschel on 15th November 1738 in Hanover, Germany. From an early age on, a career in music seemed to be in the offing for little William. His father was a military musician, and William ended up playing in the same military orchestra. In 1757 William moved to England, where he earned his living by composing, playing, and teaching of music. However, in the early 1770s, William started to develop his interest in astronomy seriously. Reading books and buying his first telescope, William's gaze was steadfastly upwards to the heavens, but he quickly became dissatisfied with the quality of his telescope. So in 1773 William resolved to build his own telescope. From then on, his telescope provided the first glimpses of our galaxy for many of Herschel's music pupils and visitors. In 1772 William's sister Caroline joined him in Bath, and William quickly trained her to become his right arm in his astronomical investigations. In a letter to Miss Maria Mitchell (the American astronomer who was the first woman to discover a comet, and after whom the Miss Mitchell's comet was named), Caroline Herschel wrote that her brother had trained her as "an adept assistant willing to struggle long hours at his side as no hired, indentured, or enslaved help would do" (Sobel, 2005: 189). In the most self-effacing manner Caroline wrote "I am nothing, I have done nothing at all; all I am, all I know, I owe to my brother. I am the only tool which he has shaped to his use – a well-trained puppy-dog would have done as much" (see <**http://www.bath-preservation-trust.org.uk/museums/herschel/biographies.php**>).

In view of Caroline's more than slavish dedication to her brother's pursuits, it is particularly ironic that on the night of 13th March 1781, when William Herschel discovered Uranus from the garden of his house in Bath, she was not by his side. Scarcely expecting to discover the first planet in modern times, William initially wondered whether he had perhaps discovered a new comet. It wasn't until November 1781, after the Herschels were "joined by I daresay half the astronomers in Europe, not to mention Russia – all fixated upon it" (Caroline in Sobel, 2005: 191) that it became clear that Herschel's comet was in fact Uranus. Having discovered the planet furthest from the sun then known (it turned out that repeated observations of Uranus could be traced as far back as 1690, but it was always considered a star; Buttmann, 1970: 6), William was heralded an astronomical hero, and in November 1781, close to his 43rd birthday, William received the Copley Medal from the Royal Society. To facilitate further astronomical research, and to alleviate Herschel's burden to make a daytime living as a music teacher, King George III awarded William an annual stipend of 200 pounds, and his sister Caroline 50 pounds for assisting him. This turned out to be money extremely well invested, because Herschel's productivity and astronomical ingenuity have created a rich legacy of fundamental insights, from his discovery of the infrared part of the electromagnetic spectrum to the mapping of thousands of star clusters, and from the discovery of the roughly disk-shaped form of the Milky Way, to the directional movement of our solar system through the galaxy. At the end of his productive life, there was no one who had explored and expanded the limits of our understanding of the galaxy as much as had William Herschel.

The relationship between William Herschel and Charles Darwin: analogies

When I learned about William Herschel's life and work, I couldn't help but be struck by several parallels with the life and work of Charles Darwin. Both Darwin and Herschel were unique among contemporaries in expanding the boundaries of our understanding about the universe and life. Both men possessed extraordinary powers of observation, which allowed Herschel to construct a more detailed map of the universe than any predecessor had achieved, and which allowed Darwin to generate the necessary grist for his theoretical mill. Both gentlemen possessed an uncompromising work ethic fired by a burning ambition to make a contribution to the natural sciences, and they adopted a tenacious single-mindedness to achieve their scientific goals. Both Darwin and Herschel saw their careers boosted, albeit in different ways due to differences with respect to financial safety and the amount of previously published scientific work, by receiving prestigious medals from the Royal Society in London in their early 40s. Herschel received his award for discovering Uranus, while Darwin was rewarded for his monographic work on living and fossil barnacles. Incidentally, at the time of their awards, Darwin and Herschel had both been working on their projects for about eight years. It was in 1845 when Darwin wrote to Hooker "I hope this next summer to finish my S. American geology, then to get out a little zoology" (see my column in issue 54 of the *Newsletter*), and he was awarded the Royal Medal in 1853. Herschel first started to develop a serious active interest in astronomy in 1773, buying books, and parts to build his own telescope. He received his medal in 1781.

Naturally, these achievements of Darwin and Herschel are disparate in terms of their subject matter, but an underlying similarity is obvious as well. For both gentlemen, the medals awarded by the Royal Society were an acknowledgement of valuable scientific work, but compared to their later successes, this initial work, however valuable, seems to have a comparatively low "oomph-factor." Although William Herschel's name may be most tightly linked with his discovery of Uranus, his later work arguably did much more to expand our knowledge of the universe, both conceptually and empirically. Similarly, Darwin's work on cirripedes only attained its full significance within the context of the evolutionary theory he elaborated and published afterwards. In fact, Darwin's barnacle monograph can be considered the first 'modern' phylogenetic work ever published, although that may not be generally realized (Ghiselin, 1996, 1997a, b). The theoretical unification of biology afforded by the *Origin* earned Darwin his deserved status as "Newton of the grassblades" (Ghiselin, 1997a: 293), but his rich documentation of nature's ways in his previous works, his barnacle monograph prominently among them, fully justifies labelling him biology's Copernicus as well.

The relationship between John Herschel and Darwin: cause and effect

The previous resemblances between the work of Charles Darwin and William Herschel are, of course, analogies only. However, a much closer connection binds Darwin and William's son John Herschel (1792–1871) (for biographical information on John Herschel see Buttmann, 1970 and King-Hele, 1992). In 1809, the year of Darwin's birth, John enrolled at Cambridge University at age 17 to begin what would turn out to be an extraordinarily wide-ranging intellectual adventure that would continue to the end of his life. Perhaps not too surprising, considering his origins as a seed sown in such a rich intellectual substrate, John turned out to be a prodigy. Intensely aware that an active intellectual life depends crucially on the successful preservation of time, the thin, tall, and restless John lived a life of almost maniacal activity. John put himself on the scientific

map in no uncertain terms by earning, at age 21, membership to the Royal Society of London for original work in mathematics. This was the start of a career that ranged widely across astronomy, chemistry, physics, mathematics, philosophy, and even including a short dabble in law, and several years as Master of the Mint (where his success, alas, was less apparent). Herschel's obvious gifts for scientific work were balanced by his aspirations in art and poetry, and he was deeply committed to his family as well. His marriage with his 19 years younger wife is simply described as "a union of unclouded happiness" (Ring in King-Hele, 1992). His many accolades include no less than five medals from the Royal Society, a knighthood, presidency of the British Association, as well as the Royal Astronomical Society, and, finally, a resting place next to Newton in Westminster Abbey. In short, for his contemporaries Herschel was the epitome of a man of science.

 John Herschel lived for several years in the mid-1830s in Cape Town, South Africa, where he mostly committed himself to completing and extending his father's astronomical observations of the heavens, securing his own reputation as a gifted astronomer in the process. It was at the Cape that he also took an interest in natural history. Keenly aware of their potential importance, Herschel sent a sample of trilobites that he received from a visitor, to Roderick 'Sir Silurian' Murchison, which provided the first evidence of the Silurian in Africa (Warner in King-Hele, 1992). Herschel had a particular interest in the local flora, especially the bulbous plants, such as amaryllids and orchids, and he collected and grew up to 200 different species in his garden. He also carried out careful morphological and comparative studies on the plants. According to Warner (in King-Hele, 1992) this instilled in John

> "ideas on character associations and the logical basis of classification that were far in advance of their time; in some cases more than a century was to pass before similar systematic observations were made and interpreted. These ideas, put forward in a letter to Herschel's friend Charles Lyell written from Feldhausen in 1836, are entirely consistent with modern ideas of cladistics and, further, were at least partly responsible for forming Herschel's belief at that time that the origination of species is a natural rather than a miraculous process."

In May 1836 the *Beagle* landed at the Cape of Good Hope. Finally Darwin had the chance to meet John Herschel, an event that Darwin must have eagerly anticipated. In his last year in Cambridge, Darwin read two works that would influence his thinking beyond anything else. The first one was Alexander von Humboldt's *Personal narrative of travels to the equinoctial regions of the new continent during the years 1799–1804*. It is hard to exaggerate how much this work stoked Darwin's enthusiasm to become a naturalist explorer. Richards (2002) even goes so far as to label Darwin effectively a German Romantic himself, based on what he perceives as the deep penetration of Humboldt's Romantic view of nature into Darwin's thinking about matter and mind. The second work that, less controversially, shaped Darwin's thinking throughout his life was John Herschel's *Preliminary discourse on the study of natural philosophy*, from 1830. Darwin wrote that the reading of these works "stirred up in me a burning zeal to add even the most humble contribution to the noble structure of Natural Science. No one or a dozen other books influenced me nearly so much as these two" (Darwin, 1995: 23).

Herschel's book set out a methodology of science, which as argued by Hull (1973), and more specifically by Gildenhuys (2004), Darwin applied throughout his own investigations. In this way

Darwin tried to solve the "mystery of mysteries," the famous phrase coined by John Herschel for the seemingly irresolvable problem of origin of organismic diversity. Since Darwin closely followed the methodological precepts laid down by Herschel to answer what Herschel himself saw as the most portentous question in natural science, one would perhaps be excused to think that Herschel would be utterly delighted with the publication of the *Origin*. What nobler monument to Herschel's scientific philosophy than to show its power to resolve the mystery of mysteries?

Herschel's second headache

Darwin included Herschel in a list of 80 or so scientists and philosophers who had the privilege to receive a presentation copy of the *Origin* that came accompanied by a nice letter. After all, what better way to ease the reception of his most important brainchild? In the opening paragraph of the *Origin* Darwin was explicit enough about his debt to Herschel:

> "When on board H.M.S. *Beagle*, as naturalist, I was much struck with certain facts in the distribution of the inhabitants of South America, and in the geological relations of the present to the past inhabitants of that continent. These facts seemed to me to throw some light on the origin of species – that mystery of mysteries, as it has been called by one of our greatest philosophers."

Unfortunately, Herschel's response was not at all what Darwin had hoped for. In a letter to Charles Lyell, Darwin wrote: "I have heard, by a roundabout channel, that Herschel says my book 'is the law of higgledy-piggledy.' What this exactly means I do not know, but it is evidently very contemptuous. If this is true this is a great blow and discouragement" (in Darwin, 1995: 220).

It was true, and it must have been a great disappointment. Darwin had created a huge headache for Herschel, because the core and most radical aspect of Darwin's new conception of nature clashed head-on with the fundamental foundation of Herschel's own outlook on life. The most radical aspect of Darwin's view of life was, of course, his uncompromising philosophical materialism. The reception of his unwavering commitment to materialism had worried Darwin from the very beginning of his theorizing. For example, in his 'M' notebook, which contained metaphysical musings, Darwin wrote: "To avoid stating how far, I believe, in Materialism, say only that emotions, instincts degrees of talent, which are hereditary are so because brain of child resemble, parent stock" (in Bowler, 1990: 85). Darwin evidently felt it was necessary to nuance his opinion that even aspects of the human mind are simply materially transmitted between generations.

It was exactly Darwin's bringing of 'mind' within the purview of 'matter' that was in deep conflict with traditional notions accepted by many of his contemporaries. It would perhaps not be accurate to say that Darwin 'reduced' mind to mere matter, but he did specify a deterministic relationship between, for example, the abstract realm of ideas and the concrete realm of the brain (see Richards, 2005). By drawing attention to the distinction between the merely abstract and the concrete, and questioning the independent existence of the former, Darwin constructed "a single theoretical system, and one that has a unitary metaphysical basis" (Ghiselin, 2000: 270). Rather than maintaining the age-old dichotomy between spirit and matter "Darwin moved concrete particular things to the center of the metaphysical world" (Ghiselin, 2005: 127). It was this metaphysical revolution in thought that was entirely unacceptable to Herschel, and which

invited his labelling of Darwin's view of nature and evolution as "the law of higgledy-piggledy." As argued by Hull (1973), Herschel believed that natural laws instituted by God governed nature. Even if the reality of evolution could be accepted, Herschel could not accept that the direction of change was independent from a higher intelligence, and from a guiding purpose.

The most fundamental modern objections to the Darwinian worldview are still cast in the same mould, by denying materialism or the concrete as the only reality. For example, in a recent article in the journal *Zygon*, which is dedicated to the exploration of the relationship between science and religion, Haught (2005: 365) writes of the "conflation of biology with materialism." Similarly, in an attempt to justify the scientific respectability of intelligent design arguments in biology, Meyer (2002) denies that materialism has a metaphysically privileged position (see my essay in issue 57 of this *Newsletter* for further discussion of Meyer's ideas). These authors would posit the existence of an independent realm of the abstract, entirely divorced from the material world, the concrete. In contrast, most modern scientists are entirely committed to materialism as the only metaphysical reality. At least, that was an expectation I had, until recently.

Scotoma in systematics

It wasn't until I carefully studied the work of Michael Ghiselin over the last year that I realized that the Darwinian revolution is still in full swing. It was a very revealing experience to discover the boundaries of my own ignorance about the profound metaphysical implications of the Darwinian view of life. I recently gave a talk at a conference at the Muséum National d'Histoire Naturelle in Paris, and there I presented the audience with three simple statements designed to provide a quick estimate of a person's metaphysical leanings: (1) I'm a member of the species *Homo sapiens*, (2) A type specimen of a species is generally a good example of that species, and (3) One of the defining features of Mammalia is hair.

The results of this little polling were very revealing. The vast majority of audience members fully agreed with the above statements. I did too, about ten months ago, until I studied Ghiselin's masterful *Metaphysics and the origin of species* (1997a). For me personally, reading this book was by far the most important step in my intellectual development for years. The basic premise and its key insight are deceptively easy to state. The premise: everything in the universe can be labelled as either a 'class' or as an 'individual.' The latter are without exception concrete. The insight: species and other taxa are individuals.

The implications of accepting or rejecting this premise and its key insight go right to the heart of the metaphysics of Darwinism. It represents the most fundamental decision any natural scientist can make in his or her career. Yet, surprisingly few of us seem actually to wrestle explicitly with this issue. The big question is why? How can it possibly be that this most fundamental aspect of Darwin's revolution in thought has either been forgotten, or has not yet been internalised by many workers? It wasn't very surprising that Herschel's migraine headaches were erased from memory. After all, as pointed out by Sacks (1995), Herschel's observations were considered to fall within the domain of medicine, one of the very few domains where Herschel's insights were not accepted as those of an insider. However, the metaphysical implications of the worldview of Herschel's most famous philosophical disciple caused him a headache of much larger proportions. Yet, a full awareness of the implications of the same Darwinian metaphysics is conspicuously lacking from the conceptual toolkit of many modern workers. In the next

issue I will attempt to explain this surprising situation, and what it means to embrace fully the Darwinian view of life, metaphysics and all.

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Cladistics for palaeontologists

Don't blame me! "Surely," I said, "everyone knows all about cladistics and the multitude of computer programs out there by now?" "Oh no," says our Editor, "there are parts of the palaeontological community where cladistic drums do not reach; there are nooks and crannies, fault lines, sink holes and caves where the words synapomorphy, paraphyly and parsimony have never been heard." Well – you could have knocked me down with a feather: all too easy now since many were attached to bloody great dinosaurs – sorry – non-avian archosaurs. "What is needed," Editor says, "is a simple walk through cladistic analysis, explaining the background theory and giving us the low-down on what the programs are doing and why – you're retired now – all the time in the world – you can bang it out before you go for your bus pass." OK, better than cleaning the car, I guess!

So here it is – cladistics in six easy sessions (Introduction, Characters, Tree building, Optimisation, Tree support and consensus, Missing values and Stratigraphy). I will emphasise the PAUP computer program in the relevant articles because this is the most comprehensive and widely available.

INTRODUCTION

Cladistics was introduced by the German entomologist Willi Hennig, who put forward his ideas in 1950. He wrote in his native language, so these were completely ignored until 1966 when an English translation of a manuscript was published under the title "Phylogenetic Systematics" (Hennig 1966). It is not an easy book to read but fortunately many others have been written that have both fleshed out and distorted his ideas. Hennig's most important contribution was to offer a precise definition of biological relationship and to suggest how that relationship might be discovered.

Taxon and character relationship

Hennig's concept of relationship is illustrated in Figure 1. Considering three taxa, then the salmon and the lizard are more closely related to each other than either is to the shark. This is so because the salmon and the lizard share a common ancestor, 'x', which lived at time t_2 and which is not shared with the shark or any other taxon. Similarly the shark is more closely related to a group 'salmon+lizard' because the shark, salmon and lizard together share a unique common ancestor – 'y', which lived at an earlier time t_1. The salmon and lizard are called sister-groups; the shark is the sister-group of the combined group salmon+lizard. By extension, the lamprey is the sister-group of shark+salmon+lizard. The aim of cladistic analysis is to discover this sister-group hierarchy, and express the results in branching diagrams. These diagrams are called cladograms, a reference to the fact that they purport to express the genealogical units or clades (the word 'Cladistics' was, ironically, coined by Ernst Mayr – a life-long opponent of cladistic classification). The aim of cladistics is to search for the sister-group, and the concept of two taxa being more closely related to each other than either is to a third (the three-taxon statement) is fundamental to cladistics.
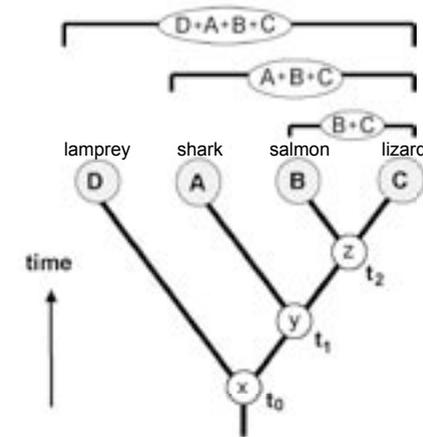

Figure 1. Hennig's concept of relationships among taxa A – D. See text for discussion.

Sister-groups are discovered by identifying characters (or character states) that are uniquely shared by two of the three groups under consideration. But not just any characters (or character states – we will deal with the relation between character and character state in the next article).

Hennig made a distinction between two types of characters (or character states) and this distinction depended on where they occurred in the phylogenetic history of a particular group. The character or the state of the character which occurs in the ancestral morphotype he called "plesiomorphic" (near to the ancestral morphology), and the derived character, or the derived state, he called "apomorphic" (away from the ancestral morphology). Here, it is only necessary to emphasise that the terms apomorphic and plesiomorphic are relative terms – relative to a particular systematic problem. In Figure 2A character state "a" is plesiomorphic and "a prime" is apomorphic. State "a prime" is presumed to have been present in the ancestral morphotype which gave rise to taxa B and C. The presence of character "a prime" – the apomorphic state – in taxa B and C is evidence of their immediate common ancestry and their sister-group relationship. "a prime" is a shared apomorphy or a synapomorphy suggesting that taxa B and C are more closely related to each other than either is to A. In Figure 2B "a prime" is apomorphic with respect to "a" but it is plesiomorphic with respect to "a double prime". So, just as the relationship of taxa is relative, so is the relationship of characters (or character states).
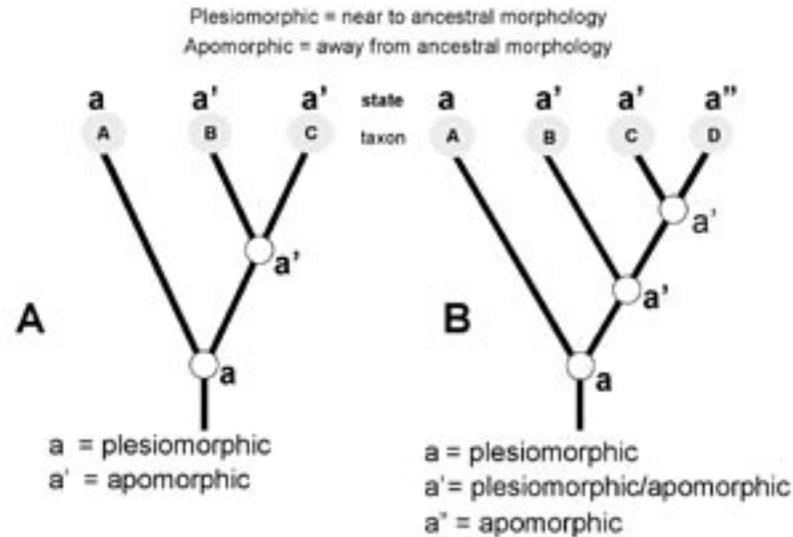
Figure 2. Hennig's ideas of relationships between character states. See text for discussion.

Hennig thought that you could decide which was the apomorphic state and which was plesiomorphic before you did the analysis. He had several criteria for this of which stratigraphic order was the most relevant to us – the state of a character that occurs earlier in the fossil record is to be regarded as the plesiomorphic state. This did not go down very well with neontologists, nor with many palaeontologists, because it relied on the faithfulness of the fossil record to document the truth. Today, there are two criteria that are used: the outgroup and ontogenetic sequence, both of which we will explore in the next article.

Hennig introduced a third state that he called autapomorphic. This is the state that occurs in only one of the taxa under consideration. And once again, autapomorphic characters in one analysis may be synapomorphies in another.

A real example is given in Figure 3. In Figure 3 characters numbered 3 and 4 are synapomorphies suggesting that the lizard and the salmon shared a unique common ancestor 'Z'. It suggests that characters 3 and 4 arose in ancestor 'Z' and were inherited by the salmon and the lizard. Shared primitive characters (symplesiomorphies) are characters inherited from a more remote ancestry and are irrelevant to the problem of relationship of the lizard and the salmon. For example, the shared possession of characters 1 and 2 in the salmon and lizard would not imply that they shared a unique common ancestor because these attributes are also found in the shark. Characters 1 and 2 may be useful at a more inclusive hierarchical level to suggest common ancestry at 'Y'. With respect to the three-taxon problem (shark, salmon and lizard) then characters 1 and 2 are symplesiomorphies and they suggest nothing other than that the shark, salmon and lizard are a group. Similarly, characters 5 – 9 and 10 – 12 are autapomorphies and irrelevant to discovering relationships since they are each found in only one of the taxa. Sister-groups are discovered by identifying shared derived apomorphic characters (synapomorphies)
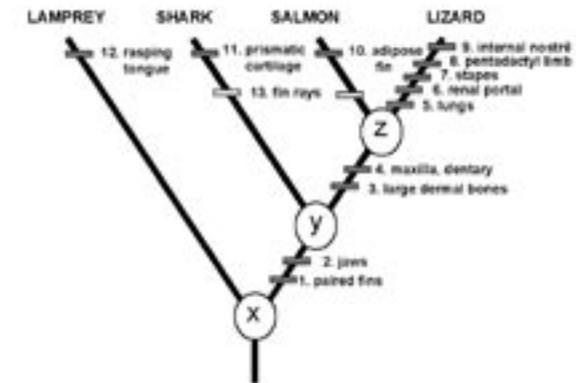

Figure 3. An example of a phylogeny showing characters by which taxa are recognised.
Characters 1 – 4 are synapomorphies, 5 – 12 are autapomorphies and 13 is an attribute seen in the salmon and the shark. See text for discussion.

inferred to have originated in the latest common ancestor and shared by descendants. These synapomorphies can be thought of as evolutionary homologies: that is, as structures inherited from the immediate common ancestor.

Another way we can think of this is to ask the question "what groups are specified by what characters?" In Figure 3 given four taxa, of (initially) unknown interrelationships, then characters 1 and 2 suggest a group Shark + Salmon + Lizard. Characters 3 and 4 suggest a group Salmon + Lizard. But characters 1, 2, 3 and 4, suggest two nested groups, one more inclusive than the other ((Shark (Salmon, Lizard)).

Parsimony and steps on a cladogram

All is not well in Figure 3. The characters do not always specify the same groups. For instance, character 13 (fin rays present in the shark and the salmon) suggests that the salmon and the shark are sister-groups relative to the lizard. So, with the characters at hand there are two theories of taxon relationship. These are shown in Figure 4. In alternative 1 the shark and salmon are sister-groups evidenced by the common possession of character 13. However, if we accept this we have to assume that characters 3 and 4 were either gained twice (once in the salmon and once in the lizard) or that they were gained in the common ancestor of shark+salmon+lizard and subsequently lost in the lizard.

Alternative 2 is that the lizard and salmon are sister-groups, evidenced by the common possession of characters 3 and 4, and we have to assume that character 13 was either gained independently in the salmon and the shark or gained in the common ancestor of shark+salmon+lizard and subsequently lost in the lizard. In other words alternative 1 is more costly in terms of the number of assumptions that we have to make about character evolution. In cladistic analysis, if given no more information, we choose alternative 2 because it assumes the least (or to turn it on its head – it explains the most in the minimum way). Alternative 2 is the more parsimonious solution and therefore is to be preferred. OK – I can hear the cries "but fin rays are more important than large

Alternative 1
Alternative 2

Theory according to character 13   Theory according to characters 3 and 4

fate of characters 3 and 4   fate of character 13

   ·······▶ Gain plus loss
    ───▶ Parallel gain
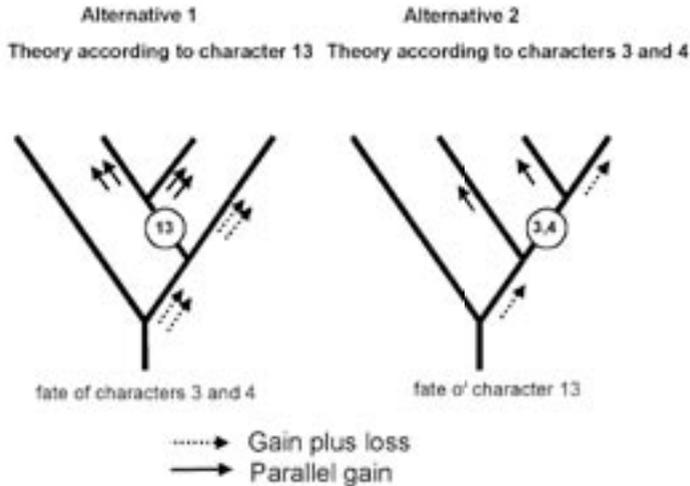
Figure 4. Parsimony. The theory to the right explains the most and assumes the least, and is to be preferred. See text for discussion.

dermal bones, maxilla and dentary." Maybe, but that is another argument and one that is usually the source of multitudes of disputes. Cladists use parsimony to choose between alternatives because parsimony is a universal rule – it can be applied everywhere in the same way. It does not mean that evolution has followed the most parsimonious course. You do not have to accept the most parsimonious solution, you just have to explain why you do not!


7 steps   9 steps   8 steps
optimal   suboptimal   suboptimal
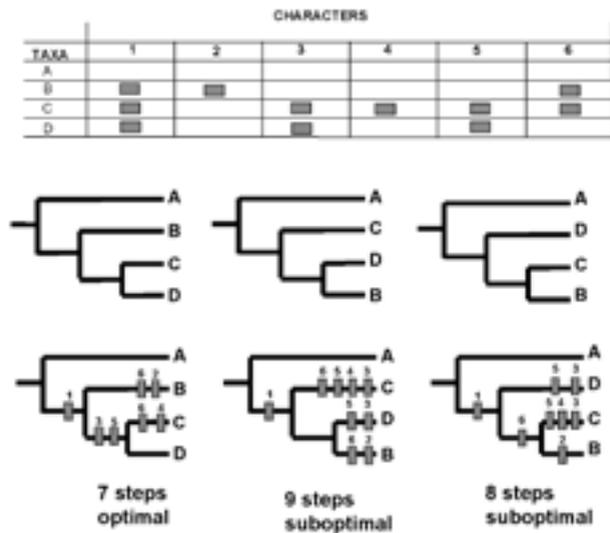
Figure 5. Optimising characters on to alternative cladograms. See text for discussion.

We can think of this in a slightly different way that is revealed in the computer programs used by cladists. In Figure 5 there are four taxa displaying states for six characters and this is displayed in the taxon by character data matrix at the top (data matrices are the daily currency of cladistics). Just for now let us assume that empty cells mean absence of something and that absence is plesiomorphic. Taxon A has none of the attributes. It is wholly plesiomorphic with respect to B, C and D. Taxa B, C and D have various complements of the other characters. Given this information there are three ways in which Taxa B, C and D can be interrelated, and these are shown in the top line of cladograms. The individual characters can be placed on each of the cladograms according to the groups that they specify. For instance character 1 specifies a group B+C+D and therefore will be placed on all cladograms just once. Characters 2 and 4 are autapomorphies and therefore they too will fit to all cladograms just once (note that these two characters do not help resolve any relationships and some people will ignore them). Characters 3 and 5 specify a group C+D and therefore will be placed on the cladogram to the left once. On this cladogram characters 3 and 5 are said to congruent; they fit the tree perfectly. On the other two trees characters 3 and 5 are said to be homoplasious because they do not fit the tree perfectly; two occurrences are needed to explain their distribution. When all characters are fitted on to the cladogram on the left then all but character 6 appears once. If we simply count up the number of times characters appear this equals seven. This cladogram is said to be seven steps long because it requires seven transformations of the characters to explain their distribution in the most parsimonious way (computer programs report the length of the cladogram and authors always give this). If all characters are fitted to all three cladograms then we will see the centre cladogram and the one to the right are longer (nine and eight steps respectively). In other words the cladogram to the left is the most parsimonious – often called the optimal cladogram. The others are suboptimal.

Notice at this stage that we have made no evaluation of HOW the characters have fit the cladogram. For characters 1, 2 and 4 there is no argument, they all fit once and that is that. Take a look at character 6 on the cladogram to the left (the optimal cladogram). It specifies a group B+C that does not appear in this cladogram (this group appears in the right-hand cladogram). In the optimal cladogram the character has been assumed to have arisen in B and separately in C; parallel origination has been assumed. It has shown two steps, both gains (absence → presence). However, we may have assumed that character 6 has been gained by B, C and D and then subsequently lost in taxon D; this is a gain and a loss (absence → presence → absence) but still records two steps on the tree. As far as parsimony is concerned there is no difference and we cannot distinguish the two scenarios. We may, however, have beliefs outside of cladistics that lead us to favour one of these transformations over the other. For example, some mammalian palaeontologists believe that the origination of a particular cusp pattern may be more closely related to diet rather than genealogy, therefore parallelism is to be preferred to gain plus loss. On the other hand most palaeontologists would assume that complex structures such as legs are unlikely to have been developed more than once and that the absence in snakes is a loss that followed a gain. Notice that these are not cladistic arguments.

The action of fitting characters to a cladogram is called optimisation. We will come across several ways for doing this and this is where we can, if we wish, build in some evolutionary scenarios. We have dealt with two so far contained within Figures 4 and 5. Assuming two parallel acquisitions is

called delayed transformation (DELTRAN in the PAUP program) because the initial transformation (absence → presence) has been delayed to near the terminal tips of the cladogram. Assuming gain plus loss is called accelerated transformation (ACCTRAN) because this way of optimising places the initial transformation nearer to the root of the cladogram.

Consensus

It sometimes happens that having been through the exercise in Figure 5 we arrive at a solution where there are more than one optimal cladograms: that is, two or more cladograms are of equal length. We have several choices at this stage: we could add more characters to try and resolve the problem, we could choose one of the cladograms because it fits the stratigraphic record better, or a palaeobiogeographic theory more comfortably, or simply because it satisfies our preconceptions. Another is to summarise the information that is common to them all and this is done through the use of consensus trees. We will devote a few paragraphs to these later.

Cladogram/tree terminology

At this point a pause may be in order to deal with some nomenclatural housekeeping and conventions. I have used the word cladogram up till now but Hennig used phylogenetic tree and technically I should have done the same in the initial descriptions in this introduction. There is an important distinction between a cladogram and a tree that we will come on to. Unfortunately the literature nearly always uses the word "tree" – tree length, tree shape, optimal and suboptimal trees, consensus trees etc. This is because "tree" is a mathematical term and much of the computing side of cladistics is basically maths. It is usually obvious when tree and cladogram are implied.

There are also some terms used to specify parts of the cladogram/tree; these are given in Figure 6 and most are self explanatory. The ingroup is made up of the taxa whose interrelationships you are interested in. The outgroup is technically the rest of life, but is usually one or more taxa that preconceived ideas hold to be closely related to the ingroup. As we will see later, the outgroup is important because it determines the plesiomorphic/apomorphic states of the characters of the ingroup.
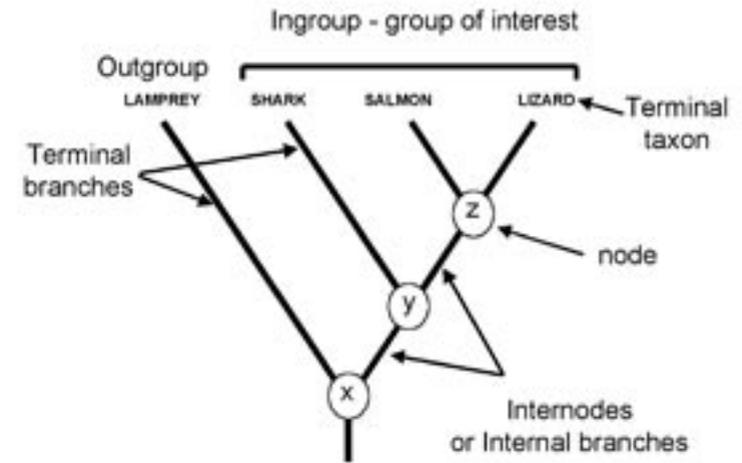

Figure 6. Terminology applied to parts of the cladogram/tree.

Sometimes cladograms/trees are drawn such that each of the branches leading to the terminal taxa and each of the internodes is of equal length, irrespective of how many character changes may be assigned to parts of the tree. This is called a non-metric tree. Another description is a metric tree in which the relative lengths of the branches and internodes are drawn to reflect graphically the numbers of character changes which may be different in different parts of the tree. The results of molecular analyses are often depicted as metric trees to emphasise the great variation in numbers of character changes that often occur in different parts of the tree.

Types of groups

Hennig identified three types of groups, which he recognised on the basis of ancestry and descent. These are shown In Figure 7.

1. A monophyletic group contains the most recent common ancestor plus *all* and *only all* descendants. In this figure such groups (with their Linnean names) would be ancestor 'Z' and Salmon+Lizard [Z(BC)] – named Osteichthyes; ancestor 'Y' and Shark+Salmon+Lizard [Y(ABC)] – named Gnathostomata; or [Z(DABC)] – named Vertebrata.

2. A polyphyletic group is one defined on the basis of convergence, or on non-homologous characters assumed to have been *absent* in the latest common ancestor (X). A group D+B containing only the lamprey and the salmon, which might be recognised on the shared ability to breed in freshwater, would be considered a polyphyletic group. Breeding in freshwater in vertebrates might be considered to be an apomorphic character but this is inferred to have arisen on more than one occasion. The character by which we might recognise it is non-homologous, it is a false guide to relationship. No Linnean taxon has ever been recognised for this group.
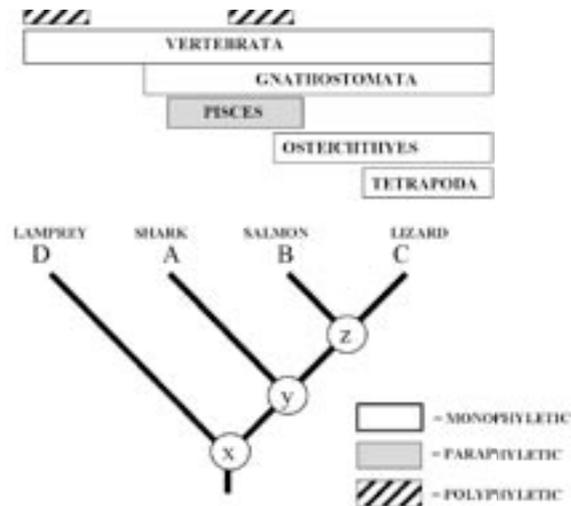
Figure 7. The types of cladistic groups recognised by genealogy with Linnean names applied.

3. A paraphyletic group is a group remaining after one or more parts of a monophyletic group have been removed. Assuming the truth of the shape of the cladogram in Figure 7 then the group shark+salmon (A+B) is a paraphyletic group that has been traditionally recognised as Class Pisces (fishes). However, one of the included members (B – the salmon) is inferred to be genealogically closer to C the lizard, which is not recognised as part of the group Pisces. The shark and salmon share an ancestor (Z) but not all descendants of that ancestor are included in the group.

Most systematists would agree with the desirability of recognising monophyletic groups, and they would also accept the artificiality of polyphyletic groups. It is paraphyletic groups which have been the source of debate, particularly among palaeontologists, because ancestral groups are, by definition, paraphyletic (Pisces ancestral to Tetrapoda, Reptilia ancestral to Aves and Mammalia).

The 'defining attributes' of paraphyletic groups, such as Pisces, are symplesiomorphies: that is, they are attributes of a more inclusive group. In Figure 3 the group Salmon+Shark shares a common ancestor Y recognised by the possession of characters 1 and 2. But these are characters of the group (salmon+shark+lizard). The group salmon+shark does not have any unique characters: in fact it can only be recognised by stating BOTH what it has (characters 1 and 2) AND what it does not have (characters 5 – 9). Since the attributes that the group salmon+shark shares with the lizard are not unique to it, then it can only be unique in what it does not have (characters 5 – 9). Unfortunately most of life also does not have characters 5 – 9). Lest you think that this is only metaphysical solipsism, the bottom line is that it is difficult to know if a newly discovered fossil is a member of an ancestral group if there are no identifiable characters by which to identify membership. And this is compounded by the fact that if we have to identify what it does NOT have, then we have to be sure that the absence is not preservational. Yet, much of the palaeontological literature is swollen with arguments over whether X or Y is the ancestor.

Another reason why paraphyletic groups have been popular in the past is that it was thought that information about evolutionary divergence could be conveyed. To recognise a paraphyletic group Pisces is also to recognise the collateral group Tetrapoda. This is done to emphasise the many autapomorphies of this latter group. In terminology of evolutionary taxonomy these tetrapod characters were seen as evidence that tetrapods had shifted to a new adaptive zone (involving life on land, receiving stimuli through air rather than water *etc.*). In a cladistic classification, such divergence would be expressed through the *number* of autapomorphies identifiable in tetrapods.

Up to this point the types of groups have been described as Hennig did – in terms of common ancestry. But groups are not discovered in this way – they are discovered through character distribution. So, we must return to characters to look again at the definition of groups. In Figure 3 the monophyletic groups salmon+lizard and shark+salmon+lizard are each recognised by synapomorphies (characters 3 and 4, and characters 1 and 2 respectively). They can be thought of as evolutionary homologies. So homology is equivalent to synapomorphy and monophyletic groups are discovered through the discovery of synapomorphies. [But notice that synapomorphies can be shown to be false if character congruence suggests a different grouping: therefore an homology is a theory that may be shown to be false – more about this in the next article.]

CLADISTIC GROUPS

Figure 8. Types of groups recognised by character distributions.

Paraphyletic and polyphyletic groups are recognised by the distribution of characters. Paraphyletic groups are those groups recognised by symplesiomorphies: that is, characters useful at a more inclusive level in the hierarchy. Polyphyletic groups are recognised by homoplasious distributions of characters. These relations are shown in Figure 8.
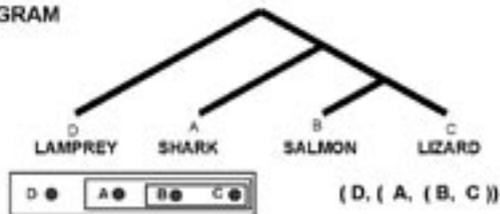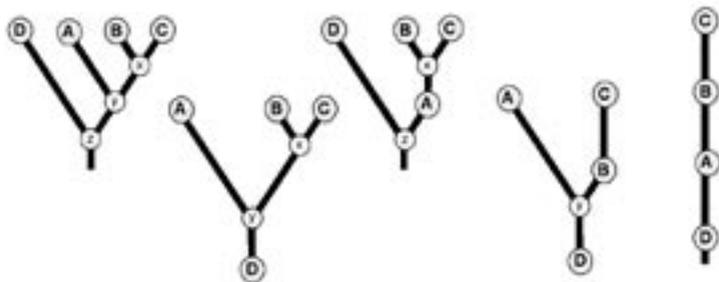
Figure 9. Cladograms and trees. The five trees shown at the bottom have an implied time axis.

Cladograms and trees

Throughout this introduction we have been slowly shifting away from Hennig's evolutionary explanations for concepts of relationship, characters and groups. We do not discover the relationships between taxa by discovering 'evolution'. We can only use the distribution of characters (and just to appease some of the hard-line palaeontologists there are some cladists who recognise stratigraphic occurrence as a character – more later). The relationships illustrated in Figure 3 can be written as a branching diagram (upright, on its side or upside down) as at the top of Figure 9. But this diagram could just as easily be illustrated as a Venn diagram, or be written in parenthetical notation as shown in the top half of Figure 9. A cladogram has no implied time axis. It is a diagram that summarises a pattern of character distribution. The nodes of the branching diagram denote a hierarchy of synapomorphies. There is no implication of ancestry and descent.

Given the character information contained in this Venn diagram there are, however, a number of equivalent evolutionary trees which include time, and which embody the concepts of ancestry and descent with modification. Five such are shown below. Some of these trees assume that one or other of the taxa (A, B, C, D) are real ancestors. Other trees include hypothetical ancestors (x, y, z). Only one tree has the same topology as the cladogram, and this is the one in which the nodes represent hypothetical ancestors. The others contain one or more real ancestors. Choice between these trees depends on factors other than the distribution of characters over the sampled taxa, the only empirical content. Selection of one tree in preference to any other may depend on our willingness to regard one taxon as ancestral to others. Alternatively, we might say that some trees containing real ancestors are less likely to be true than others because of

unfavourable stratigraphic sequence. The important point is that evolutionary trees are very precise statements of singular history, but their precision is gained from criteria other than character distributions; and these trees cannot be justified on characters alone.

The distinction between cladograms and trees is important because many people have taken the cladogram as a statement about evolution. To do this we must be prepared to accept other beliefs: for instance, that evolution is parsimonious, or that evolution proceeds exclusively by branching. Many of the criticisms of cladistics are levelled at the claim that these are unrealistic assumptions of evolution. Indeed they are. But they are not assumptions of cladistics or cladograms. They are assumptions of trees. The cladogram, as a distribution of characters, is the starting point for further analysis. Many systematists do in practice turn their cladograms into trees in order to say something about evolution. And some cladists do recognise ancestors after the analysis (more later).

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FURTHER READING

There are many, many books available. The following are relatively short and the most compatible with this series of articles.

Ax, P. 1987. *The phylogenetic system: the systematization of organisms on the basis of their phylogenesis*. John Wiley & Sons. ISBN 047 1907545. [*A weighty text book but one that clearly explains phylogenetic systematics from a Hennigian perspective.*]

Hall, B. G. 2001. *Phylogenetic trees made easy*. Sunderland Massachusetts, Sinauer Associates. ISBN 0 87893. [*A textbook stressing molecular phylogenetic systematics, but it comes from the same stable as the PAUP computer program and contains clear instructions on what the program is doing – and why.*]

Kitching, I. J., Forey, P. L., Humphries, C. J. and Williams, D.M. 1998. *Cladistics*. 2nd edition. Oxford, Oxford University Press. ISBN 0 19 850138 2. [*A textbook dealing with the theory behind cladistics and parsimony analysis.*]

Schuh, R. T. 2000. *Biological systematics: principles and applications. Phylogenetic analysis of morphological data*. Ithaca: Cornell University Press. ISBN 0 8014 3675 3. [*A hard line parsimony approach, up to date and easy to read.*]

Skelton, P., Smith, A. and Monks, N. 2002. *Cladistics: a practical primer on Cd-Rom*. Cambridge, Cambridge University Press. ISBN 0 521 52341. Pp. 1–80 [*A nice easy book with tied in computer practical.*]

Smith, A.B. 1994. *Systematics and the fossil record: documenting evolutionary patterns*. Oxford: Blackwell Science. ISBN 0632036427. [*A very well known and well used book. It contains several sections directly relevant to the more theoretical side of this series of articles and is about the only one dedicated to the palaeontological viewpoint.*]

PalaeoMath 101

Factor Analysis

Principal components analysis (PCA)—along with its basis method, eigenanalysis—is arguably the workhorse of multivariate analysis. There are multivariate methods that don't employ some aspects of eigenanalysis, but eigenanalysis-based methods easily predominate in terms of both number and application. Therefore, it behoves us to spend some time looking at the variants of PCA, going through their basic calculations, and discussing the context within which their use is justified. In this essay we'll explore factor analysis, a method often regarded as a simple variant of principal components analysis and one that used to be much more popular among palaeontologists than it seems to be today. Along the way we'll gain deeper insight into the mechanics and appropriate use of both methods

In discussing PCA last time, we asked the questions (1) what structural relations exist between our three trilobite variables, (2) whether we could take advantage of these relations to create new variables with more desirable properties, and (3) what the ordination of the species in our sample looked like when plotted against our new variables. This time, let's focus on a slightly different question, but one you might have thought we were discussing last time, 'What covariance-based structural relations exist between our three trilobite variables?'. What's the difference between structural relations and covariance-based (or correlation-based) structural relations and, since PCA is (usually) based on the covariance or correlation matrix, didn't we do that last time? It's actually not quite as simple as that. Read on to learn the difference.

As usual, we'll make use of our simple trilobite dataset (Table 1, see also Fig. 1).
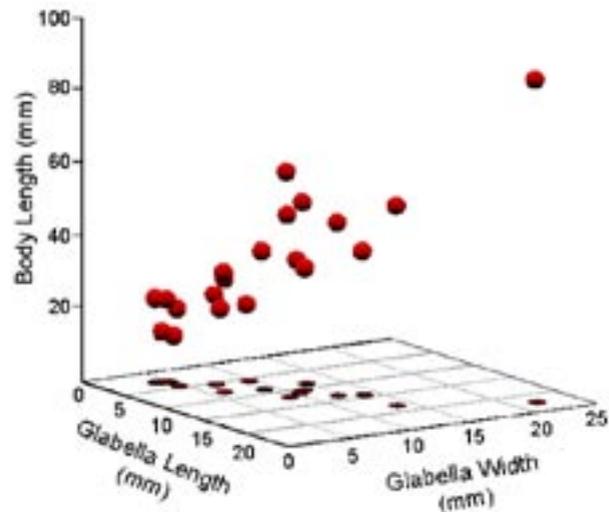

Figure 1. Scatterplot of Table 1 data in a Cartesian coordinate system.

Table 1. Trilobite data

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

Principal components analysis is used when we want to understand the structure of a set of variables based on a comparison of their variances. Remember, the eigenvalues we extract from a covariance or correlation matrix are ordered in terms of the amount of observed variance they account for. In terms of the covariance or correlation matrix, you can think of PCA as being a method that focuses on reproducing the diagonal or trace of these matrices in the most efficient manner possible. That's a very useful thing to do, as we have seen. But it's not the only thing you can do with a covariance or correlation matrix. The information in the off-diagonal elements is also interesting and useful. More to the point, it's possibly more pertinent to a large range of palaeontological problems than an assessment of the variance structure *per se*. The information carried in these off-diagonal elements is the realm of factor analysis.

Factor analysis actually has a somewhat nefarious reputation in many quarters due to the nature of its statistical model, and due to its over-enthusiastic use in the field of psychology; especially the branch of this field that deals with intelligence testing (see Gould 1981). Irrespective of this, in order to understand factor analysis one needs to understand the model on which it is based,

and there is no better way to gain this understanding than by going back to the problem which factor analysis was originally developed to solve.

Around 1900 Charles Spearman, who was interested in intelligence testing, noticed that the scores on different academic subject tests often exhibited an intriguing regularity. Consider the following correlation matrix of test scores.

Table 2. Academic Test Scores (from Manley 1994)

	Classics	French	English	Mathematics	Music
Classics	1.00	0.83	0.78	0.70	0.63
French	0.83	1.00	0.67	0.67	0.57
English	0.78	0.67	1.00	0.64	0.51
Mathematics	0.70	0.67	0.64	1.00	0.51
Music	0.63	0.57	0.51	0.51	1.00

If the effect of the diagonal values is ignored, in many cases the ratio of the values between rows of the matrix approximates a constant. Thus, for English and Mathematics …

$$0.78/0.70 = 1.114 \qquad 0.67/0.67 = 1.000 \qquad 0.51/0.51 = 1.000$$

… and for French and Music …

$$0.83/0.63 = 1.317 \qquad 0.67/0.51 = 1.314 \qquad 0.67/0.51 = 1.314$$

Spearman proposed these sorts of data had the generalized form

$$X_i = b_i F + e_i \qquad (6.1)$$

Where X_i is the standardized score the ith test, F is the 'factor' value for the individual taking the battery of tests, and e_i is the part of X_i specific to each test. Because Spearman was dealing with the matrix of correlations, both X and F were standardized, with means of zero and standard deviations of one. This fact was used by Spearman in his other factor analysis insight, that b_i^2 is the proportion of the variance accounted for by the factor (see Manley 1994 for an easy-to-understand proof of this result).

Using these relations Spearman was able to postulate that mental test scores were composed of two parts, one (F) that was common to all tests and so reflected the innate abilities—or the 'general intelligence'—of the test taker, and one (e) that was specific to the test and so could be construed as evidence of either the subject-specific aptitude of the test taker, culture-based bias in the test, or some combination of the two.[1]

Generalizing the relations presented above it can be appreciated that the model underlying factor analysis has the following form.

$$X_1 = b_{11} F_1 + b_{12} F_2 + \ldots + b_{1j} F_j + e_1 \qquad (6.2)$$
$$X_2 = b_{21} F_1 + b_{22} F_2 + \ldots + b_{2j} F_j + e_2$$
$$X_3 = b_{31} F_1 + b_{32} F_2 + \ldots + b_{3j} F_j + e_3$$
$$\vdots$$
$$X_i = b_{i1} F_1 + b_{i2} F_2 + \ldots + b_{ij} F_j + e_i$$

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[1] This seemingly straight-forward interpretation of Spearman's work later became highly controversial when estimates of a person's general intelligence were used to direct or limit their life opportunities and when the culturally biased character of many standard 'intelligence' tests was recognized (see Gould 1981 for a review).

Note the similarity between this model and the multiple regression analysis model (see *PalaeoMath 101: Regression 4 [Going Multivariate],* equation 4.1). As Jackson (2003) notes, the creators of factor analysis viewed it originally as a type of multiple regression analysis. But they had a problem. Unlike a standard regression problem in which a set of observations (X) is related to an underlying general model (Y) by specifying a rate of change (the slope m), one cannot observe the factor(s) (F) directly. As a result, their structure must be inferred from the raw data, which represents an unknown mixture of common and unique variance. In essence, you can't use multiple regression to sort this problem out because all quantities on the right-hand side of the equation are unknown.

At this juncture it's important to recognize that principal components analysis (PCA) can't resolve this problem any more than multiple regression analysis can. The PCA model (see *PalaeoMath 101: Principal Components Analysis [Eigenanalysis & Regression 5],* equation 5.1) is simply a transformation that re-expresses the observed data in a form that maximizes variance on the various PC vectors (= axes) and ensures the orientational independence of these vectors from one another. This approach focuses on accounting for variance and keeps extracting vectors until the remaining unaccounted for—or residual—variance is exhausted or drops below some arbitrarily-determined amount. Factor analysis isn't trying to account for the variance exhibited by a sample, but instead focuses on recovering the structure of the covariances among variables as completely as possible. In other words, PCA attempts to reduce the residual values of the diagonal or trace of the covariance or correlation matrix. Factor analysis tries to model the covariances or correlations in such a way as to minimize the residual values of the off-diagonal elements. You should use PCA when you want to test hypotheses about a sample's variance. You should use factor analysis when you want to model or test hypotheses about the structure of relations among variables that have been measured across a sample.

Among the many myths about factor analysis is the idea that it only differs from PCA in the sense that the number of factors extracted from the covariance or correlation matrix in a factor analysis is less than the number of variables whereas, in PCA, the number of components extracted equals the number of variables (*e.g.*, see the discussion of factor analysis in Hammer and Harper 2006[2]). Nothing could be further from the truth. Indeed, one of the principal uses of PCA is to reduce the dimensionality of a dataset from m variables to p components, where $p<m$. This erroneous view of the relation between PCA and factor analysis has been perpetuated by the innumerable over-generalized and/or superficial descriptions of both techniques that have been published in the technical literature, and especially in the user's guides of multivariate data analysis software packages within which these methods are routinely confused.

There are a number of ways to perform a factor analysis. The method I'll outline here would not be accepted by many as 'true' factor analysis; especially as it is practised in the social sciences. However, this is a basic version of the procedure most geologists refer to as factor analysis (*e.g.*, Jöreskog *et al.* 1976; Davis 2002; Swan and Sandilands 1995). It starts with a PCA. If one has reason to suspect the form of an underlying model that implies a specific number of factors, this number can be input and the factor solution computed directly. For Spearman's intelligence test data, he suspected a one-factor solution, the one-factor model quantifying his 'general

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[2] The paperback copy of this book lists 2006 as the publication year though the Blackwells website lists 1 Oct. 2005 as the publication date.

intelligence' index and the remaining test-specific variation being subsumed into the error term. For our trilobite data (Table 1) we might suspect *a priori* a two-factor model with one factor representing 'generalized size' and the other 'generalized shape', in which case the error term would represent genus-specific deviation from these generalized indices. It is often the case, however, that one has little idea beforehand how many factors are present in the data.

If you find yourself in the latter situation there is no cause for undue alarm. Factor analysis—like PCA—can be used in an exploratory mode. There are a number of rules-or-thumb for both factor analysis and PCA that can help you decide how many axes to use. If you are working with a correlation matrix, one of the most popular and easiest to remember is to consider only those axes that contain more information than the raw variables. This makes sense in that these axes are easy to identify (all will have eigenvalues > 1.0) and there seems little logical reason to make much of a fuss over composite variables that don't contain as much information as their raw counterparts. An exception to this rule, however, would be an analysis that employed a small number of raw variables. In such cases there won't be much variance to distribute over the axes anyway and a single-variable solution may not be adequate to test your hypothesis. Another popular rule-of thumb is the so-called Scree Test in which the magnitudes of the eigenvalues are plotted in rank order and a decision made on the basis of where the slope of the resulting curve breaks from being dominantly vertical to dominantly horizontal.[3] Of course, both these tests can be applied to PCA as well as factor analysis. The other quick and easy test to apply when considering whether factor analysis is appropriate is Spearman's constant proportion test (see above). If a large number of the ratios between the non-diagonal row values of the correlation matrix do approximate a constant, the data exhibit the classic structure assumed by the factor analysis model. If such a structure cannot be demonstrated, factor analysis may proceed, but should be interpreted with caution.

The PCA results for the trilobite data correlation matrix are listed below (see also the R-Mode Factor Analysis worksheet of the *PalaeoMath 101 Spreadsheet*).

Table 3. Trilobite Data Eigenvalues (Correlation Matrix)

Eigenvalues	Variance (%)	Cum. Variance (%)
2.776	92.541	92.541
0.142	4.719	97.260
0.082	2.740	100.000

Table 4. Trilobite Data Eigenvectors (Correlation Matrix)

Variables	PC1	PC2	PC3
Body Length (x1)	0.573	0.757	-0.314
Glabella Length (x2)	0.583	-0.108	0.805
Glabella Width (x3)	0.576	-0.644	-0.504

If you've read the last column you should be familiar with the interpretation of these tables, but we'll go through it again, just for practice. The overwhelming majority of the variation in these data is being expressed on PC1 (Table 3). On this axis all three variables have subequal positive loadings (Table 4). This is highly suggestive of this axis representing a generalized size index and that size variation represents the predominant component of variation in the dataset.

[3] This is called a Scree Test because the plot resembles a profile across an alluvial fan the upper part of which is composed of the large, angular rocks with a higher angle of repose that mountaineers and geologists call 'scree'.

The remaining two PC axes represent much smaller proportions of the observed variance, and the alternating signs of their eigenvector loadings indicate they represent axes of localized size (= shape) variation. Here PC2 expresses a contrast between body length and glabellar width variation while PC3 mostly expresses a contrast between glabellar length and linked body length-glabellar width variation.

Since the second eigenvalue expresses less than a third of the total variance (= 3.0) it is tempting to consider only PC1 important. After all, in the raw data each standardized variable contributes 1.0 standard deviation units to the total. However, we're going to include PC2 in our factor analysis solution because (1) we have good reason to suspect these data are composed of a size factor and a shape factor, and (2) by doing so we will be considering over 95 percent of the observed sample variance.

Unlike classical PCA, factor analysis scales the factor loadings by the covariance/correlation matrix's eigenvalues. Note in equation 6.2 the place of the *a*-values in the PCA general equation has been taken by *b*-values. The change in symbol signals this basic difference in the two loading coefficients. In order to calculate the loadings of a factor analysis the following relation is used.

$$b_{ij} = \sqrt{\lambda_j}\, a_{ij} \qquad (6.3)$$

Where b_{ij} is the factor loading, λ_j is the eigenvalue of the jth eigenvector, and a_{ij} is the corresponding PCA loading. Using this relation and calculating a solution for the two-factor model, the equations of the factor axes are as follows.

Table 5. Trilobite Data Factors (Correlation Matrix)

Variables	F1	F2	Communality
Body Length (x1)	0.954	0.285	0.992
Glabella Length (x2)	0.972	-0.041	0.947
Glabella Width (x3)	0.959	-0.242	0.979

The communality is the sum of the squares of the b_{ij} values for each variable. This quantity expresses the proportion of the variance provided by those variables to the model factor(s). The quantity '1 – the communality', then, expresses the proportion of the variable's variance attributable to the error term of the factor. As you can see from Table 5, under this two-factor solution all variables exhibit a high communality, indicating the residual error is very small.

The communality values are one thing, but we can use a little trick at this point to emphasize the difference between PCA and factor analysis. Another way of calculating the covariance or correlation matrix is to multiply the matrix of raw measurements (or standardized raw measurements, in the case of the correlation matrix) by the transpose[4] of that same matrix.

$$s = X\,X' \qquad (6.4)$$

In this expression X represents the raw data matrix, X' its transpose, and s the resulting covariance or correlation matrix. Given this relation, the degree to which the new factor loadings for a PCA or a factor analysis accounts for the structure of the original covariance/correlation matrix can be determined by multiplying the eigenvector and/or factor loading matrix by its

[4] A transposed matrix is one in which the rows and columns of the original matrix have been interchanged. In MS-Excel a tool for transposing matrixes will be found in the 'Paste Special' dialog of the 'Edit' pull-down menu.

transpose. If we do this for the two-axis PCA and factor analysis results for our trilobite data, the results might surprise you (Table 6).

Table 6. Original and reproduced correlation values for two-axis PCA and
factor analysis solutions to the trilobite dataset

	PCA			Factor Analysis		
	Original Correlation Matrix			Original Correlation Matrix		
	BL (x1)	GL (x2)	GW (x3)	BL (x1)	GL (x2)	GW (x3)
BL (x1)	1.000	0.895	0.859	1.000	0.895	0.859
GL (x2)	0.895	1.000	0.909	0.895	1.000	0.909
GW (x3)	0.859	0.909	1.000	0.859	0.909	1.000
	Reproduced Correlation Matrix			Reproduced Correlation Matrix		
BL (x1)	0.901	0.252	-0.157	0.993	0.916	0.848
GL (x2)	0.253	0.352	0.405	0.916	0.945	0.942
GW (x3)	-0.157	0.405	0.747	0.848	0.942	0.981

Notice that reproduced correlations numerically closest to the original correlations for the PCA result (0.901, 0.747) are located along the trace of the correlation matrix. This is because the purpose of PCA is to minimize deviation along this dimension of the matrix. There is also one negative value in the PCA reproduced correlation matrix, which is a bit at odds with the all-positive correlations exhibited by the raw correlation matrix. This is a somewhat spurious by-product of the small number of variables used in this example. It would not be there if all three PCA axes were used to determine the reproduced correlation matrix, and probably not be there if the number of variables and/or sample size was larger. Nevertheless, it is a good reminder that such artefacts can creep into a PCA result, especially if PCA is being used in the sense of a factor analysis. The scaling operation we used to estimate the factor loadings probably seemed somewhat trivial when you read about it above. But look at the result in terms of its ability to reproduce the original correlation matrix. In this case the two scaled factors were able to achieve a much closer approximation of the off-diagonal elements of the original correlation, while the accuracy of the diagonal elements has, to some extent, been reduced. If there were more data and/or variables in our example, this discrepancy between the PCA and factor analysis results would be even more pronounced.

Once these factor equations have been determined, they can be used to project the original data into the feature space formed by the two factor vectors. Like the scaling operation, this is a bit move involved a computation in factor analysis than in PCA. The reason is that the data matrix (X) contains a component of variation that coincides with the common factor structure (= the F-values in equation 6.1, also called latent variables) and a component that is unique to each object (= the e-values in equation 6.1). Multiplying the raw data by the factor loading matrix—as is done in classical PCA—means the common and unique components of variation are confounded. Fortunately, it's an easy matter to normalize the loading matrix for this unique component of variation in the data, by normalizing the data matrix for the residual component of variation in the covariance/correlation matrix. One can do this either by inverting the covariance/correlation matrix itself …

$$\hat{X} = X \, s^{-1} \, F \qquad (6.5)$$

… or by inverting the product of the transposed and normal factor loading matrices ($F'F$) …

$$\hat{X} = X \, F \, (F'F)^{-1} \qquad (6.6)$$

The resulting factor scores ($\hat{X}$) may then be tabulated, interpreted, and/or plotted in the normal manner (Table 7, Fig, 2).

Table 7. Trilobite factor scores

| Genus	Factor 1	Factor 2
Acaste	-1.056	-0.993
Balizoma	-1.162	0.110
Calymene	0.530	-0.889
Ceraurus	-0.924	-0.333
Cheirurus	0.168	1.737
Cybantyx	0.234	0.495
Cybeloides	-0.580	0.168
Dalmanites	-0.356	-0.854
Deiphon	-0.427	1.437
Ormathops	-1.078	0.319
Phacopidina	-0.607	0.594
Phacops	-0.502	0.433
Placopania	0.016	-0.314
Pricyclopyge	0.771	1.491
Ptychoparia	0.650	-2.753
Rhenops	1.342	0.048
Sphaerexochus	-0.963	-0.661
Toxochasmops	0.299	-0.158
Trimerus	2.921	0.031
Zacanthoides	0.723	0.091
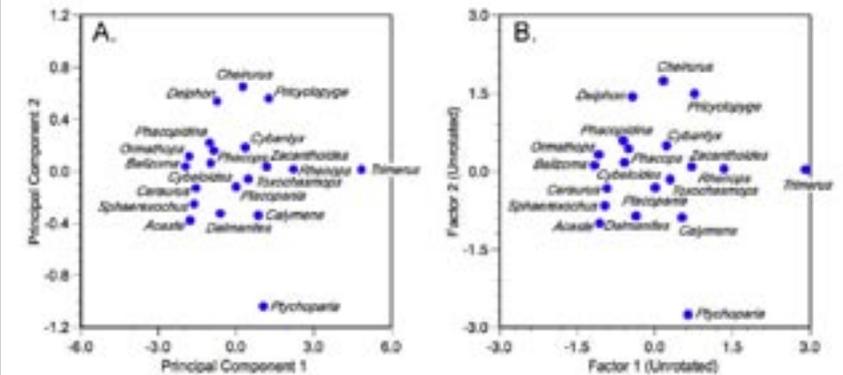
Figure 2. Plot of trilobite genus scores on the first two principal components (A) and two common factors (B) of the correlation matrix. Note similarity of the ordination despite strong axis scaling differences that arise as a result of scaling the factor axis lengths and normalization for the unique aspects of the factor solution.

Now, compare a plot of these scores to a plot of the first two PCA axes calculated from the trilobite correlation matrix. Although most features of the ordination have not changed

substantively (*e.g.*, *Trimerus* and *Ptychoparia* are still unambiguous outliers, *Pricyclopyge* and *Acaste* lie on opposite sides of the distribution), the detail has changed a bit. This is, once again, a reflection of the fundamental differences between PCA and factor analysis. The PCA ordination reflects the original geometry of the sample to a much greater extent than the factor analysis ordination. The PCA result is an optimized portrayal of variance across the sample re-expressed along two mutually independent axes. The factor analysis result, on the other hand, represents a truer picture of inter-correlations among taxa that have been optimized along two factor axes. Note also the difference in the scaling of the PCA and factor axes. The PCA ordination represents a more accurate picture of the scaling differences among taxa in the sample (albeit from standardized data). The factor analysis ordination represents a variance-reduced space that is not portraying those aspects of the raw data idiosyncratic to individual specimens. That component of variance was normalized out when computing the factor scores.

Of course, part of the reason these ordination results are very similar is that we're not working with much data. As alluded to before, more variables and/or more specimens in the dataset would likely accentuate the differences between PCA and factor analysis. Morphological data are also fairly well-behaved in this respect. Regardless, same data, different results—especially in terms of the factor loadings and the structure of the reproduced correlation matrix—because the data analysis methods are trying to do very different things. As usual, it's up to the data analyst to decide which approach best suits the needs of any particular investigation.

We've now completed a basic presentation of geological factor analysis as applied to our trilobite example, except for one final topic; axis rotation. In the comparatively simple world of classical PCA, the axes are the axes, are the axes. What you get out of the eigenanalysis (plus a bit of matrix multiplication) is what you see on the graph. Not so with factor analysis. As if all the different ways in which to do a factor analysis (see below for references) weren't enough, someone had to come along and invent axis rotation!

The intention of axis rotation is straight-forward and perfectly reasonable. Say we have a two-factor solution to a more complicated problem than our trilobite example. When we plot the factor loadings, their orientations usually look like those in Figure 3A.
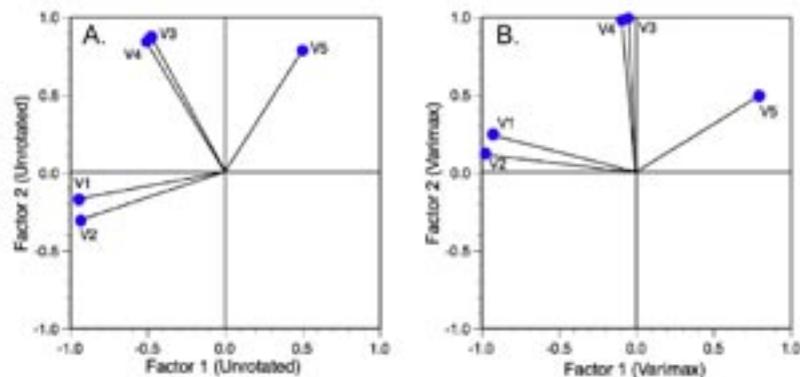

Figure 3. Unrotated (A) and varimax rotated (B) factor axis solutions to an analysis of 7 variables measured on 20 random boxes (see Davis 2002).

Obviously these variables form subsets that, for morphological data, may reflect either necessary or interesting linkages between variation in different regions of the form (*e.g.*, developmental modules). For these data there are three groups of variables. Most people familiar with PCA or factor analysis would have no trouble interpreting this result. However, when many axes are involved the interpretation can become more difficult. One way to simplify this problem is to rotate the axes rigidly about the origin of the coordinate system until they achieved a position of maximum alignment with different factor axes; something like Figure 3B.

Because the rotation has been rigid, the orientations of the variables relative to one another have not changed. This means the geometry of the analysis itself hasn't changed. The same groups of variables are present and they differ from one another by exactly the same amount. The only thing that has changed is the orientation of the vector swarm relative to the underlying factor-axis coordinate system. That's now been changed in such a way as to make the relations between the variable axes and the factor axes easier to understand and interpret. After rotation variables 1 and 2 are maximally aligned (subject to the rigid rotation constraint) with factor axis 1, whereas variables 3 and 4 are aligned with factor axis 2. Variable 5 occupies an intermediate position along both axes as a result of the fact that it does not exhibit strong covariance with any other variable.

A variety of axis rotation schemes are available for use in factor analysis to achieve this structural simplification. Indeed, there seem to be as many ways to specify an axis rotation scheme as there are to skin the proverbial cat. This is felt by many to be one of the downsides to factor analysis, insofar as there are as many solutions to a rotated factor analysis problem as there are axis rotation methods, and no good guide as to which rotation method is best in which context. Two generalized approaches to this problem exist, the 'orthogonal' (= rigid rotation) approach and the 'oblique' approach. Orthogonal rotation methods are the most popular. The most popular orthogonal method—and the one used in this example—is the varimax rotation scheme. This axis-rotation strategy only adjusts the component of variance common to the specified factor structure and does so iteratively, two axes at a time, until the improvement in the factor loading structure drops below some previously specified cut-off value.

As indicated by the name, orthogonal methods preserve the right-angle orientation of the underlying factor axis system. In other words, the variable vectors are rigidly rotated about an unchanging set of orthogonal factor axes. This having been said, there are still a large number of ways within which an orthogonal rotation can be accomplished. Mostly these methods use different weighting schemes to summarize the appropriateness of the rotation. Aside from varimax, normal varimax, quartimax, and equimax are all orthogonal rotation schemes.

Oblique rotation goes one step further, and relaxes the constraint of orthogonality on the factor axes (that is essentially derived from eigenanalysis). Under this protocol extreme variable vectors within the swarm become synonymous (or near synonymous) with individual factor axes (loadings = 1.0) and the entire space deformed such that all axes lie at various angles from one another. While this approach achieves perhaps the ultimate in simplifying the overall structure of the variable system, it does so by sacrificing the natural analogy to normal physical spaces, and can make the production of accurate graphics difficult. Oblique rotations can be useful, but they are not for the faint-hearted. As for names, olbimin, quatrimin, biquartimin, orthoblique and promax are all oblique rotation methods.

Let's finish by applying the varimax rotation to our trilobite factor results. Table 8 shows the equations of the unrotated and varimax-rotated factor loadings.

Table 8. Alternative factor loading positions for trilobite data.

Factor Loadings (Unrotated)		
Variables	F1	F2
Body Length (x1)	0.954	0.285
Glabella Length (x2)	0.972	-0.041
Glabella Width (x3)	0.959	-0.242

Factor Loadings (Varimax Rotated)		
Variables	F1	F2
Body Length (x1)	0.501	-0.861
Glabella Length (x2)	0.737	-0.636
Glabella Width (x3)	0.866	-0.480

Figure 4 shows our three variable axes in their unrotated (A) and varimax rotated (B) positions.
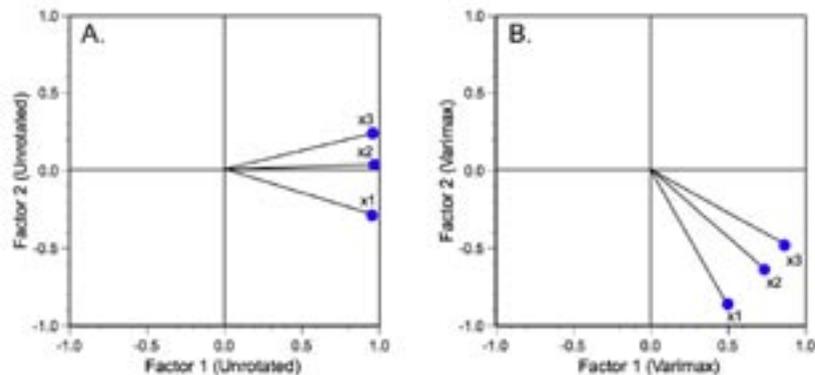
Figure 4. Alternative positioning of factor analysis reference axes for the trilobite dataset.

There are two ways to look at these tables and plots. One can either regard the factor axis coordinate system as fixed and the factor loading vectors as having rotated about the coordinate system origin (this is the sense you get from the figure), or you can regard the factor loading vectors as fixed and the factor axis system as having rotated about the common vector origin.[5] Either way the result is the same.

Because the original variables are all highly correlated with one another (see Table 6), the unrotated factor axes all exhibit low angles relative to one another. This is also typical for morphological data. The two glabellar measures lie at a smaller angle to one another than either do with respect to the body length variable. These relations are preserved during varimax rotation. But note how the rotation does make the geometric relations between the variables clearer in Table 8. This is important because the interpretation of these relations would normally be gauged on the basis of the factor loading table. After varimax rotation it is much clearer how close the orientations of these variables are on the dominant F1 axis. The linkage

[5] In this particular analysis the new axes would form an angle of 45° with the unrotated factor axes.

between the glabellar measurements is also present on the subdominant F2 axis, though it is a little harder to see because, after rotation, there are no longer any distinctions in the loading signs. Nevertheless, these distinctions are still there in terms of differences in the F2 loading magnitudes.

Because the varimax is a rigid, orthogonal rotation, interpretation of the factor scores for the set of genera is not enhanced in the same way as interpretation of the factor loadings (Fig. 5). For this example in particular, the somewhat arcuate distribution of the genera against the two common factors is largely unchanged, leading to the factor score plot being little more than a rigid two-dimensional rotation of the unrotated scores. Had more variables been involved, some adjustment of the relative positions of individual taxa within the subspace defined by the first two factor axes might have been noticed.
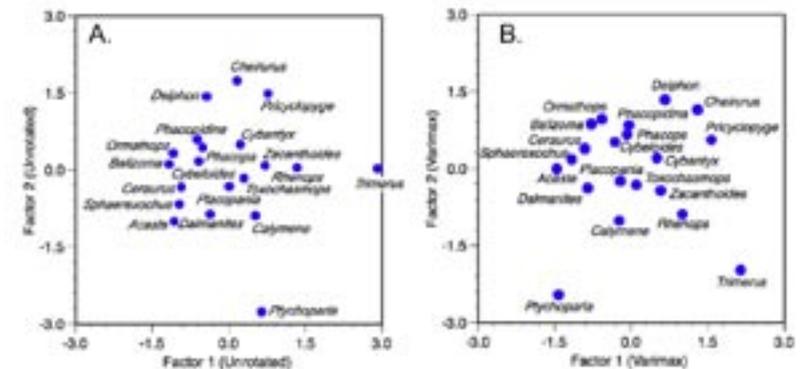

Figure 5. Unrotated (A) and varimax rotated (B) factor score plots for the trilobite dataset.

Factor analysis has a long and distinguished history in palaeontology. Imbrie and Kipp (1971) based their transfer-function approach to palaeoclimate modelling on factor analysis. The late Stephen Jay Gould—who was building an innovative career as a quantitative palaeontological data analyst before he became 'side tracked' by punctuated equilibrium—used factor analysis extensively for a variety of morphological analyses (*e.g.*, Gould 1967, Gould and Garwood 1969, Gould and Littlejohn 1973). Jack Sepkoski learned his factor analysis from Gould while at Harvard as Gould's student and went on to employ the method in his studies of Phanerozoic biodiversity (*e.g.*, Sepkoski 1981). Indeed, Sepkoski's three evolutionary faunas were originally recognized on the basis of a loading-pattern analysis on a three-factor model of his diversity data.

From a computational point-of-view, factor analysis is not problematic. Nevertheless, owing to ongoing confusion about its relation to PCA and owing to the sheer number of approaches to factor analysis available, it has not been well implemented in a number of standard data analysis packages. For the most part, these packages treat PCA and factor analysis as more-or-less variants of each other. This is understandable to some extent in that there is a genuinely large group of methods and techniques that can be applied to either PCA or factor analysis results. For example, axis rotation can be applied to the results of a classical PCA as easily as to the results of a factor analysis. The advantages of this operation will be largely the same in both cases. Similarly,

the operation that scales the lengths of the eigenvectors by the eigenvalues can also be applied within the context of a PCA as easily as in a factor analysis. Most mathematical discussions of PCA include presentation of these variations. However, for me the single computation that marks out the boundary between factor analysis and PCA is the manner in which the factor scores are calculated (equations 6.5 or 6.6). Ironically, this is the aspect of 'factor analysis' that has received comparatively little attention by those seeking to extend or vary the method. Then again, perhaps that's telling us something. This normalizing computation that lies at the heart of the factor score calculation signals a basic change in the manner in which one is treating the raw data. Under the classic PCA approach, such a normalization would not be considered because the data are not regarded as having to be 'corrected' for any intrinsic aspect of their variation. There is no error term in the basic PCA model (see *PalaeoMath 101: Principal Components Analysis [Eigenanalysis & Regression 5]*, Equation 5.1). There is—irreducibly—an error term in the factor analysis model (see equations 6.1 and 6.2). This changes everything in terms of the concepts and computations involved in factor analysis.

Therefore, if you run across a computer package (and you will) that uses anything other than the raw eigenvector matrix to compute the PC scores, it's likely that the package is confusing the distinction between classical PCA and factor analysis in favour of the latter. Similarly, though less frequently, you might find a package that computes for factor scores directly from the eigenvector matrix. In this case such a package would be confusing a factor analysis with PCA. Fortunately, the computations involved in performing both analyses are not difficult and, if you're careful, can be readily carried out in MS-Excel (see example worksheet) augmented by a macro routine to extract the eigenvalues and eigenvectors of a symmetric matrix (*e.g.*, PopTools). Alternatively, you can easily write your own PCA and/or factor analysis programs in various mathematics programs like *Mathematica* or *MathCAD*. If you must use the routines provided in dedicated, commercial software, please be careful to understand what these programs are actually doing to your data and how their results are being obtained. Otherwise you are very likely to make incorrect, or incomplete, interpretations.

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Don't forget the *Palaeo-math 101* web page at <**http://www.palass.org/pages/Palaeomath101.html**>

Addendum to *PalaeoMath 101: Principal Components Analysis [Eigenanalysis & Regression 5:*

A correspondent who wishes to remain anonymous recently pointed out that, in my preliminary discussion of allometry toward the end of the last essay I may have inadvertently confused careful readers by seeming to imply that the loadings on an isometric PCA vector must be equal. This indeed, is the case, but only once the data have been log-transformed first, as per the standard linear transform of the allometric equation ($y = x^m$ is the same as $log\ y = m\ log\ x$). As promised last time, an entire column devoted to the analysis of allometry is scheduled for the near future. Many thanks to my anonymous friend for bringing this to my attention.

MYSTERY FOSSIL

Well, it appears that – with a run of eight mystery fossils – no more mysteries remain to be resolved, or at least we've not received any more submissions. That's a pity, because the super sleuths among us have begun to make headway on our backlog.

Take bizarre and mysterious 'Mystery Fossil Number Eight' from the Pliocene–Pleistocene Nicosia Formation, Cyprus. Liz Harper at Cambridge and John Taylor at the NHM have identified this as (most likely) *Stirpulina bacillum* (Brocchi). To the uninitiated this is a bivalve from the group commonly known as "watering pot shells" – superfamily Clavagelloidea, family Clavagellidae. These strange molluscs have a tube and an anterior pedal disc with radiating projections (the 'foot' tubes in the original Mystery Fossil description). "Normal bivalve shell valves" are embedded into the tube near the base. The animals live vertically-oriented in the sediment with the posterior tube projecting above the surface and the anterior "watering can rose bit" embedded. The anatomy and functional morphology of these strange animals have been extensively studied by Brian Morton (2002a, b) and the formation of the tube by Harper & Morton (2004).
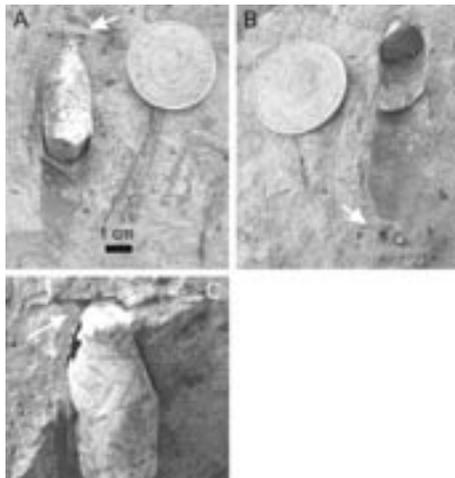
Surely there are more mystery fossils out there requiring the collective knowledge and expertise of the Palaeontological Association? If so, send a JPEG and a few details to <**c.little@earth.leeds.ac.uk**>

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——OBITUARIES——

Norman Dennis Newell
1909 – 2005

Norman D. Newell died on 18th April 2005 – a few months after celebrating his 96th birthday. Thus came to a close a distinguished and varied career that had begun in his undergraduate years at the University of Kansas in the 1920s and which had only begun to slow a year or two before his death.

Son of a dentist who died when he was only 13, Norman was raised by his mother whose support he deemed crucial to his early success as winner of a state-wide clarinet competition, and as a student embarking on what would prove to be a hugely productive scientific career. Indeed, with the Paleontological Society Medal, The Geological Society of America's Penrose Medal, plus elected memberships to the National Academy of Science and the American Philosophical Society, *etc. etc.* – Norman was an award-winner in whatever he set out to do. And though he struck one as far more interested in the job at hand than any rewards of fame or fortune his work might engender, it must also be said that Norman always took a simple, almost innocent satisfaction whenever any new piece of public recognition came his way. Clearly his mother loved him – as did his Aunt Mame, his wife Valerie of 43 years, and his constant companion Gillian, whom Norman married after Valerie's death in 1972, and who survives him now. Norman was talented – but as he himself often said, also fortunate in his life's circumstances.

Being in the right place at the right time (another thing Norman said about his life) is always a major component of success. Norman was lucky to have been exposed to the redoubtable bulwark of American invertebrate palaeontology, Raymond C. Moore, while a student at KU (he stayed there through his Master's degree, awarded in 1931). J.B. Knight was also there at the time – Norman recollecting him as a man of keen intellect and exacting standards who, as a man of independent means, was conducting a "leisurely" life of research. Though both men tried to mould young Norman to their own tastes of what an invertebrate palaeontologist should be, it was only after Norman went off to Yale for his Ph.D. (obtained in the lightning-quick speed of only two years – how times have changed!) that he fell under the sway of the retired-yet-very-much-still-active Carl O. Dunbar, the older man who seems to have impressed him most. Dunbar was apparently quite deaf by then, so he shouted his part of the conversation with his assistant, and, in his adjacent office, Norman had no problem picking up pearls of Dunbar wisdom through the wall. Norman quotes Dunbar as having said that when *he* was a youth, he could identify pretty much all the known North American invertebrate fossils; but *now* he pretty much doubted he could confidently identify a single one! It was a new age, symbolized to Dunbar by the high standards of intensity of observation and meticulous description of fossils of his former student, G. Arthur Cooper. Norman and Gus Cooper soon became friends, and remained so throughout the remainder of Cooper's long life.

Newly-minted Ph.D. in hand, Norman returned to both the Kansas Geological Survey and, additionally, to the University of Kansas as a faculty member for three years, before becoming Associate Professor of Geology at the University of Wisconsin, Madison in 1937 – a position he held until 1945. During the war years, Norman was assigned to map potential oil deposits in the jungles of eastern Peru – and is well remembered, as well, for his mapping around Lake Titicaca during the same period. Though his Peruvian work became known more for his contributions to stratigraphy and Andean tectonics than to palaeontology, it was with great delight that, as I embarked on a study of Devonian Malvino–Kaffric trilobites in the 1970s, I found a small but choice collection of specimens Norman had collected thirty years before – nicely amplifying the massive collections from Bolivia and Argentina which had come my way. Norman was always true to his first professional love: fossils!

Norman came to Columbia University and the American Museum of Natural History in the sort of joint appointment held by Bobb Schaeffer, Ned Colbert, and George Gaylord Simpson. Simpson ran the department, and the younger members often had to scrounge for research support. Invertebrate palaeontology (or so Norman used to grouse periodically) was the lowest priority in those days, and it wasn't until 1960 that Norman got the autonomy he so clearly craved, becoming chairman of the aptly dubbed "Department of Fossil Invertebrates" in 1960.

Norman is best known for his work on fossil bivalves. He loved his Upper Palaeozoic (and, later, Triassic) clams with a quiet passion, spending by far the greater part of his research time over the years collecting them, overseeing their preparation and photography, poring over them, measuring them, comparing them – and then writing them up in monograph after monograph (in later years, invariably with his colleague, former student, and man of universal good cheer, Don Boyd of the University of Wyoming). The first two volumes of the *Bivalvia* component of the *Treatise on Invertebrate Paleontology* (1969), compiled and published under Norman's direction, was a significant milestone in Norman's career in bivalve palaeontology and systematics.

And yet Norman, for all his single-minded dedication to bivalve palaeontology, always had an eye out for the deeper meaning of his fossils. It began with his monographs on Upper Palaeozoic Mytilacea and Pectinacea in the 1940s. The Pectinacea, especially, moved Norman to illustrate successive species as a phyletic series – if emphasizing a gradualistic interpretation, at least in step with historical presumptions. He did this at a time when invertebrate palaeontological discussions of evolution were at an extreme low ebb – at least in American palaeontology.

Then came Norman's homage to Charles Lyell: the Permian reef complex of West Texas attracted his attention in the late '40s – and prompted him further afield, to the carbonate sediments of the Bahamas platform, because (of course) "the present is the key to the past." Norman's work in both places was interdisciplinary and very much a team affair – with colleagues, graduate students and American Museum of Natural History support personnel all involved in what in both places was a major effort of mapping, description and analysis. If palaeoecology has sometimes seemed a derivative matter of applying ecological aperçus of the modern world to past environments, Norman actually turned the tables – finding much to say about both ancient and modern environments on their own, and by applying what he had learned in the Texas Permian in his studies of Bahamian carbonates.

There's plenty more: Norman's forays into reef formation in the Pacific (where he begged to differ a bit with Charles Darwin); his thoughts on paraconformities and the general problem of time

in stratigraphy; his study (with Leslie Marcus) on the amazingly tight correlation between the amount of CO_2 in the atmosphere and global human population (meaning you can count heads by measuring CO_2) and the ominous things such a correlation portends; and, keeping in the realm of social ramifications of his professional interests, Norman's passionate attempt to ward off creationism's threat to the integrity of science education in the United States (alas, as current events show, sadly futile).

But it is Norman's focus on mass extinction which may well prove to be his most lasting gift to us all. In the mid-twentieth century, it is fair to say that Norman D. Newell was the most prominent (I usually say "only" – but I concede I might be wrong about that) scientist of any sort who saw that mass extinctions are real events – events, moreover, that have profoundly altered the history of life.

Indeed, from today's perspective, it is easy to see that extinction is part and parcel of the evolutionary process. But, as acolytes in the late 1960s in Norman's (and Roger Batten's) graduate student seminars, we used to despair of hearing Norman discuss evolution. Extinction to us was the "down side" – we wanted to talk about evolution! (Steve Gould, a fellow graduate student in those days, once despaired after a two hour seminar session, saying "I swear that man will recant natural selection on his death bed!" Norman did no such thing, of course).

A few years later, as a very junior American Museum colleague (thanks to Norman), I got into a polite, but very intense and almost painful, argument with him about the new-fangled cladistics. I was insisting on the primacy of genealogical relationships – whether in doing systematics, or indeed understanding the evolutionary process (which I still take by far to be the more important of the two). Norman dug in his heels and quietly, stubbornly and very irritatingly (to me) insisted that *evolution is first and foremost the temporal sequence of life.* Say what you will about time missing in the stratigraphic record and the problems in recording life's traces in the rocks (taphonomy, a valuable field – but a subject, after all, invented by Charles Darwin to allow him to sidestep palaeontological inconveniences as he sought to characterize the basic elements of evolutionary pattern and process): say what you will, the stratigraphic sequence of life *is* evolution.

Norman was right. Sure, genealogy is important. But it is by no means the whole story. Clades do not evolve in a vacuum; rather biotas come and go. The way some of us are fitting these pieces together now did not always meet with Norman's wholehearted approval. But without him showing us the way – including some of his very students who in their callow youth thought him hopelessly old-fashioned – the modern relevance of palaeontology finally to effecting a theory of evolutionary process that accounts for many of the major features of life's history would not be in its promising current state.

Norman had no biological children of his own, but he left a passel of graduate

Norman Newell with Stephen Jay Gould and Niles Eldredge

student kids behind him. A partial list includes Al Fischer and Bernie Kummel (long-time faculty members at Princeton and Harvard, respectively); Victor Benavides, the Peruvian geologist; the Permian reef years produced dissertations from Roger Batten, Don Boyd, Ellis Yochelson, Frank Stehli and J. Keith Rigby; and later, Alan Cheetham, Tom Waller, Bud Rollins, Steve Gould and myself. His lineage has flourished – but his effect is not just monophyletic: for as Norman taught us to think about evolution as a succession of biotas through time, his influence transcends his close colleagues and students – and richly informs all of us in our slice of time, as we seek to make clear the lessons of the fossil record.

The Norman D. Newell fund, established in 1994 at the American Museum of Natural History in New York in recognition of Norman's long and distinguished career, supports research in invertebrate palaeontology. Grants have been awarded primarily to students, and to palaeontologists visiting the American Museum to examine fossil collections and to interact with Museum staff. Inquiries (whether for support or donations to the fund in Norman's honour) should be directed to Dr Neil Landman, Division of Paleontology, AMNH <**landman@amnh.org**>.

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Nancy Kirk
1916 – 2005

Nancy Kirk, who died on 4th September 2005, was born in Mansfield on 15th June 1916. Her mother had died when she was a young girl, so she and her older brother were brought up mainly by their father, who had worked his way up from office boy to manager of a local factory. In 1935, as a pupil at Mansfield's Queen Elizabeth's Girls' Grammar School, she won an exhibition to go up to Newnham College, Cambridge, where she read Natural Sciences. As a student she never had much money, and despite her frugal lifestyle (which continued for the rest of her life) she was always so broke that she cycled home at the end of each term.

Nancy originally intended to specialise in Botany, but found the teachers very dull. She was, however, inspired by some members of the Geology Department, particularly Brian Harland, Teddy Bullard, and Professor O.T. Jones. In 1939 she achieved first class marks in the geology finals examinations (this was before Cambridge awarded degrees to women) and was awarded the Bathurst Prize. The award of a Harkness Scholarship, followed by a Bathurst Research Studentship, allowed her to start research on

the geology of the faulted country of part of what is now Powys, between Pont Faen (Breconshire) and Presteigne (Radnorshire), under the supervision of O.T. Jones.

Her studies were interrupted by the war. In 1942, following a period in the Land Army, she was sent to the Royal Ordnance Factory, where she was involved in war work until 1945. Her experiences there were important in moulding her life, both in terms of the factory floor language that she often used, and in her attitudes to authority. On one occasion she produced a report on why so many bombs produced at the factory were being rejected. She had found that a critical part in one machine had been fitted back to front. The only apparent result of her report was that she was banned from any further checking of machinery!

Nancy returned to Cambridge in 1945 on a two year Jenner Research Fellowship, after which she supported herself on money that she had saved. She was awarded her PhD in 1949, and then worked at Birmingham University for a couple of years, before moving to live in her field area, where she continued her geological mapping. It was during this period that she submitted some very long, detailed papers on her research to the Geological Society of London, and felt that the editor's demands for major cuts were due to a chauvinistic attitude to science. Unfortunately she did not feel able to consult anyone else about the problem, and years later admitted that she should have taken more note of the fact that the Society had problems with paper rationing and was advertising the fact that they could not print any long papers. The research was never published, although Xerox copies of her map and thesis were sought-after objects by later workers.

In 1953 Nancy was appointed assistant lecturer in the Geology Department at Aberystwyth, and promoted to full lecturer in 1955. She continued working in the department long after her official retirement in 1983. At first, as one of four academic staff in the department, she had a heavy teaching load, mostly involving palaeontology, stratigraphy and map interpretation. With additional appointments, particularly in the 1960s, she managed to find more time for research. She is remembered by generations of students for the care and effort that she put into teaching, particularly the help that she gave to people who were having difficulties. She was also memorable for her dress sense (usually looking like she had just come in from the field), and her colourful language.

When, in the late 1960s, Nancy Kirk first presented her ideas about the ecology, mode of life and evolution of the graptolites to the Geological Society of London, neither she, nor the shocked graptolite experts, had any notion that the study of graptolites would take over the rest of her life. She had formulated the concept of graptolites as active colonies, using co-ordinated feeding currents to move up and down through the water column, rather than the textbook picture of passive colonies, often shown as attached to floating seaweed (although Bulman had already discarded this notion). One implication was that the experts had always thought of, and illustrated, these fossils upside down.

Nancy had developed her ideas almost by accident. She was painting her cottage, with all of her possessions piled up under dust sheets, when she realised that she had forgotten where she had left the notes for her lectures to first year undergraduates. Rather than cause havoc to her decorating, she started to write out a new set of notes and, in the process, decided that there was no basis for the traditional interpretation of these important fossils.

Had the experts simply nodded at the end of her talk, and allowed her paper to be published, she would probably have left it at that. But the condemnation of her ideas, and attempts to censor her

paper, reminded Nancy of her previous run-in with the Society's editors. She was not going to make the same mistake again. The decorating was forgotten, and for decades her possessions remained under the dust sheets.

From the early 1970s graptolite research took over much of her time. Determined to show that her ideas were supported by evidence, she embarked on a major study of the detailed structure of a complex group, the retiolites. In conjunction with her colleague, Dr Denis Bates, she spent hours every week examining samples under the scanning electron microscope, and then months poring over the accumulated images. While Denis was the expert in specimen preparation and operation of the microscope, it was Nancy who turned their joint ideas into marvellous three dimensional models. A number of beautifully illustrated papers, containing some radical new interpretations, were eventually produced, although much remains to be published. Their work gained them an international reputation and the next edition of the graptolite *Treatise* will draw heavily from their work.

Apart from her academic work Nancy will be remembered partly for the beautifully decorated pots that she made, but mostly for the magnificent garden that she created around her cottage on an isolated three acre site near Llanafan in the Ystwyth Valley. She began by planting a set of formal rose gardens, but soon ripped these out and developed a flowing palette of azaleas and rhododendrons. Most were grown from cuttings, usually taken with permission, but once the garden began to mature she concentrated on growing new varieties from her own seed. The names she gave to these new varieties reflected her impish sense of humour. She felt that new plant varieties should not always receive names that suggested romantic themes, so used names like Parazone and Harpic, after domestic cleaners.

Living in isolation mostly suited Nancy, as she was able to indulge her taste for discreet naturism. In later years she would laugh at the memory of an unexpected visit from a rather prudish senior colleague and his wife, who arrived as she was fixing slates on her roof, clad only in her walking boots. She did start to worry for her safety when, in the late 1970s, the valley was subjected to an annual invasion of hippies collecting magic mushrooms. Several properties were burgled, but fortunately they never found her garden in the woods. Eventually she moved into a bungalow closer to Aberystwyth, where she created a couple of miniature gardens.

Whatever she was doing, Nancy was single-minded in pursuit of her goal. When, at one point, there were problems with funding a new scanning electron microscope, Nancy produced much of the money from her bank account as she wanted to get on with her research. She would rope in helpers for any of her projects, and many remained willing workers for years. She could never have produced her Llanafan garden without the help of John Corfield, who first met her when she was scrounging plants from the Aberystwyth botany gardens.

Like many at Cambridge in the 1930s, Nancy was a committed Marxist. She found much of modern consumer culture distasteful, was particularly concerned about the rapidly increasing world population, and had little time for most modern politicians. Nancy never married, although there were hints that she may have been remaining true to the memory of a close friend who was killed in the Spanish Civil War. It was appropriate that the *Red Flag* was played as her body was carried to its green burial.

Antony Wyatt, with contributions from **David Loydell** and **Denis Bates**

CREATURES OF THE BURGESS SHALE

EXHIBITION AT ELGIN MUSEUM, AUTUMN 2005 TO AUTUMN 2006, ILLUSTRATED BY HANNAH CAINE

SANTACARIS

Graphite Dust on Bristol Board

HANNAH IS A 19 YEAR OLD, THIRD-YEAR GEOLOGY STUDENT AT ABERDEEN UNIVERSITY. TO COMPLEMENT HER ACADEMIC STUDIES SHE LIKES TO USE HER SKILLS AS A PALAEONTOLOGICAL ILLUSTRATOR, AND HAS NOW BEEN GIVEN THE OPPORTUNITY TO SHOW HER WORK PUBLICLY THROUGH THIS EXHIBITION.

CONTACT HANNAH FOR FURTHER INFORMATION: e-mail <**u01hlc3@abdn.ac.uk**>

Meeting REPORTS

Seventh International Congress on Rudists
The University of Texas at Austin, Austin, TX, USA   *5 – 11 June 2005*

The seven day, six night International Congress on Rudists, the first to be held in the United States and only the second to be held outside Europe, was an enormous success. This international conference, which was inaugurated in Belgrade in 1988, has also been convened in Rome, Mexico City, Marseille, Nürnberg, and Rovinj, Croatia. The most recent incarnation included 45 participants from 13 countries; the three days of formal presentations consisted of 34 oral talks and 24 posters. The meeting's official title was "Cretaceous rudists and carbonate platforms: environmental feedback",

The congress was held in Austin on 5–11 June, and was supported by the Texas Memorial Museum and the John A. and Katherine G. Jackson School of Geosciences at The University of Texas at Austin, and the Tulsa University Department of Geosciences. Ann Molineux of the Texas Memorial Museum and Bob Scott of Precision Stratigraphy and Tulsa University served as co-chairs of the meeting. This congress was dedicated to the memory of Professor Keith Young, the local doyen of regional Cretaceous stratigraphy. Although his work mostly centred on ammonites, Keith also embraced the rudist faunas of Texas and Mexico, many of which were first studied by him and his legion of students. Warm tributes were paid by some of these former research students at the ice-breaker held in the Texas Memorial Museum on Sunday night. This event was attended by most conference participants, members of Keith's family, and donors to the Keith and Ann Young Endowed Fund for Curation of Non-vertebrate Collections. We witnessed a presentation to the first recipient to be partially supported by that endowment. Keith's death in August 2004 had unfortunately robbed him of the opportunity to attend this meeting, to which he had so looked forward.

Investigation of the first of three overarching congress themes, "Depositional environments of Cretaceous carbonates," began early on Monday morning with the first poster session. These were each briefly introduced by their authors, and then allocated group viewing time. Tuesday commenced equally early with the topic "Origins, events and demise of rudist paleocommunities," while Wednesday wrapped up with our third general theme "Towards rudist taxonomy, biogeography and phylogeny". Each theme included the morning poster session as well as three oral sessions each day. These presentations addressed an impressively wide variety of topics in addition to more specifically rudistological issues, including: palaeoenvironments, sea-level change, sequence stratigraphy, geochemical signals used both for correlation and in the analysis of past conditions, mass extinction, community dynamics and sclerochronology.

The palaeoecological front was addressed on Monday by the poster of **Daniela Ruberti** and colleagues from Naples, which documented the formation of rudist lithosomes in shifting subtidal sediments filling complex channel-like depressions on late Cretaceous low-angle microtidal shelves in southern Italy. Nor were rudists the only *dramatis personae* of the palaeoecological sagas: **Alan Moro** and colleagues from Zagreb reconstructed the size and type of dinosaurs who stomped right

over the tops of rudist biostromes in Istria (Croatia), in both shallow subtidal and intertidal settings. Patterns of sedimentation over longer time-scales were addressed by **Luis Pomar** (Mallorca) with colleagues from Barcelona and Texas, who explored the interplay between rudist buildups and calcarenite wedges in the Santonian of the southern Central Pyrenees.

Adding a broader perspective, **Markus Rauch** and **Thomas Steuber** (Bochum) investigated Sr/Ca ratio changes in original rudist calcite, attributing them to changes in marine biogenic aragonite/calcite ratios (aragonite itself being a relative strontium 'mop'), and thus implicating an intriguing biotic feedback to ocean chemistry. They also expanded on Steuber's earlier work on changing Mg/Ca ratios, confirming a Cretaceous low of about 1:1 in the Barremian. In the biotic turnover department, **Müge Fenerci-Masse** and **Jean-Pierre Masse** (Marseille) classified Lower Cretaceous rudists into two broad assemblage types: one dominated by relatively large, thick-shelled forms thriving in open marine settings, and the other by smaller forms living in relatively more restricted or very shallow conditions. Surveying the changing constitution of these, they demonstrated successive preferential extinctions among the former with subsequent restocking from the latter.

On Tuesday, **Tvrtko Korbar** (Zagreb) illustrated smaller scale palaeoecology by means of serial sectioning the remarkably plastic growth of the radiolitid Biradiolites angulosus as it 'searched' laterally for attachment while growing upwards, creating quite a problem for taxonomic recognition. This latter point is an important consideration in general for rudists which, like oysters, lacked a foot and so could only grow their way out of trouble following larval settlement. At a still finer scale, the spectacular poster of **Ivan Regidor-Higuera** and **Patxi Garcia-Garmilla** (Bilbao) analyzed the characteristic layered cellular pattern of growth of the outer shell layer of radiolitids in unprecedented detail. They provided robust confirmation of tidal signatures in the cell layers, explored the diagenetic consequences of related variations in organic content in the prismatic microstructure of the cell walls, and even offered the possibility of detecting relative depths of growth with respect to the tidal range.

Participants were also treated on the Tuesday to the viewing of an Open University video on the sequence stratigraphic analysis of Albian-Cenomanian platform limestones in Istria, made immediately after the previous rudist congress there in 2002, and starring **Igor Vlahovi** (Zagreb) and **Peter Skelton** (Open University). Oxygen and carbon isotopes provided the keys for **Gavin Gunter** and **Simon Mitchell** (Kingston, Jamaica) together with **Jim Marshall** (Liverpool) to open the door onto the oceanic conditions in which diverse Maastrichtian rudist associations thrived in Jamaica; these were apparently not especially superheated, unlike their chicken, or indeed some of the earlier publications on this topic. In a poster, **Thomas Steuber** and a multinational team of co-authors used Sr-isotope stratigraphy to establish the latest Maastrichtian age of high diversity rudist assemblages in the Ciolo Limestone of Salento (SE Italy) and in megabreccias in the Ionian islands. It now seems, therefore, that Old World rudist faunas, contrary to earlier wisdom, may have suffered a catastrophic extinction at the K/T boundary, as is already demonstrated in the Caribbean.

Finally, on Wednesday, there was a feast of new taxonomic and stratigraphical data. In view of the venue, there was naturally plenty of news from the New World. **Simon Mitchell**'s study of the Caribbean multiplefold hippuritids (Barrettiinae) represents by far the most comprehensive revision of this major endemic group yet undertaken, based on consideration of an impressively wide range of characters. These have enabled him to disentangle a number of distinct lineages (implicating some new generic names) and thereby to resolve earlier taxonomic confusion, especially concerning the species of Barrettia itself. His work will surely boost the stratigraphical usefulness of these widespread and common rudists and looks set to become a classic in the field. Meanwhile **Harry Filkorn** (Los Angeles Natural History Museum) took us on a colourful adventure down a seemingly bottomless gully in California, to locate the first Praebarrettia (one of Simon's patients) to be found on the Pacific coast of North America. Further south, in Baja California, **Stefan Götz** and colleagues beautifully illustrated the well preserved inshore associations of Coralliochama. Back in the Caribbean arena, **Hernan Santos** (Mayaguez, Puerto Rico) sorted out the stratigraphy of southwestern Puerto Rico, tying its complex relationships to a combination of volcanic/tectonic activity and relative sea-level change. From one of his units, the Santonian Cotui Formation, he, **Simon Mitchell** and **Peter Skelton** described the stratigraphically oldest known antillocaprinids, which are another important endemic group that had previously been regarded as virtually limited to the Maastrichtian. This family, incidentally, includes the largest-shelled rudist species on record (up to 2 m in diameter), the aptly named Titanosarcolites giganteus (too bad that it hasn't yet turned up in Texas!). Lower in the stratigraphical column, **Bob Scott** and **Harry Filkorn** provided a rudist zonation of the US Gulf coast for the Barremian–Albian interval, linking the globally registered earliest Aptian Oceanic Anoxic Event (OAE) with the demise of the Sligo Platform. In the age-equivalent El Cajón Formation of SE Mexico, **Jerjes Pantoja-Alor** (UNAM, Mexico) and **Harry Filkorn** recorded the youngest known megalodontids. There was also plenty of regional rudistological news from the Old World, with reports from Spain, Italy, Austria, Croatia, Greece, Turkey, Iran and the Himalayas, Oman, Egypt, Tunisia and Algeria, and ranging from the Upper Jurassic to Upper Cretaceous.

As for après-conference activities, the group was entertained on Monday evening by a jazz trio and the vocal stylings of numerous participant opera enthusiasts. Extreme excitement was palpable on Tuesday afternoon as we visited an Albian rudist-packed core from the Pawnee Field, west of Houston, at UT's Bureau of Economic Geology (BEG). This tour was followed by an open session

at the Non-Vertebrate Paleontology collections, whose impressive size and breadth of rudist coverage outweighed any tiny inconvenience introduced by lack of cataloguing, inventorying, or air conditioning. Finally, Wednesday evening witnessed the launch of a rudist paddle-boat cruise on Austin's own Colorado River, accompanied by a local musician and delectable fajitas.

The Congress also included three optional and exemplary field trips, two before the Congress proper and one following. The first was led by **Charlie Kerans** of the BEG, and investigated the Pecos River gorge of West Texas. This river exposure, which consists of some 60 km of continuous section along the gorge, runs through an uppermost Albian platform (more ramp, really) succession from its northern interior towards the southern Maverick Basin. The stratal anatomy here is mappable straight from the canyon walls, a technique that Charlie and his colleagues have been performing for the last few years, using a high-tech combination of lidar and photography. This fact provided an exceptional opportunity to put the palaeoecology of these abundant rudists and other taxa into a sequence stratigraphic context. The second, one-day field trip took place on 5th June, the day before the meeting commenced. **Leon Long** of the Geology Department at UT led a fascinating trip to view the geology of the Austin area. This included a portion of the Llano Uplift, where an episodic Precambrian granitic batholith pokes through the otherwise ubiquitous Texan Cretaceous cover, and finished with a lovely set of Cretaceous dinosaur trackways.

The post-meeting field-trip, led by a veritable army of guides, spanned the entire regional Albian succession, from the Lower Albian Glen Rose Formation to the Upper Albian formations of the Edwards Plateau in the West, and included a string of classic and spectacular Texas localities. We also visited a Texas winery, including tour and tasting, and enjoyed an authentic Texas cultural experience with barbeque and music at Luckenbach, where everyone is somebody. The trip concluded with a musical (as always) dinner and a tour of a stone cutting quarry.

The meeting proceedings will be published as a special publication of the Society of Sedimentary Geology (SEPM) some time in 2006. The "Abstracts and Post-Congress Field Guide" has already been published, and is also available from the SEPM, at <**http://www.SEPM.org/**> or at the Congress website at <**http://www.tmm.utexas.edu/npl/Rudist2005/congress.htm**>. The latter also includes information regarding the conference and some very entertaining pictures. Please be advised that the next, 8th International Congress on Rudists will be held in Turkey in 2008.

Nina Triche
The University of Texas at Austin

Peter Skelton
The Open University

<table>
<tr><td>**5th Regional Symposium of the International Fossil Algae Association**
Ferrara, Italy   *30 – 31 August 2005*</td></tr>
</table>

The 5th Regional Symposium of the International Fossil Algae Association was principally organised by Davide Bassi and Anna Fugagnoli of the Dipartimento delle Risorse Naturali of the University of Ferrara. This symposium follows the tradition of successful regional meetings previously held in

Granada (1989), Munich-Vienna (1993), Cracow (1997) and Cluj-Napoca (2001) (see <**http://www.ku.edu/~ifaa/**>).

Presentations were offered in three sessions: general themes, calcareous red algae, and calcareous green algae. A total of 31 presentations were made over two days. Delegates from several countries (Italy, France, Germany, Spain, Sweden, Slovenia, Croatia, Israel, China, U.S.) attended the symposium. Two workshops were held, one focusing on the classification criteria of Dasycladales and Bryopsidales (Halimedaceae) green algae (chairman Ioan I. Bucur), and the second dealing with the palaeobiogeography of calcareous algae (chairman Juan C. Braga). Titles of the presentations can be found at <**http://www.uni-tuebingen.de/IFAA-regional-symposium/**>. The abstract book has been published in the Annali dell'Università di Ferrara, section Museologia Scientifica e Naturalistica, volume 1.

A post-meeting field excursion focused on shallow water carbonates including Middle-Upper Eocene calcareous algae and larger foraminifera (Colli Berici, Monti Lessini, north-eastern Italy), Lower Jurassic microbial structures, dasycladaleans, larger foraminifera, and dinosaur footprints (Rovereto and Altopiano di Lavarone, Trento area), and dasycladaleans at the K/T boundary (Friuli and western Slovenia areas). The field excursions were organised by the University of Ferrara, the Museo Tridentino di Scienze Naturali, the University of Naples FedericoII, the University of Trieste, the University of Tübingen, the Slovenian Geological Survey, and the Slovenia Academy of Sciences. The field trip guide-book is published in the Studi Trentini di Scienze Naturali, Acta Geologica, supplement 80 (2003).

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<bsd@unife.it>

British and Irish Graptolite Group Meeting
Cambridge, UK   *1 October 2005*

Plus ça change for Big G

A bereavement and a retirement added a certain significance to this Autumn's meeting of the British and Irish Graptolite Group in Cambridge. The date, Saturday 1st October, marked the first day of Barrie Rickards' annuity and a month after Nancy Kirk's passing. It was the end of an unbroken 108 year lineage of graptolite research at the ancient university; it is a lineage that sees its legacy in the thriving **Big G**, many of whom studied at the Sedgwick Museum before migrating elsewhere. As such, the mood was one of continuation rather than resignation.

After a few convivial coffees, the meeting proper convened with **Denis Bates'** (University of Wales, Aberystwyth) entertaining eulogy for the late Nancy Kirk and a respectful silence. Yet the mood soon turned to lively discussion as **Sue Rigby** (University of Edinburgh) revealed the interesting results of her Computational Fluid Dynamic simulations of graptolite functional morphology. Big G stayed in the computer age as **Joe Botting** (University of Cambridge) & **Lucy Muir** (Natural History Museum) advertised <**http://asoldasthehills.org/**>, their website devoted to the Builth Inlier, and **Chuck Mitchell** (State University of New York at Buffalo) unveiled his cladistic analysis of Ordovician graptolites and discussed how we might use the CHRONOS online database as a vehicle to bring the graptolite Treatise towards completion. Away from the highfaluting world of computers and PowerPoint was a series of fantastic displays by **Barrie Rickards** (University of Cambridge) on dendroids from Sweden and Australia, and an account of the first graptolites from the type Ashgill. And so it was with friendly banter that we made our way towards the Cambridge suburbs for a special lunch.

The marvellous spread laid on by Barrie and his partner, Mandy, saw a relaxed afternoon of work and chat as young and old mingled. **Liz Harper** (University of Cambridge) became an honorary graptolithologist when she and Sue brought a youth development squad along. Their children quietly played as the meeting continued: **Andrea Snelling** (British Geological Survey & University of Leicester) and **Mike Howe** (BGS) discussed taxonomic databases with Chuck; **Rachel Backus** (University of Leicester) went over her MGeol work on synrhabdosomes with **Bob Ganis** (Pennsylvania & Leicester); **Jan Zalasiewicz** (University of Leicester) described an unusual fauna he'd unearthed to **Adrian Rushton** (NHM) who was a little unsure as to whether it was page 113 or 114 of Peach and Horne that mentioned it; and amongst all this stood Barrie, one day into his retirement, talking about his latest projects with his usual combination of humility and enthusiasm. It seems there is still much to come from Big G.

So it fell to the group's founder, **Jana Hutt**, and **Peter Warren** (BGS & Royal Society), Barrie's oldest acquaintance at the gathering, to lead the retirement toasts. As the wine flowed and anecdotes bounced back and forth, Barrie called us once more to business, setting a date for the next meeting and discussing Anglo-American links for Big G with Chuck. So, all considered, British graptolithology seems far from extinction, or indeed re-radiation. It may instead be a case of *plus ça change*: Mark Williams has joined David Loydell at Portsmouth, and Jan and Sue lead respective groups at Leicester and Edinburgh; Denis will continue to publish the work on retiolites he began with Nancy; and, as ever, Barrie will still fit graptolites in around his fishing commitments.

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>>*Future* Meetings of Other Bodies

9th Meeting of the European Elasmobranch Association (EEA)
Oceanographic Museum of Monaco, Monaco   *23 – 26 November 2005*

For further details see <**http://www.oceano.mc/**>.

Journées Georges UBAGHS
Dijon, France   *30 – 31 January 2006*

The research team Biogéosciences (Dijon), the French Palaeontological Association (APF), and the French Palaeozoic Working Group (GFP) are very pleased to invite you to a two-day scientific meeting at Dijon University (Burgundy, France) in tribute to the late Prof. Georges UBAGHS (1916–2005), who was one of the greatest specialists of fossil echinoderms.

Contributions (oral presentations and posters) dealing with any aspect of fossil echinoderms (especially Palaeozoic forms), and/or the life and main scientific achievements of Georges UBAGHS are welcome. For further details, please contact Dr Bertrand Lefebvre, e-mail <**bertrand.lefebvre@u-bourgogne.fr**>, or visit the meeting website at <**http://www2.u-bourgogne.fr/BIOGEOSCIENCE/P1T.html**> (If you do not get direct access to the meeting web page, please click on "Actualités" and then "Colloques".)

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

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

IPC 2006: The Second International Palaeontological Congress
Beijing, China   *17 – 21 June 2006*

Following the successful IPC 2002 in Sydney, the Second International Palaeontological Congress will be hosted in Beijing. The conference theme is 'Ancient Life and Modern Approaches', and there will be a wide variety of plenary sessions, general and topical symposia, short courses, workshops

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and special group meetings. The programme will also feature field excursions to the fossil sites that have helped Chinese palaeontology to grab so many headlines in recent years.

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

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

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

Mark the dates in your calendar:

· 17–21 June 2006, Second International Palaeontological Congress in Beijing

· 1st March 2006, registration deadline for early birds

· A second circular about the congress will be posted by the end of October 2005

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

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

The 9th Symposium on Mesozoic Terrestrial Ecosystems and Biota (sponsored by the Palaeontological Association) will take place at the University of Manchester, England, with optional field trips before and after the scientific meeting.

Full details, key dates, contacts, and a pre-registration form can be found on the MTE website at <**http://homepage.mac.com/paulselden/MTE/**>.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Interested persons are asked to register and submit abstracts via the Congress webpage at <**http://bivalvia2006.uab.es**>.

Further inquiries may be directed to Niko Malchus (e-mail <**n.malchus@gmx.net**>).

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

For further details see
<**http://www.gli.cas.cz/GLU_AV/WIT_2006/3rd_workshop_on_ichnotaxonomy.htm**>.

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

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

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

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

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

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

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

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

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

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

FORAMS 2006: International Symposium on Foraminifera
Natal, Brazil   10 – 15 September 2006

Register now to ensure your participation on field trips, workshops, and other events. Updated meeting information (Scientific Programme for Technical Sessions and Workshops, and much more),

online registration forms, and information for the submission of abstracts are available now at the FORAMS 2006 websites so you may register at any time.

The Web addresses are:
New address: **http://www.fgel.uerj.br/forams2006/**
Mirror site: **http://forams2006.micropress.org/**

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

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

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

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

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

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

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

International Federation of Palynological Societies
Bonn, Germany   August 2008

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

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

Progressive Palaeontology 2006

Cambridge

22–23 June 2006

Department of Earth Sciences, University of Cambridge
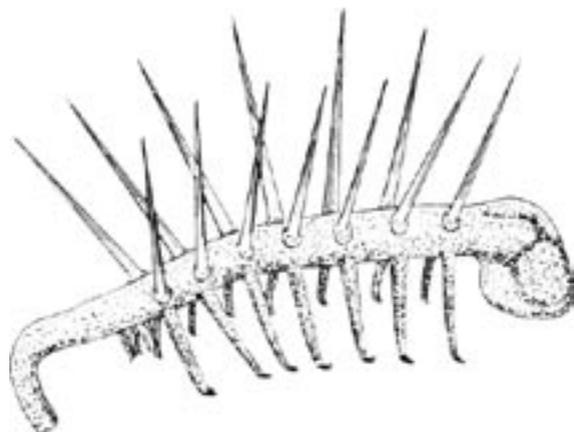
Progressive Palaeontology is an annual conference for postgraduate research students who wish to present their results at any stage of their research. Presentations on all aspects of palaeontology are welcome.

Itinerary to include:

- One day of oral and poster presentations
- Reception at the Sedgwick Museum, Cambridge
- Fieldtrip to the Mesozoic of Cambridgeshire

For more information visit <http://www.palass.org> and follow links to Progressive Palaeontology, or contact one of the following members of the organizing committee:

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

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

Supported by Oxford University Press and the Sedgwick Museum.

Book ◨ Reviews

Sedimentary Rocks in the Field: a colour guide

Dorrik A.V. Stow (2005). Manson Publishing, London, 320pp.
ISBN 1-874545-68-5 £39.95 (Hardback)
ISBN 1-874545-69-3 £19.95 (Paperback)

Manson is the publisher responsible for those two excellent books, much used by undergraduate petrologists, entitled *A Colour Atlas of Rocks and Minerals in Thin Section* and *A Colour Atlas of Carbonate Sediments and Rocks Under the Microscope*. Now they have done something similar with regard to sedimentary rocks at outcrop, in a smaller format 320 page handbook that deserves to be in the Christmas stocking of every earth sciences student in the land – and further afield. It is difficult to know who is more deserving of the plaudits that will undoubtedly accumulate for this book. The author is one of the world's leading sedimentologists, but that is not necessarily any guarantee that they can put together a teaching text of any user-friendliness at all, let alone something as good as this. But the production values are also quite exceptional and the whole design and production team at Mansons (together with the printers in Hong Kong) deserve our warmest congratulations.
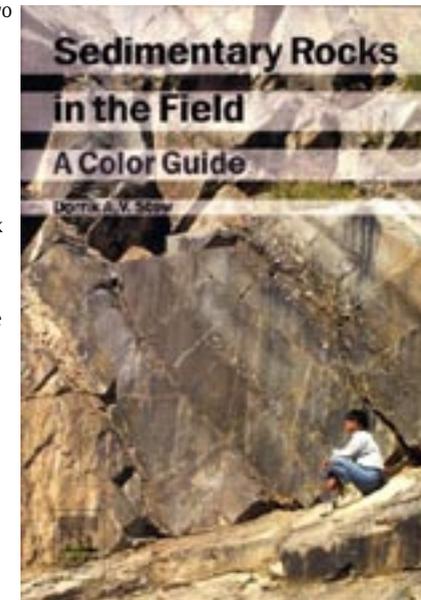
Although this is not a palaeontological publication, it is a book about the environments in which ancient organisms lived, and it deserves the attention of all but the most recalcitrant morphometricists. At one level, the book is a compendium of several hundred full colour pictures of lithologies, sedimentary textures & structures, and outcrops, supplemented by many tables and bespoke line drawings. No picture is smaller than 8 x 5.5 cm and the quality of both the original photos and of the colour reproduction is, almost without exception, quite outstanding. Such is the quality that can be achieved with modern digital techniques that there are even pictures of sediment fabrics and composition as they appear under the hand lens. The material is organised into chapters on all the main sedimentary rock types, with additional chapters on techniques, sedimentary structures, and interpreting depositional environments. Each chapter has linking text, often in the form of lists of features to look out for or to keep in mind when making descriptions.

At a further level, this is a field handbook that tells students everything they need to keep in mind when they are examining and describing sedimentary rocks for themselves, and how they need to

organise their own work in this area. As such it will supersede the long-running Geological Society book *Field Description of Sedimentary Rocks* which, notwithstanding its usefulness, now looks rather like the Beano alongside Country Life. For those of us who do less of that sort of careful description and interpretation than we used to, sit back and flick through this book to be reminded of the sheer beauty and delight of the natural world of sedimentary rocks – there are examples from over 30 countries.

Tim Palmer
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The Evolution of North American Rhinoceroses

Donald R. Prothero (2005). Cambridge University Press, Cambridge, 224pp. ISBN 0-521-83240-3 £60.00 US$100.00 (hardback).

When I started as a graduate student in 1990, I took an interest in fossil rhinos and immediately encountered the name of Don Prothero. He had co-authored a study of rhinocerotoid phylogeny (Prothero *et al*., 1986, 1989) and co-edited a volume on perissodactyl evolution (Prothero and Schoch, 1989). The latter volume summarized new developments in perissodactyl systematics, including the application of cladistic methods, in the twenty years since the work of the last major student of perissodactyls, Leonard Radinsky, to whom the book was dedicated. Interestingly, that volume also presaged a new shift in cladistic methods, as it included the first phylogenetic analysis of perissodactyls using a computer program. Since the early 1980s, Don Prothero had been working on a revision of North American rhinocerotids, based largely on the material in the Frick collection of the American Museum of Natural History, and the culmination of that study is *The Evolution of North American Rhinoceroses*. In the introduction to the book, Prothero notes that the actual study was completed in 1984, and parts of it have been published elsewhere, including the afore-mentioned 1986 phylogeny and chapters in the 1989 volume, but it has taken the intervening twenty years to get into print the vast amount of information necessary for a species-level revision of such a diverse lineage.

After the introduction, the next two chapters cover methodology and the history of the study of North American rhinocerotids. These chapters introduce the running themes of this book, namely that a lack of appreciation for intraspecific variation by early twentieth century workers has led to "over splitting" of rhinocerotid taxa, especially at the species level. Many species were recognized in the past on the basis of differences in premolar morphology, but Prothero argues that quarry samples of what are presumably conspecific taxa (such as the
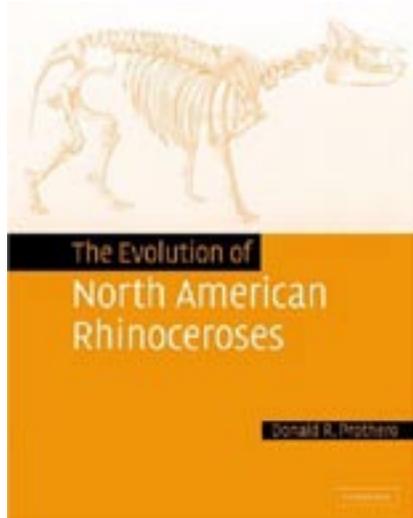
Trigonias quarry from Colorado) demonstrate that these characters vary within species and therefore have limited value for diagnosing species. These ideas are also expressed in Prothero's earlier work on rhinos. The chapter on methods almost exclusively deals with assessment and evaluation of variation; there is no discussion, for instance, of phylogenetic methods. Chapter 3: History of Investigations provides a nice review of the discovery and study of North American rhinocerotids, and will be particularly useful for those workers who deal in rhinocerotid taxonomy.

The bulk of the book is a revision of every North American rhinocerotid taxon down to the species level. Although a few new taxa are named, many more taxa are synonymized, as one would expect to follow from Prothero's conclusion that rhinocerotids are "over-split." The section on systematics is certainly the most valuable part of the book, since it provides a wealth of information on the hypodigms of various taxa, as well as their geographic and stratigraphic distribution. In many cases, Prothero provides detailed diagnoses and descriptions of taxa, but on occasion he simply refers the reader to the original sources. This can be somewhat frustrating, since many of these original descriptions are old, deficient in detail or illustration, and/or not necessarily accurate. In many cases, though, Prothero makes a point of correcting inaccuracies in the original descriptions of various taxa. Although Prothero includes a cladogram outlining the relationships among the genera, you will not find a phylogeny generated from analysis of a character matrix by a computer. Prothero's phylogeny still follows the conventions of the 1980s, with a cladogram and a list of apomorphies for each node. Prothero does acknowledge the work of Cerdeño (1995) and Antoine (2002), who focused on the even messier question of Eurasian rhinocerotid taxonomy, but he makes no attempt to emulate or incorporate their more state-of-the-art methods.

The next chapter provides a description of the postcranial osteology of North American rhinocerotids, which, given the historical emphasis on describing teeth and skulls, is a very welcome addition to our knowledge of these animals. The value of this chapter, however, is considerably diminished by a problem that plagues the book as a whole, which is the poor quality of the figures. There are a large number of figures, and Prothero cannot be faulted for relying heavily on reproductions from other sources. There are also, however, numerous photographs of museum specimens that leave much to be desired. Some of the problems are entirely aesthetic, such as photos where the background was not removed, or where the photograph is too light to see the specimen clearly. More serious, though, is that in many cases the framing of the photo cuts off a significant part of the specimen.

The last two chapters deal with macroevolutionary topics related to rhinos, including biogeography, palaeoecology, and tempo and mode of evolution. While the summary of the spatial and temporal distribution of rhinocerotids will certainly be of interest to palaeontologists of a number of stripes, there is very little in terms of quantitative analyses of macroevolutionary patterns, partly due to the nature of the fossil record.

Who, then, will want to buy this book? Clearly, this is meant for an academic audience, especially one that takes an interest in Cenozoic mammals, and it certainly is a useful selection for any library frequented by a vertebrate palaeontologist. For anyone planning to work on rhinos, it contains a wealth of information on North American specimens and the history of their study. The main deficiency of this study is that its methods have not changed much in the twenty years since the study was originally completed and aren't easily compared to more recent work on perissodactyl

phylogeny. Nevertheless, *The Evolution of North American Rhinoceroses* stands as the only modern comprehensive review of this diverse and intriguing group.

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The Microstructure of Dinosaur Bone: Deciphering biology with fine-scale techniques

Anusuya Chinsamy-Turan (2005). Johns Hopkins University Press, Baltimore, 224pp. ISBN 0-8018-8120-X, £56.50 (hardback).

If any professional palaeontological society were to give an award to a scholar who had overcome tremendous difficulty and disadvantage to achieve great academic success and make substantial contributions to the field, Anusuya Chinsamy-Turan would be the first to get my vote. As a non-white woman raised in South Africa during the apartheid years, she faced tremendous cultural disadvantages in her struggle to get a good education and make something of herself professionally. The proof of her unflagging determination is embodied in her successful academic career, her postdoctoral fellowship in the US with Peter Dodson, and her current position at the University of Cape Town, where she is doing brilliantly. And of course, in her many scientific publications, including this book.
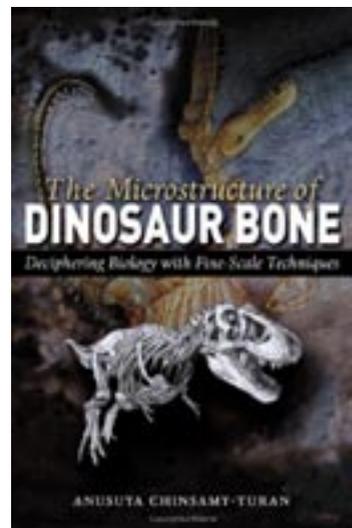
In the 1960s and 1970s, Armand de Ricqlès at the University of Paris was about the only person systematically comparing the microstructure of fossil tetrapod bones with the bones of living animals to see how they grew. Museum curators were loath to allow the destruction of fossil bones for thin-sectioning, so isolated scraps had to be cadged. Usually the skeletal provenance of these pieces was aleatory or unknown, and certainly not capable of standardization. Nevertheless, de Ricqlès and his colleagues in Paris were able to elucidate general patterns of bone growth and tissue expression in fossil tetrapod groups. What he found in dinosaurs was rather surprising, and confirmed the observations of Enlow & Brown, Peabody, Seitz, Gross, and earlier workers: dinosaur bone didn't look like typical reptile bone, but more like the bones of birds and mammals (as did the bones of some "mammal-like reptiles" close to the origin of mammals, and the bones of pterosaurs).

These bones were very well vascularized, which suggested that they grew quickly and that growth was supported by a high basal metabolism (using an actualistic model that had been accepted since the 1940s). In the late 1970s and early 1980s the term "warm-blooded" was used by many palaeontologists to refer to a constellation of physiological properties that, in general, resembled those of birds and mammals more than those of amphibians and reptiles. And, although everyone acknowledged that it was never going to be possible to measure the rectal temperature of an *Allosaurus*, the whole point of the "hot-blooded" debate seemed to be to change the paradigm of dinosaurs as slow, dull, cold-blooded giant lizards. Which model explains more of the evidence, if we use a sliding scale from "crocodile" to "bird"?

Many lines of circumstantial evidence were invoked, and none seemed decisive. There were always exceptions, caveats, red herrings, and false leads. Eventually the entire debate seemed to be in bad odour with professional societies, funding agencies, and even (horrors!) the press. Then, in the 1990s, interest in fossil bone histology picked up again. This time, the focus was on age determination and growth rates, notably in dinosaurs and their relatives. Principles and methods were stressed, and although one eye was nearly always on the general physiological capabilities that the bone tissue profiles suggested, the basic data were mounting.

Chinsamy-Turan's book is particularly strong on describing what bone is, how it is studied microscopically, and what it is capable of telling us. She begins appropriately with the bone structure of birds (living dinosaurs), and explains bone components and tissues. Moving to other living vertebrates for comparison, she constructs a basis for evaluating dinosaur bone – the variety of tissues expressed, how they grew, what they tell us about age and growth strategy, and finally physiology. As she moves from the consensus ground of tissue anatomy, techniques, and the description of tissue types in living and fossil tetrapods, the topics become more controversial. Chinsamy-Turan is variously sceptical, critical, or dismissive of many studies (including some of her own previous conclusions), and this is fine: the samples we have of many fossil taxa are sparse, and there is room for interpretation and uncertainty. But on the other hand, we know more about the ontogeny of bone tissues in some dinosaurs than we do in most large living mammals, and in some respects neontological studies have to play catch-up for a while. More than anything, the various interpretations of fossil bone histology by different researchers reflect philosophical and methodological precepts about evolution, ecology, systematics, and physiology. There is not much disagreement about basic data.

It is in the last couple of chapters that Chinsamy-Turan's interpretations of histological patterns differ from those of other palaeohistological researchers. The differences in zoological philosophy and standards of inference are too numerous and complex for a complete review here, but are

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perhaps best epitomized in two contrasting chapters in another book, the second edition of *The Dinosauria* (eds. D.B. Weishampel, P. Dodson and H. Osmolska, University of California Press, 2004). Both are on the topic of dinosaur physiology; one is by Chinsamy-Turan and Willem Hillenius, and the other is by Jack Horner and myself. Chinsamy-Turan's view of the topic, based on the data from bone histology, is well summarized in her book; but there are other interpretations.

For example, my colleagues and I (Horner, de Ricqlès, and others) have inferred from our studies of various dinosaurs (including birds), pterosaurs, pseudosuchians and other reptiles, that ornithodirans (pterosaurs and dinosaurs, and all descendants of their concestor) grew more quickly to adult size than other reptiles. This pattern emerges when we map subadult bone tissue types on a cladogram based on many other independent synapomorphies. Ornithodirans are the only reptiles to deposit fast-growing fibro-lamellar tissue throughout growth (other reptiles can do it for short periods in some parts of their skeletons, usually during early ontogeny, or when kept in hothouse conditions and superabundantly nourished). All living tetrapods that do this have high basal metabolic rates, and so far no plausible alternative physiological explanation has emerged for the extinct ones. Chinsamy-Turan would not accept most of these statements.

Subadult and adult dinosaurs deposit LAGs (lines of arrested growth, presumed to be annual) in their long bones; Chinsamy-Turan has consistently taken this as an indication of the dinosaurs' inability to resist environmental stress and grow continuously throughout the year, but we prefer another explanation. Annual LAGs are found in ALL vertebrates, except those that are growing too fast to deposit them – as often happens with young individuals, apparently including non-avian dinosaurs. We long ago reported these in elk, and many other researchers have reported them in other mammals and even large birds such as the moa. The problem with birds is that all living forms reach adult size within the first year (even the ostrich), so they do not show LAGs. They seem best interpreted as expressions of endogenous rhythms (which can be manipulated by changing photoperiodicity, as Jacques Castanet and his colleagues in Paris have shown).

Fibro-lamellar bone grows faster than lamellar-zonal bone (typical of pseudosuchians including extant crocodylians). Within the fibro-lamellar complex there are several tissue types (laminar, reticular, circumferential, radial, *etc.*) that differ in the orientation of vascular canals and other features. Ranges of appositional growth rates (microns per day) of these tissue types have been developed for some living birds, notably by Castanet and his lab at Paris. It turns out that different birds deposit these tissues at different rates, and on this basis Chinsamy-Turan concludes that one cannot estimate growth rates of fossil bone tissues based on tissue types. We would disagree for at least two reasons. First, although fibro-lamellar tissue types grow at different rates in different birds (it would be surprising if they did not vary), within the fibro-lamellar complex the order of growth rates of various tissue types does not seem to vary. And second, if one can identify two consecutive LAGs in a bone, and if the LAGs are annual, then the daily appositional growth rate is easily estimated.

As far as we can tell, dinosaurs and pterosaurs had determinate growth; furthermore, like all other vertebrate taxa, large dinosaur species grew at relatively higher rates than their smaller relatives. Birds evolved from small theropod dinosaurs, which although they seem to have grown more rapidly than crocodiles, still grew more slowly than large theropods. Our studies of the dinosaur-bird transition in histology suggest that as birds evolved they truncated that stage of growth (early post-hatching ontogeny) during which they would have grown most rapidly. Hence they became essentially miniaturized adults. Because their non-avian relatives already had feathers, which were used for insulation and other purposes, at this smaller size birds would have almost automatically enhanced the aerodynamic selective advantage of the feathers. Chinsamy-Turan would differ with these inferences about determinate growth and the miniaturization of birds.

Our conclusions in the above paragraphs are detailed in the chapter by Padian and Horner mentioned above; they have been generally supported by other researchers, including Kristi Curry-Rogers and her colleagues, Greg Erickson and his colleagues, Martin Sander and his colleagues, and others. Chinsamy-Turan's book provides a different perspective, which should be read in concert with works by these authors. The contrasts in interpretations and underlying philosophies are deeply interesting and instructive. I recommend her book if you are interested in these questions and lines of evidence, because it has a lot of very good basic data in it and it represents a concise statement of this author's view of a field in which she has made a great many important contributions. The data are by no means all in.

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Dinosaurs of Italy

Christiano Dal Sasso (2004). Indiana University Press, Bloomington and Indianapolis, 213pp. ISBN 0-253-34514-6, £24.95 (hardback).

Lacking the Mesozoic dinosaur record of Britain, France, Germany, Portugal or Spain, our Italian colleagues have long had to make do with Triassic marine reptiles, Cretaceous squamates, and assorted Neogene mammals… not that there's anything wrong with that of course. It is three interesting new dinosaur taxa, and a host of footprint discoveries, that have changed all that, however, and today Italy clearly has something quite important to say about the evolution and diversity of European dinosaurs. Discussed in depth in Dal Sasso's *Dinosaurs of Italy*, these Italian dinosaurs are an interesting bunch, comprising the little baby coelurosaur *Scipionyx*, an early basal tetanuran theropod (informally dubbed the 'saltriosaur') and a new and unusual hadrosaur. But as is so often the case, the title belies the inclusion in the volume of a far greater diversity of Mesozoic reptiles, with two chapters devoted to protorosaurs, pterosaurs, pachypleurosaurs, rauisuchians, ichthyosaurs and others. The book also includes a chapter on the evidence for the KT event preserved at Gola del Bottaccione, near Gubbio.

When first published (in 2001, as *Dinosauri Italiani*), *Dinosaurs of Italy* was the unquestioned premiere source for the new animals and discoveries it discusses. Popular articles (Dalla Vecchia 2001), a technical review (Dal Sasso 2003) and conference abstracts published since then have pre-empted much of this material for English-speaking palaeontologists, but given that most of these publications are obscure or poorly known, the contents will still be new to most readers, whether they be specialists or not.

If this book has a star it is without question the holotype of *Scipionyx samniticus*, the 23-cm-long theropod hatchling described by Dal Sasso and Marco Signore in 1998. It is entirely understandable
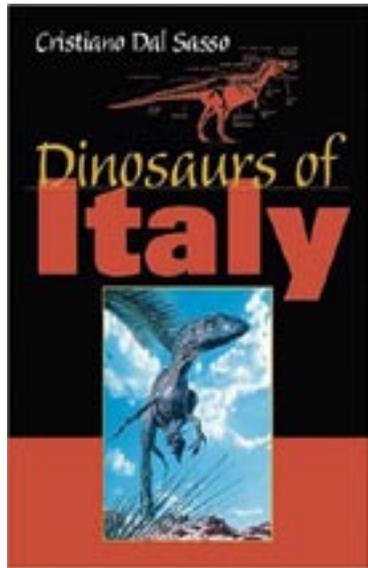
that, to Dal Sasso and his colleagues, *Scipionyx* must have seemed like the discovery of a lifetime, so it is fitting that 45 pages of this 213-page book are devoted to it. Accordingly there is more detail on the specimen's discovery and history than anywhere else, and there are some fantastic photos. *Scipionyx* was first nicknamed 'doggy' by Giovanni Todesco (its discoverer), was later dubbed 'Ciro' by the editor-in-chief of Oggi magazine, and was even later nicknamed 'Scipio' by science journalists. Technical names considered for *Scipionyx* prior to the official description included *Italoraptor*, *Italosaurus* and *Microraptor* (which isn't much of a coincidence, given that the name hardly has the world's most complex derivation).

Already *Scipionyx* has been much used and abused in the technical literature. As Dal Sasso describes, it provides further evidence that baby non-avian theropods were precocial. However, despite its undoubted hatchling status it has been allocated a position within coelurosaur phylogeny by some workers (albeit with caveats). Doing so is problematical given that we don't know how much ontogenetic transformation this species underwent and, as some have noted, its plesiomorphic morphology might be more to do with ontogeny than anything else. On the subject of ontogeny I found myself wondering whether the proportionally massive maxillary fangs of *Scipionyx* were retained into adulthood, or whether they were a special feature of juveniles. This isn't a random speculation as juveniles of a few theropod taxa (including *Ceratosaurus* and some tyrannosaurids) show that maxillary teeth got proportionally smaller with age, and what no one seems to have noted so far (to my knowledge) is that the longest maxillary teeth in *Scipionyx* were longer than the dentary was deep, a detail which has not been accurately depicted in life restorations of *Scipionyx*. This is also the case in *Ceratosaurus* juveniles: these baby theropods seem to have been 'sabre-toothed'.

Better known than any of this is the great deal of noise that has been made about the soft-tissue anatomy preserved within the specimen. A suboval abdominal mass appears to be the liver, but less convincing is the alleged partitioning of the abdominal cavity into distinct pleuroperidarcial and peritoneal cavities by a supposed diaphragm. What I find curious is that Dal Sasso was second author on the paper which asserted the presence of a diaphragm, and of a hepatic-piston mechanism, in *Scipionyx* (Ruben *et al.* 1999): an attribute 'inconsistent with *Scipionyx* having had an avian-style, lung air sac system' (Ruben *et al.* 1999, p. 515) and even, allegedly, with the derivation of birds from other theropods. This time round Dal Sasso seems far more happy with the substantial body of data indicating that theropods, and other saurischians, were pneumatic in the avian sense (see, *e.g.*, Wedel 2003a, b, O'Connor *et al.* 2005), as he should given his familiarity with theropod anatomy. The model proposed by Ruben *et al.* (1999) has been widely rejected by other archosaur anatomists, so this isn't surprising. I must note that the Brazilian theropod preserved with an abdominal vacuity adjacent to its pelvis, used by Dal Sasso as a trump card in demonstrating the presence of abdominal air sacs, was described in 2004 as the new taxon *Mirischia asymmetrica*.

Perhaps not as newsworthy as *Scipionyx* is the large tetanuran discovered at Saltrio in 1996, and also discussed at length by Dal Sasso. The Sinemurian age of the specimen makes it significant, as it is among the oldest of tetanurans. Dal Sasso notes that a possible contender for this title might be *Eshanosaurus*, an alleged basal member of the therizinosauroid lineage from the Chinese Lower Lufeng Series. If this identification for *Eshanosaurus* is correct, ghost lineages for virtually all tetanuran clades must extend right down to the base of the Jurassic, and hence the presence of big basal tetanurans (like the saltriosaur) at this time isn't such a big deal. However, a Lower Cretaceous theropod that is quite unambiguously a basal member of the therizinosauroid lineage (*Falcarius utahensis*, published in 2005) casts considerable doubt on the proposed therizinosauroid-lineage affinities, and thus theropod affinities, of *Eshanosaurus*: as several have supposed, it probably is a sauropodomorph after all. A tetanuran at the base of the Jurassic therefore still is a big deal, and we await the full technical description with interest.

As Dal Sasso points out several times, the discovery of the saltriosaur, combined with other evidence for large dinosaurs in Mesozoic Italy, necessitates a partial rethink of Italian Mesozoic palaeogeography. Areas thought to have been submerged must instead have been at least intermittently emergent and, as indicated by the presence of large predators like the saltriosaur, must in cases have been relatively large in extent. This is reinforced by the new hadrosaur from the Triestine Karst, which isn't just a one-off but among several specimens known from the region. Again, this animal (dubbed 'Antonio' and representing a new taxon) hasn't yet been technically described. Clearly it's morphologically novel, possessing particularly elongate lower limbs and a tridactyl hand. Incidentally, a name used on the Internet for this taxon is preoccupied, so isn't going to be the final choice. I won't tell you what that name is, but it's something to do with three digits, and involves 'saurus'.

As noted earlier, it's not all dinosaurs dinosaurs dinosaurs. We also get the full story behind the unusual slim-snouted Triassic ichthyosaur *Besanosaurus* that Dal Sasso and Giovanni Pinna named in 1996, x-rays of which revealed the presence of embryos. While Dal Sasso notes the phylogenetic position favoured for this taxon by Ryosuke Motani (*viz.*, that it's a shastasaurid), not noted is the alternative position recovered by Maisch and Matzke (2000) where no shastasaur clade was discovered at all – there are two sides in the ichthyosaur wars, after all. Furthermore, while Dal Sasso follows Motani in regarding *Cymbospondylus* as rather more basal than shastasaurs and even mixosaurs, there is also Sander's (2000) analysis where *Cymbospondylus* is still a shastasaur, and is in fact sister-taxon to *Besanosaurus*. A controversy that Dal Sasso doesn't touch on is whether *Besanosaurus* is the same thing as *Mikadocephalus*, named in 1997 for a skull from Monte San Giorgio. There is more to this than nomenclatural trivia, in that specimens from Spitsbergen have been referred to *Mikadocephalus*, so if this taxon and *Besanosaurus* really are the same thing then there is evidence for this animal well beyond Italy.

Still on marine reptiles, the brief coverage of pachypleurosaurs, placodonts, nothosaurs, thalattosaurs and the enigmatic *Eusaurosphargis* was welcome but, in my opinion, all too brief, especially given the lengthy coverage given to the more familiar animals. In fact there is easily enough literature on these less-famous groups to fill a book the same size as *Dinosaurs of Italy*, if only a popular volume devoted to thalattosaurs and placodonts would sell as well as one with the word 'dinosaur' on the cover.

Finally, I have a few minor gripes. A brief discussion of Dale Russell's 'dinosauroid' is far too sympathetic and reads as if the idea of the possible evolution of post-Cretaceous humanoid theropods is widely accepted as valid, whereas it really isn't. One could argue that it is misleading to present to lay audiences the idea that palaeontologists really think that tetrapod evolution is predetermined in this way, or that the evolution of humanity or something like it is inevitable. I suppose whole books have been written about this subject however (Gould 1989, Conway Morris 2003). *Eudimorphodon* does not mean 'double-shaped true teeth' as Dal Sasso states, but rather 'true two types of teeth' (the taxon was so named because *Dimorphodon*, named a great deal earlier, is markedly less heterodont), and I was a bit confused about his reference to serrated teeth in ziphiid (beaked) whales when writing about the distribution of tooth serrations within tetrapods. No ziphiid has serrated teeth, though of course there are several fossil whale groups that did. The name *Lagosuchus* is used a few times in the book: this name is presently regarded as a nomen dubium, and the valid taxon once referred to it (and oft used as the archetypal proto-dinosaur) is *Marasuchus*. Some of the illustrations look a bit familiar, strongly resembling earlier works by David Peters and Greg Paul. Finally, remarkably, there is no index.

Overall, *Dinosaurs of Italy* is pleasant and enjoyable, the translation and editing are excellent and, to nerdy completists like me, the book is essential for all the unique details it provides on the taxa it discusses. I recommend it to those truly interested in Mesozoic reptiles.

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Evolution of the Insects

David Grimaldi and Michael S. Engel (2005). Cambridge University Press, Cambridge, 772pp. ISBN 0-521-82149-5. $75.00. £45.00 (hardback).

Insects, by any definition, are important creatures. They account for three quarters of all described animal species: almost a million named so far (compared with only 4,000 or so mammals), and probably several million more awaiting discovery. Their presence simply cannot be ignored by humans, for reasons both good and bad: they provide commodities such as honey and silk, and include among their numbers crop pollinators (*e.g.* bees), crop pests (locusts) and disease vectors (mosquitoes). Their ecological significance can also not be over-stated. If man were to disappear, Earth's beleaguered terrestrial ecosystems would make a slow recovery; were insects to go, these ecosystems would collapse.

The fossil record of the insects is much patchier than that of many other groups (*e.g.* bivalves) because of their comparative delicacy and their near-restriction to non-marine habitats. Fossil insects are also less 'glamorous' than, say, dinosaurs or ammonites, so have on the whole received less amateur and professional attention. However, when insect fossils occur (mostly in lake sediments or amber), their remains can be abundant and astonishingly well-preserved, offering insights into their long and fascinating history.

The insects, then, are certainly well worthy of pampering in top-quality publications, and this book is one of them.

First off, it is an imposing and handsome volume, running to over 700 pages, and would make a fine adornment to any coffee table that could withstand its weight. And it is remarkably good value at £45. Beyond the cover, it also does not disappoint. There have been many good books covering the diversity and habits of modern insects, but none I am aware of that have blended this so well with their fossil history. The book's dedication reads: 'For the entomophiles, winged and larval', and I think that it could, indeed, appeal to a wide readership. At the one extreme, my two young 'larvae', aged five and six, were intrigued by some of the bizarre bugs captured in the colour photos. At the other extreme, even specialists are likely to find something new, or at least take pleasure from the copious images of impressive fossil specimens, many not previously seen in print. More general readers will find the text on the whole an interesting and quite easy-going read. Very little prior knowledge is assumed by the authors. Scientific terms and methods are clearly explained in the text and there is an extensive glossary towards the end of the book. The references run to 70 pages, facilitating the investigation of topics in more depth.

This American-authored volume follows fairly hot on the heels of, and forms an interesting complement to, another excellent and substantial palaeoentomological publication, this one multi-authored and Russian (but written in English): *History of Insects* (Rasnitsyn & Quicke, 2002). Although there is inevitably some overlap, the latter volume is aimed more squarely at the specialist and places more emphasis on topics such as insect taphonomy and palaeoecology, while offering a more cursory treatment of modern insects. Differences between the two volumes in systematic practices and even in the choice of formal names of insect orders suggest that insect classification is still a lively and contentious activity.

The first chapter of *Evolution of the Insects* introduces the reader to the insects' phenomenal diversity and ecological importance, before moving on to consider the part insects played in the

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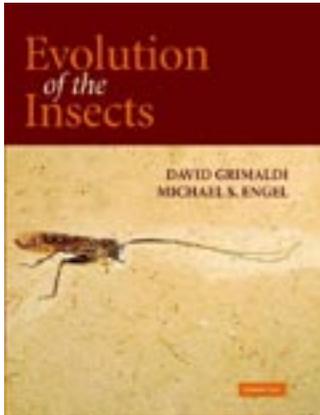
historical development of evolutionary theory. Principles of classification are explained and there is a discussion of the roles of genetics and palaeontology in the reconstruction of insect evolutionary history. Chapter 2 looks at insects as fossils, describing the various ways in which their bodies can be preserved, and the types of insect trace fossils that can also be found (*e.g.* their burrows or preserved nibblings on plant remains). There follows a review of major fossil insect deposits worldwide, accompanied by photos which are, however, sometimes printed too small to be easy on the eye. Chapter 3 considers the place of the insects within the Arthropoda, briefly detouring to visit other members of that vast phylum, such as trilobites, spiders and millipedes. It then documents what we know of the insects' first tentative steps on to the land 400 or more million years ago. Chapter 4 gently delves into the fundamentals of insect morphology, before considering the history of fossil insect research, introducing in the process some of the often-colourful characters involved, such as the occult-inclined researcher who tried to recruit a mystic to breathe life into the huge fossil 'dragonflies' he was studying.

Chapters 5 to 13 comprise the real body of the book, covering, with a wealth of detail, the entire range of insect higher taxa, both living and extinct. For each insect order there is an initial summary of distinguishing features followed by an overview of the diversity and habits of modern representatives (for those orders that still have them), and then consideration of fossil taxa and their evolution. There are also a number of worthwhile diversions including discussion of the origins of insect sociality, bloodsucking, parasitism and flight (they were the only flying creatures for probably over 100 million years until the reptiles took to the air). These chapters contain the majority of the book's 900+ illustrations, comprising mostly detailed line drawings and photographs of living and fossil insects (mostly in colour, apart from the scanning electron micrographs, which are, nevertheless, delightfully detailed). Perhaps most visually stunning are the photos of insects in amber. Any mundane fly that can still be studied in minute detail millions of years after its death makes a fine picture, but some of the images in the book, for example of entombed ants still grasping their honeydew-producing mealy bug livestock, are truly breathtaking.

Chapter 14 focuses on the final third of insect evolution, the heady rush towards Recent faunal composition in tandem with the flowering plants. There is also a discussion of the factors influencing the geographical distribution (particularly in the Southern Hemisphere) of ancient and modern insect groups, followed by an appraisal of how the insects fared in the asteroid-induced end-Cretaceous mass extinction. At family level, it seems, they were relatively unperturbed, but may have been more badly affected at species level because there is a decline in diversity of insect feeding damage to plant fossils. The book's authors sensibly caution that this evidence is based only on a small number of North American localities (so may not reflect events worldwide), but also, less sensibly, perpetuate the misconception that there were fewer than ten species of dinosaurs still alive at the end of the Cretaceous – a figure also based on a small number of North American localities.

The editorial standard of the book is generally high, but inexplicably slips slightly in this chapter. Sometimes fairly critical words are omitted (readers will be either amused or bemused to encounter

'Wegener's theory of continental') and several times I wondered what relation 'angiopserms' had to 'angiosperms'. Nevertheless, this chapter is an enthralling read, and I think the book would have benefited if the large amount of information on the first two-thirds of insect history, disseminated throughout hundreds of pages of text, were also summarised in a succinct chapter.

The short final chapter considers the insects' future. It dispels the myth that man has failed to eliminate a single species of insect (although this is essentially true for major pest species, and in some cases the indiscriminate use of pesticides has actually led to the evolution of even hardier 'superpests'); the reality is that insect species, the vast majority benign or even useful (and all interesting), are almost certainly disappearing much faster than we can count them. The authors give some poignant examples of insect 'dodos', such as the Californian Xerces Blue butterfly and make what is obviously a heartfelt plea for the preservation of insect diversity. Endangered insects (and other invertebrates) figure much less in the public perception (and consequently receive less funding) than, say, large mammals, and this is a situation which needs redressing.

All in all, this is a superb book, and anyone who is not already an entomophile most likely will be after browsing through it.

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Evolving Eden. An Illustrated Guide to the Evolution of the African Large-Mammal Fauna

Alan Turner and Mauricio Antón (2004). Columbia University Press, New York, 304pp. ISBN 0-231-11944-5. $39.50. £24.50 (hardback).

Any layperson sitting in on a vertebrate palaeontology conference would be hard-pressed to find reconstructions of whole animals or ancient mammalian ecosystems amid all of the esoteric debates about ridges on bones and crests on teeth; indeed, a casual bystander might justifiably wonder if students and professionals in attendance had spent much, if any, time thinking about how their favourite taxon fit into the broader palaeoecological picture. Of course, as palaeontologists we can't help but be obsessed with details when the taxa that we discover and describe are rarely represented by more than a few jaws or isolated teeth, but an unfortunate side effect of increasing specialization and an ever-growing corpus of anatomical and analytical jargon is that the fascinating stories that have been revealed by the mammalian fossil record often end up being totally inaccessible to the general public. In *Evolving Eden*, Alan Turner and Mauricio Antón help to remedy this situation by, in their words, aiming to "…provide an accurate visual impression of the species that make up the changing large-mammal fauna of Africa and to set these species in an appropriate landscape".

Evolving Eden is full of these "impressions" – that is, Mauricio Antón's wonderful part- or whole-body reconstructions of numerous extinct taxa from predominantly post-Fayum (<30 million-year-old)

African faunas, either alone or alongside sympatric species. But it isn't simply a palaeontological picture book. Antón's artwork is based on detailed anatomical knowledge of living and extinct taxa, as demonstrated by his use of a "layered" approach to reconstruction that first uses the morphology of preserved elements as a guide for the origin, insertion, and size of deep and superficial musculature, and only thereafter adding what are, necessarily, much more speculative details of external morphology. It will be reassuring to academics that these reconstructions are accompanied by interesting information about each of the extinct animals, their distributions in time and space, and their probable lifestyles. It's easy to find similar books that are strictly dedicated to hominin evolution, but extinct non-hominin African mammals – and particularly those that lived before the close of the Miocene – have always received much less attention. In this regard, Turner & Antón's book nicely fills what was apparently a vacant niche.
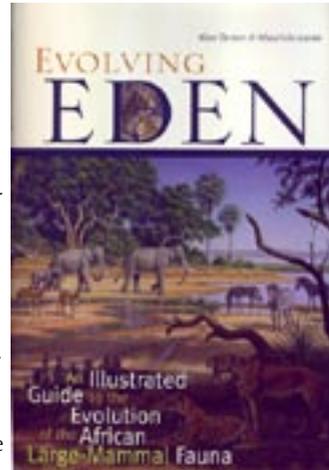
The first two chapters of *Evolving Eden* provide very brief introductions to dating methods, the role of continental drift in mammalian evolution, climate change, and the physical geography of Africa. Most advanced undergraduates studying vertebrate palaeontology or palaeoanthropology will already be familiar with such information. More than half of the book is taken up by the third chapter, "African mammals, past and present," which discusses and reconstructs a number of Miocene, Pliocene, and Pleistocene African mammals, most of which will not be familiar to the layperson or undergraduate student. The bulk of the art and text is dedicated to hominins, carnivorans, proboscideans, perissodactyls, and artiodactyls. For each of these groups, the reader will find considerable variation in the amount of detail – for instance, about 32 pages on carnivorans and 39 on artiodactyls, but only 9 pages on proboscideans and 7 on perissodactyls. Much shorter bits on small mammals (generally one or two paragraphs, and an image) appear to be something of an afterthought. There are some errors here and there in discussions of Palaeogene African mammals and smaller Miocene-to-Recent mammals, but as these topics fall outside the intended scope of the book, such errors do not really detract from its overall usefulness.

The fourth chapter provides information on most of the major Miocene and Pliocene mammal localities in Africa, and discusses each site's faunal content, likely mode of deposition, and palaeoenvironmental setting – thus helping to place the taxa discussed in chapter 3 into a more coherent ecological context. Antón provides a number of nice reconstructions of these mammalian palaeocommunities. The final chapter synthesizes all of this information, bringing the reader through a series of landscapes from the early Oligocene up to the terminal Miocene (using snapshots from around 30, 20, 15, and 8 million years ago), and detailing the impacts that faunal immigration, emigration, and climate change appear to have had on these different assemblages. Plio-Pleistocene faunas are discussed primarily within the context of turnovers in the "ungulate" and carnivoran constituents, and the possible driving role of climatic fluctuations in shaping the modern African mammal fauna. Again, as might be expected from Turner & Antón (also authors of *The Big Cats and Their Fossil Relatives*), there seems to be a somewhat disproportionate amount of attention paid to carnivorans and predator-prey dynamics through all of these chapters. The chapter concludes with a short section on hominin evolution, including the evidence for early tool-making and dispersal(s) out of Africa.

Evolving Eden should be of interest to anybody who wants a user-friendly, jargon-free introduction to the more recent (primarily <20 million-year-old) evolution of mammals in Africa, and the environments in which hominoids and early hominins evolved. Therefore this book will be of particular use for the layperson that either isn't prepared to, or doesn't want to, delve into the more technical specialist literature on these topics. I would also recommend the book for advanced undergraduate and first-year graduate students who are interested in pursuing vertebrate palaeontological work in the African Neogene, because it nicely provides a "big picture" starting-point that doesn't come quite so easily from hundreds of scattered original taxonomic descriptions. The book would be a particularly good companion for a student attending a palaeoanthropological field school in Africa. And although professional palaeontologists will certainly find reason to quibble about details (or lack thereof), I can't imagine that anybody working on these fossil mammals wouldn't be excited to see them brought back to life in Antón's skilled reconstructions.

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Ediacaran palynology of Australia

Kathleen Grey (2005). Association of Australasian Palaeontologists, Memoir 31, 439 pp. AUS$141.00 (Australia) AUS$150.00 (Overseas). Prices include surface postage. Australian prices include GST.

If you are interested at all in the Cambrian explosion, or the origin of animals, or merely the foremost division in the whole of geological time, then you need to know about the Ediacaran. This newly ratified, terminal Proterozoic period documents the last 90-odd million years leading up to the Phanerozoic and holds the data, possibly even the answers, to many of the big evolutionary questions. And although much recent emphasis has been on the spectacular metazoan embryos recovered from the first half of the period, and the problematic macrofossils of the second, the most informative source of Ediacaran data may turn out to be palynological. Certainly organic-walled microfossils provide a degree of stratigraphic continuity not met by other more taphonomically constrained data.

As with any fossils, Ediacaran palynomorphs can be approached either as organisms, worthy of palaeobiological interrogation in their own right, or as biostratigraphic tools in the battle to subdue deep time. In this massive monograph on the palynology of the "Centralian Superbasin," Australia, Kath Grey sides enthusiastically with the biostratigraphers, the punch-line being a proposal for five acritarch-based biozones with which to divide up the first *ca*. 50 million years of the Ediacaran. Such stratigraphic resolution is entirely unprecedented in the Proterozoic record, and promises a

major recalibration of Ediacaran history.

Acritarchs are organic-walled vesicular microfossils of unknown taxonomic affinity, and are classified by means of an artificial form taxonomy wherein different shapes, sizes and distributions of morphological features – mostly surface ornamentation – define individual form-genera and form-species. Most ornamented, so-called acanthomorphic, acritarchs are Palaeozoic; however, a distinctive suite of Proterozoic forms has come to light over the past few decades, most famously in the early Ediacaran Doushantuo Formation of South China (*e.g.*, Zhang *et al.* 1998) and the early Ediacaran Pertatataka Formation of central Australia (*e.g.*, Zang and Walter 1992). Indeed, it is now clear that this Doushantuo/Pertatataka microbiota (DPM) marks a major break from all previous biotas, representing an order-of-magnitude increase in both diversity and evolutionary turnover (Peterson and Butterfield 2005). Certainly this is the kind of data necessary to develop a useable biostratigraphy – and with its thick, undisturbed, widely distributed and extensively cored Neoproterozoic strata, the Centralian Superbasin is probably the best place to try it out.

As befits a major biostratigraphic endeavour, this monograph presents a systematic and exhaustive account of local and regional geology, with an emphasis on correlation between its constituent parts: the Adelaide Rift Complex to the SE, the Officer Basin to the SW and the more or less central Amadeus and Georgina basins. Apart from the biostratigraphic scheme under development, intra- and inter-basinal correlation draws heavily on δ13C chemostratigraphy and the presence of a widespread ejecta layer from the early, but not earliest, Ediacaran Acraman bolide impact. By cross-referencing acritarch assemblages with both carbon isotope signatures and the ejecta layer, Grey proposes an earliest Ediacaran interval dominated by simple sphaeromorphic acritarchs (the "Ediacaran Leiosphere Palynoflora" or ELP), followed by four biozones defined on unique assemblages of acanthomorphic acritarchs (the "Ediacaran Complex Acritarch Palynoflora" or ECAP). All four ECAP zones are said to lie stratigraphically above the Acraman layer but below the first appearance of Ediacaran macrofossils.

It is not difficult to poke holes in this stratigraphic scheme. As Grey mostly acknowledges, the absence of any distinctive constituents in the ELP rules out any useful biostratigraphic application, and the limited extent of the Acraman ejecta layer means that the stratigraphic control between the two most usefully fossiliferous regions (the eastern Officer Basin and Amadeus Basin) is left hanging on somewhat tenuous carbon isotope signatures and yet-to-be-tested acritarch biostratigraphy. And, when scrutinized in any detail, the acritarch data is often far from compelling: for example, there is but a single ECAP-bearing borehole from the Adelaide Rift Complex, a single ECAP-bearing borehole from the Amadeus Basin, and none at all from the Georgina Basin; the proposed uppermost ECAP biozone is based on a single two-metre interval within a single borehole; acritarch distribution in the two principal fossiliferous boreholes of the eastern Officer Basin clash conspicuously with other stratigraphic indicators; and in one instance, ECAP-type acritarchs are reported as occurring below the Acraman ejecta layer.

Of course all biostratigraphic schemes are founded on limited, localized data, and gain respectability only as zones are adjusted and patterns corroborated. To her credit, Grey has managed to knock out a genuinely testable hypothesis from what is turning out to be a tangle of accruing early Ediacaran data. She has also been more forthright than others in stating her premises, arguing explicitly that the acritarchs she is working with are the resting cysts of phytoplankton, and that their distribution
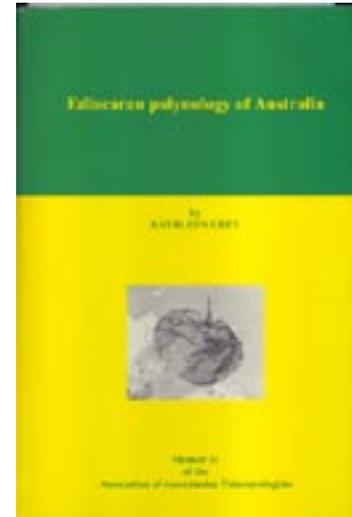
is largely independent of facies. Indeed, it is these assumptions that set the scene for her relatively literal interpretation of the fossil successions, and thus their biostratigraphic utility. It is a worthy hypothesis, but, to my eye, the premises are not sustainable. ECAP/DPM-acritarchs have long been noted for their enormous size (typically an order-of magnitude larger diameter than their Palaeozoic counterparts) and the absence of excystment structures that characterize phytoplankton cysts. Moreover, there is a strong case – based on size, sedimentology and associated, environmentally sensitive microfossils – for identifying most ECAP/DPM fossils as limited to conspicuously shallow water settings (Butterfield and Chandler 1992). If this is the case, then the succession of fossils within the Centralian Superbasin probably has more to do with fluctuating environment than evolutionary turnover.

A non-cyst habit also has important implications for form-taxonomic diversity, since metabolically active organisms exhibit a fundamentally greater range of ontogenetic, ecophenotypic and taphonomic variation. Grey identifies 64 acritarchs in this study (including 26 new form-species and six new form-genera), of which 49 are acanthomorphs, 12 are sphaeromorphs (unornamented acritarchs), and four are identified as coenobia. All of these are meticulously described and illustrated, with previous authors regularly – and usefully – being taken to task for missing citations, failure to comply with the rules of nomenclature and generally woolly thinking. This is all to the good, but I am still left wondering what this lucid form-taxonomy actually tells us. To my untrained eye, more than a few of these form-taxa look to be variations on a theme – and if they turn out to be the remains of metabolically active organisms, that is very likely what they are.

Whether or not the early Ediacaran can be divided into stratigraphically discrete biozones, there is no question that the ECAP/DPM documents a major evolutionary regime change – nothing less than the first measurable radiation in the whole of the fossil record. And given its proximity to other terminal Proterozoic phenomena, it will inevitably figure in to any overarching scenario of the interval. Grey, for example, has made much of the fact that the new biota expands to dominance shortly after the post-Marinoan Acraman impact, proposing that "cyst-forming" ECAP "phytoplankton" had a competitive advantage over their (non-encysting) ELP incumbents in the resulting carnage. By contrast, Kevin Peterson and I (2005) have argued that the sudden appearance of diverse new acritarch morphologies should be recognized as a coevolutionary response to the appearance of eumetazoans. There is no shortage of other hypotheses for explaining the Ediacaran–Cambrian transition, and these too will need to recognize and incorporate the palynological record. In the meantime, there is a pressing need for more, good, primary data with which to determine the underlying patterns. On this front, at least, Grey sets the new, very high, standard.

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Oceans of Kansas – a Natural History of the Western Interior Sea

Michael J. Everhart (2005). Indiana University Press, Bloomington and Indianapolis, 322pp. ISBN 0-253-34547-2, \$39.95 (cloth).

Don't go into the water! I'm told that when faced with the unfortunate and rather grizzly event of a shark attack, my best chance of survival comes from calmly and collectedly poking the fishy foe in the eye. But if I were to take a plunge in a Cretaceous ocean, sharks would be just one of many ferocious marine predators I may be attempting to prod in the face. I don't know if the same course of action applies to a fifteen metre long mosasaur, but luckily for keen surfers, these terrors are of course now prehistory. Yet they are not forgotten … as revealed by Michael J. Everhart in his new book: *Oceans of Kansas – a Natural History of the Western Interior Sea*.

The book was borne out of popular demand. Mike Everhart's website, Oceans of Kansas (<**http://www.oceansofkansas.com/**>) went online almost ten years ago in 1996, yet it remains to this day a valuable and popular online resource for all manner of information on the fossil-bearing rocks of Kansas and the extinct fossil animals they yield. The strength of the website lies in the depth and scope of the material, and particularly in the emphasis on visuals – a picture does, after all,
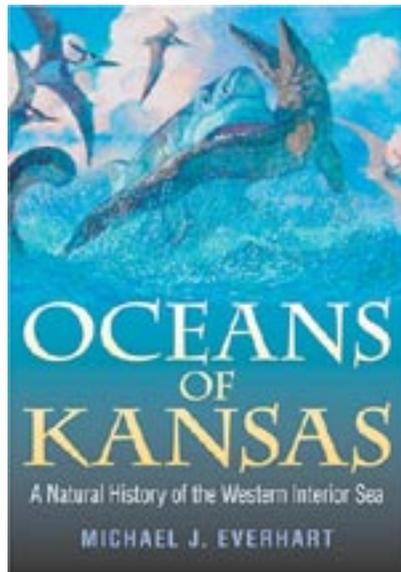
say a thousand words. "But where is the book?" visitors to the website would ask, and Mike has endeavoured to create one for us. It forms a part of the Indiana University Press' extensive *Life of the Past* series, edited by James O. Farlow.

Like the website, *Oceans of Kansas* is dedicated to the inhabitants of the depths and shorelines of the Western Interior Sea. This inland sea completely covered what is now known as the state of Kansas during the Late Cretaceous. It stretched across the middle of North America from the Gulf of Mexico in the south to the Arctic Circle in the north, dividing the continent, and formed a home for a wide diversity of marine organisms. The faunal list includes invertebrates, fishes, marine reptiles, pterosaurs and marine birds, which frolicked in these 'oceans of Kansas' during the deposition of the Upper Cretaceous, Smokey Hill Chalk Member (the focal point of the book), and the over- and under-lying horizons.

Oceans of Kansas the book occupies a more-or-less empty literary niche. Existing popular literature is sparse with regard to fossil marine reptiles, which form a large proportion of Everhart's book. Richard Ellis' (2003) *Sea Dragons – predators of the prehistoric oceans* was the first popular volume dedicated to fossil marine reptiles since Williston's (*c.*1914) 'Water Reptiles of the Past and Present' (downloadable for free as a PDF from Arment Biological Press (<**http://www.herper.com/ebooks/titles/Water.html**>). Yet, where Ellis interpreted fossil marine reptiles purely as living creatures, Everhart concentrates on the actual fossils too. In this respect, the volume benefits the active researcher by consistently providing institution and specimen numbers, and by figuring fossil specimens.

After an introductory chapter, and a chapter describing the historical discovery of the deposits and the stratigraphy, the book is nicely structured taxonomically as Everhart runs through each of the groups living in and around the ancient oceans. We begin with a review of the invertebrates, plants and trace fossils (chapter 3) and move quickly into the vertebrates – sharks (chapter 4) and fishes (chapter 5). Some of the shark remains belong to the ginsu shark (*Cretoxyrhina*) pictured on the front cover attacking a medium sized mosasaur. The first group of marine reptiles to feature are the relatively rare turtles (chapter 6), followed by the mysterious long-necked elasmosaurid plesiosaurs (chapter 7), the short-necked plesiosaurs (polycotylids and pliosaurids) (chapter 8), and the mosasaurs (chapter 9), including the giant *Mosasaurus* and the durophagous *Globidens*.

Chapter 10 takes us into the sky above the oceans to meet the pterosaurs, particularly the genus *Pteranodon*, and here we stay in part for a look at the flying and swimming toothed birds (chapter 11). The last group of animals are the dinosaurs (chapter 12), of which a few must have been washed out to sea from the surrounding shorelines. The book is neatly tied up in the final chapter (13), 'the big picture', which reminds us, this time in a stage by stage setting, of all we have learned.

Each chapter is interlaced with tales of historical and personal discovery, with insights into the excitement of excavation. We are told the more infamous tales from history: the discovery of the first Maastricht mosasaur, Cope's erroneous reconstruction of *Elasmosaurus* with the head on the end of the tail, and the fish-in-a-fish specimen of *Xiphactinus* for example. But we are also relayed a number of equally binding but less well-known anecdotes: how he has discovered new specimens in the field, how parts of the same specimen have been matched up after many years, and the feud between Williston and Eaton regarding the anatomy of pterosaurs also comes to mind.

REVIEWS

The volume comes complete with a gallery of 12 colour plates: a showcase of Dan Varner's palaeoart. These paintings are complemented by many (black and white) palaeo-restorations throughout the text (by Russell Hawley), and succeed in portraying the fauna of the oceans as dynamic living creatures. There are also many useful photographs and scientific illustrations/reconstructions accompanying the text.

Minor flaws (typos and figures without scale bars) are few and far between, and are ultimately of little consequence on the impact of the book. Due to the wide taxonomic diversity covered by this book, I recommend it to anyone with a general interest in marine vertebrate palaeontology, but especially (of course) to anyone with an interest in these deposits in particular, and the organisms they yield. It is also perfect for anyone with an interest in the history of North American palaeontology. *Oceans of Kansas – A Natural History of the Western Interior Sea*, is an informative and enjoyable read and it is certainly a welcome addition to my bookshelf!

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Early Silurian trilobites of Anticosti Island, Québec, Canada

Chatterton, B. D. E. and Ludvigsen, R. (2004). Palaeontographica Canadiana No. 22. Canadian Society of Petroleum Geologists and Geological Association of Canada, Calgary, 264p. ISSN 0821-7556, ISBN 0-919216-93-5. Canadian Orders CDN\$109.00 (shipped by Canada Post). US Orders US\$90.00 (shipped expedited parcel). International Orders US\$90.00 (shipped small packet surface mail).
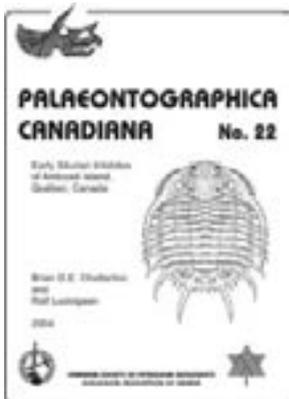
Over 20 years ago I reviewed the very first issue of *Palaeontographica Canadiana* and, highly impressed by the quality of production, I expressed the view that if a steady supply of good contributions could be maintained then the monograph series would gain an important place in the palaeontological literature. Happily, that hope has been realised, especially for those of us interested in Lower Palaeozoic fossils, and Brian Chatterton, one of the authors of that first issue and of four others along the way, has produced a veritable *tour de force* with Rolf Ludvigsen in this, the 22nd in the series.

Some 52 species, 32 of which are new, belonging to 30 genera (one new) are described and superbly illustrated in 84 plates

and, in some instances, very clear line drawings. An 85th plate shows the fauna of the uppermost Ordovician formation on Anticosti. The work will justifiably become a standard trilobite taxonomic monograph, but there is much else that will be of wider interest to Silurian workers. In addition to historical reviews of the island and of previous work on the trilobites and a summary of the lithostratigraphy, the introductory parts of the work place the Silurian (Llandovery and possibly lowest Wenlock) faunas in their temporal and palaeoenvironmental context both locally and globally.

A trilobite biostratigraphical scheme is established largely for correlation of the latest Ordovician and Silurian on Anticosti Island. It comprises six 'faunas' (considered equivalent to biozones) based on the stratigraphical distribution of species. These are mapped onto the lithostratigraphy and stage-level chronostratigraphy, but beyond a few notes in the text on the conodont zones, there is no direct indication of the equivalence of the faunas to the biostratigraphical schemes based on other groups on the island. A few of the trilobite species are known from successions elsewhere, but the correlation potential of the Anticosti trilobites and the possibility of the wider applicability of the biostratigraphical divisions seem very limited at present.

A taphonomic discussion assesses the occurrences of the trilobites in a range of carbonate and mudrock settings from low energy environments to (most commonly) tempestites and rare mass flow deposits. There are good links between probable modes of life and environmental perturbations, including the recognition of tightly enrolled specimens below thick storm-generated obrution deposits. There are also important observations of the effects of abrasion and diagenesis on the preserved surface microstructure of some species; cautionary tales for the recognition of taxonomic character states.

The assessment of taphonomy and a clear statement of the sampling strategy (in most cases aimed in the field at maximising species numbers and obtaining the best preserved material) provide the necessary background to a consideration of the recurring generic associations of trilobites in the faunas. Four main biofacies are defined and illustrated by histograms and pie charts of representative samples. They are named on the basis of the numerically dominant genera: *Calymene*, *Acernaspis*, *Encrinurus* and *Proetus*. In the case of the first of these, four component assemblages also of presumed ecological significance are defined. A further two, rarer, biofacies are also defined and represent the shallowest (<30 m) and deepest (80–100 m) water environments yielding trilobites in the Anticosti succession. On a larger scale, the palaeogeographical significance of some of the trilobites (and some notable absences from the succession on Anticosti) is also described. The consideration of the palaeoecology includes a very useful discussion of Silurian trilobite associations described in the literature from around the world, and a comparison of the Anticosti biofacies with them. All this is particularly important as it helps document the recovery of trilobites after the Hirnantian extinctions and a return to alpha diversities that are comparable to those of the preceding Cambrian and Ordovician. The value of this monograph thus extends beyond its undoubted taxonomic strength and it is a very welcome addition to an excellent monograph series.

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The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis

D. McIlroy (editor) (2004). Special Publication 228, The Geological Society, London, 490pp. ISBN 1-86239-154-8. £95.00 (Hardback).

This Special Publication of the Geological Society arising from the Lyell Meeting in 2003 contains 20 contributions involving 36 authors. The volume is thus a substantial contribution to ichnology, containing both detailed analyses of specific ichnofaunas, and papers providing useful overviews. In his introduction to the volume the editor states that the aim of the volume is "to provide a summary of recent progress, with an up-to-date summary of most themes in modern ichnology." This is a laudable aim, and many papers do provide such summaries, but the aim is possibly rather difficult to achieve through individual contributions to a conference volume. The editor clearly made a valiant attempt to keep authors on track, and to organise the great variety of papers into a coherent volume.

The introductory paper by McIlroy covers some of the major concepts of ichnology, and reviews methods and applications, giving a personal view on the study of traces in core. This paper has broad appeal, providing a useful introduction and references for those who are not specialist ichnologists. Pemberton *et al.* provide a valuable contribution of wide relevance, extending and summarising previous work on the recognition of significant stratigraphic surfaces using trace fossils. They are careful to stress the importance of studies that integrate information from all possible sources: palaeoecology, substrate, and sedimentology. The academic and economic applications to stratigraphic studies are enthusiastically stressed, with numerous illustrations and examples. Glaub investigates microborings in mollusc shells collected off the coast of Mauretania in an area of upwelling currents. The borings are well illustrated and described, and the potential for interpretation of water depth, and allochthonous deposits in the fossil record on the basis of borings, are discussed. An interesting contribution by Goldring *et al.* investigates climatic control of modern coastal and shoreface sediments. They are able to suggest three climatic zones distinguished using echinoid and crustacean burrows. Furthermore, they trace these latitudinal zones back into the Tertiary. Doubtless other such latitudinal variation existed in earlier times, such as the Permo-Carboniferous, when there was great latitudinal variation in climate. A paper by Manning investigates the information that can be gained from dinosaur tracks, using experiments on substrates with differing densities and moisture contents. Such experiments aid the recognition of surface and transmitted tracks, and enable conclusions to be drawn regarding the sediment consistency in the palaeoenvironment. He emphasises the fact that vertebrate-produced ichnotaxa do not correspond to zoological taxa; a basic tenet of ichnology, but one that still bears emphasis.
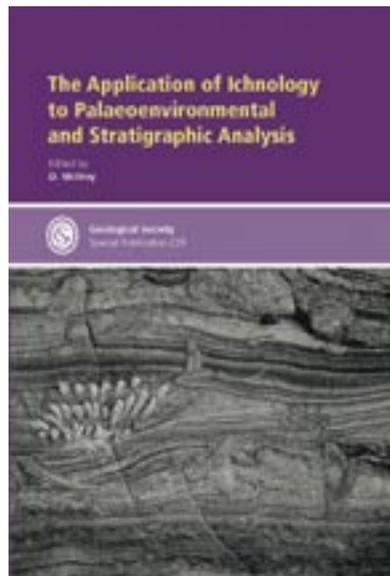
The rest of the papers are loosely organised in an environmental order from deep to shallow marine, and then over the shoreline into non-marine areas, with a few papers towards the end of the volume addressing changes in ichnofaunas through time. The papers are a mix of reviews and case studies, with the reviews being the most attractive to myself, but there would be no reviews without the basic data provided by case studies, so both are valuable to science. Uchman discusses the history of deep-sea traces on the basis of 151 'flysch' formations; the term flysch, and the associated references, bring back memories from the first great turbidite bandwagon. Uchman's analysis dispels some previous conceptions that did not have the benefit of the presently accumulated data.

Martin reviews published models relating oxygenation to trace fossil assemblages, and uses two classic sections – the Blue Lias at Lyme Regis and the Toarcian of Ravenscar – to compare trace assemblages with previously interpreted oxygen levels of the strata. She concludes that substrate consistency, as well as oxygenation, may control the distribution of traces. Mangano and Buatois continue their prolific output with a study of Carboniferous tide-influenced environments in North America, and characterise the assemblages from differing tidal flat environments. In a second paper in the volume they review traces and ichnofacies in freshwater environments; part of Seilacher's original 'Scoyenia' ichnofacies, providing useful clear diagrams illustrating ichnofacies distribution. My personal gripe would be the application of *Mermia* to an ichnofacies. As a trace it is a variably demented squiggle, and since the type material of *Mermia* came from sediment pockets in Lower Old Red Sandstone lavas, a more suitable representative might have been chosen for sublacustrine environments.

The volume continues with case studies of a good variety of environments. Bann *et al.* investigate the marine to estuarine variation in the Permian of the Sydney Basin, and Baldwin *et al.* the Cambrian Bright Angel Shale in Arizona. McIlroy takes us offshore to a Jurassic tide-dominated delta in the Norwegian Haltenbank area with a very detailed study that aimed to improve the sponsors' knowledge of hydrocarbon reservoir facies. We then find ourselves back in the Permian of Australia with Bann and Fielding looking at shoreface and delta facies. Melchor investigates Triassic lacustrine deltas from Argentina, and provides a review of described examples from the Devonian to the present; he suggests that it might be possible to subdivide the Mermia ichnofacies in his example. All authors have 'generic' points to make, but the inevitable romp through time and space is mind-bending.

At last we reach the land with papers by Genise *et al.*, and later in the volume by Genise, on ichnofabrics in palaeosols. One paper provides useful guidance on how to study traces in soils, and the other provides a review of such traces through time.

Back in the sea, Droser *et al.* give interesting evidence from burrows that early Cambrian marine substrates were firm close to the sediment/water interface, and that the zone of mixing increased in depth through the Cambrian as trace fossil size and diversity increased. Twitchett and Barras review the trace fossil record with respect to extinction events, and find evidence that ichnodiversity, burrow size, and bioturbation depth are reduced immediately after extinction events, and that traces provide information on faunal recovery.

The volume concludes with a stratigraphic review of marine bioerosion by Bromley, who provides a chart of taxa through time. Four possible 'ages of bioerosive activity' are recognised, but the

changes do not appear to be dramatic, or to be connected with mass extinctions. Problems are noted with the known ranges of borings and supposed makers; doubtless this chart will inspire further study.

I have tried to mention the subject matter in the volume, and if you have waded through the above, you will have gathered that there is an eclectic mix as is frequently the case with conference volumes. The lengths of some contributions would certainly have been cut for publication in a journal. The standard of production is that expected from the Geological Society, but the photographs of trace fossils in several papers could show more contrast to improve clarity. In several cases this is a consequence of the use of field photographs, probably originally in colour. However, this is an interesting volume with a good mix of description, theory and philosophy; a must-have for ichnologists. The introductory chapter by McIlroy, whilst containing much that will be already familiar to ichnologists, will be valuable to palaeoecologists, sedimentologists and stratigraphers. Students of palaeontology will find the book a valuable source of information and references to add to coursework.

A challenge for ichnologists is to separate climatic, evolutionary and environmental associations of trace fossils without inventing a myriad of ichnofacies names that will impress nobody outside the ichnological world. Maybe what is now needed in ichnology is a well-illustrated multi-author book adopting a common framework and documenting ichnofacies through time, environments and geography. Is anybody brave enough for that?

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The sponges of the Middle Cambrian Burgess Shale and Stephen Formations, British Columbia

J. K. Rigby and D. Collins (2004). Royal Ontario Museum Contributions to Science vol. 1, 155 pp.

This is the third version of a Burgess Shale sponge monograph, and two questions immediately spring to mind. Firstly, is it necessary? (I'll come to that shortly.) And secondly, why is it being reviewed here – surely it's too specialised a work for the *Newsletter?* Well, perhaps, but what also perhaps raises it above a purely taxonomic work is that it also contains a list of localities, with their sponge fossil content, from the wider Burgess Shale area rather than just the classic sites, and also a substantial summary of the early history of fossil sponges. The latter forms what should be a very useful summary of occurrence and possible phylogeny. In short, it uses a revision of the taxonomy as an opportunity to give a much more coherent picture of early sponge evolution. So, does it succeed?

Partly. In some ways, it is a critical volume, with the number of species and genera going up from 34 and 20 in the last incarnation (Rigby 1986), to 48 and 26 respectively in this one. They are generally described in the meticulous detail that we expect from J. Keith Rigby, and some of the new taxa, such as *Ulospongiella*, are quite startling creatures. The new taxa are described in about as much detail as is possible without going to extremes that few would condone, often using Rigby's favoured strategy of describing all significant specimens in turn, rather than just a summary of
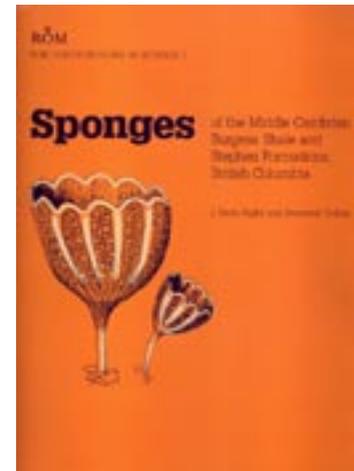
the characters of the taxon. It might be easier for the reader to extract things like intra-specific variability if the data were presented graphically at times, with, for example, correlation plots of important parameters, but the important thing is that the information is mostly present in the descriptions. There is no doubt that the taxonomic content is, for the specialist at least, both fascinating and important. The standard of illustration is in general very high, with good detail visible even in difficult material. Some are a little fuzzy, but that is difficult to avoid in a work of this size. So far, so good.

There are frustrations, however, and some of them are significant. Of least significance, perhaps, there are a few taxonomic assignments that appear strange, to say the least. *Fieldospongia bellilineata*, for example, appears from the photographs (of the second known specimen, with significant new detail) to have a structure effectively identical to the probably keratose demosponge *Vauxia*, and yet it is classified as closer to the lithistids. There is not even any discussion of the apparent similarity; perhaps the authors have good reason to keep the genera separate, but that is not obvious from either the illustrations or the description.

In other cases, the justification for the relationships proposed between new and existing genera is open to question, and the arguments sometimes, to me, seem less than persuasive (for example, with *Hamptoniella* and *Hamptonia*, where some features are similar, but what I would regard as probably more fundamental differences in skeletal structure are disregarded). This is closely tied to what I also see as problems in the phylogeny and early sponge history section. The evolutionary diagrams are actually little changed from the 1986 monograph, with the addition of new taxa but little rearrangement. In the case of the demosponges, the numerous lineages effectively form an unresolved polychotomy, and only sometimes do the authors suggest definite relationships between genera, although there is a loose ordering of many of them into a diverging phylogenetic fan. Their support for the arrangements given in the hexactinellids and demosponges seems weak in many places, and more worryingly, without a clear framework. With a useful phylogenetic hypothesis it should be clear when a new taxon is discovered, if not where to fit it in, then at least how to approach the job. To be brutally honest, I'm not even sure, with their scenario, which characteristics would need to be examined in order to incorporate a new genus.

That's not to say that sponge taxonomy is easy; in fact, it's excruciatingly tricky, with convergence (particularly of strengthening structures within the early, thin skeletons) seeming to be absolutely rife. The shared presence of spicule tracts, for example, cannot be treated as proof of a close relationship by itself, and the number of different tract arrangements is sometimes bewildering. There is certainly a temptation either to throw up one's hands in despair and declare it impossible, or to produce scenarios based on a few aspects of morphology, and stratigraphic position. But stratigraphy is another element that we cannot trust, simply because the record is so incomplete. There must be more reliable characters that can shed light on phylogeny, even if we cannot be certain at this stage what they are. The only way to progress seems to me to be, in true scientific

fashion, to try to use precise and well-defined frameworks that can accommodate known taxa, and test them with new data. We'll be wrong almost every time, but at least we'll be able to find out how we're wrong.

Rigby & Collins' hypothesis is certainly a scenario that can be tested, but without explicit statement of which considerations have resulted in the chosen arrangement, progress is very difficult. There are now perhaps three main phylogenetic hypotheses for the early evolution of hexactinellids, and in order to resolve them, the most fundamental requirement is a clear statement of how they differ. With the ones presented here, I'm not sure that is really possible. It's likely that all the published scenarios are wrong, but the interesting part is in finding out how they're wrong, and to learn from that which types of character might be more reliable. For that, we need to know clearly and precisely which characters the authors consider to be reliable.

So that's what I mean by 'frustrating.' There is, in a volume with such important new material, the potential to give a very detailed and interesting discussion of potential phylogenetic scenarios, but the chance was sadly missed. The summary of the early sponge record is very welcome, and is indeed probably the best yet published, but the interpretation doesn't go far enough to be satisfying.

The same could be said of the detailed occurrence and locality data that starts the volume. The data itself is interesting, complete, and potentially very useful. It is, however, very difficult actually to use it, partly because there is no overview figure or table. In order to find ecological correlations between different species, it is necessary for the reader to produce a summary diagram of localities against taxa. Such a simple presentation doesn't give any more information, but is more a fundamental courtesy than anything else – you only notice it when it's not there. Also, and in the same way as the phylogeny section, there is another missed opportunity here: the absence of any discussion of the ecological distribution of the taxa. The information for a treatment of tiering, patchiness, community composition and habitat modification is probably available in the volume, but it takes a lot of work on the part of the reader. Instead, it could have been a very interesting story in itself. Perhaps such a study is pending, and I do the authors a disservice, and if so then I look forward to it with relish. But it's still frustrating. The whole thing feels rather rushed, which is surprising.

So, can I recommend it? Definitely, and without hesitation, to any specialist (although it is expensive), because it contains so much raw data on a host of very important, and new fossils. I can't let any dissatisfaction with some aspects affect the fact that it's got a lot of important work in it. The illustrations and descriptions are worth it in themselves; in fact no one working extensively in this area is likely to be able to do without it. Which is all just as well, because the interpretative elements of the volume might just leave you grimacing a little.

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ABSTRACTS