41st Annual Meeting Cardiff, 1997

ABSTRACTS

Compiled by Chris Berry

Diversification of coralline and dasycladalean calcified algae during the Cretaceous and Cenozoic

Julio Aguirre and Robert Riding

Department of Earth Sciences, University of Wales Cardiff, Cardiff CF1 3YE

Coralline red algae originated in the Early Cretaceous, diversified almost continuously to the Early Neogene, and reached their maximum species diversity in the Early Miocene. Thereafter, diversity dramatically collapsed to a Late Pliocene minimum of 55 species, the lowest level since the Cretaceous. The Cretaceous-Pliocene diversification history of dasycladalean green algae is quite different, with two maxima and two troughs. Following a maximum in the Barremian-Aptian, diversity fell sharply in the Albian and this continued until a minimum was reached in the Campanian. Dasycladaleans then diversified in the Maastrichtian to reach a peak in the Palaeocene, followed by progressive decrease throughout the remainder of the Cenozoic. At the present-day, only about forty species of dasycladaleans are extant.

These two algal groups differ considerably in their light and temperature ranges. Corallines occur to depths of 270 m, and occupy habitats from tropical reefs to polar shelves. They are much less sensitive to both sea-level and temperature change than the shallow warm-water dasycladaleans. These differing requirements of corallines and dasycladaleans may, at least in part, account for the differing diversity patterns of these two major groups of calcified algae, as they responded to global environmental change during the past 145 Ma.

Soft tissue preservation in the pterosaur *Sordes pilosus* and its palaeobiological significance

N. N. Bakhurina and D. M. Unwin Department of Geology, University of Bristol, Queen's Road, Bristol BS8 1RJ

Evidence of soft tissues has contributed important details to our knowledge of pterosaur anatomy, but, frequently, the limited extent of preservation (in terms of quantity and/or quality) has restricted understanding of important structures such as the wing membranes and the integument. *Sordes pilosus*, a long-tailed pterosaur from the Upper Jurassic of Karatau, in Kazakhstan, is exceptional in that there are extensive tracts of well preserved soft tissues including wing membranes, the integument, 'hair-like' structures, claw sheaths, a tail-flap and foot-webs. Soft tissues are preserved in

two ways: as impressions and pseudomorphed by what appears to be mineralised organic residues.

The wing membranes are completely preserved and clearly demonstrate extensive attachment to both fore and hind limbs. Exceptionally well preserved wing fibres show that these structures were composite, with a variable morphology, and present throughout the flight patagia. Short fine filaments arising from the external surface of the integument covering the head and body seem to be remains of 'hair-like' structures. Otherwise the integument appears to have been relatively smooth and there is no evidence of scales or scutes.

The Middle Ordovician fauna of the Welsh Basin; its use in defining a chronostratigraphic standard

Richard Bettley

Department of Earth Sciences, University of Oxford, Parks Road, Oxford OX1 3PR

Proposals have been made to redefine the Ordovician series boundaries of the historical type area (Fortey et al. 1995) at more globally recognisable horizons. Extensive fieldwork in the Anglo-Welsh region has aimed to study these horizons, to relate them to the regional zonal schemes, and provide potential GSSP sections for use as regional or global reference standards. Mixed trilobite-graptolite faunas have been collected from single, measured sections across the region to produce a database of appearance-extinction events and a composite standard sequence. Quantitative methods can be applied to the data and offer greater accuracy and resolution over the classical methods previously used in correlating these isolated inliers.

The collecting of large populations from closely spaced stratigraphic intervals has also resulted in representative populations suitable for quantitative measurement. One particular line of study is of great interest in allowing the comparison of parallel evolutionary shifts in trilobite species of the Builth Inlier (Sheldon 1987), with those of new areas. This not only tests their candidature as genuine evolutionary changes, but also tests their stratigraphic usefulness.

Endocerida in the Silurian of Siberia

Olga K. Bogolepova

Department of Historical Geology & Palaeontology, Institute of Earth Sciences, Uppsala University, Norbyv‰gen 22, S-752 36, Uppsala, Sweden

Very rare Silurian representatives of the Order Endocerida (Cephalopoda), which flourished during the Ordovician Period, are described for the first time from the Mojerokan Formation (Llandovery) of eastern Siberia. These data complete the Silurian record of Endocerida described previously from Wales and the Canadian Arctic (Evans & Holland, 1995).

Keeping track of Palaeozoic terrestrial arthropods

Simon Braddy

Department of Geology, University of Bristol, Queen's Road, Bristol BS8 1RJ

Trace fossils have tremendous potential to provide information on the timing, palaeoenvironmental

distribution and diversity of the early terrestrial arthropods. Arthropod trackways occu *in situ*, may extend the range of some groups (e.g. arthropleurids) and can record the behaviour (e.g. walking techniques) of the producer. Ichnological data are also fraught with conceptual problems and considerable reinterpretation and taxonomic rationalization is required before the temporal and palaeoenvironmental distribution of the terrestrial arthropods can be assessed. Some ichnotaxa have been established on the basis of only slight behavioural and preservational variations from other ichnotaxa. The translation of ichnological evidence into diversity data is inhibited by the convention that ichnotaxa are based on the morphology of the trace rather than the identity of the tracemaker (i.e. different arthropods could create a single ichnotaxon or a single individual could produce various ichnotaxa by using different behaviours).

Understanding the functional mechanics of trackway production is fundamental to interpreting the trace fossil record of arthropod terrestrialization. Computer modelling (using LocoBug) is used to analyse the locomotion and indentify the trace maker. LocoBug enables a generic, three dimensional arthropod body plan to be animated by the three gait parameters (i.e. Gait, Opp., Suc.). LocoBug determines which legs are on the substrate at each instant of the step cycle and plots a 'stability polygon' relative to the animal's centre of mass, allowing the speed-stability relationship and optimal walking techniques for different body plans to be determined. LocoBug also generates theoretical trackways, which can be used to determine the degree of morphological variation that results from behavioural variation. Reinterpretations of various arachnid, eurypterid and arthropleurid trackways are presented and discussed, using data derived from LocoBug.

Getting a head in the Cambrian: cephalic composition and evolution in early arthropods

Graham E. Budd¹ and Ruth A. Dewel²

¹Department of Historical Geology and Palaeontology, University of Uppsala, Norbyv‰gen 22, Uppsala, Sweden.

²Department of Biology, Appalachian State University, Boone, North Carolina, USA.

The composition of the arthropod head has provided a focus for some of the most protracted and heated arguments in arthropod research. Modern arthropod heads are complex capsules of fused segments with the possible addition of a presegmental "acron", of which the exact number and homology are controversial. However, stem-group arthropods have a much simpler arrangement, ranging from the remarkably primitive system of the onychophorans through the linear heads of tardigrades and basal anomalocaridids. The complexity of the euarthropod head seems to have arisen as a correlate of shifts in feeding strategy from predominantely cephalic appendage-feeding in lobopods through to predatory gnathobasic thoracophagy in advanced anomalocaridids and basal euarthropods.

Recognition of homologies between anomalocaridids and euarthropods allows the insights gained from the simplest arthropod heads known to be applied to more advanced forms, and provides important data for phylogenetic reconstruction. In doing so some fascinating problems arise. For example, an appendage present in the earliest forms (the "frontal appendage"), undergoes a mysterious vanishing act in more derived taxa - unless of course it is homologous with the first antenna, which raises difficulties all of their own. The resolution of these issues will require

information from fossils, molecular development and classical morphology: but new advances in all of these fields mean that an answer may be closer than ever.

Evolution and habitat changes in Eocene hantkeninids

Helen Coxall¹, Paul Pearson¹ and Nick Shackleton²

¹Department of Geology, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ

²Godwin Laboratory, Department of Earth Sciences, University of Cambridge, Cambridge CB2 3RS

The hantkeninids are a group of attractive, planispiral planktonic foraminifera that evolved in the early middle Eocene and went extinct at the Eocene - Oligocene boundary. Because they are widely distributed and have ornate, character-rich shells, there is great potential for biostratigraphic, evolutionary and palaeoceanographic studies. SEM observations and the discovery of rare "missing links" demonstrate that *Clavigerinella eocanica* was the ancestor. The group then underwent substantial morphological evolution, such that a total of 32 morphospecies have been described. Nevertheless, it is doubtful whether more than two cladogenetic (branching) events occurred.

Previous geochemical evidence for the life habitat of the hantkeninids is very sparse. In this study, hantkeninids from a number of localities and ages were subjected to oxygen and carbon isotopic analysis, including material from various DSDP and ODP sites and some beautifully preserved specimens collected from the upper Eocene of the U.S. Gulf Coast. The results shows that the early hantkeninids were relatively deep, thermocline-dwelling forms, but later hantkeninids were surface-ocean dwellers. The period in which the group shifted its habitat corresponds to the phase of most rapid morphological change, during a time of global oceanic and climatic cooling. The possibility that this evolution was driven by the acquisition of photosynthesising symbionts is discussed.

Long-term evolutionary patterns of Jurassic low latitude Radiolaria

Taniel Danelian¹ And Kenneth G. Johnson²

¹Department of Geology and Geophysics, University of Edinburgh, West Mains Road, Edinburgh EH9 3JW

²Department of Geology and Applied Geology, University of Glasgow, Glasgow G12 8QQ

We analyse a compilation of 3227 Middle and Upper Jurassic (175-135 Ma) radiolarian occurences of 341 species in 131 samples which come from western Tethyan and central (proto-) Atlantic oceans. All samples are independently calibrated by other age diagnostic fossil groups, such as ammonites, calcareous nannofossils and calpionellids, and isotope stratigraphy. A negative peak in diversification is revealed for the early Bajocian, which is formed mainly by accelerated extinctions. Moreover, the mid/late Tithonian is characterized by an increase in originations combined with very few extinctions. These peaks correspond with well known palaeoenvironmental (geochemical and sedimentological) events in western Tethys, including the dramatic environmental changes during Tithonian time marked by the widespread accumulation of calcareous nannofossil oozes in western Tethys and the proto-Atlantic. However, analysis of sampling completeness and stratigraphic permutation tests suggest that the observed patterns might have resulted from uneven sampling.

Morphological and palaeobiological diversification of the earliest ophiuroids [Echinodermata]

Juliette Dean

Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD

Asteroids and ophiuroids first appear in the lower Ordovician and numerous Lagerst‰tten provide an unrivalled record of their early divergence. Although a number of features distinguish extant asteroids and ophiuroids, these differences are much less apparent in the Ordovician, resulting in many problematic taxa. Type material for at least one species of every genus of Ordovician 'ophiuroid' has been re-examined and incorporated into a morphological analysis to produce a phylogenetic hypothesis of ophiuroid origins and relationships. This information has been used to map out the functional and ecological diversification of early ophiuroids.

Solving the conodont growth conundrum

Phil Donoghue

School of Earth Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT

Despite the recognition that the conodont feeding apparatus represents one of the earliest experiments with a mineralised skeleton amongst the vertebrates, we are still relatively ignorant as to how the elements of the apparatus grew. The reason why this has remained the most intractable problem in conodont palaeobiology is because of the paradox between evidence that the elements must at least periodically have been embedded in soft tissue, and evidence indicating that they functioned as teeth. Bengtson's classic model of element evertion, analogous to the claws of cats, neatly obviates this problem, but is incompatible with homology between the hard tissues of conodonts and vertebrates. An alternative model must be sought.

A comprehensive study of the way in which conodont feeding elements grew has revealed that elements of similar morphology were constructed in dissimilar ways. The way in which the elements of ancestral taxa grew elucidates a mode of growth compatible with evidence of soft tissue cover, the function of conodont elements, the mode of growth of more derived taxa, and also comparable systems of exoskeletal growth in other vertebrates. Conodont elements grew in alternating phases of extended function punctuated by considerably shorter phases of growth. This pattern of growth is directly comparable with the "growing dentition" of lungfish and acanthodians, although it is suggested that the locus of formation of conodont elements was shallow, and so closer comparison with growing scales of these and other groups of fish may be more appropriate.

Ichthyoliths as biostratigraphic and palaeoenvironmental tools in the Carboniferous of Ireland.

Mags Duncan

Department of Geology, Trinity College, Dublin 2

Irish Carboniferous marine biotas as portrayed in the literature are almost exclusively composed of invertebrates. In fact, a majority of limestone samples subjected to acid etching, yield ichthyoliths, microscopic hard tissues of fish.

The ichthyoliths recovered comprise teeth, scales, and in some instances bone fragments, most of which can be assigned to major taxonomic groups of fish, such as chondrichthyans, actinopterygians and acanthodians. Taxonomy of ichthyoliths at the level of genera and species raises problems analogous to, but more acute than, those encountered in conodonts. At present, most ichthyoliths are treated as morphospecies using open nomenclature.

Many ichthyoliths such as palaeoniscoid type teeth are ubiquitous and apparently will not be useful in detailed biostratigraphy or facies analysis. These taxa are particularly poorly recorded members of the Carboniferous biotas. Other taxa, for example the chondrichthyan *Thrinacodus ferox* are more restricted in their distribution both in terms of stratigraphy and palaeoenvironment. Many Carboniferous chondrichthyans, actinopterygians and acanthodians appear to have a world-wide geographic distribution.

The cephalopod fauna of the Durness Group of northwest Scotland

David H. Evans

English Nature, Northminster House, Peterborough PE1 1UA

Cephalopods have been known from the Lower Ordovician carbonate successions of Durness and Skye since the middle of the 19th century. The North American affinity of the fauna was recognised by Salter (in Murchison 1859), although very different inferences were drawn regarding climate and geographical distributions. Many individuals are dolomitised or incompletely silicified, leading to problems in preparing material through acid digestion. Apart from specimens collected during the past 20 years, very little is known as to the precise horizons and locations from which much of the material came. To some extent, the more recently collected material has helped to resolve this problem. The cephalopod fauna consists so far of a range of taxa including representatives of the Ellesmeroceratidae, Bassleroceratidae, Tarphyceratidae, Piloceratidae, Proterocameroceratidae, Endoceratidae, and Protocycloceratidae. Piloceratids from the Durness Group show an extraordinary range in morphology, suggesting that the group is far more diverse than previously understood; while studies of *Protocycloceras* indicate that North American forms of this genus are over-split at species level. In the terminology of Flower and others, this cephalopod fauna indicates the presence of the Gasconadian, Demingian, Jeffersonian and Cassinian stages within the Durness Group, although breaks in the succession may occur.

A new enigmatic fossil from the Ordovician Soom Shale Lagerstätte

Sarah Gabbott¹, Richard Aldridge¹ and Johannes Theron²

¹Geology Department, Leicester University, Leicester LE1 7RH

²Department of Zoology, University of Stellenbosch, Private Bag X1, 7602 South Africa

The Ashgill Soom Shale Lagerst‰tte preserves the soft tissues of several taxa, sometimes with a subcellular level of fidelity. A number of specimens of a new enigmatic fossil have been found at three localities; the affinity of these animals is most likely to lie among the arthropods, although none displays jointed appendages. Aspects of the soft-tissue anatomy are, however, excellently preserved with some three-dimensionality. The most complete specimen is dorso-ventrally compacted, and exhibits forty segments, a gut trace, lateral lobes and other features. An incomplete specimen in

lateral aspect shows details of the internal features including fibrous musculature and an axial row of triradiate structures. The soft tissues are preserved through replacement by illitic and alunitic minerals and are associated with concentrations of rare earth elements. Complete feeding apparatuses of prioniodontid conodonts occur close to two of the specimens, suggesting that the conodonts may have been scavenging.

Coprolites as evidence of nutrient cycling in early terrestrial environments Kate Habgood

Department of Earth Sciences, University of Wales Cardiff, PO Box 914, Cardiff CF1 3YE

Numerous fossil assemblages and palaeosols indicate that terrestrial communities were in existence by the Late Silurian. These localities include the remains of vascular and non vascular plants, fungi and primitive arthropods. The existence of simple food webs has been inferred from this evidence, although evidence for plant-animal interaction is rare.

Coprolites have been recovered from Upper Silurian and Lower Devonian localities in the Welsh Borderlands. These contain abundant plant matter and are interpreted as evidence of a cycling of primary productivity. The nature of the source of such coprolites is enigmatic since non-predatory animal remains of an appropriate size have not been recovered from these localities. A majority of the coprolites recovered are predominantly composed of (apparently) undigested plant spore walls suggesting that little nutrient was extracted.

Comparison of spore size distributions in coprolites with those of *in situ* and dispersed spore assemblages, has potential to provide evidence for the origin of the spores within coprolites and hence the feeding strategy of the coprolite producer. Experiments on the palatability of various modern fern, moss and liverwort spores to modern myriapods (*Julus scandinavius*) have been undertaken. These have provided faeces comparable to the Silurian and Devonian coprolites in size, shape and composition. Experiments currently in progress test the effects of spore age, size, ultrastructure and degradation by fungi on the palatability and digestibility of spores.

The evolution and biodiversity of Cretaceous planktonic Foraminiferida.

Malcolm B. Hart

Department of Geological Sciences, University of Plymouth, Drake Circus, Plymouth, Devon, PL4 8AA

Planktonic Foraminiferida originated in the Triassic (?) or Early Jurassic but only expanded markedly in the Early to mid-Cretaceous. It is during the mid-Late Cretaceous that they evolved into a wide range of morphotypes and were able to colonise a much greater range of environments and regions. During the mid-Cretaceous, in particular, they developed a range of strategies ("k" and "r" selection) which allowed them to move from eutrophic surface-water environments into oligotrophic environments, especially those much deeper in the water column.

The general increase and/or turnover of taxa was punctuated by a number of major "events" - e.g., the Bonarelli event in the latest Cenomanian. Between these major biotic crises there are a number of smaller events, some of which can be attributed to small anoxic events, although others may be more

closely related to eustatic changes.

The data appear to indicate that there are patterns of extinction and radiation that relate to cyclical stimuli. The major changes in taxonomic composition of the fauna are also related to major extinction/radiation events where, if proper criteria are followed, individual taxa appear to change genus rather than species! The mechanisms involved in such changes are complex, but in the Cretaceous the level of dissolved oxygen in the water column, coupled with sea-level changes, appear to be quite important.

Implications of members of the Permian Cathaysian flora on spermatophyte phylogeny

Jason Hilton

Department of Palaeobotany, Institute of Botany, Chinese Academy of Sciences, Xiangshan, 100093 Beijing, P.R. China.

The Cathaysian flora of the Sino-Korean platform dominated floral assemblages in China from the Late Carboniferous through the Permian. The flora was initially termed the *Gigantopteris* flora due to the preponderance of the members of this spermatophyte lineage in its assemblages. However, subsequent investigations identified the Gigantopterid flora to be representative of only the latest stages of the floral transition, leading to the adoption of the term Cathaysian flora to encompass the entire East Asian flora of this period. From what is known about the spermatophyte composition of this flora it is abundantly clear that they, like the other components of this flora, are distinct from other contemporaneous floras (e.g. Glosspterid and Angaran floras). In particular there is a lack of reliable information on the Cathaysian conifers although data from contemporaneous floras indicate this to be a crucial period of evolutionary diversification for this group. As such, the Cathaysian flora presents a great potential for adding new data on spermatophyte evolution and phylogeny. A detailed and systematic study of several new taxa of spermatophyte ovulate structures will be presented from this important palaeogeographical area, and the implications of these new findings on the evolution and phylogeny of the spermatophytes considered.

Finite Element Analysis of cranial mechanics in Permian therapsid 'sabretoothed' predators

Ian Jenkins

Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ

Permian therapsid (mammal-like) 'reptiles' exhibit considerable skull diversity. The constructional anatomy of their crania is weakly analogous to extant predators - both sauropsid and mammalian. Hence the approach of basic physical principles was used to study structural aspects of their cranial evolution. This was especially pertinent for the 'sabretoothed' forms of the Permian: gorgonopsians, plus scylacosaurid and lycosuchid therocephalians. The skulls of long-snouted forms are theoretically weak in axial skull torsion arising from unilateral canine biting. However, their abundance during the Permian testifies to an adaptive success. Finite Element Analysis (FEA) was used to model the rostra of these groups. Model-generated stress trajectories were compared with the pattern and orientation of force transmission pathways observed in fossil crania. Stress trajectories extending from the canaines to the supraorbital region were produced at unilateral canine loading. The primary palate

functions as a spring, restricting stress to its working side. Significant compressive forces occurred at the supraorbital rim and region of the contralateral ectopterygoid. Gorgonopsians exhibit a unique adaptation to strengthen this region of the primary palate. Anatomical reinforcings show congruence with modelled stress patterns. Morphological variation between these groups suggests trophic partitioning resulting from diverse structural skull mechanics.

Miocene diversification of the Caribbean reef-coral fauna: new data from the Tamana Formation, Trinidad

Kenneth G. Johnson

Department of Geology and Applied Geology, University of Glasgow, Glasgow G12 8QQ

Ongoing analysis of the patterns of Neogene Caribbean reef coral species occurrences suggests that the Early and Middle Miocene reef-coral fauna was characterized by low species richness and low rates of species turnover. However, these older deposits are not as extensively preserved as Late Miocene and Pliocene material, and differences in estimated rates of faunal change are likely to be a function of differential sampling. To describe better the older Neogene coral fauna, large collections were made from the Middle Miocene Tamana Formation of Trinidad. Nearly 50 species were recovered, including 20 species first occurrences (FOs) but only 7 last occurrences (LOs). Approximately 30 of the records are new, including 7 FOs and 4 LOs. New rates of species turnover estimated using these additional data are still not as high as Pliocene estimates. Local diversity levels are similar to other assemblages from throughout the Neogene, suggesting that greater species diversity during the Pliocene is caused by local to regional variation in species assemblages (patchiness) rather than more speciose local communities. Therefore estimates of regional species richness and turnover rates are likely to remain underestimated for Early and Middle Miocene corals.

The Boreal ammonite succession and zonal sequence in the Early Cretaceous of Greenland

Simon R.A. Kelly¹ and Peter F. Rawson²

¹CASP (Cambridge Arctic Shelf Programme), West Building Gravel Hill, Huntingdon Road, Cambridge CB3 0DJ

²Department of Geological Sciences, University College, Gower Street, London WC1E 6BT

The Early Cretaceous ammonite succession in Greenland is reviewed and placed in a zonal framework. During recent field work in East Greenland several ammonite faunas have been discovered which have been hitherto unknown in Greenland. Over forty ammonite genera are now recognised and are distributed in at least 17 principal faunas. Comparison of these faunas is made with the standard 37+ zones identified in the northwest European Early Cretaceous succession. Locally correlation can be achieved down to subzonal level. Correlations with other boreal as well as tethyan ammonite successions are discussed.

Palaeozoic stromatoporoid and tabulate growth bands and their palaeobiological implications

Stephen Kershaw $^{\mathrm{1}}$ and Graham A. Young $^{\mathrm{2}}$

¹Department of Geography and Earth Sciences, Brunel University, Uxbridge, Middlesex UB8 3PH,

²Manitoba Museum of Man and Nature, 190 Rupert Avenue, Winnipeg, Manitoba R3B 0N2, Canada

Examination of stromatoporoids and corals from selected Ordovician and Silurian sites in several facies and regions demonstrates that both groups generated growth banding with consistent patterns. The regularity of such banding in some samples is interpreted as due to episodic factors such as sedimentation or seasonality because, in both groups, banding commonly coincides with ragged margins generated by sedimentation killing the flanks of the skeleton, followed by recovery. Tabulate coral growth banding consists of an alternation of denser and more closely spaced skeletal elements with less dense and more widely spaced elements. This pattern is similar to that seen in modern scleractinians; each couplet is considered to represent one year's growth. Tabulate banding varies in scale and intensity among taxa, facies and regions; recorded vertical growth rates range from estimated 1-20m/yr. Stromatoporoid growth banding is a more subtle phenomenon. Where clearly visible, it falls into two scales; latilamina scale with prominent growth disruptions, commonly c.10mm; and lamina scale, commonly 1-3mm. Modern calcified sponges grow 0.1-0.5 mm/yr, but at such rates Palaeozoic stromatoporoids would have taken thousands of years to grow even moderately large individuals, and comparison with intergrown corals indicate fast growth in the fossils. Preliminary measurements suggest that reefal stromatoporoids grew faster than those in muddy facies, because the banding is thicker in the former, although interpretation of the banding as annual remains uncertain. The present study is the first comprehensive comparison of banding in corals and stromatoporoids, permits an improved understanding of its controls, and illustrates the potential of banding as a tool for assessment of ancient environmental parameters influencing the sea bed.

The taphonomy of a Waulsortian carbonate buildup

Jeff Lord

Department of Geology, Trinity College, Dublin 2, Ireland

Recent work has suggested that parts of the surface of Waulsortian buildups were covered by a mucilage-rich, microbial film, which stabilised the surface sediment to the extent that depositional dips of up to 40(were maintained. The taphonomy of a diverse assemblage of crinoids, bryozoans, brachiopods and molluscs in a Waulsortian carbonate buildup of late Tournaisian age at Mullawornia, County Longford, Ireland has been investigated in order to establish the physical conditions on the surface of the mound.

The fauna is parautochthonous. The brachiopods and bivalves are mostly preserved as conjoined valves and show little evidence of transport. However, their orientation is random and they are rarely preserved in life position. There is no evidence of bioturbation; the re-orientation of shells must have resulted either from currents or through the collapse and settlement of the semi-coherent sediment as organisms such as sponges decayed. The component parts of crinoids in many cases do not appear to have been dispersed very far. Fenestrate bryozoans, in contrast, are commonly comminuted, suggesting that at least at some times current energy levels on the bank surface were high. Sorting ratios of conodont elements may provide some information as to what extent currents were an important feature of the surface of a buildup.

Early Silurian sea-level changes

David K. Loydell

Department of Geology, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3OL

Global sea-level fluctuated markedly during the early Silurian, probably as a result of the waxing and waning of ice-sheets in the South American portion of Gondwana. A new sea-level curve for the Early Silurian is presented which appears to differ significantly from those published previously.

Facies (and faunal) changes in the Lower Silurian do not support the P and S model, but are consistent with the sea-level changes proposed here.

Mid Telychian marine red beds appear to have been deposited during a minor sea-level fall immediately after a period of very high sea-levels, rather than during a transgressive episode as previously suggested.

Comparison of the sea-level curve presented herein with those constructed in the past is hampered by the lack of precision currently possible in the correlation of early Silurian deep water (graptolitic) and shallow water (shelly) sequences. Improving the precision of this correlation should be a priority for future research.

Crinoid stem ossicles as biostratigraphical and palaeoecological tools in the Carboniferous of northwest Ireland: problems and potential

Kay Mannifield
Department of Geology, Trinity College Dublin, Dublin 2, Ireland

Complete crinoid specimens are rare in the Carboniferous shale and limestone sequences of northwest Ireland. By contrast, columnals and pluricolumnals are abundant.

More than 40 different columnal types have been distinguished. However, relating the columnal morphotypes to biological taxa is difficult. Few complete crinoids have been found with which to compare the disarticulated stem material; as a result columnals cannot usually be identified in terms of species erected on the basis of complete material. In some crinoid families there appears to be little variation in column morphology, so that it is unlikely that it will be possible to distinguish species and even genera within them on the basis of columnals. In other families, individual species appear to have distinctive columnals, which are useful biostratigraphical and palaeoecological tools. However, in xenomorphic stems two or more columnals of different appearance may in fact be conspecific. This may lead to an overestimation of taxonomic diversity.

Despite these problems, it is clear that different stratigraphical horizons in the Carboniferous of northwest Ireland are characterised by distinct assemblages of crinoid columns. Crinoid columnals also yield a much less biased estimate of crinoid diversity than that given by counts of thecae.

A novel early Mid Devonian reproductive structure

J.E.A. Marshall

Department of Geology, University of Southampton, Southampton Oceanography Centre, European Way, Southampton SO14 3ZH

A new early land plant reproductive structure has been discovered in East Greenland in rocks of Early Mid (Eifelian) Devonian age. This reproductive structure is relatively large (9x7x4 mm) and borne on a specialized stalk with an abscission structure. It contains a single internal organic walled inner body invested by an external tissue and appears to have an apical opening. It is interpreted as a large dispersed megasporangium containing a single megaspore rather than a specialised spore filled sporangium. It is of possible lycopod affinity. It shows parallels with the unrelated progymnosperm and lycopod 'seed-megaspores' which it significantly pre-dates. Functionally it is interpreted as an adaptation to reproduction in a seasonally ephemeral upper fan environment.

The life and times of *Dunbarella*

Chris Peel

Department of Earth Sciences, University of Leeds, Leeds LS2 9JT

Black shale biodiversity is often dominated by thin-shelled, flat-valved bivalves referred to here as 'paper pectens'. Throughout the Namurian and Westphalian marine bands of the UK, the genus *Dunbarella* was prolific and often formed pauci- or mono-specific assemblages. The interpretation of *Dunbarella* autecology will contribute to understanding the palaeoecology of black shales. The life strategies of this enigmatic taxon are discussed here. Functional morphology and faunal relationships suggest that *Dunbarella* was a benthic epibyssate animal. Size frequency plots show that individuals, within a population, are clustered around a narrow size range, indicating brief colonisation by single cohorts. An inflated prodissoconch and the lack of specimens much less than 10mm imply a teleplanic larval stage, and hence a dichotomy in the *Dunbarella* life cycle. The presence of shell damage may be evidence of predation in these harsh dysaerobic environments.

Class Obolellata - the earliest rhynchonelliformean (calcareous shelled) brachiopods

Leonid E. Popov¹, Lars E. Holmer², Michael G. Bassett³

¹VSEGEI, Srednij Prospect 74, 199026 St. Petersburg, Russia

²Institute of Earth Sciences, Historical Geology and Palaeontology, Norbyv"gen 22, S-752 36

Uppsala, Sweden

³National Museum of Wales, Cathays Park, Cardiff CF1 3NP

Recently revised classifications of the brachiopods recognise three subphyla and nine classes, replacing the traditional subdivision into "inarticulates" and "articulates". The Class Obolellata represents the earliest known calcareous-shelled brachiopods, appearing in the early Atdabanian and becoming extinct at the end of the Middle Cambrian. The obolellates include forms both without articulation, and those with primitive articulatory structures, consisting of paired ventral denticles and dorsal sockets; this type of articulation appears to have evolved independently from other Cambrian calcareous shelled lineages. The muscle system in the Obolellata is closely comparable with that of other rhynchonelliformean brachiopods. In*Obolella*, the ventral muscle scars are located peripherally within the visceral area, but in the majority of genera they form a single muscle field, with the adductor scars located medially. In some "articulated" obolellides and naukatides, the attachment scar

of the internal oblique is located posterior to the axis of rotation, suggesting that the internal oblique muscles may have served as diductors. In the Order Naukatida, a high ventral muscle platform is developed, somewhat comparable with the free spondylium of protorthoideans, but probably evolved independently. Obolellides are the most abundant Early to Middle Cambrian rhynchonelliformean brachiopod faunas of North America and Siberia, whereas naukatides are known mainly from tropical Gondwana (Australia) and associated island arcs as well as occurring sparsely in North America.

Lower Silurian palaeotaxodont bivalves from Wales and the Welsh Borderland

Vivian Alexander Ratter

Department of Earth Sciences, University of Wales Cardiff, PO Box 914, Cardiff CF1 3YE

Lower Silurian palaeotaxodont bivalves from Wales and the Welsh Borderland have received little attention since the last century, and consequently are poorly understood. Current research is revising the taxonomy and resolving their phylogeny and autecology.

Attention is presently focused on bivalve assemblages dominated by palaeotaxodonts from the Llandovery of the Malvern Hills and the Wenlock of Pembrokeshire and Cardiff. An investigation of the Llandovery succession has established two new genera, whilst the Wenlock sediments in South Wales have yielded a further two new genera and four new species. Several taxa bridge gaps in the knowledge of palaeotaxodont morphology between the Upper Ordovician and Devonian, and indicate the rapid evolution of some nuculoid families during the lower Silurian. A new nuculid species is one of the earliest examples of a bivalve possessing a resilifer, whilst new ctenodontid genera suggest a distinctive evolutionary lineage from the Ordovician genera *Ctenodonta* and *Tancrediopsis*. The autecology of a number of palaeotaxodont assemblages has also been investigated. Life habits have been ascertained using morphology and biometric data. Results reveal that the majority of deposit-feeding nuculoids were medium-depth, rapid burrowers, and consequently, well adapted for the near-shore, unstable substrate in which the majority lived.

Astraspis - reconstructing and recoding an Ordovician fish

Ivan J. Sansom¹, M. Paul Smith¹ and Moya M. Smith²

¹School of Earth Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT

²Division of Anatomy and Cell Biology, UMDS Guy's Hospital, London Bridge, London SE1 9RT

Articulated specimens of Ordovician fish are rare, with reports from only three localities; in Australia, Bolivia and the USA. Amongst these, the Harding Sandstone Formation (Caradoc, Ordovician) of Colorado is the only one that has also yielded histologically identifiable material. A new specimen of the pteraspidomorph *Astraspis desiderata* Walcott 1892 was recovered from the Harding in 1994, which exhibits details of the structure of the headshield and tail scales. Together with a reassessment of the previously recorded articulated specimens and the exoskeletal histology, these new data permit the first integrated anatomical account of an Ordovician fish. Many of the features seen in previous reconstructions of *Astraspis* prove to be erroneous, and a number of the published character codings for the genus also require revision.

Plant-insect interactions in the Triassic of South Africa and the problem of

taphonomic bias

Andrew C. Scott¹, John Anderson² and Heidi Anderson²

¹Geology Department, Royal Holloway University of London, Egham, Surrey, TW20 0EX

²National Botanical Institute, Private bag X101, Pretoria 1001, South Africa

The Molteno Formation of Late Triassic (Carnian) age in South Africa has yielded more than 200 plant species from 100 plant assemblages at 69 localities (30,000 catalogued slabs) as well as more than 300 species of insect. Damage to leaves caused by insects is widespread on a diverse number of plant species at numerous localities. The damage includes feeding traces, predominantly continuous marginal feeding traces, leaf mines including linear and possible blotch varieties and probable leaf galls. Damaged taxa include a wide variety of gymnosperms including the conifer Heidiphyllum, the ginkgophytes Ginkgo and Sphenobaiera and the pteridosperms Dicroidium, Taeniopteris and Dejerseya and the genera of uncertain affliliation Yabeiella and Taeniopteris. Quantitative data (3000 specimens examined) on the insect damage was obtained for four sites: Waldeck, Kapokkraal, Aasvoelberg and Birds River. Quantitative data indicate that leaf damage between sites varies from 3 to 25% and within species from 1-50%. Some evidence of host specificity is presented. The variation in damage to the same taxon between sites and even the overall herbivory seen at the different sites, makes the interpretation of the general levels of hebivory in the Molteno difficult to assess. Herbivory levels in Northern Hemisphere Triassic plant assemblages appears to be significantly lower and this is also the case with the succeeding Jurassic floras worldwide. It is not yet clear to what extent taphonomic bias may influence the calculation of overall herbivory levels for a given time period.

Cambrian bradoriid and phosphatocopid Arthropoda of North America

David J. Siveter¹ and Mark Williams²

¹Leicester University, Leicester LE1 7RH

²British Geological Survey, Keyworth, Nottingham NG12 5GG

North American species were among the first bradoriid and phosphatocopid arthropods documented. They occur throughout the Cambrian of N America most abundantly in the Canadian Atlantic Provinces, British Columbia and Arizona and to a lesser extent in New York State and Tennessee. The total known fauna comprises 16 genera and 26 species and is much less diverse at the specific level than previously indicated (about 100 species). Several genera have a phosphatic carapace, thus endorsing the notion that carapace composition cannot be used as a diagnostic criterion for distinguishing bradoriids and phosphatocopids. The bradoriid and phosphatocopid faunas of N America occur as low diversity marine assemblages and were probably mostly benthic or nektobenthic. Most species are short ranging but have only local geographical occurrence. A few species have intercontinental biostratigraphical potential being coeval in Canada, Britain and Scandinavia. Provinciality of the bradoriid and phosphatocopid faunas supports the notion of an Iapetus Ocean in the Cambrian. Eastern Canadian (Avalonian) faunas are characterized by Beyrichona, Cyclotron and Hipponicharion; Arizona (Laurentia) has Walcottella and Dielymella. Bradoria is known from both the Avalonian and Laurentian parts of N America; the cosmopolitan Anabarochilina occurs only in the Laurentian part. Faunas of the distal shelf of Laurentia have Asiatic (Liangshanella and cambriids) and Australian (Indota) bradoriids.

Late Ordovician deep water conodonts: patterns of species change during a marine transgression

*C.J. Smith¹&², H.A. Armstrong¹ and A.W.Owen²

¹Department of Geological Sciences, University of Durham, Durham DH1 3LE

²Department of Geology and Applied Geology, University of Glasgow, Glasgow G12 8QQ

Until recently it was assumed that deep water environments would be impoverished in species but recent studies have revealed them to be ones of prolific speciation and high species diversity. Ocean state models predict that deeper water faunal assemblages will appear at progressively higher levels on the continental slope at times of transgression as a response to changing conditions. Transgressive episodes can therefore provide a window into both deep water faunas and their environments, allowing patterns and processes of speciation to be elucidated.

The widespread Nod Glas Formation represents a late Caradoc deepening of the Welsh basin. Sedimentological analysis of the phosphatic limestones from this unit suggests that the initial deepening occurred during the deposition of the lower part of the formation. Further deepening is reflected by the shales with graptolitic horizons towards the upper part of the formation. Although conodont samples have only been obtained from the basal few metres, distinctive faunal assemblages there reflect the changing environmental conditions and have wider implications for both deep water conodont palaeobiology and basin evolution.

Ecological competition and macroevolutionary patterns in post-Palaeozoic bryozoans

Paul D. Taylor¹, Frank K. Mckinney² and Scott Lidgard³

¹ Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD

²Department of Geology, Appalachian State University, Boone, North Carolina 28608, USA

³Department of Geology, Field Museum, Chicago, Illinois 60605, USA

Do biotic interactions over ecological time shape macroevolutionary patterns through geological time? Post-Palaeozoic bryozoans consist mainly of two orders - Cyclostomata (Ordovician-Recent) and Cheilostomata (Jurassic-Recent) - which develop a similar range of colony-forms and generally co-occur. On average, recent cheilostomes outcompete cyclostomes for food and living space. Furthermore, evidence from skeletal overgrowths shows that cheilostomes have won the majority of spatial competitive encounters with cyclostomes since at least the mid-Cretaceous. But has this long-term ecological superiority led to faunal replacement?

Three alternative measures of changes in the relative 'success' of cyclostomes and cheilostomes are now available: (1) global taxonomic (family) diversity; (2) within-fauna species richness; and (3) within-fauna skeletal mass. Concurrently with the mid to late Cretaceous radiation of cheilostomes, the slower radiation of cyclostomes that had commenced in the late Triassic reached a plateau in terms of global family diversity. At the same time, within-fauna species richness of cyclostomes declined slightly from its mid-Cretaceous peak. Within-fauna skeletal mass of cyclostomes relative to cheilostomes decreased through the late Cretaceous before rising abruptly after the K-T boundary and then decreasing again towards the present day. Therefore, different measures of relative success may

provide different perspectives on the relationship between ecological competition and macroevolutionary pattern.

Evolutionary implications of the extent and pattern of exploitation of skeletal morphospace by animals of the Burgess Shale

R.D.K. Thomas and Rebecca M. Shearman

Department of Geosciences, Franklin & Marshall College, Lancaster, Pennsylvania 17604-3003, U.S. A.

A comprehensive analysis of the skeletons of Burgess Shale animals reveals that they incorporate 146 of the 182 design elements that constitute our multivariate Skeleton Space. Within 15 million years of the emergence of animal skeletons, 83% of design elements recognized among all living and extinct marine organisms had been exploited.

The morphological disparity of skeletal design elements increased in parallel with the diversity of higher taxa, much more rapidly than the diversity of families and genera. The rapid saturation of available morphospace following the emergence of a key innovation confirms that maximum disparity is determined by the passive constraint of limited viable options. In contrast, emerging developmental mechanisms and the adaptive exploitation of environmental opportunities are efficient causes of increasing diversity.

A similar analysis of Tommotian skeletons from the Lena River region shows that these are composed largely of simple rods, plates and cones. The Burgess Shale animals record an extraordinary proliferation of design elements involved in the growth of metamerically segmented, external skeletons. Internal and remodeled skeletal elements are greatly under-represented. Developmental controls associated with the growth of internal lever-skeletons, based on the duplication of *Hox* gene clusters and diversification of bone matrix proteins, must have evolved much later than those responsible for the growth of otherwise similarly complex external skeletons.

Late Cambrian and Early Ordovician conodont clusters in abyssal deposits of south-central Kazakhstan

Tatiana Tolmacheva VSEGEI, Srednij Prospect 74, 199026 St. Petersburg, Russia.

Early Palaeozoic ophiolites in southern Central Kazakhstan include condensed sequences of radiolarian cherts, which originally formed some of the earliest known radiolarian oozes formed on an abyssal plane. Together with radiolarians these cherts contain numerous conodonts of the Upper Cambrian Eoconodontus nothchpeakensis Biozone to the Middle Ordovician Pygodus anerinus Biozone. Sporadic occurrences of lingulate brachiopods, e.g. Paterula, and hexactinellide sponge spicules provide possibly the earliest direct evidence of benthic faunas inhabiting abyssal depths. A unique character of the conodont faunas is the abundance of natural assemblages of elements. The conodonts preserved in clusters includes proto-, para- and eoconodont taxa, e.g., Phakelodus tenuis, Prooneotodus aff. P. rotundatus, Coelocerodontus bisulcatus, Drepanodus arcuatus, Oepikodus evae, Oelandodus sp., Paracordylodus gracilis, Paroistodus proteus, Periodon flabellum, Prioniodus adami, P. elegans, Rossodus sp., Scolopodus? peselephantis, Teridontus sp., etc. Almost all the

natural clusters are preserved in coprolites, including elements of various sizes and growth stages, but juveniles are the most abundant. The material makes it possible not only to add detail to characters and the composition of some multielement conodont apparatuses, but also to study ontogenetic development of elements in some species of paraconodonts and eoconodonts, and to trace the succession of formation of distinctive units of conodont elements.

Geochemical vertebrate taphonomy: Rare earth element analysis of terrestrial vertebrate assemblages

Clive N. Trueman

Department of Geology, University of Bristol, Queen's Road, Bristol BS8 1RJ

Several studies have determined the rare earth element (REE) distribution patterns of ancient vertebrate remains from terrestrial samples, but no extensive data are available to assess the variation in REE distribution patterns of fossil bones either within or between assemblages; or the effect of varying sedimentological conditions on bone preservation.

In this talk, data are presented from two broadly contemporaneous terrestrial assemblages from the Campanian (Upper Cretaceous) of Montana, U.S.A., and Alberta, Canada. Although both of these assemblages were produced in fluvial environments, the sedimentology of the two deposits differs significantly in detail. The Two Medicine Formation of the Willow Creek Anticline, Montana is dominated by flood plain sediments and is characterised by low rates of reworking, whereas the Dinosaur Park Formation of Dinosaur Provincial Park is dominated by channel sediments and is characterised by high rates of reworking.

The REE chemistry of the vertebrate remains differs significantly between these two assemblages, and may be used to distinguish between channel and flood plain environments of early diagenesis. Both assemblages also contain bone bed vertebrate accumulations. In the Willow Creek Anticline assemblage, the variation in REE patterns of bones from the bone bed can be compared to that found in 'background' bone accumulations. The bones from the bone bed show much more consistent REE patterns, suggesting that the bone bed was not formed by simple concentration of 'background' bones, but had a unique, environmentally restricted source.

The REE are therefore shown to present a powerful new tool for the taphonomic analysis of terrestrial vertebrate assemblages.

Hind limb kinematics of pterosaurs during terrestrial locomotion

D. M. Unwin

Department of Geology, University of Bristol, Queen's Road, Bristol BS8 1RJ

Two different interpretations of how pterosaurs used their hind limbs during terrestrial locomotion have emerged in recent years. Some have argued that pterosaurs were bipedal digitigrades, with their legs tucked under the body in a fully erect position, permitting a nimble and rapid gait. Others opt for a more traditional, quadrupedal, plantigrade reconstruction with the legs sprawling outwards in a semi-erect position, allowing an effective, if ungainly waddle. So far, the imperfect preservation of pterosaur bones has fueled rather than resolved this controversy.

New, complete, uncrushed hind limbs of pterosaurs from the Santana Formation of Brazil, show that the traditional view is largely, if not entirely correct. The femur jutted out sideways and forwards from the pelvis and progression was largely achieved by flexion and extension of the lower leg at the knee. The digits could not hyperextend, as in birds, thus the foot was plantigrade and typically angled forwards and outwards. This interpretation of hind limb posture perfectly matches tracks attributed to pterosaurs and is also consistent with their role as the posterior wing spar of the flight apparatus.

Comparative biomineralization in cheilostome and cyclostome bryozoans

Michael J. Weedon and Paul D. Taylor

Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD

Modern bryozoan faunas largely comprise two orders which independently evolved calcified skeletons: the dominant Cheilostomata and the Cyclostomata. Biomineralization in cyclostomes originated in the Ordovician, whereas calcified skeletons in cheilostomes first appeared in the Jurassic. Colony forms in the two orders occupy similar morphospace. However, at the zooidal level cheilostomes display a much greater disparity than cyclostomes. Is this contrast in disparity between the orders paralleled at the level of skeletal ultrastructure? Cyclostome skeletal walls are invariably dominated by laminar fabrics, with small amounts of granular and planar spherulitic structures. Cheilostome skeletons comprise a much wider range of fabric types, with wall perpendicular prismatic fabrics (absent in cyclostomes), wall-parallel prismatic and planar and transverse spherulitic fabrics, rod-like fabrics (again unique to cheilostomes), as well as a range of laminar fabrics including rhombic "semi-nacre". Furthermore, many cheilostome species have aragonitic skeletons, skeletons of mixed mineralogy or weakly-calcified, flexible skeletons: conditions unknown among cyclostomes. Therefore the two closely-related clades exhibit strikingly different skeletal ultrastructures, reflecting their independently evolved calcification and the strong influence of biological control on details of skeletal growth and fabrics.

The Permo-Triassic mass extinction in East Greenland

Paul Wignall and Richard Twitchett

Department of Earth Sciences, University of Leeds, Leeds LS2 9JT

The Permo-Triassic boundary in East Greenland is ostensibly complete and occurs within a siltstone and mudstone dominated marine succession. A major facies change occurs near the end of the Permian with highly bioturbated silty mudstones of the Foldvik Creek Formation giving way to finely laminated, pyritic shales of the Wordie Creek Formation. The shales contain concretions which yield ammonoids and beautifully preserved fish, some showing preservation of soft parts. Many Permian taxa disappear near to this facies change but the precise level of the mass extinction has long been controversial due to the presence of Permian fossils (brachiopods and bryozoans) from up to 100 m above the base of the Wordie Creek Formation. These Permian taxa have prompted some authors to suggest that a Permian fauna survived in Greenland long after the extinction elsewhere; whereas other authors interpret these specimens as "reworked". This fauna is generally encountered in limestone clasts from conglomeratic lenses that are probably turbidite feeder channels. Many of the limestone clasts are lithologically similar to known Permian limestones in the region implying that they are indeed reworked. However, thin intervals of bioturbated mudstones from within the Triassic

contain a "mixed" fauna of Triassic bivalves and Permian bryozoans which are unlikely to be reworked. Furthermore, some turbidite sandstones contain well preserved valves of brachiopods at their base. It would therefore appear that the East Greenland region provided a temporary Triassic refuge for some Permian taxa.

Structure and taxonomic significance of the graptolite prosicula

S. Henry Williams and Lorne C. Clarke

Department of Earth Sciences, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X5, Canada

Studies on graptolite taxonomy and phylogeny in recent years have placed great emphasis on proximal development of the rhabdosome, particularly the presence or absence of a virgella and early thecal growth patterns. As the prosicula was the earliest part of the graptolite skeleton to be secreted, we consider that it may also reveal fundamental information about evolutionary relationships within the Graptoloidea. Parameters investigated include the overall form, transition into the nema, pattern of secondary longitudinal ridges and spiralled trace. A variety of Ordovician taxa ranging in age from Tremadoc to Ashgill have been examined using a combination of light microscopy, SEM and TEM. In addition to these features, we are also paying attention to peridermal microstructures that may point to the method and order of secretion of the various components of the prosicula. Subsurface samples recovered during recent hydrocarbon exploration in the Lower Paleozoic of western Newfoundland have shown that graptolite prosiculae are commonly found in palynomorph preparations from strata in which more complete graptolite remains are lacking. If prosicular morphology thus proves to be a useful taxonomic feature, graptolite prosiculae might also be used biostratigraphically in the absence of more complete material.

Phylogenetic and phenetic approaches to crustacean evolution

Matthew A. Wills

Department of Geology, University of Bristol, Wills Memorial Building, Queen's Rd., Bristol BS8 1RJ

The crustaceans exhibit enormous plasticity of form, having evolved many distinctive bodyplans since their origins in the Cambrian. Homoplasy within the clade is high, and there may be superficial similarities in overall form and function for distantly-related taxa in similar habitats. A better understanding of the evolution of the clade requires: 1. a more complete picture of the phylogeny of both Recent and fossil groups, and, 2. insights into the pattern of morphospace filling through time. Ultimately, this will necessitate the thorough integration of cladistic, phenetic and stratigraphic data.

A data base comprising 135 morphological characters scored for orders and sub-orders was produced to address some of these questions. Gross cladistic topology is: (Eumalacostraca vs Maxillopoda) vs Phyllopoda (paraphyletic). A few Cambrian fossils (e.g., *Canadaspis, Waptia* and *Odaraia*) fall close to the base of large clades, but occupy key regions of morphospace, such that Cambrian disparity approached half its present level. The Ordovician and Silurian saw a marked decrease. The appearance of the eumalacostracans and branchiopods in the mid and late Devonian signalled two rapid and marked disparity increases, with levels reaching another plateau (about 80% of Recent levels) from the Permian to the Tertiary. Most intervals preserve a range of forms more disparate than the mean of random samples, but not significantly so (with the exception of the end Devonian).

Trackways of juvenile dinosaurs

Joanna L. Wright

Department of Geology, University of Bristol, Wills Memorial Building, Queen's Rd., Bristol BS8 1RJ

Fossil vertebrate trackways are the only direct evidence of the way in which extinct animals moved about on land. Tiny fossil trackways from the early Jurassic of the Eastern United States are thought to have been made by juvenile theropod dinosaurs. The tracks show that these small dinosaurs moved on average relatively more quickly than larger theropods. The makers of these tracks seem to have used some unusual gaits, which would not have been suspected from skeletal morphology alone.

Relationships between internal and external morphology in *Paleofavosites*

Graham A. Young¹ and Robert J. Elias²

¹Manitoba Museum of Man and Nature, 190 Rupert Avenue, Winnipeg, Manitoba R3B 0N2, Canada ²Department of Geological Sciences, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada

Growth of coral colonies resulted from the interaction of environmental and genetic mechanisms. Astogenetic and structural factors generated the primary skeletal elements, but the pattern of organization of modules could have been affected if colony form changed in response to environment. By comparing internal and external characters through colony growth, we can determine how factors combined to produce growth form. This study is based on *Paleofavosites subelongus* from the uppermost Ordovician to lowermost Silurian of the east-central United States. Corals of this species are morphologically simple, but are variable in characters related to corallite size and packing, and in external growth form.

The final colony form was generated by changes in maximum growth angle of marginal corallites through astogeny; this angle changed in concert with growth surface shape. These features were coordinated with corallite characters. Initial colony growth was apparently under a high degree of genetic control; genetic constraint of subsequent growth probably worked through relationships among characters of internal and external morphology. Frequent variations in growth angle and growth surface shape during astogeny indicate fluctuations in the environmental factors affecting growth form. It is likely that sedimentation and possibly colony subsidence were the major environmental factors influencing growth form.

POSTERS

Trepostome bryozoans from the Tramore Limestone (Ordovician), County Waterford, Ireland

¹Caroline Buttler and ²Patrick Wyse Jackson

¹Department of Geology, National Museums & Galleries of Wales, Cathays Park, Cardiff CF1 3NP

²Department of Geology, Trinity College, Dublin 2, Ireland

The Tramore Limestone Formation (Llandeilo, Ordovician) crops out on the south east coast of County Waterford, Ireland. It is a muddy nodular limestone reaching 65m at its thickest. The

Tramore Limestone Formation contains trilobites and a diverse brachiopod fauna, which have been shown to have affinities with Baltica, as well as bryozoans. The most common bryozoan colonies have a distinctive hemispherical dome-shaped morphology. The zoaria range in size from 9mm to 75mm and have previously been identified as *Monticulipora*, *Stenopora* or *Favosites* species. Unfortunately the majority of the zoaria are re-crystalised making identification difficult. There are some species in which the internal structures remain. Examination of these have shown them to be *Diplotrypa petropolitana*. The colonies are all abraded and some have *Trypanites* borings on the upper surface. The lower surface of the colonies are rugose and sometimes concave. The bryozoan fauna is not monospecific, decalcified bryozoans of undetermined ramose trepostome forms have been identified.

Chasmataspids come in from the cold

Jason A. Dunlop

Institut für Systematische Zoologie, Museum für Naturkunde der Humboldt Universität zu Berlin, Invalidenstrasse 43, D-10115 Berlin, Germany

Arthropods from the Severnya Zemlya Formation, October Revolution Island, Siberia (Lower Devonian, Lochkovian) are reported. The fossils derive from a single collecting trip in 1978 and the palaeoenvironment is interpreted as a quiet lagoon. As well as ostracodes (not described) the fauna includes a new phyllocarid (Crustacea: Phyllocarida). There is also a new, eyeless cheloniellid (Arachnata: Cheloniellida) with probable affinities to the Ordovician genus Duslia. Most significant are some 60 specimens of chasmataspids (Chelicerata: Chasmataspida) which resemble previous finds from the Devonian of Germany, e.g *Diploaspis*. These new chasmataspids confirm that chasmataspids had 13 opisthsomal segments, a reduced tergite 1, a preabdomen comprising tergites 2-4 and a postabdomen comprising segments 5-13. The material shows that the preabdomen could telescope with fossils preserved as both 'long' and 'short' forms. Intriguingly these fossils also suggest that chasmataspida had a eurypterid-like metastoma and genital appendage. This implies that Chasmataspida and Eurypterida may be sister groups.

Palynomorph distribution in a late Wenlock shelf sequence, Farley Member, Coalbrookdale Formation, Shropshire, England

Craig Harvey

Centre for Palynology, The University of Sheffield, Mappin Street, Sheffield S1 3JD

The Farley Member is a 24-27 metre sequence of repetitive alternating nodular argillaceous limestones and calcareous mudstones developed between the Apedale Member of the Coalbrookdale Formation and the Much Wenlock Limestone Formation. Quantitative analysis shows diverse assemblages of acritarchs and chitinozoans to be found throughout at abundances of 200-2000⁻¹. Typical sample species diversities range between 48-62 for acritarchs and 5-9 for chitinozoans. Selected samples were taken laterally along reference stratigraphic horizons and from adjacent calcareous mudstones and nodular limestones. Results reveal in all samples the main acritarch genera are consistently recorded as *Leiosphaeridia*, *Micrystridium*, *Veryhachium* and *Diexallophasis*. Chitinozoan assemblages are dominated by *Conochitina* or *Ancyrochitina*. Lateral samples were internally consistent with regard to species composition. Palynomorphs in nodules are consistently preserved in three dimensions, reflecting early diagenetic nodule formation, in contrast to their

flattened nature in the mudstones from post depositional compaction. Qualitatively assemblages from adjacent limestone/mudstone couplets are broadly comparable, but they differ significantly in absolute abundance. At a broader scale than the limestone/mudstone couplets, there are significant changes in a few key acritarchs. Assemblages are representative of the middle part of the *Eisenackidium wenlockensis* acritarch Biozone.

Biodiversity changes through Late Cretaceous floras from the Antarctic Peninsula Peta Hayes

Department of Earth Sciences, University of Leeds, Leeds LS2 9JT

The radiation and diversification of angiosperms across the Southern Hemisphere is poorly understood since few southern Cretaceous floras have been documented. Although the northern tip of the Late Cretaceous volcanic arc, now represented by the Antarctic Peninsula, was at about 65 degrees south, it was extensively forested and the remains of the plants are now preserved within the James Ross Basin. Surprisingly, new studies of plant fossils show that there was a remarkably diverse angiosperm component within these southern polar forests. The excellently preserved impressions of the leaves are separated into taxa using architectural characters such as venation patterns and marginal features. Comparisons between the angiosperm leaf floras of the Hidden Lake Formation (Coniacian-Santonian) and the Santa Marta Formation (Campanian) are drawn.

The evolution of the scombroid fishes

Kenneth A. Monsch

University of Bristol, Department of Geology, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ

The teleost suborder of Scombroidei poses some intersting questions regarding their evolution. Some of the supposed scombroids are warm-blooded, an exceptional feature in fishes. Up to this date, phylogenies of scombroids have been based by including solely Recent taxa. The different phylogenies thus proposed differ radically on some points. Although there is a superb fossil record, it is for the first time now that evolutionary studies are carried out with it. A phylogeny, based on Recent and fossil taxa will be constructed. The inclusion of fossils will hopefully solve problematic ancestral relationships which cause controversies regarding scombroid interrelationships. Interesting questions like the evolution of warm blooded-ness in this fish group will be looked at. Fossils and Recent specimens from the BM (NH), the Palaeontological Institute in Moscow and the Smithsonian Institute will be described and incorporated in the phylogenetic analyses.



Mark Purnell (map2@le.ac.uk)