The
Palaeontological
Association

45th Annual Meeting
15th-19th December, 2001
Geological Museum
University of Copenhagen

ABSTRACTS

Abstracts of oral presentations

Compiled and edited by David A.T. Harper

The tristichopterid fishes: Almost, but not quite, tetrapods

Per Erik Ahlberg
Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK **<pea@nhm.ac.uk>**

The clade Tristichopteridae occupies a relatively high position within the tetrapod stem group; it is the most advanced "osteolepiform" group, and forms the sister taxon to *Panderichthys* + tetrapods. The best known tristichopterid is the primitive early Frasnian genus *Eusthenopteron*, but the clade persisted to the end of the Devonian.

The phase of rapid morphological change traditionally identified as the "fish-tetrapod transition" begins with the late Givetian *Panderichthys* and continues through to Famennian stem-group tetrapods such as *Acanthostega* and *Ichthyostega*. By contrast, the less crownward "osteolepiform fish" part of the stem group shows limited morphological change and no obvious overall trend towards terrestriality. However, within the Tristichopteridae there is independent acquisition of a *Panderichthys*-like body morphology. Recently, the advanced late Frasnian tristichopterid *Mandageria* has been found to possess a true neck joint, previously thought to be a unique tetrapod character. The extent, nature, and likely ecological significance of the convergence between tristichopterids and tetrapods will be discussed in the light of these findings.

Phylogenetic analysis of the tetrapod stem group has shown that the lower, "fish" part consists of (in ascending sequence) the clade Rhizodontida, a paraphyletic array of osteolepiforms, the clade Tristichopteridae, and *Panderichthys*. In morphological terms, the "fish-tetrapod transition" begins at the level of *Panderichthys*.

Lower Cretaceous Valanginian ammonites of East Greenland

Peter Alsen
Geological Institute, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark **<petera@geo.geol.ku.dk>**

During the Mid Jurassic there was a total separation of the faunas of East Greenland from those of both Northwest Europe and the Tethys. Faunal communication was resumed in the Late Jurassic but the faunas show a high degree of endemism, and provincialism was pronounced. In the latest Jurassic faunal communication again ceased but in the Valanginian, for the first time since Early Jurassic, a fully marine connection between the Boreal and Tethys Ocean was established due to the subsiding East Greenland Rift basin. Enhanced circulation and ventilation of oceanic waters are reflected in the East Greenland Valanginian fauna, which in places is very rich and highly diverse: Tethyan forms from warm southern seas are found as far north as the East Greenland Boreal Arctic mixed with northern Boreal forms reflecting long-distance migration from south to north and the breakdown of biogeographic barriers. Polyptychitid ammonites and Buchia typical of the Boreal Realm dominate the East Greenland fauna. The ammonite genera *Lytoceras*, *Phylloceras* and *Delphinites* are common, while nautiloids, brachiopods and inoceramid bivalves occur rarely.

Larval shells and further news of the Late Palaeozoic conocardioid rostroconchs

Michael R.W. Amler and Nicole S. Rogalla
Institut für Geologie und Paläontologie am Fachbereich Geowissenschaften der Philipps-Universität Marburg, Abt. Invertebraten-Paläontologie, Hans-Meerwein Straß, D-35032 Marburg, Germany <**amler@mailer.uni-marburg.de**> and <**rogalla@mailer.uni-marburg.de**>

When some 30 years ago the class Rostroconchia POJETA et al., 1972 was first established and described, the univalved protoconch served as one of the diagnostic characters of the class, although larval shells of rostroconchs were known only sporadically. Nevertheless, rostroconchs remained biologically and systematically dubious and not fully understood, mainly due to insufficient preservation. Extensive investigation during the last ten years on advanced Mid and Late Palaeozoic Conocardioidea offer considerable new data on their presumed palaeobiology. Analyses of shell microstructure and architecture as well as detailed information on the ontogenetic development of the shell provide new insights on probable life habits and phylogenetic relationships. Based on extensive SEM analyses, new data are available about position, size and growth of the conocardioid protoconch. Contrasting with bivalves, in which the prodissoconch is situated in the dorsalmost part of the two valves, the univalve protoconch of conocardioids is placed behind the two beaks, directly on top of the dorsal face of the rostral base. Protoconchs of conocardioids vary in size and shape; small, but strongly inflated as well as distinctly endogastrically coiled types were observed. Particularly, the endogastric protoconchs show distinct growth varices which delimit an early stage (protoconch I) from a later stage (protoconch II). The pseudo-bivalved condition develops from strongly allometric growth of the protoconch II. During further, less common growth, the typical, laterally inflated adult shell develops, whereas the early, coiled protoconch is detached, creating a rounded or oval scar on top of the rostral base which indicates the shell margin of the former protoconch.

Placing a Lower Cambrian enigmatic fossil: *Mickwitzia* Schmidt

Uwe Balthasar
Department of Earth Sciences, University of Cambridge, Cambridge CB2 3EQ, UK

The Lower Cambrian genus *Mickwitzia* is a distinct component of the Cambrian problematica of Laurentia, Baltica and northern Gondwana. Its planoconvex, organophosphatic shell is reminiscent of that of the phosphatic brachiopods, but its unusual size (up to 72 mm in diameter) and the occurrence of abundant "canals" perforating the shell has made its inclusion within the Brachiopoda contentious.

The study of new, well-preserved specimens from the Lower Cambrian Mural Formation of the Canadian Rocky Mountains allows a more detailed description of the shell structure than previously possible. The thin outermost layer shows a fine concentric ornament. It seems not to be penetrated by the abundant "canals", which questions earlier views that these "canals" functioned to deter predators. The middle layer consists of fine organophosphatic laminae with differing organic content. The most obvious features of this layer are the prominent "canals" that build inward-pointing protuberances. The third, innermost layer is not laminated, shows the highest concentration of organic material and covers the space between the protuberances.

The structure of the middle layer appears to be similar to co-occurring lingulid shells and insofar as laminated organophosphatic shells are exclusive to linguliformean brachiopods, *Mickwitzia* is likely to

be related to them. The peculiar "canals", however, are different from any known shell feature of any brachiopod group and hence make it difficult to include *Mickwitzia* within the brachiopod crown-group. It therefore is likely that *Mickwitzia* represents a stem-group brachiopod and might as such help to resolve relationships between the Brachiopoda and adjacent phyla.

The past and present of biomineralized animal sclerites

Stefan Bengtson
Swedish Museum of Natural History, Stockholm, Sweden

Biologically induced mineralization is probably as old as life itself (often a side effect of life processes) whereas biologically controlled mineralization generally requires sophisticated physiological mechanisms and appears later in evolution. The use of biominerals to strengthen animal skeletons is a further development of controlled mineralization that calls for an intricate integration of organic and inorganic materials. When skeletons appeared in animal evolution near the Precambrian-Cambrian boundary, a small selection of the many available biominerals were used for this purpose. The occurrence of particular biominerals in particular lineages has been interpreted in different ways: as phylogenetically constrained necessities, as temporary choices which can be inverted later in evolution, or as reflections of the initial conditions under which the particular skeletons evolved. A number of animal groups appearing in the Early Cambrian evolved dermal sclerites of various structure and composition. The variety of sclerite shapes and biominerals in the Cambrian, as well as an unexpected find of a modern analogue of Cambrian sclerite-bearing animals, suggest that the phylogenetic significance of sclerite shape is limited, that the choice of skeletal mineral reflects the environmental conditions under which the skeleton first evolved, and that, once established, the originally selected mineral is not replaced.

How many four-legged fishes? The diversity and distribution of *Ichthyostega*

Henning Blom
Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK **<henb@nhm.ac.uk>**

The Late Devonian tetrapod *Ichthyostega* from East Greenland is known from a large collection of skulls and post-cranial elements. The largest amount of material has been collected from two formations, with a good stratigraphical control, at several localities on Gauss Halvø. The Britta Dal Formation, the uppermost and most productive formation, is clearly separated from the slightly poorer Aina Dal Formation by the unfossiliferous Wiman Bjerg Formation (about 100 m thick). The skulls from Gauss Halvø divide into two stratigraphically separate populations with distinct differences in skull proportions and maxillary dentition. The *Ichthyostega* population from Britta Dal Formation is more robust than that from the Aina Dal Formation, and has a shorter and wider skull with a lower number of maxillary teeth.

Specimens collected as loose blocks at the north side of Celsius Bjerg, Ymer Ø have been compared with the populations of Gauss Halvø. This comparison shows that the stratigraphically unconstrained skulls of Celsius Bjerg are morphologically distributed within and between both populations of Gauss Halvø. In the original description of *Ichthyostega*, several separate species were recognised from Celsius Bjerg. Their validity can now be evaluated in the light of the populations recognised on Gauss Halvø.

The "Bohemian type" bivalves in the Silurian of Arctic Russia

Olga K. Bogolepova and Alexander P. Gubanov
Department of Earth Sciences, Uppsala University, Norbyvägen 22, SE-752 36, Uppsala, Sweden

The bivalve genera *Dualina*? and *Sibirinka* are reported for the first time from the Severnaya Zemlya Archipelago of Arctic Russia, where they occur in limestone concretions within the Sredninskaya Formation. Graptolites from the same concretions indicate the upper *crispus–griestoniensis* biozones (Llandovery). This is the second record of the earliest epibyssate pteriomorphs to appear in Siberia, which flourished later in the basins of central and southern Europe. During the early Llandovery the first representatives of Antipleuridae, Lunulacardiidae and Pterineidae appeared in Siberia and later, members of these families occur in the "Bohemian type" bivalve-dominated communities; these are characteristic of the Silurian (Wenlock-Prídolí) and Lower Devonian cephalopod limestone biofacies of peri-Gondwanan Europe and Perunica. In addition to the records from present day Europe, Silurian cephalopod limestones are also known to occur in northern Asia (Siberia, Novaya Zemlya, northern Taimyr, New Siberian Islands), where they form thin beds up to 2 m thick, or occur as isolated nodules or lenses within black graptolitic shales.

The Cardiolidae are still poorly known in these areas, but are one of the principal components of these faunal associations. A new record of ancestral forms of "Bohemian type" bivalves in the cephalopod limestones of Severnaya Zemlya is very important from a palaeogeographic point of view, as no members of these families have been recorded in this area, and from this time interval. Appearing in the late Rhuddanian (*Climacograptus cyphus*?–*Demirastrites triangulatus* biozones) of Siberia, the range of *Sibirinka*, for example, expanded into Severnaya Zemlya during the Telychian (*crispus–griestoniensis* biozones). During the Wenlock some elements of the "Bohemian type" fauna inhabited the Arctic Canada, Alaska, Gotland, and reached South America, Florida and Kazakhstan during the Ludlow. The distributions of the Bohemian-like fauna, from Siberia to Severnaya Zemlya, Sweden, Arctic Canada together with Alaska, and from Siberia to Kazakhstan, Caucasus, Podolia, and the peri-Gondwanan areas, can be explained by the current directions of Silurian surface circulation. Nevertheless is Siberia and Severnaya Zemlya the centre of origin of the "Bohemian type" Bivalvia forms?

A Berriasian "Wealden-fauna" from Bornholm, Denmark

Niels Bonde
Geological Institute, University of Copenhagen, Øster Voldgade 10, DK-1350 København K, Denmark

The large gravel pit at Robbedale, Bornholm, has yielded a "Wealden-fauna" from the basal part of Jydegaard Formation (Upper Berriasian). Molluscs and vertebrates occur together in sand and clay, with bivalves especially concentrated in the basal clay-ironstone, the *Neomiodon* Bed, where mass-mortality layers are covered by the eponymous genus. Fish remains also occur in this clay and in the sand overlying it, which in addition contain terrestrial vertebrates and thin clay-beds filled with the freshwater gastropod, *Viviparus*. The vertebrates comprise hybodont sharks, *Lepidotes*, amnioids, pycnodont dentitions and fragments of primitive teleosteans, as well as turtles and crocodiles; significant are the unique discoveries of lacertilians and a carnivorous dromaeosaurid, the first Danish dinosaur, represented by one tooth collected in 2000.

Fringe swellings in the Marrolithinae (Trilobita, Trinucleidae)

A. Bowdler-Hicks
Division of Earth Sciences, University of Glasgow, Gregory Building, Lilybank Gardens, Glasgow G12 8QQ, Scotland, UK **<a.bowdler@earthsci.gla.ac.uk>**

Marrolithine trilobites, most widely known perhaps from the PalAss logo, inhabited a spectrum of shelf environments in and around the Rheic Ocean and southern part of the Iapetus Ocean during the Ordovician. As with other trinucleid trilobites, variations in the patterns and numbers of pits on the bilamellar fringe that surrounds the cephalon are key diagnostic characters for species definition. In addition, some members of the Marrolithinae are distinguished by swellings on one or both lamellae of the fringe. Several types of swelling can be recognised. In some taxa they are restricted to a portion of either the lateral or posterior part of the fringe but extend across several arcs. In others they extend along a considerable section of a single pit arc. The strength of the swellings and their distribution between the two lamellae also varies between taxa. Conversely there is considerable intraspecific geographical variation in the development of lateral swellings in some species of *Marrolithus*. In some instances, temporal variations in swellings may reflect shifting depth-related, environmental gradients rather than evolutionary lineages. A better understanding of the fringe swellings is helping to clarify the taxonomy and phylogeny of the Marrolithinae.

A mystery trace fossil revisited: The work of a deposit-feeding bivalve from the Palaeocene of California, USA

Richard G. Bromley[1], Murray Gregory[2], Alfred Uchman[3] and Anthony Martin[4]
[1]Geological Institute, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark
[2]Department of Geology, The University of Auckland, Private Bag 92019, Auckland, New Zealand
[3]Institute of Geological Sciences, Jagiellonian University, Oleandry St. 2a, 30-063 Krakow, Poland
[4]Department of Environmental Studies, Emory University, Atlanta, Georgia 30322, USA

In recent years, several cases of the co-occurrence of a particular group of discrete structures, comprising compound trace fossils, have been interpreted as representing bivalve locomotion and feeding activity. These structures include locomotion of split-foot bivalves through sediment (resembling ichnogenus *Protovirgularia*), feeding by means of palpal tentacles (resembling *Lophoctenium*), and shell impressions during resting phases (resembling *Lockeia*). A particularly well-preserved and large example of such bivalve activity is described from submarine canyon deposits in the Palaeocene Carmelo Formation at Point Lobos, Monterey, California. The trace fossil is colourful, spectacular, and has previously been the subject of mystery and wild speculation. In this case, however, *Protovirgularia*-like and *Lockeia*-like structures are replaced by a tubular structure containing a meniscate fill. This is interpreted as the track of the shell and foot of the bivalve. The lack of *Protovirgularia*-like structure suggests this is not the work of a split-foot bivalve, but rather of a wedge-foot bivalve. However, *Lophoctenium*-like structures are particularly well developed. A deposit-feeding wedge-foot bivalve suggests a member of the Tellinidae. Tellinids have separate in- and exhalent siphons, and the *Lophoctenium*-like probes were probably made by sweeps of the inhalent siphon. In

the upper part of the trace fossil a series of long, upward-stretching tubes is preserved. These tubes are interpreted as successive probing positions of a tellinid bivalve's siphons as the feeding animals moved slowly forward.

Reaching for the crown: A new phylogenetic reconstruction of the euarthropod stem group, and its morphological implications

Graham E. Budd
Department of Earth Sciences, Uppsala University, Norbyvägen 22, SE-752 36 Uppsala, Sweden

Cambrian arthropods have long caused difficulties to phylogeneticists, and a recent string of efforts at resolving their phylogenies have been contradictory. Here, I add one more attempt, this time to show that a large group of taxa previously thought to be only distantly related actually fall into a new clade near the top of the euarthropod stem-group. This clade includes, most notably, many of the bivalved arthropods that have sometimes been thought to be true crustaceans. The new reconstruction allows a much clearer picture to be obtained of arthropod head evolution than previously possible. Rather than being a highly variable character as is often claimed, arthropod head segmentation seems to have evolved in a fairly orderly fashion. In conjunction with recent work on extant taxa such as the onychophorans, the options of how the euarthropod head might be constructed are considerably narrowed by the fossil evidence, although the "endless dispute" is still far from over. In addition to the head segmentation evidence, the composition of the crown-group euarthropod body-plan is further clarified, with taxa such as *Sidneyia* and *Burgessia* apparently lying very close to the base of the crown group. This work plugs an important gap in our understanding of arthropod evolution, and provides the most complete view of the origin and assembly of any invertebrate body plan.

Stepping into the Tournaisian: Five toes and two fingers for early tetrapods

J.A. Clack
University Museum of Zoology, Downing St., Cambridge, CB2 3EJ, UK

The only articulated tetrapod specimen from the Tournaisian fits temporally, morphologically and phylogenetically between the Devonian forms and those of the later Early Carboniferous, bridging a 30 million year gap in the fossil record. The specimen preserves two digits on the manus, one of which is extremely small. It is most similar to the supernumery digits found in the manus and pes of the known Devonian forms, and may suggest a polydactylous manus. The pes of the Tournaisian specimen preserves five digits, two complete and one nearly complete. However it can no longer be assumed that this pes is the earliest known pentadactyl limb; small supernumery digits might have been lost from this pes. One feature suggests that nevertheless, this pes shows a terrestrial adaptation otherwise seen only in later Carboniferous forms. The metatarsals are proximo-distally asymmetrical, possibly associated with bringing the foot into an anteriorly directed position. Cladistic analysis shows that this animal and *Whatcheeria deltae* from the Visèan of Iowa form the next most primitive clade after the Devonian *Ichthyostega*. However, including them in an analysis breaks up the traditional taxon "anthracosaurs". This result accords with some recent published analyses, but not those previously found by the author.

Categorising Dead Bugs: Biometric revision of the Palaeozoic bryozoan genus *Stenophragmidium* (Trepostomata, Bryozoa: Bassler, 1952)

Duncan Cleary
Department of Geology, Trinity College, Dublin, Ireland
<duncancleary@hotmail.com>

Palaeontologists rarely have the luxury of D.N.A. analysis when classifying fossil organisms. This results in the need for other methods to be employed in order to classify specimens into reasonable taxonomic units, such as species. Colonial organisms provide a particular challenge in this respect, as they possess several levels of genetic individuality. This study classifies a genus of trepostome bryozoan (similar to *Tabulipora*) from the Upper Palaeozoic, which is documented from Europe, North America and China. Rather than applying a series of subjective classification methods, a rigorous statistical approach was adopted, utilising univariate, bivariate and particularly multivariate analyses, including P.C.A. and cluster analyses. Combined with cladistic analysis, this methodology proved very robust in classifying specimens into species. The strength of this particular approach lies in its universal applicability to all areas of palaeontological classification, where objective analysis of large volumes of biometric data is required.

The Palaeocene/Eocene thermal maximum (PETM) and land environments in S. England

Margaret Collinson[1], Jerry Hooker[2] and Darren Gröcke[1]
[1]Department of Geology, Royal Holloway University of London, Egham, Surrey, TW20 0EX, England, UK **<M.Collinson@gl.rhul.ac.uk>**
[2]Department of Palaeontology, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK

Floras from near the Palaeocene/Eocene thermal maximum (PETM) in S. England have been shown to contain distinctive key diagnostic elements which distinguish them from younger floras of the early to mid Eocene (Collinson 2000 *GFF*, **122**, 36-37). Recently, a temporary exposure of lignite (at Cobham, Kent), has provided a unique and unexpected window into conditions at the PETM. Carbon-isotope results document a carbon-isotope excursion (CIE) comparable to that recorded in the marine realm and from soil carbonates in continental strata in the USA. Macroscopic fusain (= charcoal), indicative of repeated fires, is exceptionally abundant throughout. This unique phenomenon is not repeated elsewhere in the entire Cenozoic succession of southern England. Preliminary results show that the charcoal includes twig-like pieces and fragments of larger woody axes of dicotyledons as well as probable fern axes. Palynological studies indicate high abundance of some fern spores. Some horizons contain megaspores and microspore massulae of the heterosporous water fern *Salvinia* (a free-floating aquatic) which is also known from the other English PETM floras. The dominant vegetation elements are unchanged across the CIE.

Ordovician bivalves as palaeolatitude indicators

John C.W. Cope[1] and Fang Zong-jie[2]
[1]Department of Earth Sciences, Cardiff University, PO Box 914, Cardiff CF10 3YE, UK
[2]Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China

Early Ordovician bivalves were confined to siliciclastic facies of the Gondwanan shelves, but by the Mid Ordovician had spread to other continental shelves. Late Ordovician bivalves were cosmopolitan and not facies-controlled. Despite the scarcity of Early Ordovician faunas, recent work has shown clear latitudinal differences between high- and low-latitude faunas. In the Mid-Ordovician latitudinal differences became more marked and show a clear preference of pteriomorphians for low latitudes and heteroconchs for high latitudes. The development of low-latitude carbonate platforms in the Late Ordovician led to a major diversification of the pteriomorphs where they developed semi-infaunal and epifaunal habits.

Comparisons between bivalve diversity and abundance yield some surprising results—in particular that nuculoids are both more diverse at the species level and form a much higher percentage of the bivalve population, in terms of individuals, at low latitudes.

This information proves useful in areas of complex terrane accretion, such as south-western China, where bivalve faunas show distinct latitudinal differences between adjacent terranes, and makes palaeocontinental reconstruction more robust.

Freshwater hybodont sharks in the Aptian-Albian of Tunisia and Thailand

Gilles Cuny[1], Varavudh Suteethorn[2], Eric Buffetaut[3] and Mohamed Ouaja[4]
[1]Geological Museum, University of Copenhagen, Øster Voldgade 5-7, 1350 Copenhagen, Denmark **<cunyg@netscape.net>**
[2]Department of Mineral Resources, Rama VI Road, Bangkok 10400, Thailand **<varavudh@dmr.go.th>**
[3]Centre National de la Recherche Scientifique, 16 cour du Liégat, 75013 Paris, France **<eric.buffetaut@wanadoo.fr>**
[4]Office National des Mines, BP 215, La Charguia, 1080 Tunis, Tunisia

The first hybodont sharks are known as early as the Late Devonian and they disappeared in the Maastrichian, but it is generally accepted that they showed a maximum diversity during the Triassic and that their numbers were greatly reduced by the Cretaceous. New data from the Lower Cretaceous from both the northeastern margin (in Thailand) and the southwestern margin (in Tunisia) of the Tethys show on the contrary that they were still very successful in freshwater environments. The Khok Kruat Formation (Aptian) of Thailand has yielded at least five genera of hybodont sharks: *Hybodus*, *Thaiodus*, *Heteroptychodus* plus two new genera, while the fish fauna of the Chenini Formation (Albian) in Tunisia is dominated by the hybodont *Tribodus*, confirming its presence in Africa. Moreover, it is during the Late Jurassic–Early Cretaceous interval that hybodont sharks developed for the first time a cutting dentition with *Thaoidus* in Asia and *Priohybodus* and *Porohiza* in Africa.

Palaeontological and molecular evidence for the origin of silica secreting marine organisms

Taniel Danelian[1] and David Moreira[2]
[1]Univ. P. and M. Curie (Paris 6), Dépt. CNRS-FRE2400, Paléontologie and Stratigraphie, C. 104, T. 15-25, E4, 4, place Jussieu, 75252 Paris Cedex 05, France
[2]Univ. P. and M. Curie (Paris 6), CNRS-UMR 7622, Développement et Evolution, Bâtiment B, E6, 4, place Jussieu, 75252 Paris Cedex 05, France

There are three groups of silica-secreting organisms with a fossil record that occur in modern oceans: the Bacillarophyta/Diatoms (unicellular algae), the Polycyctine Radiolaria (Protozoa) and the siliceous sponges (Hexactinellida and Demospongia, considered now as part of the Metazoa). Each of these three eukaryotic groups extracted substantial amounts of silica from the oceans and over time profoundly transformed the oceanic silica cycle. But when did each group appear and how does it fit onto the universal tree of life? Given some recent Cambrian discoveries suggestive of closely living association and morphological similarities between these two groups, how close is the phylogenetic relationship between sponges and Radiolaria? Recent ideas and currently available palaeontological and molecular data are discussed with respect to the evolutionary appearance of both groups in the marine biosphere.

Based on the dispersed distribution of silica-secreting organisms on the molecular phylogenetic tree of the eukaryotes, two competing hypotheses can be constructed, the first more likely. The capacity to inject silica in the cytoplasm to build skeletons: (1) is a common, anciently-acquired character, which has been retained and used only in some organisms (*i.e.*, sponges, Radiolaria); (2) appeared several times independently in different eukaryotic groups, demonstrating an evolutionary convergence.

Eoteuthis Størmer—its place in cephalopod evolution

Desmond T. Donovan
Department of Geological Sciences, University College London, Gower Street, London WC1E 6BT, UK

The genus *Eoteuthis* was described by the late Wilhelm Størmer from an X-ray photograph of a fossil from the Lower Devonian Hunsrückschiefer of Eifel, Germany. Originally thought to be a belemnite-like animal, it was later published as a squid. Other authors re-interpreted it as an orthoconic nautiloid.

Eoteuthis is re-examined on the basis of an enlarged X-ray photograph. There are seven or more tentacles, but no sign of suckers, cirri or hooks, or of the differentiation seen in Recent *Nautilus*. There is a possible funnel. The slender, tapering body does not show any features of an orthocone shell. Its irregular outline does suggest a soft body rather than a shell. *Eoteuthis* is possibly a cephalopod, of uncertain affinity.

Ichnology and palaeoenvironment of the Middle Miocene Grand Bay Formation of Carriacou, The Grenadines, Lesser Antilles

Stephen K. Donovan[1], Ron K. Pickerill[2] and Roger W. Portell[3]
[1]Department of Palaeontology, Nationaal Natuurhistorisch Museum, Postbus 9517, 2300 RA Leiden, The Netherlands
[2]Department of Geology, University of New Brunswick, Fredericton, New Brunswick, Canada E3B 5A3
[3]Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611-7800, U.S.A.

The eastern coast of Carriacou in the Grenadines, Lesser Antilles, exposes Miocene siliciclastic and carbonate strata of four formations, namely the Belmont (Lower Miocene), Kendeace (Lower-Middle Miocene), Carriacou and Grand Bay formations (both Middle Miocene). The Grand Bay Formation is the most widely exposed unit, consisting of a succession of volcaniclastic sandstones with associated interlayered calcareous mudstones and minor conglomerates.

Palaeoenvironmental interpretations of this formation disagree, considering it to be of either deep- or shallow-water origin. The strata are abundantly fossiliferous, including diverse assemblages of scleractinian corals, isocrinids, terebratulid brachiopods and, particularly, benthic molluscs. Although uncommon, several of these groups contain borings, including *Caulostrepsis cretacea*, *C. spiralis*, *C.* cf. *taeniola*, *Gastrochaenolites cluniformis*, *G. difugus*, *G. torpedo*, *Oichnus paraboloides*, *O. simplex*, *Petroxestes pera*, *Rogerella* isp. and *Trypanites solitarius*. Soft-sediment ichnotaxa (*i.e.*, burrows) are also present. Although their detailed systematics are still under study, the following ichnogenera are prevalent; *Chondrites*, *Diplocraterion*, *Gordia*, *Planolites*, *Scolicia*, *Skolithos*, *Teichichnus*, *Thalassinoides*, *Zoophycos*.

Collectively, this latter ichnofaunal assemblage compares well with others described from deep-water sequences, particularly those from Cretaceous deep-sea chalks of northern Europe. We suggest that the Grand Bay Formation is similarly a deep-water sequence. Our conclusions are supported by both sedimentological and faunal evidence.

A trilobite accumulation from Waulsortian Limestone (upper Tournaisian; Carboniferous) of County Westmeath, Ireland

Niamh Douglas, George Sevastopulo and Patrick Wyse Jackson
Department of Geology, Trinity College, Dublin 2, Ireland

Trilobites are a ubiquitous but relatively minor component of the fauna of upper Tournaisian Waulsortian carbonate mudmounds in Ireland. Typical abundances are estimated to be less than fifty specimens (usually pygidia, cranidia and free cheeks) per cubic metre of limestone. A block of upper Tournaisian Waulsortian limestone from Leny, County Westmeath in the Geological Museum, Trinity College is approximately 1.85 10^{-3} m^3 in volume and contains several hundred specimens of *Cummingella* cf. *raniceps* (Phillips). The material consists of disarticulated cranidia, free cheeks, hypostomes, thoracic segments and pygidia, and more complete carapaces, some of which are apparently enrolled. Some disarticulated material was broken before burial. Specimens are preserved randomly convex or concave up. The matrix is micrite that also contains abundant smooth ostracodes,

mostly single valves, and a calcareous microfossil of unknown affinity. The surface between the trilobite-bearing matrix and overlying micrite is sub-horizontal, sharp but irregular, and is apparently encrusted by specimens of the bryozoan *Fistulipora* growing downwards.

The accumulation is interpreted as the fill of a horizontal cavity in the mound into which the trilobites retired to moult. Other dense accumulations of trilobites in Carboniferous mudmounds may have a similar origin.

Palaeoecology of an early Callovian 'belemnite battlefield': Bed 13, Peterborough Member, Oxford Clay Formation, England

Peter Doyle[1] and Jason L. Wood[2]
[1]School of Earth & Environmental Sciences, University of Greenwich, Chatham Maritime, Kent, ME4 4TB, UK **<p.doyle@gre.ac.uk>**
[2]Department of Earth Sciences, The Open University, Walton Hall, Milton Keynes, Buckinghamshire, MK7 6AA, UK **<j.l.wood@open.ac.uk>**

Belemnite battlefields are accumulations of belemnite rostra forming distinct shell beds in the fossil record. Although often dismissed as the product of time-averaging, recent studies suggest primary inputs to such accumulates from mass-mortality, or the action of predators. Bed 13 of the Peterborough Member, Oxford Clay Formation (Jasoni Zone, Callovian), is an important and intriguing example. Excavation and fine-scale surface mapping demonstrate that it is a condensed shell bed of abundant ammonites and belemnites and associated epibyssate and grypheate bivalves. Many of the ammonites are scavenged and broken. Belemnites are particularly common, with surface densities of between 150 and 325 per m^2. Three species are present: *Cylindroteuthis pusoziana*, *Belemnopsis* sp. and *Belemnotheutis*, with *Cylindroteuthis* by far the most common. Most are well-preserved with no significant current orientation. A significant number display corrosion inconsistent with simple breakage, suggesting passage through the digestive system of large predators. Surprisingly, the majority of the *Cylindroteuthis* are juveniles, with at least four distinctive ontogenetic phases, broadly consistent with estimates of belemnite longevity of around four years. The preservation states and abundance of juveniles militates against a simple explanation of time-averaging alone for this 'belemnite battlefield'. Population structure suggests mortality of normal populations of *Cylindroteuthis* in preferred feeding grounds. Such feeding grounds would in turn attract predators, and the presence of corroded belemnites suggests regurgitates. Study of this surface will provide a greater understanding of the Jurassic marine ecosystem.

An early Devonian harvestman (Arachnida: Opiliones) from the Rhynie Chert, Scotland

Jason A. Dunlop[1], Lyall I. Anderson[2], Hans Kerp[3] and Hagen Haas[3]
[1]Institute f. Systematische Zoologie, Museum f. Naturkunde, D-10115 Berlin, Germany **<jason.dunlop@rz.hu-berlin.de>**
[2]Department of Geology and Zoology, National Museums of Scotland, Edinburgh EH1 1FJ, UK **<l.anderson@nms.ac.uk>**
[3]Department of Palaeobotany, Westfälische Wilhelms-Universität, D-48143 Münster, Germany **<kerp@uni-muenster.de>**

Harvestmen (Arachnida: Opiliones) are a relatively abundant and diverse group of arachnids which are distinguished from spiders principally by their compact body in which the prosoma and opisthosoma are strongly fused together. Fossil harvestmen are rare and the previous oldest record is an unnamed specimen from the Lower Carboniferous of East Kirkton, Scotland. Here we describe the earliest known harvestmen from the Rhynie Chert, Scotland (Lower Devonian: Pragian). This remarkable material includes cuticle-lined internal structures. Both sexes appear to be preserved as shown by a penis (male) and an ovipositor (female) lying within the opisthosoma. These fossils also include a pair of large, branching trachea, the oldest record of arachnid tracheal respiration and confirmation that these animals were terrestrial. These long-legged Rhynie harvestmen are very similar to the common, extant long-legged harvestmen which are abundant in grassland habitats today. Based principally on the appendages and the annulate, setose ovipositor the Rhynie fossils can be referred to an extant opilionid tribe (Eupnoi) within the suborder Palpatores. Correspondingly, these fossils do not represent the most basal opilionid taxon (the suborder Cythophthalmi) and imply a pre-Devonian opilionid radiation.

Pinnatiramosus: the ultimate Chinese puzzle?

D. Edwards[1], Li Cheng-Sen[2], Wang Yi[3] and M.G. Bassett[4]
[1]Department of Earth Sciences, Cardiff University, PO Box 914, Cardiff CF10 3YE, UK
[2]Institute of Botany, Beijing, People's Republic of China
[3]Institute of Palaeontology, Chinese Academy of Sciences, Nanjing, People's Republic of China
[4]Department of Geology, National Museum of Wales, Cardiff CF1 1NP, UK

Chinese assemblages of Silurian and Lower Devonian plants show such striking disparity that they have demanded reassessment of evolutionary and geographic radiations of early land plants. Most spectacular of all, and occurring in Llandovery (basal Silurian) rocks of Guizhou province, is *Pinnatiramosus qianensis* Geng which consists of an extensive vascularised axial system showing complex pinnate branching. The latter is morphologically far more advanced than the strictly dichotomous branching exhibited in slightly younger fossils believed to derive from the earliest tracheophytes, and the permineralised xylem possesses tracheary pitting first documented in the Middle Devonian elsewhere. The orientation of the branches suggests that the fossils are autochthonous, and not transported into the entombing marine rocks which are dated by brachiopods. The lecture will evaluate evidence for two contrasting scenarios, namely that the fossils were the rooting systems of Llandovery plants, or that they came from much younger plants which colonised weathered Silurian surfaces in the late Palaeozoic.

Mesofossil evidence of Late Cretaceous vegetation on Table Nunatak, Antarctica

Helena Eklund
School of Earth Sciences, University of Leeds, Leeds, LS2 9JT, UK
<h.eklund@earth.leeds.ac.uk>

Mesofossil evidence of a mixed vegetation including angiosperms (flowering plants), gymnosperms (*e.g.*, conifers) and pteridophytes (*e.g.*, ferns, club mosses) has been recovered from an Upper Cretaceous (Santonian) outcrop at Table Nunatak, Antarctica. The fossils are preserved as more or less three-dimensional or slightly flattened charcoalifications, most of which are remarkably small, ranging from one or two to a few mm in length. While reproductive structures such as isolated fruits and seeds are diverse and abundant, flowers, isolated pollen-producing structures and megaspores are more rare. However, a few types of flowers have been recognised and these represent not only the earliest known flowers from Antarctica, but they are also the only known charcoalified flowers from the Southern Hemisphere. Vegetative structures include isolated leaves, fragments of wood and conifer axes, and circinate fern rachises.

The fossil flora from Table Nunatak is of great interest because it comprises the first Cretaceous mesofossil assemblage including angiosperms reported from the Southern Hemisphere. In view of this, a systematic comparison between the Table Nunatak assemblage and several well-known Late Cretaceous mesofossil assemblages from the Northern Hemisphere will be given.

Unravelling the spiral holdfasts of the Ordovician crinoid Iocrinus Hall

William Fone[1] and Stephen K. Donovan[2]
[1]Staffordshire University, College Road, Stoke on Trent, ST4 2DE and The Open University in the West Midlands, 66-68 High Street, Harborne, Birmingham B17 9NB
[2]Department of Palaeontology, Nationaal Natuurhistorisch Museum, Postbus 9517, 2300 RA Leiden, The Netherlands

Localities yielding articulated fossil crinoids are rare in the British Llanvirn. Previously, only six such localities have been reported in the literature; only two are Lower Llanvirn.

The abundant shelly fauna of the Shelve Formation of the Shelve Inlier, Shropshire, has been extensively studied since the 19th century. Three new localities containing crinoid-bearing horizons have been identified. Two have yielded articulated specimens of the gracile disparid *Iocrinus* sp. cf. *I. pauli* Donovan and Gale. The distal end of the stem shows spiral coiling, an adaptation for attachment. Distal stems consist of mainly wedge-shaped columnals separated by larger, parallel-faced columnals; the number of wedge-shaped columnals increases distally. When broken, the column spiralled between the parallel-faced columnals, commonly at the distal end. This is interpreted as due to through-going ligaments attaching between the parallel columnals holding the stem straight; when this strong ligament is damaged weaker ligaments between the apex of the wedges draw them closed to cause the column to curve. A section of mid stem that was damaged has curved into an arc of almost 360 degrees, whereas above and below this region remained normal.

Microplankton changes through a mass extinction: The Early Silurian Ireviken Event

David Gelsthorpe
Department of Geology, University of Leicester, Leicester, LE1 7RH, UK
<dng1@le.ac.uk>

The Ireviken extinction Event in the early Silurian (Llandovery/Wenlock boundary, 428 Ma) has been related to a major change in global climate. Within the Event at least eight extinction horizons in the conodonts (early vertebrates) have been reported. It has been established that the changes in the phytoplankton (acritarchs and prasinophyte algae) at this time were severe (Le Hérissé 1989), but until now these have not been analysed in detail.

The Ireviken Event was first recorded in the Visby Beds on the island of Gotland (Sweden). It has been interpreted as an example of the change between P to S climate state (Jeppsson 1993), reflecting severe changes in the ocean-atmosphere system.

The data set shows a significant turnover in the phytoplankton at the Ireviken Event, with most of the extinctions occurring at the end of the event, when many of the conodont extinctions have taken place. Most of the species that become extinct belong to the genus *Oppilatala*. The originations occur very gradually across the whole event, apart from around the Upper Visby Beds/Lower Visby Beds boundary where they mostly cease. If the P and S model is correct, these data indicate a higher diversity of phytoplankton occurred in the S state, perhaps reflecting greater specialisation in a low-nutrient environment.

The phylogenetic relationships of fossil and Recent galliform birds

Bonnie E. Gulas[1] and Gareth J. Dyke[2]

[1]Department of Geology and Geophysics, Yale University, New Haven CT 06520, USA **<gulas@amnh.org>**
[2]Department of Ornithology, American Museum of Natural History, New York NY 10024, USA **<gdyke@amnh.org>**

Of the more basal clades of modern birds (Neornithes), the "landfowl" or galliforms are the most diverse. This unquestionably monophyletic avian order includes such well-known birds as pheasants, quails, guineafowl, turkeys, and chickens. Using osteology, we conducted the first phylogenetic analysis of these birds that includes most extant genera as well as a number of well preserved fossil taxa. Results of our analysis are congruent with traditional classifications and with available molecular evidence. Using parsimony, we show that the megapodes (mound-builders) are the most basal clade within Galliformes, followed by the cracids (*e.g.*, currassows) and phasianoids (*e.g.*, pheasants, guineafowl and partridges) as successive sister-taxa. Within this latter grouping, a number of traditional "family-level" clades are also well-supported. Although many supposed fossil galliforms have been described from the Mesozoic, without exception this material is fragmentary, consisting only of isolated skeletal elements. The first fossil records of the order that are well-preserved enough to be informatively coded within phylogenetic analysis come from the Palaeocene and Lower Eocene of Europe (*e.g.*, *Paraortygoides* Mayr) and North America (*e.g.*, *Gallinuloides* Eastman).

Early Ordovician faunal development of the Laurentian platform in NE Greenland

D.A.T. Harper[1], Svend Stouge[2], W. Douglas Boyce[3], Jørgen Christiansen[4] and Ian Knight[3]
[1]Geological Museum, Øster Voldgade 5-7, DK-1350 Copenhagen K, Denmark **<dharper@savik.geomus.ku.dk>**
[2]Geological Survey of Denmark and Greenland, Thoravej 8, DK-2400, Copenhagen NV, Denmark **<ss@geus.dk>**
[3]Government of Newfoundland and Labrador, Department of Mines and Energy, Geological Survey Division, Regional Geology Section, PO Box 8700, St John's, Newfoundland A1B 4J6, Canada
[4]Holbæk College of Education, Seminarieparken 2, DK-4300 Holbæk, Denmark

Lower Ordovician successions in NE Greenland contain a variety of platform carbonates developed within the Dolomite Point, Antiklinalbugt, Kap Weber, Narhval Sund and Heim Bjerge formations. The Ordovician successions range in age from earliest Canadian to the late Whiterock and formed an integral part of the Laurentian margin. Contrary to previous studies a wide range of carbonates including mudmound and reefal facies have been identified, ranging from algal and sponge developments during the Canadian, cropping out on Ella Island, to the presence of stromatoporoid mounds in the younger parts of the succession exposed, farther north, on Albert Heims Bjerge. Restricted carbonate facies and faunas were periodically modified by the input of silciclastics, eustatic changes in sea level and at least one oceanographic event during the Arenig. Particularly spectacular are the carbonate complexes developed in the Antiklinalbugt Formation on Ella Island where a range of brachiopod, gastropod and trilobite dominated communities are commonly associated with bioclastic facies at the base of algal and sponge reefs correlated with the top of the *Cordylodus intermedius* conodont Zone and the base of the *Cordylodus angulatus* conodont Zone. Together the faunas represent an early developmental stage of the Laurentian Province, at this stage fundamentally different from benthic faunas elsewhere in the Iapetus Ocean.

Benthonic Foraminifera from Stevns Klint (Denmark); new data from the K/T boundary

Malcolm Hart, Sean Feist and Greg Price
Department of Geological Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK

The classic K/T boundary section of Stevns Klint has been re-sampled at three locations and the material investigated for Foraminifera (especially benthonic taxa) and stable isotopes. The benthonic Foraminifera are only marginally affected by the extinction event at the boundary, although there are subtle changes in the distribution/dominance of key taxa. The isotopic analysis (based on bulk rock and selected genera of benthonic Foraminifera) shows the typical Maastrichtian pattern, including the negative $\delta^{13}C$ excursion within the Fish Clay. Within the expanded Fish Clay succession in the northern part of the section there are some significant variations in the $\delta^{13}C$ record and a number of "cycles" are recorded. Above the "hardgrounds" in the uppermost Maastrichtian, the chalk appears to be redeposited, forming the well-known mound structures, as the normal isotopic signals of the Maastrichtian are missing and the fauna shows some signs of reworking.

Evolution of early planktonic Foraminifera: links to eustatic sea-level and ocean change

M.B. Hart[1], M.J. Oxford[1] and M.D. Simmons[2]
[1]Department of Geological Sciences, University of Plymouth, Plymouth, PL4 8AA, UK **<m.hart@plymouth.ac.uk>** and **<m.oxford@plymouth.ac.uk>**
[2]CASP, University of Cambridge, 181A Huntingdon Road, Cambridge, CB3 0DH, UK **<mike.simmons@casp.cam.ac.uk>**

The taxonomy and biostratigraphy of the early planktonic Foraminifera have been reviewed and new records have been made of Jurassic planktonic Foraminifera from localities where they were previously undescribed, such as from the Jurassic sediments of the UK. These new data suggest that there is a strong link between the evolution of the earliest planktonic Foraminifera and eustatic sea-level change and global oceanic events. Bursts of planktonic Foraminifera evolution seem linked to the opening of environmental niches directly after sea-level rise and/or anoxia. The earliest possible planktonic Foraminifera are assigned to the genus *Praegubkinella*, although it seems likely that this genus had at best only a meroplanktonic mode of life. This genus occurs in Toarcian sediments directly above the Bifrons Zone anoxic event and sea-level rise. The next evolutionary event within the planktonic Foraminifera is the appearance of *Conoglobigeria* in the latest Bajocian–earliest Bathonian, a time of major eustatic sea-level rise (Zigzag Zone maximum). The earliest holoplanktonic Foraminifera (*Globuligerina*) appear around the time of the latest Bathonian sea-level rise, and further bursts of abundance and evolution of this genus correspond to maximum flooding events and/or anoxia events such as in the Mariae Zone at the base of the Oxfordian.

Planktic Foraminifera from the lowermost type Danian of Stevns Klint, Denmark

Claus Heinberg[1], Jan A. Rasmussen[2] and Eckart Håkansson[3]
[1]Department of Environment, Technology and Social Studies, Roskilde University Center, Box 260, DK-4000 Roskilde, Denmark **<heinberg@teksam.ruc.dk>**
[2]Department of Stratigraphy, Geological Survey of Denmark and Greenland, Thoravej 8, DK-2400 Copenhagen NV, Denmark **<jar@geus.dk>**
[3]Geological Institute, University of Copenhagen, Øster Voldgade 10, DK-1350 København K, Denmark **<eckart@geo.geol.ku.dk>**

The planktic foraminiferan fauna from the lowermost type Danian strata at Stevns Klint, Denmark is to date essentially unknown. New, rich assemblages of planktic Foraminifera procured from the *Cerithium* Limestone considerably improve this situation, boosting stratigraphic resolution for the sequence of events immediately following the Iridium event marking the K-T boundary across the Danish Basin. The new assemblages show an overall dominance of *Chiloguembelina* spp. and *Globoconusa daubjergensis*. In spite of the presence of several stratigraphic key species, such as *Eoglobigerina eobulloides* and *Guembelitria cretacea*, the comparatively low diversity of most samples complicates correlation with global-zonation schemes. However, other parameters of the planktic assemblages in the *Cerithium* Limestone appear to be potentially useful in both intra-basinal and more global correlations. Thus, the total lack of Foraminifera larger than 125 microns in the *Cerithium* Limestone is paralleled in both the boundary stratotype section at el Kef, Tunisia, and across the Danish Basin. Also the ratio between biserial, triserial and spiral tests may provide a high-resolution

correlation tool in the Danish Basin, where a seemingly gradual shift from biserial dominance to a more 'normal' situation with dominance of spiral forms has been recorded in all sections investigated. This development may also be relevant on a global scale.

Controls on crystal growth during coccolithogenesis - Evidence from Atomic Force Microscopy

Karen Henriksen[1,2,3], Jeremy R. Young[2], Paul R. Bown[3] and Susan Stipp[1]
[1]Geologisk Institut, Kobenhavns Universitet, Øster Voldgade 10, DK-1350 Copenhagen, Denmark
[2]Palaeontology Department, The Natural History Museum, London SW7 5BD, UK
[3]Geology Department, University College London, London WC1E 6BT, UK

Atomic force microscopy (AFM) is an ultra-high resolution imaging technique that requires no surface coating and can be used in air or under solution at ambient conditions of temperature and pressure. The technique is relatively novel and has not previously been applied to coccoliths, so we have conducted a pilot project exploring its potential for providing new information on coccolith biomineralisation.

Coccoliths of various species were investigated with regards to morphology, ultrastructure, crystallography and the nature of the organic coating. Morphological surveys reveal the presence of growth fronts and different surface textures, which can either be ascribed to the organic coating, or to the underlying calcite; distinguishing between the two was possible through imaging of coccoliths where the organic coating had been removed by oxidation. Dissolution experiments were carried out which showed that the organic coating protects the faces of coccolith elements from dissolution, but suggests an absence of inter-element organics.

This study shows that AFM is a technique of great potential in coccolith biomineralisation research, capable of giving new information on the nature of the coccolith crystals and the organic material associated with them. Elucidating the interaction of these two—inorganic crystals and organic molecules—is critical to understanding biomineralisation.

Lucky for Some—13-rayed Silurian starfish and the origins of multiradiate asteroids

Liam Herringshaw
School of Earth Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK <**LGH865@bham.ac.uk**>

Five-part symmetry is a feature generally cited as typical of echinoderms, but there are notable exceptions. Asteroids (starfish), and to a lesser extent ophiuroids (brittle stars), show deviation from pentamerism at a number of levels, from specific to ordinal, such that a number of questions are raised about the nature of echinoderm symmetry.

Of 34 extant asteroid families, 20 are exclusively pentaradial, nine include both five-rayed and many-rayed species, and five are solely multiradiate (Hotchkiss 2000). Fossil starfish with more than five rays are extremely rare. All Ordovician asteroids are pentaradial, barring occasional teratological six-rayed specimens, and the same is true of Llandovery species, but the Much Wenlock Limestone Formation of Dudley, England, contains the consistently 13-rayed *Lepidaster grayi* Forbes, 1850. This is the first

example of a multiradiate asteroid in the fossil record, and is the only Silurian case known. It is not until the early Devonian that a second non-pentaradial species is encountered.

All extant multiradiate asteroids for which post-metamorphic growth has been studied begin with five rays, but the subsequent pattern of ray addition is highly variable. Possible explanations for *Lepidaster grayi* having 13 rays will be outlined, as will the functional and ecological implications. The phylogeny of multiradiate asteroids will also be discussed.

Terrestrial and marine mass extinction at the Triassic/Jurassic boundary synchronized with initiation of massive volcanism

Stephen P. Hesselbo[1], Stuart A. Robinson[1], Finn Surlyk[2] and Stefan Piasecki[3]

[1]Department of Earth Sciences, University of Oxford, Parks Road, Oxford OX1 3PR, UK
[2]Geological Institute, University of Copenhagen, Øster Voldgade, DK-1350 Copenhagen K, Denmark
[3]Geological Survey of Denmark and Greenland, Thoravej 8, DK-2400 Copenhagen NV, Denmark

The mass extinction at the Triassic-Jurassic (Tr/J) boundary at 200 Ma ranks amongst the five most extreme in the Phanerozoic and occurred approximately at the same time as one of the largest volcanic episodes known from the geological record, that which characterized the Central Atlantic Magmatic Province (CAMP). New organic carbon-isotope data from key sections in the UK and Greenland demonstrate that changes in flora and fauna from both terrestrial and marine environments occurred synchronously with initiation of a short-lived light-carbon isotope excursion, and that this happened significantly earlier than the conventionally established marine Tr/J boundary. The results also indicate synchronicity between the extinction event and eruption of the first CAMP lavas, suggesting a causal link between loss of terrestrial and marine taxa and the very earliest eruptive phases. Following a temporary return to heavier values, relatively light carbon again dominated the shallow-marine and atmospheric reservoirs for at least the next 600 kyr.

The leptaenid brachiopods of the Silurian of Gotland: Ecology and functional morphology

Ole A. Hoel
Department of Earth Sciences, Uppsala University, Norbyvägen 22, SE-752 36 Uppsala, Sweden

The leptaenids are the most diverse strophomenids on Gotland. At least five species occur. *L. rhomboidalis* has very deep rugae, a transverse, often irregular shape, and large, functional pedicle foramen. It occurs mostly in the early stages of reef development. *L. depressa* has low, rounded rugae, a quadratic shape, lacks a pedicle foramen in the adult stage, and has a long, upward-bent trail. It occurs mostly in muddy environments. Several forms seem to be intermediate between both species, especially in the more limestone-rich areas in the NE of the island. *L. sperion* is a very large leptaenid found in level-bottom limestones whereas *Scamnomena rugata* is small and flat and seems to be confined to high-energy reef flank environments. The large and wide *Lepidoleptaena poulseni*

dominates in the upper Wenlock and Ludlow; *L. rhomboidalis* is found mostly in reefs and generally in the NE parts of Gotland. Thus it preferred higher energy environments. The high level of encrusting and breakage of the shells indicate an exposed lifestyle. *L. depressa* occurs mostly in marls in the SW, and are rarely encrusted, indicating an infaunal way of life. Intermediate forms bolster the notion that the morphology of *Leptaena* was largely environmentally influenced.

Palaeosols of the Cretaceous fossil forests of Alexander Island Antarctica

Jodie Howe
School of Earth Sciences, University of Leeds, Leeds, LS2 9JT, UK
<J.Howe@earth.leeds.ac.uk>

The Cretaceous rocks of Alexander Island, Antarctica contain abundant *in situ* fossil plants and trees rooted within well-defined, organic-rich palaeosols. The palaeosols developed upon the floodplain of a braided river system within a fore-arc basin and supported dense stands of araucarian and podocarp conifers with understoreys of ferns and shrubs. Periodically the rivers flooded, inundating the floodplain with sediment, covering the soils and their vegetation. Repeated sequences of palaeosols overlain by flood-derived volcaniclastic sandstones and siltstones show that when the waters subsided new soils formed and plant colonisation began again.

The palaeosols show two distinct horizons: a claystone upper horizon (mollic epipedon) that is organic-rich, mottled and contains plant debris and delicate, branching *in situ* rootlets; and a lower horizon (cambic layer) that predominantly shows characteristics of the bedrock with roots, ped structures and clay cutans. The palaeosols have also been overprinted by zeolite facies minerals formed from the breakdown of volcanic glass within the sandstones during diagenesis. Although these soils have a volcaniclastic component they are more developed than a volcanic ash andisol and are classified as mollisols. Palaeosol structure and composition indicates that the prevailing high latitude Cretaceous climate was markedly seasonal, with alternate wet and dry periods.

"Sclerosponges"—a new element in the Neogene of the eastern Mediterranean

Eckart Håkansson and Margret Steinthorsdottir
Geological Institute, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen, Denmark **<eckart@geo.geol.ku.dk>**

Since their rediscovery in the 1960s, 'sclerosponges' have been reported sporadically throughout the tropical realm, where they may constitute an important element of cryptic communities. Today most biologists regard 'sclerosponges' as an informal, polyphyletic group of sponges unified by a solid calcareous skeleton, which is usually associated with siliceous spicules. However, the understanding of sponge systematics is still far from adequate, a situation which is even more apparent when it comes to fossil sponges.

In accordance with their apparent temperature requirements, 'sclerosponges' appear to be largely unknown from the modern Mediterranean Sea as well as in the Neogene faunas associated with the development of this 'ocean'. The discovery of a 'sclerosponge' species in a fossil cave, within the Pliocene part of the marine Kolymbia Formation on the island of Rhodes in the eastern Mediterranean, therefore constitutes an interesting extension of the known distribution of the group. Thus this

'sclerosponge', in the Pliocene fauna of Rhodes, may constitute yet another tropical relict having relatives within the Tethyan precursor of the Indian Ocean.

The new 'sclerosponge' is characterized by largely equi-dimensional, rounded to polygonal calicles with stout tabulae, but it has yet to be established whether siliceous spicules are still preserved in the skeleton. The new form has been recorded only from a single locality, where it is a prominent member of the encrusting, cryptic community constituting the last, epilithic phase before the final, Pliocene infill of the cave.

Late Cretaceous and Early Paleogene echinoderms from Denmark—an update

John W.M. Jagt[1] and Sten L. Jakobsen[2]
[1]Natuurhistorisch Museum Maastricht (OCWS), P.O. Box 882, NL-6200 AW Maastricht, The Netherlands **<mail@nhmmaastricht.nl>**
[2]Geological Museum, Øster Voldgade 5-7, DK-1350 Copenhagen K, Denmark **<slj@savik.geomus.ku.dk>**

New finds of echinoderms from the Maastrichtian white chalk facies of Møn and Sjælland and the overlying Danian (Early Palaeocene) bryozoan limestone of Sjælland (Denmark), as well as a revision of material contained in the collections of the Geological Museum (Copenhagen), allow these faunas to be assessed in greater detail. Echinoid, asteroid, ophiuroid and crinoid faunas from the Maastrichtian type area (SE Netherlands, NE Belgium), of Maastrichtian and Palaeocene age, have recently been revised. Changes in these faunas across the Cretaceous-Tertiary (K/T) boundary suggest local extinction within several groups and earliest Palaeocene migration events in others to have taken place. The new Danish material may shed light on the dating and trajectory of these events.

In addition, the shallow-water settings of the Maastrichtian type area may now be compared in greater detail with the deeper water environments represented by the Danish white chalk and bryozoan limestones. This in turn will allow our views of the impact of K/T boundary perturbations to be sharpened.

Examples illustrated include the first complete specimens of the goniasterid and astropectinid starfish *Metopaster kagstrupensis* Brünnich Nielsen, 1943 and *Lophidiaster*? gr. *punctatus/postornatus*, well-preserved individuals of brittle stars, including the type of *Ophiomusium rahbeki* Brünnich Nielsen, 1942, as well as *Ophiotitanos serrata* (Roemer, 1840) and the *granulosum/subcylindricum* species group of *Ophiomusium*, and an interesting accumulation of well-preserved cidaroid echinoid tests from Fakse.

A new spin on the Lower Cambrian medusoid fossil Kullingia; scratch circles, not chondrophorine cnidarians

Sören Jensen[1], James G. Gehling[2] and Mary L. Droser[1]
[1]Department of Earth Sciences, University of California, Riverside, CA 92521, USA
[2]South Australian Museum, Adelaide, Australia.

The Chondrophora are pelagic colonial hydrozoans with chitinous multichambered disclike floats. More than 10 genera of fossil chondrophorines have been identified but generally their interpretation is problematic. *Ovatoscutum* is the only remotely possible terminal Proterozoic candidate, and purported Cambrian chondrophorines are dubious at best. Mindful of this, Narbonne et al. (1991:

Journal of Paleontology **65**, 186-190) interpreted *Kullingia* from the Lower Cambrian of Newfoundland as impressions of chondrophorine floats, thereby providing new support for deep roots of these cnidarians. However, the type material of *Kullingia* from the Lower Cambrian of Sweden possesses features which show that the nested concentric ridges were formed by the rotation of a tubular organism; this is conclusively demonstrated by specimens that preserve impressions of a segmented tubular organism centred on and conterminous with the disc. New material of *Kullingia* from Newfoundland, including a specimen with a tube, shows that these *Kullingia* also represent scratch circles. The earliest chondrophorines must be sought in post-Cambrian material.

The Cenomanian Stage in Egypt: Macropalaeontology, integrated biostratigraphy, and inter-regional correlation

Ahmed S. Kassab
Geology Department, Faculty of Science, Assiut University, Assiut 71516, Egypt
<kassab@acc.aun.eun.eg>

The present study aims to establish an integrated ammonite, echinoid and oyster biozonation for refined age determination and a precise correlation of the Cenomanian Stage in Egypt. It is based on palaeontological and stratigraphical analyses of several sections exposed on western and southern Sinai, the north and central Eastern Desert, and the north Western Desert.

Based on palaeontological and stratigraphical data, several related oyster and ammonite species previously identified in the literature as separate species are considered here as variants and synonyms of dimorphic species. Biostratigraphically, the fossiliferous Cenomanian strata have been subdivided into three ammonite zones coeval with four oyster and three echinoid zones of Late Cenomanian age. Some of these macrozones are absent at certain localities. An integrated ammonite, oyster, and echinoid zonation is presented. The ammonite zones are those of *Neolobites vibrayeanus*, *Metoicoceras geslinianum* and *Vascoceras cauvini*. The oyster zones are those of *Ilymatogyra africana*, *Ceratostreon flabellatum*, *Gyrostrea delettrei*, and *Exogyra olisiponensis*. The echinoid zones are those of *Arciacia pescameli*, *Holyctypus excisus*, and *Hemiaster pseudofourneli*. These macrozones are calibrated with associated planktic Foraminifera for the purpose of regional stratigraphy and inter-regional correlation.

In most of the sections, the Cenomanian/Turonian boundary is marked by the occurrence of the ammonites *Vascoceras proporium*, *Vascoceras obesum* and/or *Pseudaspidoceras flexuousum*. In others, this boundary is coincident with an erosional surface suggesting an hiatus of varying magnitude between the Cenomanian and Turonian. No Lower Cenomanian index fauna has been identified from these outcrops. The palaeobiogeography of the fauna will be discussed.

An integrated biostratigraphic approach to the Albian/Cenomanian boundary in eastern Greenland

Simon R.A. Kelly[1], Bill Braham[2], John Gregory[3], A. Munif Koraini[4], Hugh G. Owen[1] and Andrew G. Whitham[1]

[1]CASP, West Building, 181a Hundington Road, Cambridge GB3 QDH, UK

[2]11 Corner Hall, Hemel Hempstead, Hertfordshire HP3 9HN, UK

[3]Department of Palaeontology, The Natural History Museum, London SW7 5BH, UK

[4]Petronas Research & Scientific Services SDN BHD, Lot 3288 & 3289, off Jalan Ayer Itam, Kawasan Institusi Bangi1 43000 Kajang, Selangor Darul Ehsan, Malaysia

Combined collection of Cretaceous macrofauna and microbiota in eastern Greenland has enabled the precision of dating the dinocyst zonation to be refined. Initial dating of sediments based only on dinocyst evidence of Nøhr Hansen (1993, *GGU Bull.* **166**) placed the Albian-Cenomanian boundary above the *Epilopidosphaeridia spinosa* Subzone in the upper part or top of the *Subtilisphaera kalaalliti* Zone. However, in the present study, the Albian-Cenomanian boundary was discovered to be located much lower in the dinocyst succession. In this revised scheme the boundary is placed within the *Wigginsiella grandstandica* Subzone in the early part of the *kalaalliti* Zone. The reason for the modification is the co-occurrence of reliable Cenomanian macrofauna, such as the ammonite *Schloenbachia varians* and bivalves of the *Inoceramus crippsi* group in association with dinocysts of the *Wigginsiella grandstandica*, *Odontichitina ancala* and *Ovoidinium*? sp. 1 zones. A revised integrated macro- and microbiostratigraphical zonal scheme is proposed for parts of the Albanian and Cenomanian stages in eastern Greenland. It is based on ammonites, mainly hoplitids, gastroplitinids, schloenbachiids and mortoniceratids, inoceramid bivalves, belemnites, dinoflagellate cysts and foraminiferans. The *kalaalliti* Zone ranges from Upper Albian, through the Cenomanian and possibly into the Turdnian stages. It is expected that this revised scheme of zones will be of significance for offshore biostratigraphic studies in the North Atlantic region and in the Arctic.

Correcting diversity counts using ghost ranges—new hope or phantom menace?

Abigail Lane

Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol, BS8 1RJ, UK

The traditional 'taxon counting' method of estimating ancient biodiversity is open to many criticisms, not least of which is the problem of inconsistency in the preservation of fossil organisms, and the associated error on first and last appearance times of taxa. The use of cladistics to construct phylogeny has provided a way of correcting the first appearance of a taxon based on the origination time of its sister group. This extension of a taxon or taxon group's range back in time is known as adding a 'ghost range', and it has been suggested that ghost ranges as well as actual fossil ranges should be included in diversity counts.

As logical as this phylogenetic method of correcting diversity may seem, it has problems—in particular the bias inherent in altering origination, but not extinction times, and the potential for incorrect addition of ghost ranges if the ancestor of a taxon is defined as its sister. To investigate these uncertainties a new random number computer simulation has been designed which creates a phylogeny, samples it and then adds ghost ranges, with diversity counts being made at all three stages. The results enable the performance of both the traditional and phylogenetic methods to be assessed.

3-dimensional reconstruction of a Thylacocephala

S. Lange and F.R. Schram
Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Post Box 94766, NL-1090 GT Amsterdam, The Netherlands

The Thylacocephala consist of a number of marine Palaeozoic and Mesozoic apparent crustaceans, with a common body plan that usually consisted of large carapace, large compound eyes, three pairs of raptorial limbs, a battery of small posterior limbs and several pairs of large gills.

Study of sections of some exceptionally well preserved fossils of the Jurassic thylacocephalan *Dollocaris ingens* makes it possible to present a 3D reconstruction of the thylacocephalan body that includes interpretations of the position and morphology of internal organ systems, noticeably the digestive system and part of the circulatory system. The reconstruction offers an interpretation of the functional morphology of the gills as well as an improved understanding of the raptorial limbs and the posterior limbs. The knowledge gained from the reconstruction promises to elucidate more of the questions still surrounding this enigmatic group.

Morphological changes in the trilobite *Olenus* and *Homagnostus* (Upper Cambrian, Sweden): Iterative gradual evolution re-examined

Bodil Wesenberg Lauridsen
Geological Institute, University of Copenhagen, DK-1350 Copenhagen K, Denmark
<Bodill@geo.geol.ku.dk>

Kaufmann (1933a) suggested that *Olenus* species (Trilobita) in the Upper Cambrian *Olenus* Zone at Andrarum, Southern Sweden, evolved following an iterative gradualistic pattern. Four species lineages comprising six species show the same pattern of gradual narrowing of the exoskeleton. The purpose of the present study is to re-examine these morphological changes. Further the morphological changes of the contemporary trilobite *Homagnostus obesus* and the palaeoecology of the *Olenus* Zone will be discussed.

The study is based on image analysis of almost 5,000 photos taken of the shale surfaces collected in the Andrarum Shale Quarry. The differences in the morphological changes displayed by the relevant pygidia and cephala were tested statistically. The faunal composition of the *Olenus* Zone was recorded in order to track palaeoenvironmental changes. The variation in V/(V+Ni) was measured and the changes were tested statistically. Finally, the morphological changes of the two genera were compared with the palaeoenvironmental changes. It is not possible with modern statistical methods to confirm a gradual iterative evolution of the skeletal elements from either the *Olenus* species or *H. obesus*. The Plus ça change model is therefore presented as an alternative explanation of the morphological changes in the *Olenus* Zone.

Assembling a hyolithid

Mónica Martí Mus[1] and Jan Bergström[2]
[1]Department of Earth Sciences, Historical Geology and Palaeontology, Uppsala University, Norbyvägen 22, SE-752 36 Uppsala, Sweden **<monica.marti@pal.uu.se>**
[2]Department of Palaeozoology, Swedish Museum of Natural History, P.O. Box 50007, SE-104 05 Stockholm, Sweden **<jan.bergstrom@nrm.se>**

The skeleton of hyolithids consists of a conch, an operculum and a pair of long, curved "spines" called helens. These elements tend to disarticulate easily after death, which has hindered knowledge of the morphology of the complete organism. In particular, the fragile helens have remained poorly known. Abundant muscle scars occur on both conch and operculum and have been the basis for controversial reconstructions of soft parts. The study of exceptionally preserved hyolithids has provided new insights into the functional morphology of the hyolithid skeleton. The helens were solid and had a shell microstructure consisting of concentric lamellae. They grew by terminal accretion following a logarithmic spiral. The proximal portion of the helens was internal and held free in the dorsal plane of the aperture; the distal portion was entirely external. Upon closure of the operculum, each helen was locked between the conch and operculum with the dorsal edge tilted forwards. Helens were involved both in locomotion and stabilisation. Comparative study of muscle scars indicates that hyolithids did not have serially-arranged muscles involved in a hydrostatic skeleton. Instead, they had distinct, non-seriated muscle bundles operating the articulation of the skeletal elements.

Palaeosaurus—an integrated biostratigraphy collections management initiative at the British Geological Survey

Tim McCormick
British Geological Survey, Keyworth, Nottingham NG12 5GG, UK
<tmcm@bgs.ac.uk>

If palaeontology is to maintain a profile as a relevant and dynamic science, it is increasingly important that institutions housing fossil collections collate and make available structured information on their holdings. The British Geological Survey hosts the most comprehensive biostratigraphy collections relating to Britain and its continental shelf found anywhere. The estimated three million samples include representatives of virtually all major groups, and occur in a variety of formats including hand specimens, core samples, slides, photographs, and thin sections. The collections are the result of over 150 years of intense surveying and collection plus numerous important donations.

"Palaeosaurus" is an ongoing initiative to develop an integrated biostratigraphy collections management system in BGS. It brings together for the first time information on the provenance, systematics, stratigraphy, citations, loan status and location of material, and supports links to other relevant BGS data resources. Palaeosaurus is designed to be a single point of contact for basic information on all BGS fossil holdings.

In order for the database to remain viable in the long term, care must be taken in design of data structures. Particular issues are associated with stratigraphical and taxonomic attributes. Some approaches to circumventing problems will be outlined.

Fossil nanobacteria from the basal Cambrian

Malgorzata Moczydlowska
Department of Earth Sciences, Uppsala University, Norbyvägen 22, SE-752 36 Uppsala, Sweden

Life on Earth has existed for over 3.87 Ga and bacteria were probably the first organisms to evolve, yet the records are rare and in most instances reveal their metabolic processes and activity (biogenic minerals, molecular fossils, isotopic fractionation, stromatolites) rather than the body fossils themselves. Slightly permineralized bacteria preserved three-dimensionally in their natural habitat and surrounded by biogenic pyrite as a by-product of their metabolism are reported from Lithuania. The fossil nanobacteria are preserved in situ on the tube of the extinct animal *Sabellidites*, which is about 540-544 Myr old. The nanofossils are cylindrical, non-septate filaments with rounded terminations, 209-324 nm wide, occurring in large numbers. The filaments are organic, as proven by their elemental composition, and indigenous to the host specimen and rock.

They are slightly pyritized, silicified and coated by phosphate, and interwoven with the authigenic, early diagenetic crystals of pyrite and gypsum. Under anoxic conditions at the sediment-water interface, these anaerobic, sulphate-reducing bacteria infested post-mortem the *Sabellidites* tube and began to decompose its organic matter. The nanofossils were saprogenic but their systematic affiliation remains uncertain. This is the first record of fossil nanobacteria that are in fact smaller than any previously published bacterial microfossils.

The *lundgreni* (Wenlock, Silurian) graptolite extinction event in the Welsh Borderland

Lucy Muir
Department of Geology and Geophysics, University of Edinburgh, Grant Institute, West Mains Road, Edinburgh, EH9 3JW, UK **<Lucy.Muir@glg.ed.ac.uk>**

Graptolites experienced many extinction events during their history. One of the most severe was the event that occurred at the end of the *lundgreni* graptolite biozone (Wenlock, Silurian). Hypotheses for the cause of the *lundgreni* event include the spread of anoxia in the oceans and the retreat of anoxia in the oceans. In a section along Trewern Brook in the Welsh Borderland the event is marked by an interval where graptoloids are completely absent. This absence is interpreted as being caused by migration out of the study area. There is a sea level fall and a change in the state of the sea floor from anoxic to oxic at this time. This finding contradicts the hypothesis that the *lundgreni* event was caused by the spread of anoxia in the oceans, and confirms the hypothesis that the event was caused by the retreat of anoxia.

The *Leptoplastus* Zone (Upper Cambrian) at Slemmestad, Norway

Arne T. Nielsen
Geologisk Museum, Øster Voldgade 5-7, DK-1350 København K, Danmark
<arnet@savik.geomus.ku.dk>

The Middle Cambrian-Tremadoc Alum Shale Formation of Scandinavia acted as decollement level for the Caledonian thrust sheets. The Alum Shale of the Oslo Region is therefore rather strongly folded and

faulted. No measured sections have been published. However, although exposures of the Alum Shale look rather chaotic it appears that the stratigraphic succession can be pieced together with a high degree of confidence. An example is shown from the Slemmestad Harbour, located adjacent to the Oslo Fjord approximately 30 km southwest of Oslo. Here the Upper Cambrian *Leptoplastus* Zone is exposed in an anticline. In both flanks the highly fossiliferous limestone horizons within the shale have been systematically sampled bed-by-bed.

The *Leptoplastus* Zone is approximately 2.7 m thick and comprises in ascending order the *L. raphidophorus*, *L. ovatus*, *L. angustatus*, *L. stenotus* and *L. neglectus* subzones *sensu* Westergård (1947). No limestone horizons represent the basal *L. paucisegmentatus* Subzone, but it appears that shale just above the uppermost limestone horizon of the *Parabolina* Zone contains leptoplastids associated with *Parabolina*. Accordingly this shale may represent the *L. paucisegmentatus* Subzone, hitherto regarded as missing in the Oslo area. More importantly, there is no space for the *L. crassicorne* Subzone, introduced by Henningsmoen in 1957 between the *L. raphidophorus* and *L. ovatus* subzones. *L. crassicorne* is common, but restricted to the *L. ovatus* Subzone. Likewise the *Protopeltura holtedahli* Subzone, erected by Henningsmoen cannot be recognized (the species has not been found), and *Protopeltura broeggeri*, being the index fossil of a third subzone erected by Henningsmoen, occurs associated with *L. angustatus*. Therefore these subzones should be abandoned.

Material subsequently sampled from a nearby section through parts of the *Parabolina* Zone may represent *P. holtedahli*, but this needs verification. Nevertheless, *P. holtedahli* seems very closely related to *P. aciculata*, and should perhaps be ranked only as a subspecies. It is concluded that we should revert to the subdivision of the Leptoplastus Zone, published by Westergård in 1947, with the only emendation that *Eurycare latum* has a longer range and should not be used as an index fossil. At Slemmestad this species is indeed most common in the *L. ovatus* Subzone (cf. Westergård), but it ranges throughout the *Leptoplastus* Zone.

Evolution of the Eocene *Turborotalia* lineage (planktonic Foraminifera)

Paul N. Pearson and Matthew Carroll
Department of Earth Sciences, University of Bristol, Queen's Road, Bristol BS8 1RJ, UK

Turborotalia cerroazulensis and related forms are a common constituent of upper Eocene planktonic foraminifer assemblages worldwide and have been extensively used in biostratigraphical correlation. Here we investigate an old suggestion that *Turborotalia* is descended from the middle Eocene species *Subbotina frontosa* by gradual evolution. This hypothesis has not been generally accepted because *Subbotina* and *Turborotalia* are far removed from one another in almost all aspects of their shape and microstructure. Long stratigraphic records of *Turborotalia* are investigated from several sites in the Pacific, Atlantic and Mediterranean regions. Populations of up to 200 specimens from individual samples have been picked and various measurements made using image analysis software. We have confirmed from stratophenetic linkage between large numbers of samples from different levels that long-term gradual transition from *S. frontosa* morphotypes to *Turborotalia* did occur, but the pattern is complicated by some clear cladogenetic events and substantial geographic variability. This may indicate the existence of multiple closely related sibling species that are difficult to resolve using traditional taxonomic approaches. The *T. cerroazulensis* lineage became extinct a few tens of thousands of years before the Eocene–Oligocene boundary. More than ten million years later, very similar morphologies re-evolved from unrelated species.

Innovations, constraints, and the complexity of conodonts

Mark A. Purnell
Department of Geology, University of Leicester, Leicester LE1 7RH, UK
<map2@le.ac.uk>

After more than a century of taxonomic work and decades of intense biostratigraphic activity the changing fortunes of conodonts through time have been thoroughly documented. Their fossil record is widely acknowledged to be among the best of any of the Metazoa and although interpreting compiled taxonomic datasets is fraught with problems the pattern of conodont diversity and evolution is not something that palaeontologists can easily ignore. Most interpretations of conodont diversity have focused on its relationship with sea level; there have been few attempts to consider the intrinsic biological factors that must have been important in conodont evolution. How has the complexity of the conodont skeleton changed through time? Do intervals of increasing diversity reflect adaptive radiation—the appearance of evolutionary novelties and key innovations? How important were evolutionary constraints? The lack of answers to these questions reflects what has been a central paradox of the conodont fossil record: Numbers of taxa and stratigraphic ranges have been well documented, but little was known of conodonts as organisms. In the last few years this has changed. With new knowledge of conodont skeletal architecture, apparatus composition, element function and phylogenetic relationships, we can now start to investigate innovation, constraint, and adaptation through the 300 million year record of conodont evolution.

Palaeobiogeography of Cenozoic larger Foraminifera in SE Asia

Willem Renema
Nationaal Natuurhistorisch Museum, PO Box 9517, 2300 RA Leiden, The Netherlands **<Renema@naturalis.nl>**

The Indo West-Pacific is the most diverse area for shallow marine organisms, including larger Foraminifera, in the modern-day ocean. In this paper the Cenozoic history and character of this fauna are discussed in terms of both morphological and taxonomical diversity.

During the Cenozoic, there are only few genera of larger Foraminifera in SE Asia, compared to Europe or other places in the Western Tethys. Within the nummulitids not only the taxonomic, but also the morphological diversity is lower. This diversity increases gradually to a maximum in the Mid Miocene, after which many genera become extinct. In the Plio-Pleistocene many new genera appear again. A major turn-over event occurred in the Priabonian-Rupelian. Parameters affecting the diversity distribution of larger Foraminifera in the Cenozoic act on several levels. First there is the worldwide recognizable subdivision of the Cenozoic into two or three faunas, the Palaeocene-Eocene fauna, the Late Oligocene to Mid Miocene fauna and the Recent fauna, which occur as interactions with global events. Secondly there is interaction with regional and local parameters that partitions these global patterns into local and regional patterns.

Xiphosurid behaviour as deduced from tracks of Middle Jurassic age, Cleveland Basin, Yorkshire

Mike Romano and Martin Whyte
Environmental and Geological Sciences, University of Sheffield, Dainton Building, Brookhill, Sheffield, UK

Traces attributed to a limulinid xiphosurid (arthropod) maker were first described from marine Middle Jurassic rocks (Scarborough Formation) of the Cleveland Basin, Yorkshire, by the authors in 1987. Since then, while investigating rocks of the Ravenscar Group for dinosaur tracks, a number of limulinid traces and trackways have been discovered in the non-marine units. The ichnofossils may be assigned to *Kouphichnium clevelandensis* n. isp. and *'Kouphichnium' rossendalensis*. The former clearly demonstrates the heteropody of the maker, and their occasional asymmetry indicates a slight rotation of the body relative to the direction of locomotion. The latter ichnospecies provides further evidence of the feeding behaviour of these Jurassic limulinids. The Saltwick Formation has generally been regarded as a coastal plain deposit, and the presence of limulinid tracks reinforces the suggestions of periodic marine influences and/or the fresh water tolerance of these essentially marine Mesozoic arthropods.

Uncovering the biogeographical history of the common scleractinian reef coral Acropora: The Anglo-French connection

Brian Rosen[1] and Carden Wallace[2]
[1]Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK **<B.Rosen@nhm.ac.uk>**
[2]Museum of Tropical Queensland, 78-102 Flinders Street, Townsville, Qld 4810, Australia **<Carden@mtq.qld.gov.au>**

Acropora (staghorn coral) occurs today throughout most of the tropical Indo-Pacific and Caribbean reef regions, and is the most abundant, widespread and species-rich reef coral genus, often in extensive mono-generic assemblages. With increasing concern about the stability, and even survival, of modern reef communities in the face of global and environmental change, it is relevant to ask how old this pattern is. The oldest known record of *Acropora* is from the late Palaeocene of Somalia, but by the mid-Eocene it is known from Europe and tropical America. There are no records yet from the Indo-Pacific until the late Oligocene. Its palaeontology has been very neglected, but Wallace's recent comprehensive revision and phylogeny now provides a timely framework to begin a reassessment. Remarkably, the collections of The Natural History Museum revealed an unexpected palaeonvironmental context for the early history of Acropora. The best preserved, oldest specimens come from mid-Eocene *non*-reefal, *non*-tropical (ca 50°N) deposits of southern England and northern France. Although the material consists of small broken pieces, preservation of skeletal detail is surprisingly good, allowing provisional allocation of specimens to various lineages in Wallace's phylogeny. In this talk we discuss the intra-generic affinities of this fossil material and preliminary thoughts on the biogeographical history of *Acropora*.

Wallace, C.C. 1999. *Staghorn Corals of the World; a revision of the genus Acropora*. CSIRO Press, Melbourne. 422 pp. Wilson, M.E.J. & Rosen, B.R., 1998. Implications of paucity of corals in the Paleogene of SE Asia: plate tectonics or Centre of Origin? In: Hall, R. and Holloway, J.D. (eds.). *Biogeography and Geological Evolution of SE Asia*. Backhuys Publishers, Leiden, The Netherlands, pp.165-195.

The preservation of woods in volcanic pyroclastic flows and surges and implications for the study of fossil plant assemblages from volcanic areas

Andrew C. Scott
Geology Department, Royal Holloway, University of London, Egham, Surrey, TW20 OEX, UK

Hot pyroclastic flows and surges from the Soufrière Hills Volcano, Montserrat, in 1997 entombed local vegetation. The hot ash charred the woods that comprised living, dead and rotted woods. Some of the woods remained buried in hot ashes for several months. Specimens were recovered from the 21st September flows from near Bramble Airport and were studied by scanning electron microscopy and by reflectance microscopy. All recovered specimens (up to 15 cm in diameter and 20 centimetres long) were charred throughout. Unlike charcoalified logs resulting from wildfires these tended to remain intact and not break into the characteristic cubic shapes. SEM studies show excellent anatomical preservation of the wood. Wood from trees which may have been living when hit by the hot ash show evidence of sudden rupturing of the wood. All the studied specimens were angiospermous. Reflectance values from the woods indicate a range of temperatures to which the woods were subjected, mainly in the range 200-340°C, possibly up to 450°C. A suite of charcoalified logs and twigs has also been studied from the North Island of New Zealand. Specimens were studied from the Taupo Ignimbrites (1.8Ka) and the Kaharoa pyroclastics (650Ka) (collected by Colin Wilson). The pyroclastic flows and surges incorporated vast quantities of vegetation (probably 1km^3) and most of what has survived to the present day is charred, uncharred vegetation having rotted away. The specimens included both angiosperms and conifers, and included logs and twigs ranging from 0.5-15 cms in diameter and up to 33 cms long. SEM shows excellent anatomical preservation of the woods. Reflectance data between sites indicates a wide variety of charring temperatures, from above 450°C to 225°C from 11km to 43km from the vent. These studies indicate that volcanic pyroclastic flows and surge deposits may preserve charcoalified plants that may yield data not only on the vegetation which was entombed but also yield data on the nature of the deposits themselves.

Acritarchs at the Cambro–Ordovician boundary: Biostratigraphy or ecophenotypism?

Thomas Servais[1], Michael Montenari[2] and Ludovic Stricanne[2]
[1]Paléontologie—Sciences de la Terre, UPRESA 8014 CNRS, Cité Scientifique SN5, F-59655 Villeneuve d'Ascq Cedex, France
[2]Institut und Museum für Geologie und Paläontologie, Eberhard-Karls-Universität, D-72076 Tübingen, Germany

The galeate acritarchs are an important constituent of Late Cambrian and Early Ordovician phytoplankton assemblages. New studies of well preserved and diversified assemblages of sandstones and shales in the basal Tremadoc (Early Ordovician) of the Hasi Rmel area in Algeria (type area of two galeate genera) has led to a better understanding of the variability of this plexus of morphotypes. The new investigation integrates statistical analyses of morphological parameters observed within the large populations, and tries to determine if palaeoenvironmental conditions could have influenced the morphology and the distribution of the individual morphotypes of the galeates.

Eleven classical morphological criteria have been used in the dataset. The results indicate that most of these morphological parameters show a continuous variability and that it is almost impossible to draw

a border between individual morphotypes, which are so far described in literature as separate species or genera.

The statistical analyses show that some of the parameters related to the processes, such as their length, their basal structure or their distal terminations, are probably the most important features in understanding the variability of the galeates. In addition, the results of the investigations may indicate that these parameters are possibly related to water depth.

The origin of massive downslope rudist/coral limestone bodies in the Upper Cretaceous of Central Tunisia: Giant olistoliths?

Peter W. Skelton[1], M. El Hédi Negra[2], Eulàlia Gili[3] and F. Xavier Valldeperas[3]
[1]Department of Earth Sciences, Open University, Milton Keynes MK7 6AA, UK
<P.W.Skelton@open.ac.uk>
[2]Université de Tunis II, Faculté des Sciences de Bizerte, Departement de Géologie, 7000 Bizerte, Tunisia
[3]Departament de Geologia, Universitat Autònoma de Barcelona, Edifici C, Bellaterra, 08193 Barcelona, Spain

The Merfeg Formation (Upper Campanian) of Central Tunisia, which crops out around the western periclinal termination of Jebel El Kébar, near Sidi Bouzid, comprises a curious mixture of facies. At its base are several discrete mounds of featureless micrite with rudist- and coral-rich units especially in their upper parts. They are separated laterally from one another by platform-derived megabreccias and conglomerates, and are overlain by pelagic limestones, within which are intercalated at least two more, somewhat thinner rudist/coral limestone units. This complex of facies is laterally equivalent to thicker basinal limestones of the Abiod Formation, exposed in other jebels. The massive bodies have previously been interpreted as *in situ* downslope mudmounds that became capped by rudist and coral formations, cemented, then surrounded by erosively emplaced debris flows, and finally buried in pelagic sediments. However, our detailed studies of rudist orientations imply variable and relatively high angles of bedding in the masses, with respect to the regional dip, that are unlikely to have been primary. Accordingly, we offer an alternative hypothesis that the masses were gigantic platform-derived olistoliths, emplaced along with the associated debris flow deposits. Whether the proposed catastrophic collapses of a neighbouring (unexposed) platform were triggered by tectonics or instability induced by sea-level fall remains uncertain.

Small Shelly Fossils from the Lower Cambrian of North-East Greenland

Christian Skovsted
Department of Earth Sciences, Uppsala University, Norbyvägen 22, SE-752 36, Uppsala, Sweden

Most studies on late Early Cambrian fossils from Laurentia are concerned with trilobites or brachiopods, and only a few Small Shelly faunas have been described. Ongoing investigation of Small Shelly Fossils from the Bastion and Ella Island formations of North-East Greenland offers new insights into the diversity of shelly fossils in the Lower Cambrian of Laurentia. The fauna from North-East Greenland can be closely compared with a recently described fauna from the Browns Pond Formation in the Taconic Allochthon of New York State. Weaker connections to the slightly younger Forteau Formation of

Labrador and western Newfoundland also exist, and a mid-Dyeran age for the North-East Greenland fauna is suggested. Greenland trilobite faunas appear to be useful for intercontinental correlation in the Lower Cambrian, but the good preservation of the North-East Greenland Small Shelly Fossils promises further to facilitate correlation. Faunal links with the early Botomian of Siberia and Australia are especially promising.

Arthropod trackways from the Lower Devonian of South Wales: A functional analysis of producers and their behaviour

A. Smith[1], S.J. Braddy[2], S.B. Marriott[3] and D.*E.G.* Briggs[2]
[1]Department of Geology, National University of Ireland, Galway, Galway, Ireland
[2]Department of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK
[3]School of Geography and Environmental Management, University of the West of England, Bristol, BS16 1QY, UK

Trace fossils are vital for providing data on the palaeoecology and behaviour of extinct arthropods, and tracking their conquest of the land. Lower Devonian red beds from Pant-y-Maes quarry in the Brecon Beacons of South Wales contain abundant arthropod trackways, assigned to two variants of *Diplichnites gouldi*. Probable producers were selected from contemporaneous body fossils and their hypothetical trackways simulated via computer modelling; body plan data (*e.g.*, size, leg lengths, spacing, and angle of swing) were derived from published reconstructions and new specimens. By varying gait parameters (*i.e.*, gait ratio, and opposite and successive phase differences), the most efficient, stable gait patterns were identified. Kampecarid and eoarthropleurid myriapods were thus identified as the producers. They employed an in-phase (swimming stroke-like) gait, rather than the most stable walking technique. This, combined with sedimentological evidence, and lateral displacement of some trackways (attributed to currents), indicate that these trackways were produced subaqueously. As similar trackways have been recorded from sub-aerial settings elsewhere, this indicates that kampecarid and eoarthropleurid myriapods adopted amphibious habits.

Rates of morphological change and heterochronic evolution in Cretaceous rudist bivalves revealed by Strontium isotope stratigraphy

Thomas Steuber
Ruhr-Universität, Institut für Geologie, Mineralogie und Geophysik, 44801 Bochum, Germany **<thomas.steuber@ruhr-uni-bochum.de>**

Strontium isotope stratigraphy of numerous localities of rudist-bearing formations in the region of the former Mediterranean Tethys has provided a reliable and precise stratigraphical frame for the evaluation of morphological change in hippuritid rudist bivalves during the Coniacian-Campanian. Phyletic size increase and peramorphic evolution involving hypermorphosis appears to be a common theme. A doubling of the length of the mantle margin occurred within 5 myr in two lineages which were studied in detail.

Strontium isotope stratigraphy has resulted in a considerable revision of the ranges of some of the species investigated. As the stratigraphy of Tethyan carbonate platforms frequently relies on the distribution of rudist bivalves, and the species investigated have frequent records in the region of the central-eastern Mediterranean Tethys, the history of many Late Cretaceous carbonate platforms must be re-evaluated.

Stratigraphy and biogeographic affinities of the Lower-Middle Ordovician conodonts of the Yangtze Platform, South China

Svend Stouge
Geological Survey of Denmark and Greenland (GEUS), Division of Stratigraphy, Thoravej 8, DK-2400 Copenhagen NV, Denmark

Results of taxonomic and biogeographic studies of conodonts from the Yangtze Platform of South China are presented. The investigated assemblages derive from the Daping Section ranging in age from early to mid Ordovician. The succession comprises six biozones, which can be correlated over wide areas. The taxonomic composition and stratigraphic distribution of the Lower Ordovician conodont assemblages show great similarities with shallow-water low-latitude faunas from SE Asia and Australia. During the "*evae*-transgression" there were close faunal affinities between the Yangtze platform deposits and the margin to slope deposits of North America and the Precordillera of Argentina, South America. Common species belong to the genera *Bergstroemognathus*, *Gothodus*, *Juanognathus*, *Oepikodus*, *Protoprioniodus* and *Tropodus*. From the mid Ordovician onwards increasingly stronger similarities (taxonomic affinities and stratigraphic ranges) developed between the South Chinese assemblages and the mid-high latitudinal Baltoscandian area, characterized by the genera *Baltoniodus*, *Microzarkodina*, *Scolopodus* and *Trapezognathus*. These trends are inferred to represent environmental gradients within a framework of hypothesized palaeoceanographic surface circulation patterns during the early to mid Ordovician.

The Silurian chelicerate *Offacolus:* a three-dimensional exploration

Mark D. Sutton[1], Derek *E.G.* Briggs[2], David J. Siveter[3] and Derek J. Siveter[4]
[1]Department of Earth Sciences, University of Oxford, UK
[2]Department of Earth Sciences, University of Bristol, UK
[3]Department of Geology, University of Leicester, UK
[4]University Museum, University of Oxford, UK

The small non-biomineralised arthropod *Offacolus kingi* is the most common body fossil of the Herefordshire (UK) Konservat-Lagerstätte, and is now identified firmly as a chelicerate. A recently published description is now supplemented by three-dimensional computer models obtained from serial grinding of specimens, providing a detailed understanding of external morphology. *Offacolus* possesses a deep prosoma with an anterior gape, and an opisthosoma that consists of a preabdomen with three articulating segments and a postabdomen of at least four fused segments. The postabdomen bears a mobile spine with a distal articulation and bifurcation. *Offacolus* has a prosomal appendage array (including chelicerae) closely comparable to that of *Limulus*, but supplemented by a set of robust and setose outer rami on appendages II-V that lack homologues in other arthropods. Opisthosomal appendages are flap-like and broadly comparable to the book-gills of *Limulus*. Cladistic analyses place *Offacolus* basally within the Chelicerata, as a sister taxon to the eurypterids and extant chelicerates, but more derived than the Devonian *Weinbergina*.

Did bryozoans miss the Cambrian explosion?

Paul Taylor[1] and Andrej Ernst[2]
[1]Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK **<P.Taylor@nhm.ac.uk>**
[2]Institut für Geowissenschaften der Universität zu Kiel, Olshausenstr. 40, D-24118 Kiel, Germany **<ae@gpi.uni-kiel.de>**

The oldest unequivocal bryozoans are of Tremadoc age. The absence of bryozoans from the Cambrian fossil record makes them unusual among routinely fossilized phyla. Did bryozoans miss the Cambrian Explosion and originate after most other metazoan phyla, or were they present in the Cambrian but not represented in the fossil record? Phylogenetic analysis could solve this problem. However, neither anatomical nor sequence-based phylogenies have produced a clear-cut picture of the relationships between bryozoans and other phyla. Catastrophic metamorphosis of the bryozoan larva, along with reduction in individual complexity correlating with a colonial lifestyle, are both factors inhibiting anatomical analysis of interphyletic relationships, while sequence data are still very sparse. The fossil record reveals a rapid appearance of higher taxa in the Early Ordovician. These include borings produced by soft-bodied ctenostome bryozoans, raising the possibility of non-boring ctenostomes being present in the Cambrian. Unfortunately, none have yet been identified from the Cambrian Lagerstätten, nor is there much prospect of finding bioimmured ctenostomes given the paucity of skeletonized encrusters in the Cambrian. A newly compiled generic diversity curve for Ordovician bryozoans shows an approximately exponential pattern, with the possibility of a low diversity initial phase—'macroevolutionary lag'—extending back into the Cambrian.

Faunal turnover in the Caribbean Plio-Pleistocene: Molluscan food webs implicate plummeting nutrient supply

Jonathan Todd[1], Jeremy Jackson[2], Kenneth Johnson[2], Helena Fortunato[3], Antoine Heitz[4] and Peter Jung[4]
[1]Department of Palaeontology, The Natural History Museum, London SW7 5BD, UK **<J.Todd@nhm.ac.uk>**
[2]Geosciences Research Division, Scripps Institution of Oceanography, La Jolla 92093-0244, USA
[3]Smithsonian Tropical Research Institute, Box 2072, Balboa, Panama
[4]Naturhistorisches Museum Basel, Basel CH-4001, Switzerland

The major regional molluscan faunal turnover in the Plio–Pleistocene of the Tropical Western Atlantic has been attributed to drops in temperature or primary productivity, but without considering how taxa with widely differing ecologies might vary in relative susceptibilities to extinction or speciation. To discriminate between the two turnover hypotheses we compiled molluscan life-habits and trophic composition data from 463 quantitative collections newly made by the Panama Paleontology Project. These bulk-sampled collections extend through 12myr of dominantly shallow shelf deposition from the southwestern Caribbean, including comparable, time-averaged, dredged Recent collections. Analysis of bivalve feeding and life habits and gastropod feeding show shelf ecosystems to have altered markedly in trophic structure since the Late Pliocene. Massive cross-habitat declines in abundance, but not diversity, of predatory snails and suspension-feeding clams are consistent with a macroecological

transition from heterotrophic and nutrient-rich to more phototrophic and nutrient-poor ecosystems in which reef-dwellers (*e.g.*, cowries and worm-snails) became common. In contrast, all other ecological life-habits remained remarkably stable. These food-web changes provide the strongest support for the hypothesis that declining regional nutrient-supply produced through oceanographic changes associated with Isthmian uplift had an increasing impact on regional macroecology, culminating in a faunal turnover at 2Ma. Although the timing of turnover and origin of the 'modern Caribbean fauna' is similar, the detailed diversity dynamics of clams and snails, and reef corals are distinct.

Early Triassic ophiuroids: their taphonomy, palaeoecology and distribution

Richard J. Twitchett[1] and Joshua M. Feinberg[2]
[1]Department Earth Sciences, University of Bristol, Queens Road, Bristol, BS8 1RJ, UK
<**R.J.Twitchett@bristol.ac.uk**>
[2]Department of Earth and Planetary Science, University of California, Berkeley, CA 94720, USA
<**jmfeinbe@uclink.berkeley.edu**>

Recent fieldwork has revealed that Lower Triassic sediments in eastern Nevada and the Italian Dolomites contain a rich accumulation of ophiuroid body fossils, disarticulated ossicles and trace fossils, including the first Triassic ophiuroids reported from North America.

Resting traces are almost exclusively confined to fine sandstones in marine red bed intervals that were deposited in very shallow-water settings above normal wave base. Usually, they are associated with a low diversity, shallow penetrating, deposit-feeding community. Palaeoenvironmental considerations (shallow water, tropical palaeolatitude, greenhouse climate) suggest that these ophiuroids could withstand high temperatures and fluctuating oxygen and salinity levels.

Fully articulated body fossils occur in silty limestones and calcareous fine sandstones, which were rapidly deposited below wave base during storm events. The animals would have been engulfed by a storm, swept downslope and buried. The ophiuroids are all small (body disc diameters of 2-5 mm). Thus, in common with other marine taxa, Early Triassic ophiuroids exhibit very small body size (the Lilliput effect).

Disarticulated ossicles occur in bioclastic storm beds throughout the carbonate-siliciclastic, shallow-marine settings of the Werfen Formation (Italy) and the Thaynes Formation (Nevada). Ophiuroids were present from the Griesbachian (*isarcica* Zone) and were a significant component of the epifaunal community from the Dienerian.

New arthropods and problematica from the Ordovician of Morocco

Peter Van Roy
Research Unit Palaeontology, Department of Geology and Soil Sciences, Ghent University, Krijgslaan 281 / S8, B-9000 Ghent, Belgium <**peter.vanroy@rug.ac.be**>

The shallow marine coarse clastics of the Upper Ordovician Upper Ktaoua Formation in south-eastern Morocco (Erfoud-Rissani-Alnif-Zagora area) have recently been shown to contain fossils of soft-bodied and poorly sclerotized organisms in association with more classical shelly elements and trace fossils. Preservation of soft tissues in the Moroccan sites is strikingly similar to that of some of the more resistant "frond-like" Ediacaran organisms. Most of the Moroccan fossils do not seem to have been transported before burial.

Represented by over fifty specimens from three sites, cheloniellids belonging to Duslia are the most numerous among the newly discovered arthropods. This genus was hitherto only known from the Czech Republic. Some Moroccan specimens preserve the gut as a fine sedimentary infill. Other arthropod fossils include rare fragments of possible aglaspidid and eurypterid affinity and, from the Zagora area, a single complete specimen of a possible basal chelicerate.

With several hundreds of specimens collected from four sites, soft-bodied paropsonemid eldonioids are the most abundant fossils. The *in situ* preservation of these otherwise rare problematica suggests a benthic mode of life for these animals.

Co-occurring at three sites with the paropsonemids are discoidal fossils of uncertain affinities, showing similarities to both *Protolyellia* and *Ediacaria booleyi*.

Palaeozoic Archidesmida (Diplopoda: Helminthomorpha) from Scotland: The Most Ancient Millipedes Known

Heather M. Wilson[1] and Lyall I. Anderson[2]
[1]Department of Entomology, 4112 Plant Sciences Building, University of Maryland, College Park, MD 20742, USA **<wilsonhm@wam.umd.edu>**
[2]Department of Geology and Zoology, National Museums of Scotland, Chambers Street, Edinburgh, EH1 1JF, UK **<l.anderson@nms.ac.uk>**

The first archidesmid millipede, *Archidesmus macnicoli*, was described by B.N. Peach in 1882 from the Lower Devonian of Tayside, Scotland. Peach demonstrated that *A. macnicoli* was a flat-backed millipede with tuberculate ornament and paranota, and suggested an affinity with extant Polydesmida. Subsequent to Peach's work, knowledge of archidesmid morphology remained unchanged. New specimens recently collected from the Tillywhandland Quarry SSSI near Forfar preserve previously unknown details of the sternites and gonopods. The sternites are broad with laterally set coxal sockets and paramedian pores. Recognition of the form of the sternites and gonopods in *A. macnicoli* provides evidence that some Cowie Formation millipedes are also archidesmids. The Cowie Formation, part of the Stonehaven Group, was originally thought to be Upper Silurian (Prídolí) in age. However, recent work on palynological assemblages has indicated a mid Silurian age (late Wenlock to early Ludlow) (Marshall 1991; Wellman 1993), making the Stonehaven archidesmid millipedes the oldest known terrestrial arthropods. Although archidesmids represent the most ancient millipedes known, they are by no means the most primitive, having a relatively derived body plan. Archidesmids may have affinities with the Eugnatha (= Nematophora + Merocheta + Juliformia) and, based on the ring structure and sternal morphology, it is suggested here that Archidesmida may be a sister group to the spiny Carboniferous Euphoberiida.

Cruciplacolithus neohelis and the K/T Boundary

Jeremy R. Young[1], Ian Probert[2], Jacqueline Fresnel[2], Alberto Saez[1,3] and Linda Medlin[3]

[1]Palaeontology Department, The Natural History Museum, London SW7 5BD, UK
[2]Lab. Biologie and Biotechnologies Marines, Université de Caen, France
[3]Alfred Wegener Institute, Bremerhaven, Germany

A perplexing feature of the coccolithophore record across the K/T boundary is the occurrence just above the boundary of "incoming" species not known from the Maastrichtian. Perhaps the most cryptic of these is *Cruciplacolithus primus* which subsequently gives rise to a diverse set of genera, constituting the families Coccolithaceae and Calcidiscaceae. *Cruciplacolithus* itself is characterised by coccoliths with an axial cross in the central area and is generally regarded as disappearing from the fossil record in the Late Eocene. There is, however, one extant species which has often on grounds of gross coccolith morphology been assigned to *Cruciplacolithus–C. neohelis*. This is a small, poorly known, neritic coccolithophore with little or no fossil record. We have recently carried out a multi-species analysis of the molecular genetics of coccolithophores. One intriguing result of this was that *C. neohelis* did not prove to be a recently derived taxon but rather shows a deep divergence from its sister taxon *Coccolithus pelagicus*. Molecular clock estimates place this divergence at ca 60-80Ma, strongly favouring the alternative hypothesis that *C. neohelis* is a genuine *Cruciplacolithus* and may be representative of the ancestral Coccolithaceae. In this case a possible explanation for the cryptic origin of *Cruciplacolithus* in the earliest Danian is that it migrated out of neritic environments, following elimination of the oceanic plankton. Consideration of the ecology of the other "survivor" and "incoming" taxa suggests that this may have been a common pattern.

Abstracts of poster presentations

Compiled and edited by David A.T. Harper

Holocene molluscs and climatic variability in Argentina (South America)

Marina L. Aguirre
Departamento Paleontología Invertebrados, Museo de Ciencias Naturales, Paseo del Bosque, 1900 La Plata, Argentina **<maguirre@museo.fcnym.unlp.edu.ar>**

In Argentina, Holocene Interglacial deposits (9-1.4 Ka) have provided contradictory evidence for the occurrence of the Climatic Optimum (Hypsithermal): for example, it was minimized or absent over the entire littoral zone (microfossils), well documented in the Bonaerensian coastal area (molluscs) or absent in the Patagonian littoral zone (molluscs). However, being a world-wide event, at least some influence on benthic molluscan associations should be expected.

An updated review of molluscan assemblages from 21 Holocene coastal deposits, preserved in the Buenos Aires, Río Negro, Chubut, Santa Cruz and Tierra del Fuego areas, has allowed a reinterpretation of climatic variability since the last transgressive maximum, as shown by compositional, diversity and distributional changes in molluscan assemblages through time.

All 111 taxa (61 gastropods, 50 bivalves), from four Bonaerensian (8-1.4 Ka) and 17 Patagonian (9-2 Ka) areas, conform to four ecologic groups (cosmopolitan, warm-temperate, cool-temperate, exclusive to cold water masses) by analogy with their modern distributions. Their occurrence and relative abundance within assemblages relate to the age and latitudinal position of the deposits. Additionally, qualitative and quantitative comparisons with modern molluscan associations show a greater abundance of warm-water elements and suggest a higher SST during the mid-Holocene than at present. There is, however, a decreasing trend southwards: there are more warm (35%) and less common (6%) cold-water taxa ca. 7.5-4.5 Ka (Bonaerensian) and more warm-temperate (47%) and less common (33%) cold-water species ca. 9-6 Ka (Patagonia). A combination of the following may have been responsible for relative displacements of these fossil molluscan assemblages when compared with those of the present day: (1) A southward displacement of the mid-Holocene (8-4.5 Ka) palaeoceanographical pattern. (2) A stronger influence from the Brazilian warm-water current than at present. (3) Shifts of the Subtropical Convergence and of the South Atlantic Anticyclonic Centre.

A New Theory of Spatial Development in *Homo sapiens sapiens* with implications for an Environmental Evolution Trigger for Humans

J. Gail Armstrong-Hall
Wayne State University affiliation, Troy Public Schools, 2503 Coral, Troy, Mi. 48085, USA **<Paleo20@hotmail.com>**

Analysis using a Manova on state-wide standardized science-testing results yielded surprising and significant data. This information led to the formulation of Armstrong-Hall's Theory of Parallel Opposing Spatial Skill Development in *Homo sapiens sapiens*, a modification of the Hunter-Gatherer Theory of Spatial Sex Differences; where eight spatial abilities (four female and four male) are outlined. Abstract thought may be directly linked with the process of hunting. Suggestions for research with an aboriginal tribe may yield the key to understanding the leap from primitive to modern man.

Freshwater molluscs and biostratigraphy of the rift deposits to the north of Lake Edward (Congo)

Baharak Bashar, Achiel Gautier and Dirk Van Damme
Research Unit Palaeontology, Department of Geology and Soil Sciences, Ghent University, Krijgslaan 281 / S8, B-9000 Ghent, Belgium
<fatemehbaharak.bashar@rug.ac.be> and **<dirkvandamme2001@yahoo.com>**

This study concerns the fossil freshwater molluscs and the biostratigraphy of the rift deposits to the north of Lake Edward, situated in the northern part of the Western Rift Valley, on the Congolese side. The investigated material was collected by de Heinzelin in 1958, from outcrops in the Upper Semliki region, and has remained unstudied since. This material derives from lacustrine deposits (the Lusso Beds), dating as Pliocene. The fossils are concentrated in peloidic ironstone beds, characteristic for the Lusso Beds. The current research aims to compare the recently established biostratigraphy for the area with previous work, taking into account the latest taxonomic revisions of the malacofauna of this region. This study resulted in an adjustment of the stratigraphical ranges of some species, possibly caused by regional differences in the composition of the molluscan assemblages. Biozonal comparisons indicate that at the end of the deposition of the Lusso Beds an impoverishment of the endemic molluscan fauna took place. This leads to the conclusion that the previously established biostratigraphies are still valid, but are less detailed than the biozonation incorporated in this study.

The Frasnian–Famennian mass extinction from the Holy Cross Mountains of Poland

Dave Bond
School of Earth Sciences, University of Leeds, Leeds, LS2 9JT, UK
<d.bond@earth.leeds.ac.uk>

The Frasnian-Famennian boundary marks one of five Phanerozoic mass extinctions. Proposed mechanisms include sea-level and climate changes, volcanism and bolide impact. Transgressive pulses and warm oceans are considered to have promoted two widespread anoxic "Kellwasser Events" during the Frasnian, typified by black shales and limestones in Germany, the "Kellwasser Horizons". The equivalent beds have been investigated in the Holy Cross Mountains of Poland.

This region was characterised by two basins: the Lysogory (north) and Checiny Zbrza (south), separated by the Kielce Swell. A continuous F-F sequence is exposed in Kowala Quarry (southern basin). This is represented by interbedded shales, micrites and calcarenites, with several distinct facies. Nodular horizons and colour variations support changing oxygen conditions. Two distinctive radiolarian-rich cherts occur at the F-F boundary. The Frasnian contains a varied fauna which becomes drastically reduced to an impoverished *Orbiculoidea* assemblage in the earliest Famennian before recovering. Kellwasser equivalents are identified as are other oxygen deficient periods, notably an Annulata Shale equivalent.

Biotic response to Mid-Cretaceous palaeoceanographic events : insights from the Vigla pelagic succession of the Ionian zone in Greece

Taniel Danelian, François Baudin, Silvia Gardin and Catherine Beltran
Univ. P. and M. Curie (Paris 6), CNRS-FRE2400, Paléontologie and Stratigraphie, C. 104, T. 15-25, E4, 4, place Jussieu, 75252 Paris Cedex 05, France

The response of the marine biosphere to Oceanic Anoxic Events (OAE) is of much interest to palaeobiology. Preliminary results on calcareous and siliceous microfossils and organic geochemistry are discussed for the 'upper siliceous zone' of the Lower Cretaceous pelagic carbonates of the Ionian zone in Greece, a Jurassic-Cretaceous tropical trough starved of any major siliciclastic or platform carbonate input. This siliceous interval is characterized by the abundance of radiolarites that seem to have accumulated during the Aptian-Albian, an interval characterized by several widely recognized OAEs, possibly as the result of enhanced productivity driven by abnormally high volcanism and an intensified greenhouse climate. Towards the base of these radiolarites a 5 m-thick organic-matter-rich horizon (up to 6.6% of Total Organic Carbon) has been recognized, which we believe is coeval with the Lower Aptian OAE1a. Nannofossils observed in marls at this horizon constitute an oligospecific assemblage, characterized by abundant and 'giant' nannoliths, and the total absence of any *Nannoconus* morphotypes. A radiolarian assemblage yielded from a chert within this horizon is suggestive of an early Aptian age, but curiously it is characterized by high diversity and displays no particular sign of biological distress.

A new crustacean from the Pragian Rhynie Chert, Rhynie, Aberdeenshire, Scotland

Steve Fayers and Nigel H. Trewin
Rhynie Research Group, Department of Geology and Petroleum Geology, Meston Building, University of Aberdeen, Aberdeen, Scotland, AB24 3UE, UK

A new crustacean is described from the Rhynie Chert. Recently the faunal list of this famous deposit has increased significantly, notably following discoveries in the Windyfield Chert. This discovery, however, is the first unequivocal addition to the crustacean element of the fauna since the discovery of the enigmatic lipostracan *Lepidocaris rhyniensis*.

The material comprises 36 almost complete individuals plus fragmentary remains. The head is usually present but is frequently detached from the body, and damage to the anterior of the thorax suggests that most specimens are exuvae. The largest specimen has a length of 8mm. The head region appears domed with a labrum and a pair of robust mandibles and long biramous antennae. A few specimens exhibit what may be a detached and poorly preserved univalve carapace. The trunk is long and multi-segmented, both thorax and abdomen possessing similar ring-like somites. The thorax comprises six segments with long foliaceous appendages. The abdomen possesses 10-12 foliaceous appendages, one per somite, and up to 28 posterior apodous segments. The tail comprises a telson with two caudal furcae.

The new animal is a branchiopod, possibly belonging in the subclass Calmanostraca. This new crustacean is associated with *Lepidocaris rhyniensis*, charophytes and probable cyanobacteria within a 'mulm'-like chert texture, indicative of deposition in a subaqueous environment, most probably a temporary pool.

Tail of two trilobites—The importance of considering locality information in species recognition

William Fone
Staffordshire University, College Road, Stoke on Trent, ST4 2DE and The Open University in the West Midlands, 66-68 High Street, Harborne, Birmingham B17 9NB, UK

The provenance of fossil specimens is important in establishing stratigraphical, palaeoenvironmental and palaeobiological contexts. Palaeogeography is another context that might be established if precise locality details are known. In the past the precise contexts of specimens have not always been established and the robustness of any subsequent scientific analysis using such material is reduced as a consequence. Statistical analyses of encrinurid tubercle patterns (Tripp *et al.*, 1977, *Palaeontology* **20**, pp. 847-867) have been re-examined using fresh samples. The experiment considered local palaeogeography as a significant factor. The results bring into question some of the inferences drawn from the original study and highlight the need to preserve, where possible, the locations of figured material.

A *Tetraxylopteris*-like Progymnosperm from the Devonian of Venezuela

Susan Hammond
Department of Earth Sciences, Cardiff University, PO Box 914, Cardiff CF10 3YE, UK **<hammonds2@cf.ac.uk>**

Coalified compressions of *Tetraxylopteris*-like progymnosperms were collected from the Middle or lowermost Upper Devonian Campo Chico Formation, Sierra de Perijá, Venezuela. One exceptionally good specimen with three-dimensional preservation of sterile morphology clearly has three branch (axis) orders, and ultimate appendages consisting of small and several-times dichotomous branch systems. Further specimens yielded information on a larger order of axis to which the first order branches are attached (probably the stem), and others information about the diverse nature of ultimate appendages—both their position and their morphology. Ultimate appendages are helically arranged but exact positioning is unclear, and they vary from being three-dimensional to apparently planar. All three branch orders (with possible exception of the first-order) arise multiply from nodes. This plant may belong to either *Tetraxylopteris* Beck or *Proteokalon* Scheckler and Banks because much of its sterile morphology is identical/similar to both. The new plant has occasionally dichotomising branches like *Proteokalon*, and probable three-dimensional ultimate appendages like *Tetraxylopteris*. Future research into fertile morphology may finally clarify the generic affinity and/or determine whether *Tetraxylopteris* and *Proteokalon* are synonymous.

Some Scottish Lower Carboniferous Trilobites

John Hampton
7 Harpenside Crescent, Dirleton, North Berwick, East Lothian, EH39 5DW, UK

Trilobite faunas are not well developed in the Scottish Carboniferous and where they do occur are restricted to a very small number of genera and species. The Neilson Shell Bed is an important stratigraphical marker horizon in the Scottish Lower Carboniferous (Brigantian; P2) allowing precise correlation over the entire Midland Valley. It contains a small trilobite fauna entirely dominated by *Paladin mucronatus* (M'Coy, 1844). *Paladin cuspidatus* (Reed, 1943) also occurs, but other genera are restricted to extremely rare examples of ?*Brachymetopus* and ?*Archegonus* species. The presentation illustrates these components of the fauna from several Midland Valley Neilson Shell Bed localities and shows the typically very fragmentary nature of the trilobite fossils from this horizon in general.

A review of the Bathonian-Callovian Rhynchonellida (Brachiopoda) from the Coal Mine succession of Northern Sinai

Adel A.A. Hegab
Department of Geology, Faculty of Science, Assiut University, Assiut, Egypt

The rhynchonellids from the Bathonian-Callovian coal mine succession of Gebel El-Maghara are revised. Among them, there are large, wide and strongly costate Rhynchonellida derived from reddish yellow shales and claystones. These brachiopods belong to a new genus which was previously included by the author in *Rhynchonella masajidensis* without description. Feldman described serial sections and published photographs of similar material from Gebel El-Maghara in 1991 and placed them in Cooper's Pycnoria. The descriptions and illustrations of Feldman are not identical with those of Cooper neither in their internal structures nor diagnostic characters. Feldman's specimens are removed from *Pycnoria* and assigned to a new genus. This study establishes the diagnostic characters of the new genus as well as for *Pycnoria magna* in order to compare them and correct their systematic position within the northern Sinai development of the Ethiopian faunal realm.

Taphonomical observations of Upper Miocene mammal bones from Kerassia (Euboea Island, Greece)

George Iliopoulos
Department of Geology, University of Leicester, Leicester, UK **<gi6@le.ac.uk>**

The taphonomic investigation of Upper Miocene (MN 11-12) fossil mammal bones from Kerassia was undertaken on material from seven different sites near Kerassia. These sites consist of roadside cuttings (K1 to K7) where at least two fossiliferous horizons occur. The taphonomical aspects highlighted here are the biogeochemical and histological alterations of the bones.

Geochemical analytical techniques (XRD, ICP, Electron Microprobe) were utilized to unravel the chemical composition of the bones, and SEM plus optical microscopy were used to observe thin sections of bone. Correlations and comparisons were made by using bone material from other Upper Miocene localities of Greece, as well as Recent bone. Hydroxyapatite ($Ca_{10}(PO_4)_6(OH)_2$) is the observed dominant mineral phase of the bone with calcitic infills in most bone cavities. REEs show different patterns from the two horizons, indicating that they underwent different depositional environments.

The histology of the bone is generally good. Microcracks in the bones with calcitic infills can be ascribed either to pre-burial weathering or to post-burial compaction, or to shrinking of the bone post-preparation. Extensive damage of the bone tissue is caused by microbial focal destruction (most probably by bacteria) that can be seen around the perimeter of the bones, around the marrow cavity and as randomly scattered foci.

Reconstructing and interpreting 3-dimensional structures associated with dinosaur footprint formation from tracks from the Middle Jurassic of Yorkshire

Simon Jackson
Environmental and Geological Sciences, University of Sheffield, Dainton Building, Brookhill, Sheffield, UK **<glp00sjj@sheffield.ac.uk>**

There is a multitude of dinosaur tracks exposed in the Middle Jurassic strata along the Yorkshire coast, reflecting their diversity at this time. Because skeletal remains are very rare from this time/area, the dinosaur fauna has been neglected, until recently.

Many of the Yorkshire tracks are transmitted tracks, and the true track surface is concealed within the fossil itself. Research is presently aimed at understanding this (sub-surface) deformation within the track and how the track morphology varies with depth throughout the track. This study uses vertical sectioning of tracks to reveal the complex 3-dimensional nature of the track and is currently using computer software to model some of these structures, among other methods. The reconstructions of these 3-dimensional phenomena offer important insights into footprint formation and subsequent preservation.

Atmospheric Carbon Dioxide levels and Cenozoic mammalian community structure

Christine M. Janis
Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA **<Christine_Janis@Brown.edu>**

The community structure of herbivorous mammals, including species aspects such as body mass, diet (*e.g.*, browser *vs.* grazer), and digestive fermentation system (hindgut *vs.* foregut) is highly sensitive to the vegetational habitat. The vegetation, in turn, is determined by environmental factors such as temperature, precipitation, and seasonality. Thus present-day mammalian communities are good indicators of environmental conditions. Past communities nonanalogous with any today may contain information about nonanalogous past environmental conditions, possibly indicative of higher levels of atmospheric CO_2. High levels of CO_2 result in high levels of plant productivity, but with lower levels of plant quality (nitrogen/carbon ratio). Abundant but low quality vegetation (high CO_2 regime) would favour hindgut fermenters, whereas the converse would favour foregut fermenters. The change in faunal dominance from hindgut to foregut fermenters in the mid/late Eocene, long attributed to competition, may instead be related to the significant drop in atmospheric CO_2 at that time. Secondly, while controversy remains about early Miocene levels of CO_2, the very large numbers of browsers in individual faunas, up to twice as many as in comparable habitats (woodland or savanna) today, suggests a level of plant productivity unmatched today, possibly reflecting higher levels of atmospheric CO_2.

Late Ordovician trilobites on the brink of extinction

Kathleen L.D. Keefe
Division of Earth Sciences, University of Glasgow, Gregory Building, Lilybank Gardens, Glasgow, G12 8QQ, Scotland, UK **<kathykee@earthsci.gla.ac.uk>**

The Rawtheyan faunas of the Girvan district, southwest Scotland, including those of the famous Lady Burn Starfish Beds, provide the most complete census of trilobites from the Laurentian margin immediately prior to the end-Ordovician extinction event. They include 40 genera whereas only five are known from the succeeding Hirnantian Stage at Girvan. An online database including type and figured specimens in the Hunterian Museum, Glasgow, is being created and the fauna analyzed in terms of the palaeogeographical history of its components. The trinucleids are a microcosm of the diverse origins of the fauna linked to the closure of the Iapetus Ocean. *Cryptolithus praeteritus* was one of the last members of a Laurentian lineage. *Tretaspis persulcatus* was derived from an earlier species at Girvan whereas *T. sortita* is a widespread species known also from Wales and Norway and had its origins either in Avalonia or Baltica. *Nankinolithus granulatus* was a deep-water immigrant originating on the margins of higher latitude plates. This mixture of endemic and immigrant taxa typifies the Upper Drummuck trilobite faunas. No trinucleids survived into the Hirnantian at Girvan although a few poorly preserved specimens of *Cryptolithus* and *Tretaspis* are known from that stage elsewhere.

Palynological contributions to the stratigraphy and palaeoecology of the Lower and lower Upper Cretaceous rocks of Egypt

Magdy S. Mahmoud
Geology Department, Faculty of Science, Assiut University, Assiut P.O. Box 71516, Egypt **<magdysm@yahoo.com>** or **<magdysm@aun.eun.eg>**

Much palynological work has been published on the Cretaceous rocks of Egypt. An overview of the most interesting stratigraphical and palaeoecological knowledge that has been achieved from palynomorphs is presented. In the last few years the author in collaboration with other colleagues has erected some new palynomorph taxa, from central Egypt, of considerable stratigraphic potential. Based on the palynological data the geological settings of certain rock units are revised for this central region of Egypt. A very recent sample set from the area is discussed together with some interesting geological interpretations.

The World's oldest melanosclerites and foraminiferal linings, from the Lower Cambrian Lontova Clay, Estonia

D. McIlroy[1] and T. Winchester Seeto[2]
[1]Department of Earth Sciences, Liverpool University, Brownlow Street, Liverpool, L69 3GP, UK
[2]Centre for Ecostratigraphy and Palaeobiology, Department of Earth and Planetary Sciences, Macquarie University, N.S.W. 2109, Australia

The Lontova Clay is a smectite-rich claystone, which has undergone little diagenesis, due to its position on the margin of the stable Siberian craton. The claystone is rich in the fossil agglutinated foraminiferans *Platysolenites* and *Spirosolenites*, with exquisite preservation of foraminiferal tests,

including the juvenile (prolocular) regions, which are otherwise unknown (McIlroy *et al.* 1994, Lipps and Rozanov 1996, McIlroy *et al.* 2001).

Melanosclerites are organic microfossils of uncertain affinity, first identified by Alfred Eisenack, and were previously only known from palynological residues ranging from the Ordovician-Devonian. The occurrence of melanosclerites in the Lontova Clay extends their lower range from the Ordovician to the sub-trilobitic lower Cambrian and includes *Semenola semen* Schallreuter, 1981, and species of *Melanosteus* Eisenack, 1942 and possibly *Melanoclava* Eisenack, 1942.

While agglutinated Foraminifera are known from the Precambrian–Cambrian transition, their tests are delicate and not commonly recovered from acid-digested samples. The organic test-linings found in the Lontova Clay allow identification to generic level and include *Saccammina*, *Psammosphaera* and a small, broken tubular form (?*Bathysiphon*), which supplements the previously described *Platysolenites* spp., *Spirosolenites spiralis* and *Psammosphaera* sp. which are known from their agglutinated tests.

Terrestrial trace fossils from the Lower Old Red Sandstone (Lower Devonian) of southwest Wales

Lance B. Morrissey and Simon J. Braddy
Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ, UK

While diverse terrestrial ichnofaunas are well known from the Lower Devonian of the Midland Valley of Scotland, elsewhere in the UK the record is less complete. A new assemblage of terrestrial trace fossils is described from the Lower Old Red Sandstone of Pembrokeshire, southwest Wales, preserved mainly in fine-grained fluvial facies (channel margin and overbank sediments, deposited by ephemeral streams within a semi-arid environment), and thin tuffaceous horizons. The ichnofauna is dominated by an extensive, but low diversity *Beaconites ichnocoenosis*, comprised of the meniscate backfilled burrow *Beaconites barretti*. The concentration of these burrows (up to thirty per square metre) shows a multimodal size distribution, representing periodic colonisation events (probably in response to seasonal desiccation) of subaerially exposed (partly indurated) sediments, by a population of amphibious eoarthropleurid myriapods, pentrating to the level of the water table in order to aestivate and/or moult. Arthropod trackways also characterise an active, gregarious arthropod epifauna of arachnids (*Palaeohelcura*; first Welsh record) and myriapods (two forms of *Diplichnites* up to 16 cm wide) and *Diplopodichnus*. Additional ichnotaxa include arthropod foraging and resting traces [*Cruzianna*, *Rusophycus*, 'scratch arrays' (cf. *Stiallia*), and *Selenichnites*], and worm burrows (*Cochlichnus*, and *Palaeophycus*).

Acritarch and Prasinophyte algal biostratigraphy of the type Ludlow Series, Silurian

Gary L. Mullins, Ruth E. Richards, Richard J. Aldridge and David J. Siveter
Department of Geology, University of Leicester, University Road, Leicester LE1 7RH, UK

Two high-resolution biostratigraphical schemes based on the acritarchs and prasinophyte algae (microphytoplankton) recovered from the type Ludlow Series, Silurian, Ludlow, Shropshire are presented. Samples were collected generally at 1 m intervals, with closer spacing across formation and series boundaries. Initial results have allowed the identification of six biozones. Four biozones are

based on the first appearance of the acritarchs *Ammonidium ludloviense*, *Gorgonisphaeridium*? *listeri listeri*, *Leoniella vilis* and *Triangulina sanpetrensis*. Two biozones are based on the first appearance of prasinophyte algae *Glyptosphaera helterskelter* and *Cymatiosphaera mortimerensis*. Work in progress on samples from the Lower-Upper Bringewood and Lower-Upper Whitcliffe formations, middle and upper Ludlow Series, of the type area will further enhance these biostratigraphical schemes.

Our high resolution study will provide a firm basis for accurate comparison of the Ludlow type area with contemporary sections elsewhere. Our data also have great potential for determining palaeoenvironmental fluctuations at a much finer scale than previously possible, and for testing evolutionary and climatic models. In addition, collaboration with Ken Dorning, Alain Le Hérissé, Paul Hill, Stewart Molyneux, Paul Swire and Jane Washington-Evans will provide information on the biostratigraphy, palaeoecology and evolutionary history of acritarchs and prasinophyte algae in the Wenlock Series of the Wenlock type area, Much Wenlock, Shropshire.

A Cracoean Reef fauna from southwest Ireland

John Murray, George D. Sevastopulo and Patrick N. Wyse Jackson
Department of Geology, Trinity College, Dublin 2, Ireland **<murray2@tcd.ie>**

Cracoean Reefs developed during the mid to late Viséan (late Holkerian to early Brigantian) around the margins of the Shannon Basin in southwest Ireland. The sedimentology of these particular carbonate mudbanks has been largely neglected in the literature and their fauna, which is quite prolific in places, has not been illustrated before. Specimens have been collected from one particular reef 'knoll' which is well exposed at Oyster Hall, c. 6.5km east from the village of Fenit in County Kerry. The lithology is quite variable; however it is composed predominantly of massive micrite, generally lacking any sign of a supporting or baffling framework.

The biota is dominated by crinoids, brachiopods and bryozoans. Brachiopods are commonly articulated. Productoid forms are particularly abundant and may even have delicate spines preserved. Other forms include reticularioids, spiriferoids and rhynchonellides. Fenestellids comprise the bulk of the bryozoan fauna, however pinnate forms such as *Baculopora megastoma* and *Penniretepora elegans* also occur. Several corals have been recovered including *Siphonodendron* sp. and *Cladochonus* sp. Non suspension feeding members of the community include the gastropod *Bellerophon* sp., the nautiloid Orthoceras sp. and occasional trilobites. *Gnathodus bilineatus* and *G. girtyi* dominate conodont faunas, confirming an Asbian age for the assemblage.

Eemian bivalve and barnacle taphofacies from Northern Russia

Jan Kresten Nielsen and Svend Funder
Geological Museum, University of Copenhagen, Øster Voldgade 5-7, DK-1350 Copenhagen K, Denmark **<jankn@savik.geomus.ku.dk>**

Marine Eemian sediments along the Pyoza River in the Arkhangelsk region (northern Russia) constitute a shallowing-upward succession from offshore to foreshore/shoreface and contain a rich macrobenthic fauna, especially of bivalves and barnacles. The shells were examined for taphonomic features formed by abrasion, bioerosion, disarticulation, dissolution, encrustation and fragmentation to define taphofacies for a palaeoenvironmental model. Five bivalve taphofacies and three barnacle taphofacies are distinguished. Both bivalves and barnacles were poorly preserved in foreshore/shoreface

environments, as the shells were subjected to extensive transportation by currents. The shells were best preserved in offshore environments, where rapid episodic sedimentation enabled within-habitat preservation, some even *in situ*. No barnacles occur in the most fine-grained offshore sediment, probably caused by clogging clay and lack of a suitable substrate. Such dissimilarities suggest that the number and distribution of taphofacies depend on which fossil groups are used. Additionally, remarkable interspecific variability may exist within the individual taphofacies. For example, the barnacles are better preserved than the mussel *Mytilus*, although both are fixosessile suspension feeders. It indicates that not only life habits but also shell structure influences preservation. Thus, taphofacies analyses should encompass taphonomic features, interspecific life habit and shell properties together to determine overall preservation patterns.

Molecular and morphological species discrimination: Developing a marine gastropod model system for Neotropical radiations

Timothy A. Rawlings[1], Jonathan A. Todd[1], and Richard H. Thomas[2]
[1]Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, England, UK
[2]Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, England, UK

The marine gastropod genus *Polystira* provides an exceptional opportunity to explore the effects of large-scale environmental changes on the evolutionary dynamics of Neotropical species radiations. Unlike most taxa studied to date, this genus is extremely well represented in both Recent faunas and in fossil assemblages spanning the past 17 myr, and appears to be exceptionally diverse, with an estimated 80+ Recent and fossil morphospecies. The successful use of this genus to unite extant and palaeontological perspectives on species radiations, however, relies on our ability to delimit species accurately, especially among sympatric morphospecies that are only narrowly distinguishable morphologically. We propose to do this by linking a detailed morphological analysis of this taxon through time to a molecular-based analysis of phylogenetic relationships among extant morphotypes. Here we present our initial explorations of relationships among a subset of Recent morphospecies of *Polystira* from tropical America. We examine the correspondence between morphological and molecular based characters in species discrimination, identify the most reliable morphological characters for use in species recognition, and discuss the implications of these results for exploring evolutionary trajectories within this genus. Freshwater molluscs and biostratigraphy of the rift deposits to the north of Lake Edward (Congo).

The microfauna of the Lower Cornbrash (Middle Jurassic) of Ketton Cement Quarry, Rutland

K.J. Riddington
School of Earth Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK **<KJR887@bham.ac.uk>**

Since the early work of Jones (1884), the microfauna of the Bathonian (Middle Jurassic) has been extensively studied. However, a comprehensive study of the Lower Cornbrash, which occupies the uppermost part of the Bathonian Stage, above the Forest Marble, has yet to be carried out. The

macrofauna of the Cornbrash Formation has been extensively studied and a change in the fauna has previously been noted at the Lower-Upper Cornbrash (Bathonian-Callovian) boundary. It is at this horizon that Raup and Sepkoski (1984, 1986) placed the missing peak in their mass extinction periodicity theory; this study will provide an opportunity to test this controversial hypothesis.

At Ketton Quarry, the entire sequence from the Lincolnshire Limestone (Lower Bajocian) through to the basal Oxford Clay (middle Callovian) is exposed. The top of the Blisworth Clay has also been studied for comparison with the already well documented fauna of the Forest Marble. The microfauna of the Lower Cornbrash is varied and includes ostracodes, Foraminifera, vertebrate teeth and gastropods. The diversity of the Foraminifera increases from the Blisworth Clay through to the top of the Lower Cornbrash. The ostracode and foraminiferan assemblages are abundant and diverse throughout, and allow correlation of this interval using the existing biostratigraphic framework.

Phylogeny of Araneae: The fossil evidence and its interpretation

Paul Selden and David Penney
Department of Earth Sciences, University of Manchester, Manchester M13 9PL, UK

A phylogenetic tree combining all known fossil spider records with cladograms of Recent spider families is presented. This diagram reveals a number of interesting features. First, we rely heavily on Fossil-Lagerstätten for the fossil record of spiders; by their fragile nature, spider fossils define the occurrence of a Lagerstätte. Second, the vast bulk of fossil spiders occur in Cenozoic strata, because of their common occurrence in amber of that age (mainly Baltic and Dominican Republic). Most modern spider families, and a few fossil ones, occur in Cenozoic strata. Third, there are very few Mesozoic and Palaeozoic spiders, known mainly from single specimens or a few from a single locality, but they tell us a great deal about the evolutionary history of the Araneae. Most Mesozoic spiders belong in modern families, and a picture is emerging of great longevity of many spider families. Fourth, it is rational to concentrate on Mesozoic spiders in order to fill out our knowledge of the geological history of Araneae and, fortunately, many new specimens are coming to light from strata of this hitherto dark age in the history of spider evolution.

Biostratigraphy of the Coniacian-Santonian sequence in West Central Sinai, Egypt

H.A. Soliman, A.S. Kassab, N.A. Obaidalla and N.A. Abdel-Maksoud
Geology Department, Faculty of Science, Assiut University, Assiut, Egypt

Six sections were measured in detail, covering the area of west central Sinai, and samples for micro- and macro-fossil identification were collected for biostratigraphical analysis through the Coniacian-Santonian succession. The sequence is represented by the siliciclastic and carbonate rocks of the Matulla Formation overlain by the chalky limestone beds of the Sudr Formation. Based on the vertical distribution as well as the co-existence of the index fauna of ammonites and planktic Foraminifera, an integrated biostratigraphical zonal scheme has been developed for the Coniacian-Santonian sequence of west central Sinai. The ammonites zones are: the Coniacian *Barroisiceras onilahyense–Forrestrea brancoi*, *Metatissotia fourneli*, *Subtissotia africana*, and the Santonian *Texanites texanus–Tissotia semmamensis* zones. The planktic foraminiferal zones comprise the Coniacian *Dicarinella primitiva*, the Coniacian–Santonian *Dicarinilla concavata*, and the Santonian *Dicarinella asymetrica* zones. The *Dicarinilla concavata* Zone is here subdivided into two subzones, namely the *Dicarinella imbricata* of Coniacian age and the

Archeoglobigerina blowi of Santonian age. The proposed zones have been correlated with zonal schemes of other well-dated sections and a precise age determination of the rock units has been provided. The Matulla Formation is considered as Coniacian–Santonian in age. The measured lower part of the Sudr Formation is referred to the Santonian.

The known and the neglected—Ordovician biodiversity patterns on the Laurentian margin

Sarah E. Stewart
Division of Earth Sciences, University of Glasgow, Gregory Building, Lilybank Gardens, Glasgow G12 8QQ, UK **<sarahste@earthsci.gla.ac.uk>**

The Ordovician radiation saw the greatest sustained rise in marine biodiversity in the Phanerozoic. Whilst the global and regional patterns of diversity change within major clades are becoming clearer, relatively little emphasis has been placed on changes in spatial or temporal diversity of entire shelly faunas. This includes the relatively rare or neglected organisms.

The well-known Ordovician sedimentary succession of the Girvan District, SW Scotland is an ideal location to study basin-scale diversity change of the whole fauna. It preserves a spectrum of environments, from which groups such as trilobites, brachiopods, conodonts and pelmatozoans are mostly well documented. However molluscs, other echinoderms, non-trilobite arthropods, colonial organisms such as bryozoans and also the rare or more problematic taxa, including machaeridians and conulariids, have largely been neglected. Preliminary work indicates that these groups may be significant or even numerically dominant components of some faunas. The question arises as to whether their preservation at some horizons represents the rare occurrence of unusual environments, or of a taphonomic window into the 'normal' shelly benthos. Either way, the documentation of new occurrences will provide a fuller understanding of the Mid and Late Ordovician diversity patterns on the Laurentian margin.

Evidence for Swimming in the dicynodont reptile *Lystrosaurus* from the Lower Triassic of Russia

Mikhail Surkov[1], Nikolas Kalandadze[2] and Michael Benton[1]
[1]Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ, UK **<mv.Surkov@bristol.ac.uk>** and **<mike.benton@bristol.ac.uk>**
[2]Paleontology Institute, Moscow, Russia

There has been much speculation about the mode of life of the famous Early Triassic mammal-like reptile *Lystrosaurus*, which ranged from strongly aquatic habitats to a fully terrestrial life-style. Investigation of the cranial and postcranial remains of *Lystrosaurus georgi* from the Moscow syncline revealed that this species had, most probably, a semiaquatic life-style and lived on the shore of the palaeobasins. This suggestion is based on comparative analysis of possible locomotion between *L. georgi* and *Dicynodon*, as well as on an analysis of the data from semi-aquatic Recent and fossil tetrapods. There are nine specialized features in the skeleton of *L. georgi* which suggest a semi-aquatic life-style. 1. Raised eyes and nostrils. 2. Shortening of the neck relative to the forelimbs. 3. Size and shape of the ribcage. 4. Increased mobility of the humerus in a transverse plane and power of its

retraction. 5. Reduced role of muscles to raise the body. 6. Increased areas of attachment for femur retractors. 7. Increased attachments for crus flexors. 8. Length of the femur reduced compared to the length of the humerus. 9. Pearl-shaped external nostrils and postero-ventral ridge, perhaps indicating sealable nasal passages.

Proboscidea from the Upper Miocene of Kerassiá (Euboea, Greece)

G. Theodorou[1], A. Athanasssiou[1] and G. Iliopoulos[2]
[1]Department of Historical Geology and Palaeontology, University of Athens, Athens, Greece **<gtheodon@geol.uoa.gr>** and **<aathan@cc.uoa.gr>**
[2]Department of Geology, University of Leicester, Leicester, UK **<gi6@le.ac.uk>**

During the last nine years, systematic excavations carried out by the University of Athens are in progress near the village of Kerassiá in Northern Euboea (Central Greece). To date seven fossiliferous sites have been discovered in the area, which yielded a rich and diverse fauna of Turolian age. In the present report we describe the currently available proboscidean findings, which we refer to ?*Choerolophodon* sp. and *Tetralophodon* cf. *longirostris*.

The Rhynie Chert—A Web-based teaching and learning resource

Nigel H. Trewin[1], Steve Fayers[1] and Lyall I. Anderson[2]
[1]Rhynie Research Group, Department of Geology and Petroleum Geology, Meston Building, University of Aberdeen, Aberdeen, Scotland, AB24 3UE, UK
[2]Department of Geology & Zoology, National Museums of Scotland, Chambers Street, Edinburgh, Scotland, EH1 1JF, UK

We have created, with funding from the Joint Information Systems Committee (JISC), a Web-based teaching and learning resource based on the Rhynie Chert and its flora and fauna. The resource is designed for use as an Honours level palaeontology course, but has application for botanists, zoologists, hot-spring enthusiasts and interested amateurs.

The database includes sections on History of Research, Geology of the Rhynie area, the biota, and comparisons with modern hot-spring environments. A glossary and extensive reference list are also included. An illustrated description is given for each of the major plants and animals so far described from the chert.

A 'teaching manual' section gives ideas for tutors on course content and assessment, with suggested essay and examination question topics. This particular section will be password-protected; tutors interested in accessing this should contact the authors.

The learning resource may be accessed through the University of Aberdeen, Department of Geology and Petroleum Geology Web site at **http://www.abdn.ac.uk/geology/**

The authors would welcome suggestions for improvements and feedback from tutors using the course. The site will be updated as new material is described in the literature.

The Late Carboniferous tetrapod ichnofauna of Alveley, South Shropshire

Lauren Tucker

Palaeobiology Research Group, School of Earth Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK **<LXT758@bham.ac.uk>**

The Late Carboniferous to Early Permian represents a key stage in the evolution of tetrapod faunas. The aquatic, amphibious assemblages of the Carboniferous decline with the appearance of the amniotes during the later stages of this period, producing a transition to predominantly terrestrial communities that continues into the Early Permian. A diverse Late Carboniferous (Westphalian D) ichnological assemblage from the Alveley Member (Salop Formation, Warwickshire Group) of the Wyre Forest, South Shropshire is a significant example of a transitional tetrapod community. The footprints occur as positive casts within fine and medium-grained sandstone beds of Butts Quarry, Alveley. An alluvial floodplain community is represented by trackmakers ranging from small temnospondyl amphibians to larger pelycosaurian amniotes. Possible amphibian body traces have been identified, as well as plant fossils and the tracks of arthropods. This fauna, together with sedimentological data, will be used to produce a palaeoenvironmental reconstruction of this ecosystem, providing an important insight into the terrestrial and semi-terrestrial communities of the Late Carboniferous.

Life and death in the Lower Palaeozoic: Testing models of extinction and oceanic cyclicity using the conodont fossil record

Linda M. Wickström
School of Earth Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK **<LMW034@bham.ac.uk>**

The conodont fossil record is widely appreciated for its 'completeness' and throughout the Palaeozoic it has been used to establish the timing, tempo and magnitude of extinction events, oceanic cycles and a variety of other phenomena. All of these hypotheses implicitly assume an approximately complete conodont fossil record and make a variety of predictions, such as patterns of speciation, all of which are open to test.

I am attempting to test these hypotheses against the evolutionary relationships of a number of distinct conodont lineages that span the Late Ordovician-Late Silurian interval. Conodont interrelationships are traditionally resolved through morphological analysis of the taxonomically diagnostic P1 elements, and biased heavily in favour of the stratigraphic distribution of taxa. My approach is to consider all elements in the feeding apparatus in cladistic analysis, and to consider stratigraphic data only secondarily, in its fit to phylogenetic hypotheses that are based upon morphology alone. In maintaining a distinction between these datasets, I have been able independently to assess the completeness of the conodont fossil record and stratigraphic support for phylogenetic hypotheses. Results so far have been based upon the genus *Kockelella* and will be augmented in future by analysis of clades representative of other major groups of conodonts.

Experimental compression of extant millipedes and reconstructing the ring structure of the Carboniferous millipede *Pleurojulus*

Heather M. Wilson[1] and Joseph T. Hannibal[2]
[1]Department of Entomology, 4112 Plant Sciences Building, University of Maryland, College Park, MD 20742, USA **<wilsonhm@wam.umd.edu>**
[2]The Cleveland Museum of Natural History, 1 Wade Oval Drive, Cleveland, OH 44106, USA **<jhanniba@cmnh.org>**

Pleurojulus is an extinct Upper Carboniferous millipede, with an Euramerican distribution, that had free sternites, pleurites and tergites. *Pleurojulus* is typically found preserved in one of two positions: either dorsoventrally compressed with the pleurites preserved in a paramedian position; or laterally compressed with the pleurites preserved articulated at the lateral margin of the tergites. Two major hypotheses have previously been posited regarding the reconstruction of the ring structure in *Pleurojulus:* (1) the ring structure was similar to that of juliform millipedes, only with the sternites and pleurites free; (2) the pleurites were located in a near-horizontal position beneath the tergites as in Colobognatha.

In an attempt to distinguish between these competing hypotheses, a variety of extant millipede taxa, with differing ring structures, were compressed to assess how ring structure might influence patterns of deformation or breakage during taphonomy of fossil millipedes. The specimens, preserved in EtOH, were treated with protease to mimic limited decay and then compressed using a materials testing device to a maximum force of approximately 400 Newtons. Although aspects of the deformation pattern in other millipedes were similar to that of *Pleurojulus*, overall, Polyzoniid millipedes (Colobognatha) deformed in a manner most similar to that seen in *Pleurojulus*.

The Ordovician brachiopod *Platystrophia* in North America: Are there some "Vikings" from Baltica?

Michael Zuykov

Department of Paleontology, St. Petersburg State University, 29, 16 Liniya, 199178 St. Petersburg, Russia **<zuykov@riand.spb.su>**

The rhynchonelliformean brachiopod *Platystrophia* (Orthida) is one of the most distinctive and common components of the Late Ordovician brachiopod faunas in Baltica and Laurentia, which supported two different biogeographic provinces on the opposite sides of the Iapetus Ocean. A recent review of Laurentian *Platystrophia* reveals the existence of two different morphological groups. A core of the Laurentian *Platystrophia* comprises such taxa as *P. annieana*, *P. colbiensis*, *P. cypha* and *P. ponderosa* which show a distinctive structure to the cardinalia and dorsal muscle field. However, there are some species (*e.g.*, *P. daytonensis* and *P. acutilirata*) closely linked to the lineage of aboriginal Baltic *Platystrophia* in characters of the dorsal interior. The Baltoscandian Basin was the major centre of diversification and subsequent dispersal of *Platystrophia* during the Ordovician. Some of them managed to cross the narrowing Iapetus Ocean and reach Laurentia in the Caradoc. There is however an indigenous Laurentian lineage showing the external characters of *Platystrophia*, but with a distinctive internal morphology. The origin of the latter group may be the result of rapid morphological evolution within isolated ancestral populations soon after immigration to Laurentia, or it could be an example of morphological convergence evolved in some native Laurentian plectorthoideans.