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## Oral presentations

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

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A programme of field excavation undertaken by National Museums of Scotland staff, volunteers and other interested parties during early July 2003 had three main aims. Firstly to relocate the exact position of the 'Eurypterid Bed', a fossiliferous sediment which in the late 1880's yielded the world's most diverse assemblage of Silurian chelicerate arthropods, secondly to characterise the likely sedimentary depositional setting and preservational mechanics of this Fossil Konservat-Lagerstätte, and thirdly to investigate the wider relevance of this fossiliferous unit to the more fully known sequences lying stratigraphically higher in the inlier as detailed by the work of Clarkson et al. (2001). After extensive excavation, the 'Eurypterid Bed' lithology was located *in situ* on the banks of the Gutterford Burn stream section. Detailed sedimentary logging and sampling indicated that volcaniclastic sediments played a major role in the formation of the bed; both discrete ashfall bands and ash-rich sediment were discovered in the metre-thick unit along with monograptids. Overlying the 'eurypterid bed' occur sporadic horizons yielding dendroid graptolites and numerous (at least 12) thin, discontinuous bands of decalcified marine limestone, rich in invertebrate remains. The fauna within these bands shows a degree of similarity with that identified in the overlying Deerhope Formation.

### Variability of setal arrangements in the early evolution of brachiopods

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

pseudointerarea of *Mickwitzia*? cf. *occidens* and the shell of *Mickwitzia*? *muralensis* indicates significant differences in the respective setal apparatuses and their functionality. A detailed study of the microstructure of *Mickwitzia*? *muralensis* demonstrates that its shell perforating setae were secreted in a follicle. Based on functional grounds it appears unlikely that this apparatus was acquired underneath the shell, but represents an inner epithelial follicle that became incorporated into shell secreting outer epithelium. The apparatus of the shell protruding setae of *Micrina* and *Mickwitzia*? cf. *occidens* did not include a follicle and represents a more basic design.
These results show that shell or sclerite perforating setae evolved at least twice during the early evolution of brachiopods.

**Cambrian Brachiopoda of the Rift Valley, Jordan and Israel**
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The middle Numayri Dolomite member of the Burj Formation, exposed extensively in the Safi area to the east of the southern Dead Sea coast, comprises mostly very shallow water, transgressive sequences of dolomites (including sabkhas) and dolomitic limestones with a number of discrete horizons containing linguloid, obolellid, acrotretoid, matutelloid, protorthoid, kutorginoid and nisusioid brachiopods. Some of the assemblages are preserved in life position, but they are mostly found in storm generated, silicified coquinas of disarticulated valves. The age is late Lower Cambrian (Toyonian).
*Kutorgina, Psiloria* and *Trematobolus* form distinct assemblages at some levels, whilst other beds contain discretely scattered valves of *Trematosia*, *Trematobolus, Eoobolus, Psiloria* and *Vandalotreta*. Associated fauna includes the problematic sclerite *Stobostromus* together with hyoliths, hexactinellid sponge spicules, and *Chancelloria*. Very small carbonate build-ups appear to be bound by calcareous algae.
Approximately co-eval beds in the Timna National Park of the southern Negev, Israel contain a less abundant assemblage of *Chile*, *Kutorgina, Trematosia, Israelaria, Glyptoria* and *Leioria*, accompanied by hyoliths and helcionellid molluscs.
Biogeographically, protorthides are distinctive components of peri-Gondwanan terranes. *Glyptoria* and *Chile* are known otherwise only from Kyrgyzstan. As a whole, the faunas demonstrate a compositional structure precursory to the Palaeozoic Evolutionary Faunas, with *Leioria*, for example, being a likely ancestor of the pentameride clade.

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

**A new enteropneust-like hemichordate from the Middle Cambrian Burgess Shale**
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The early fossil record of soft-bodied hemichordates is meagre (though various Cambrian fossils have been interpreted as hemichordates). This is unfortunate, as hemichordates are likely to have an important role in understanding the evolutionary relationships of the morphologically disparate deuterostomes.
A previously undescribed enteropneust hemichordate is one of the most common taxa found in the Burgess Shale of British Columbia. The specimens have the typical enteropneust tripartite body-plan of proboscis, collar and trunk. The internal collagenous skeletal rods (of the dorsal branchial region), that would have supported the gill slit apparatus, are well preserved, as are several other internal features of interest. The morphology of these specimens suggests that the major characters of the enteropneust body-plan have remained in a remarkable degree of stasis since the Middle Cambrian.
The transport and subsequent preservation of the material (including the influence of decay and rotting prior to fossilization) will be considered in light of the soft-bodied nature of enteropneust hemichordates and the currently prevailing models of transport and deposition of the Burgess Shale fauna. In addition, the non-cuticular nature of modern enteropneusts poses a few, puzzling taphonomic questions for current models of Burgess Shale preservation. Here it is proposed that secreted mucus and organo-bromides may have played a part in the preservation of these soft-bodied hemichordate fossils.

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

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Late Silurian arthropod trackways, back-filled burrows and unusual foraging traces, from the Clam Bank Formation in Newfoundland, eastern Canada, bolster evidence suggesting that arthropods were already exploiting terrestrial environments by the Late Silurian. Among these trace fossils are three *Diplichnites* trackways, which were produced by myriapods. Based on biomechanical formulae of arthropod locomotion and theoretical *bauplans* based on computational and functional analyses, probable producers (*e.g.* eoarthropleurid and kampecarid myriapods) are assigned to these trackways.
Additionally, the Clam Bank Formation has recently produced a *Beaconites* burrow, demonstrating an adaptive burrowing/aestivation strategy amongst these arthropods to cope with the strenuous terrestrial landscape. Furthermore, a distinct array of scratch-bundles, which resembles *Striatichnium* (known previously only from the Rotliengendes of Germany), extends the stratigraphic range of this rare ichnogenus, and provides convincing evidence for foraging behavior in a myriapod or euthycarcinoid producer.

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

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The origin of the bilaterian animals has long been one of the most controversial topics in palaeontology and zoology. The particular problems involved include a continuing extremely poor

understanding of basal bilaterian relationships in the modern fauna, a shortcoming that has hampered recognition of of putative basal members of clades in the fossil record. Another problem has been a consistent failure to apply stem- and crown-group distinctions to Cambrian fossils, leading researchers to stumble into a series of predictable snares. As the subject matures, however, Cambrian fossils are increasingly being regarded as being pivotal in our understanding of the origins of major modern groups, and a surprisingly large number of (albeit controversial) examples where this is the case are now emerging. Several extremely fruitful areas of research stand out in particular. The first is that the stem-/crown-group distinction can be used to probe the timing of the origins of groups, a point of considerable controversy between palaeontologists and molecular biologists. The second is the reconstruction of functional routes of evolution of the major body plans, providing a framework and a constraint around which currently popular “evolution of development” hypotheses must be fitted. Finally, stem-group reconstruction at this level potentially allows a greater understanding of the relationships of the living “minor phyla”, providing an important point of cross-fertilization between the fossil record and the extra information available from extant taxa.
Despite the great potential of Cambrian taxa, many problems remain in their interpretation. Not least of these is recognising the subtle stem-/crown-group boundary itself, which has proved to be highly problematic in several Cambrian cases, and may be a more general problem worth a wider investigation. Even with the recognition that not all phylum-level crown groups have definitively emerged by the Middle Cambrian, this bare fact should not necessarily be interpreted as meaning that all important body-plan evolution took place after this time: the disinction involved may in some cases be a semantic one.

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

**Taphofacies of the Burgess Shale**
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Evaluation of post-mortem effects, biostratinomy and diagenesis, is crucial in assessing the quality of any fossil deposit. For the Burgess Shale, most taphonomic studies have focused on the

diagenetic conditions necessary for soft tissue preservation and biostratinomic analysis has attracted relatively little attention. In this study, the biostratinomy of the sponge *Eiffelia*, the brachiopod *Micromitra*, the hyolith *Haplophrentis*, the scleritome-bearing animal *Wiwaxia*, and the arthropods *Marrella*, *Olenoides*, *Sidneyia*, and *Waptia*, is compared in 36 individual fossil assemblages from the “Greater Phyllopod Bed.”
Fossils range in preservation from fully articulated individuals, sometimes showing soft parts, to isolated skeletal elements within individual fossil assemblages. Organisms that are fully articulated are thought to have been alive at the time of burial. Most disarticulated specimens were animals that were dead and had started to decay prior to their final burial. The presence of both a “live” and a “dead” assemblage at the same site of deposition indicates that most individuals have not been transported out of their original life habitat. Variations in the relative frequency of articulated specimens across species and assemblages demonstrate the presence of different taphofacies, and provide clues for the reconstruction of temporal and spatial dynamics of the Burgess Shale community.

**Assembling a tetrapod body-plan: definition, slippage, and stems.**
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Stem groups precede crown groups: their definition and significance has been summarized elegantly in several articles (e.g. Budd 2001). Body-plans and bauplans are hypotheses of general and specialized shared conditions abstracted from crown group memberships. Thus, body-plans and last common ancestors of living groups have tended to blur one into the other, and stem groups have emerged as a unique means of investigating the evolutionary sequence (and possible significance) of body-plan assembly. However, the most basal fossil taxon matching a crown-based body-plan is likely to branch from below the crown-node. So the generally accepted definition of, in this case, Tetrapoda, will probably include the crown group plus a chunk of the stem. But fossils are incomplete, thus raising issues about assumed conditions of unknown parts. Moreover, this problem increases towards the stem base, where membership was probably less diverse, fewer characters unite taxa with the crown, fossils are rare and fragmentary, and hypotheses of stem-membership are more controversial. Theories of bauplan assembly suffer accordingly.
Stem groups should not be interpreted as ancestor-descendent sequences, and neither should their body-parts (i.e. character states). The pectoral fins of *Eusthenopteron* did not transform into the polydactylous forelimbs of *Acanthostega* (Coates *et al*. 2002). Conjectured homologies between these structures are based upon morphological similarity, but explanations consist of hypothesized shared developmental conditions. Therefore, anatomical markers in stem taxa (such as paired fins, digits or feathers) deliver minimum hypotheses of developmental evolution. Finally, stem groups are often used to explore the sources of classic evolutionary innovations, such as 'the tetrapod limb'. Such innovations are often presented as causal to functional and ecological change. Here, a summary of stem group tetrapod fins and limbs will be used to consider the detailed pattern of changes, and the extent to which these support standard textbook scenarios of the fish-tetrapod transition and vertebrate terrestrialization.

BUDD, G. 2001. Climbing life's tree. *Nature* 412: 487
COATES, M.I., JEFFERY, J.E. and RUTA, M. 2002. Fins to limbs: what the fossils say. *Evolution & Development* 4, 390-401

**Oceanic anoxic events (OAEs) and plankton evolution: a case study from mid-Cretaceous Radiolaria**
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The impact of OAEs on the marine biosphere is of interest to palaeobiology because OAEs represent major environmental perturbations of the ocean-climate system. As a siliceous group with a long evolutionary history, Radiolaria constitute an interesting proxy to gauge the biotic response of zooplankton. Previous studies suggest that Radiolaria experienced important faunal turnovers during the mid-Cretaceous OAEs. We have focused on the members of family Archaeodictyomitridae (Early Jurassic-Palaeocene) for which we have first analysed the phylogenetic relationships of its various Cretaceous morphospecies. Our analysis was based on literature review, collection of new material with a high resolution sampling and phenetic analyses performed with the help of PAST software.
We find that some previously thought extinctions of Archaeodictyomitrid species during OAE1b (late Aptian – early Albian) are in fact pseudoextinctions. Indeed, our material from Albania suggests that a major diversification took place at the base of this OAE.
A high-resolution study across the Bonarelli level (OAE2) confirms the step-by-step pattern of numerous real extinctions (end of lineages), some of which started in the late Cenomanian, long before the C/T boundary. This might suggest that extinctions were not driven by abrupt environmental changes, but by the *ca.* 2 Ma environmental deteriorations which began with the mid-Cenomanian event.

**Stem groups, the fossil record and molecular dates for the origins of major clades**
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The veracity of the fossil record as a repository of the evolutionary history of life on Earth, and in terms of its ability to inform on the timing of origin of major clades, is now in question more than at any time in the past. This situation has been arrived at, in particular, from the development of so-called molecular clocks. At their simplest, molecular clocks estimate the time of origin of clades by calibrating molecular phylogenetic hypotheses to time, using palaeontological dates to correlate one or more branches to time, and using this quantitative relationship to constrain the time of origin of all the other branches. Although some molecular clock and palaeontological estimates show close approximation there are many infamous examples of disagreement and, in almost all instances, dates derived from molecular data are considerably older than those based on palaeontological data. This is attributed either to systematic biases in molecular clocks, or the vagaries of the fossil record.
Despite the fact that molecular biologists generally couch their taxonomic concepts solely within the framework of living taxa, i.e., the crown-groups of clades, molecular clock estimates pertain to the time of divergence of clades from their nearest living sister-groups, i.e., the origin of total groups. This can, and has led to confusion, both between molecular biologists and palaeontologists, and amongst molecular biologists themselves, over precisely which taxon putatively competing analyses are aimed at. The discrepancy in time estimates can be very considerable.
Finally, the distinction between the time of origin of total- and crown-groups has been used as a possible rapprochement for the consistent pattern of disparity between molecular clock and palaeontological estimates. This is based on the idea that lineages diverge long before they acquire morphological apomorphies and, thus, lineage divergence is likely to be invisible to the palaeontological record until each of the lineages diversify (and so molecular clocks estimate the origin of the total group while palaeontological estimates better reflect the origin of the crown-group). However, this fails to take account of the hierarchical nature of total- and crown-groups,

wherein the time of origin of one crown-group is also the time of origin of its constituent total groups - and there is no evidence that molecular clocks and palaeontological estimates are proportionally any better at lower taxonomic rank.

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

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

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

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

**First Permian spider and the diversity of late Palaeozoic mesotheles**

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

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

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Tree-rings in pre-Quaternary fossil woods have long been used as important quantitative indicators of palaeoclimate. In this paper, a global analysis of the relationship between climate and tree-ring parameters is presented that appears to invalidate the use of fossil woods in this way. Three parameters, specifically, mean ring width, mean sensitivity, and percentage latewood, were analyzed from 1000 sites worldwide using data reprocessed from the International Tree-Ring Data Bank. Results reveal that variability in modern trees related to taxonomy, ontogeny, and ecology tends to obscure the palaeoclimatic signal except where sample size is very large, and sample taxonomy and ontogenetic age is constrained. As it is unlikely that such conditions can ever be met in fossil studies, the validity of using quantitative tree-rings parameters as indicators of Pre-Quaternary climates would seem questionable.

**Stem groups and angiosperm origin**

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Considerable progress has been made over the past few years towards a better understanding of phylogenetic relationships among angiosperms and phylogenetic analyses based on molecular data have begun to produce consistent ingroup topology. The recognition of Amborellaceae, Nymphaeales, Illiciales, Trimeniaceae, and Austrobaileyaceae as the earliest diverging lineages at the base of the angiosperm tree has been an important step towards the formulation of a new concept of early angiosperms diversification. The new model conflicts with previous phylogenetic reconstructions, but it has received support from the fossil record as well as morphological and developmental studies and it appears to clarify character patterns that have otherwise been difficult to explain, e.g. patterns of carpel closure, one of the most critical features (papers in Zimmer et al. 2000). There are, however, a number of major, unresolved problems that have to be solved before a robust model for angiosperm origin and early evolution will be in place. One of these problems is

to establish the position of angiosperms in relation to other seed plant groups and to precisely root the angiosperm tree. Phylogenetic models based on morphological data strongly supported an anthophyte clade with angiosperms nested within the seed plants together with Gnetales and Bennettitales. Molecular analyses have indicated alternative positions, including a strongly supported model that resolves angiosperms as sister to all other seed plants and nests Gnetales within the conifers (e.g., Chaw et al. 2000). Currently, however, molecular studies do not appear to be sufficient for the unambiguous identification of relationships among seed plants (Rydin 2002) and information from the fossil record therefore appears crucial in the reconstruction of phylogenetic patterns leading to the crown group angiosperms. So far no stem group angiosperms have been recognised. This could partly be explained by the lack of fossils with key reproductive features preserved, but difficulties are exacerbated by the lack of a solid phylogenetic framework for seed plants as a whole.

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RYDIN, C., KäLLERSJö, M. and FRIIS, E.M. 2002. Seed plant relationships and the systematic position of Gnetales based on nuclear and chloroplast DNA: conflicting data, rooting problems and the monophyly of conifers. *International Journal of Plant Sciences* **163**(2), 197-214.
ZIMMER, E.A., QIU, Y.-L. ENDRESS, P.K and FRIIS, E.M. 2000. Current perspective of basal angiosperms. *International Journal of Plant Sciences* **16 (6 Supplement)**, S1-S248.

**The preservation of Early Cambrian animals of the Chengjiang biota**

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The diversification of animal life in the Cambrian is one of the most significant events in the history of life and continues to source controversy. Investigation of this event utilizes the fossilized remains of mineralised and non- and lightly-mineralised Cambrian animals, study of the latter being vital in providing a more inclusive representation of Cambrian life. The Early Cambrian Chengjiang biota of Yunnan Province, China is of prime importance in this respect, because it contains the earliest known diverse metazoan record.
Gauging preservational bias is crucial in providing a potential assessment of the completeness of this fauna and whether it represents a true depiction of early Cambrian life. We present a new model to explain the exceptional preservation and details of the decay process. Pyrite replaced mineralised, lightly-mineralised and non-mineralised tissues. The geochemistry of the sediment provides an insight into the bottom and pore water conditions which were important in preservational processes. This study provides a foundation for interpretation of Chengjiang fossils by revealing bias in the preservation processes.

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

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The shape of the mammalian glenoid varies widely. It ranges from the tight transverse hinge of some carnivorans, through the mildly concave surface found in humans, to the longitudinal slot of hystricomorph rodents. These variations in morphology are normally explained in terms of allowing particular styles of mastication to be performed. Nevertheless it is probable that other aspects of

cranial morphology influence the form and position of the temporo-mandibular joint.
The relationship of the glenoid to the pharyngeal region and braincase in extant Lipotyphla was examined using geometric morphometrics. It was found that: 1) the shape of the glenoid varies with the anteroposterior length of the auditory region; 2) the position of the glenoid moves posteromedially as basicranial flexure decreases (as indicated by pharyngeal narrowing and the foramen magnum becoming more posteriorly directed), with this rotation seeming to conserve the length of the vector of the lateral pterygoid muscle; and 3) the position of the lateral margin of the glenoid changes with basicranial flexure and braincase width.
In order to broaden this work to encompass glenoid morphologies not present today, this analysis is being extended to fossil lipotyphlans including *Apternodus*, *Oligoryctes* and *Domnina*.

**Tertiary cold seeps in the Caribbean region**

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Cold seeps are unusual environments populated by low-diversity animal communities in which the dominant mode of nutrition is chemosymbiosis. The primary producers in this ecosystem are bacteria, which metabolise reduced chemical compounds in the seep fluid in order to fix carbon and produce organic molecules. This process – chemosynthesis – is closely linked to the formation of distinctive carbonate deposits, which allow cold seep sites to be recognized in the fossil record. Modern cold seep communities occur in varied geographical settings and are relatively well known in terms of ecology and animal physiology. However the biogeographic distribution of cold seep fauna, as presently known, is poorly understood. The reasons for the high degree of endemism among cold seep species; disparities between the Atlantic and Pacific seep faunas and the links between cold seep taxa on a regional to global scale are as yet undiscovered. Answers to some of these problems may lie within the fossil record of cold seeps.
This study concerns Tertiary cold seeps in the Caribbean region – an area of unique palaeobiogeographical significance since the Caribbean Sea previously provided a direct, open water connection between the Atlantic and Pacific Oceans. Cold seep deposits are described from Barbados, Trinidad and the northern coast of Venezuela. Biodiversity of the seep fauna is documented. Comparisons are made between this fauna and published data on modern Caribbean seep communities, and fossil Tertiary seep communities in Eastern Pacific, Western Pacific and Mediterranean regions. Implications for the origin and distribution of modern seep faunas are discussed.

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

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An exceptionally preserved biota of Upper Silurian (Ludlow Series) age is found in submarine channel fill deposits around Leintwardine in the central Welsh Borderland. The deposits are of importance as they represent a rare example of exceptional preservation in organisms of Silurian age; they also provide a unique palaeoenvironmental setting.
The channel biota comprises a range of Upper Silurian marine animals; approximately 50 species of invertebrates have been recorded. Along with typical Silurian forms such as brachiopods, graptolites and trilobites, there are also more unusual taxa such as abundant and diverse echinoderms (ophiuroid and asteroid sea stars, echinoids, crinoids and ophiocistioids), eurypterid and xiphosurid chelicerates, phyllocarids and worms. The asterozoans are one of the most

interesting and diverse groups of the fauna. The ophiuroids are by far the most abundant of the echinoderms; the asteroids are rare in comparison. The degree of disarticulation varies throughout the invertebrate fauna; the echinoderms are mostly complete, whilst the majority of the arthropod material consists of disarticulated components. Asterozoan specimens are almost always preserved intact, revealing the finest morphological detail. Almost all of the fossils are preserved as 'hard-parts'; occasional soft-body preservation of palaeoscolecid worms may occur. The unusual channel fauna generally occurs in concentrated horizons through the channel fill; much of the remainder of the fill is relatively barren. The starfish fauna appears to occur exclusively within these horizons, although some of the other unusual fauna such as eurypterids and phyllocarids also occurs at other levels.

**Ediacaran microbial colonies**

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

**Summer temperatures of Late Eocene to Early Oligocene freshwaters**

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The first major glaciation of the Cenozoic (Oi-1) affected Antarctica in the Early Oligocene. Recent published work attributes ~1‰ of the 1.2‰ +$\delta^{18}O$ isotope shift in marine benthic foraminifera to increased ice volume rather than to temperature decrease. Expanding upon new techniques (Grimes et al. 2003 GCA, In Press) we report the first oxygen isotope derived freshwater palaeotemperatures from the Late Eocene to the Early Oligocene. Three absolute summer season palaeotemperatures for southern England (values unaffected by changes in ice volume) were derived from multiple palaeoproxies (rodent tooth enamel combined with three different freshwater biotic carbonates) at each of six horizons. Each of these independent palaeotemperatures displays similar trends and indicates a variable warm subtropical climate throughout the Late Eocene to early Oligocene. We also calculated time-averaged Mean Annual Temperatures (MAT), which, like

temperatures derived from $\delta^{18}O$ in the marine realm, are affected by changes in ice volume. At the Oi-1 glaciation our trend in MATs decouples from the trend in summer temperatures, which is consistent with a change in global ice volume. Published work on marine fish otoliths and molluscs indicates that temperature decrease in low latitudes at the Eocene - Oligocene transition selectively affected the winter season. Combined results suggest that the climate at low and mid-northern latitudes was not strongly affected by the southern hemisphere Oi-1 glaciation. Our technique provides a new method of independently testing climate trends and of obtaining absolute palaeotemperatures for the continental realm.

**Insights into Neoproterozoic embryology**

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

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

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

combined with morphometric measurements on microfossils to document stratophenetic series in two co-occurring taxa at multiple locations within the basin. As a means of demonstrating the method, an application of the Bayesian inversion procedure to synthetic data is presented.

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

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

**Who wants to eat a brachiopod?**

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

*Apletosia maxima* from the Coralline Crag. The South Georgian and Pliocene brachiopods lived in communities alongside a full range of predatory taxa whereas the fauna of the Antarctic Peninsula is well known to lack major fish and crustacean groups.

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

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

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

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

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

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For a monophyletic group with still extant members, Hennig distinguished between the total group (Gesamtgruppe), the crown group (*Gruppe) and the stem group (Stammgruppe). The total group comprises all forms, extant or extinct, which are more closely related to the extant members of the group than to anything else still extant. The crown group comprises the latest common stem species of the extant members of the group, plus all its descendants extant or extinct. And the stem group comprises all members of the total group which are not members of the crown group. Passing through every stem group is the stem lineage, all members of which are direct ancestors of the crown group. Every fossil belongs to one and only one stem group, in a less or more crownward position.
The monophyly of the Deuterostomia has been confirmed on DNA evidence, with the probable parenthetic structure (Chordata ((Echinodermata + Hemichordata) Xenoturbella)). Among recent animals, only the echinoderms retain a skeleton with each plate a single crystal of calcite. Parsimony based on extant animals might therefore suggest that all such fossils are more closely related to extant echinoderms than to any other extant group. The anatomically complex “carpoids”, however, comprising fossils with such a calcite skeleton but no radial symmetry, probably include the stem groups of the echinoderms, ambulacrarians (= hemichordates + echinoderms), hemichordates, craniates, tunicates, acraniates and chordates, implying that the calcite skeleton has several times been lost. Among primitive deuterostomes, therefore, the distinction between stem groups and crown groups is capital.

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

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

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

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Charophytes, a non-marine green algae, are the ancestor of higher land plants and have been around at least since the Ordovician. However, the fossil record of charophytes is relatively sparse, with typically only the calcified female gametangia, or gyrogonite, being preserved. One of the oldest known charophytes is *Palaeonitella cranii* (Kidston and Lang) Pia, found in the Early Devonian Rhynie chert, Aberdeenshire, Scotland. *P. cranii* has been silicified enabling the preservation of the thalli, antheridia and non-calcified gyrogonite and providing a unique opportunity to compare the structure of a Palaeozoic charophyte with that of the extant family Characeae. *Palaeonitella cranii* is a relatively small charophyte with long thin stems that give rise to whorls of multicellular branchlets; the male reproductive organs (antheridia), preserved in life position, are attached to these branchlets by a short stalk. The structure of the thalli and the position of the antheridia are remarkably similar to that of species belonging to the extant Nitelleae tribe. However, the gyrogonite of *P. cranii*, which is composed of six sinistrally spiralling cells and has six coronula cells arranged in one single tier, is more reminiscent of the Chareae tribe. This suggests that *P. cranii*, although retaining some of the characteristics of the Nitelleae, is an ancestor of the Chareae, supporting existing molecular studies which indicate that the Nitelleae are basal to the Chareae within the Characeae.

**Land plant origins: body-building from scratch**

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

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

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*Charniodiscus* is one of the most widespread and best-known representatives of the Ediacara biota (terminal Neoproterozoic; 575-543 Ma). This soft-bodied, leaf-shaped organism consists of an ornamented frond attached to a stem that was anchored to the seafloor by a basal attachment disc. The scarcity of complete specimens has previously hindered the evaluation of the taxonomy and biology of *Charniodiscus*. The presence of literally hundreds of complete specimens from the Avalon Zone of Newfoundland has allowed for detailed morphometric analyses and construction of

growth series, which permits the recognition of features that vary with growth (e.g. stem length, frond width, and disc diameter) versus those that reflect taxonomic differences (e.g. number of primary branches, presence of a distal spine, frond shape ratios). Ratio plots and principal components analyses (PCA) distinguishes two feeding strategies within the *Charniodiscus* population at Mistaken Point Newfoundland. The first strategy consisted of building a large, wide frond with a short stem, thereby maximizing food gathering from the lower tiers. The second form sacrificed frond area in order to construct a longer stem that elevated the feeding structure above the lower tiers, permitting feeding up to 50 cm above the sea floor. The competition for resources in this deep water community resulted in the sympatric speciation of *Charniodiscus* into two, morphologically distinct species unique to the Mistaken Point Formation. By feeding from different tiers, the adult forms of both species effectively reduced the competition for resources and represent two similar, yet ecologically distinct forms of stalked filter feeders.

**Sex and brainstorming in mitrates**

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

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

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Stromatolites represent a dominant feature of Precambrian and Cambrian warm and shallow-water environments. After the evolution of organisms that graze on these (mainly) cyanobacterial mats, stromatolites were relegated to a relatively minor role for most of the Phanerozoic and are described mainly from restricted environments. The situation in the western part of the Prague Basin near Holoubkov represents an unique record from an apparently restricted environment where stromatolites are preserved as iron-ores around volcanic centers. Polished slabs reveal a variety of different morphologies from biolaminites to stacked hemispheroids.
No macrofossils are known from these successions, which supports the idea of unfavourable life conditions. This poses the problem of no direct biostratigraphic information for determining the age

of the sedimentary ore unit. A Lower Ordovician age (Tremadocian to Arenigian) is given by the regional lithostratigraphic framework. Recently published models demonstrate the possibility that the ferric iron in the Precambrian BIFs may have been generated by microbial activity. We propose a major role for microorganisms, rather than chemical precipitation, in the formation of Fe-stromatolites and Fe-laminites from Holoubkov.

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

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

**On the stem lineage of Arthropoda**

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

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

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

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

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

**Exceptional preservation of amphibians from the Miocene of NE Spain**

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

**Phylogenetic systematics of early (Tremadoc-Arenig) hollinoidean ostracods**

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The study is aimed at resolving the phylogenetic systematics and evolution pattern of early (Tremadoc-Arenig) hollinoidean (Palaeocopa) ostracods, an important component in the fossil assemblages, lacking, however, any modern representatives.
Baltoscandia, showing the greatest record of the studied taxa, seemingly served as the centre of radiation for most important families, both towards the low latitudes (to Laurentia and also to Siberia) and towards the Perigondwanan area. Another important centre of radiation was Siberia.
50 ostracod genera were analysed cladistically, using the PAUP programme. The 27 selected characters were mostly non-ornamental, being more stable in generic taxa and having higher systematic value. The characters coded valve contact features, general valve sculpture, details of sulcation and lobation, cristal sculpture, admarginal sculptures and type of dimorphism, peculiarities of adventral sculpture in heteromorphs and in tecnomorphs.
The results of the analysis prove, that the Palaeocopa of Tremadoc-Arenig from Baltoscandia, Siberia and Australia form a monophyletic clade. The ancestral palaeocopes show affinity to the monophyletic Siberian Soanellide clade, but the Siberian Cherskiellids form a distinct monophyletic clade. Distinction between Tetradellidae, Ctenonotellidae and Tvaerenellidae needs further study and perhaps a revision in future.

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

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Synziphosurines are an extinct paraphyletic group of primitive Xiphosura, a Class represented today by only four species within three genera (e.g. the well-known 'living fossil' *Limulus polyphemus*). New synziphosurine material from the Lower Silurian of Wisconsin and the Middle Silurian of Iowa, USA, represents at least two new taxa, significantly increasing our understanding of the morphological diversity of this poorly known group. Along with *Bembicosoma pomphicus* from the Pentland Hills of Scotland, they are also among the earliest-known representatives of this group. The new material bears most resemblance to the family Weinberginidae (a higher taxon in some need of revision), which currently contains the monospecific genera *Weinbergina opitzi*, *Legrandella lombardii* and *Willwerathia laticeps*. The preservation of six pairs of prosomal appendages in the exceptionally preserved Wisconsin material is in contrast to the seven pairs seen in *W. opitzi*, from the Lower Devonian Hunsrück Slate. This suggests this taxon occupied a more derived position than *W. opitzi* despite its older age. A preliminary cladistic analysis of synziphosurines, including the new taxa, will be presented.

**Gastropod evolution at the Palaeozoic-Mesozoic transition**

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

**Resistance of spiders to Cretaceous–Tertiary extinction events**

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Throughout Earth history a small number of global catastrophic events leading to biotic crises have caused mass extinctions. Here, using a technique that combines neontological and palaeontological data in the form of a phylogenetic tree and also using independent numerical data derived from

relative abundance of amber spider inclusions, we consider the effects of the Cenomanian--Turonian and Cretaceous--Tertiary mass extinctions on the terrestrial spider fauna. We provide the first evidence that spiders suffered no decline at the family level during these mass extinction events. On the contrary, a weighted regression analysis shows that they increased in relative numbers through the Cretaceous and beyond the K/T extinction event. This trend for spiders is similar to that observed for insects. However, the increase in insect palaeodiversity over time masks underlying extinction and origination events. This is not true for spiders. Extinction resistance in spiders may be facilitated by their generalist predatory strategy.

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

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Brachiopod faunas may represent an important source of information about the response of the biosphere to palaeogeographic and climatic change during the Carboniferous Period. However, little is known about how those changes modified brachiopod assemblages. To address this question, studies on Pennsylvanian brachiopods from the eastern Great Basin, Nevada (USA), have been conducted. These brachiopods were selected because of their stratigraphic context within cyclic depositional sequences, the origin of which may be related to eustatic sea-level change linked to fluctuations in ice volume on Gondwana.
Rapid fluctuations in sea-level changed the structure of benthic communities, affecting the populations of brachiopod faunas. A chaetetid-like colonial coral is found in association with the brachiopod species *Heteralosia slocomi*, but only in the shallowest facies of the sedimentary cycles. The size of the populations of this brachiopod species increases when this coral is present, as does the morphological variation shown during the ontogeny of the brachiopod. The presence of this coral seems to be beneficial for the brachiopod. A symbiotic relationship is suggested in which the brachiopod would provide nutrients and the coral, shelter against predation. Analyses of these data suggest that rapid sea-level changes linked to climatic change alter the ecology of benthic organisms. These studies, therefore, may provide a better understanding of the effects of climatic change in the development of benthic communities.

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

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Phylogeography, the study of intraspecific evolution using molecular markers, has revolutionized research on living species because speciation, divergence, and migration leave their imprint on gene sequences. Phylogeography is possible because molecules evolve quickly, allowing reconstruction of intraspecific relationships. Except in cases where DNA has been recovered from fossils, phylogeography has bypassed palaeontology because morphological data, as traditionally analyzed, do not offer such fine resolution. We have studied quantitative morphological traits of the type typically preserved in the vertebrate fossil record to assess their suitability for phylogeographic analysis.
We find that morphology evolves at rates that differ trait to trait and group to group. A particular trait is suitable only if it evolves quickly enough for measurable divergence to have accumulated, but slowly enough not to be unduly ‘saturated’ by evolutionary reversals. Multivariate traits, such as geometric morphometrics, are often superior for palaeophylogeographic work because, *ceteris paribus*, the probability of exact evolutionary convergence decreases with dimensionality, although,

univariate traits, diverge more quickly. Maximum-likelihood phylogenetic analysis is particularly suitable to multivariate morphometric data. Tree support can be assessed by bootstrap in which the members of each population are resampled, population means recalculated, and reordination and tree construction iteratively performed.

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

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

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

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The Lower Cretaceous sequence of the Kopet Dagh basin includes the Shurijeh, Tirgan, Sarcheshmeh and Sanganeh formations. The sequence starts with red sandstones and conglomerates of the Shurijeh Formations. The change from the thick-bedded limestones of the Tirgan Formation to the marly and shaly limestone beds of the Sarcheshmeh Formation marks a significant sea-level rise, during which Late Barremian heteromorphs such as *Martelites* and *Heteroceras* and planispiral forms such as *Turkmeniceras* invaded the basin. During the Early Aptian sea-level fluctuations the most important genus is *Deshayesites*.
When deposition of the shales and siltstones of the Sanganeh Formation commenced in the western part of the basin during Early Aptian times, smooth-shelled genera such as *Aconeceras*, *Melchiorites* and *Pseudosaynella* entered the area. These forms failed to penetrate further east, where the Sarcheshmeh Formation was still being and deposited. The Late Aptian sea-level rise introduced some ribbed forms such as *Hypacanthoplites* and *Parahoplites*.
In most cases the first appearance of new taxa happens in transgressive and highstand systems tracts. The most abundant ammonite faunas also often coincide with these tracts. Although sea-level changes appeared to influence the first appearance of particular taxa, ecological and local

bathymetric conditions also influenced the distribution of ammonites within the basin.

**The affinities of sinacanthid fishes**

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

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

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

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

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HIV, the AIDS virus, is a human tragedy and medical challenge of global proportions. HIV is also a phenomenal model system for research in molecular palaeontology. Most of this research is being done now by researchers with no training in nor even awareness of the field of palaeontology; there are significant challenges and opportunities here for palaeontologists who dare to enter the world of

molecular systematics. Open problems include the nature and origin (in both time and space) of major crown groups, which have the HIV-specific taxonomic rank of subtype. Do HIV-1 M subtypes represent (a) separate transmissions from chimpanzee to human hosts, or (b) recombinations between distantly related strains, or (c) major epidemic outbreaks, or (d) some other phenomenon? We support the global HIV research community by building and curating public databases (http://hiv-web.lanl.gov), providing analysis tools (online and/or downloadable), publishing annual compendia, and conducting research both independently and in collaboration with laboratory research groups. Our research is strictly computational, and the focus of my own research is on estimating the time of origin of major clades of HIV.

**Ordovician biodiversity trends in Girvan, SW Scotland**

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Arguably the greatest sustained rise in diversity in the Phanerozoic took place in the Ordovician. Some groups, including molluscs and the more problematic taxa, have often been neglected in the study of many shelly faunas, and hence their contribution to the Great Ordovician Biodiversification Event may be far from completely understood. The richly fossiliferous Ordovician succession from Girvan, SW Scotland, provides a variety of environments, close to the Laurentian margin, in which the diversity of these taxa, and of whole faunas, can be assessed.
Recent sampling and study of museum collections show that gastropods are ubiquitous throughout most of the Llanvirn to Ashgill at Girvan. The problematic bellerophonts diversified through the Caradoc and into the following Ashgill, particularly in siliciclastic facies, with some species being selective in substrate type. Unequivocal bivalves appear in the Caradoc and are mainly small infaunal nuculoids and ctenodontids in siliciclastic facies. Following the global pattern, epibyssate forms occur in the upper Caradoc faunas, and most modes of life had appeared by the Ashgill. Of the more neglected molluscs, polyplacophorans occur throughout the succession, albeit at low diversity, and in most instances low abundance. However at one locality they are extremely abundant and occur with a diverse but highly unusual shelly fauna in which other molluscs are very rare.

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

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*Bdellacoma* is an asteroid hitherto known only from the Ludlow of Leintwardine. New specimens from the Wenlock Herefordshire Lagerstätte are fully articulated and preserved in three-dimensions. Computer reconstructions have been prepared from coarse-scale serial-sawing data to reconstruct gross morphology, and from fine-scale serial-grinding data to reconstruct detailed anatomy. The latter reveal details of elongate tube feet, which are collapsed medially, but preserve flared tips that may represent suckers. They are expanded into ampullae at their bases, confirming the long-held assumption that these structures were housed in the open podial basins of Palaeozoic asteroids.

Fine-scale reconstructions also reveal details of a delicate aboral plating structure on the arms, and a complex arrangement of spines. A set of short sub-cylindrical spines adorn the aboral surface, while long curvi-planar spines flank the ambulacral groove, forming a complex overlapping mesh from which the tube feet emerge. Additionally, *Bdellacoma* arms bear large articulated pedicellariae of the *Bursulella* type, previously thought to belong to an echinoid rather than an asteroid.

**The taphonomy of the Bear Gulch Lagerstätte**

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

**Arenig ostracod assemblages and biofacies in the Baltoscandian palaeobasin**

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Fairly well preserved ostracods of the Baltoscandian Middle Ordovician carbonate shelf succession provide an exceptional opportunity to explore early ostracod assemblages and biofacies in detail. 260 ostracod samples from twelve sections of the Baltoscandian area have been analysed using multivariate statistical methods.
Although the number of documented ostracod species reaches 50, the ten most abundant species form up to 95 percent of the total fauna. The generally low-diversity ostracod fauna is dominated by palaeocopes *O. bocki*, *B. palmata* and *R. mitis*. However, two eridostracan species - *C. socialis* and *I. ventroincisurata* belong to the most abundant species of the studied fauna, the former showing also wide distribution over the whole study area and throughout the entire study interval.
Different cluster analyses reveal about 10 ostracod assemblages, of which the high-diversity *C. socialis* and *I. ventroincisurata* assemblages are spatially and stratigraphically widespread, the low-diversity *T. primaria*, *B. palmata* and *O. bocki* assemblages, on the contrary, restricted to certain stratigraphic levels or facies regions.
At least three ostracod biofacies can be distinguished in the study area, representing different depth zones of the epicontinental sea. However, the analysis also reveals the alternation of the shallow-water ostracod faunas with ostracod faunas associated with deeper water conditions, reflecting sea level fluctuations of the basin.

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

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Vertebrate palaeontology lags well behind scientific archaeology when it comes to the awareness, application and development of geochemical methods to extract information from ancient bones. This despite that fact that most equipment used to study ancient bone is housed in geology and/or biology departments. Such a relative ignorance of chemical applications is partly explained by the difficulty of dealing with substantially older materials. The severe alteration of bone during diagenesis (fossilisation) has meant that many techniques that could be applied to relatively recent bone remains could not be applied to ancient fossils. Recent conceptual advances in the study of bone diagenesis, however, warrant re-evaluation of geochemical techniques and their potential for vertebrate palaeontology.
In this presentation, I will outline the current state of knowledge regarding mechanisms and rates of bone diagenesis, and will briefly discuss three geochemical techniques with reference to recent case studies:
Survival and analysis of ancient bone proteins
Direct and relative dating of bone mineral
Stable and heavy isotope composition of ancient bone mineral.
These techniques are still under development, but have great potential to advance many fields of vertebrate palaeontology.

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

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**The origin of birds, feathers and flight: have palaeontologists solved the problem?**
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Deconstructing and understanding major evolutionary transitions such as the origin of birds and flight and then communicating this understanding to other scientific (and non-scientific) disciplines is

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

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

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

Ingham, J.K. 1966. The Ordovician Rocks in the Cautley and Dent Districts of Westmoreland and Yorkshire. *Proceedings of the Yorkshire Geological Society*, 35, 455-504.
Rickards, R. B. 2002. The graptolitic age of the type Ashgill Series (Ordovician) Cumbria. *Proceedings of the Yorkshire Geological Society*, 54: 1-16.

**Thylacocephalan arthropods: their Early Cambrian origin and evolutionary significance**

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The Thylacocephala are bivalved arthropods with a long fossil record (Lower Silurian to Upper Cretaceous), a worldwide distribution (Europe, North America, Australia, China and South America) and a most peculiar morphology exemplified by a rostrum-bearing bivalved carapace, hypertrophied visual organs and, in some species, long raptorial appendages. Despite key-information obtained over the years from several Lagerstätten (Solnhofen, Germany; Mazon Creek, Illinois and La Voulte-sur-Rhône, France), the Thylacocephala has long remained an odd group of animals with unknown origin and uncertain affinities within the Arthropoda (e.g. crustaceans). The discovery of thylacocephalans in the Maotianshan Shale Lagerstätte of South China opens new evolutionary perpectives and reveals the importance of the group.
1) Thylacocephalans have Early Cambrian ancestors (*Zhenghecaris shankouensis*).
2) the myodocopids (Upper Ordovician-Recent), abundantly represented in present-day marine environments, may originate from the thylacocephalan stock and may no longer be considered as ostracods. This new evolutionary scenario is supported by morphological, ontogenetical and molecular evidence from 18S ribosomal DNA sequences that all indicate an important gap between the myodocopids and the ostracod lineages. It contradicts the classical view of Ostracoda as a monophyletic taxon and leads to a redefinition of this major group of extant crustaceans.
3) Enigmatic Cambrian globally-distributed taxa such as *Isoxys*, *Tuzoia* and other bivalved arthropods probably belong to Thylacocephala, making the group a new important component of the Early marine communities.

**The position of rugose corals in the Anthozoa**

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This study presents the first attempts at ordinal level revision of the Rugosa based on the results of phylogenetic analysis. It aims to: (1) test monophyly of the Rugosa; (2) assess at which hierarchical taxonomic level the characters commonly used in rugose systematics are informative, and (3) formulate a hypothesis of the position of the Rugosa among Metazoa.
To accomplish these goals a revision of two Orders of the Rugosa, Cystiphyllida and Stauriida *sensu* Hill (1981), was performed. The phylogenetic analysis used these two orders as the ingroup, and a combination of fossil corals and extant Anthozoa as the outgroup (126 characters; 90 biomineralised, 36 "soft tissue"). Two phylogenetic analyses were performed. The first analysis used Alcyonaria as the prime outgroup yielding 6 trees that were merged into a single tree after optimisation. The second analysis used *Tabulaconus*, a Cambrian fossil coral, and yielded six trees. These trees were combined into a single tree after optimisation, to produce the most informative tree for the problem at hand.
The analysis supports monophyly of Rugosa, but eight of the sixteen sub-orders of the Stauriida are rejected. The Rugosa is the adelphotaxon of a group formed by fossil corals and the Scleractinia with cyclic septal insertion. The major implications for the Anthozoa are: (1) the subclass Zoantharia

is rejected and replaced by the subclass Hexacorallia; (2) the Alcyonaria is rejected as a subclass, becoming a family within the Hexacorallia; (3) the time of origin of the Anthozoa is accepted as Early Cambrian. A new classification for the Anthozoa is provided.

**An early Silurian armoured polychaete?**

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The Polychaeta are a successful and diverse marine class but their body fossil record, with the exception of jaw elements (scolecodonts), is sparse. Even chaetae, which are produced in vast numbers by most species, are extremely rare. We report abundant disarticulated associations and articulated arrays of chaetae from a widely occurring, but enigmatic, Lower Silurian organism. Its chaetae share a number of characteristics with the setae of polychaetes but are substantially more robust, and appear to differ in their arrangement.
The restriction of the chaetae to graptolitic black mudstones is curious. Whilst some modern polychaetes can withstand dysoxia or short bouts of anoxia, the absence of any associated trace fossils or shelly benthos with the fossils appears to preclude them having had a benthic ecology. Similarly, there is no evidence to suggest that they had been transported in from more shallow marine settings, and they appear to have been too heavily armoured to have formed part of the plankton.

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

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Jurassic freshwater ostracods have their origins in those Namurian and early Permian species that survived the end-Permian Extinction Event. By the Cretaceous, diverse non-marine ostracod fauna had evolved, some surviving the 65Ma Extinction Event to develop into modern taxa. But a fundamental question remains, *when did ostracods originally become non-marine*? Most Early Palaeozoic to Devonian species colonised marine-shelf habitats, although some leperditiids inhabited more marginal marine settings. But, unequivocal ‘freshwater’ taxa were unknown until the Namurian.
In central Scotland the Ballagan Formation (early Carboniferous, Tournaisian) occupies the transition between the Old Red Sandstone lithofacies and the more marine-influenced later Viséan succession. Deposition occurred in quasi-marine and non-marine (lacustrine, coastal floodplain and

fluviatile) environments, which supported paraparchitacean, platycope and podocope ostracods. Although these groups are generally considered to be marine, all provide firm evidence of colonising non-marine habitats. The stable isotope ratios of ostracod carapaces ($^{13}C/^{12}C$ and $^{18}O/^{16}O$), macrofaunas and host sediments provide consistent non-marine signatures. Some platycopes associate with algal palynomorphs including *Botryococcus*, suggesting low salinity (freshwater?). Some paraparchitaceans and certain podocopes associate with *Modiolus* (Bivalvia), thought to signal brackish water. Other paraparchitaceans occur in sediments interpreted as alluvial fan deposits. Thus, ostracods had made their most fundamental ecological shift by the early Carboniferous, colonising a range of non-marine aquatic habitats.

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

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**Poster presentations**

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

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

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

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Pre-Llandeilo Ordovician ostracods are rare in Avalonia, and only five species in total are currently recorded from the Builth Inlier, from the Llandeilo and Caradoc. New localities in the uppermost *murchisoni* and upper *artus* biozones (Llanvirn) have yielded diverse mouldic faunas of binodicopes and lesser palaeocopes. Although several genera can be recognised, many of the specimens are morphologically intermediate. In particular, the binodicope genera *Bullaeferum*, *Laterophores* and *Klimphores* form a continuous group, with few consistent species. Some early specimens of *Bullaeferum* show a velum, and an additional posterior node, suggesting a relationship to the tetralobate palaeocopes; in this case, *Laterophores*, *Klimphores* and perhaps some other binodicopes must also be re-examined. Since very few certain binodicopes are known prior to the Llanvirn, this genus group may be relevant to their derivation from palaeocopes.
Several additional localities are being investigated, and a biostratigraphic succession of ostracod taxa in the inlier is being prepared. In outline, diversity and disparity increase rapidly during the early stages of volcanism (upper *artus* Zone), and remain high, with indistinct species boundaries until the lower *teretiusculus* Zone, when volcaniclastic sedimentation decreases. Thereafter, a few species dominate, and by the *gracilis* Zone, only *Conspicillum bipunctatum* and smooth taxa are recorded. Although the record is complicated by environmental and taphonomic variations, this is consistent with models of genetic heterogeneity encouraged by volcanic disturbance.

**Heteractinids and hexactinellids: unravelling basal sponge relationships**

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The relationships of the sponge classes are highly controversial. A compilation of molecular, zoological and palaeontological data suggests that demosponges and hexactinellids are sister groups, with Calcarea more primitive; it is normally assumed that mineralization was independent between Calcarea and siliceous sponges. However, a new specimen of the heteractinid calcarean *Eiffellia globosa* Walcott, and a re-examination of the type specimens, has revealed the presence of diagnostic hexactinellid spicules as a substantial component of the skeletal mesh. The arrangement of these spicules in *Eiffellia* is shown to be precisely equivalent to that of various protospongiid hexactinellids, and growth occurred through an identical pattern. Contrary to established views, on morphological grounds, the Eiffelliidae and Protospongiidae cannot be clearly separated. The only

significant distinction is the presumed compositional difference, although spicules of early representatives of each group are invariably completely recrystallised. Nevertheless, features of the taphonomy of *Eiffellia* can be used to provide a speculative account of the mineralogical transition. The heteractinid Calcarea are thus suggested to be paraphyletic with respect to the Silicespongea.

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

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

**Palaeoenvironments and taphonomy of the Upper Carboniferous Coseley Lagerstätte**

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The Late Carboniferous Coseley Lagerstätte from the West Midlands, UK, contains exceptionally preserved plant and animal fossils found within siderite nodules that occur within Westphalian B mudstones of the Coal Measure Group. The interbedded sandstones, mudstones and coals represent a freshwater lacustrine environment that formed within a typical coal measure swamp forest. The biota includes a diverse assemblage of plant and animal fossils that show soft tissue preservation. The plant specimens include lycopsids, sphenopsids, ferns and pteridosperms represented by a wide selection of plant organs including stems, leaves, cones and seeds. The animal specimens are dominated by a diverse arthropod and fish assemblage that includes xiphosurans, arachnids, millipedes, winged insects, crustaceans, cartilaginous jawed fishes and bony fishes.
The soft tissues have been replicated by clay minerals, notably kaolinite and very fine detail is preserved, such as colour banding on insect wings. This very early clay mineralisation is closely followed by sulphide and carbonate precipitation where void filling sphalerite, pyrite and galena have formed within the siderite nodules. The Coseley Lagerstätte is closely comparable with the more famous Mazon Creek Lagerstätte of Illinois, USA and is closely comparable with the fresh to brackish water Braidwood biota of the latter but there is no equivalent of the marine Essex fauna. Taphonomically, the Coseley Lagerstätte differs from the Mazon Creek in being preserved by a more complex range of mineral phases.

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

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

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

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

### *Ichthyostega*: the makeover

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

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

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

### *Billingsella* associations from Iran (Cambrian Brachiopoda)

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Shallow marine biotopes on the inner shelf of most palaeocontinental margins in the late Cambrian contain a distinctive, recurrent assemblage of rhynchonelliformean brachiopods dominated by the genus *Billingsella* (Bassett *et al*. 2002). Whilst the *Billingsella* Association is part of the Cambrian Evolutionary Fauna, it has a precursory ecological structure heralding those of the Palaeozoic Evolutionary Fauna, including components that can be traced phylogenetically into Ordovician descendants.
Cambrian rocks are fairly widespread through Iran, and the *Billingsella* association is well developed in three regions: 1) Tabas, in Yazd Province, where the eponymous genus is abundant in storm generated coquinas of the Derenjal Formation, accompanied by other brachiopods such as *Archeorthis* and *Palaeostrophia*; trilobites and echinoderms are present in thin limestone units; 2) Zardeh-kuh in Isfahan Province in shale and siltstone sequences with dominant *Billingsella* accompanied mostly by related orthoideans; 3) At Kuh-i-Nanak in the Zagros Mountains of south-west Iran, where *Billingsella* accompanied by echinoderm plates occurs in limestone blocks incorporated within salt-plugs of probable Permian age. In this region the presence of redlichiid trilobites suggests that the allochthonous blocks are also partly of late Lower Cambrian age.

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

**Observations on the acritarch microflora**

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

**Protein control over calcium carbonate biomineralisation**

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Biominerals are inorganic-organic composite materials in which the organic component exerts control over mineral development. The organic fraction consists of proteins, glycoproteins and carbohydrates, and varies in both concentration and composition between taxa. The proteins present within the biomineral control mineral nucleation, morphology and polymorph type. Proteins from the calcium carbonate skeletons of three marine invertebrates and an avian eggshell have

been extracted and characterised in relation to molecular weight and isoelectric point by polyacrylamide gel electrophoresis (SDS-PAGE) and isoelectric focusing (IEF) respectively. The four systems provide a range of ultrastructures and two calcium carbonate polymorphs. The bivalve *Mytilus edulis* has an outer prismatic calcite layer and an inner layer of aragonite. The articulated brachiopod *Terebratulina retusa* has a primary layer composed of acicular calcite and a fibrous secondary layer, while the inarticulated brachiopod *Novocrania anomala* has an acicular calcite primary layer and a secondary layer of calcite semi-nacre. The calcite eggshell of the domestic fowl (*Gallus gallus*) differs in that it is precipitated rapidly within a distinct environment. By characterising the protein component we can identify the proteins that control polymorph type and the formation of these four calcium carbonate biomineral systems.

**The Endocerida – a divided order?**

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

**An intriguing new plesiosaur from the Pliensbachian of England**

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A plesiosaur skeleton recently collected from Blockley, Gloucestershire (*luridum* subzone, *ibex* zone, Lower Pleinsbachian, Lower Lias) represents a previously undescribed taxon. The specimen is a relatively small adult (approximately 3 metres in length), and is remarkably robust in overall morphology.
The material shows a mosaic of characters, and does not at first sight appear to fall neatly into an existing plesiosaur family. Twenty-three cervical vertebrae are preserved, and initial analysis shows that the neck may have had in the region of 27 vertebrae. The cervical neural spines are inclined and expanded which, along with the comparatively short neck, suggests pliosauroid affinities. Unfortunately, the length of the rostrum and lower jaw symphysis are unknown. However, in the skull the frontals are large and form the anterior border of the pineal foramen, the premaxillary facial process is short, and the teeth are long and slender. These are all plesiosauroid characters. The clavicular arch is large and forms a significant part of the pectoral girdle structure, which is the plesiomorphic state for plesiosaurs. However the humerus has a significant preaxial expansion and the epipodials are short and broad, both of which are derived characters.
Initial phylogenetic analyses using existing datasets have so far proved inconconclusive. The taxon

moves between major branches of the cladogram depending on the subset of characters (e.g., cranial or postcranial) analysed.

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

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New diagnostic morphological features discovered following further preparation and re-examination of the holotype of the myriapodous arthropod *Leverhulmia mariae* Anderson and Trewin, 2003 from the Windyfield chert are discussed. Leg appendages have been discovered with attached pretarsi comprising a pair of lateral claws, a fixed median claw and possible unguitractor plate, suggesting affinities with non-ellipuran Hexapoda. We interpret the holotype as part of an abdomen bearing at least five pairs of segmented cercal leglets. The condition of the pretarsi is strongly reminiscent of Diplura, Archaeognatha and Zygentoma (= Thysanura *s. str.*), and the presence of segmented cercal leglets on the abdomen show similarities with fossil representatives of these clades known from the Carboniferous.
*Leverhulmia* is the second hexapod species found in the cherts at Rhynie, the only other form being the collembolan *Rhyniella praecursor* Hirst and Maulik, 1926. Showing closer affinities with the Diplura, Archaeognatha and Zygentoma, *Leverhulmia* may well represent the earliest fossil apterous insect known to date.

**School is where it all begins**

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

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

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

remains of a single species by Jaekel. These fossils are rare and limited in range, it seems unlikely that this is an entirely coincidental association. Discussion of the similarities in the echinoderm and trilobite faunas leads to the conclusion that material from Great Britain and the Czech Republic may need to be compared and revised.

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

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The Early Jurassic "*Lithiotis*" facies bivalves radiated rapidly and dominated tropical nearshore ecosystems. Much confusion has surrounded these bivalves, which have been compared to rudists because of their large size (≤ 1 m) and unusual morphologies. However, previous research had assigned these bivalves to estuarine environments with very low growth rates, unlike rudists. This study combines growth band increment data with stable isotopes to quantify growth rates. Stable isotope analyses were performed on *Cochlearites loppianus* and *Lithioperna scutata*. Two younger bivalves were sampled for comparison. A *Crassostrea titan* (Miocene) was selected as its large size and prominent growth bands enabled easy and consistent sampling. *Isognomon janus* (modern) was selected because of its proposed phylogenetic affiliation. Peaks and troughs in the δ18O isotopes correspond to internal and external growth bands in both *Lithioperna* and *Cochlearites* specimens. These growth bands are interpreted as representing annual growth bands. Proposed growth rates were calculated for *Lithioperna* (17.6 mm/year), *Cochlearites* (11.2 mm/year). If the assumption of an annual growth rate is extended to *Lithiotis problematica* specimens, then *Lithiotis* had rates between 10.8-34.1 mm/year, depending on the region. The upper range is similar to published values of two late Cretaceous rudists, *Gorjanovicia* cf. *costata* and *Vaccinites ultimus*.

**Conservation of process for vertebrate dentitions of their own design**

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

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

***tupiniquim***

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*Saturnalia tupiniquim* from the Carnian of Brazil is one of the earliest dinosaurs known. As the most basal sauropodomorph discovered so far, the forelimb myology of *Saturnalia* was probably close to the plesiomorphic condition for both Sauropodomorpha, and Saurischia as a whole.
The muscles of the forelimb and pectoral girdle were reconstructed using the extant phylogenetic bracket method (Bryant and Russell, 1992; Witmer, 1995). This approach allowed the humeral attachment sites for the coracobrachialis, deltoides, pectoralis, scapulohumeralis, subscapularis, supracoracoideus, extensor and flexor muscles, to be determined. In addition the method suggests that certain other muscles (e.g. the brachialis) were probably present in *Saturnalia*, as they are found in all extant reptile groups. However as their attachment sites vary in extant taxa, their locations in *Saturnalia* are uncertain and they have not been reconstructed.

BRYANT, H. N. and RUSSELL, A. P. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Philosophical Transactions of the Royal Society of London*, **B 337**, 405-418.
WITMER, L. M. 1995. The Extant Phylogenetic Bracket and the importance of reconstructing soft tissues in fossils. Pp. 19-33. In Thomason, J. J. (ed.). *Functional morphology in vertebrate palaeontology*. Cambridge, Cambridge University Press.

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

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

**A Scottish Lower Carboniferous macrofossil Assemblage**

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New material from a disused East Lothian quarry in the uppermost Lower Carboniferous (Dinantian,

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

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

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

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

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

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Abundant and diverse coral and mollusc faunas characterize the Plio-Pleistocene carbonate successions of the Netherlands Antilles. The Seroe Domi Formation on Curaçao, however, contains important brachiopod, arthropod and echinoid associations in an ecosystem that marked the southern margin of the late Cenozoic Caribbean basin. The micromorphic brachiopod *Thecidellina* is abundant, disarticulated and rarely found cemented to the substrate. The valves are well preserved and show variable degrees of asymmetry, probably forming cryptic communities, cemented within cavities in the coral buildups. This biofacies contrasts with coeval deeper-water

assemblages dominated by the pedunculate *Argyrotheca*, *Terebratulina* and *Tichosina* elsewhere in the basin. Common crustaceans include the coral-inhabiting barnacle *Ceratoconcha* occurring in association with their coral hosts and as isolated shells. Six species of decapods occur, the most plentiful being the frog crab *Ranilia* commonly found as complete carapaces. Next in abundance is a box crab found as chelipeds and isolated fingers. The formation has now yielded c. 12 echinoid taxa, making this the most diverse echinoid fauna within the Antilles. Taxa range in size from pea-like regular echinoids to *Clypeaster rosaceus* Linné up to 200 mm in length. Marginal ossicles provide the first evidence for fossil asteroids from Curaçao.

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

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The stratigraphic sequence of the Jurassic rocks in Gebel El-Maghara of northern Sinai has attracted the attention of many workers in the world. The measured stratigraphic sequence is part of El-Maghara massif. El-Maghara represent the first salient massif about fifty kilometers south of the Sinai Mediterranean coast and is situated between longitude 330 10/ and 330 40’ E and latitude 300 35’ and 300 50’ N incorborating an area of about 1300 Km2. The aim of the present work is to study the rhynchonellid Brachiopoda from the coralline limestone of Mahl Member (Bajocian age) as well as the calcareous shales (Bathonian-Callovian ?) from Gebel El-Maghara. These rocks have yielded *Burmirhynchia gutta* Buckman, *Torquirhynchia roueriana* (d’Orbigny) and new genus and species *Septirhynchella hassi* respectively. These fossils are serially sectioned at different intervals in order to study their internal characteristics.The analysis of internal structure of the latter new genus has revealed that it is characterized with a well developed septalium, septalial plates and canalifer type of crura in addition to ventral umbonal septa.

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

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

**What can machaeridian microstructure tell us?**

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

Machaeridian sclerites possess at least two calcite layers where the thin outer layer is produced by lamellar deposition along a growing margin and a thicker inner layer consisting of calcite elements radiating from the umbo, clearly visible in the Kanash material. This inner layer seemingly grew by addition and incorporation of new elements as the sclerite widened. The distinct granulation universally seen on the inner surfaces of the sclerites is a feature of the inner layer as well, and in well preserved material the granulation appears closely aligned with the radiating elements. Marginal spines when present may be a third component enveloping the margin and producing the doublure especially evident on the inner surface of turrilepadid sclerites.
Although morphologically very different the problematic Multiplacophora is one of the few taxa with sclerites that appear to posses two calcite layers roughly similar to those found in machaeridian sclerites. The inner layer displays radiating elements and the outer layer is produced by marginal accretion.

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

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

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

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

subdivided into: the *Barroisiceras onilahyense - Forresteria brancoi, Metatissotia fourneli,* and *Subtissotia africana* biostratigraphic zones*.* The established ammonite zones are calibrated with foraminiferal as well as other macrofaunal zones for the purpose of regional stratigraphy and inter-regional correlation.
The basal Coniacian is marked by FOD of the faunal assemblage of the ammonite *Barroisiceras onilahyense - Forresteria brancoi* Zone, as well as by LOD of the Turonian ammonites of *Coilopoceras* spp. The Coniacian/Santonian boundary is delineated by FOD of the basal Santonian *Texanites texanus* and/or *Tissotia semmamensis* and LOD of the Late Coniacian *Subtissotia africana* and other Coniacian ammonites*.*
The biostratigraphic character of the fauna, chronostratigraphic correlation of the proposed zones, and lithological framework show that the sedimentation in the Egyptian lands was interrupted by several minor breaks, probably diastems, during the Coniacian time. Besides the intra-Coniacian minor breaks, the Coniacian succession is bounded by two unconformity surfaces coeval with the Turonian-Coniacian and Coniacian-Santonian boundaries in several localities.

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

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

**Biotic response to OAE1b precursor event at Blake Nose, North Atlantic**

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Oceanic anoxic events (OAEs) are exceptional episodes in Earth history; their investigation has significant relevance for understanding of dramatic and abrupt fluctuations in climate, such as those seen in the world today. ODP Site 1049 at the Blake Nose in the North Atlantic hosts a near-continuous and exquisitely preserved sequence of mid-Cretaceous sediments, including those deposited during the early Albian OAE 1b event. OAE 1b is represented by a single black shale

horizon and associated ∂C13 excursion. Approximately two metres below the black shale another negative ∂C13 excursion is recorded (Gröcke et al, 2002) associated to significant colour and lithology change. Here, we present planktonic and benthonic foraminiferal population counts over this interval. Relative planktonic species counts and correspondence analysis (CA) show distinctive pre-, syn- and post-∂C13-excursion assemblages, accompanied by a major decline in pelagic abundances and diversities. Increased benthonic foraminiferal accumulation rates and a major decline in planktonic/benthonic ratios suggest elevated palaeoproductivity, whilst a decrease in benthonic foraminiferal oxygen index values record lower bottom water oxygenation at this time. It appears that a significant disruption of oceanic circulation and/or productivity affecting ecosystems in entire water column occurred prior to the main black shale event, suggesting onset of OAE1b may have taken place preceding black shale deposition in the north Atlantic. We compare the event in the north Atlantic with that of the Niveau Kilian black shales of the Vocontian Basin, south-east France, and suggest an associated regional event to have occurred at Blake Nose which did not result in sapropelic deposition.

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

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The basal part of the Sabaya Formation (Ezab El-Qasr-3 well, core depth 560-566 m) encounters the columellate *Afropollis operculatus/zonatus* group. Other significant pollen such as *Tucanopollis annulatus* and *Tucanopollis* cf. *crisopolensis* occur. These taxa favour an Aptian age, but the stratigraphic position above the well-dated Abu Ballas Formation (Lower Aptian) suggests an Upper Aptian age. Consequently, the previous assumption that the Sabaya Formation could range down into the Aptian is acceptable. A fairly humid palaeoclimate is supported by the presence of abundant araucariacean pollen, ferns (e.g. *Deltoidospora*), water ferns (*Crybelosporites*) and freshwater algae (*Botryococcus* and *Ovoidites*). Humidity is thought to have existed during deposition of the upper part of the formation (Ismant-1, core depth 301-307 m). In this interval the non-columellate *Afropollis jardinus* appeared. *A. jardinus* (an Albian-Cenomanian angiosperm) is associated with *Integritetradites porosus* and *Crybelosporites pannuceus*. *I. porosus*, when erected by Schrank and Mahmoud, 2000 is regarded as Cenomanian pollen. Therefore, an Albian-Lower Cenomanian age is suggested. However, the nexinal body in *A. jardinus* is sometimes being divided into two parts. Based on this and on the morphological similarities, size ranges and the patterning of the reticulate exines in all members of the species, a dimorphism might be suggested.

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

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

mammoth have been found *in situ*, to be able to reconstruct a late Pleistocene ecosystem. The picture that arose is that of a waterbody surrounded by rather dry grassy plains with a diverse flora and fauna.

**A scolopendromorph centipede from the Cretaceous Crato Formation of Brazil**

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

**Micropalaeontology of Oligomiocene deposition, southwest of Tehran, Iran**

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Saveh is located in central Iran 120 km of southwest of Tehran. Most of the area is covered by plutonic and volcanic masses of Eocene to Miocene age, and Quaternary fluvial and lacustrine deposits, but lesser outcrops of limestone and marble also occur. The thickness and percent of marble increase from east to west, and 120 samples from limestone beds were taken from north and northwest of Saveh for palaeontological and stratigraphical investigations. Thin sections were studied for microbiostratigraphic aims.
This study has recognized important species of foraminifera, such as *Neoalveolina melocurdica*, *Peneroplis evolutus*, *Dendritina rangi*, and *Meandropsina iranica*. This fauna indicates a Burdigalian (Lower Miocene) age, and microfossils such as *Miogypsina irregularia*, *Miogypsinoides complanata*, *Operculina complanata* and *Amphistegina lessoni*, which range from Aquitanian to Burdigalian indicate equivalence to members C4, E and F in the stratotype. This indicates that during the latest Aquitanian and Burdigalian The Qum sea north and northwest of Saveh covered the Tertiary volcanic masses, depositing coral limestone and marble. The Qum sea was a continental and warm sea with coral reefs which have low dip in this area.

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

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*Undichna*, trails produced by swimming fish are relatively uncommon within the fossil record. Alluvial deposits of the St. Maughans Group (Lower Old Red Sandstone, Early Devonian) of Tredomen Quarry, near Brecon, South Wales have yielded the oldest known trails of swimming fish as well as body fossils of heterostracan and osteostracan vertebrates. *Undichna unisulca* comprises

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

**phytoPal: a database of Palaeozoic phytoplankton**

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

**The synonymy of the osteolepid fish *Thursius***

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In 1888 Ramsey Traquair created the genus *Thursius* to accommodate *Dipterus macrolepidotus* and a new species *Thursius pholidotus*. Later, in 1948 Erik Jarvik created a new species *Thursius moythomasi* based on scale row counts and differences in the proportions of the plates of the head. The two authors whilst conducting fieldwork in Scotland have found it difficult to distinguish between *T. macrolepidotus* and *T. moythomasi*. On examining Jarvik's description and specimens used, we have discovered that the two species actually represent the two end ranges of a very variable species. We have also collected many new specimens that fit between these ranges and so *T.*

*moythomasi* must be regarded as a synonym of *T. macrolepidotus*. In the course of this study, it has also been found that *T. pholidotus* is so different from *T. macrolepidotus* that it cannot belong in the same genus (a view also suggested but not acted on by Jarvik) and we propose the new genus name *Andrewsia* to accommodate this species. We have also found that the various worldwide species referred to *Thursius*, where generically diagnostic, belong in *Andrewsia*.

**Upper Carboniferous syncarid crustaceans from the Montceau Lagerstätte (France)**

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

**On the palaeoecology of dolichosaurs (Squamata)**

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

that may have foraged within small crevices and/or utilized a predatory strike. Overall, the palaeoecological evidence shows that dolichosaurs share similarities with the Upper Cretaceous limbed snake *Pachyrhachis*.

**Simulating evolution of shape over palaeontological timescales**

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Evolution of morphology can be simulated using the covariance matrix of geometric morphometric variables. This method automatically incorporates correlations from functional integration or developmental constraints, because these are embedded in the matrix. The matrix is first rotated to its principal components and a time-series simulation is applied to each individually. The collective results of the simulations are rotated back to the original shape space to produce the end morphology. The simulation can incorporate different evolutionary models, from completely random to highly constrained.
This method can be used to study the relationship between microevolution and macroevolution. When the matrix is based on a single species, the simulation can be run for millions of iterations (representing the number of generations elapsed over palaeontological time scales), and the results compared to real morphological differences between taxa. Any disparity indicates that the model or rate is not realistic. Application to mammalian molar shape suggests that either strong stabilizing selection, small rates of evolution, or low heritability have been the case because unconstrained evolution, even at moderate rates, produces results that are too disparate.

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

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Almost all aspects of modern conodont palaeontology, including systematics, taxonomy, palaeoecology and palaeobiology rely on an understanding of conodonts as skeletal apparatuses, not just as isolated elements. Unfortunately, the conodont fossil record consists almost entirely of disarticulated remains, and for the vast majority of taxa the skeletal apparatus must be reconstructed using indirect methods. The confidence that can be placed in these reconstructions varies, but even the best are nothing more than hypotheses, the ultimate test of which is the discovery of the constituent elements as an articulated skeleton.
Among conodonts with morphologically complex apparatuses, taxa currently assigned to the order Prioniodontida are particularly problematic because articulated skeletons have been described from only two species, and there is uncertainty concerning the number of elements in prioniodontid apparatuses. This is frustrating, because the prioniodontids are important in understanding the evolutionary history of complex conodonts. The discovery of a partial skeleton of *Distomodus kentuckyensis* Branson and Branson, only the third prioniodontid to be described from a natural assemblage, has a direct bearing on these uncertainties.

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

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The elongate sphenodontid *Pleurosaurus* currently contains two species. *Pleurosaurus goldfussi* is known from the Solnhofen Formation of Germany while *P. ginsburgi* is described from the Canjuers Formation, of France. The latter species has been hypothesised to represent a more advanced stage in aquatic adaptation, with a greater reduction in forelimb length and increase in body length. Recent discoveries have cast doubt upon this distinction. The species are now thought to coexist spatially and temporally. Furthermore, the presence of intermediately proportioned forms from Solnhofen questions their morphological separation. The present study incorporates data from over fifty pleurosaur specimens. Multivariate and bivariate statistics have been used on numerical data such as humerus length, skull length and presacral length. The results support the presence of two adult morphologies, varying in limb proportions.
The current investigation reveals no other metric or qualitative anatomical differences that support the division made by limb proportions. Because of the spatial and temporal co-occurrence of these morphologies, as well as the small degree of difference between them, I do not consider them separate species but prefer their interpretation as sexual morphs of *P. goldfussi*.

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

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Preliminary study of an echinoderm fauna from the late Viséan of the Montagne Noire, southern France suggests that it is more similar to faunas of comparable age in Britain and Ireland than to those in north Africa. Late Viséan crinoid faunas from the former areas contain few camerates, whereas coeval faunas from the Béchar Basin, Algeria are characterised by a diverse assemblage of camerates. The fauna under study contains the following taxa which also support affinities with faunas from Britain and Ireland: the codiacrinids *Cydonocrinus* and *Lageniocrinus*; a new genus of allagecrinid, known previously only in northwest Europe and a new species of *Litocrinus* known previously only in Ireland. The suggested faunal affinity will be further strengthened if it can be confirmed that the aberrant blastoid *Astrocrinus*, tentatively identified from a fragment on the basis of its distinctive ornament, is really a part of the fauna from the Montagne Noire. An unexpected component of the crinoid fauna is the codiacrinid *Clistocrinus*, reported previously only from the Pennsylvanian of Alaska.
Palaeogeographical reconstructions of Tethys during the Mississippian generally show the ocean closing to the west so that the Montagne Noire on the Euramerican Plate and the Béchar basin on the advancing Gondwana Plate were in close proximity. The evidence from the echinoderm faunas suggests that the western end of Tethys closed later than late Mississippian. Analysis of the palaeobiogeographical affinities of the rich faunas of brachiopods, bryozoans and corals from the Montagne Noire is required to substantiate this suggestion.

**Phosphatized embryos from the Lower Cambrian of Kuanchuanpu, China**

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Insoluble residues of the Kuanchuanpu Lagerstätte contain abundant phosphatized globular bodies.

Among these, two types of unambiguous microfossils can be distinguished besides numerous globules with a polygonal surface pattern of equivocal biotic origin.
One of these microfossils is *Olivooides* Qian 1977, for which a developmental series including presumed postembryonic, i.e. hatched, stages has been described recently (Yue and Bengtson 1999). The morphology of the postembryonic stages, which are rare, suggests the presence of more than one species. One of such specimens exhibits a pentaradial symmetry on the whole body, as it is present in the embryonic stages but differing from the postembryonic stages described by Yue and Bengtson (1999; they show pentaradial symmetry only at their apex).
The second kind of globular microfossil so far undescribed can be readily distinguished from *Olivooides* by its considerably smaller size and different topography. Here, too, a developmental series can be recognized, although the available range of stages is far narrower. Postembryonic stages are absent, which makes determination of the direction of development difficult. On one pole of the globe, the presumed embryo bears an array of plate-like compartments. The fossil displays biradial symmetry, therefore it is not possible to determine an anterior-posterior orientation. Structures on the opposite pole of the fossil are less prominent, but a smooth region delimited by furrows can be discerned. Because of the limited insight in the developmental series, with the absence of postembryonic stages, attempts towards a phylogenetic placement were not successful so far. Our foremost aim at this point of investigation is the adequate documentation of this microfossil.

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

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

**A new cheloniellid arthropod from the Ordovician of Morocco**
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Cheloniellids are rare and poorly-known Palaeozoic arachnomorph arthropods characterized by a

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

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

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

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**Missing molluscs: captured in the Carboniferous!**

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

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

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The occurrence of three-dimensionally preserved digestive tracts of hyoliths from the Lower Cambrian of the Montagne Noire, France, presents a unique opportunity to study their behavioural ecology. The guts are preserved by phosphate within orthothecid conchs and have a simple U-shaped morphology, which differs markedly from other known orthothecid guts found in Australia, France and Antarctica which are much longer and sinuously coiled.
There appears to be a correlation between conch size and gut preservation potential in that only very small conchs (<3mm) contain the preserved guts. This may be related to the presence of a detached operculum in the juvenile which could be withdrawn into the shell creating a sealed microenvironment in which preservation of the soft-parts was possible. If so, it is possible that juvenile orthothecids possessed fairly simple digestive tracts which lengthened and coiled when reaching adulthood, presumably as a result of a change in diet and/or gut to body volume ratio. Occurrences of well preserved guts in hyolithids shows them to also have a simple U-shaped morphology, although this is in an adult form, raising the possibility that the hyolithids and orthothecids may be linked by heterochronous evolution.

**The morphology of *Platystrophia* group (Brachiopoda)**

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Ongoing revision of the Ordovician to early Silurian rhynchonelliformean brachiopod genus *Platystrophia* from Laurentia, Avalonia and Baltoscandia has led to an improved understanding of

their morphology. It concerned a spinose ornamentation, dorsal cardinalia, median septum and adductor scars. The hollow spines on the external shell surface show two types in their diameter and density: (1) 0.05 to 0.08 mm in diameter (on well preserved specimens they are large curved, ‘hook-shaped’), 45- 60 per mm2; (2) 0.03 to 0.06 mm in diameter (orthogonal spines), 90-120 per mm2. Three types of cardinalia are identified. Two are comparable with those previously named by Schuchert and Cooper (1932, p. 37) as the “*Orthis*-*Hesperorthis* type” and the “*Plectorthis* – *Hebertella* type” and the third was described by Jin (1989) in the *Platystrophia*-like genus *Gnamptorhynchos*. There are two different arrangements of the posterior adductor scars in dorsal valve: (1) closely placed posterior adductor scars divided by a strong median septum; and (2) widely separated posterior adductor scars lacking a median septum. Morphological diversity amongst taxa presently referred to *Platystrophia* has direct implications for its taxonomy and our understanding of the evolutionary and biogeographic history of the genus.