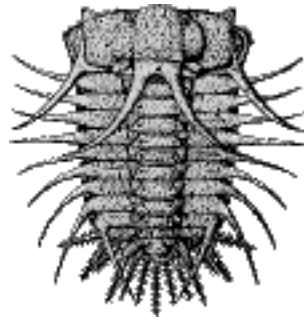


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Abstracts

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Trilobites, phylogenetic context, and the Palaeozoic Evolutionary Fauna

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Trilobites represent the dominant component of Sepkoski's (1981, 1984) Cambrian Evolutionary Fauna. As a clade, they reached peak taxonomic diversity from the Late Cambrian to the Middle Ordovician. Their subsequent history reflects crisis at the end-Ordovician mass extinction followed by continuous reduction until their end-Permian disappearance. Conventional interpretation of this pattern recognizes a transition near the base of the Middle Ordovician (Whiterockian), involving a shift in marine communities from earlier trilobite-dominated assemblages to articulate brachiopod-rich faunas of the rapidly radiating Palaeozoic Fauna. The actual mechanisms remain controversial (e. g. passive dilution *v.* active displacement), but there is little question that trilobites as a whole became relatively minor components of many mid-Palaeozoic communities.

The overall pattern of Ordovician-Silurian trilobite decline is, however, misleading. While the clade as a whole was in quantitative taxonomic decline, no single natural subgroup of trilobites has a diversity history corresponding to this cumulative pattern. In addition, the best available estimates of trilobite alpha diversity (Adrain and Westrop, 1996) indicate stasis in within-community trilobite species richness from Upper Cambrian to Upper Silurian.

This disparity is accounted for in part by a new phylogeny-based compilation of trilobite generic abundance. When post-Ordovician trilobites are resolved as suprageneric monophyla, these clades

may be traced to encompass their Ordovician origins. Collectively, the subset of overall trilobite diversity thus identified overwhelmingly displays a coordinated pattern of explosive and sustained mid-Ordovician to Silurian diversification. Post-Ordovician trilobites are conventionally viewed as the dwindling 'tail' of Cambrian Fauna diversity. It may be more accurate to consider this group on its own merits: as a robust participant in the initial establishment and success of the Palaeozoic Evolutionary Fauna.

A coral-algal reef from the Lower Cretaceous of Portugal

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Despite the profusion of late Jurassic coral-algal reef communities, by the late Cretaceous carbonate platforms were typically ramps characterised by rudistid-foraminiferal associations. The carbonate-siliciclastic succession of west central Portugal contains a true coral-algal reef, which evolved during this period of apparent decline of such buildups. This succession consists of highly cyclic deltaic, estuarine and shelf clastics interbedded with lagoonal to shelf carbonates. These provide evidence of frequent environmental change and along strike variations in sediment input and nearshore dynamics. This is illustrated by the development of a reef, of Hauterivian age, in only one section. Facies analysis indicates that reef stabilisation occurred on a muddy shelf substrate following a delta-abandoning transgressive event. The initial phase of reef growth was strongly influenced, and periodically interrupted, by the sporadic increased influx of terrigenous clay.

Palaeoecological analysis has identified the presence of i) an organic framework, in which three biofacies exist representing fore-reef, reef-crest and reef-flat, and ii) relief, inferred from the presence of thick channel fill successions, forming penecontemporaneously with reef growth. The latter are analogous to the energy dissipating channels found in the recent reef of Discovery Bay, Jamaica. Despite the presence of reef building metazoans in sections of the same age along depositional strike, a true reef only developed in the Cabo Espichel section. Rudistid bivalves, normally important contributors to Cretaceous reef biota, are completely absent from the section, both in the reef structure and the associated lagoonal facies. This study illustrates and accounts for the apparently unusual environmental conditions which led to the development of this reefal buildup.

Ultrastructure of a Silurian dendroid

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Fragments of stipes of ?*Dendrograptus* sp., from the Silurian of Gotland, are described using the SEM and TEM. Young specimens have thin walls, and denticulate thecae; gerontic specimens have greatly thickened walls. The fusellum is formed of fuselli with thin (0.13 mm) fibrils orientated at 40-70 to the surface of the previous fusellus, bounded by a compact granular layer with thicker (0.2 mm) smooth fibrils loosely embedded in it. The cortex is formed of similar granular layers again with smooth (0.3-0.5 mm) fibrils. Differences between this ultrastructure and those described in *Dictyonema* and other dendroids are discussed.

Dinosaurs and other tetrapods in an Early Cretaceous bauxite paleosol, NW Romania

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The bauxite mine at Cornet, near Oradea, north-western Romania, produced thousands of bones in an excavation in 1978, representing ornithopod dinosaurs, and rare pterosaurs and supposed birds. The fossils are disarticulated bones in good condition which occur in highly concentrated lenses within bauxite clays, which are dated as Berriasian (earliest Cretaceous). The bauxite represents detrital material washed into deep fissures and caves formed within a karst of uplifted Tithonian (latest Jurassic) marine limestones. The area represented one of several islands on the northern shore of Tethys, and it was inundated by the sea later in the Early Cretaceous. The ornithopod dinosaurs may represent several taxa, but they are smaller on average than an assemblage of typical Wealden ornithopods, perhaps because of dwarfing on the island. The fauna is geographically significant since it shows relationships with Western Europe, and with Asia. It is also the oldest reported assemblage of several bird species.

Architectural innovations in trimerophyte derivatives in the Middle Devonian flora

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Although primitive plant groups persisted into the Middle Devonian, the main innovations in plant architecture were to be found amongst those plants derived from the Lower Devonian trimerophyte lineages. The ribbed xylem column of the main axis of these plants, together with lateral dichotomous branching systems, may have been the basis for the eventual emergence of iridopterid, cladoxylopsid and progymnosperm organisations which become prevalent in the Middle Devonian. Recent observations on Middle Devonian plants from Venezuela (collected on a Sylvester-Bradley Award-funded expedition), Scandinavia, Europe (in collaboration with Muriel Fairon-Demaret) and the USA have provided new data on the morphology and anatomy of plants within the complex of potential trimerophyte derivatives. From this new information it is hoped to establish a clearer understanding of radiation within this group, particularly with regard to the as yet enigmatic origins of ferns and horsetails.

***Anaspyroceras pseudocalamiteum* (Barrande, 1852) (Cephalopoda) in the Scyphocrinites Bed of the Carnic Alps**

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Anaspyroceras pseudocalamiteum (Barrande, 1852) (Cephalopoda), well known from the Silurian of the Prague Basin, Sardinia, and Tajmyr (Eastern Siberia), is recorded for the first time from the Scyphocrinites Bed of the Carnic Alps (Austria). Morphological features and facies distribution reflect a pelagic adaptation of the molluscs.

Soft-bodied fossils from a Silurian volcanoclastic deposit

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A remarkably preserved assemblage of fossils from the Silurian (Wenlock Series) of Herefordshire, UK, falls within a 100 million year interval from which few soft-bodied animals are known. The relatively deep water marine environment represented is dominated by new arthropods and polychaetes. This is the first report of soft-bodied fossils from carbonate concretions within a volcanic ash deposit. The discovery identifies an important new source of evidence of the evolutionary history of soft-bodied taxa.

Exploration of a new method to assist in phylogenetic analysis and evolutionary pathway reconstruction

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A simple, non-cladistic, statistical test is described, which when computerised reveals much about the internal structure of phylogenetic data. Theoretical models suggest that this test can identify convergent and 'noise' characters as well as hierarchical ordering of characters, which has a direct correlation to a character's position within the sequence of character appearance. Similar structures have been found in the exploration of real data sets. Where multiple data sets exist for a given collection of phena (e.g. morphological, chemical, behavioural and DNA) similar patterns of species radiation can often be produced from the differing data sets. However, the trees commonly differ from those produced by cladistic methods. At its most basic level this method may provide one possible way of assessing character weights.

Guts and guano: a record of Cambrian alimentation

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Active accumulation and processing of organic material is basic to metazoan biology; thus, a record of Cambrian-age guts, gut contents, and faecal pellets/strings should help to illuminate the development of modern marine ecosystems, as well as the autecology of individual forms. Fossilized guts are limited to instances of exceptional preservation and are conspicuous in a number of the Burgess Shale fossils. The gut of the priapulid *Ottoia*, for example, is essentially a straight tube which occasionally includes its metazoan prey. By contrast, the gut of *Leanchoilia* has a highly convoluted internal structure, probably an adaptation to maximize surface area; small spheroidal structures conceivably represent symbiotic gut bacteria. A phosphatized gut in a hyolithid from the Middle Cambrian Mount Cap Formation shows it to have been U-shaped, but otherwise unconvoluted.

Faecal material is abundant in the Mount Cap and the Middle Cambrian Hess River formations and includes extensive bedding-plane accumulations of millimetre-sized pellets, strings and curiously segmented structures. Organically preserved pellets/strings often contain spheroidal acritarchs - presumably phytoplankton - and a general absence of bioturbation suggests that most of this material is the product of zooplankton/nekton.

In addition to increasing potential ecosystem complexity, the repackaging of organic material into relatively concentrated faecal structures must have had a profound impact on the distribution and biogeochemical cycling of C, P and N through the Precambrian/Cambrian transition. The induced feedback effects likely played a central role in determining the course of the Cambrian explosion.

Gotland chitons and Silurian rocky shores

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New silicified assemblages of Silurian chitons (Polyplacophora, Mollusca) from Gotland, Sweden are diverse. Previously described taxa comprise *Chelodes* and *Gotlandochiton*, and although the large, thick sclerites of *Chelodes* are known more widely, records of early Palaeozoic chitons are few. The new material is dominated by a new *Chelodes* species, in sufficient numbers to demonstrate growth patterns, and several plates from one animal although no articulated specimens are present. Other genera are mostly less robust and smaller, and include several with holoperipheral growth, usually restricted in Recent chitons to tail sclerites. Muscle insertion scars are used to reconstruct function of sclerites, which lacked the insertion plates for articulation found in Recent chitons.

Several of the Silurian genera were elongated animals, without or with limited overlap between plates, or with individually elongate plates. Others were smaller and more ovoid in form, similar to Recent chitons. Most modern chitons are sluggish grazers in intertidal or upper littoral zones of rocky shores, clinging onto rocks using the wide attachment area of the muscular foot. Gotland chitons are restricted to very few localities, in inshore, shallow shelf facies. Rocky shore environments are rarely preserved, but the localised distribution of Gotland chitons at intervals during Wenlock and Ludlow times appears to reinforce evidence for shoreline proximity.

Vertebrates from the Tetori Formation (Lower Cretaceous) of Japan

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The Tetori Formation contains the only major microvertebrate assemblages from Japan. The bone-bearing sediments described are located near Shokawa Village, Gifu Prefecture, central Japan. A variety of taxa, including fish, amphibians, reptiles and birds, is preserved in fine-grained terrestrial/freshwater sediments. The fossils are generally well preserved, with no sign of *in situ* weathering and only slight abrasion.

A phylogenetic classification of the Bivalvia

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The early Ordovician was the period when bivalves first diversified. By the close of Cambrian times, all known bivalves appear to belong to one family, but by the end of early Ordovician times no fewer than 18 families have been hitherto recognised and these can be assigned to six subclasses. With the recent description by the author of a large early Arenig bivalve fauna and the identification of the probable origin of the filibranch gill, it has been possible to identify the likely origins of the principal bivalve groups. Parsimonious analysis of characters of the subclasses has allowed the probable shell microstructure of early Ordovician forms to be determined and a picture has emerged of the fundamental diversification of the Class Bivalvia. Most of this diversification occurred within the early Ordovician, but the evolution of the seventh subclass occurred later, probably in late Ordovician times. No further bivalve subclasses evolved after this time and the Bivalvia appear unique in being the only major invertebrate group in which all subclasses (or comparable higher-level taxa) are extant.

Could we still study isolated primitive shark teeth without a SEM?

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Since Reif's (1973) work, neoselachian sharks teeth have been easily distinguished from those of

hybodont sharks on the basis of their enamel ultrastructure. The latter have a Single Crystallite Enameloid (SCE) while the neoselachians possess a triple-layered enameloid. In 1993, however, Duffin described *Rhomphaiodon nicolensis* from the Upper Triassic of northeastern France, a species that he attributed to the neoselachian sharks because of its triple-layered enameloid, although the external morphology of the teeth is practically indistinguishable from that of the genus *Hybodus*. Recently, my own work has revealed a triple-layered enameloid in a new taxon from the Upper Triassic of the Jura (northeastern France) and, again, the morphology of these teeth is very close to that of a *Hybodus* shark. Teeth from *Hybodus minor*, from the Rhaetic of England, display a Parallel Fibred Enameloid (PFE) very different from the SCE of hybodont sharks. Finally, some teeth from the Rhaetic of the Jura have a very similar morphology to those from the neoselachian *Synechodus* but display a SCE.

It appears that if the ultrastructure of the enameloid is truly the key feature of neoselachian sharks, a matter which could be contested taking into account the new discoveries described above, it becomes impossible to study isolated shark teeth without the use of SEM.

Mammal-like occlusion in conodonts

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Two main debates have featured in the last 140 years of conodont palaeobiological research. The first, concerning the affinities of conodonts, is drawing to a close, and many now recognise the animal as possessing the earliest vertebrate mineralised skeleton. The second debate, concerning the function of conodont elements, remains contentious because of an almost complete lack of direct evidence, which has resulted in a number of competing hypotheses. Recently, new evidence has provided unequivocal support for a tooth-like function and raised a number of important new questions.

The evolution of teeth is believed to have been closely linked with the evolution of jaws, the structure upon which they are borne and articulated. Many types of tooth function require a great degree of control and according to traditional hypotheses this can only be provided by jaws. Conodonts did not possess jaws, and new research into the functional morphology of pairs of elements dissected from bedding plane assemblages has indicated that some taxa performed sophisticated tooth functions rarely recognised outside mammals. How did conodont elements perform any tooth function, least of all one that requires the greatest degree of spatial control of all dental mechanisms? The answer to this question lies in the complex morphology of the elements themselves. Many conodont elements in posterior positions developed long anterior blades which performed a jaw-like function, acting in a manner which restricted movement of the functional surfaces to one of strict opening and closure in a plane parallel with the blades. This type of element motion restricted possible function to one of crushing.

Chasmataspids - not the ancestors of arachnids

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Chasmataspids are a rare and problematic group of Palaeozoic arthropods, which have variously been allied to the Xiphosura, Eurypterida and Arachnida. Chasmataspids are known from two occurrences, the Ordovician of Tennessee and the Devonian of Germany, and the Ordovician and Devonian forms are quite distinct. However, both types are characterised by a unique pattern of opisthosomal segmentation with a 3-segmented preabdomen and a 9-segmented postabdomen. Restudy of the

original chasmataspid material has allowed a revised interpretation of their morphology, particularly with respect to their respiration, and new reconstructions of the fossils are presented. Chasmataspids represent a distinct taxon within Chelicerata, diagnosed on their autapomorphic opisthosomal differentiation, and are provisionally placed as sister group to Arachnida + Eurypterida. An unpublished Upper Cambrian trace fossil may have been made by a chasmataspid and if so this would be evidence for the oldest unequivocal occurrence of chelicerates in the Cambrian.

Orthoconic nautiloid accumulations in the upper Ordovician of Cumbria

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Concentrations of orthoconic nautiloids from the Keisley Limestone were collected during the previous century, most of which are now preserved in museum collections. The configuration of the orthocones within individual blocks suggests the presence of steep palaeoslopes in the vicinity of Keisley.

A second accumulation of orthocones was noted by McNamara (1978) from the Troutbeck Formation of the Dent Group above Troutbeck. McNamara considered that the distribution of these orthocones was random, while the shells were trapped in a stromatolitic overgrowth. Recent study of this accumulation suggests that the distribution of orthocones may not be random. The stromatolites, combined with a virtually complete lack of other organisms, suggest that this may represent a rather unusual environment in the upper Ordovician of northern England.

Paddling in the Portlandian: A new record of dinosaur footprints from the Purbeck/Portland transition, Portland

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A new set of dinosaur footprints has been discovered on the Isle of Portland on an exposed bedding surface in a disused quarry. The footprints are shallow impressions of small (up to 14 cm in length), broad three-toed prints, very similar to those made by bipedal tridactyl ornithopods such as *Iguanodon*. They do not appear to form a distinct trackway, more of a 'meandering stroll' assemblage. The footprints occur on the upper surface of a transitional bed between the underlying marine shelly oolites of the Portland Stone Formation and the overlying palaeosols and algal limestones of the Purbeck Lulworth Formation. This bed represents a change from high energy carbonate shelf facies to shallower, lower energy conditions prior to the onset of terrestrial soils/hypersaline lagoon environments. This is the lowest stratigraphic occurrence of footprints known in the Purbeck Group, since previously recorded footprints occur much higher in the Middle Purbeck Durlston Formation. These footprints show that ornithopod dinosaurs paddled happily in the shallows of the Portlandian seas in the Mediterranean climate that prevailed at that time.

The taphonomy of the Soom Shale (Ordovician, South Africa): how geochemistry affects preservation

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In the fossil record the most common authigenic mineral to replace soft tissues is apatite; more rarely, and usually with less fidelity, replacement by pyrite and carbonate has occurred. However, the soft tissues in the Soom Shale are uniquely composed of clay minerals. Under the anoxic-euxinic conditions which prevailed in the Soom Shale depositional basin, in the presence of cations, colloidal

clay particles may have had an affinity for organic substrates. This unusual taphonomic pathway may have been a consequence of low carbonate and iron concentrations in the sediment; hence there was no mechanism to buffer or fix the H₂S produced by organic matter decomposition. The hydrodynamic and geochemical properties of constituent sedimentary elements may influence the likelihood of soft-tissue preservation in any black shale. In particular, it seems that deposits where soft-tissue preservation occurs are characterized by a low ratio of heavy elements contained in detrital minerals (e.g. Si, Zr, Ti) against organic carbon and V, Cu, Ni, Mo, and/or phosphate and rare earth elements. This observation provides promise of a geochemical method for prospecting for new black shale lagerstätten.

Evolutionary response by bivalves to changing Phanerozoic sea-water chemistry

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Sedimentological evidence suggests that sea-water chemistry has oscillated between 'Aragonite' and 'Calcite' seas during the course of the Phanerozoic. During 'Calcite' sea periods aragonite was highly unstable and dissolved rapidly on the sea-floor. Here we propose, using a survey of familial diversity, that during times of such corrosive seas bivalved molluscs which secreted their shells entirely of aragonite were at a selective disadvantage compared to those with calcitic outer shell layers. This is the first case in which it has been suggested that there was a dynamic link between sea-water chemistry and the evolution of a particular taxon throughout the Phanerozoic.

***Teredolites*-infested log-grounds from the Cretaceous of the Cauvery Basin, South-East India**

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A rich assemblage of *Teredolites*-infested log-grounds is described from the Garudamangalam Sandstone Formation (Upper Turonian - Coniacian) of the Cauvery Basin, SE India. The borings, possibly created by the boring bivalve *Opertochasma* sp. are described. The abundance of log-ground material within this part of the Cretaceous succession is used to assist in the determination of the sequence stratigraphy of this mid-Cretaceous succession. The log-grounds are associated with some quite considerable tree fragments (one of which is 18 m in length), monospecific shell banks and conglomeratic horizons.

The log-ground fauna was discovered as part of a complete re-assessment of the lithostratigraphy and biostratigraphy of the Cauvery Basin; an area made famous by the classic works of Blanford, Stoliczka and Kossmat. The basin was formed by the rifting of India from Antarctica during the Early Cretaceous, preserving an interesting mid-Upper Cretaceous marine succession. While parts of the succession record sea-level changes induced by local tectonics, an occurrence of these log-grounds in the Late Turonian - Coniacian confirm the global effect of the Late Turonian regression.

Late Cretaceous angiosperm leaf floras of the Antarctic Peninsula

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Using previously unstudied plant fossils from the late Cretaceous strata of the James Ross Basin,

Antarctic Peninsula, new information is provided about the composition of southern polar forests. During this period, the volcanic arc now represented by the Antarctic Peninsula was at about 65 S. However, the area was extensively forested and would have provided a major gateway for biotic exchange between east and west Gondwana. The Cretaceous to Tertiary sequence of the James Ross Island area is one of the most complete in southern Gondwana and many of the floras within it are amongst some of the best preserved in the southern hemisphere. The Hidden Lake Formation of Coniacian-Santonian age within the Gustav Group contains plant fossils occurring as impressions in the sandy siltstones. Despite the lack of cuticle, the marginal features and venation patterns of the angiosperm leaves are clearly visible and taxonomic identification is possible through the morphological analysis of characters such as these. Initial studies show that a range of angiosperm leaves are present, including members of the Lauraceae, Nothofagaceae, Annonaceae and Proteaceae. These leaves represent the remains of temperate rainforests that grew in this area of Gondwana during the Cretaceous and many aspects of the flora are analysed to determine the palaeoclimate of this region.

A carbon and oxygen stable isotope stratigraphy for the early Silurian of Estonia

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The Early Silurian was a time of recovery following the Ashgill extinction, however there were smaller extinctions in plankton and benthos during the Llandovery. Recent studies of Late Ordovician events have shown that the Ashgill extinction was associated with a period of major glaciation, related glacio- eustatic sea level changes and a large positive excursion in ^{18}O and ^{13}C in marine carbonates and organics. It has been suggested that the Early Silurian events are also related to changes in ocean state, or sea- level fluctuations associated with climatic change. To test this model a carbon and oxygen stable isotope stratigraphy is being established for the Llandovery and lowermost Wenlock. Data have been obtained from brachiopod calcite from Estonian shallow water carbonate sequences, chosen for their shallow burial and low thermal maturity. Results of the initial analyses show a gradual trend towards more negative ^{18}O values through the Llandovery, and nearly constant values of ^{13}C except for two small positive excursions (2 and 1 perthousand) which are based on limited data. In the early Wenlock there is a large positive excursion in both oxygen (2 perthousand) and carbon (3 perthousand) which persists for three graptolite biozones and is associated with extinctions amongst planktonic faunas.

Stable isotopes in the shell of the queen scallop *Aequipecten opercularis* (L.) as indicators of Holocene palaeoenvironments in the North Sea

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Stable isotope profiles of bivalve shells have proved useful tools in the reconstruction of palaeotemperatures and other palaeoceanographic variables. Cores of North Sea Holocene sediments taken by the Land-Ocean Interaction Study (LOIS) contain well-preserved shells of the queen scallop *Aequipecten opercularis*. Living scallops were grown over winter to establish that growth occurs in this season, and analyses of the shells of the scallops cultured under monitored conditions have confirmed that shell carbonate is laid down at or close to isotopic equilibrium. Good correlations have been obtained between the isotope ratios of scallop shells grown in the same net. Several of the sub-fossil shells have been serially sampled to give information on seasonal changes in environmental conditions and have revealed isotope profiles that show fine- scale seasonal

information. The results obtained show the utility of *Aequipecten* as a palaeoenvironmental indicator.

Silurian nautiloids from the Carnic Alps

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The Carnic Alps form a mountain chain along the Austrian-Italian border west of the village of Villach in the province of Carinthia. In this region, a dominantly carbonate sequence ranging from the Upper Ordovician to the Lower Carboniferous is exposed. The fossiliferous Lower Palaeozoic sequences exhibit four marine facies representing platform to basinal environments. The Wolayer and Plocken facies of the central Carnic Alps have long been famous for their rich occurrence of cephalopods and the Silurian '*Orthoceras*' limestone facies at the Cellon and Rauchkofel sections are being studied in detail with regard to their biostratigraphic potential.

A detailed study of the taphonomic features and palaeoecology of the Lower Silurian nautiloid fauna from these two sections in the Carnic Alps is discussed with regard to minor changes in sea-level within the sequence and possible environmental settings for the nautiloids based on their hydrostatic limits.

Origin and radiation of the Trimerellida (Brachiopoda, Craniiformea)

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Trimerellides are some of the most distinctive elements in mid to late Ordovician and early Silurian warm water brachiopod faunas from low palaeolatitudes. They were long known mostly from the Silurian, but with recent discoveries of diverse trimerellide faunas from the mid and late Ordovician of Australia, South China, and Kazakhstan it is now evident that these enigmatic, often very large brachiopods evolved rapidly and diversified mostly during the Caradoc and early Ashgill. In general, trimerellides apparently tended to form low diversity, high density communities in shallow, low energy marine environments, although some Silurian associations formed high-energy banks. The Kazakhstani terranes have yielded the earliest known trimerellides, where they occur just below the first appearance of graptolites suggesting a late Llandeilo or early Caradoc age (*Nemagraptus gracilis* Biozone). This assemblage includes *Ussunia*, which appears to retain many craniopside-like characters. The Order Craniopsida is the most probable ancestral group.

The most diverse Ordovician trimerellide faunas known are from Kazakhstan, South China and Australia, whereas in other regions they are represented usually only by one, rarely two genera. The observed pattern of geographical distribution of Ordovician trimerellides can be explained as the result of two major migrations from the Kazakhstani terranes: 1) during the early Caradoc, to South China, Gondwana (Australia) and Laurentia (North America); 2) during the late Caradoc, to Baltica and Angaria. The Ordovician trimerellide fauna from South China is unique in that it contains taxa with excavated and vaulted visceral platforms (e.g. *Trimerella*); this pattern of shell morphology is otherwise unknown in Ordovician trimerellides, but became widespread in the Silurian. Nearly all local trimerellide lineages outside of South China and, maybe, Australia became extinct just before the Hirnantian, and there is no record of trimerellides in the Hirnantian and Rhuddanian brachiopod

faunas. They re-appeared in the mid- to late Llandovery (mostly *Dinobolus*). During the Wenlock, trimerellide faunas dominated by *Monomerella*, *Trimerella* and *Dinobolus* had a near cosmopolitan distribution; however, *Gasconsia* is the only trimerellide that survived into the Ludlow, after which the group became extinct.

**Appendages of the arthropod *Kunmingella* from the early Cambrian of China:
its bearing on the systematic position of the Bradoriida and the
fossil record of the Ostracoda**

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The first discovery of the appendages of Bradoriida *s.s.* (Arthropoda) - hitherto generally supposed to be ostracodes - is reported from *Kunmingella* from the early Cambrian soft-bodied 'Chengjiang' Lagerstätte of China. Although this evidence does not particularly clarify the affinities of *Kunmingella* within the Arthropoda, it does demonstrate that this genus and, by implication, taxonomically allied bradoriids in general, are neither ostracode, crustacean *s.s.* nor closely related to the Phosphatocopida (also conventionally classed as ostracodes). This has a far-reaching implication for the stratigraphical distribution and evolution of the Class Ostracoda: that much (all?) of their Cambrian record is most likely spurious. The find also endorses the fact that arthropod radiation involved several different types of convergently bivalved groups.

Quillworts from the Wealden of the Weald

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With the exception of certain horsetails, *in situ* plants are rare in the non-marine Lower Cretaceous of southern England. This is usually attributed to repeated deposition and erosion of the alluvial flood plain by Wealden rivers. Mineralised quillworts, *Isoetites* sp. nov., have been reported previously accompanied by the spore *Minerosporites*. However, these are reworked in Quaternary deposits and are not found *in situ*.

We now report the first Wealden quillworts in life position, '*Isoetites* sp. 2', from the top Ashdown Formation (Hastings Group, at Cliff End, Pett Level; near Hastings, East Sussex). Numerous plants are exposed and eroded by the sea in consolidated but uncemented fine sand showing short upright stems, leaf bases, corms and radial rootlets. Megaspore-like structures have been noted in the field, but are yet to be isolated from the matrix. An isolated *Isoetites* sporophyll with megaspore has been found in the Upper Weald Clay at Smokejacks Brickworks (near Ockley, Surrey) showing that quillworts occur in the Barremian as well as the Berriasian-Valanginian of the UK. Cliff End and Smokejacks are popular fieldwork localities and these finds demonstrate that much remains to be found in the Wealden.

A tale of two clades: differential survivorship of holasteroids and spatangoids at the Cretaceous-Tertiary boundary

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Previous estimates of extinction levels amongst echinoids at the Cretaceous-Tertiary boundary have been as high as 70% at the generic level. However, such estimates have been plagued by inconsistent taxonomic usage in the literature. To overcome this problem, a revision of Maastrichtian and Palaeocene atelostomate echinoids has been undertaken to create a taxonomically standardized data set. This demonstrates that holasteroids and spatangoids suffered markedly different fates at the Cretaceous-Tertiary boundary. Whereas holasteroids lost over 60% of their generic diversity at the end of the Cretaceous, less than 20% of the spatangoids became extinct at that time. However, a further 32% of spatangoid genera had disappeared by the Thanetian (late Palaeocene). These differential extinction levels clearly suggest that some degree of selectivity was in operation. Generic and species level cladistic analyses have been used to clarify patterns of survivorship selectivity amongst holasteroids and spatangoids and to determine the effects of geographic distribution, environment and taxonomic diversity on extinction levels. The effect of the extinctions on disparity within the two clades has also been explored.

On the small size of Bathonian (Middle Jurassic) bivalves in southern England

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Analysis of an extensive monographic database reveals that the mean size of Bathonian (Middle Jurassic) marine bivalve species from southern England is substantially less than that of Oxfordian (Upper Jurassic) forms. Subsets of the data (subclasses and life-position categories) in every case show the same pattern as the total fauna. For no subgroup is the mean size of Bathonian forms greater than 75% that of Oxfordian species, and for some it is less than 50%. Closely-studied scallop and oyster lineages similarly provide evidence of substantially smaller size in the Bathonian, with additional indications of geographic reduction in size from south to north. Palaeogeographic and sedimentary-facies considerations suggest a control by freshwater influx from the north. The notion of reduced (or fluctuating) marine salinity appears to be contradicted by the high diversity of Bathonian bivalves in southern England and the occurrence of cephalopods, echinoderms, corals and calciate brachiopods. This conflict can be resolved by invoking a measure of adaptation to reduced salinity amongst normally stenohaline-marine taxa. An important lesson of the study is that cryptic environmental change may be involved in cases of phyletic size increase.

Sampling error and the interpretation of evolutionary patterns

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Uneven or incomplete sampling is a significant source of error in the analysis of the temporal distribution of fossils. One useful measure of sampling effort is the ratio of the number of taxa found in a particular interval to the number which occur both before and after the interval. If differential sampling exists, permutation tests can be used to assess its potential to create spurious patterns. One approach is to compare the observed evolutionary pattern to a distribution of thousands of artificial patterns generated through permutation of the stratigraphic distribution of samples. In an analysis of Neogene Caribbean coral distributions, completeness indices indicate that sampling is relatively poor

during Early to Middle Miocene time. This corresponds to periods with low estimated rates of taxonomic turnover, suggesting that accelerated Plio-Pleistocene turnover is caused by differential sampling and does not reflect real evolution. However, permutation tests refute this result, suggesting that rates of origination and extinction were higher than expected during the Pliocene. In contrast, an earliest Pleistocene extinction pulse cannot be distinguished from these data.

The skeletal taphonomy of *Archaeopteryx*: a quantitative approach

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A quantitative study of the preservation of *Archaeopteryx* shows that, even where only small numbers of individuals are involved, numerical studies can provide fresh insights into vertebrate taphonomy. The skeletal remains of *Archaeopteryx* can be assigned to two preservational types. Differences between these categories are related primarily to the length of time elapsed between death and burial, though, undoubtedly, many other factors contributed to the spectrum of decay patterns observed. There is no evidence for a regional drift pattern and the death posture of *Archaeopteryx* is best explained as a response to the conditions within the Solnhofen lagoon, most likely hypersalinity. The digital crossover on the hands of *Archaeopteryx* is interpreted as a post-mortem artefact.

How eurypterids swam

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This presentation will address the problem of how to deduce the likely locomotion of animals exclusively from fossil evidence. A computer model, based on fundamental hydrodynamic principles, has been devised in order to predict the swimming capabilities of eurypterids, extinct arthropods of the Palaeozoic. The model is tested using morphological data from the living swimming crab *Portunus puber*, whose swimming abilities and techniques are well-documented. The empirical optimal swimming scheme which is predicted corresponds well with that demonstrated by the animal, and the deviations which do occur can be explained.

A range of eurypterids, *Baltoeurypterus*, *Pterygotus*, *Salteropterus*, *Dolichopterus* and *Carcinosoma*, are examined using hydrodynamic data obtained from flume tank experiments with clay reconstructions of the animals. The computer model suggests that some species of eurypterids were highly capable swimmers, with the adults employing a range of lift-based techniques comparable with those of similar-sized marine mammals of the present. Swimming in juvenile eurypterids, on the other hand, was drag-based. The transition from one swimming mode to the other during the growth of *Baltoeurypterus* is examined.

Homologies in stylophoran echinoderms

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The Stylophora represent one of the most controversial groups of Palaeozoic echinoderms, as their organization and mode of life are interpreted differently by three rival theories. Great confusion results from this debate and there is, so far, no agreement on the orientation and on the recognition of

homologous thecal faces in the members of the two orders (Cornuta and Mitrata) into which the Stylophora are usually divided. It becomes necessary to reconsider the question, starting by delineating a clear model of homologies for all stylophorans. We stress here the importance of four of them: the aulacophore (or arm), the apophyses, the adoral plates and the zygal crest (or septum). Analysis of each structure leads to the conclusion that the flat faces of mitrates and cornutes are homologous. Consequently, the 'calcichordate' model is invalid. This investigation also shows that all Stylophora share the same basic skeletal organization and that, therefore, the distinction between cornutes and mitrates is artificial.

Between a rock and a hot place: The fossil record of hydrothermal vent communities

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Hydrothermal vents are found at mid-ocean ridges and back-arc basins in the deep-sea where new ocean crust is forming. The vent environment is a challenging one, characterised by extreme pressure, complete darkness and thermal gradients from 2 C to 400 C over a few centimetres. Yet vent sites support diverse communities of animals, including the well-known giant gutless tube worms. These communities are remarkable in many ways, not least because 95% of their constituent species are endemic to this habitat. Furthermore they rely entirely on chemoautotrophic primary production by bacteria, mainly using hydrogen sulphide in the hydrothermal fluid as an energy source. Some of the endemic vent animals have been regarded as 'relic' taxa, isolated in vent site refugia since the Mesozoic or Palaeozoic. Here I will present data from the six known ancient vent deposits that contain fossils and show that while some elements of vent assemblages have remained constant since the Silurian, the shelly fossils have changed. This suggests that vent sites are not the refugia that they were suggested to be.

Function and development of the eye in pelagic trilobites - evidence from a lower Ordovician genus

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Much is now known about the structure, operation, and ontogenetic development of the holochroal trilobite eye. Past studies have tended to focus on benthic trilobites. Some trilobites interpreted from independent evidence as having had a pelagic mode of life possessed markedly hypertrophied, globular eyes. One such is the lower Ordovician genus *Carolinites*. We can analyse these eyes in terms of general form (shape, relative size, field of view), and detailed lens arrangement (shape and size of lenses, density and style of lens packing, presence and location of areas of increased lens density) to obtain information regarding the function of the eye and hence draw inferences about its workings and the mode of life of the animal itself. In particular, calculation of the 'eye parameter' from measurements of size and angular separation of the ommatidia offers potential for characterising the photic depth at which the eye would have operated optimally, and hence the water depth in which the organism would probably have lived.

Just when you thought it was safe to go back to the water - the biggest pliosaur yet

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Kronosaurus from the Albian of Queensland, estimated length *c.* 14 m, has always been regarded as the largest pliosaur. Historical records of Oxford Clay (Callovian) faunas have indicated that another large pliosaur lived earlier (Middle Jurassic - Early Cretaceous). Comparisons of *Kronosaurus* with this historical material show that the cervical vertebrae of the Jurassic form were about 40% larger than *Kronosaurus*. Estimates of the overall length of the new form range from 17-20 m and the (mass) weight to be about 50 tonnes. This equates closely with modern whales and is larger than extant toothed whales *Orca* and *Physeter*.

Differential transport of spores within a single Devonian lake

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The Devonian of East Greenland comprises a thick sequence of continental clastic sediments. West of the main bounding fault to this basin are scattered Devonian outliers which formed within small extensional basins. One such basin is represented by the Devonian sequence on Ella Ø, where close to the basal unconformity four lacustrine beds occur intercalated with conglomerates. Detailed analysis of one lake unit shows it to have significant lateral variation. At proximal localities high on the unconformity surface it mostly comprises lacustrine turbidites whilst at distal locations were within a deep stratified lake. Significantly this lakes shows a sequence of progressive deepening with the development of stratification and anoxia followed by shallowing and ultimately drying out. Water depth estimates determined following restoration of the unconformity surface for post-Devonian tectonic rotation are of the order of 100 meters at maximum depth in distal locations.

Macrofossil plant debris within the lake sediments shows differential transport with fronds (primarily *Svalbardia/Archaeopteris*) and frond debris at proximal localities but only logs present within distal lacustrine sediments. Conspicuous within the palynological assemblages are *G. lemurata* and *C. optivus* which are the known *in situ* microspores and megaspores for *Svalbardia/Archaeopteris* and presumed to have originated from the same parent plant. Three logged sections within a single lake unit were profiled for 'absolute' abundances of microspores, megaspores *G. lemurata* and *C. optivus* in addition to spore diameter for *G. lemurata*, kerogen type, TOC calcite content and atomic H/C ratio. This provides detailed information within which to interpret changes in palynomorph abundance with sedimentary environment both laterally between sections and vertically within single sections. These data permit comparisons of differential transport between the megaspore and microspore pair and demonstrate significant changes in palynological assemblage composition occur. This has major implications for the use of abundance data in defining spore assemblages for biozonation.

Oxygen isotope composition of fossil shark teeth as a palaeoclimate proxy

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The suitability of oxygen isotope analysis of fossil shark teeth as a proxy for marine palaeotemperature determination is assessed. Shark teeth may be useful for palaeoclimate reconstruction because they are common fossils, generally well-preserved, possess a long geological history, and are readily identified to generic, if not specific level. While many forms are cosmopolitan in habitat, individual taxa are fairly conservative, allowing certain palaeoecological assumptions to be made. Shallow marine shark taxa (odontaspids, lamnids and carcharhinids) were collected from the Miocene Upper Marine Molasse of southern Germany. Jurassic shark teeth (hybodont and neoselachian taxa) from a variety of ages and marine palaeo-environments of the northern Europe epeiric sea were also analysed. The rapid growth and replacement of teeth means that the oxygen isotope composition of the tooth hydroxyapatite should not be affected by physiological or ecological changes with time, but instead, reflect temperature and isotopic composition of the water at the time of formation. A series of samples from the separate phosphatic phases (enameloid, orthodontine and osteodontine) of individual teeth was taken, to check for oxygen isotope heterogeneity across a tooth. In addition, several samples from within one sedimentary unit and across several layers were taken to evaluate inter-tooth heterogeneity and possible diagenetic alteration of the phosphate. Crystallinity is determined through XRD and trace element analyses.

Taxonomy and evolution of the Cretaceous ammonite genus *Hamites*

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Hamites and *Stomohamites* are among the most interesting of the heteromorph ammonites because they appear to show many of the morphological trends displayed by the heteromorphs as a whole. Examples of morphological variation within the genus range from simple open spirals, to ptychocones and helices. This would appear to suggest that as a group they were morphologically and functionally diverse. The *Hamites* and *Stomohamites* of southern England can be divided into a number of successive phases: Lower Greensand origins, Gault Clay diversification; and, finally, Cenomanian decline. This study uses cladistics to investigate the evolution of these enigmatic ammonites, and an ecological model is proposed.

Bioturbation and the closure of the deep-marine taphonomic window: evidence for the prosecution

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Plots of the temporal and environmental distribution of Konservat-Lagerstätten during the Phanerozoic reveal that they are overabundant in deeper-marine (slope and basin) settings of Cambrian age. To date, discussion of the role of bioturbation in the closure of a 'deep-marine taphonomic window' has been hampered by the lack of data that would allow changes through time in that specific environmental setting to be monitored.

In this study, fifty ichnofaunal assemblages interpreted, on sedimentological criteria, to have been emplaced in deep-marine settings, were considered; these spanned the interval Cambrian to Carboniferous. There are pronounced ethological differences between ichnofaunal assemblages of Cambrian and post-Cambrian age. Those of Cambrian age are dominated by examples of surficial

and near-surface repichnia, stationary domichnia, and semi-stationary fodinichnia; only 47% of the assemblages studied have single, or at most, two, examples of agrichnia and/or pascichnia. In contrast, examples of agrichnia and/or pascichnia are present in 82% of the assemblages of Ordovician age; the figures for the succeeding three geological periods are, in turn, 75%, 100% and 100%. Further, by the early Silurian (at the latest), lateral partitioning of agrichnia and pascichnia into different ecological niches within the deep-marine environment had developed; this included the establishment of equilibrium communities in more marginal ecological niches, e.g. low-oxygen environments.

The post-Cambrian introduction of a more mobile, actively-bioturbating, infauna to deep-marine environments correlates with, and may explain, the virtual restriction of Konservat-Lagerstätten to deeper-marine settings of Cambrian age.

A deep shelf trilobite fauna from the Ashgill of eastern Ireland and its palaeobiogeographical significance

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The early Caradoc faunas of the Grangegeeth terrane of eastern Ireland were closest to Scoto-Appalachian/Laurentian faunas, suggesting that the terrane lies to the north of the final Iapetus suture. A newly discovered, younger trilobite fauna containing at least ten genera confirms the mid-Ashgill age suggested by Harper and Mitchell (1982) who also documented a deep water *Foliomena*-type brachiopod fauna from the same formation. The trilobite fauna has undergone some transport and is dominated numerically by mesopelagic cyclopygids. Fewer than half of the benthic species lack or have very small eyes and thus this is not an atheloptic assemblage typical of many Ordovician slope facies. The benthic assemblage can be considered in terms of a bathymetrically arranged spectrum of faunas and is closest to that of the deep shelf *Phillipsinella parabola* - *Staurocephalus clavifrons* fauna, also known from the late Ordovician of Avalonia, Gondwana, Baltica and S.E. China. This is the first record of such a fauna from Ireland and helps demonstrate an important aspect of the late Ordovician breakdown of provincialism in the Iapetus Ocean.

Squashed heads and soft sea-beds: taphonomy of conodont apparatuses

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The fossil record of conodonts consists almost entirely of the dissociated parts of their feeding apparatus. Fossils that preserve together the skeletal elements of individual conodonts are comparatively rare, but these 'bedding-plane assemblages' and 'fused clusters' are, nonetheless, of paramount importance in the development of conodont taxonomy and anatomical notation, in apparatuses reconstruction, in the recognition of homologies and in the interpretation of evolutionary pathways. They represent the only direct evidence of the three-dimensional architecture of the conodont feeding apparatus, and have also been used to infer details of the body shape of conodont animals.

The post-mortem processes that led to the formation of these important fossils are not well understood, yet this information is vital if primary biological data are to be disentangled from taphonomic effects. From analysis of apparatus collapse patterns in bedding-plane assemblages and clusters we have determined the position of repose of dead conodonts; contrary to our expectations, the majority of conodont carcasses did not lie with the long axis of the head parallel to the sea floor.

The possibility that these counterintuitive results reflect the shape of the conodont body or head is unlikely. Rather, the distribution of conodont head collapse orientations is probably correlated with substrate density and carcass penetration.

Biotic recovery after the end-Ordovician glaciation - evidence from the conodont and sedimentary record of Anticosti Island, Québec

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The Lower Palaeozoic greenhouse was punctuated by the end-Ordovician glaciation. This resulted in a major re-organisation of the biosphere through mass extinction and subsequent recovery. Detailed sedimentary and faunal analysis of the mid- to outer shelf carbonate sequence exposed on Anticosti Island (Québec), has enabled the study of the evolutionary patterns and processes controlling conodont recovery. On Anticosti Island, the onset of glaciation occurred within the Richmondian (upper Vauréal Formation). The glacial maximum (*extraordinarius* Biozone) may be partly missing and represented by a hiatus. Initial transgression (*persculptus* Biozone) is represented by oncolite and bioherm deposition in the Point Laframboise Member. Bioherm growth was terminated by the deposition of the Becscie Formation (*acuminatus* Biozone) during the major post-glacial transgression, though carbonate deposition continued throughout the Llandovery. The initial conodont recovery was dominated by the stepwise appearance of crisis progenitor taxa, first occurring within the Point Laframboise Member. Cyclic increases in species diversity allowed continued recovery through the Llandovery, culminating in high diversity faunas in the upper Telychian. However, recovery was short-lived with renewed global extinction in the Upper Llandovery to Wenlock.

Relationships between Early Ordovician conodont provincialism and palaeoecology

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Two major conodont provinces existed through all but the earliest part of the Ordovician around the Iapetus Ocean. Traditionally, the Midcontinent Faunal Region characterised Laurentia and Siberia, while the North Atlantic Faunal Region included Baltoscandia and the easternmost part of Laurentia (the Appalachians and western Newfoundland). Increased knowledge of conodont life and behaviour indicates that the distribution of most conodont taxa was dependent on environmental factors, which means that it is necessary to perform palaeoecological analyses before faunal province models can be tested. The present study is based on multivariate analyses of published and unpublished presence-absence conodont data from several localities surrounding the Iapetus Ocean, all from the basal Llanvirn (*L. variabilis* - *E. suecicus* Zones in Baltica and *H. holodentata* - *P. harrisi* Zones in Laurentia). Cluster analyses demonstrate that the relatively high similarity between Baltoscandia and eastern Laurentia during the Lower Llanvirn is mainly due to the co-existence of pandemic shelf margin or slope taxa of the *Protopanderodus* - *Periodon* Biofacies and not to typical platform taxa. This indicates that the North Atlantic Faunal Region should be restricted to Baltoscandia and probably South China, and the Midcontinent Faunal Region should include the Laurentian platform as well as the eastern margin areas.

The hydrodynamics of the graptolite rhabdosome recorded by

laser doppler anemometry

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Laser doppler anemometry has been used to measure changes in fluid velocity over a range of graptolite models. Flow is seen to be altered significantly by spines on the sicula and by the morphology of thecae themselves. A single virgellar spine retards flow along the 'naked' side of the sicula and directs it instead over the thecae. More complicated sicular spine arrays in Ordovician biserial graptolites produce turbulence. Fluid is deflected over the sicular aperture, creating a small stagnant region. As fluid passes over simple thecae an area of recirculation is generated, with a small amount of fluid flowing back into the thecal aperture. When this aperture bears spines, a similar pattern is seen, but with the generation of trailing vortices which flow along the rhabdosome. Flow velocity increases between these spines. The turbulence created by spines increases with distance from their point of origination, so that fluid flow in the nema region is highly turbulent. Two important conclusions emerge. Firstly, graptolites are stable in fluids only when flow is from sicula to nema. They must have arrayed themselves in this fashion relative to motion in the oceans. In this position, with flow controlled by sicular and thecal morphology, the zooids would be unlikely to have fed within the stagnant zones of the thecal apertures. It seems more likely that they fed at some distance from these apertures, either with lophophores extended into the sea or having crawled along spines. Secondly, this tool offers a means of quantitatively assessing the hydrodynamic function of aspects of graptolite morphology and the potential to understand the specific oceanic conditions for which graptolites were evolved.

Stromatolite decline: reassessment of the concept of metazoan competition

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Apparent patterns of stromatolite abundance in the Proterozoic and scarcity in the Phanerozoic have led to the widely held view that stromatolite decline was a result of metazoan competition. But this is inconsistent with two key features of Proterozoic-early Palaeozoic microbial history: i) stromatolite decline in the Proterozoic preceded metazoan radiation, instead of following it, and cannot therefore be regarded as a result of metazoan interference; ii) microbial carbonates are very abundant in the Cambrian, reflecting an increase in their importance that coincided with metazoan radiation. It is proposed here that these patterns are better explained by variations in environmental factors that influenced microbial growth and calcification. According to this Environmental Constraint Model, variations in physical and chemical factors have determined the extent of microbial growth and calcification, and this has also impacted upon metazoan success. When microbes declined (as in the mid-Proterozoic) then metazoans were able to expand, but when microbes were abundant (as in the mid-Cambrian) then metazoans declined. It remains to be seen whether metazoans were limited more by competition from the microbes themselves, or by the environmental factors that stimulated microbial growth and calcification.

Benthic origins of zooplankton: an environmentally determined macroevolutionary effect

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Zooplankton show a unique pattern of evolution with successive waves of invasion into the water column from the benthos. We have found that 18 of 21 planktic groups whose ancestry can be traced originated in the benthos. New recruits have survived and radiated if preadapted to remain in the plankton, but no major clades have evolved there (with the possible exception of some protists). The innovative steps into the planktic realm do not coincide with major global events such as mass extinctions. Recruitment into the plankton can occur either at the larval stage or in adulthood. No groups have returned to a benthic mode of life from a planktic one, except possibly some of the cnidarians. This unusual pattern of evolution, a one-way track into a particular environment, demonstrates the profound effect of the ecosystem on large-scale patterns and processes of evolution.

Plus ça change - a model for stasis and evolution in different environments

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'Plus ça change, plus c'est la même chose' - The more that changes, the more it's the same thing. The Plus ça Change Model proposes that morphological stasis is the usual response to widely fluctuating physical environments on geological timescales (until thresholds are reached). The lineages that survive in an environment of fluctuating sea level, climate, substrate etc., are those that are relatively inert to each environmental twist and turn, in contrast to more sensitive lineages in less changing environments. Generalists in this long-term sense are species with properties that enable them to survive throughout wide environmental fluctuations for millions of years: they are thus distinct from ecological eurytopes. The model predicts a tendency for continuous, gradualistic evolution on land in the tropics and in the deeper sea, and for more stasis (and occasional punctuations) in shallow waters and temperate zones.

Punctuated equilibrium could be mistakenly perceived as the overwhelming pattern in the history of life because the environments in which gradualism predominates are rarely preserved in the fossil record (the vast majority of which comes from dynamic shallow marine settings in which stasis is expected).

Relatively little evolution may be occurring worldwide at present, compared with, say, 3 million years ago. The last 10,000 years of stable climate since the end of the Pleistocene upheavals may not have been a sufficiently long interval of stability to relax the promotion of stasis. Evolution that *is* happening today (where not human-induced) should be easiest to detect on land in the tropics.

Studies on the postulated Jurassic-Cretaceous boundary mass extinction

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Previous studies of the Jurassic-Cretaceous boundary (most notably by Raup and Sepkoski 1984) indicate that this interval represents a mass extinction, though smaller in magnitude than the end-Cretaceous event. Many of the data used so far come from literature on the Jurassic-Cretaceous boundary beds of southern England and southeast France. In the south of England sections, apparent extinctions are noted, although these can be attributed to a profound facies change from marine to freshwater. Classic field areas in France exhibit either substantially incomplete boundary sections or are sparsely fossiliferous, forcing authors to use a variety of biostratigraphic schemes which inevitably lead to tenuous correlation between areas. In the light of this, it is hard to see how

'extinction' as a result of such local ecological change, or within uncorrelatable areas showing apparent stratigraphic gaps can be translated into a true global mass extinction event. Crude stage-level data on familial extinction and origination across the interval from basal Kimmeridgian to uppermost Valanginian are presented, and confirm the existence of an extinction peak during this interval. Preliminary faunal data collected from the most complete boundary section in the Volga Basin of Russia, and from the successions near Caravaca, SE Spain show that both are largely complete, any minor stratigraphic gaps being confined to less than one ammonite Zone. Both sections display continuous marine sequences and represent deposition within the Boreal and Tethyan faunal realms respectively. They therefore provide an ecologically unbiased and palaeogeographically broad foundation on which to make assessments of the nature and magnitude faunal composition changes (if any) at the Jurassic-Cretaceous boundary.

Cretaceous ostracods with preserved appendages from Brazil

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The Santana Formation in the Araripe Basin, NE Brazil, is a world famous lagerstätten which preserves vertebrates and invertebrates, including the ostracod *Pattersoncypris micropapillosa*. These ostracodes are present in large numbers in nodules containing fish and are occasionally found to be phosphatized, thus preserving fine detail of their soft parts. These specimens comprise the most abundant well-preserved ostracods with preserved appendages in the fossil record and, therefore, furnish significant information about the palaeobiology and evolution of the group. Their body plan, morphology and ontogeny is very similar to Recent Cyprididae, thus indicating how little podocopine ostracods have changed over the last 100 million years. The monospecific nature of the ostracode fauna suggests that these possible nektobenthic ostracodes inhabited unusual environmental conditions.

Experimental observations on predator deterrence by pronounced shell ornament in epifaunal bivalves

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A series of laboratory experiments was undertaken to determine the effectiveness of pronounced shell ornament in epifaunal bivalves against predatory shell boring by subtropical muricid gastropods and extraoral feeding by asteroids in Hong Kong. The results suggest that natural and artificial spines deter muricid predators from attacking ornamented areas of the bivalve shell but do not have a similar effect upon the asteroids. These findings are discussed in relation to the extant and often highly spinose cementing bivalve families Spondylidae and Chamidae. The adaptive radiation of the Muricidae in the Albian may have resulted in selection for highly ornamented epifaunal bivalve taxa in shallow, warm water rocky shore environments where the epifaunal habit renders sessile prey particularly vulnerable to attack by roving durivorous predators. The ability to produce spines in the family Spondylidae, however, was already apparent in ancestral Pectinacea in the late Palaeozoic. It is concluded that the pronounced shell ornament of the free valves of warm water cemented epifaunal bivalve taxa is functional against shell boring muricids, although other hypothesised functions may have been equally or more important throughout the evolution of highly ornamented groups.

Functional morphology and the burrowing habit in Lower Palaeozoic linguloid brachiopods

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The Linguloidea is represented in Recent faunas by the genera *Lingula* and *Glottidia*, which share an infaunal habit. Fossil linguloids of a broadly similar form are known from throughout the Phanerozoic, and have often been assumed to have had a similar life habit. Some Palaeozoic forms undoubtedly were infaunal, and the posterior internal morphologies of these are similar to those of Recent lingulids. However, most taxa in the Cambrian and Lower Ordovician have a somewhat different posterior morphology, which appears poorly adapted to the egress of a posteriorly directed pedicle, a requirement for a lingulid style infaunal habit. These forms seem rather to be adapted for a pedicle to emerge *posteroventrally*, suggesting their mode of life to have been essentially epifaunal. These functional considerations allow provisional diagnosis of the burrowing habit from morphology alone, although *in situ* finds remain important as confirmatory evidence. Examples of fossil linguloids interpreted as infaunal and epifaunal are given from the Lower Ordovician of the Anglo-Welsh Basin, and the taxonomic extent of this mode of life in the Linguloidea is investigated.

The Ctenostomata - the historical importance of a forgotten major clade

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The ctenostomes are a major group (traditionally an 'order') of primitive yet extant, unmineralized, marine bryozoans. Their existence has been consistently ignored in palaeoecological and phylogenetic studies despite their having a known range from the Early Ordovician. This is in large part due to the Palaeozoic taxa (and, until recently, the majority of Mesozoic taxa) being known solely from a limited diversity of borings. Nevertheless the borings are morphologically highly informative and are an untapped source of systematic information. When combined with a cladistic (PAUP) analysis of Recent ctenostome superfamilies they show that almost all of these may have originated by the Ordovician, implying vast ghost lineages. Fortunately such unmineralized encrusters may be systematically collected in large numbers, preserved by bioimmuration (organic overgrowth by a neighbouring skeletonized encruster). Snapshots of Mesozoic marine hard substrate communities with their full complement of mineralized and unmineralized denizens, are routinely provided by bioimmuration. Many of these communities contained, and sometimes were dominated by, members of a single, highly diverse family of extant encrusting ctenostomes: the Arachnidiidae. Apart from revolutionising our knowledge of such communities, the apparent ubiquity of this clade in Mesozoic shelf seas forces a re-evaluation of the ecological importance of ctenostomes throughout much of the Phanerozoic. Preserved with submicron-scale fidelity, and sometimes with soft parts, many taxa are more completely known than their Recent counterparts. Stem-group members of this family, in particular, provide previously inaccessible information which necessitates a revision of current notions of bryozoan phylogeny and classification. Indeed, PAUP analysis reveals that the dominant and most speciose group of bryozoans today - the cheilostomes - nest amongst, and were derived from, probable stem-group arachnidiids. Despite an often rich suite of characters, high-level cladistic analysis of post-Palaeozoic Bryozoa is still in its infancy. Study of bioimmurations has largely removed the taphonomic 'calcification barrier' which had previously prevented a clear view of the inter-relationship of ctenostomes and cheilostomes, two of the three major extant groups of bryozoans.

A new model for the recovery of the soft-bodied marine community following mass extinction events

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Ichnology can be a very powerful tool in modelling the extinction and recovery of soft-bodied benthos. The identity of most trace makers can be resolved to at least class level, especially from resting or dwelling traces. This model has been developed from a study of the end-Permian mass extinction.

The initial post-extinction ichnofauna is very sparse and consists of isolated thin horizons of *Planolites*. These represent brief periods of colonisation by opportunistic, deposit-feeding annelids (probably polychaetes). The next stage involves the appearance of filter-feeding organisms (producing *Skolithos* and *Arenicolites*), the appearance of nematodes (*Cochlichnus*) and an increase in deposit-feeding polychaetes. Next to appear are the 'higher' invertebrates (crustaceans and other arthropods) and by the Spathian the trace fossil assemblage (and hence soft-bodied community) is of comparable richness to the upper Permian.

The sequential re-appearance of trace fossils after the mass extinction is unrelated to facies change and seems to be a global phenomenon. There are two possible reasons for the temporary disappearance of each ichnotaxon: i) the original trace maker(s) became extinct and then a different organism re-discovered the same behaviour; or, ii) the trace maker(s) survived in an unknown refuge before returning as conditions improved. Interestingly, the pattern of trace maker return is very similar to the recovery of the soft-bodied benthos following modern, small-scale defaunation events.

Two legs bad, four legs good: the truth about pterosaur tracks

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Distinctive tracks of a quadrupedal animal with a three (occasionally four) digit manus print and four digit pes print have been reported from Jurassic and Cretaceous coastal sediments of North America and Europe. At first, these ichnites, named as *Pteraichnus*, were interpreted as pterosaur tracks, but later, in the 1980s, they were reinterpreted as crocodylian. New material, principally from France and the USA, shows that the original identification was correct since two features (indications of elongate penultimate phalanges in digits two to four of the pes, and manus trackways up to three times the width of pes trackways) can only be attributed to pterosaurs. Recent improvements in our understanding of pterosaur anatomy and functional morphology explain remaining difficulties regarding some unusual features of the ichnites, such as the orientation of the manus digits, and the absence of some expected ichnological features. *Pteraichnus* and *Pteraichnus*-like tracks demonstrate that, when grounded, pterosaurs were plantigrade, quadrupedal, and had a semi-erect stance and gait. This is consistent with exceptionally preserved remains of pterosaurs which show extensive attachment of the wing membranes to the hind limbs and resolves a long-running debate regarding the terrestrial ability of this group.

Microevolution and environmental change in bivalves of the Oxford Clay

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The Plus ça Change Model (see Sheldon, this volume) has extended the debate about microevolutionary patterns in the fossil record. The model predicts that the evolutionary pattern *within a single lineage* will be stasis when there is greater environmental fluctuation, and net directional change and/or more widely fluctuating morphologies when environments are more narrowly fluctuating.

The predictions of the model are being investigated using bivalve lineages from the Oxford Clay. The two main lineages studied are *Mesosaccella morrisoni* and *Meleagrinnella braamburiensis*. *M. morrisoni* was probably an infaunal deposit feeder, whereas *M. braamburiensis* was a very thin-shelled suspension feeder. A pendent mode of life for *M. braamburiensis* has been assumed until now because the sediment was believed to have been too soupy for its survival at the sediment-water interface. However, given its great abundance, especially in clusters, and the apparent rarity of plant and wood debris for potential attachment, *M. braamburiensis* may actually have lived on the sea floor. A taphonomic study of all the fauna, together with isotopic data, will yield detailed information on changing environments within the Oxford Clay.

Results have been obtained from two different areas: Calvert, Buckinghamshire and the Peterborough region. *M. morrisoni* appears to show a tendency for more morphological change within the relatively stable environment and more stasis within the fluctuating environment. Analysis of the *M. braamburiensis* lineage, which is more complicated due to allometry, will also be discussed.

Exceptionally preserved early land plants with *in situ* spores: integrating and interpreting the early land plant megafossil and microfossil records

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The fossil record for early land plants comprises megafossils and dispersed microfossils (spores and fragments). However, these two lines of evidence are difficult to integrate and have often been treated as disparate. Assemblages of exceptionally preserved early land plants have recently been recovered from late Silurian - early Devonian deposits from the Welsh Borderland. The fossils preserve exquisite cellular detail and are providing an unprecedented insight into the anatomy of these plants. Analysis of such material permits deliberations on functional anatomy (e.g. of stomata and vascular tissue) and reproductive biology (e.g. spore development and sporangial dehiscence). Furthermore, numerous specimens contain well preserved *in situ* spores. The *in situ* spores can be compared with dispersed spores, isolated from coeval deposits, in order to identify dispersed spore/parent plant relationships. Consequently, utilising information from *in situ* spores, the early land plant microfossil record, which is believed to be reasonably good, can be interpreted in terms of the megafossil record, which is notoriously poor. Such research permits more fruitful interpretation of the early land plant fossil record, shedding light on patterns of evolution, palaeophytogeography and diversity, in addition to providing evidence regarding early land plant affinities and phylogenetic relationships.

The end-Palaeozoic double whammy

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Recent intensification in the study of the Late Permian mass extinction has begun to overturn much of the long-established dogma concerning this, the most severe crisis in the history of life. In particular, the view that the event was a prolonged one, spread over the last 5-10 million years of the Permian has been challenged. Recent compilations have shown that the event can be separated into two distinct extinction episodes. The first mass extinction occurred within the Maokouan Stage (Guadalupian Stage of North America) and affected ammonoids, brachiopods, echinoderms, corals and fusulinid forams. The fact that ammonoids, brachiopods and to a lesser extent rugose corals and fusulinids all radiated in the later Permian indicates that the Maokouan extinction was distinct from the end Permian extinction. Previous studies have tended to amalgamate both extinction events thereby giving the impression of a prolonged crisis.

The apparent absence of high latitude, Late Permian sections has hindered investigation of the Late Permian extinction events and much of what we know comes from Tethyan sections. Only the sections of NE Greenland and Spitsbergen contain an abundant and diverse late Permian benthos dominated by brachiopods and bryozoans with lesser corals, forams and bivalves. The age of this fauna has proved contentious due to the absence of any biostratigraphically -useful conodonts and ammonoids. The benthic taxa appear to be no younger than Guadalupian/Maokouan age which suggests that there is a major late Permian hiatus in the Boreal region. Recent organic C isotope evidence indicates, on the contrary, that there is a complete Late Permian-Early Triassic transition in Spitsbergen. If this chemostratigraphic correlation is true then it indicates that the Boreal fauna was not greatly affected by the Maokouan crisis and survived to the end of the Permian before succumbing to the second 'whammy'.

Fossil vertebrate trackways from the Purbeck Limestone Group of Dorset

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The Purbeck Limestone Group of Dorset has yielded one of the richest mid- Mesozoic terrestrial faunas in the world. It also contains one of the most diverse dinosaur footprint assemblages in Britain, due largely to the number of quarries for building stone that formally operated in this area. Dinosaur footprints have been known from the Purbeck for over a hundred years. Most of these tracks were previously attributed to *Iguanodon* but more recently it has become apparent that the fossil footprint fauna is much more diverse. A trackway of an iguanodontid walking quadrupedally is preserved. Quadrupedal dinosaur tracks have also been found; these were probably made by nodosaurid ankylosaurs. Most recently, some tracks have been recognised as pterosaurian in origin. The recognition of these trackway producers is important in augmenting our knowledge of the fauna of the Purbeck Limestone Group.

Poster abstracts

The bases of middle Ordovician series in their type areas and their usefulness for global correlation

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The Anglo-Welsh area provided the first classifications of middle Ordovician stratigraphic units, and a basis for the definitions of the Llandeilo and Caradoc Series on shelly fossils, and the Llanvirn Series on graptolites. These series have been used to correlate to areas outside of Eastern Avalonia and have been widely accepted until recent years. The main problems to their use have been: The restricted geographic ranges of the trilobites and brachiopods used by Bancroft (1933) and Williams (1953).

How these shelly zones relate to the graptolitic zones which are being used elsewhere to define global units of time.

A more recent problem to have occurred is that of the validity of the *teretiusculus* graptolite zone which was originally defined at Builth and which has been used by Fortey *et al.* (1995) to define their Llandeilian Stage. Collecting of continuous measured sections in the mixed faunas of the Shelve Inlier, the Builth Inlier and the Mydrim area should help to:

Correlate the shelly, non-graptolitic units with the key graptolite horizons.

Correlate infrazonally across the Welsh Basin.

Clarify the taxonomy of some of the critical, poorly defined species and their stratigraphic ranges.

Select a new first appearance event for the base of the *teretiusculus* zone.

The Cambrian explosion of molluscs and possible shrapnel in Silurian hydrothermal vents

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Amongst the most prominent of the shelly fossils to appear in the geological record of the latest Vendian are microscopic, problematic molluscs. They are also characteristic of the earliest Early Cambrian. These problematic molluscs are a major component of the faunas which appeared in the 'Cambrian explosion', the great diversification of highly organised life which took place at or just before the base of the Phanerozoic.

Although generally referred to the Gastropoda or Monoplacophora, Cambrian problematic molluscs bear little morphological similarity to members of these extant classes. Abundant in the Early Cambrian, they had virtually disappeared by the Early Ordovician and were replaced by ancient representatives of the modern classes of Mollusca. However, molluscs recently discovered in Silurian hydrothermal vent sediments of the Urals may represent a final fragment of the great Cambrian explosion.

In most modern schemes of early molluscan phylogeny, a central position is ascribed to *Latouchella*. The large morphological diversity within the genus is important to our understanding of evolutionary trends within the early molluscs.

Palaeoclimatic and palaeoecological reconstruction of an Upper Oligocene flora from western Germany

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Tertiary plant fossils provide an excellent archive for palaeogeographic and palaeoclimatic research in terrestrial ecosystems. In this study an Upper Oligocene flora, located in the Tertiary volcanic area of the Westerwald (northwest of Frankfurt, Germany), has been examined in respect to its palaeoclimatic and palaeoecological significance. The lacustrine sediments, yielding the fossil flora, comprise laminated oilshale alternating with reworked volcanic material deposited in a caldera. The sediments have been dated with eomyid mammal teeth as Upper Oligocene (MP 28; 25.8 Ma).

Beside faunal remains (fishes, frogs, tadpoles, insects, salamanders, eomyids and a turtle) more than 1,500 well-preserved leaves, fruits and seeds (altogether 83 species) were collected.

Climatic analysis of the plants were made using the coexistence approach of the 'nearest living relative' method. This allows a quantitative reconstruction of different climate parameters. Mean annual temperature and precipitation being determined as between 13.8 C to 16.8 C and 1003 mm to 1355 mm respectively.

The reconstruction of the vegetation dynamics is of especial interest, because the influence of the volcanic events on the vegetation can be proved taxonomically, ecologically and also, geochemically with carbon isotope techniques. The comparison of this flora with other Oligocene floras in central Europe contributes to the understanding of vegetation zonation and also to the reconstruction of terrestrial climate evolution during the Oligocene.

Palaeoecology of the Lower Oligocene 'Zementmergel' Formation of the Lower Inn Valley (Tyrol, Austria)

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The Lower Oligocene 'Zementmergel Formation' of the Lower Inn Valley (Tyrol, Austria) has been investigated with respect to palaeoecological and palaeoclimatological reconstructions. This includes not only the interpretation of different lithologies, especially carbonates, but also a detailed study of the rich mollusc associations. This study is part of a Collaborative Research Initiative (SFB 275) of the Faculty of Geosciences at the University of Tübingen.

Carbonates occur either at the base of the marls of the 'Zementmergel Formation', or as intercalations within the latter. These intercalations are interpreted as mass- flow deposits due to the allochthonous nature of the included components and the internal sedimentary structures of the beds. Microfacies analysis show that the carbonates consist of very poorly- sorted rudstones dominated by coralline algae, corals, large and small benthic foraminifera, bryozoans, bivalves and echinoderms in a muddy matrix.

The well- preserved molluscs of the 'Zementmergel Formation' include both aragonitic shelled gastropods and bivalves, as well as calcitic pectinids and oysters. Although historically described, a thorough taxonomic revision is necessary. At least two different faunal associations can be recognized: an autochthonous soft-bottom, deeper water fauna; as well as an allochthonous shallow water fauna which was swept into the basin along with the carbonate sediments.

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