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ABSTRACTS and PROGRAMME

The apparatus architecture of prioniodontids

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Conodonts are among the most prolific fossils of the Palaeozoic, but it has taken more than 130 years to understand the phylogenetic position of the group, and the form and function of its fossilized feeding apparatus.
Prioniodontids were the first conodonts to develop a complex, integrated feeding apparatus. They dominated the early Ordovician radiation of conodonts, before the ozarkodinids and prioniodinids diversified. Until recently the reconstruction of the feeding apparatuses of all three of these important conodont orders relied mainly on natural assemblages of the ozarkodinids. The reliability of this approach is questionable, but in the absence of direct information it served as a working hypothesis.
In 1990, fossilized bedding plane assemblages of *Promissum pulchrum*, a late Ordovician prioniodontid, were described. These were the first natural assemblages to provide information about the architecture of prioniodontid feeding apparatus, and showed significant differences from the ozarkodinid plan. The recent discovery of natural assemblages of *Phragmodus inflexus*, a mid Ordovician prioniodontid with an apparatus comparable with the ozarkodinid plan, has added new, contradictory evidence.
Work is now in progress to try and determine whether the feeding apparatus of *Phragmodus* or that of *Promissum pulchrum* is most appropriate for reconstructing the feeding apparatuses of other prioniodontids. This work will assess whether *Promissum pulchrum* is an atypical prioniodontid, or whether prioniodontids, as currently conceived, are polyphyletic.

Parasitism on graptolites

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We present here spectacular evidence of parasitism on a planktic graptoloid, in the form of tubular periderm outgrowths on an Ordovician biserial from the Viola Limestone of Oklahoma. Such parasitic outgrowths must have had a major influence on the hydrodynamics of the rhabdosome, in terms of both its overall morphology and its weight distribution. We will also illustrate various other evidence for parasitism on graptolites, indicating that these most conspicuous components of the Palaeozoic plankton were host to a variety of parasitic organisms.

The skin of chancelloriids

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Chancelloriids are Cambrian organisms characterized by a sack-like body covered with composite star-shaped sclerites in a manner reminiscent of cacti. When first described from the Burgess Shale by Charles Walcott, they were interpreted as sponges. Later they have been reinterpreted as close relatives of the Cambrian halkieriids, based on the similar construction of the sclerites, which appear to have been formed by partial mineralization of a soft cuticle. Recent challenges to this interpretation are based on claims that chancelloriid sclerites were fully or partly formed from the outside. On this basis, relationships with sponges and ascidians, respectively, have been proposed. Specimens of chancelloriids from the famous Lower Cambrian Chengjiang biota of Yunnan Province, China, preserve exquisite details of the flexible cuticle between the sclerites. The cuticle has a regular rhombic pattern, apparently reflecting the bases of spine-like processes. No structures resembling ostia, such as would be expected in a sponge, have been observed. Nor does the rhombic pattern resemble the cellular pattern in a sponge pinacoderm or the flattened, imbricating, spicular processes of some sponges. There is no evidence of the cuticle covering the sclerites, as has been claimed in support of the ascidian model. The skin of the Chengjiang chancelloriids was an integrated unit consisting of a flexible bristly cuticle with regularly placed batteries of sharp calcareous spines.

Is the Palaeozoic fossil record worse than the post-Palaeozoic?

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Some palaeoecological evidence suggests that the fossil record does not necessarily deteriorate backwards in time. This common assumption has been queried by studies of shell beds, but it is hard to make such studies comprehensive and global. The postulated deterioration has been tested in a different way, using comparisons of phylogeny and stratigraphy. A large number of cladograms and molecular trees were divided into those with Palaeozoic, and those with post-Palaeozoic, originations. There is no major difference between the two sets in terms of congruence of the fossil record with postulated phylogeny, and
hence no evidence for deterioration.

Ordovician cephalopods and inarticulate brachiopods from the Carnic Alps of Austria

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Recent study in the Austrian Carnic Alps reveals a new fossil record of cephalopods and lingulate minute brachiopods. From the upper Ordovician Uggwa Limestone six species of ortho- and tarphycerid cephalopods (Arionoceratidae gen. et sp. indet., *Geisonoceras* sp., *Lituites*? sp., *Michelinoceras* sp. 1, *Michelinoceras* sp. 2) and three species of inarticulate brachiopods (*Acrotretella tenuis* sp. nov., *Lingulella* sp. and *Rowelella*? sp.) are described. The faunal affinities of the described fauna will be discussed with respect to the latitudinal setting of the Proto-Alps during the Ordovician.

Permian Polaroids: snap-shots of ancient environments and animal activities

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Ichnological evidence is particularly significant when deducing the biomechanics and behaviour of extinct animals. Many trace fossils are 'snap shots' of the activities of extinct animals and provide insights on the palaeoenvironment of the time. This theme is illustrated by two Permian ichnoassemblages.
The late Permian Ganfontein palaeosurface (near Fraserburg, Karoo, South Africa) represents a crevasse splay formed after a flooding event on a vast alluvial plain. Spectacular sedimentary structures indicate that shallow pools were left after the flood; their margins preserving the activities of the animals living on the flood plain. The traces include *Bradysaurus* and dinocephalian trackways, sinuous fish trails, the trackways of freshwater crustaceans (*Umfolozia*, *Tasmanadia*), scorpions (*Paleohelcura*, *Siskemia*) and beetles (*Permichnium*), and beaded worm trails.
The Lower Permian Robledo Mountains ichnofauna (New Mexico, USA), regarded as the most abundant and diverse assemblage of Permian terrestrial trace fossils in the world, represents a marginal marine setting including tidal flats, non-marine red beds and freshwater conditions. The vertebrate traces include temnospondyl amphibian, araeoscolid, ?diadectid and pelycosaur trackways (the latter of biomechanical significance) and enigmatic sidewinding snake-like (?aïstopod) trails. The invertebrate traces include 14 ichnogenera of arthropod trackways, recording the activities of myriapods, arachnids, eurypterids, xiphosurans, crustaceans and several different types of insects, and various new undescribed arthropod resting traces.

All about (metazoan) Eve: A critical reassessment of the early fossil record of animals

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The conventional picture of the Cambrian explosion is that metazoan phyla appear abruptly in the fossil record with little hint of their forbears or how the distinctive 'body plans' that characterise extant animals were assembled. This picture appears to be incorrect, however, because when critically assessed, most Cambrian metazoans do not actually qualify for membership of the extant phyla, which instead appear gradually in the Phanerozoic. Character and functional analysis of the extant bilaterian phyla suggests that their last common ancestor must have been a large and relatively complex organism, a conclusion at odds with the various hypotheses invoking tiny metazoans existing well before the Cambrian. As well as the Cambrian body fossil record being suspect, the Precambrian trace fossil record also withers under scrutiny, with no convincing trace fossils older than 600 Ma (or, more probably, 570 Ma). All moderately diverse trace fossil assemblages may be younger than 550 Ma. Given that the last common ancestor of the bilaterians would almost certainly have been capable of leaving a trace fossil record, we conclude that the fossil record strongly supports a time of origin for the first bilaterian animal at around this time. Such a conclusion is at odds with recent molecular estimates of metazoan diversification times, but should not be dismissed merely on that account.

A re-interpretation of the braincase of the Devonian tetrapod *Ichthyostega stensioei*

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Re-examination of the braincase of the Upper Devonian tetrapod *Ichthyostega* has produced a radical new interpretation and the first identification of a stapes. Earlier descriptions were unable to interpret the braincase elements of *Ichthyostega* in terms comparable to those recognized in other early tetrapods or sarcopterygian fishes. However, our study has identified most conventional braincase parts in a structure which, apart from a few primitive features, is highly specialized in its morphology and organization. The otic region is extremely narrow, and to each side of it lies a large open chamber free of bony structures except for the inflated but lightly ossified stapes. It is not clear whether this chamber would have housed air, water, fatty tissue or muscle, although air or water are most likely, since the chamber was probably associated with the spiracular system. The contents in life would have determined whether the chambers were concerned with hearing, sound production, buoyancy, gas exchange or some other function in the living animal. At present, it is not possible to attribute a function, except that aerial sound reception seems one of the least likely. In its peculiar and extremely specialized braincase morphology, *Ichthyostega* may be an instance of the phenomenon of 'early diversification, later stablization' which has been seen in the evolution of other tetrapod and also invertebrate features. Other features of its anatomy are still considered primitive, and it remains phylogenetically near the base of the tetrapod tree.

Relationships of Cambrian conodonts

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A histological study of the Late Cambrian-early Ordovician *Proconodontus* euconodont lineage has revealed that the elements comprise a lamellar crown of enamel overlying a basal body composed of spherulitic atubular dentine or, in some cases, globular calcified cartilage, and confirms their vertebrate affinity. This is concordant with studies of later euconodonts, and further emphasises the diversity of tissues that are found in euconodont basal bodies. A generally accepted hypothesis of euconodont origins is that euconodonts evolved via the paraconodonts from the protoconodonts during the Mid-Late Cambrian. In order to test part of this hypothesis, the histology of *Prooneotodus rotundatus*, a paraconodont, has been compared with the morphologically similar euconodont genus *Proconodontus*, and the results will be presented. A second euconodont lineage incorporating *Teridontus* appears to be unrelated to the *Proconodontus* lineage, and raises the possibility that euconodonts, as currently defined, are polyphyletic. Protoconodont and paraconodont relationships are even more uncertain. Protoconodonts are generally considered to be a sister group of the Chaetognatha (arrow-worms) on both anatomical and histological grounds. Since chaetognaths and vertebrates are not closely related, the protoconodont-paraconodont-euconodont evolutionary model is not reconcilable with the vertebrate affinity of euconodonts.

Taphonomy of a microvertebrate assemblage from a Lower Triassic fissure deposit at Czatkowice, Crakow Uplands, Poland

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In 1978 a bone-bearing fissure fill deposit was discovered preserved in Carboniferous Limestone at Czatkowice Quarry, Poland. These Lower Triassic sediments preserve a diverse and taxonomically significant microvertebrate fauna and include taxa adapted to fully aquatic, amphibious, and fully terrestrial life styles. These animals lived in the vicinity of ephemeral pools found in the dune fields that covered large areas of Poland during the early Triassic. Analysis of the microvertebrate remains follows the techniques of two major research areas: the fossils have been classified using the 'traditional' taphonomic weathering, abrasion and fragmentation indices, and geochemical techniques such as ICPMS analysis of uranium, thorium and Rare Earth Elements (REEs), and XRD analysis of the mineralogical composition of the bones. A combination of these methods has allowed taphonomic and diagenetic pathways for the assemblage to be constructed.

The origin of heterodont bivalves

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Heterodont bivalves are today the most diverse of the seven bivalve subclasses, but their origins are obscure. The most fundamental bivalve radiations occurred in the early Ordovician, following the

evolution of the filibranch gill. Because Arenig faunas contain representatives of most bivalve subclasses, it is clear that the principal radiations must have occurred before this, yet so far there are only some nine or ten species known from the Tremadoc Series. Some workers avoid the problem of differentiating between the Palaeoheterodonta and the Heterodonta by combining the two in a subclass Heteroconchia, but as shown by Cope (*Palaeontology*, **40**, 713-746), the shell microstructure of the two groups suggests that they have been long separated. In the absence of shell microstructural evidence, other criteria for distinction must be employed. Analysis of dentition suggests that some long-accepted palaeoheterodonts are in fact heterodonts, and that even in the early Ordovician heterodonts were already present. This implies that all modern bivalve subclasses (with the possible earlier exception of Lipodonta) arose from palaeotaxodont ancestors within a 5-10 million year interval in the earliest Ordovician.

Re-investigation of classic Scottish Middle Old Red Sandstone fish-bearing nodule localities

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Classic nineteenth century 'nodule bed' Devonian fish sites adjacent to the Moray Firth, are being re-investigated. Excavations have taken place at Tynet Burn with more recent field work at Edderton and Gamrie. Detailed logging of both fish and sedimentology is yielding considerably enhanced information on preservation, faunal distribution and palaeoenvironments.
The nodule beds are approximately equivalent in age and the fish assemblage consists of placoderms, acanthodians, an actinopterygian, porolepiforms, osteolepiforms and a dipnoan. The assemblage is typical of the 'Achanarras Fauna' of Givetian age which is widespread in the Orcadian basin, representing a time of generally high lake levels. However, it is apparent that minor lake level fluctuations are superimposed on the general trend.
The localities are interpreted as near shore lacustrine environments. At the Tynet Burn locality during an early stage in diagenesis, synchronous with concretion formation, chemotrophic bacteria invaded open fractures and partially oxidized the fish remains. This event was responsible for the characterstic vibrant red to purple colours of Tynet Burn fossils and took place at a time of low lake level when the fish bed was subjected to oxidation in the vadose zone. Comparisons between the occurrence of fish at different localities is yielding new information on the possible modes of life of fish genera.

Conodont affinity, chordate phylogeny and the origin of the vertebrate dermal skeleton

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For much of the past 140 years the affinity of conodonts has been one of the most vigorous and

poorly constrained subjects of debate in systematic palaeontology. Prior to the discovery of soft tissue remains in association with the characteristic feeding elements, conodonts had been attributed to three kingdoms and almost every major animal phylum. The elucidation of conodont anatomy has led to almost universal acceptance of chordate affinity, but despite this systematic constraint, the debate has become even more controversial. Conodonts have been interleaved with many of the primitive jawless vertebrates and every permutation amongst the invertebrate chordates has been postulated. However, although most hypotheses have been couched in cladistic terminology or expressed in the form of a cladogram, not one is the result of a formal cladistic analysis. Instead, each hypothesis represents either the result of hanging conodonts off a pre-existing cladogram by pre-established synapomorphies, or else classifying conodonts according to unsubstantiated *a priori* assumptions of character polarity in chordate phylogeny. This is unfortunate as conodonts clearly have an important contribution to make to our understanding of chordate evolution, or else they would not evoke so much controversy.
Our analysis suggests that the systematic position of conodonts lies at the critical point in chordate relationships, between the extant jawless vertebrates which lack any form of mineralised dermal skeleton, and the familiar groups of extinct jawless vertebrates which possessed a well developed mineralized dermal skeleton in the form of scales and plates. These results corroborate recent hypotheses for the origin of the vertebrate skeleton and provide a refined understanding of chordate phylogeny. The affects of alternative codings for contentious characters are discussed, along with their implications for relationships.

Fossils, palaeodepth and tectonics: Miocene evolution of Carriacou, The Grenadines, Lesser Antilles

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The stratigraphical succession of Carriacou consists of an Eocene-Miocene sequence of volcanics, volcaniclastics and subordinate limestones. Previous interpretations of the fossiliferous Miocene succession suggested that they were laid down in a uniformly shallow water setting. The implication from this is that uplift during and after the Miocene has been minimal.
Preliminary analyses of selected fossil groups suggests that this simple interpretation is incorrect. Volcaniclastic units contain abundant fossils that commonly occur in deeper-water environments in the tropical western Atlantic at the present day, including pteropods, brachiopods and stalked crinoids. Shell concentrations in the Belmont and Grand Bay formations are packed with numerous shells of at least three taxa of large terebratulide brachiopod, including some in situ `nests' of gregarious individuals. Columnals of isocrinids are locally common, with rare columnals of a gracile bourgueticrinid. These data suggest at least a deeper water shelf environment, supported by the rare occurrence of the trace fossil *Zoophycos*. The Middle Miocene Carriacou Formation rests unconformably on the volcaniclastic units.
A revised mid Tertiary geological history of Carriacou suggests early-mid Miocene deposition on the deeper water island shelf. This succession was uplifted in the early mid Miocene, with later mid Miocene limestone deposition in a shallower water setting.

A Cambrian pantopod larvae from Orsten and its significance for chelicerate phylogeny

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Pantopods (or pycnogonids) are the odd-looking arthropods which hide in zoology textbooks as a class of the Chelicerata. Their relationships remain controversial. Authors who studied the group often interpreted them as unrelated to chelicerates, or any other arthropod group. Reinterpretation of the few Devonian pantopods may solve 'problems' of their appendage number and reduction of the opisthosoma. An Upper Cambrian fossil from the most prolific Orsten Lägerstatte in the Kinnekulle area, Västergötland, Sweden, was proposed by Müller and Walossek (1986) as a larval chelicerate with possible pantopod affinities. This fossil has rudimentory appendages in front of a chelate appendage pair, followed by two pairs of gnathobasic limbs with a single ramus. We confirm its earlier interpretation as a pantopod protonymph and, following Walossek and Müller (1997), argue that it supports two important hypotheses. Firstly, arthropods originally had a head with four appendage pairs (a pair of antennae and three pairs of biramous limbs) and Chelicerata have lost appendage 1, the antennae, during their evolution, making the chelicerae the 2nd head appendage. Secondly, Pantopoda are sister group to all other Chelicerata, on the synapomorphy of chelicerae, but retain as plesiomorphies remnants of the antennae and an anamorphic ontogeny starting with a head larva, with the autapomorphy for the chelicerate stem species being a more advanced pattern of development.

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Construction and ecology of late Palaeozoic algal reefs

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Late Carboniferous to Early Permian reefs in south-western USA are generally considered to be ecologically simple communities, constructed predominantly by leaf-like 'phylloid' algae, sphinctozoan sponges and various problematica (*Tubiphytes* and *Archaeolithoporella*). Lack of recognized framework builders in these reefs and high proportions of micrite have led to a sediment-baffling (mainly by phylloid algae) interpretation for reef construction.
Detailed ecological study of the biota, however, reveals novel construction mechanisms within late Palaeozoic reefs, most notably interaction between biological growth mechanisms and early marine cementation. Phylloid algae, sponges, *Tubiphytes* and *Archaeolithoporella* have complex patterns of

mutual encrustation, both *in-vivo* and post-mortem, and these control the basic structure of the reefs. Phylloid algal thalli are shown to have currently undescribed growth forms and are capable of supporting primary reef voids with associated cryptic biota. Large volumes of early marine cement, together with putative microbial micrite, are instrumental in stabilizing the reef framework to produce positive topographic relief. This active growth of reef frameworks in the late Palaeozoic contrasts with the passive mechanisms of sediment trapping previously proposed.

Some palaeobiological aspects of the European Jurassic Trigoniidae

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During the Jurassic and Early Cretaceous, the Trigoniidae were among the dominant members of the shallow burrowing bivalve infauna. The family is characterized by its large and peculiar dentition along with a strong and elaborate external ornament, which has lent itself well to a thorough morphological analysis. Through the use of biometric methods, natural species groupings have been identified. Severe taxonomic splitting by previous workers has been recognized and thus, for each genus within the European Jurassic, the number of species is reduced to a handful. Ascending the Jurassic, trends within *Myophorella* include a gradual size increase along with a reduction in the density of tubercle spacing upon the valve exterior. Morphological differences within this genus have also justified its division into two subgenera: *Myophorella* and *Promyophorella*, a division rejected by previous workers. The lack of a continuous record of trigoniids in the European Jurassic has made it difficult to ascertain the particular mode of speciation. There is no evidence for gradualism; a punctuated equilibrium model appears to be a more likely alternative.
The occurrence of trigoniids within the Jurassic appears to be confined to certain stratigraphical horizons. Combined with the fact that some species occur only locally this suggests that their distribution was environmentally controlled. Through field work in Dorset and the Cotswolds the assumption that trigoniids occupied coarse-grained sediments in somewhat unstable environments would appear, for most species, to be correct. However, it has been observed that some inhabited highly argillaceous sediments in quiet water settings.

Jamoytius kerwoodi White: an unimaginative interpretation

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The anatomy and affinities of *Jamoytius kerwoodi* White have long been controversial. Its preservation as a flattened organic film makes the interpretation of features equivocal when solely based on comparison of their shapes. For such problematical fossils, a methodology emphasizing taphonomy and incorporating three-dimensional modelling allows features to be identified more rigorously by providing evidence of their composition and three-dimensional architecture. A comparator, moreover, must be carefully chosen. A small number of least equivocal features should initially be used to place the organism within a phylogenetic context, within which the other features can be identified. Applying this technique to *Jamoytius* indicates that it is an agnathan vertebrate. Its preserved features include W-shaped phosphatic scales, more than ten pairs of branchial openings,

optic capsules, a round ventral mouth, a terminal nasohypohysial opening and continuous ventrolateral fin folds. A cladistic analysis shows *Jamoytius* as the most primitive vertebrate that possesses scales and ventrolateral fin folds. In this context, discussions about the origins of dermal armour and paired appendages should consider *Jamoytius*. The evidence from *Jamoytius* indicates that vertebrate paired appendages may be primitively continuous, and it may support the suggestion that the armour of the agnathans derives from trunk neural crest.

Middle Jurassic benthic associations and palaeoenvironments of the Kachchh Basin, western India

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The Kachchh Basin, a Mesozoic rift basin situated at the western margin of the Indian plate, was filled in the Jurassic with largely siliciclastic sediments. They represent environments ranging from coastal plain, fan delta, and brackish water embayments to shallow marine ramp and low energy basin, the latter exhibiting, at times, signs of sediment starvation. Sedimentation took place cyclically, controlled by eustatic sea level changes of different orders of magnitude as well as by regional tectonic events and by climate.
During the Bathonian-Oxfordian, the basin was populated by a diverse benthic macrofauna (approximately 450 taxa) that belonged to the Ethiopian faunal province. This fauna was dominated by bivalves, with brachiopods, gastropods, corals, serpulids, bryozoans, and sponges as additional elements. A cluster analysis of 220 quantitative samples with more than 23000 individuals yielded 42 associations and several assemblages. The analysis of the spatial distribution pattern of these associations shows a clear relationship to substrate, energy level, salinity and climate. Many associations replaced each other along onshore-offshore transects. In the deeper parts of the basin the diversity of associations occurring in a particular facies type is higher than in shallower parts, but the size of individuals is, in most cases, distinctly smaller. The temporal distribution pattern of the associations is governed, on one hand, by shallowing-upward cycles, on the other hand by large-scale climatic changes. Thus, due to an assumed change from warm-arid to cooler and more humid conditions around the Bathonian-Callovian boundary, tropical elements of the fauna such as the bivalve *Eligmus*, high-diversity coral meadows, and meadows of lithistid and hexactinellid sponges disappear. The concurrent change from oligotrophic to more eutrophic conditions resulted in the dominance of low-diversity associations characterized by deposit-feeding nuculid bivalves in the deeper parts of the basin.

Functional morphology of the hand of *Deinonychus antirrhopus* and its importance for the origin of flight

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The transformation from grasping hand to wing while retaining functionality throughout the transition is one of the most persistent questions in the origin of avian flight. New data from hand morphology of basal maniraptors provides insight into how this may have occurred. The third digit of

Deinonychus antirrhopus (Ostrom) has a curious morphology: bowed gracile metacarpal, buttressed joints between the first, second and third phalanges so that they move as a single unit and the finger is held slightly flexed, and a 50 degree twist in the long axis of the finger so that the ungual (claw) faces medially. This morphology, shared by *Archaeopteryx*, *Confuciusornis*, *Velociraptor*, and possibly *Protarchaeopteryx* and *Caudipteryx*, allows for the third digit to cross underneath the second digit. I suggest that this unique hand allowed the semi-opposable first and third digits to retain their grasping ability while the feathers (originating from the second digit) were elongated. This allowed feathered maniraptors to retain a functional grasping hand during the early development of a wing.

Structural-functional aspects in the evolution of the lid corals (Rugosa)

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The Rugosa show some very conspicious examples of solitary corals. These corals do not have a round shape but a unilaterally flattened shape (slipper like shape, *Calceola*) or they have a rectangular shape (*Goniophyllum*). Furthermore, these corals have a lid by which they can close their polypars. The internal structure of the soft bodies of these corals and some of their structural-functional aspects are reconstructed on the basis of biological and morphological knowledge of the recent corals, in order to give a testable model for an evolutionary pathway from the rugose bauplan to the bauplan of *Calceola* and *Goniophyllum*. The soft body of a rugose coral consists of a gastrovascular cavity that is filled by water, an actinopharynx that closed in a valve like manner, internal single mesenteries that act as tethers between the oral disc, pedal disc, and body wall, and tentacles that are formed on the oral disc at the sites of the mesenteries. During their individual development, new mesenteries are added only in four insertion zones. Septa and mesenteries behave like casts and moulds and as a consequence septa are added only in the four zones where new mesenteries are inserted. This arrangement of the soft body of the Rugosa causes structural-functional limitations for their evolution and for their abilities to form colonies or reefs. But in some cases structural-functional limitations open new evolutionary pathways. The examples of the lid corals represent such new pathways in evolutionary transformation of the rugose bauplan. *Calceola* as well as *Goniophyllum* evolve by quite simple modifications of the general bauplan of a rugose coral. Their peculiar shapes, the lids and especially the even hinges between the calyx and the lid(s) are caused only by mechanical necesseties. Under special conditions (such as high sedimentation rates) these bauplans represent suitable survival strategies.

Classification and distributional trends within the punctate orthide brachiopods

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Cladistic organization of the dalmanellidine brachiopods, involving over 150 genera and based on 42 coded characters, has provided a testable classification for the suborder; nevertheless the analysis indicates the homoplastic development of many features, dictated by functional considerations, locally within parts of the clade. Two superfamilies the Dalmanelloidea and the Enteletoidea are

recognized on the basis of their contrasting cardinalia and include 14 and six families, respectively; both shared a common ancestor probably during the mid-late Cambrian. When matched with stratigraphical data both Relative Completeness and Stratigraphical Consistency indices for the damanellidine clade are high and statistically significant. Investigation of biodiversity within the suborder reveals a major spike during the late Ordovician with subsidiary peaks during the early and mid Devonian associated with first the colonization of deeper-water habitats and second radiations in carbonate environments. Diversity stabilized during the late Palaeozoic when only three groups, the rhipidomellids (dalmanelloid), enteletids and schizophoriids (enteletoids), survived; all three taxa show some similarities in having biconvex profiles, deep notothyrial cavities and large muscle scars.

The reliability of micropalaeontological data: an example from the Kimmeridge Clay of Dorset

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Biostratigraphical and palaeoenvironmental interpretations based on micropalaeontological assemblages generally assume that surface or sub-surface point samples are representative of the heterogeneous complex of species populations that comprise foraminiferal assemblages.
To investigate the reliability of such assumptions, a replicate based sampling scheme was devised to study temporal and spatial variation in benthic foraminiferal assemblages from the type sections of the Kimmeridge Clay and from adjacent boreholes drilled as part of the NERC Special Topic Rapid Global Geological Events (RGGE). This sampling scheme allows direct measurement of the degree to which core samples are representative of the assemblages they sub-sample.
Multivariate analysis of census data from over 300 samples indicates significant vertical and horizontal variation over small scales (cm to m) in outcrop and significant variation between outcrop and core (5 km from the type section). Thus, faunal patterns obtained from surface or sub-surface point samples can reflect a localised subset of the range of assemblage patterns existing within a lithological unit. A fuller understanding of the types of distribution patterns that occur at a variety of spatial scales may be necessary before biostratigraphical and palaeoenvironmental interpretations based on micropalaeontological (and, indeed, macropalaeontological) distribution data are accepted with the level of confidence that we currently employ.

Benthic foraminiferal response to the development of low oxygen conditions in the Pliensbachian-Toarcian (Lower Jurassic) of North-West Europe

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Whilst the existence of a minor extinction event in the Early Jurassic has been confirmed by analyses of upper Pliensbachian and lower Toarcian macrofaunas, the microfaunal response has not received as much detailed attention. High resolution sampling of Pliensbachian-Toarcian intervals in the United Kingdom, southern France and south-west Germany has revealed a fundamental turnover in the foraminiferal assemblages in the Toarcian Falciferum Zone during which many foraminiferal taxa

became extinct. Whilst large scale benthic foraminiferal trends have been previously identified this study has revealed the existence of opportunist or disaster foraminiferal species. These species occur during times of environmental stress and exploit available habitat space for short periods of time. Uniserial forms such as *Nodosaria*, *Frondicularia* and *Lingulina* which dominate Pliensbachian assemblages become less important in Toarcian and subsequent assemblages whilst the coiled forms like *Lenticulina* dominate after the event. Generalists, e.g. *Lenticulina*, most probably had certain adaptations that allowed them to survive low oxygen conditions and contribute to the rapid recovery that started in the falciferum Subzone (Falciferum Zone) of the Early Toarcian. The response of benthic foraminifera during the late Pliensbachian-early Toarcian interval can be linked to the changes in sea-level and the resulting development of low oxygen conditions.

Developmental mode and macroevolutionary correlates in temnopleurid echinoids

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It is widely accepted that developmental strategy is closely linked with a number of biogeographical and macroevolutionary correlates, such as geographical range, geological longevity, speciation rate and survivorship at times of mass extinction. Many of these claims are anecdotal and none has been tested within a rigorous phylogenetic framework. Echinoids are unusual amongst marine invertebrates in that developmental mode can be simply and unambiguously deduced from examination of the adult test. The temnopleurid echinoids embrace taxa exhibiting all three primary modes of development: planktotrophic, lecithotrophic and brooded. A phylogeny of the temnopleurids is presented which allows an estimation of the number of times nonplanktotrophy has arisen in this group and enables the investigation of the links between larval type and macroevolutionary correlates.

Quaternary reefs of eastern Sicily: growth history and control in a tectonically active region

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Uplifted Quaternary reefs on the eastern Sicily coast are frameworks of coralline algae and vermetid gastropods as veneers on steep bedrock surfaces. Reefs grew while sea level changed, so they are not biotically zoned. The reef at Aci Trezza near Catania grew in the early Holocene sea-level rise on eroded early Etnean basalt, and has a very complex growth history, seemingly involving interplay of tectonic and sea-level control, but finally underwent tectonic uplift over the last *c.* 8000 years, dated from boring bivalves. 40 km north, at Capo Sant Alessio, the upper surface of a reef coincides with a bedrock notch previously dated at *c.* 5000 y, representing the mid Holocene quasi-stillstand and the oldest age of this reef. The reef was simply uplifted in later Holocene times. 10 km south of Capo Sant Alessio, at Capo Sant Andrea near Taormina, an (algal) reef grew on the 45 degree dip of an eastward-dipping old fault plane in limestones associated with the Malta Escarpment-Messina fault

system. The reef extends to *c.* +12 m, but is notched at *c.* +5 m (= *c.* 5000 y) and presumably grew during early Holocene times. It was drowned and buried in micrite prior to uplift. Sediments in contact with the fault do not show strain, so apparently it has not moved for a few thousand years. At Capo Milazzo peninsula in north-eastern Sicily, a coral from +2 m, previously dated at 6270+/- 140 y BP, indicates either a small uplift, or a more complex history of uplift and subsidence. Observations from the biota in these four sites, combines with the fact that bedrock notches between Catania and Milazzo show poor correlation between sites, except over short distances. The reefs are therefore a useful tool to demonstrate differential uplift in eastern and north-eastern Sicily, to assist tectonic models of the region.

Temporal separation of basin restriction and the latest Palaeocene warm water pulse in the North Sea: high resolution palynofacies data

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The terminal Palaeocene of the North Sea Basin is characterized by a number of important events. In particular, there is evidence of the widely documented late Palaeocene warming and a phase of maximum basin restriction. Well 22/10a-4, situated in the Everest Field of the Central North Sea yielded more than 100 m of continuous, well preserved core, representing a continuous section through the late Palaeocene Maureen, Lista and Sele formations of Knox and Holloway (1992). The stratigraphical interval of interest in Well 22/10a-4 spans the Lista/Sele boundary and the Sele Formation.
The palynofacies assemblages show a significant change at the Lista/Sele boundary from a sparse assemblage dominated by black (oxidized) wood in the green, bioturbated claystones of the Lista Formation to a more diverse assemblage dominated by brown (unoxidized) wood in the dark grey to black laminated mudstones of the Sele Formation. This significant palynofacies change reflects a change from well oxidized, open marine conditions in the Lista Formation to restricted, anoxic conditions in the Sele Formation. The tectonic event causing the significant restriction of the North Sea Basin is clearly temporally separated from the late Palaeocene warming, which in Well 22/10a-4 is indicated both by an influx of the warm water wetzelielloid dinocyst *Apectodinium* and para-tropical pollen, which first appear in the Sele Formation, some 15 m above the Lista/Sele boundary. The preliminary data collected therefore indicate that the onset of maximum basin restriction and the late Palaeocene climatic warming are not coeval, being separated by some 15 m of sediment deposition at this locality.

Knox, R. W. O'B. and Holloway, S. 1992. Paleogene of the Central and Northern North Sea. *In* Knox, R. W. O'B. and Cordey, W. G. (eds). *Lithostratigraphic nomenclature of the UK North Sea.* British Geological Survey, Nottingham.

Jurassic vent

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The Figueroa massive sulphide deposit, located in Franciscan Complex rocks in the San Rafael Mountains of California, preserves the only known Jurassic hydrothermal vent fossils. The Figueroa fossil assemblage is specimen-rich but of low diversity and comprises, in order of decreasing abundance, vestimentiferan worm tubes, the rhynchonellid brachiopod *Anarhynchia* cf. *gabbi* and a species of ?nododelphinulid gastropod. The Figueroa community of animals lived at a deep-water, high-temperature vent site located on a mid ocean ridge or seamount at equatorial latitudes. The fossil vent site was then translated north-westward by the motion of the Farallon Plate and subsequently accreted to its present location. An iron-silica exhalite bed, the probable lateral equivalent of the Figueroa deposit, contains abundant filamentous microfossils with two distinct morphologies and probably represents a lower temperature diffuse flow environment. This is stratigraphically overlain by a 15 m thick sequence of bedded cherts containing early Jurassic radiolarians. The Figueroa fossil community was subject to the same environmental conditions as modern vent communities but it is unique amongst modern and other fossil vent communities in having rhynchonellid brachiopods.

Acid rain and Strangelove oceans over the Cretaceous Tertiary Boundary

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Mass extinction of marine phytoplankton following the Cretaceous Tertiary (K-T) boundary event resulted in the collapse of the carbon isotope depth gradient in marine sections, the so called strangelove oceans. Coal and clay samples from the Raton Basin, New Mexico spanning the K-T boundary were examined for isotopic and elemental ratio variations. Results show a sudden positive d34S excursion at the boundary and a large increase in the concentration of sulphur as shown through C/S and S/N elemental ratio analysis. A large negative d13C excursion occurring after the K-T boundary is also detected. These events are interpreted as evidence for sulphuric acid rain and marine extinction driven degassing of CO2 as proposed under the strangelove ocean model.

Fracture and osteomyelitis in PII of the second pedal digit of *Deinonychus antirrhopus* (Ostrom) an Early Cretaceous 'raptor' dinosaur

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We report here on a healing transverse, displaced, midshaft fracture of PII of the second pedal digit of Yale Peabody Museum 5205, the type specimen of *Deinonychus antirrhopus* (Ostrom). The affected phalanx bore the sickle-shaped talon for which the animal is named.
Radiographic examination of the fossil shows a caudal and ventral displacement of the distal fragment. The presence of osteomyelitis is supported by lytic areas at the fracture site with evidence of a sequestrum. Oblique views provide no evidence of longitudinal fracturing. Radiographs support the diagnosis of a fracture due to bending, which is compatible with damage during a slashing motion of the talon. However, pathologic fracture subsequent to primary osteomyelitis cannot be ruled out at this time.
Sufficient stability/immobility allowed partial healing to occur prior to the animal's death, as evidenced by lack of callous, remodelling and smoothing of dorsal and medial sides. That this animal survived for an unknown length of time with an injury to one of its purported major defence and food-gathering mechanisms may support Ostrom's analysis of gregarious/pack-hunting behavior for *Deinonychus*.

The link between sea levels and climatic change in a non-glacial world: evidence from the Palaeozoic sequence of the Falkland Islands

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Palynomorphs have been found throughout a section in West Falkland. This section is, to date, the best and in fact only known high latitude palynostratigraphical reference section. These palynological assemblages contain a number of readily identifiable spores and chitinozoans which are known from both Laurasia and/or north Gondwana and which can be used to assign ages. But it apparent that not only does assemblage composition differ in comparison with north Gondwana and Laurasia but that the inception of key marker spores can be much delayed. This can be seen from comparison of macrofossils, chitinozoans and spores in the lower part of the Emsian Fox Bay Formation.
Within the West Falkland Group the key correlative horizons are the transgressive shales. As such the West Falkland Group can be correlated and sub-divided in the same way as the correlative Bokkeveld and Witteberg groups in South Africa. As recognized within South Africa, these shale horizons represent elements of a sea level curve and provide the method for more precise extra-Gondwanic correlations. Within each marine incursion the spore assemblages become more diverse and show the inception of species known from lower Devonian latitude. As such the linkage between sea level and climate change can be recognized. This high latitude observation is potentially very significant in our understanding of the mechanism for Devonian sea level change.

Microevolutionary transitions in a lower Ordovician pelagic trilobite lineage

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Microevolution patterns are typically characterized in terms of the end-member cases of punctuated equilibria and phyletic gradualism. If punctuational evolution is, as usually described, the result of allopatric processes, then gradualism can be predicted to occur in organisms not prone to such processes; i.e. organisms whose population structure and environment tend to preclude formation of peripheral isolates. Pelagic marine animals are prime candidates.
The trilobite *Carolinites* has been convincingly shown to have been epipelagic. A recent analysis of its visual geometry underlined this interpretation. *Carolinites* occurs with greater or lesser abundance at some 11 horizons spanning Ross-Hintze shelly fossil zones H (Ibex) to M (lower Whiterock) in the lower-middle Ordovician succession at Ibex, western Utah, a succession which itself meets the necessary geological requirements for an evolution case study.
Geometric morphometric analysis suggests that the visual impression of transitional change in the lineage is the result of subtly (sometimes less subtly) changing allometries affecting different parts of the exoskeleton. 'Allometric paedomorphic' and 'allometric peramorphic' processes affect different structures. The case study highlights a number of issues of importance in characterizing evolution patterns, and in particular the difficulty of quantitatively demonstrating gradualistic change.

Biostratinomy of *Uintacrinus* Lagerstätten: Upper Cretaceous of Kansas and Colorado, USA

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New, well-documented field occurrences in Kansas and Colorado, in laminated chalk (Niobrara Formation) and black shale (Mancos Shale) respectively, and re-examination of museum collections have provided new information pertaining to the biostratinomy of *Uintacrinus* assemblages. In both facies, dense aggregations are preserved as thin lenses with articulated calyces and arms only on the lower surface, in contrast to disarticulation on the upper surface. Calyces may be imbricated within a lens and are mostly compressed laterally but specimens may also be preserved oral side up or down. Some specimens displaying the oral side retain soft part preservation of the tegmen, anal tube and ambulacra. Several aggregations display a spoke-like pattern in which arms are aligned towards the centre of the slab, suggesting inward collapse of crinoids with arms entangled centripetally. The dense aggregations also reveal a number of new preservational observations, including marginal indentations, hyporeliefs and reversal of typical upper surface disarticulation. These features indicate the likely occurrence of a cyanobacterial component of necrolytic origin which may have provided cohesion, explaining many of the taphonomic features. Microbial sealing during decay may help to explain other instances of similar crinoid preservation, including both benthic and pelagic forms, in which articulation is confined to lower surfaces.

Supposed *Scomberomorus saevus* (Scombridae, Teleostei) hypural plates from the lower Tertiary, and scombrid relationships

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Scomberomorus saevus is a fish species from the family Scombridae, described from the Palaeocene and Eocene. Some of the hypural plates (bones from the tail region) used to describe this species and other specimens of hypural plates, that fit the descriptions of *S. saevus*, proved to be different scombrid genera and species. Hence, the validity of *Scomberomorus saevus* is questioned. The material includes a new fossil species of *Acanthocybium* and a species of a new bonito genus. This new genus provides evidence for a sister group relationship between bonitos and Spanish mackerels, with the Spanish mackerels as the plesiomorphous sister group.

Direct correlation between the Llandovery-Wenlock (Silurian) chitinozoan and graptolite biostratigraphical schemes

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The Banwy River section (mid Wales, UK), palaeogeographically situated close to the shelf edge, contains graptolites from the upper Llandovery-lower Wenlock series (?*turriculatus*) *crispus* to *riccartonensis* graptolite biozones (Loydell and Cave 1996). The Llandovery-Wenlock series boundary (as currently defined) has been identified for the first time in the UK in the graptolitic facies of Banwy River and graptolites have enabled correlation with sections in Bohemia and Scandinavia.
Samples from known graptolite biozones have been processed for the recovery of Chitinozoa to enable the direct correlation between the graptolite biostratigraphical scheme and the chitinozoan biostratigrapical scheme. This study has enabled the first direct correlation between the base of the *Margachitina margaritana* Biozone and the graptolite biostratigraphical scheme and it also provides further evidience to suggest that the base of the *Angochitina longicollis* Biozone occurs in strata younger than previously thought.
The direct correlation between the *margaritana* chitinozoan Biozone and the graptolite scheme also indicates that the base of the Wenlock Series may correlate with an older graptolite biozone than currently defined (the base of the Wenlock Series is presently considered to be coincident with the base of the *centrifugus* graptolite Biozone).

Loydell, D. K. and Cave, R. 1996. The Llandovery-Wenlock boundary and related stratigraphy in eastern mid-Wales with special rerference to the Banwy River section. *Newsletters on Stratigraphy*, **34**, 39-64.

The Silurian of Gotland - a 'Fossil-Lagerstätte' of Palaeozoic calcareous micro- and nannofossils

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The Silurian of Gotland, Sweden, consists of about 450 m of carbonate sediments accumulated in a warm epicontinental sea near the Silurian equator. The strata never underwent tectonic stress or deep burial conditions. Therefore, the sediments show only minor late diagenetic alteration and an excellent preservation of microfacies characters and fossils, particularly those with originally calcitic skeletons. With the aim to understand the formation of micritic limestones and the development of limestone-marl alternations several hundreds of polished, slightly etched rock samples from the Silurian of Gotland were investigated with the SEM. One of the most surprising results of these investigations was the discovery of excellently preserved calcareous micro- and nannofossils, most of which remained unknown to date. Only few morphotypes can be assigned with varying degrees of confidence to organisms which are described in literature. These are possible ancestors of the foraminifera and diverse algal remains. Additionally, very abundant small spherical calcitic microfossils ('nannospheres' and 'calcispheres') and several other enigmatic groups of microorganisms ranging in size between 5 um and 100 um have been observed. The importance of these calcareous micro- and nanno-organisms in the production of Palaeozoic carbonate muds is so far unknown and needs further investigations.

Clio's revenge: using historical data to explore tree-based historical reconstructions

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Historical explanations should never be confused with historical data themselves. Some new approaches in evolutionary biology invoke history in the form of phylogenetic trees when making among-species comparisons. Such historical reconstructions are used to explain correlations, character distributions, and other observations in extant taxa. But these reconstructions do not draw directly on historical data. Palaeontological data can potentially falsify such hypotheses.
A phylogenetic tree of fossil carnivorans (Viverravidae, Eutheria) from North America was used to explore this possibility. Branches of the tree were 'pruned' at the early Eocene and the resulting 'tips' were treated as extant taxa in calculating ancestor-node reconstructions. The reconstructions were compared with the actual palaeontological samples hypothesized to lie at those tree-nodes.
This experiment highlights several points: the original reconstruction methods are extremely sensitive to tree-topology, to the extinction of taxa, and to estimates of time-since-divergence; the addition of palaeontological data counterbalance these, but introduce phylogenetic issues about whether fossil samples fall at tree-tips or tree-nodes and statistical issues with comparing estimated means with sample means.

Feeding mechanisms and the evolution of jawless fish

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Probably the most widely held view of the early evolutionary history of the vertebrates explains

diversity changes as a classic Darwinian struggle driven by competition for food resources. Jawless vertebrates radiated by outcompeting potential rivals for food or by moving into unoccupied niches; they in turn were outcompeted and replaced by gnathostomes with superior feeding mechanisms. Unfortunately, there are almost no data to support this scenario, and recent work raises serious doubts. These hypotheses of competition rely heavily on interpretations of the feeding mechanisms employed by extinct agnathans, and these are poorly known. Speculation regarding feeding in heterostracan fishes, for example, ranges from predation to mud grabbing, microphagous suspension feeding, deposit feeding, algal frond snipping, algal scraping, plankton feeding, detritivory, or sea-bottom mud ploughing. Similarly, anaspids have been interpreted as microphagous suspension feeders, suction feeders or macrophagous predators with a rasping tongue. This range of confusing and contradictory opinions has developed because of the scarcity of evidence for feeding mechanisms, and a lack of constraint in analyses of agnathan functional morphology. Rather than relying on analogies with extant jawless fish, direct analysis of functional morphology in extinct agnathans allows constrained and testable hypotheses of feeding mechanisms to be proposed.

Microframe reefs built by calcified microbes, middle Cambrian, Jinan, North China

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Mid Cambrian reefs with microframe structure built by calcified microbes, probably cyanobacteria, are well-exposed in the Zhangxia Formation near Jinan in Shandong Province. Members of the *Epiphyton*, *Renalcis* and *Girvanella* groups are almost solely responsible for a series of extensive biostromes, individually up to 15 m thick, in which metazoans are scarce. These reefs are surrounded by coarse cross-bedded oolite-pisolite, reflecting rapid growth in a high-energy environment.
The two main reef lithotypes present are: (1) matrix-rich *Tarthinia-Tubomorphophyton* thrombolite-dendrolite microclusters, and (2) *Gordonophyton-Razumovskia* thrombolite microframes. The latter were created by rectilinear arrangement of prostrate and vertical microbial filaments, and the small (millimetric) size of the cavities contributed to framework strength.
Similar, but usually less well-preserved, mid-late Cambrian reefs appear to be widespread in Asia and North America. These North China examples establish microbial microframes as a distinctive reef-structure, and show that frame-building continued during the Cambrian despite archaeocyath demise.

Volcanically mediated plankton blooms in the Silurian of the Southern Uplands

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At Thirlestane Score, in the Southern Uplands of Scotland, the occurrence of graptolites corresponds closely with the occurrence of particular lithologies. All graptolite bearing horizons cluster around bentonite layers, and are found as a couplet of distinct populations. In the lower element of the couplet, which is found in a bioturbated, beige coloured and nodular layer, the graptolites are common, siculae are abundant, specimens are generally small and populations show a straight survivorship curve. In the upper element of the couplet, a dark coloured, laminated layer, the graptolites are relatively rare, siculae uncommon, specimens large and populations show a convex survivorship curve. The rest of the section appears to be barren.
The ingress of ash into the system seems to have stimulated primary productivity and hence graptolites. The beige couplet population pattern is consistent with an unstable environment, such as would be expected in a nutrient rich system (Rosenzwieg, 1971). The upper element of the couplet has a pattern consistent with lower nutrient levels creating a more stable system. The most likely nutrient being added by ash falls is iron, suggesting that macronutrients were available in the system.

Rosenzweig, M. L. 1971. Paradox of enrichment: destabilisation of exploitation ecosystems in ecological time. *Science*, **171**, 385-387.

Miocene palaeotemperatures of the Mediterranean region from zooxanthellate corals: application of the diversity-energy relationship

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Fossil corals have long been used for palaeoenvironmental interpretation using simple uniformitarian qualitative extrapolation from the restriction of many extant taxa to warm shallow tropical marine waters. A preliminary attempt is made here to derive actual palaeotemperatures from the Miocene coral record of the Mediterranean region by invoking the 'energy hypothesis'. This is an inference from the empirical relationship (known in a variety of marine and terrestrial groups) of taxonomic richness to climate (ultimately solar energy input), e.g. richness of modern zooxanthellate coral genera increases in relation to mean prevailing temperatures.
A Miocene palaeotemperature curve based on 15 Mediterranean coral localities is generated from this relationship. Results show an overall cooling, with warmest conditions (*c.* 20deg.C) in the early Miocene. From the mid Miocene to late Miocene, climate cooled at an accelerating rate through about 4.5deg.C. This trend matches oxygen isotope evidence surprisingly well, although the coral-derived cooling lags behind the isotope curve by about 5 Ma. Reasons for this and other anomalies will be discussed, particularly with respect to dating and increasing biogeographical isolation of the Mediterranean over this time.

Fire ecology of Cretaceous vegetation in the Isle of Wight, England and Nova Scotia, Canada

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Fusain (fossil charcoal) is common in early and mid Cretaceous terrestrial sediments in England and Nova Scotia. In the Wealden sediments of the Isle of Wight, England, fusain is abundant in the Vectis Formation. Marginal marine channel sandstones contain abundant conifer wood charcoal whilst higher in the sequence siltstones within gutter casts on coastal plains bordering fresh-saline lagoons, contain charred fern fronds.
In central Nova Scotia in the Shubencadie and Musquodoboit basins, drilling beneath Quaternary cover has shown the presence of mid Cretaceous non-marine sediments filling palaeovalleys. These sediments include lignite horizons which are probably organic-rich sediments rather than true *in situ* peats. Charcoal occurs in many closely spaced layers. Uncharred plants include conifers which have leaves with xeromorphic characters such as sunken stomata and papillae. Charred plants include ferns and conifers which indicate the occurrence of crown, understorey and possibly surface fires. Evidence of post-fire soil erosion comes from the presence of large quartz grains in the lignite and diverse arthropod coprolites including those from termites.
Growth rings in conifer charcoal from Nova Scotia and England and from permineralized woods from England show evidence of a seasonal climate. Fire appears to have been a frequent feature in these two areas. Homogenized cell walls of the woods indicate charring temperatures greater than 275°C.
In the Isle of Wight evidence suggests the occurence of conifer woodlands and fern dominated 'prairie' . In Canada the ferns and conifers appear more mixed but fern dominated horizons may indicate that fire frequency prevented the re-estabishment of the climax vegetation. The occurrence of charcoal in such contrasting geological settings in the early-mid Cretaceous emphasizes the importance and significance of regular wildfires in pre-angiosperm dominated vegetation.

Explaining the Quaternary paradox

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'The current facts and understandings of population genetics would be thoroughly compatible with major changes in the adaptations of most lineages of animals and plants during the last million years. Instead, a large proportion of Recent species are essentially identical to their Pliocene ancestors." (George C. Williams, 1992, *Natural Selection*, p. 131). According to the Plus ça Change Model, morphological stasis over geological timescales tends to arise not from the stability of physical environments, but from their *instability*. Because of the Quaternary climate upheavals, many of today's species may be relatively inert to environmental twists and turns. They are generalists in a long-term, non-ecological sense, with properties that have enabled them to survive with little change throughout wide fluctuations in various aspects of the physical environment for about 2 million years. Were it not for human influences, relatively little microevolution might be occurring world-wide: indeed, most reported cases of rapid microevolution in macroorganisms today are in new environments associated with human activity. Although the climate of the last 10000 years has been relatively stable, this interval has not been long enough to relax the influences promoting net stasis. Of course, many fossil lineages also show approximate stasis at times other than the Quaternary. According to the model, this is because most of the fossil record comes from dynamic shallow marine environments, whereas the relatively stable environments in which gradualism tends to occur (such as on land in the tropics and in the deep sea) are rarely represented.

Evolution in a fluctuating environment

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As a population of organisms evolves towards a hypothetical optimum morphology, the range of variation in the population will increasingly straddle the optimum. Consequently, the rate of evolution declines gradually, with a convex curve, until the mean morphology equals the optimum. If the environment is fluctuating, the optimal morphology fluctuates accordingly. This has the effect of sampling a range of evolutionary rates and the convexity of the curve results in this sampling producing a slower mean rate of evolution. This effect can be seen in genetic algorithm simulations. The implication is that evolution will be slower in climatic zones, environments or times when conditions fluctuate; comparisons can be made with Sheldon's (1996) 'plus ça change' hypothesis, which predicts stasis under these conditions.

Permian non-marine ichnofaunas from the Falkland Islands; the South Africa connection

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Thick Permian deltaic to turbiditic sandstones and mudrocks were deposited in the eastern end of the Karoo Basin of South Africa, and following Mesozoic break-up of Gondwana are now located in the Falkland Islands. The deeper water, off-delta facies which include glacial rhythmite and turbiditic sandstone and shale units locally contain a spectacularly well-preserved ichnofauna.
Characteristic forms are *Umfolozia* arthropod trackways comparable with SouthAfrican forms, and *Undichna* produced by swimming fish. The *Undichna* traces include a new form as well as abundant *U. bina* which is also characteristic of rocks of the Ecca Series in South Africa.
Other traces present include *Cochlichnus*, *Diplocraterion*, *Haplotichnus*, *Helminthoidichnus*, *Isopodichnus*, *Kouphichnium*, *Planolites*, *Scoyenia*, *Skolithos*, *Stelloglyphus* and several new or unidentified forms.
The assemblages collected strongly resemble those of late Palaeozoic freshwater basins in South America, which are generally assigned to deep water lacustrine conditions. However, it is thought that oxygenation levels and substrate type were the major controlling factors rather than water depth.

The preservation of bone

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Fossil bones are fairly common in many sedimentary systems, and have been extensively collected for 150 yrs or more. However, biogenic apatite is more unstable in pore waters than biogenic (shell)

calcite. To be preserved, biogenic apatite must recrystallize to a less reactive mineral. Despite the huge number of fossil bones found, from a wide variety of locations, very few fossil bones are pseudomorphed by minerals other than apatite. In all cases bones fossilize by recrystallization of biogenic apatite to francolite (carbonate fluorapatite). This recrystallization is pervasive and affects all portions of the bone, but commonly very fine histological detail is preserved. These observations can be explained by a simple model of bone recrystallization, which requires specific geochemical and hydrological conditions for preservation of bone. These conditions vary both between burial sites and within bones, and affect the relative rates of bone recrystallization and degradation. Having established a simple model for bone preservation, we are better equipped to predict taphonomic biases, and to select bones for geochemical analysis.

'And the small shall inherit the Earth...'

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The Permian-Triassic strata of East Greenland have yielded an abundant, diverse and exceptionally well-preserved fossil fish fauna. From an evolutionary point of view fish are extremely interesting as they are often said to be unaffected by mass extinction events and may even radiate through such times of global crisis. However, study of the Greenland fauna has shown that these are myths and that fish suffer in a similar way to the rest of the marine fauna.
One very obvious characteristic of the post-extinction Lower Triassic fauna is its very small size. Late Permian species have a mean body length of some 0.5 m, with a number of genera exceeding several metres in size. In contrast, basal Lower Triassic species rarely exceed 0.25 m long (most are around 0.1 m). This 'Lilliput Effect' is observed in all other marine organisms at this time: e.g. shelly invertebrates, foraminifera, burrowing infauna etc. In addition, palaeoecological data show that all these fish were benthic or nektobenthic predators. The other major group of nektobenthic vertebrate predators in the Permian-Triassic (conodonts) also show a similar size reduction in the post-extinction fauna. Small size in post-extinction survivors has also been documented in other mass extinctions (for both fish and conodonts).
The reason for this 'Lilliput Effect' is unclear. While some authors suggest that animals with large body size may be more prone to extinction events, the data are equivocal. A more likely explanation is that small size develops in response to a prolonged decrease in food supply after the extinction event. Isotopic evidence (low d13C) suggests that plankton biomass was much reduced for most of the Griesbachian. A similar isotopic signature also appears after all other mass extinction events.

The palynology of the upper Wenlock Series (Silurian) of the Much Wenlock and Ludlow areas, Shropshire, England

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The upper Wenlock Series from the Sheinwoodian-Homerian to Homerian-Gorstian boundary includes the upper part of the Coalbrookdale Formation and the Much Wenlock Limestone Formation

in the type area. The palynological assemblages are generally well preserved and of low geothermal alteration, with acritarchs, prasinophycean algae, chitinozoans and terrestrial sporomorphs regularly recorded. In most samples, acritarchs are the most abundant palynomorphs present, with *Leiosphaeridia*, *Michrystridium*, *Multiplicisphaeridium*, *Diexallophasis*, *Helosphaeridium*, *Cymatiosphaera*, *Gorgonisphaeridium* and *Veryhachium* the common genera recorded.

Poikiloaerobic, exaerobic and dysaerobic biofacies - which is correct?

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Many, if not most, organic-rich, laminated shales contain abundant, low diversity assemblages of benthic species often concentrated on discrete bedding planes. Intense debate in the past decade has seen the proliferation of names for this biofacies. For the most part, this discussion reflects a dichotomy in interpretation that was first realised in the debate between Seilacher and Kauffman over the origin of the benthic fossils of the Posidonia Shale of Germany. Exaerobic, quasianaerobic and (the original definition of) dysaerobic biofacies were interpreted to record persistent, but low benthic oxygen levels, whereas poikiloaerobic and episodically dysaerobic biofacies record alternating anoxic and dysoxic benthic conditions. Measurement of pyrite framboid sizes in these biofacies may help to distinguish between these conflicting interpretations.
Modern pyrite framboids are observed to form rapidly in a narrow zone at the top of the sulphate reduction zone (SRZ) where iron oxidation occurs. In euxinic environments, where the SRZ extends into the lower water column, pyrite framboids can only reach small sizes (5 ：m) before sinking to the seafloor. In contrast, diagenetic framboids from dysoxic environments can grow to considerably larger sizes. Analysis of framboid sizes from the benthos-rich, organic-rich shales of the Kimmeridge Clay (Upper Jurassic, Dorset) reveals that they are dominated by syngenetic framboids with only a tiny proportion of larger, diagenetic framboids. This implies that shale deposition records long-term euxinic conditions interrupted by a few brief oxygenation events of perhaps a few months duration. This interpretation of the Kimmeridge Clay shales is closest to Seilacher's original interpretation of the Posidonia Shale.

POSTERS

New Early Devonian arthropods from the Windyfield Chert, Rhynie, Aberdeenshire, Scotland

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An intensive drilling and trenching program centred around the Early Devonian Rhynie chert hot spring deposit during the summer of 1997, has provided many new insights into the stratigraphy, sedimentology and palaeontology of this unique style of Konservat-Lagerstätte where early terrestrial

land plants and animals are preserved within siliceous sinters. Part of this work involved the location and study of the Windyfield cherts, a similarly hosted, yet apparently discrete hot spring centre some distance from the Rhynie cherts and perhaps at a different stratigraphical level in the local succession. This is reflected in the floral and faunal composition of these beds, which have revealed a new early land plant taxon and a number of new arthropods including whole body fossils and cuticle fragments of millipedes, eurypterids, scorpions, crustaceans and as yet unidentified groups. Cuticular fragments are widespread throughout all chert textures, as well as the enclosing clastic sediments, whilst complete arthropods tend to be concentrated within a discrete layer approximately 20 mm thick which appears to be rich in micro-coprolites. The discovery of these additional faunal elements at Rhynie indicates a broad compositional similarity between this and other preserved early terrestrial ecosystems such as Alken an der Mosel, Germany and Gilboa, USA.

Vertebrate taphonomy of the Cromhall Quarry palaeokarst

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A pseudoplanktonic inarticulate brachiopod attached to graptolites and algae

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Small inarticulate brachiopods from graptolitic facies have typically been interpreted as pseudoplanktonic on an unknown, probably algal host. Clusters of valves, sometimes associated with organic stains on bedding planes have supported this conclusion, although an alternative explanation relates to the benthic colonization of decaying algae on the sea floor.
The Upper murchisoni Shales of the Llanvirn (Darriwillian) of the Builth Inlier of Central Wales contain abundant specimens of the small inarticulate *Schmidtites*? *micula*. Recent discoveries above a bentonite show clusters of *S. micula* valves associated with the graptolite *Pseudoclimacograptus scharenbergi*. Attachment is either directly to the rhabdosome, or secondarily, via filamentous algae. Clusters of valves with no obvious nucleus, presumably representing a purely algal host, are abundant. Associations do not occur with *Didymograptus murchisoni*, *Callograptus* sp., an orthoconic nautiloid, or the larger inarticulates, *Palaeoglossa attenuata* and *Monobolina crassa*.
The implications of these specimens include a definite pseudoplanktonic lifestyle for *S. micula*, the recognition of graptolites as a host for Early Palaeozoic pseudoplankton, possible fine-scale depth zonation among the epeiric graptolites, and the importance of ash-fall in the preservation of planktonic associations.

Evolution of the *Turborotalia cerroazulensis* lineage (Eocene planktonic foraminifera)

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Palaeoecological reconstruction of Lower Cretaceous (Barremian-Aptian) shallow-water coral communities of the Neo-Tethyan Realm

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Equable climatic conditions coupled with high sea level stands in the Early Cretaceous gave rise to periods of significant coral development on expansive carbonate platforms in the Neo-Tethys. The coral units are frequently laterally extensive and exhibit diverse palaeoecologies, geometries and sedimentary systems. Whilst there have been local studies of Barremian-Aptian coral communities, there has been no attempt to produce an overview. Documentation of a significant number of coral-bearing sequences in Europe and the Middle East will allow the formulation of a regional palaeoecological synthesis.
Field observations in Provence and the French Pyrenées intimate the existence of four groups of coral-bearing units based on geometry and sedimentology: (1) biostromes dominated by shallow-water carbonates; (2) small reefal mounds dominated by shallow-water carbonates; (3) biostromes proximal to, or intimately related with, muddy sediments; and (4) broad reefal mounds closely associated with muddy sediments. The coral and associated faunas studied are subject to laboratory examination to verify taxonomic affinities. Nevertheless, preliminary systematic assignments have revealed that hydnophoroid Scleractinia such as *Hydnophoromeandraraea* sp. and *Eohydnophora* sp. are important components of the communities within each of the above groups.

Covert creatures from the Carboniferous: *Stenophragmidium* (Trepostomata, Bryozoa) from the Lower Carboniferous of the British Isles

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The bryozoan *Stenophragmidium* has been described from various parts of the Lower Carboniferous of Britain and Ireland. It is a trepostome bryozoan with erect ramose, hollow erect, adnate sheet and encrusting colony forms. It is very similar to *Tabulipora*, but differs in that it possesses features that can consistently distinguish it from all other trepostomes. These features, called hemiphragms, are processes that extend from the proximal wall of the autozooecial chamber. Previous work on *Stenophragmidium* has led to some confusion in the literature, therefore a complete taxonomic revision of the genus is being carried out. As part of this revision, multivariate statistical techniques have been applied to the data available and the results appear to agree with other more traditional systematic methods. It appears that previously described material in some cases belong to the same taxon, while the number of known taxa has increased substantially. *Stenophragmidium* ranges from the latest Tournasian to the Brigantian in Britain and Ireland. It is found in a range of rock types from deep water shales to shallow water oolites. It perhaps has potential as a biostratigraphical tool in the

absence of other better known markers.

A morphometric analysis of the hind limbs of flying vertebrates

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The diverse angiosperm leaf flora of the Late Cretaceous Antarctic Peninsula

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In the Late Cretaceous Antarctica was connected to South America, Australia and New Zealand, which allowed the migration of animals and plants across Gondwana. The Antarctic Peninsula, which was an active volcanic arc at about 65deg.S, was a crucial link during the radiation and diversification of the angiosperms. Fossil plants from the Hidden Lake Formation (Santonian) and the Santa Marta Formation (Santonian-Campanian) on James Ross Island, east of the northern peninsula, provide new evidence about forests with a diverse angiosperm component flourishing in the region. Although there is no cuticle present, the leaf impressions are excellent and show intricate detail of the leaf architecture.
Many of these ancestral leaf fossils cannot be clearly assigned to modern families. Numerous and subtle variations in angiosperm leaves of the mid and early Late Cretaceous are such that they appear to form a morphological continuum. For this reason multivariate statistical methods were used to cluster the leaves using characters such as the style of the apex and base, angles, marginal features, and primary, secondary and tertiary venation patterns. There are 18 clusters of leaves within the Hidden Lake Formation, representing 18 form genera of Antarctic Cretaceous angiosperms and exposing a diverse polar flora.

A conodont, thelodont and acanthodian fauna from the lower Prídolí (Silurian) of the Much Wenlock area, Welsh Borderland

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Conodonts, thelodonts and acanthodians have previously been collected from the Prídolí of the Welsh Borderland from bone beds such as The Ludlow Bone Bed. In general, specimens collected from these types of deposit are very abraded and make taxonomic studies difficult. This poster shows well preserved thelodont microelements from two samples from the Downton Castle Sandstone Formation (Prídolí, Silurian) of the Much Wenlock area of the Welsh Borderland. Head scales, a wide variety of transitional scales, and pore scales of the lateral line sensory canals of the thelodont *Paralogania*

ludlowiensis (Gross) are shown for the first time. A new acanthodian *Nostolepis linleyensis* sp. nov. and elements from the apparatus of the conodont *Ozarkodina*? *hemensis* sp. nov. are illustrated from the same samples. The thelodonts in both samples are typical of upper Ludlow-Prídolí faunas from across the Welsh Borderland, and are also present in smaller numbers in the Ludlow Series of Gotland Island, Sweden, Saaremaa Island, Estonia, and in Latvia and Lithuania. The conodont *O.*? *hemensis* sp. nov. is restricted to this area of the Welsh Borderland. The co- occurrence of well preserved elements of conodonts and thelodonts suggests that they were deposited fairly rapidly with little or no re-working and that a restricted marine environment prevailed in the early Prídolí in the Much Wenlock area of the Welsh Borderland.

Heterochrony in cavusgnathid conodonts and possible paedomorphism of the 'Granton Animals'

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The fossils preserving traces of conodont soft tissues have revolutionized many aspects of the study of conodonts: after more than 100 years of uncertainty and speculation we finally have some understanding of the nature of conodonts as animals. Reconstructions of conodont anatomy are an important component of this new conceptual framework. Not only do these reconstructions satisfy our basic curiosity about a group of enigmatic, extinct organisms, they are a powerful influence on developing concepts of conodonts as living animals, and reconstructions themselves become the subject of biological interpretation and speculation.
Almost all recent reconstructions of conodonts are based primarily on the best known and best preserved material: the Carboniferous cavusgnathids (*Clydagnathus windsorensis*) from Granton, Scotland. But how well do these few specimens represent the Conodonta as a whole? Analysis of apparatus growth in cavusgnathid conodonts based on the Granton specimens and natural assemblages from Montana, provides strong support for the hypothesis that *Clydagnathus windsorensis* is progenetic (i.e. paedomorphic). This does not call into question any of the key anatomical attributes of conodonts, or their assignment to the vertebrates. Neither does it indicate that the Granton conodonts are larval forms. It does suggest, however, that some details and proportions of reconstructed animals may reflect juvenile morphology rather than that of a typical adult conodont (whatever that may be).

Graptolite adolescence - the awkward age

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When Graptolites moved from the benthos into the plankton early in the Ordovician, the free-floating planktonic forms rapidly evolved highly organized geometric shapes. Many of these changes were adaptations to life in the open water, and were largely driven by hydrodynamic considerations.
The key to studies of fluid dynamics is the Reynolds number, which determines how a fluid flow

behaves. `Equality of Re does not mean that forces are unchanged, but patterns of flow will be the same even if one fluid is a gas and the other a liquid' (Vogel 1981). This allows valid experimentation using different fluids; in this case air instead of water.
My work to date has focused on *Amplexograptus maxwelli*, using models of early growth stages. I am investigating the effect of proximal spines through the asymmetrical period when the graptolite develops from an individual to a colony. The sicular spines had a profound effect on flow over the model colonies which appears too dramatic to be coincidental, and therefore they are likely to have had a hydrodynamic function. Results indicate that the spines are intended to disrupt vortex formation during the building of th11 and th12 only.

Vogel, S. 1981. *Life in moving fluids.* Willard Grant Press, 352 pp.

Natural assemblages of *Phragmodus* and the apparatus architecture of prioniodontid conodonts

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The composition of the apparatus of the Ordovician conodont *Phragmodus* is well known, but the number of elements and their spatial arrangement are more problematic. This can only be determined directly from natural assemblages, without which hypotheses of apparatus architecture must be derived from inferred element homologies with Late Palaeozoic taxa assigned to the order Ozarkodinida. The reliability of this approach is open to question as it is unclear whether architectural and skeletal templates based on ozarkodinids are applicable to prioniodontids such as *Phragmodus*. Similarly, although the architecture of the giant late Ordovician prioniodontid *Promissum pulchrum* is well understood, the degree to which its apparatus reflects the architecture of other prioniodontids remains untested.
Natural assemblages of *Phragmodus inflexus* reveal the architecture of the apparatus. The rostral array comprised nine subparallel, bipennate S elements, above the cusps of which lay a pair of dolabrate M elements. Caudal to the S elements were opposed pairs of Pb and Pa elements, arranged with their long axes almost perpendicular to the long axes of the S elements. This has important implications for the reconstruction of other prioniodontid taxa and the recognition of homologies. The architectural similarities between *Phragmodus* and taxa assigned to other orders supports the hypothesis that the conodont apparatus was more conservative than has been thought.

The phylogeny of the Ichthyosauria, characters and congruence

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Exceptionally preserved dendroid graptolites from Silurian *Konservat-Lagerstätten*

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Dendroid graptolites have been collected from two *Konservat-Lagerstätten* localities in east central USA: from the Racine Dolomite Formation (Wenlock) at Thornton Quarry, Illinois and the Brandon Bridge Formation (Upper Llandovery) at Waukesha Lime and Stone Quarry, Wisconsin. At Thornton, two dendroid-rich beds have been identified in the non-reef strata below the overlying reef flank beds. Dendroid graptolites at Waukesha are found abundantly in ten beds but are completely absent in others.
The aim of my research is to investigate all aspects of Silurian dendroid graptolites from *Konservat-Lagerstätten*. This will include: taphonomy, to determine the methods of preservation and variations in preservation; and taxonomy, particularly the potential use of ultrastructure in classification. I will also be looking at morphological variation within species and at the affinities of some species of the genus *Inocaulis* which may be marine algae. Further areas of research include palaeoecology, the use of ultraviolet light to reveal soft tissue; abnormalities as environmental indicators and the potential use of dendroid graptolites in biostratigraphy.

Crinoid faunas of the Much Wenlock Limestone Formation of the UK

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The lack of interest in Wenlock Crinoidea in recent years has left the taxonomy of the group in great need of work. A reliable taxonomic framework relies heavily on a thorough understanding of variations among species, something not considered in detail when the majority of taxonomy was done in the last century. *Marsupiocrinus coelatus* is an example of the variability in arm number commonly observed among the Camerata yet ignored in past studies. The species typically has four arms per ray, 20 arms in total, yet many individuals have two, three, or five arms in any number of rays. Arm gain is very rare among the collections but arm loss, particularly of a single arm per ray, is very common. Studies of the orientation of deformed rays and the distributions among different specimen sizes offer little in the way of an explanation for the variations. Environmental pressures can be ruled out as 'normal' specimens share common attachment sites, and similar sized specimens have different arm numbers. Modern crinoids are known to grow back more arms than they had prior to an attack by a predator. This would provide an explanation for arm gain; however, there are no damaged plates visible in these rays, nor is there any evidence of predation in the case of arm loss.

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