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## Chapter 2 Silurian palaeontology

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### Introduction

The fossil remains of Silurian life have both a national and international significance, which is largely derived from the fundamental role they played in the original definition of the Silurian System by Murchison in 1835. The importance of the fossils continued to grow throughout the 19th century with the acknowledgment of the Silurian as an internationally recognizable division of geological time, with the development of biostratigraphy and the more recent formalization of Silurian chronostratigraphical boundaries and subdivisions.

Fossil remains from the British Silurian have helped reveal important aspects of evolution, such as the distinctiveness of the Palaeozoic biota, the early evolution of fish, the first land living animals and vascular plants, the application and development of the concept of marine benthic communities within the Silurian and their evolution within the Lower Palaeozoic. Consequently, both national and international significance has been conferred on a considerable number of GCR sites largely on the basis of their fossil content. Some of these sites were selected independently for the GCR for their palaeontological significance, and are also described in other GCR volumes such as those on the *Palaeozoic Palaeobotany of Great Britain* (Cleal and Thomas, 1995) and *Fossil Fishes of Great Britain* (Dineley and Metcalf, 1999). Fossils are also directly or indirectly important in all other Silurian GCR stratigraphy sites described here because they form the basis for relative dating and correlation of the sites.

### Palaeontological studies and the recognition of the Lower Palaeozoic systems

#### Historical recognition and subdivision

Fossils have played a critical role in the initial development of our ability to distinguish sequences of rock strata, establish a general stratigraphical succession of strata, subdivide geological time and correlate between separate surface outcrops of strata of similar age, despite occasional apparent mismatches between their lithologies. However, the original (early 19th century) hope that the method of using fossils would provide a simple key to correlation of strata, both locally and abroad, soon encountered problems as the complexities of the fossil record became apparent. There were difficulties in characterizing fossil species and understanding their stratigraphical distribution in time and space.

By the 1830s, when the first systematic investigation of the strata of the Transition or Grauwacke Series and Primary rocks was undertaken in Wales by Roderick Murchison and Adam Sedgwick, geological mapping and stratigraphical procedures were already well established. A decade or so earlier, Georges Cuvier and Alexandre Brongniart in France and William Smith in England, had independently discovered and practically demonstrated that successive strata could be characterized, sequenced and correlated by their contained fossils. This method allowed the construction of a new type of geological map and sections, which could represent three-dimensional geological structures. However, even as late as 1830, these techniques had only been applied in any systematic way to the 'Mountain Limestone' (the Carboniferous Limestone of today) and younger strata in England (excluding the south-west) and parts of Wales. The older Transition (or Grauwacke) and Primary rocks of Wales, the Lake District, southwest of England and most of Scotland remained '*terra incognita*', as shown by Smith's 1817 geological map and section of England and Wales (Figure 2.1) and the more sophisticated 1820 compilation map of Greenough.

Murchison claimed that he was proceeding by 'Smithian' stratigraphical principles and certainly took care, from the start, to characterize his rock units by listing their fossil contents. The geological situation that confronted Sedgwick was much more complex. Not only are the strata of North Wales difficult to subdivide in terms of their lithological character, and generally lacking in fossil content but they are often highly deformed by folds and displaced by faults. Sedgwick struggled to make sense of the order of the strata and even when he did find fossils, he was not so assiduous as Murchison in identifying them. Sedgwick's initial failure to list his Cambrian fossil fauna allowed the subsequent conflict over the

definition of the boundary between the Cambrian and Silurian to escalate.

Murchison was no palaeontologist but he recruited a number of experts such as J. de C. Sowerby, J.L.R. Agassiz and W Lonsdale to help illustrate and describe his Silurian faunas in his famous three part work of 1839, *The Silurian System* (for a detailed background to this work see Bassett, 1991). Over the following decades, Murchison elaborated upon 'his' Silurian System and in 1854 published the first edition of *Siluria. A History of the Oldest Fossiliferous Rocks and their Foundations...*, which, as its title indicates was not only a synthesis of his many academic publications but laid claim to the origin of life within the Silurian (Figure 2.2). The book went into a number of editions over the years and its wide distribution helped promote acceptance of the Silurian System both nationally and internationally. But it was the adoption of the Murchisonian version by the Geological Survey of Great Britain and Ireland, which finally painted so much of the Lower Palaeozoic outcrop of these islands the characteristic Silurian blue, a situation that lasted until the early 1900s.

### **International recognition and promotion of the Silurian System**

As early as 1836, the dissemination of the term 'Silurian' was helped by its use in a number of popular geological books such as Buckland's *Bridgewater Treatise on Geology and Mineralogy...* (1836) and the first American edition of Lyell's *Principles of Geology...* (1836). By 1838, Silurian fossils were identified as far away as the Falkland Islands by Charles Darwin when he visited the islands during the voyage of the *Beagle*. However, it was largely through Murchison's international network of contacts that he managed to 'recruit' a number of influential geologists, such as Verneuil, von Such, von Keyserling and Barrande, into accepting the existence of the Silurian System within the Transition rocks of their own countries. Keyserling and Verneuil subsequently collaborated with Murchison in his expeditions across eastern Europe to the Urals, which culminated in the 1845 publication of *The Geology of Russia in Europe and the Ural Mountains*.

In this book, Murchison established the Permian System, proved the extension of the Devonian System beyond Britain and identified and mapped what he regarded as Silurian strata lying directly above Azoic' metamorphic rocks, thus excluding any recognition of the Cambrian. The critical acclaim of this work beyond the confines of the geological world, resulted in a knighthood for Murchison and seemed to put an official 'seal of approval' on his expanded Silurian 'empire', to the exclusion of Sedgwick's Cambrian. But, as Conybeare pointed out at the time, such a downward extension defeated the original purpose of their venture, in that in many ways it did not improve upon the old classification as Transition Series.

Amongst the most important and influential of Murchison's supporters abroad, from the palaeontological point of view, was Joachim Barrande, a French engineer, who lived in Prague and devoted his energies to describing and illustrating the abundant fossils of the Transition rocks of Bohemia. From 1846 until 1883, Barrande published over 29 volumes entitled *Système Silurien du centre de la Bohême*, which describe and illustrate the remarkably rich fossil biotas of several thousand species, many of them new, from the limestones, shales and sandstones of the Bohemian structural basin.

The quality of preservation and illustration of these fossils was unsurpassed at the time and was not to be matched by illustration of British Silurian faunas until Davidson published his monograph on Silurian brachiopods between 1866 and 1871. Barrande's monographs had a considerable international impact and helped further the establishment of the Silurian System in Europe and beyond. He vehemently defended his espousal of the enlarged version of the Silurian to his death in 1883.

### **Historical views of Silurian life**

In the pre-Darwinian world of the 1830s, the investigation of fossil remains was still to a considerable extent at the 'natural history' stage of discovery. Murchison and his palaeontological collaborators were part of a general international effort to describe all aspects of the natural world including the history of life on Earth. There were still lingering adherents to the interpretation of fossils entombed in strata as the remains of life caught up in the Noachian deluge but generally amongst geologists there was an acceptance of a very great age for the Earth, in the order of many millions of years, although no-one had yet devised an acceptable method of measuring its antiquity in years. Even the problematic

question of whether or not extinction had happened had been convincingly affirmed by this time. Of more concern was the question of whether life had appeared progressively from primitive to more advanced forms or whether all forms of life had been present right from the original 'creation' — the gradualist view versus the uniformitarian argument of Lyell.

### **Life began in the Silurian?**

The investigation of the British Silurian played a significant role in undermining Lyell's concept, which had initially been adhered to by most British geologists, including Murchison and Sedgwick. Inevitably the concept was tied into the question of how and when life had originated. And the resolution to this lay in the fossil evidence contained within what were at the time thought to be the oldest sedimentary strata within the Transition Series.

Murchison's claim that the origin of life itself was recorded within 'his' Silurian System was widely accepted at the time. It was portrayed in one of the very first attempts to chronicle the history of life pictorially, published in an English broadsheet entitled *The Antediluvian World* (1849; (Figure 2.3)). By 1858, this view was even more widely distributed by its depiction in the second edition of Unger's popular book on the *Primitive World in Its Different Periods of Formation* (1858, see Rudwick, 1992, p. 97 *et seq.*, fig. 67). However, by the 1860s it had become clear to many geologists that there was a distinct Cambrian fauna to be found below the Silurian and that therefore life had originated much earlier.

From the 1840s, the development of the conflict between Sedgwick and Murchison over the definition of the boundary between the Cambrian and Silurian, resulted in Murchison extending the base of the Silurian downwards (for a detailed account see Secord, 1986). This allowed Murchison to claim that the very origin of life, as represented by the oldest organic remains, was to be found within an enlarged Silurian. But if this was true, it had a very far reaching implication for Sedgwick's Cambrian because it excluded the possibility that Sedgwick would be able to define the Cambrian on the basis of its contained fossils. By Murchison's definition, any fossils that were found were Silurian and therefore the rocks that contained them were also Silurian. Murchison seemed to be supported by evidence from Bohemia, where Barrande established a sequence of 'étages' (stages 'a' to 'g') within the Silurian. Étage 'c', contained what Barrande called the 'First' or 'Primordial Fauna', below which were the even older unfossiliferous rocks. Some members of this limited fauna of Étage 'c' were in fact genera that British Geological Survey palaeontologist J.W. Salter found in North Wales in 1854 and which he used to justify his percipient but ill-received suggestion that the upper limit of the Cambrian be drawn at the Tremadoc Beds.

During the late 1840s and 1850s, fossils from Barrande's Primordial fauna were also found in Scandinavia and North America and its distinctiveness from the Silurian fauna gradually became more apparent. Furthermore, there was emerging evidence of primitive life, such as the trace fossil *Oldhamia* from Ireland (Forbes, 1848), having existed in the older rocks. Murchison eventually conceded in the second edition of 'Siluria' (1859) that such ill-defined fossils might be Cambrian in age but still adhered to a Silurian age for well-defined and stratigraphically useful shelly invertebrates, such as trilobites and brachiopods.

### **The Ordovician resolves the problem**

The problems of definition of the Cambro-Silurian boundary took a long time to resolve. Although Charles Lapworth was able to demonstrate and justify the separation and reallocation of much of the Lower Silurian as a major division in its own right in 1879, it was several decades before this new tripartite division of the Lower Palaeozoic was generally accepted. Lapworth had named his new division the 'Ordovician System', after the Ordovices, a Romano-British tribe inhabiting south-east Wales (Figure 2.4). From investigations in the Southern Uplands of Scotland, Wales and the Lake District and using his newly discovered detailed knowledge of the vertical distribution of graptolite fossils, Lapworth was able to subdivide and correlate Lower Palaeozoic strata with a refinement and confidence that had previously been unobtainable. Detailed biozonation of this kind had been developed by the German palaeontologist Opperl (1856–1858) within younger strata of the Jurassic using ammonites.

Lapworth's breakthrough in the development of biozonation marked the beginning of the modern phase of Lower Palaeozoic biostratigraphy and the redefinition of the Silurian System. Despite repeated efforts of successive international geological congresses from 1878 onwards, to standardize global stratigraphical nomenclature and its usage,

it was not until the late 1950s and 1960s that the movement finally succeeded in relation to the Lower Palaeozoic systems (Holland, 1989).

## **The Silurian biota**

### **Habitats and environmental setting**

The early 19th century recognition of Murchison's Silurian System meant that it was the first of the Lower Palaeozoic systems to have its fossil fauna extensively investigated and described. Because much of the initial British work was carried out within the Welsh Borderland and central Wales by Murchison and a number of his correspondents, there was a focus on the strata and fossils of this particular area to begin with. However, this was rapidly extended as the different sedimentary environments represented by the successions of the Lake District, Southern Uplands and Midland Valley of Scotland were mapped and their fossil faunas described. Some of the distinctive faunal elements, such as the jawless fish of the Midland Valley and the graptolites of the Southern Uplands and Lake District were subsequently to play important roles in the development of understanding the evolution of life within the Silurian.

From a modern perspective and analysis, it can be seen that these Silurian strata conserve sedimentary deposits (facies) and life habitats mainly from within a marine subtropical realm. Many of these facies were geographically restricted and temporally short-lived. With hindsight it is not surprising that they were difficult to correlate. Fossils have played a significant role in the diagnosis of these facies, which reflect a range from shallow water brackish or possibly freshwater, through continental shelf into deeper, off-shelf marine basin environments. The latter accumulated thick piles of turbiditic and hemipelagic deposits. Consequently, within the relatively restricted geographical area of the British Silurian outcrop, a considerable variety of marine environments and their biotas have been preserved.

Within the temporal span of the Silurian there was a significant amelioration of global climate following the end Ordovician glaciation and this is reflected in the fossil faunas. Despite the low latitudes (about 30°S or less) of the tectonic plate elements of the British Isles (Avalonia and part of Laurentia), it was not until late Wenlock times that significant thicknesses of platform carbonates and associated reef forms developed within this subtropical realm. The location of these major organic-based carbonate structures was controlled by a combination of climate and sea bed topography, related to the regional tectonic history and larger scale changes in sea level.

Such interpretations of palaeogeography and palaeoclimate have only been developed from independent lines of evidence within the last few decades. New interpretation and understanding of the fossils, sediments and tectonic structures and the provision of latitudinal constraints from palaeomagnetic studies, have all contributed to the dramatic change over the last 160 years in our view of how environments and life developed throughout the Silurian of the British Isles.

### **The diversity of Silurian life**

Silurian times are now known to have been occupied, from the beginning, by representatives of most of the major groups (phyla) of extant marine animals. From free-swimming fish and cephalopods to sedentary bottom dwelling corals, clams and actively burrowing 'worms', the Silurian biota has some taxonomic familiarity to us today. However, there are also many important differences. In detail, the organisms almost all belong to different genera and most belong to extinct family groupings. Furthermore, a significant number of the important marine groups, such as the trilobites, graptolites and conodonts are members of the distinctive and extinct Palaeozoic fauna, which was first characterized by Phillips in 1860. The dominant shelly macro-invertebrates of Silurian times were brachiopods, a relatively uncommon group today, whose habitats have been taken over by the bivalved molluscs. The main biological innovations of the Silurian are associated with the radiation of the fish and the invasion of the land by animals and plants.

The main early radiation of the Lower Palaeozoic marine invertebrates and vertebrates took place in the preceding Cambrian and Ordovician times. Although the rate of diversification at higher taxonomic levels had slowed down by Silurian times, rates of speciation were generally maintained. However, the late Ordovician glaciation, with its lowered sea levels and major changes in ocean circulation, produced a significant marine extinction at that time. Many

invertebrate groups were severely affected but most made fairly rapid recoveries in the early Silurian. However some, notably the trilobites, never really recovered.

As with almost all fossil biotas, there are the additional discrepancies in diversity and abundance between those groups of organisms that are preserved by the processes of fossilization and the original living biota that the fossil record samples.

### **Preservational bias**

The complicated (taphonomic) processes of recruitment of the remains of organic life to the sedimentary record, and their burial and lithification within the rock record are highly selective (Figure 2.5). Modern research has shown that the fossil record generally preserves a poor sample of organisms that were once alive, just as the stratigraphical rock record only preserves a small sample of original habitats and sedimentary environments. Occasionally, exceptional circumstances of preservation provide rare views of those parts of the biota not normally conserved, such as organisms that are very small, soft-bodied or have organic exoskeletons.

Within the British Silurian, most preservation of non-biomineralized organisms is restricted to the arthropods and associated agnathans of the Llandovery and Wenlock shallow marine facies of the Midland Valley of Scotland (e.g. see the Gutterford Burn and Ree Burn–Glenbuck Loch site reports). Recently however, the discovery of a soft-bodied and lightly sclerotised biota in Wenlock age marine volcanoclastic deposits of Herefordshire (Briggs *et al.*, 1996; (Figure 2.32)) opens up the possibility of further finds in similar deposits elsewhere within the Silurian.

The macrofauna of this Herefordshire deposit is dominated by small arthropods (29%) and polychaete worms (>27%), associated with fewer trilobites (8%), graptolites (4%) and high spired gastropods (2%). It is accompanied by a microfauna, which includes radiolarians, not normally preserved in the British Silurian (see (Figure 2.10)) and altogether gives a better idea of true biological community relationships within a particular facies of relatively deep-water carbonate muds. These relationships indicate that whilst the majority of Silurian benthic sessile organisms had relatively short food chains and little ecological interaction, the free swimming forms probably had evolved more elaborate niche division and trophic tiering than was previously thought.

The fossil record, in general, is dominated by the remains of more readily preservable inhabitants of marine continental shelf deposits. The shelves are the main sites of colonization deposition and long-term burial of sediment, consequently there is an overall preservational bias towards these facies and the life forms they supported.

The taphonomic processes that intervene between the death of organisms and the transformation of their remains into fossils within rock strata are highly selective. The result is a biased sample of the original communities and a very generalized idea of their original inter-relationships and spatial distribution. The business of reading and interpreting the fossil record, in order to understand the nature of the data has become very sophisticated in recent years (see Brett and Baird, 1997, for a review). Despite the considerable constraints of such poor samples and sample bias, new understanding of taphonomic processes has made it possible to deconstruct fossil assemblages in order to derive much more complete and reliable pictures of ecological relationships in space and time. Palaeontologists have developed palaeoecological techniques for assessing the degree of representation of ancient biological communities by fossil assemblages.

For the most part, the macroscopic fossil remains are those of marine invertebrates with 'shells' of various compositions but dominated by exoskeletons of calcium salts (carbonates, e.g. molluscs; phosphates with traces of organic material, e.g. vertebrates). Other materials are important in particular groups, such as non-crystalline quartz (silicon dioxide) in sponges, or organic compounds such as collagen-like proteins and cellulose in graptolites and plants respectively. The preservation of these materials in the fossil record depends largely on the post-depositional history of the sediments, especially changes in the chemical environment. These generally lead to information loss through preferential solution or replacement of the original skeletal material. Nevertheless, even the empty sediment moulds of shells, which are typically found in fine-grained Silurian clastic deposits, can reveal the specific identity of the original organism.

## Silurian fossil groups

Because of the 19th century impetus given to the role of fossils in mapping and identifying strata in Britain, there is an international significance to some of the pioneering work of British palaeontologists. Furthermore, because of the early prominence of the Silurian System within the Lower Palaeozoic and the prolonged struggle to characterize its boundary with the Cambrian, there has been a considerable emphasis on the nature and identity of Silurian fossils. So much so that some 19th century British geologists, with interests in other aspects of geology, complained that the Geological Society of London had gone 'fossil mad' (Bassett, 1991)

Despite such occasional protests, the detailed monographical work of description and illustration of British Silurian fossils has stood the test of time, with most of the species identified in the 19th century being still recognized today, although their generic affinities and higher taxonomic groupings have been subsequently refined. Early monographical description, illustration, and systematic work of particular importance includes corals (Milne-Edwards and Haime, 1855), brachiopods (Davidson, 1866), ostracods (Jones and his collaborators, see Siveter, 1978 for a review), graptolites (Nicholson, 1872) and trilobites (Salter, 1864/1867). Subsequently, many, but by no means all, important Silurian fossil groups have received detailed attention.

The following is a brief outline of the main fossil groups found within Silurian strata. They are generally typical of the chief components of the overall Lower Palaeozoic biota such as brachiopods, trilobites, graptolites, cephalopods and conodonts. The descriptive sequence generally follows the systematic arrangement in *The Fossil Record 2* (Benton, 1993), from which detailed taxonomies and stratigraphical ranges may be obtained.

### Primitive life forms

Whilst the primitive life forms of the Monera (bacteria and blue-green algae) and Fungi are of great evolutionary importance and their very sporadic record extends back into the Precambrian, so far their scarce Silurian representatives have, as yet, no biostratigraphical significance. By comparison, there are several groups of organic-walled microfossils that are generally placed within the Algae' and have important Silurian fossil records. These were primarily members of the marine plankton and are grouped together as 'acritarchs'. The appearance of the calcified and bottom-dwelling charophyte algae in the Silurian may, however, be of importance in the overall evolution of the early plants (Kenrick and Crane, 1997) but they are exceedingly rare as fossils and are not elaborated upon here.

For nearly fifty years now, since the 1950s, Silurian and other Palaeozoic sedimentary rocks have been chemically processed for extraction of any microscopic organic material that has survived the generally deleterious processes of fossilization and lithification. As a result of this research, organic microfossils belonging to a number of different groups of organisms (some extinct) have been recovered. Several groups have subsequently become of considerable academic interest and practical use, especially for biostratigraphical correlation. These fossils include acritarchs, chitinozoans, plant spores and scolecodonts.

### Acritarchs

Acritarchs are microscopic (mostly 25–200 microns in diameter), organic walled vesicles or bodies of uncertain biological relationships, which have an extensive geological age range from late Precambrian (around 1.4 billion years ago) to Recent times. Generally, they have a more or less spherical form and are characterized by robust walls and varied surface sculpture, which gives them a high preservation potential and has allowed a vast range of morpho-species (c. 10 000) to be distinguished within several hundred acritarch genera. Many are of undoubted algal affinity but others are of unknown origin. Consequently, the group is artificial and the name 'acritarch' a utilitarian 'dustbin' term, without formal status (Edwards *et al.*, 1993, P. 33).

It is thought that most acritarchs are the reproductive cysts of marine green algae, which need to be tough to survive the physical, chemical and biological rigours of the marine environment similar to the way that the spores and pollen of higher plants have to in terrestrial environments. The relative abundance of acritarchs (and other microorganisms) in ancient marine sediments probably reflects the productivity of the oceans and phytoplankton of the time. Consequently,

recognition of their fossil occurrences has the potential to provide important 'windows' on the world of the microplankton and marine productivity in Silurian times. It is also considered that, as an ancient fossil group, acritarchs represent an important link between the green algae and other green plants.

From the earliest Palaeozoic, the acritarchs increased in diversity and structural complexity to an acme in Siluro–Devonian times. Several hundred taxa have now been described from the Silurian. Some acritarchs from the Silurian, such as the large tasmanitids (up to 0.5 mm in diameter and just about visible on a rock surface) and leiosphaerids, have even been assigned to the Prasinophyta, within the green algae. In Welsh Borderland sites, such as the Long Mountain, the increasing abundance of tasmanitids upwards through the late Ludlow strata into the Pridoli, is probably a good measure of shallowing water and the increasing proximity of land.

The investigation of acritarchs in the British Silurian was pioneered by Downie (1963) and subsequently their biostratigraphical potential has been developed by Lister (1970) and Dorning (e.g. 1981a). Downie charted (1984) the stratigraphical distribution of over a hundred selected taxa for Britain and elsewhere and Martin (1989; (Figure 2.6)) has provided a synopsis and informal scheme of six acritarch assemblage biozones for the Silurian. Acritarchs have also proved to be invaluable in correlating those Silurian successions with no available macrofossils (Cramer and Diez, 1977, 1979; Martin, 1989).

### **Chitinozoans**

Like the acritarchs, the commonly vase-shaped chitinozoans are another problematic group of organic walled microfossils (mostly 50–250 microns in diameter). They have their acme in Silurian strata (some 100 or so recorded species) but unlike the acritarchs are an extinct group and more restricted in their range (Ordovician to Devonian and possibly Carboniferous). They are only preserved in marine sediments and are generally not as common as acritarchs. Sometimes they are found in connected strings and have been widely claimed to represent the egg cases of invertebrates, even graptolites (because of the coincidence of their stratigraphical range) but there is no direct evidence of this affinity.

Like acritarchs, many chitinozoans have short stratigraphical ranges (Figure 2.7) and thus considerable biostratigraphical potential. Seventeen global chitinozoan biozones, for the Silurian have been proposed by Verniers *et al.* (1995). In Britain the most extensive work has been undertaken in Ludlow strata of the type area, where Sutherland (1994) introduced 12 informal biozones. Brief reviews of chitinozoan distribution through the British Silurian were published by Aldridge *et al.* (1979) and Dorning (1981b), and the distribution of species across the type Llandovery–Wenlock boundary was documented by Mabillard and Aldridge (1985).

### *Plant spores*

Silurian strata have provided some of the most interesting 'acritarch-like' microfossils (sporomorphs) from marginal marine and deltaic deposits, which are thought to be non-marine in origin. They were derived from the first plants to invade the land and whilst fossils of the 'parents' tend to be exceedingly rare and fragmentary, the resilient sporomorphs are often exceedingly abundant in Silurian marginal marine sediments (Richardson and McGregor, 1986), having been transported via rivers and 'flushed out' to sea before becoming incorporated in these deposits (Figure 2.9).

The microfossils consist of monads, dyads, triads and tetrads (clusters of one, two, three or four bodies) and some of them have distinctly thicker walls than any other known acritarchs. Some closely resemble the spores of modern bryophytes, such as the liverwort and others resemble the spores of the earliest known vascular plants. Spores of these types have in fact been recorded as far back as the late Ordovician (Gray *et al.*, 1982; Wellmann, 1998) and their origin has been highly contentious, since macrofossils of neither bryophytes nor vascular plants have been found until later on in younger Silurian strata. Few Silurian spore taxa can be related to macroplants because of their different modes of distribution and recruitment to the fossil record. Consequently only those few spore taxa that have been found in plant reproductive structures can be related to the parent plants.

Despite the theoretical problems of relating the spore and macroplant record, the evolution, abundance and high fossilization potential of the spores in fine-grained sediments have made them very useful biostratigraphical and

palaeoenvironmental indicators. Spore-based biozonation of the Silurian has been developed by Gray (1985a, 1988) and Richardson and McGregor (1986). Some seven assemblage biozones of sporomorphs have been recognized for the Silurian over an almost global area (Richardson and Edwards, 1989; (Figure 2.8)).

### **Scolecodonts**

Scolecodonts are the other group of small organic fossils (100–200 microns in length), which may be found in acid residues, associated with acritarchs and chitinozoans. When they were first recognized as fossils by Eichwald (1854) and Pander (1856), their affinities were uncertain and thought possibly to lie with the fish but the biological identity of scolecodonts is not now in doubt. They can be homologized with the mouthparts or jaw apparatuses' of living marine polychaete annelids.

These small (c. 1 mm in length), serrated and tooth-shaped bars, are jaw elements arranged in pairs, similar in form to conodonts but of a different, purely organic composition. They have been recovered from Lower Palaeozoic sedimentary rocks of early Ordovician age and range through to present time. Although they are amongst the most common kind of Silurian microfossils that can be chemically isolated from carbonate rocks, relatively little research has been done on them compared with other microfossils (see below). That they have considerable biostratigraphical and palaeoenvironmental potential, has been shown by Kielan-Jaworowska (1966) for the Polish Silurian and more recently by Bergman (1989) and Eriksson (1997) for part of the Baltic Silurian succession. Like the conodonts they were sensitive to changes in ocean circulation patterns and nutrient supply and were affected by events such as the Ireviken extinction at the end of the Llandovery. Eriksson suggests that there is a close relationship in relative abundance between scolecodonts and chitinozoans which shows a bathymetric control. Little work has been done on them in the context of the British Silurian but there is clearly considerable potential for comparison with the European studies.

### **Protozoan microfossils: radiolarians and foraminiferans**

The oceans today contain two important groups of shelled unicellular or protozoan microorganisms, the radiolarians and foraminiferans secrete preservable skeletons, which can be extremely abundant. The symmetrical and often spinose spherical skeletons of the radiolarians are composed of silica and can occasionally be chemically isolated from mudrocks. Foraminiferans have mainly calcium carbonate skeletons, which rarely can be isolated. Both groups are more commonly identified under the microscope, within rock thin sections. And, both protozoan groups have fossil records that extend back to the Cambrian and should therefore be present within the British Silurian.

Silurian Radiolaria have been recorded from only a few localities worldwide: Texas, Nevada, the Urals, Japan and the Canadian Arctic. They have an abundance and importance in, for example, the Silurian basinal shale-carbonate successions of the Canadian Arctic archipelago (e.g. Holdsworth, 1977; Goodbody, 1986), where they are associated with other planktonic organisms such as graptolites and the free-swimming orthoconic nautiloids. There is no doubt that radiolarians were present in the deeper waters of the offshore basins of the British Silurian but, in the main, have either not been preserved or not yet found within the deposits of these basins. The potential for future finds has been highlighted by the recent discovery and chemical isolation of radiolarians from carbonate nodules within a Wenlock volcanoclastic deposit in the outer shelf sequence of Herefordshire, the first record of the group from the British Silurian ((Figure 2.10); Briggs *et al.*, 1996).

Foraminiferans are a group of protozoans, amoeba-like organisms, which secrete a protective and coiled shell or test with growth chambers, generally made from calcium carbonate but which also can be constructed from agglutinated sand grains. Their habits range from bottom dwelling (benthos) to living in near-surface waters as part of the plankton. Records of Silurian foraminiferans have been very few but the sporadic occurrence of arenaceous foraminiferans was noticed by Aldridge *et al.* (1981) in acid residues from microfossil preparations of a range of Silurian carbonate rocks. Their potential abundance was particularly emphasized during detailed work on the microbiotas of the basal Wenlock boundary stratotype ((Figure 2.11); Mabillard and Aldridge, 1982), when several thousand specimens were recovered. Subsequently Kircher (1989) surveyed the occurrence of arenaceous agglutinating foraminiferans from shelf mud-carbonate sediments across the Welsh Borderland. She showed that some 24 genera could be recognized but that they are relatively long ranging and have limited biostratigraphical potential.



The poor representation of foraminiferans in the British Silurian may be as much a matter of lack of recognition as lack of preservation and both foraminiferan and radiolarian groups hold considerable potential for future research.

## **Benthic colonial invertebrates**

Even 400 or more million years ago in Silurian times, there was a considerable diversity of colonial organisms that lived on the sea bed. Of the Silurian fossil groups of these sessile, bottom-dwelling invertebrates, many secrete preservable siliceous or calcareous skeletons such as the sponges, stromatoporoids, corals and bryozoans. Within the Silurian context of the British Isles, the most important of these are the corals, bryozoans and stromatoporoids, all of which are not only common fossils but were significant organisms within the ecology of the continental shelf deposits of the time.

### **Sponges**

In Britain, the Silurian sponge record is impoverished, even though as a group, they are more widespread in their habitats than the corals. Sponges that secrete an endoskeleton of siliceous spicules have colonized deeper off-shelf deposits since Cambrian times and have a well-developed fossil record from the Silurian of Arctic Canada (Rigby and Dixon, 1979; Goodbody, 1986) but they are not well known within the British succession.

### **Stromatoporoids**

By comparison, stromatoporoids were, like the corals, of considerable importance as both rock formers and diverse members of Silurian benthic reef communities, especially within the British shelf mud-carbonate facies. They are rare within elastic facies and preferred warm water, high-energy carbonate buildups on open shelf environments. Originating in Ordovician times, stromatoporoids radiated to their acme in the Silurian (17 families). There was some faunal turnover at the ordinal level between the Ordovician and Silurian, with the Labechiida declining and the Clathrodictyida, Stromatoporida and Actinostromatida becoming increasingly important (Scrutton, 1989). Most orders extend into the Devonian but the whole group then suffered a major decline at the end of this period. Today they are rare cryptic reef dwellers and are thought to be taxonomically related to the sponges (Rigby *et al.*, 1993).

Stromatoporoids are colonial organisms that secrete calcareous structures made up of both sponge-like spicules and layered skeletal features, similar to those found in tabulate corals. The colonies formed both framework and binding elements within Silurian reefs and are very variable in shape and size, ranging from tabular to mound-shaped and a few millimetres in diameter to a metre or so. The surface is often mammilated with canals (astrorhizae) radiating from the centre of the bosses.

Most modern research on Silurian stromatolites has been done in North America and the Baltic region (for a recent review of Silurian stromatoporoids see Nestor, 1984; Scrutton, 1989). There are considerable problems with the establishment of acceptable taxa of stromatoporoids, which generally seem to be long ranging and have strong ecological control on their distribution. Nevertheless, some species are claimed to have surprisingly wide distribution and may make a contribution to biostratigraphy and correlation.

### **Corals**

Corals are anthozoan cnidarians (like sea-anemones) that increased exponentially in number and diversity from Ordovician through to mid-Devonian times. However, during the Llandovery there was something of a plateau in their expansion, which probably reflects changes in global climate and sea levels. The mid-19th century study of British and Irish Silurian corals was pioneered by M'Coy (1850, 1851c) and Milne-Edwards and Haime (1855). Silurian corals belong, like most other Palaeozoic corals, to the extinct tabulate and rugose groups, whose relationships to the common living scleractinian corals is unclear. There are, however, many morphological similarities between the skeletal remains of living and fossil groups, which allow close comparison and functional analysis.

Like their modern descendants, Silurian corals secreted supporting calcareous structures, generally cone-shaped (2–30 mm in diameter), which in the Rugosa were single in solitary forms and multiple and interconnected in those which reproduced by asexual budding of the polyps. The more common and diverse tabulate corals were clustered into various

disc and hemispherical shapes as colonial forms, which generally grew to 100 mm or so in height (although some reach several metres). These latter and the colonial forms of *Rugosa* were important in forming the framework of reefs of the British region at the time (see Copper and Brunton, 1991; Scoffin, 1971). The robust calcareous skeletons of corals have high preservation potential and they are common fossils within Silurian shelf mud-carbonate deposits, especially within the Wenlock (Figure 2.12).

In general, Silurian corals are taxonomically distinct from those of the preceding Ordovician and succeeding Devonian but there are no clear-cut boundaries between the successive faunas. Scrutton (1989) has reviewed the biostratigraphy of Silurian corals, showing that their potential has been well developed in North America, China, the former Soviet Union and in the Baltic states. Klamann in particular has developed 12 biozones for the classic Silurian sections in Estonia, based on tabulates, and he has extended correlation to Gotland (1982). Although tabulate distribution is clearly facies dependent, the scheme shows considerable promise for application to the British carbonate sequences and their coral faunas.

## **Bryozoans**

Zoologically, bryozoans are an advanced group of lophophorate metazoan invertebrates, which commonly secrete a calcareous (calcitic) skeleton and are generally sessile in habit. However, their size, form and lifestyle is similar to that of the other colonial epibenthic organisms described above and so they are often grouped, ecologically and for general convenience, with the corals and stromatoporoids. The earliest descriptions of British Silurian bryozoans is contained within monographical works on corals by M'Coy (1850, 1851c) and Milne-Edwards and Haime (1855).

A bryozoan colony interacts with the surrounding environment as a complete organism but some of the individual zooids may have specialized form and function, giving a degree of polymorphism to the colony. The sessile colonies of tiny (millimetre sized) zooids secrete protective calcareous tubes or boxes, which may be linked together to form a wide range of morphologies from branching tree-like fronds to mounds, sheets or discs up to several centimetres in size.

From Ordovician beginnings, the Palaeozoic bryozoans diversified rapidly but suffered a marked setback with the glacially driven extinction event at the end of the period. Recovery was slow through the Silurian and there were fewer genera and species than in the Ordovician. However, Brood (1989) considers that this decline may be more apparent than real, as a result of the lack of appropriate carbonate facies preserved in the Llandovery sequences of Britain and western Scandinavia.

Their diversity and variable form allowed them to occupy a wide range of habitats from coral reefs to the surfaces of empty shells lying on deeper water soft mud substrates and they may have colonized the hard surfaces of living shelled invertebrates. Altogether, they became important organisms within Silurian seas and made significant contributions to the skeletal content of the carbonate sediments of the time.

Bryozoans were frequently associated with the other common suspension-feeding lophophorates of the time, the brachiopods (see below), competing for substrate space with them and tabulate corals. Generally they are facies dependent and hence ecologically sensitive, so that they have considerable potential as environmental indicators. However, most of their fossil remains have been transported by sedimentary processes from the original sites of occupation, so their fossil record has to be treated with caution for interpretation of palaeoenvironments. Their fragmentary remains and marked intraspecific variation has led to some instability in definition of the taxa. And, with long-ranging species they have not become of biostratigraphical importance.

However, since bryozoans are common and widespread fossils for which taxa are generally well defined, they do have potential for correlation and biogeography. In general, the study of British Silurian bryozoans has been neglected (Taylor, 1991) and even those of the Baltic Silurian, where they are particularly abundant in the limestones and marls and have been recently researched (e.g. Brood, 1984), contain many undescribed taxa.

## **The 'shelly invertebrates'**

As a term of convenience 'shelly invertebrates' is often used to describe the bulk of macrofossils found in marine sediments but taxonomically it does not have much meaning since it can incorporate molluscs, brachiopods, arthropods and echinoderms, etc.. It essentially refers to those fossil groups that have readily preservable calcareous shells.

The molluscs (Phylum Mollusca) are remarkably diverse animals with many familiar extant groups and a long fossil record. Their very variable form and habit ranges from that of the seabed dwelling sessile bivalves through to the highly active and free swimming cephalopods. Much of this diversity was present in Silurian times when they were already important members of the marine ecosystem but the relative importance of the different groups was quite different from that of the present day.

### **Bivalved molluscs**

Bivalved 'clams' were the most common of the benthic molluscs in Silurian times within the British outcrop but they only played a really significant role in a few facies, those of shallow- water clastic deposits and offshore deeper water mud substrates (Figure 2.13). As a group, the bivalved molluscs had successfully radiated through the Ordovician but were reduced from 65 to 26 genera by the extinction event at the end of the Ordovician (mu, 1984; Palmer, 1989; (Figure 2.14)). From this setback, they slowly recovered through the Silurian but in most facies were dominated in terms of abundance and diversity by another group of sessile benthic filter feeders, the brachiopods. Their relative abundance in relation to all other fossil invertebrates seems to have gradually increased from about 2.5% (250 species) in the Ordovician, through 3.8% (196 species) in the Silurian to 4.6% (532 species) in the Devonian. Only after the Permo-Triassic extinction did they jump to 15% plus of the total invertebrate fossil record (Palmer, 1989).

Some bivalves, especially the nuculoids are infaunal deposit feeders and are found scattered through the shallow-water muddy facies of the British Silurian, in which they were active burrowers. They were accompanied by some byssate filter feeding bivalves, modiomorphaceans and grammysiids, which were also shallow burrowers. The ability of bivalves to survive in some of these shallow-water deposits, compared with the brachiopods, may have been due to their greater tolerance of substrate disturbance by other burrowing organisms and/or current activity. Many of the filter feeding Silurian bivalves such as the cardiolids and praecardiids were semi-infaunal nestlers or shallow burrowers and colonized other types of mud substrates. They evolved from byssate forms according to Kříž (1984) and were again most successful where the competition from the brachiopods was reduced but in their case it was in the low energy, deeper water, laminated mud-silt facies. This common facies in the Welsh Basin also supported a sparse bivalve fauna of byssate bivalves such as the pteriniids, lunulicardiids, butovicellids, etc. which accumulated with the remains of pelagic and planktonic organisms (graptolites, cephalopods, ostracods etc., see below).

Since the distribution of most of these bivalves is facies dependent and their species duration is relatively long, they, like many other endemic shelly fossils, are of limited biostratigraphical use in the British succession. However, in the Silurian of the 'Barrandian' area of Bohemia, Itha has developed a biozonation based on its more abundant bivalves. Some of these Bohemian species, such as *Slava fibrosa* and *Butovicella migrans*, were more cosmopolitan than most bivalves and do occur within the Welsh Silurian.

### **Gastropods**

The univalved coiled gastropods are the most diverse of molluscs today and even in Silurian times the number of taxa exceeded that of the bivalved molluscs (Figure 2.15). According to Knight *et al.*, (1960) there were around 110 genera, predominantly archaeogastropods, and Peel (1989) records more than 300 species of Silurian gastropods from North America and a further 200 from Britain and Gotland. However, despite this numerical abundance, they have had but a minimal influence on Silurian biostratigraphy. Relatively few genera are characteristically Silurian and many are derived from the Ordovician and continue into the Devonian. However, many of these taxa have not been revised since the 19th century and it is possible that new work on well-preserved specimens may reveal a very different picture. Indeed, Peel (1974) has already shown that evolutionary lineages of the trilobed bellerophontins *Tritonophon* and *Plectonotus* do have a limited biostratigraphical value from the late Ordovician through into the Permian.

Silurian gastropods were less diverse in their habits than modern marine gastropods and their aragonitic carbonate shells are rarely well preserved except in certain shallow-water carbonate facies, such as reefs and sublittoral environments. Here, their greater abundance was perhaps related to their herbivorous feeding habits and the presence of shallow-water algae, whose delicate fronds are not often preserved as fossils. However, Peel (1984) has argued that the remarkable shallow-water abundances of *Turbocheilus helicites* (the *Platyschisma* of older records) at the base of the Downton Group of the Welsh Borderland, may have been a result of its acquisition of ciliary feeding habits. A few Silurian gastropods (bellerophonitiforms) are thought to have been infaunal burrowers (Peel, 1984) but it is questionable as to whether any occupied the niches filled by limpet or carnivorous gastropods today. Like the bivalves, the gastropods of the British Silurian are not common enough, despite their considerable taxonomic diversity, to have any biostratigraphical potential but they are one of the most neglected of fossil groups in the British Silurian and in need of further investigation.

### **Nautiloid cephalopods**

Perhaps the one molluscan group with more obvious stratigraphical potential in the Silurian is that of the nautiloid cephalopods: carnivorous squid-like creatures that occupy conical chambered shells (rarely, up to a metre in length). Like their surviving relatives, the majority of the nautiloids of the Palaeozoic were actively free-swimming but unlike the few remaining survivors, they were abundant and diverse in Ordovician and Silurian seas. A radiation of nautiloids in the early Ordovician produced some 130 genera (House, 1988) and was followed by a marked reduction to less than 50 genera with the end Ordovician extinction event. The Silurian recovery to over a 100 genera was short-lived and by the end of the period there seems to have been a fallback again to less than 50 genera. The earliest comprehensive view of Silurian nautiloid cephalopods was provided by Barrande (1867–77) for the Bohemian basin and Blake (1882) for Britain. As Holland (1989) points out, there are many Silurian taxa that have been inadequately defined and there may be many more Silurian forms than presently realized.

There was considerable diversity in form of the shells from simple straight 'orthocones' (Figure 2.16) to various curved (cyrticone) and coiled (gyrocone) types, which reflect different modes of life from fast free-swimming to slow benthic forms (Holland, 1984). The greatest diversity of nautiloid form is found in the Wenlock age mud-carbonates of the shelf platform with its associated reefs. Thin-shelled orthoconic forms were well adapted for a free-swimming mode of life and so their remains are particularly associated with the fossil assemblages of deeper water. The silty mudstone substrates of these basins supported little in the way of autochthonous benthos and so accumulated the remains of pelagic and planktonic organisms like the nautiloids and graptolites.

Despite their relative abundance in the Silurian, the preservation of nautiloid cephalopods is often inadequate for precise identification. The original aragonitic calcium carbonate of the shell is either replaced by coarsely crystalline calcite or more commonly dissolved away with neither the calcite replicas nor the remaining moulds and casts retaining enough detail for specific identification. These preservational problems have hampered or perhaps inhibited modern research on the stratigraphical distribution of British Silurian nautiloids but as Holland (1984, 1989) has pointed out, their relative abundance and cosmopolitanism gives them potential as biozonal indices. This potential has already been suggested for *Leurocycloceras whitcliffense* in *post-Bohemograptus bohemicus* Biozone strata in the Welsh Basin (Holland and Palmer, 1974; Holland, 1989).

A variety of small (about 1 cm in length), narrow and cone-shaped shells are found in the British Silurian. Mostly, these belong to extinct fossil groups such as the conulariids (see Jerre, 1993), hyolithids (Marek and Yochelson, 1976) and tentaculitids (Boudek, 1964; Blind and Stürmer, 1977). Whilst these extinct fossil groups are generally regarded as having molluscan affinities, roughly similar shells of the extant scaphopods also occur and are undoubted molluscs. The small calcareous sclerites (individually 2–4 mm in length but arranged in rows up to 30 mm in total length) of the extinct machaeridians have a similar problematic status. Originally described from the Wenlock Limestone of Dudley by Woodward (1865) as barnacles (Cirripedia), they also show affinities with the molluscs and annelids (Höglström, 1997). Although none of these fossil groups achieve any biostratigraphical significance in the British Silurian at present, some are common enough in certain facies (especially carbonate mudstones) to have biostratigraphical potential.

### **Trilobites**

Arthropods are by far the most common creatures on Earth today and are dominated by the insects. However, the fossil record of arthropods in Silurian times was almost entirely marine, but for the very rare remains of some of the earliest known land-living animals. The marine forms are dominated by two groups, the extinct trilobites and the crustacean ostracods, both of which are of considerable importance to our understanding of the past.

Trilobites, like so many other marine invertebrates, suffered a marked decline in diversity at the end of the Ordovician with many well-established families becoming extinct (Thomas and Lane, 1984). From a high point of over 60 families, they were reduced to around 20 and then fewer within the Silurian (Romano *et al.*, 1993). Beyond this, they never did regain their Ordovician level of diversity.

Nevertheless, the remains of trilobites can be common enough within Silurian sediments, especially the mud-carbonates of the continental shelf. Partly this is due to their high preservation potential resulting from their multi-element mineralized exoskeletons and their typical arthropod habit of moulting in order to grow. Consequently, any one animal produces a large number of moulted and preservable elements within its lifetime but entire trilobite exoskeletons are much less common. Reliable identification can, however, be achieved from some individual skeletal elements, especially the head shields.

Trilobites were first recognized as a distinct group of fossils in the latter part of the 18th century (Walch, 1771). They have been seen as part of the characteristic Silurian fossil fauna since Murchison's investigations in Wales. Indeed, they are amongst the most distinctive and readily recognizable of all extinct fossil groups, which have attracted common folklore names, such as the so-called 'Dudley locust' (*Calymene blumenbachii*). These calymenids (see Siveter, 1985, 1996) were relatively common in the Wenlock limestones, which were extensively quarried in the Dudley area of central England during the 19th century (see the Wren's Nest site report).

Trilobites are arthropods with a common basic design — somewhat flattened, flexible and 'tri-lobed' bodies covered with a mineralized exoskeleton, thickened dorsally and made of articulating plates. Ventrally, the lighter exoskeleton carries numerous paired and jointed appendages used for locomotion, feeding and respiration but these are rarely preserved. Consequently, our knowledge of the habits and mode of life of these common fossils is quite limited and based on a knowledge of present day arthropod analogues and fossil distribution patterns. In detail, trilobites show considerable variation in form and hence probably function. Furthermore, it is apparent that their distribution is generally related to facies; see, for example Thomas (1980), Mannil (1977) and Chlupad (1987) for trilobite distribution in the Welsh Basin, the Baltic area, and the Barrandian area of the Czech Republic, respectively.

In the Anglo-Welsh area, for instance, some phacopids and encrinurids are exclusively associated with marginal marine conditions, which may reflect a greater tolerance of salinity changes (Thomas and Lane, 1984). Only a few species, such as some odontopleurids (e.g. *Odontopleura ovata*) transgress major facies boundaries and this has been argued to indicate a pelagic habit.

Despite their relative abundance and diversity in the Silurian they have not achieved the biostratigraphical value of other groups such as the graptolites. This is due to a number of factors (see discussion by Thomas *et al.*, 1984), especially the benthic habits, biofacies and lithofacies controls on Silurian taxa. However, recent refinement of the stratigraphical ranges of selected genera has shown considerable biostratigraphical potential (Thomas *et al.*, 1989). The modern study of evolutionary lineages, such as that of the odontopleurids (Chatterton and Perry, 1983) has shown how this potential can be realized. Thomas *et al.* (1984) have proposed a trilobite biozonal scheme for the British Silurian and some links from this can be recognized elsewhere in Europe (Thomas *et al.*, 1989). In addition, individual species have been shown to have short vertical ranges and sufficiently wide distribution to act as good markers for biostratigraphical and correlation purposes. One such is *Alcymene puellaris*, which is typical of the Upper Leintwardine Formation and correlatives throughout the Welsh Borderland and Lake District (see Siveter, 1983 and Ramsköld *et al.*, 1994).

## Ostracods

The ostracods are an exceedingly abundant and diverse group of extant, water living micro-arthropods with a well-recorded fossil history. The body is enclosed within two shells, typically 1–3 mm in length and rarely up to 10 mm or

more. As with other arthropods, ostracods grow by regular moulting of the exoskeleton, which has enhanced their preservation in the fossil record. Mineralization of the 'shells' (carapace valves) by calcium carbonate also has increased their preservation potential.

As with many groups of shelly invertebrates in the British Silurian, post-depositional solution of the shell carbonate has left impressions (internal and external) of ostracod valves in the sediment. Moulds of this kind frequently preserve enough fine detail of shell ornament and internal structures such as muscle scars to allow specific identification and they form an important component of ostracod fossil faunas.

Ostracods have occupied a variety of niches, mostly within the marine realm, from early in the Palaeozoic. Indeed, most of the habitats of living ostracods were already occupied by Silurian times, apart from that of the deep sea and possibly freshwater (Siveter, 1984). Most Silurian ostracods were stenohaline benthic forms, although a few, such as the leperditiids, may have been euryhaline. Mostly, they lived by crawling and swimming at the sea bed (Figure 2.17), and some may have burrowed in soft sediments. Consequently, many ostracods are facies- and depth-controlled in their distribution at the species level and many have relatively restricted geographical ranges.

However, some benthic species clearly ignore facies boundaries; moreover, the relatively rare pelagic forms are also generally much more cosmopolitan than typical benthic forms (Figure 2.18). It is in the Silurian that we have the earliest, really good evidence that some ostracods (the myodocopes 'entomozoids' and 'bolbozoids') were living essentially off the bottom, as a part of the pelagic biota (Siveter *et al.*, 1987, 1991; e.g. see the Meeting House Quarry site report).

A problem with palaeoecological analysis of Silurian ostracods is their taxonomic distance from living forms, in that all the Lower Palaeozoic taxa are extinct at the family level. Following an extensive early Ordovician radiation, ostracods suffered significant taxonomic reduction at the end of the Ordovician. Their recovery within the Silurian and common occurrence as fossils has led to ostracods becoming increasingly important as biostratigraphical and palaeoenvironmental indicators.

From early recognition of a few genera by Murchison (1839) and Barrande (1872), it was the pioneering researches of T.R. Jones and his collaborators in the latter part of the 19th century (see reviews in Siveter, 1978 and Siveter and Lord, 1997), which really promoted the study of British Silurian ostracods and their biostratigraphical potential. However, it was not until the 1960s and the modern renaissance in Silurian ostracod studies, led by Martinsson (e.g. 1962, 1967), that this potential was properly developed.

Altogether, their abundance as fossils, their relatively rapid rates of evolution and their distribution has made Silurian ostracods very useful biostratigraphical indices. Silurian ostracod genera are, in general, widely distributed and although species cannot be correlated worldwide many species are intercontinental and interprovincial in their distribution; for example, the well-known facies-breaker *Frostiella groenvalliana* occurs in elastic and carbonate substrates in Maine, the Baltic and Britain (see the Ludford Lane and Ludford Corner GCR site report). Biozonal schemes have provided important correlation between British, Baltic, southern European (including Ukrainian) and eastern North American successions throughout the Silurian (see review by Siveter, 1989). These schemes become particularly refined within the upper parts (middle Ludlow and younger horizons) of the British Silurian. Moreover, as conodonts are not commonly present in British Palaeozoic strata, and graptolites are absent above the upper Ludlow, ostracod biostratigraphy assumes particular importance for the upper part of the Silurian sequence.

### **'Other arthropods'**

Numerous other arthropod groups, such as the phyllocarids, xiphosurans, eurypterids, scorpions and myriapods have different levels of significance for Silurian biostratigraphy and palaeontology. From the evolutionary point of view, the role of arthropods, such as the myriapods, in colonizing the land and the fossil evidence for this event in Silurian or earlier times is of considerable importance. Fossil fragments of arachnid and centipede cuticle from the British Silurian have provided the first direct evidence in the world for animals living on land (Jeram *et al.*, 1990; see site report on Ludford Lane and Ludford Corner). However, these arthropods have no biostratigraphical significance as yet and are only mentioned in relation to the early vascular plants and their Welsh Basin sites.

Xiphosuran (king-crab) and phyllocarid evolution is of considerable biological interest but only the shrimp-like phyllocarids are mentioned here because of their role as part of the pelagic fauna of the Silurian (see Rolfe and Beckett, 1984). The extinct chelicerate eurypterids and protoscorpionids are worth brief consideration, for although they too are of little biostratigraphical use, their life habits have been the subject of speculation for over a century (Woodward, 1866–78).

These chelicerates were amongst the most impressive and largest organisms (up to 1.5 m long) of Silurian times for which we have fossil records, apart from some of the orthocone cephalopods, which may have reached lengths of two metres or more. Eurypterids, which are similar in appearance to living terrestrial scorpions, were aquatic forms which evolved in the Ordovician and reached their acme in the Silurian when they developed their greatest diversity and abundance (Selden, 1984). Overall, they were euryhaline and ranged from marine-brackish across to fresh waters and with their well-protected gills were probably able to spend short intervals on dry land. Well-preserved Silurian eurypterids have been found within the shallow water successions of the Midland Valley of Scotland and are commonly associated with agnathan fish faunas (see the site reports on Gutterford and Lynslie Burn in the Pentlands and Ree Burn–Glenbuck Loch in the Hagshaw Hills).

It has long been recognized that eurypterids were highly adaptable in their locomotion and many were capable of walking, burrowing or swimming, whilst some were more specialized and efficient at one particular mode. Selden has demonstrated (1984) that some Silurian eurypterids (e.g. *Lanarkopterus*) were accomplished swimmers and armed with enlarged chelicerae, they were also effective raptorial style predators, which may have fed on agnathan fish and other eurypterids. Others are more likely to have been more generalized organic detritivores, which fed on carrion.

The protoscorpionids evolved in the Silurian and as their name indicates are scorpion-like in appearance but were, according to Rolfe and Beckett (1984), aquatic in habit and euryhaline, like the eurypterids with which they are generally found. They had an overall range from truly marine to fluvial although individual genera had more restricted distribution. The huge chelicerae of the Lesmahagow scorpion (*Lanarkopterus*) suggests that they had to deal with tough prey and the association with faecal strings of thelodont denticles, indicates that the prey may have been agnathan fish.

As with other Lower Palaeozoic periods, it is highly likely that the overall diversity of arthropod faunas is severely under-represented by the general nature of the fossil record. The British Silurian generally lacks sites of special preservation but a promising discovery from the Wenlock of the Welsh Borderland (Briggs *et al.*, 1996) may help to redress the balance. Here a new arthropod (3–4 mm long) with a non-mineralized exoskeleton dominates the fauna, along with softbodied polychaete worms (see (Figure 2.32)), neither of which are normally preserved. Further study of this fauna will show the continuing potential for better understanding of Silurian faunas that are not normally fossilized.

## Brachiopods

Brachiopods, commonly known as 'lamp shells', form a fundamental part of the Palaeozoic biota and although they are still part of the marine benthos in some seas today, their abundance, diversity and distribution has been progressively diminished since the Permo-Triassic extinction. As with so many other of the Silurian invertebrates, their early extensive radiation through Cambro-Ordovician times was set back by the terminal Ordovician extinction, although recovery in the Silurian was rapid. Their importance is derived from a number of factors — their abundance and domination of many benthic fossil assemblages and their widespread distribution in time and space. These factors have led to a biostratigraphical use, based on the most rapidly evolving lineages and a palaeoenvironmental use, based on facies and depth controls on their spatial distribution.

The role of brachiopods within the Silurian dates back to the original palaeontological characterization of strata of this period by Murchison in the 1830s. Investigation of the group was promoted by the monographical studies of Davidson (e.g. 1866) and the exceptional quality of his illustrations and anatomical comparisons with living taxa. Since the 1950s, the study of Silurian brachiopods has been enhanced enormously by the investigations of numerous specialists in Britain and abroad, resulting in a database and level of understanding that is not matched in many other groups of Silurian fossils.

These bivalved, benthic invertebrates are taxonomically placed in a separate phylum (Brachiopoda) and traditionally were divided into two classes (Articulata and Inarticulata). However, recent analysis (Holmer and Popov, 1996; Williams *et al.*, 1998) of the characters of the surviving groups of brachiopods suggests a reorganization at a high taxonomic level into two major groups, based on shell composition, rather than the nature of the shell articulation, as was previously used.

Brachiopods were often the commonest macroorganisms on Silurian shelf substrates (Figure 2.19). Many were anchored by a fleshy stalk, the pedicle, throughout their lives but others become detached early in their development and were immobile free-living forms, a few were semi-infaunal burrowers and some cemented to hard substrates. Overall, they evolved a considerable diversity of form and habit (Bassett, 1984) but were never as 'plastic' as the more adaptable bivalved molluscs, which have now inherited many of the niches originally occupied by brachiopods. In particular, the dominant articulate brachiopods have never been able to retreat into the sediment to become infaunal burrowers and escape predators as bivalved molluscs have done.

All brachiopods seem to have been lophophorate filter feeders with the shells enclosing and protecting the delicate immobile lophophore, which acted as a filter pump for finely particulate (and possibly molecule-sized) organic matter and oxygen.

The shells of the articulate brachiopods are calcitic with an organic matrix and tend to be better preserved than the aragonitic shells of molluscs in carbonate sediments. However, in clastic deposits, brachiopod valves are like most other carbonate shells, generally removed by solution and the quality of preservation of the moulds depends on the fineness of the sediment grains. In silts and shales, even the minute details of the muscle scars are commonly preserved and allow identification to the species level. The less common inarticulate brachiopods have shells with mixed compositions, which often include a high proportion of organic proteins and calcium phosphates. This often enhances their preservation potential, especially in fine-grained clastic deposits, so that fossil record of lingulids and orbiculoids may be relatively good in some shallow-water and deep-water clastic deposits (see report of the Lower Wallop Quarry site in the Pridoli of the Welsh Borderland).

Despite the recognition that most genera and many species of brachiopods are long ranging, recent decades have seen the study of more rapidly evolving lineages of certain genera. These have demonstrated their biostratigraphical use for local correlation and biogeography, summarized by Bassett (1989b) for the Silurian. For example, delineation of the sequence of stricklandiide and pentameride species has been used to correlate Llandovery and Wenlock successions (e.g. Bassett and Cocks, 1974; Cocks *et al.*, 1984). Other genera have similarly been used for Ludlow sequences.

One of the most important extensions of such evolutionary studies has been the recognition of their ecostratigraphical role. This was pioneered by Ziegler (1966) for the Llandovery and arose from his study of speciation of the stricklandiide *Eocoelia*. From the co-occurrence of *Eocoelia* species with certain other brachiopod assemblages through time, Ziegler described (1968) a sequence of time related brachiopod based Llandovery benthic 'communities' in Wales and the Welsh Borderland (Figure 2.29). Furthermore, he claimed that they were depth related and ranged from a shallow-water marine *Lingula* 'Community', through four or five gradually deepening 'communities' across the continental shelf into a deeper water graptolite 'community'. For the Llandovery, the spatial distribution of these brachiopod dominated fossil assemblages did indeed seem to parallel the palaeobathymetry of the Welsh Basin and its elastic facies distribution (see 'The spatial distribution of the Silurian biota — The shelly facies', p. 62).

## **Pelmatozoans**

The echinoderms are biologically one of the most interesting and diverse of invertebrate groups with a long fossil record. From Cambrian beginnings, the main diversification of the phylum took place in Ordovician times followed by a decline at the end of the period coincident with that suffered by so many other groups, followed by partial recovery within the Silurian. Despite the Silurian 'dip', at least 800 species of echinoderm distributed amongst some 225 genera are recorded for the period (Sevastopulo *et al.*, 1989) and this is thought to be a serious underestimate.



The Silurian fossil record of the echinoderms contains sporadic remains of the main living and extinct groups from the blastoids, cystoids, crinoids, asteroids, holothurians and echinoids to the ophiuroids. As a consequence of this diversity, widespread distribution and occurrence in different facies, they should have considerable biostratigraphical potential. But so far this has not been realized, except in a few instances, largely because of preservational problems. Of this great diversity of animals, only the pelmatozoans (crinoids and blastozoans) are of any great significance in the Silurian biostratigraphy of the British Isles.

Like most echinoderms, the calcareous skeleton of the pelmatozoans is made up of plates that generally dissemble after death into their numerous parts. Individually these elements are not often diagnostic of the parent animal. However, more or less entire remains of crinoids are not uncommon in Silurian carbonate facies and over 200 genera are known (see Brett, 1984 for a review of the ecology of Silurian pelmatozoans). Most were sessile, passive, suspension feeders that grew up to 100 cm above the substrate to which they were permanently anchored by holdfasts. The overall form approximates that of a tree, with the basal structure giving rise to a flexible stem of numerous articulated discs rising like a backbone and carrying at its apex a cup and several feathery arms. The latter were used as a filter fan for feeding and respiration with the food being carried by ciliary action to the mouth on the top of the cup, which contained the body organs.

The global Silurian record of crinoids reaches its acme in the Wenlock and this is reflected in the British sequence with 63 species recorded from the Much Wenlock Limestone Formation (Ramsbottom, 1953) but this is probably an underestimate and, according to Sevastopulo *et al.*, (1989), the fauna is in need of much revision. By comparison, the Silurian crinoid fauna of Gotland is better known and contains 193 species. Also contemporary North American crinoids, derived from the rich carbonate facies, have shown their biostratigraphical potential with both endemic and cosmopolitan genera, such as *Pisocrinus* showing particular promise (Ausich, 1977). In the European context, crinoids have had more attention in the Penedol, where the distribution of the pelagic *Scyphocrinites* has been investigated in relation to the Silurian–Devonian boundary (Stukalina, 1977; Witzke *et al.*, 1979).

## Graptolites

From the abundant fossil remains of graptolites in certain facies of the Silurian and other Lower Palaeozoic strata, it is evident that these extinct marine colonial organisms were originally very common in parts of the ancient oceans and seas, possibly to the same extent that jellyfish are today. Somewhat like jellyfish in life habits, the graptoloid graptolites (with millimetre wide branches and an overall colony diameter of up to a metre; (Figure 2.20)) were, for the most part, free-living animals that probably fed on the plankton and followed its diurnal migration within the surface waters of the oceans.

The graptoloids coexisted with another group of rooted, bottom-dwelling graptolites, called the dendroids (small multibranched bushy forms, up to 10 cm in height), from which they originally evolved back in late Cambrian times.

Both graptolite groups are taxonomically very different from the cnidarian jellyfish and are placed in the Class Graptolithina within the Phylum Hemichordata along with the surviving graptolite-like pterobranchs (Rigby, 1993).

Graptoloids were planktonic, and are most important within the British Silurian and for its stratigraphy. However, there is considerable argument over the extent to which the colonies were capable of independent movement (Rickards *et al.*, 1998). They probably had very limited powers of locomotion and some were undoubtedly assisted by special hydrodynamic effects induced by colony shape (e.g. spiral form of the cyrtograptids). Much of their geographical distribution depended upon currents and tides and many of them have cosmopolitan, ocean-wide distributions, although many others have much more endemic or provincial distributions, limited to individual seas or ocean basins. Nevertheless, the combination of their abundance, wide distribution in space and high rates of evolution, have given the graptolites a very significant role in Silurian biostratigraphy (Figure 2.21).

Whilst the early focus on the shelf sediments of the Welsh Borderland by Murchison and his collaborators revealed the presence of graptolites, their biostratigraphical potential was not revealed until some time later. In the 1860s, James Hall pioneered the accurate description of graptoloid species in the 'Silurian' (Ordovician) around Levis, Quebec (1865).

However, it was Charles Lapworth who first recognized in the geologically complex Southern Uplands of Scotland that graptoloids occurred in distinct associations, which changed through time (Lapworth, 1870, 1878, 1879–1880b).

By working out the biozonal succession of assemblages, Lapworth was able to correlate rocks of similar age over large areas, even when the physical relationship of individual outcrops was confused by complex tectonic structures. Indeed, for the first time in Palaeozoic rocks, mapping of fossil distribution helped to elucidate the geology, rather than the other way round (where the stratigraphical sequence was used primarily to establish the faunal succession). Lapworth compared the stratigraphical utility of the graptoloids with that of the Mesozoic ammonites, whose detailed biozonation had been demonstrated by Oppel in 1856.

In essence, Lapworth's graptoloid biozonation of the Ordovician and Silurian has survived the test of time and its value has been formally recognized by the establishment of the Ordovician–Silurian international stratotype boundary at Dob's Linn (see site report). Subsequently, graptolite biozones were extended beyond the Llandovery of the Southern Uplands up into the Wenlock and Ludlow by Elles (1900) and Wood (1900). Their biozonal scheme, based on British sequences became the international standard, accepted and used worldwide for over 50 years, until new discoveries, especially of graptolites in younger (high Silurian and low Devonian) strata, required substantial revision (Horný, 1962).

Continued investigation in this century (see Palmer and Rickards, 1991, for a recent overview) has further refined the scheme so that there are some 40 graptoloid biozones for the Silurian worldwide, of which 27 are generally recognized in the British sequence (Rickards, 1989b, 1995; (Figure 2.22)). Those younger Silurian, Pridoli age, strata have not yielded graptolites from the shallow and quasi-marine deposits that make up this series in Britain. Elsewhere, Bohemia for example, rocks of this age are fully marine and graptolitic. The total duration of the Silurian was some 30 Ma according to radiometric dating of associated igneous rocks. On a mean average basis such biozonation provides subdivisions of less than a million years, a remarkably fine calibration that is equalled only by the conodonts within the Palaeozoic.

The occurrence and preservation of abundant graptolites is associated with particular sedimentary environments, especially those with mud substrates and low levels of benthic activity. Such facies are typical of outer shelf or basin environments, where oxygen levels and rates of autochthonous clastic sediment input are low, inhibiting the development of the benthos and allowing the remains of free-swimming (nektonic) and floating (planktonic) organisms to accumulate. These deposits have been characterized as 'graptolite facies' (see discussion below), where the graptolites have not been too 'diluted' by high volumes of silt or mud. The latter situation is more typical of the basinal turbiditic facies and even there, the muddy pelagic intervals may contain graptolites and their faunal associates (see the site report on Penstrowed Quarry in the Wenlock Series).

## Conodonts

Until recently, conodonts have been one of the most taxonomically elusive groups of fossil organisms ever known. For much of the 140 years since their original discovery in the middle of the 19th century; the tiny, tooth-shaped fossil remains of conodonts had no systematic home, and palaeontologists were unable to say with any certainty what group of extinct organisms they belonged to. Commonly less than 1 mm or so in length, the fossil conodont elements are barely visible on a rock surface to the unaided eye. Nevertheless, they are very abundant in some types of marine sedimentary rocks, especially continental shelf limestones, from which they can be extracted by chemical preparation.

Abundance and widespread occurrence throughout strata of Cambrian to Permian age led to the recognition of their potential as biostratigraphical zone fossils long before their zoological affinities were determined. Although the Russian naturalist Christian Pander, who first described them in the early 19th century, regarded them as fish teeth, they have since been placed by various authors in a very wide range of invertebrate groups. However, recent research (Aldridge *et al.*, 1986, 1993b; Sansom *et al.*, 1992) has confirmed conodonts as teeth elements of a vertebrate feeding apparatus. The discovery of fossilized conodont animal softparts from Carboniferous rocks near Edinburgh (Wardie Shore GCR site, see Briggs *et al.*, 1983; Aldridge *et al.*, 1993b) shows that these were small eel-shaped creatures, mostly a few centimetres in length but occasionally as much as 0.5 m in length (Aldridge and Theron, 1993; Gabbott *et al.*, 1995).

From their anatomy and from the widespread distribution of some of the fossils through different facies and over large geographical areas, the conodonts were clearly free-swimming animals, many with a pelagic marine habit. Some were carnivorous predators (Aldridge and Jeppsson, 1984; Purnell *et al.*, 1995), using their multi-element conodont apparatuses to capture and consume small planktonic or nektonic prey. The facies dependence of many conodonts shows that overall they were diverse in behaviour and habitat. Endemic shallow water, near-shore specialists can be recognized, while others preferred deeper water offshore environments and some were cosmopolitan ocean dwellers, which coexisted with the graptolites. However, it is also clear that conodont distribution does not fit a simple onshore–offshore ecological scheme. Detailed patterns of extinction and radiations in the evolving lineages of both the conodonts and graptolites have shown that there were significant faunal turnovers throughout the Silurian. These biotic events have been related to oceanic (*primo–secundo*) episodes and events involving changes in oceanic circulation and productivity of the plankton by Jeppsson (1990, 1997), Aldridge *et al.* (1993b) and Jeppsson *et al.* (1995).

The first conodont biozonal scheme for the Silurian was developed by Walliser (1962, 1964), who defined 12 biozones based on a section in the Carnic Alps of Austria. Several of these biozones have become widely recognized but since part of the Llandovery is missing from the original section, it cannot serve as a standard. Aldridge and Schtinlaub (1989; (Figure 2.23)) revised Walliser's scheme and expanded it to encompass 13 biozones, which can be widely recognized beyond the British Isles. This has now been further extended to 15 biozones by Jeppsson (1997) and matched as far as possible to the graptolite biozonal scheme and oceanic regime.

## The evolutionary innovations

### Fossil fish

When Murchison started his investigations of the Welsh Silurian, it was thought that the Old Red Sandstone represented the 'Age of Fishes' (Agassiz, 1844–1845) and that the earlier Transition Series were characterized by shelled organisms and other more primitive forms of life. However by 1855, fossil fish had been found within the Silurian strata of Lesmahagow and other localities in the Midland Valley of Scotland. This discovery pushed the origin of the vertebrates down into the Silurian and revealed novel, often well-preserved and entire fossil remains of a diverse fauna of strange jaw-less (agnathan) fish many of which were quite unlike any that had previously been discovered. Some of the fish were covered in tiny shark-like body scales (thelodonts), whilst others had bony body scales and head shields. A few of the fish had the horseshoe-shaped, bony head shields characteristic of fish known from the Passage Beds at the base of the Old Red Sandstone in the Welsh Borderland.

Modern research shows that the origin of the agnathan fish now lies much deeper back in time and within the early Cambrian (Figure 2.24), (Figure 2.25). Nevertheless, the Scottish Silurian fish fauna is still one of the most diverse and best preserved of these early agnathans in the world. The fauna records the early radiation of a number of agnathan groups such as the anaspids, petromyzonids and cephalaspids (for review see Blicek and Janvier, 1991). This palaeontological importance places considerable conservation value on the sites from which the agnathans originate (see the Gutterford Burn and Ree Burn–Glenbluck Loch site reports and Dineley and Metcalf, 1999). The tiny individual scales (ichthyoliths) of some of these fish have been shown to have characteristic morphologies for individual species. Also, the distribution of some species crosses from carbonate to clastic facies and beyond individual basins of deposition. They therefore have considerable biostratigraphical potential and this has been realized with respect to the British Silurian in recent years. Eight biozones and several faunal provinces have been established between the tectonic plates of Laurentia and Avalonia and that of Baltica (Scandinavia), (Turner, 1973; Märss, 1989, ((Figure 2.26)), (Figure 2.27); Blicek and Janvier, 1991).

Until very recently, some of the earliest evidence for the origin of the jawed fish (gnathostomes) was also to be found in Silurian strata of the Welsh Borderland, with fossil remains of spines, scales and teeth from the extinct acanthodian fish. These fossils were first known from the 1830s, when they were found in the Ludlow Bone Bed, within the Passage Beds, which were thought at the time to be Old Red Sandstone in age. Subsequently, the 'Passage Beds' or 'Tilestones' were brought into the Silurian as the Downton (now within the Pŷdoli, e.g. see the site report on Ludford Lane and Ludford Corner). Other gnathostome fish groups such as early representatives of the chondrichthyans and osteichthyans have been found elsewhere and in older Silurian strata. Most recently chondrichthyan scales have been found in late

Ordovician strata of North America (Sansom *et al.*, 1996). However, the fragmentary remains from the British Silurian still represent important evidence for the early radiation of the acanthodians and hold the potential for further research (Dineley and Metcalf, 1999).

The Silurian radiation of the fish, both the dominant jawless forms (agnathans) and the newly evolving jawed forms (gnathostomes), is recorded in deposits of widespread shallow-water epicontinental seas and marginal marine embayments. The often well-preserved Scottish agnathans are found in finely laminated mudrocks typical of quiet water lagoonal/lacMärssne environments with anoxic bottom conditions which inhibited the benthos and promoted whole-body preservation. By comparison, the Welsh Basin agnathans and a few of the Scottish ones, especially the osteostracans with their tough, bony head shields, are found in coarser clastic deposits of shallow, well-oxygenated running water. Similarly, the fragmentary and disseminated fossil remains of gnathostomes of the Pridoli Series are found within shallow, well-oxygenated, marginal marine deposits. Here the fossils are associated with the marine regression marking the end of Silurian deposition in the Welsh Basin.

### **Fossil land plants and animals**

The same retreat of the sea across the Welsh Borderland region at the end of Silurian times deposited sediments that contain the fossil remains of vascular land plants and arthropods and record one of the most important innovations in the history of life — the invasion of terrestrial environments. Although the first fossil plant discoveries were made in the 1840s by officers of the Geological Survey (Phillips, 1848), it was not until Lang's detailed investigation (1937) of their structure that the full significance of these primitive rhyniophytoid plants, such as *Cooksonia*, was realized. Since the 1970s, a new programme under the guidance of D.E. Edwards (University of Wales at Cardiff) has re-evaluated the original finds. Edwards and her collaborators have also discovered new and better preserved material from these Welsh sites, producing 'the most complete record of Silurian land-plant fossils in the world... [that] has played a central role in developing a phylogenetic and palaeoecological model for the terrestrialization of vegetation' (Cleal and Thomas, 1995, p. 29).

The plant fossils are, at first glance, unspectacular in that they are generally small (1–4 cm high), carbonized thin stems with simple dichotomous branches, terminated by globular reproductive organs. Only rarely preserved are the critical histological and structural features, such as water conducting vessels, stomata and sporangia, that identify them as vascular plants, capable of surviving and reproducing under the stresses of life in a light, dry gaseous environment such as the atmosphere. Nevertheless, some of these features have now been discovered and revealed by electron microscopic study, particularly of species of *Cooksonia* from Welsh Borderland localities (e.g. see the site reports on Perton Road and Quarry, and Ludford Lane and Ludford Corner). This plant fossil evidence from the British sites has been of international importance in developing our understanding of early vascular plant evolution (Figure 2.28).

The most commonly preserved plant fossils are their microscopic reproductive spores, which are produced in great numbers. The spores are decay-resistant and light enough to be readily transported by even the lowest energy water and air currents. Consequently, spores are commonly found in a wide range of associated sediments, such as coastal marine sediments, far beyond the location of the parent plants. A problematic result of this separation of parent plant and reproductive spore, is that the identity of the parents of most spores are unknown. However, the abundance, wide dispersal and evolution in morphology of these plant spores has made them very useful biostratigraphical markers and has led to the development of spore-based biozonal schemes.

The distribution in time of plant spores has shown a remarkable anomaly, in that vascular plant-type spores have now been found as far back as mid-Ordovician times, whilst the macro-plant fossil record does not begin until the Silurian. This anomaly suggests that the full fossil record of the early evolution of the vascular plants has yet to be found, perhaps because of the scarcity of suitable preservational environments in the rock record. New finds from the lower Silurian of China and elsewhere support these suggestions of an earlier and more diverse land flora. However, the British material and sites retain considerable potential for further study and will continue their historic importance for conserving and providing examples of an important phase in early land plant evolution and radiation (for a review see Kenrick and Crane, 1997).

Some of the earliest fossil evidence for land-living animals and their interactions with the first plants is also derived from the same British Silurian sites. Tiny, millimetre-sized, fragments of terrestrial arthropod cuticle have been chemically isolated from the sedimentary rocks at Ludford Lane and Ludford Corner, in the Welsh Borderland (see site report). Despite their small size and fragmentary nature, they are distinctive enough to have been identified (Jeram *et al.*, 1990) as belonging to the earliest known arachnids and centipedes.

Furthermore, the remarkable discovery of spore-laden coprolites (faecal pellets, 0.5–3 mm long) at the same site (Edwards *et al.*, 1995) indicates that there were plant-eating animals present at the time. The association of the coprolites with vascular plant fossils and the exoskeletal remains of aquatic eurypterid arthropods shows that all the fossil remains were assembled in shallow marine offshore sediments. Whilst there is no direct evidence to connect one particular arthropod as the herbivore that excreted the coprolites, the fossil remains include millipede-like animals of a suitable size. Analogy with living millipedes, which are plant detritivores, supports this connection. The most important aspect of the finds is their role as the earliest evidence of herbivory and cycling of primary productivity in early plant dominated terrestrial ecosystems, and the potential for new research.

## **The spatial distribution of the Silurian biota**

Since the early 19th century there has been a recognition that particular kinds of fossils are associated with particular kinds of sedimentary rocks, for example in the Silurian, corals, crinoids and stromatoporoids are typically associated with limestones and graptolites with shales. In Murchison's time, there was some conflation of various Silurian shale and limestone horizons because of the superficial similarity of their fossil faunas, which sometimes led to confusion of the overall stratigraphical succession. Only detailed identification and description of their fossils allowed the stratigraphical separation of otherwise similar lithologies.

Understanding of the nature of fossil distribution in space and time was, however, further confused by Barrande's work on the Silurian succession in Bohemia. Barrande found what seemed to be 'islands' of limestone strata containing fossil 'colonies' of a different age from those found in the surrounding 'normal' sequence of shales. His observation seemed to contradict the generally accepted principle of the order of superimposed strata with characteristic fossils and caused considerable debate. It also worried Darwin because it seemed to provide evidence that contradicted his theory of 'the slow and gradual modification (of species), through variation and gradual selection' (Darwin, 1859). However, Darwin (1882, p. 320) thought that Lyell's explanation as case of temporary migration from a distant geographical province...', for Barrande's colony theory, seemed 'satisfactory'. Barrande subsequently adopted and developed Lyell's explanation, arguing vehemently against growing evidence that the whole basis for his theory was flawed. Finally, the Cambridge geologist J.E. Marr (1880a), demonstrated that the 'out of stratigraphical context' colonies had been produced by strike-slip faulting and had no biological basis.

By the latter part of the 19th century, the simplistic 'layer-cake' view of the distribution of sediments and their contained fossils, in time and space, was revised by the Waltherian concept of 'facies' cross-cutting timeplanes. Research on the temporal distribution of Jurassic ammonites introduced a more sophisticated understanding of the complex relationships between abundances and ranges of fossils in strata. This led to the development of biostratigraphical zones beyond Oppel's original (1856) concept of the range zone of a species to that of an 'acme' zone, marked by the maximum abundance and geographical distribution of a species (see Brett and Baird, 1997, for a recent review).

More recently, the link between the ecology of Silurian organisms and their stratigraphy has been further explored, especially by Boucot (1986). And, there has been a recognition that the sediment record is characterized by a hierarchy of palaeontological events of varying temporal and spatial magnitudes that are nearly contemporaneous. Such events may be taphonomic (with selective preservation of taxa not usually recorded), ecological (e.g. environment controlled population explosions) or incursions (temporary invasions across basin boundaries). Some of these events extend beyond individual basins of sedimentation and are global in scale. Study of these events provides the potential for a successional history of biotic events which are the palaeontological equivalent of sequence stratigraphy (see Brett and Baird, 1997).

## The Shelly facies

Perhaps the most important development in Silurian palaeontology of recent decades has been the recognition of the ecologically based patterning of species distribution and the evolution of these patterns through time. The ecological base for the clustering of living benthic marine organisms and the spatial patterning of such clusters has been established since the pioneer work of Petersen (1918). However, fossil assemblages are more diffuse and complicated. These difficulties were partly removed by the study of the sedimentary processes of preferential recruitment and new understanding of how taphonomic bias in burial and fossilization occurs (see Schafer, 1972, for an overview). The advent of bulk rock sampling and statistical analysis of fossil assemblages promoted the recognition of repeated associations of particular species and regular dominants. Such patterns are characteristic of living benthic communities.

In the 1960s detailed studies by Ziegler (1965) of the macrofossil assemblages of the various clastic facies of the Welsh Llandovery, showed a recurrence of particular associations generally dominated by a few species of brachiopods. The pattern followed the established palaeobathymetry of the Welsh Basin and Ziegler claimed that they reflected a succession of depth-controlled brachiopod 'communities'.

These fossil 'communities' as Ziegler called them are something of a misnomer and should not be confused with true biological communities within which degrees of interdependence or interaction have been observed. Fossil communities are probably better referred to as associations, since they are based on counts of fossil remains that may not be in their original habitats. Nevertheless, from the subtidal *Lingula* 'Community', four further brachiopod associations were established down across the shelf slope, namely those of *Eocelia*, *Pentamerus*, *Costistricklandia* and *Clorinda*, followed by a deeper water graptolite dominated association (Figure 2.29).

The Llandovery facies are predominantly clastic and complications arose when the same type of analysis was subsequently applied to the younger Wenlock, Ludlow and Pridoli strata (Cocks and McKerrow, 1978; Hancock *et al.*, 1974; Watkins, 1979). These sediments are more varied with mixed carbonates and clastics distributed across a wider and less inclined shelf slope.

Consequently there seems to be more of a facies- rather than a simple depth-control on the spatial pattern of associations. Comparison with living benthic communities shows that this is only to be expected where the dominant benthic organisms are filter feeders.

Nevertheless, the possibility of mapping ecologically meaningful associations of macrofossils in the Lower Palaeozoic had been successfully established. The further possibility of showing how these associations had evolved through Lower Palaeozoic time was explored and demonstrated by Boucot (1975, 1990). He developed a biogeographically based model of evolving biofacies and their benthic assemblage zones, which also reflect larger scale changes in climate and ocean circulation. This is particularly manifested in the broad division into the southern hemisphere Malvinokaffric Realm of cool water and the North Silurian Realm with carbonate-rich warmer water.

Typically, these shelf associations are dominated by two or three brachiopod species with a variable number of minor associates depending largely upon the degree of ecological stress the environment placed on the original community.

Generally there are half a dozen or more associated macroorganisms ranging from other brachiopods and molluscs to bryozoans, corals and pelmatozoans. However, where there were significant carbonate buildups (see below), the diversity often increases greatly and the brachiopods are overshadowed by corals, bryozoans and stromatoporoids. Relative abundance is more evenly spread with cephalopods, trilobites and many other minor associates joining the overall assemblages. Within the Wenlock these biotic/carbonate associations were developed into reefs.

## Reef formers

True reefs are not very well developed within the British Silurian strata compared with the contemporary sediments of regions like Baltica or Laurentia. The reefs are restricted to the Wenlock of the Welsh Borderland, a time when there was the greatest global development of Silurian reefs. This acme of reef-building may have been associated with global

climatic warming, which allowed reefs to develop at the edge of the subtropics, where Avalonia was positioned at the time (Figure 2.30).

Murchison first recognized Silurian reef forms in 1833 in the Wenlock limestones of the Wenlock Edge area of Shropshire and then in Gotland in 1847. Further detailed study had to wait another hundred years or so, despite the availability of modern analogues from 1842 when Darwin first published his book on living coral reefs.

Since the 1950s, it has been realized that the Wenlock reefs of the Welsh Borderland, along with those of Gotland and Estonia, are amongst the best preserved and most richly fossiliferous reef structures of this time in the world. Those of the Welsh Borderland (e.g. the GCR site Easthope–Harley Hill) are very limited in size and only represent patch reefs developed on a carbonate platform close to the shelf-edge (Copper and Brunton, 1991; Riding, 1981; Scoffin, 1971), there are no barrier or fringing reefs. The largest reefs were less than 15 m in height with diameters of no more than 300 m and most were much smaller. Nevertheless, the reef limestones and associated inter-reef and flanking muddy carbonates of the Much Wenlock Limestone Formation provided an extensive range of habitats, which were occupied by a wide variety of organisms. Skeletal debris accumulated in the adjacent sediment traps.

The dominant organisms were sessile framework builders, generally colonial organisms that secrete calcareous supporting and protective cups, plates and tubes of various kinds, as seen in the tabulate corals, stromatoporoids, bryozoans and branching rugose corals (Figure 2.31). The framework is bound together by cemented calcareous skeletons from genera of the same fossil groups plus calcareous algae and most importantly stromatolites. The remaining voids and interstices provided niches which were occupied by a range of brachiopods (over 30 species have been recorded) pelmatozoans, gastropods, trilobites and smaller organisms such as conodonts, ostracods, acritarchs and chitinozoans.

The early post-depositional lithification of these reefs and their associated carbonates into limestones helped preserve the contained fossil remains, especially some of the small and delicate or thin-shelled interstitial organisms. The carbonates can also be chemically treated with relative ease for the extraction of organic-walled microorganisms and conodonts.

### **The graptolite facies**

At the deeper end of the spectrum of benthic assemblage zones across the shelf facies, the dominance of the brachiopods in the faunal associations gives way to the graptolite association (for reviews see Watkins and Berry 1977; Palmer, 1991; Underwood, 1993). Here, the substrate consists largely of laminated shales, silts and sporadically intercalated turbiditic sands. The shales and silts contain the remains of organisms that lived within the water column and those benthic forms that could tolerate soft substrates and lower oxygen levels. The benthic fauna appears to have been mainly bivalved molluscs such as cardioids, pterineids and lunulicardiids, which were most tolerant of the prevailing substrate and water conditions in these environments throughout the Silurian of the various basins within the British sequences. In addition there are rare epifaunal colonizers of the occasional hard substrate (generally empty shells) such as pedunculate brachiopods, crinoids and calcareous tube worms. The autochthonous benthic elements vary in density and are often outnumbered by the remains of a variety of other macrofossils recruited from the water column above.

This latter planktonic and nektonic macrofauna mainly includes graptolites and cephalopod molluscs with occasional phyllocarids and ostracods (see the report on the Ludlow age Friends Meeting House Quarry site). The accompanying microfauna includes abundant plankton such as the organic-walled acritarchs and chitinozoans along with scolecodonts, conodonts and ostracods. Many of these organisms evolved rapidly, were widely distributed and provide the bases for biozonal schemes. In the context of the British Silurian, the graptolites play the major biostratigraphical role in this facies, with a biozonal scheme elaborated from that first established by Lapworth (1879–1880b), elaborated by Elles and Wood (1900, 1901–18) and now developed in modern form by Koren (1989) and Rickards (1995).

### **Trace fossils and facies of the bathyal zone**

Many organisms leave traces of their existence and behaviour in the sediment without any hard parts necessarily being fossilized but very rarely soft bodied organisms are preserved (Figure 2.32). Such trace or Ichnofossils' may be produced by the activities of a very wide range of organisms from the burrows of soft bodied 'worms' of various kinds to the footprints, tooth marks and faeces of vertebrates (for a recent review see Bromley, 1996). Although trace fossils are produced in most sedimentary environments, those of particular interest in the present context are the trace fossils found in Silurian deposits, which are otherwise bereft of body fossils. Such preservational conditions are particularly found within the fine-grained pelagic and hemipelagic deposits from offshore basins beyond the reach of normal, shelf-sea traction currents. Deposits of this kind are common within the Silurian of central and northern Wales (e.g. see the Aberarth–Morfa and Penstrowed Quarry site reports), the Lake District (e.g. see the Brathay site report) and Southern Uplands (e.g. see the Thornylee Quarry site report).

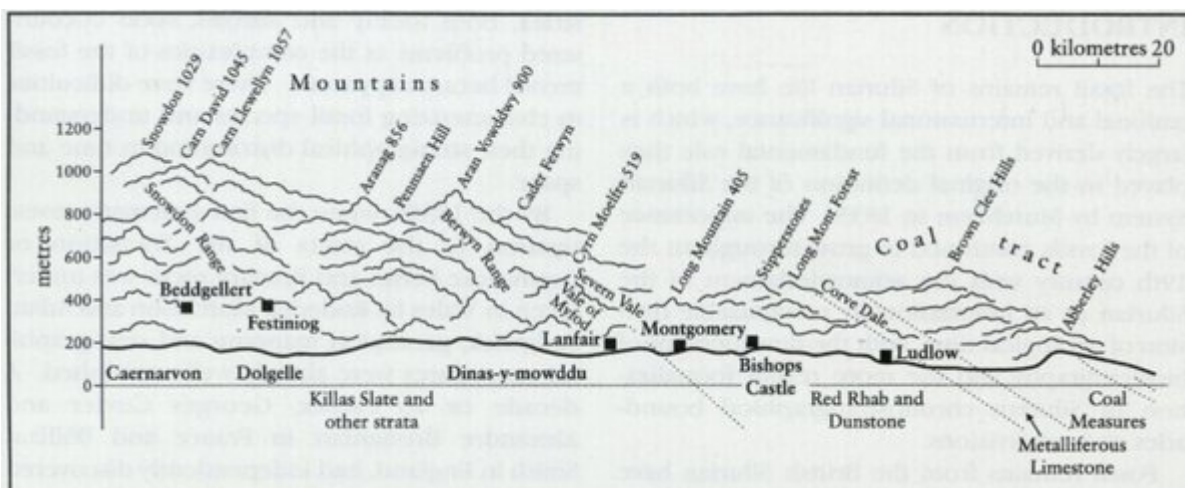
Basinal environments are typically formed beyond the shelf edge and below 200 m, from the bathyal zone down into the abyssal zone. Various factors, such as low oxygen levels in bottom waters at these depths, inhibit and may even prevent the development of bottom dwelling benthic faunas. The resulting sediments are typically fine-grained and laminated silts and muds (pelagites and hemipelagites, see Kemp, 1991, and Chapter 1) into which the episodic deposits of turbidity currents are introduced in particular environmental conditions.

In the Silurian this facies is often populated by the graptolite assemblage described above. However, the introduction of abundant short-lived turbiditic event beds can so dilute the slow supply of autochthonous muds that the recruitment of the remains of pelagic organisms is drastically reduced. But where there is enough oxygen in the bottom waters and there is sufficient nutrient supply, these autochthonous muds (division Te of the turbidite sequence of Bouma, 1962; (Figure 3.40) this volume) can be colonized by a range of largely infaunal, soft-bodied organisms. Indeed the presence of trace fossils in these sedimentary environments are important records of changes in basin aeration (Kemp, 1991).

Distinctive patterns of traces generated by the behavioural traits of organisms inhabiting these bathyal and abyssal depths have long been recognized and characterized as the 'Zoophycus' and 'Nereites' zone assemblages (Seilacher, 1962; Leszczynski and Seilacher, 1991; Wetzel, 1991). Indeed, *Nereites* was first described and named from the Welsh Basin turbidite succession in Murchison's *Silurian System* (1839). Crimes and Crossley have since (1991) identified 25 kinds of trace fossils (ichnogenera) from the turbiditic sandstones of the Aberystwyth Grits Group.

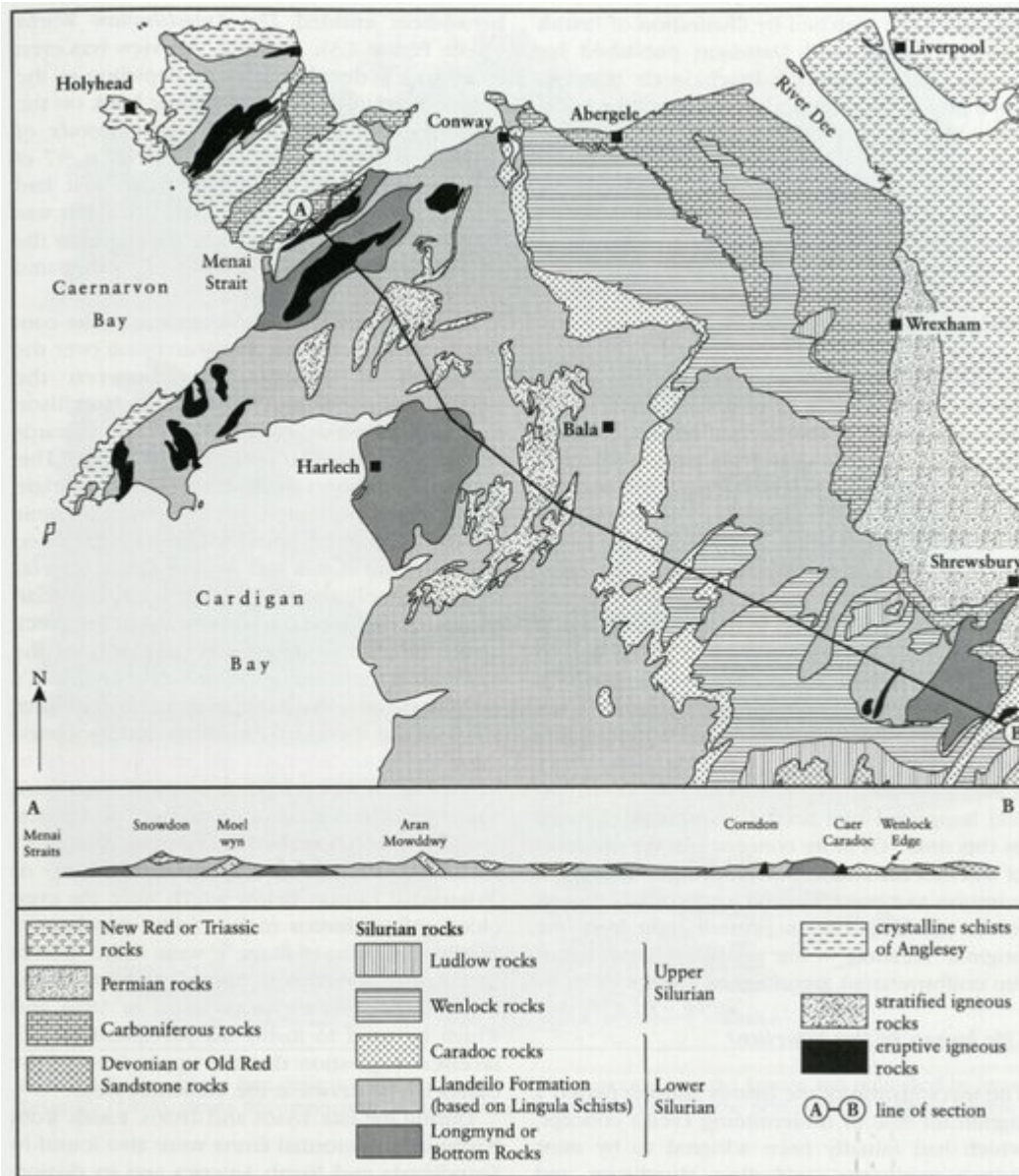
A further distinction in Welsh Basin ichnofaunas has been identified by Orr (1995) between pre- and post-turbidite assemblages of trace fossils. Before the incursion of turbidite flows, surface trails and shallow burrows developed in the autochthonous mud substrates. Turbidity currents often stripped some or all of this mud before casting the surface traces on the sole of the turbiditic sandstone. The upper surface of the sandstone was then burrowed by a somewhat different biota. The sedimentological nature of the deposits provides an excellent medium for the preservation of traces of activities such as burrowing and sediment feeding. It is now recognized that these ichnological signatures provide a potentially powerful tool for the diagnosis and interpretation of event beds as well as indications of palaeobathymetry (for a review see Pemberton and MacEachern, 1997).

## References

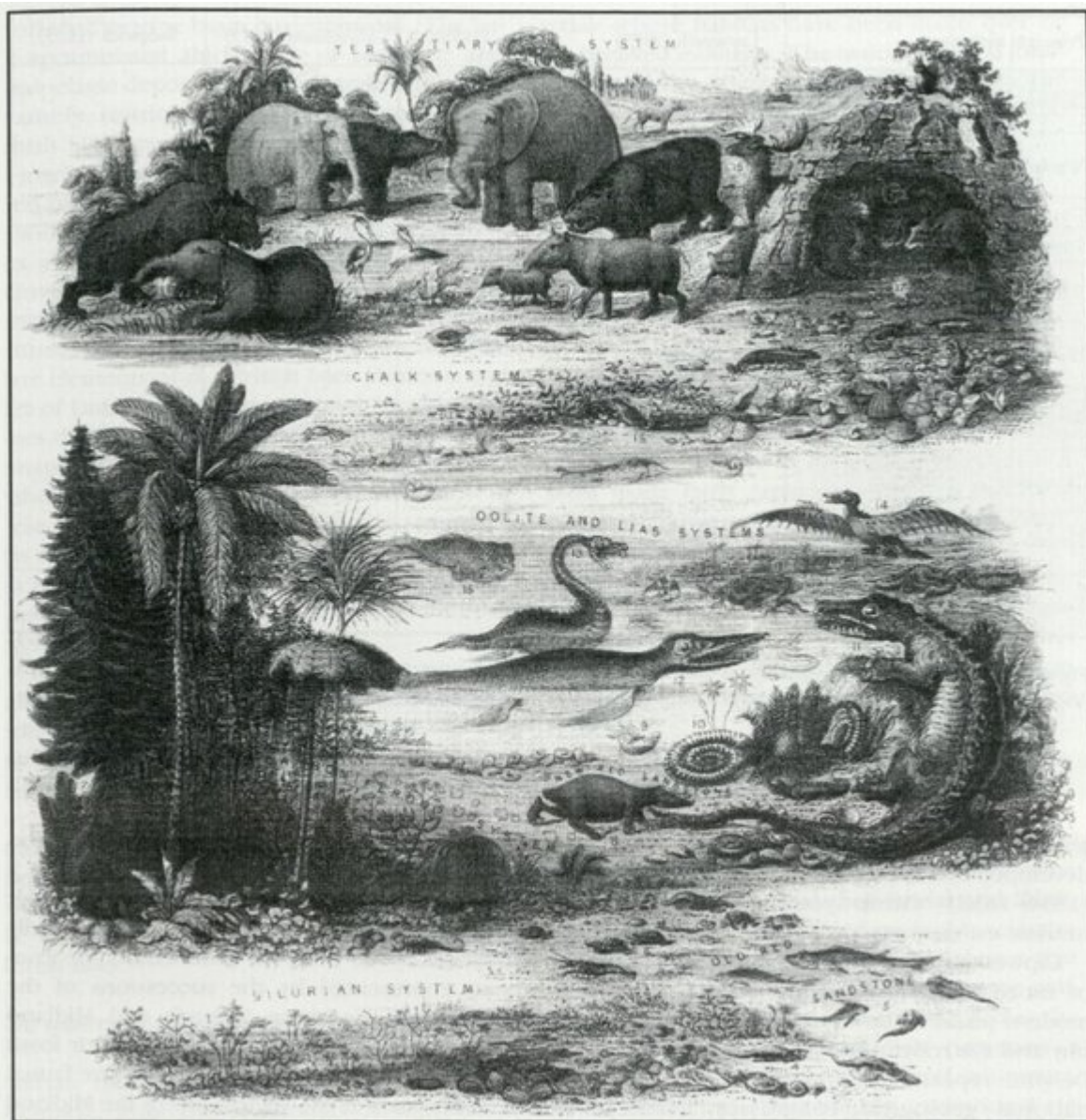




(Figure 2.1) The undivided Lower Palaeozoic strata in the Welsh part of William Smith's 1817 cross-section from London to Snowdon, redrawn from Fitton, W.H.F. 1832, 'Notes on the History of English Geology', Philosophical Magazine 1, Plate 2, fig. 4.



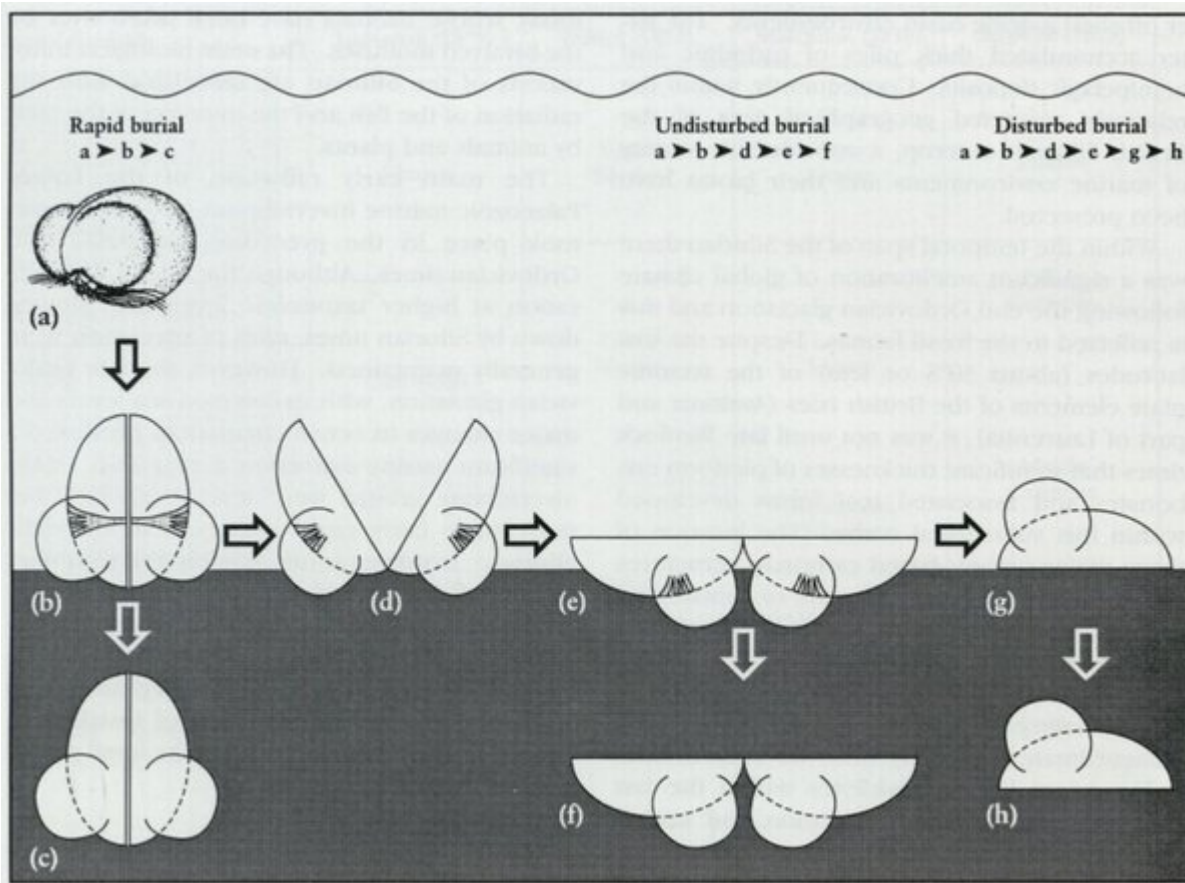
(Figure 2.2) North Welsh part of Murchison's 1854 map and section of the Silurian Rocks of England and Wales, which accompanied his first edition of *Siluria*. The Lower Palaeozoic is divided into Upper and Lower Silurian with Sedgwick's Cambrian subsumed into the basal part of the Lower Silurian (Longmynd or Bottom Rocks).



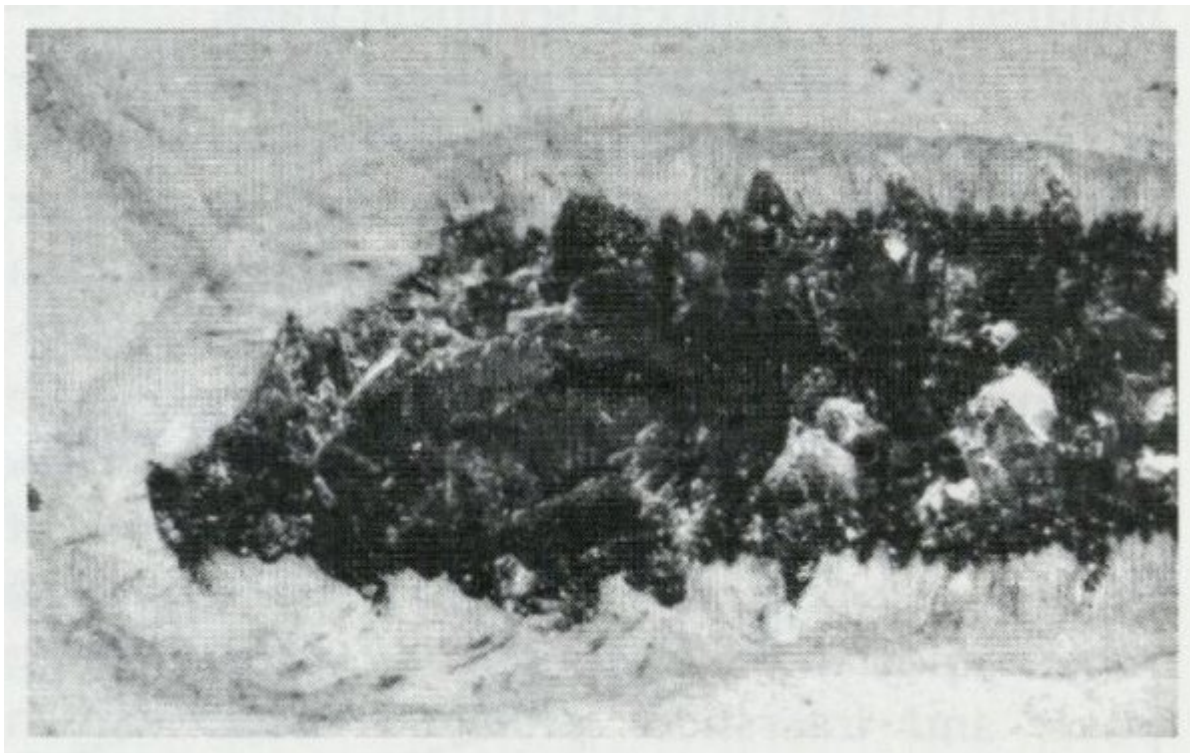
(Figure 2.3) One of the first depictions of the history of life, engraved by John Emslie and published by James Reynolds (1849), shows life originating (at the bottom of the figure) within the period of the Silurian System.

Principal divisions		Lapworth (1879)	Phillips (1855)	Murchison (1859)	Sedgwick (1855)
Ludlow	1	Silurian	Upper Silurian	Upper Silurian	Silurian
Wenlock	2				
Upper Llandovery = May Hill	3				
Lower Llandovery		Ordovician	Lower Silurian	(Primordial Silurian)	Upper Cambrian
Bala = Caradoc Sandstone	4				
Llandeilo	5				
Arenig	6				
Tremadoc	7	Cambrian	Cambrian	Cambrian	Middle Cambrian
Lingula Flags	8				
Longmynd	9				
					Lower Cambrian

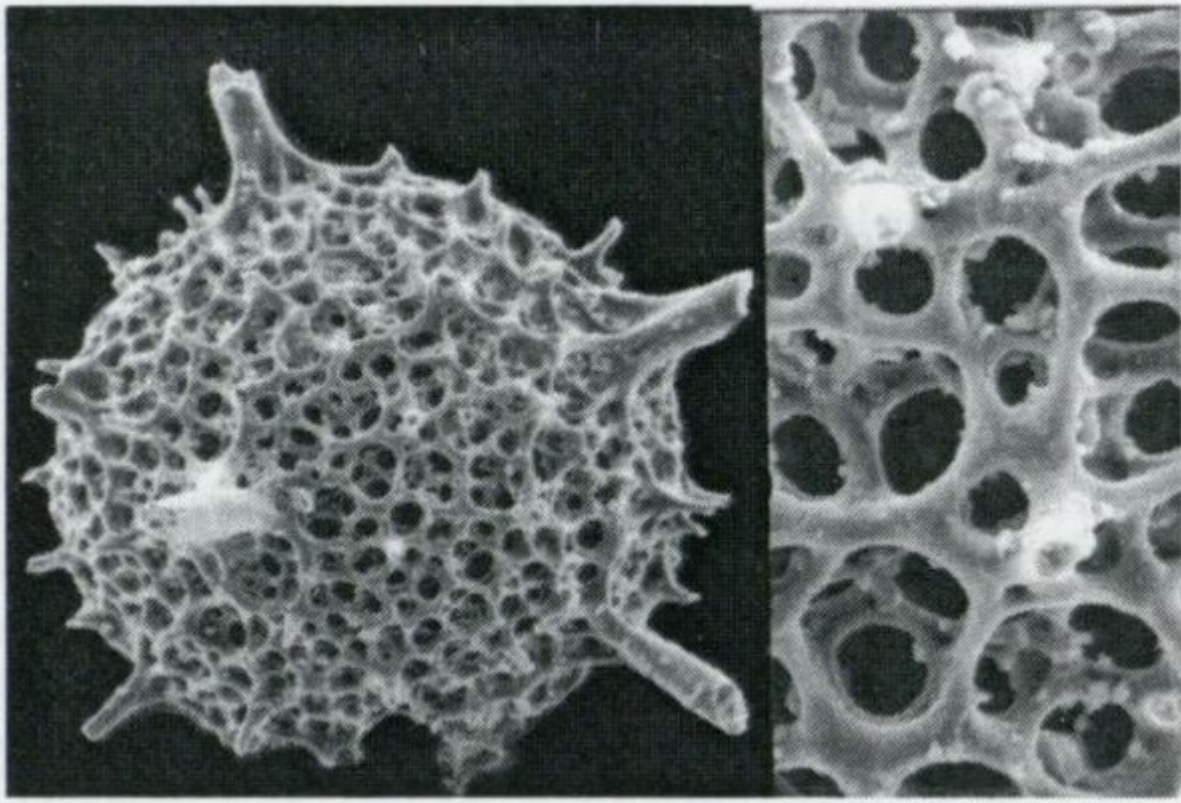
(Figure 2.4) Successive classifications and subdivision of the Lower Palaeozoic rocks of Britain from 1855 to 1879, when Lapworth introduced the Ordovician between the Silurian and Cambrian periods.



(Figure 2.5) An example of taphonomic processes of fossil burial, showing the various modes of preservation of Silurian myodocope ostracods (from Siveter et al., 1991).



(Figure 2.32) Worm: Wenlock Series, Herefordshire; x7.5. (Photo: Derek J. Siveter; from Briggs et al., 1996).

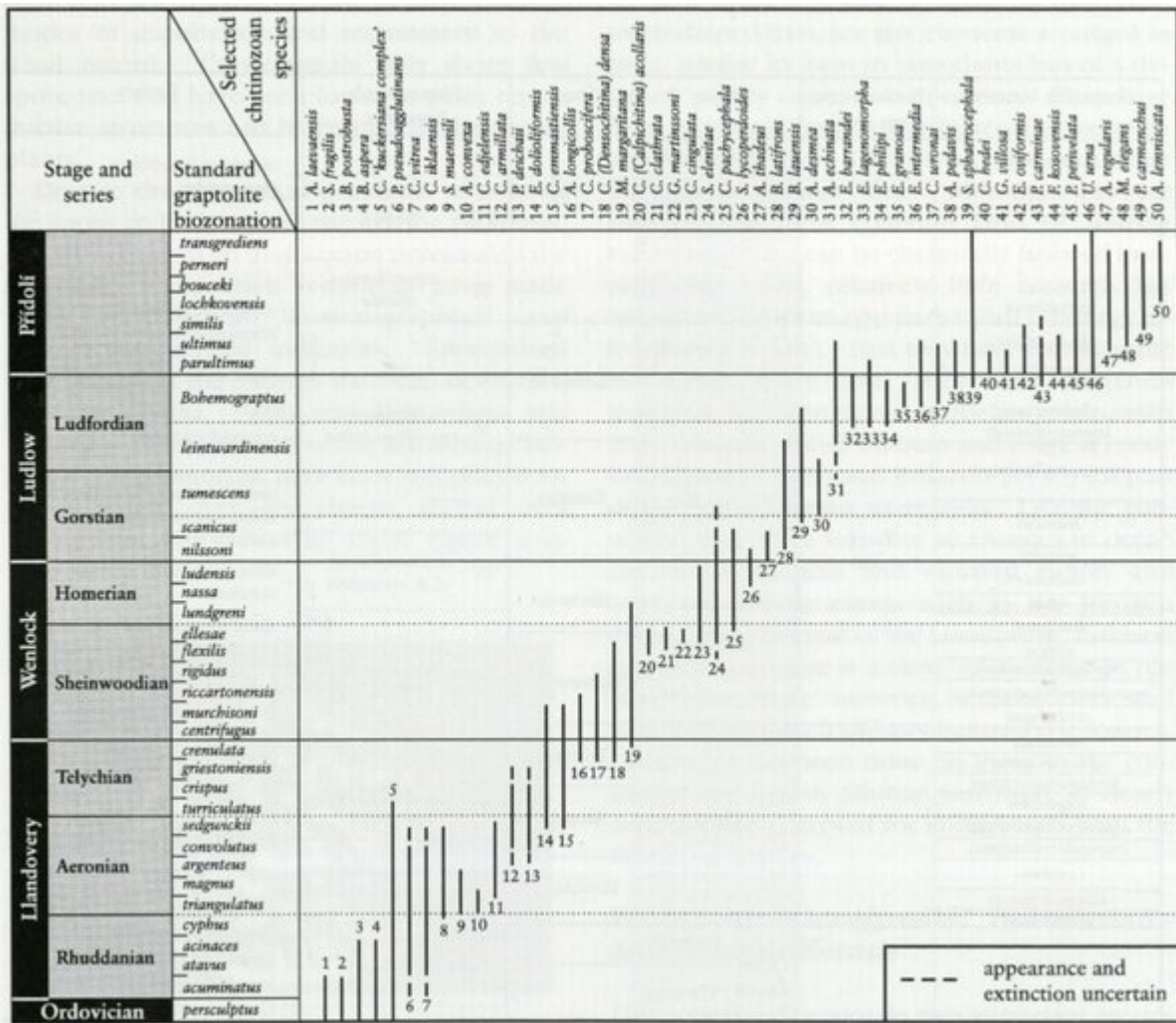


(Figure 2.10) *Astropherid radiolarian*, Wenlock Series, Herefordshire. Left: complete specimen, x 130. Right: detail of test, x 520. (Photos: David Siveter; from Briggs et al., 1996.)

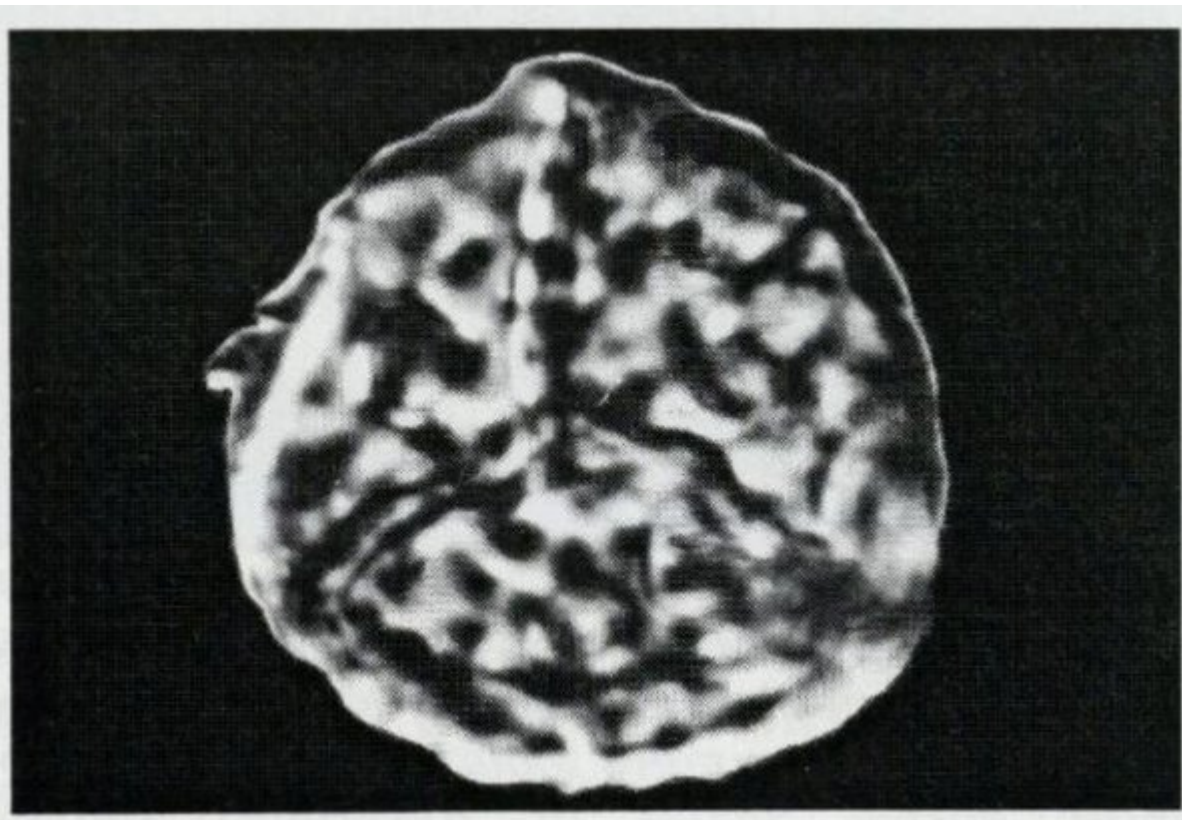
Series	Stage		Acritarchs
	Stage	Stage	
Priddoli Ludlow Gorstian Wenlock Sheinwoodian Telychian Llandoverly Aeronian Rhuddanian			<i>Gro. oligospinosum</i> <i>M. cabottii</i> <i>Tylotopalla</i> sp. <i>Eac. aff. E. ampulliformis</i> * <i>H. visbyensis</i> <i>Eac. rochesterensis</i> <i>El. williereae</i> <i>Do. limaciformis</i> <i>Da. estillis</i> <i>N. carminae</i> <i>Ca. maplewoodensis</i> <i>Do. algerensis</i> <i>Do. trispinosa</i> <i>De. furcata</i> <i>Di. williereae</i> <i>Do. amphora</i> <i>El. aurora</i> <i>Solita</i> sp. <i>De. monospinosa</i> <i>De. ramusculosa</i> <i>Geron</i> sp. <i>Gr. encantador</i> <i>S. rugulosum</i> <i>V. dilatispinosa</i> <i>Florisphaeridium</i> sp. <i>Pk. chondrocheus</i> <i>Cy.?</i> <i>carinosum</i> <i>Cy. pilaris</i> <i>L. carminae</i> <i>Onondagaella</i> sp. <i>Pe. stipitospinata</i> * Informal acritarch assemblages
			6
			5
			4
			3
			2
			1

\* recorded on one continent only     
 --- appearance and extinction uncertain     
 ?-?-? extension doubtful     
 ← → present also in Ordovician and Devonian

(Figure 2.6) An acritarch biozonal scheme for the Silurian proposed by Martin (1989).



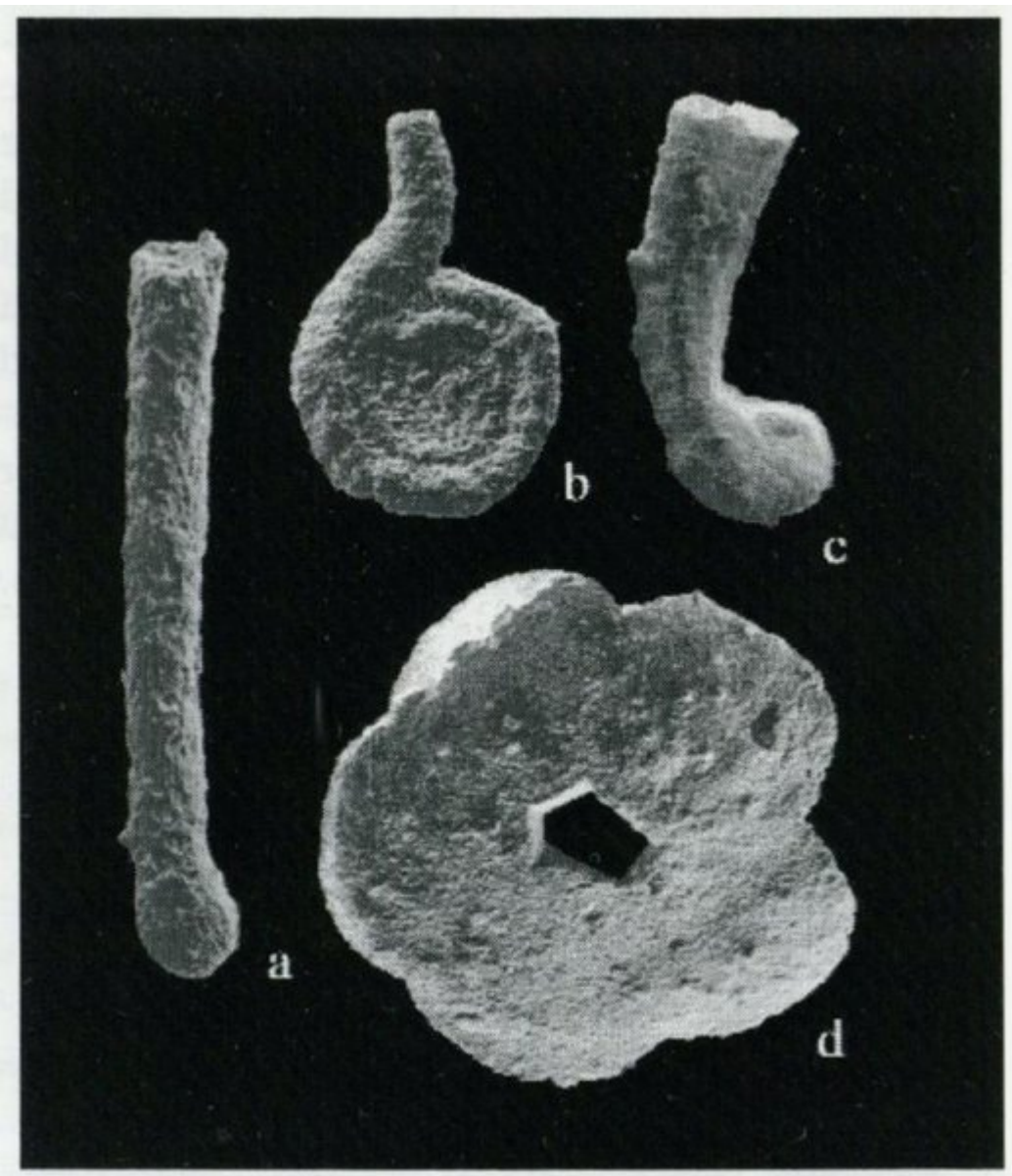
(Figure 2.7) The stratigraphical ranges of selected chitinozoans, compared with the graptolite biozones of the Silurian (after Paris, 1989).



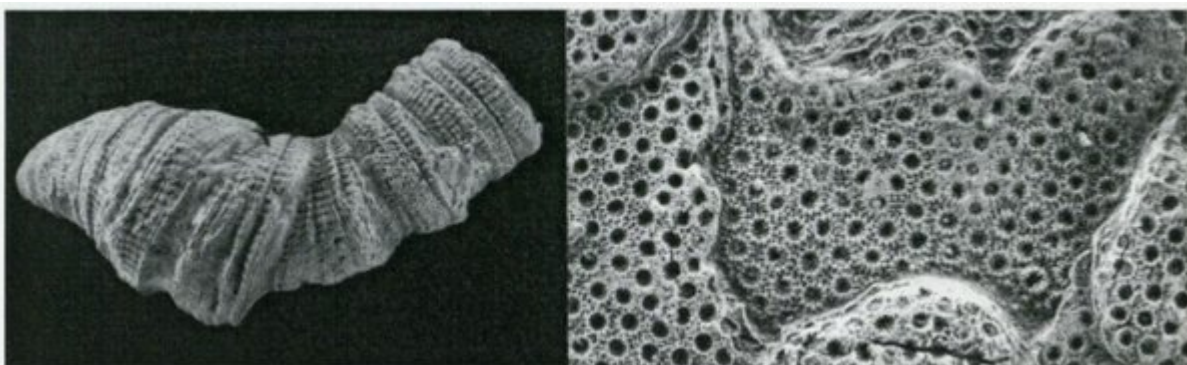
(Figure 2.9) Spore: *Synorisprites tripapillatus*, Cliffords Mesne Sandstone Formation, Gorsley, Herefordshire; x 2000. (Photo: John Richardson.) Detailed correlation with the graptolite biozonation has yet to be fully realized because the occurrence of diagnostic sporomorphs does not generally coincide with that of diagnostic graptolites.

Graptolite biozones	Radiometric age (Ma)	Series	Stage	Sporomorph biozones	Events
<i>transgrediens</i>	412	Devonian		VIII Zone B	incoming <i>Streelispora</i> , <i>Aneurospora</i>
		Prídolí		VII Zone A	
<i>parultimus</i>	414		Ludlow	Ludfordian	VI <i>tripapillatus-spicula</i>
( <i>kozlowskii</i> ) ( <i>thuringicus</i> ) ( <i>bohemicus</i> ) <i>leintwardinensis</i>		V <i>libycus-poecilomorphus</i>			
<i>tumescens/incipiens</i>	420		Wenlock	Gorstian	
<i>scanicus</i>		Homerian			
<i>nilssoni</i>	425		Llandovery	Aeronian	IV cf. <i>protophanus</i> -cf. <i>S. verrucatus</i>
<i>ludensis</i>		III <i>chulus-nanus</i>			
<i>nassa</i>	435		Ordo-vician	Ashgill	
<i>lundgreni</i>		Telychian			
<i>ellesae</i>	435		Rhuddanian	Ia <i>murusattenuata-murusdensa</i>	
<i>rigidus/linnarssoni</i>		II <i>avitus-dilutus</i>			
<i>murchisoni/riccartonensis</i>	435		Caradoc	Ib 'permanent' tetrads and dyads	
<i>centrifugus</i>					laevigate permanent tetrads, Caradoc cuticles
<i>crenulata</i>					
<i>griestoniensis</i>					
<i>turriculatus/crispus</i>					
<i>sedgwickii</i>					
<i>argenteus/convolutus</i>					
<i>triangulatus/magnus</i>					
<i>cyphus</i>					
<i>atavus/acinaces</i>					
<i>acuminatus</i>					

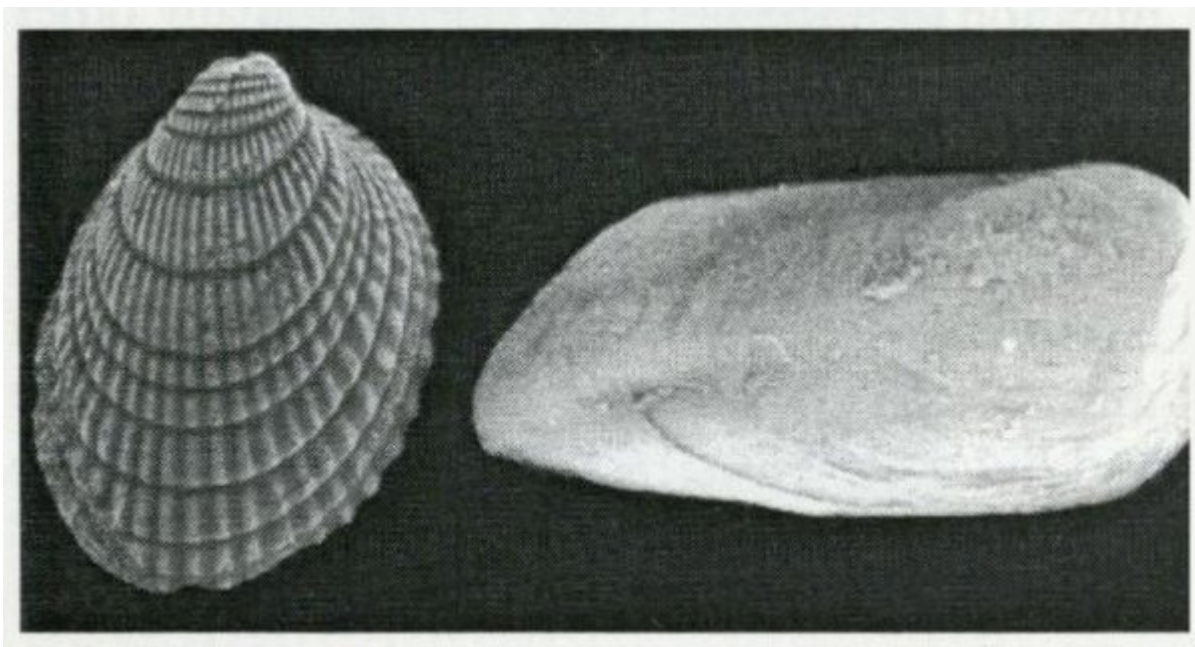
(Figure 2.8) Sporomorph biozones and plant megafossil events from the late Ordovician to earliest Devonian, compared with the graptolite biozones (after Richardson and Edwards, 1989).



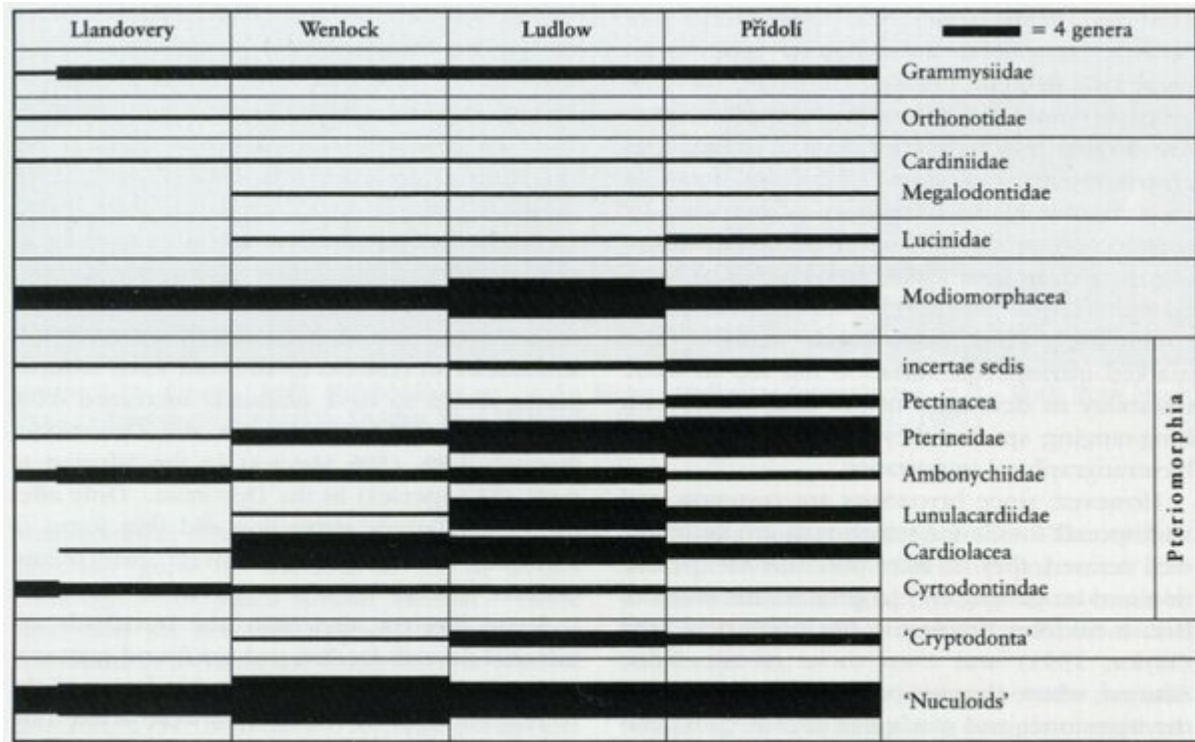
(Figure 2.11) Foraminifera: (a) *Hyperammina barrisi*; (b) *Ammodiscus exsertus*; (c) *Lituotuba?* sp.; (d) *Hemisphaerammina thola*. All from the uppermost Purple Shales or lowermost Buildwas Formation, Llandovery–Wenlock boundary beds, Wenlock Edge, Shropshire, x 70. (Photos: from Mabillard and Aldridge, 1982.)



(Figure 2.12) Corals: Left *Ketophyllum* sp., x 1. Right: *Heliolites interstinctus*, x 2. Both from Much Wenlock Limestone Formation, Dudley, West Midlands. (Photos: from Siveter et al., 1989.)



(Figure 2.13) Bivalves. Left: *Cardiola interrupta*, Ludfordian Stage, Ludlow Series, Usk, Gwent; x 1. Right: *Fuchsella amygdalina*, Whitcliffe Group, Ludlow Series, Malvern Hills, Herefordshire; x 2. (Photos: from Siveter et al., 1989.)

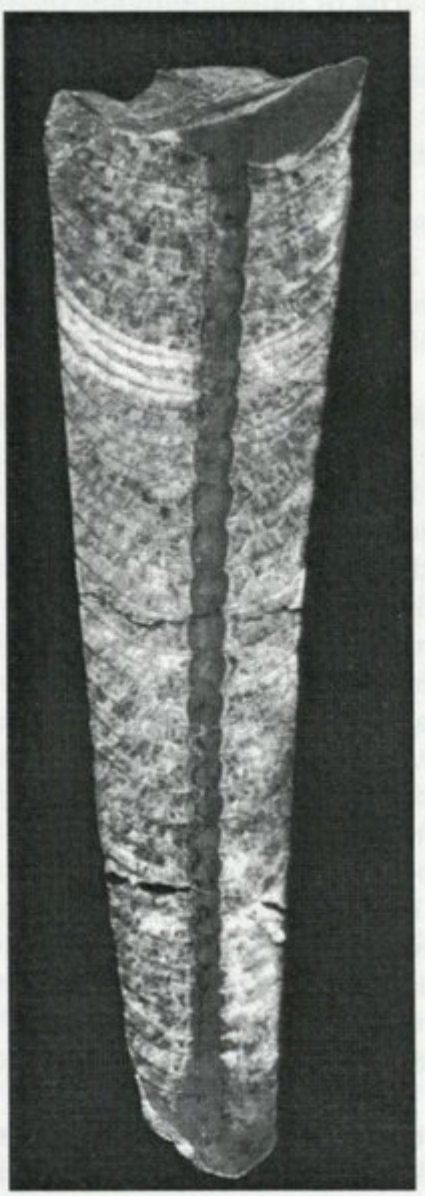


(Figure 2.14) The relative abundance (number of genera per stratigraphical interval) of various bivalve groups through the Silurian (from Kilt, 1984).

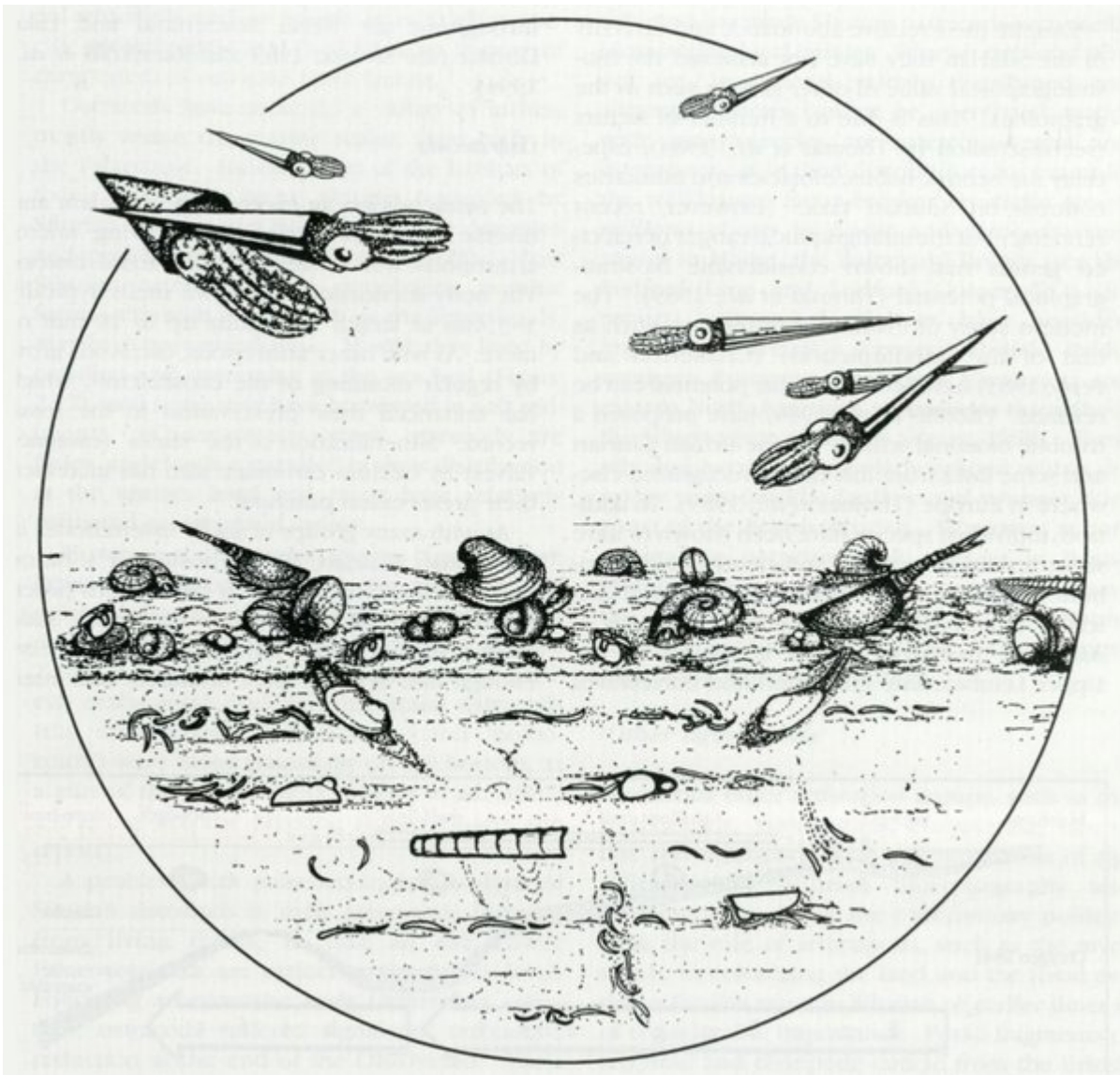




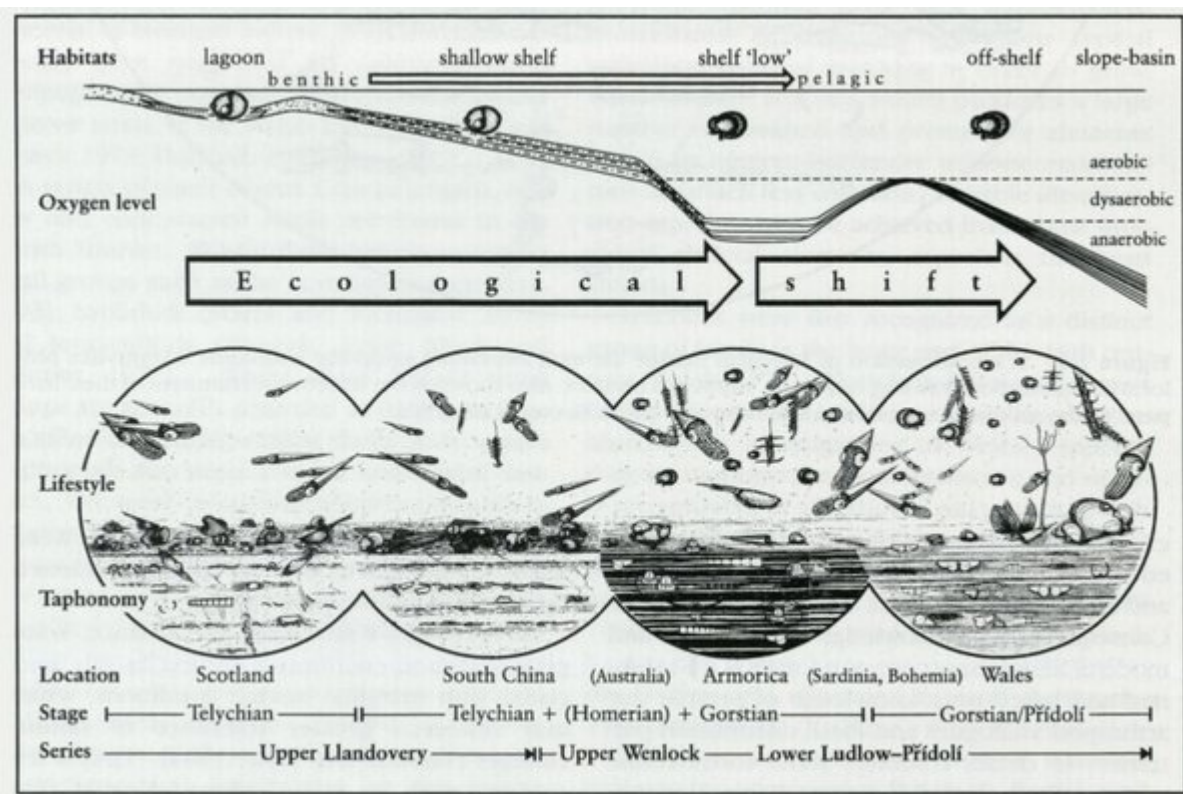
(Figure 2.15) Gastropod: *Poleumita discors*, Much Wenlock Limestone Formation, Wenlock Edge, Shropshire, x 0.5.  
(Photo: from Siveter et al., 1989.)



(Figure 2.16) The nautiloid *Polygrammoceras bullatum*, Oxford University Museum C.94., Lower Bringewood Formation, Ludlow Series, Ledbury, Herefordshire; longitudinal section, x 1. (Photo: C.H. Holland.)



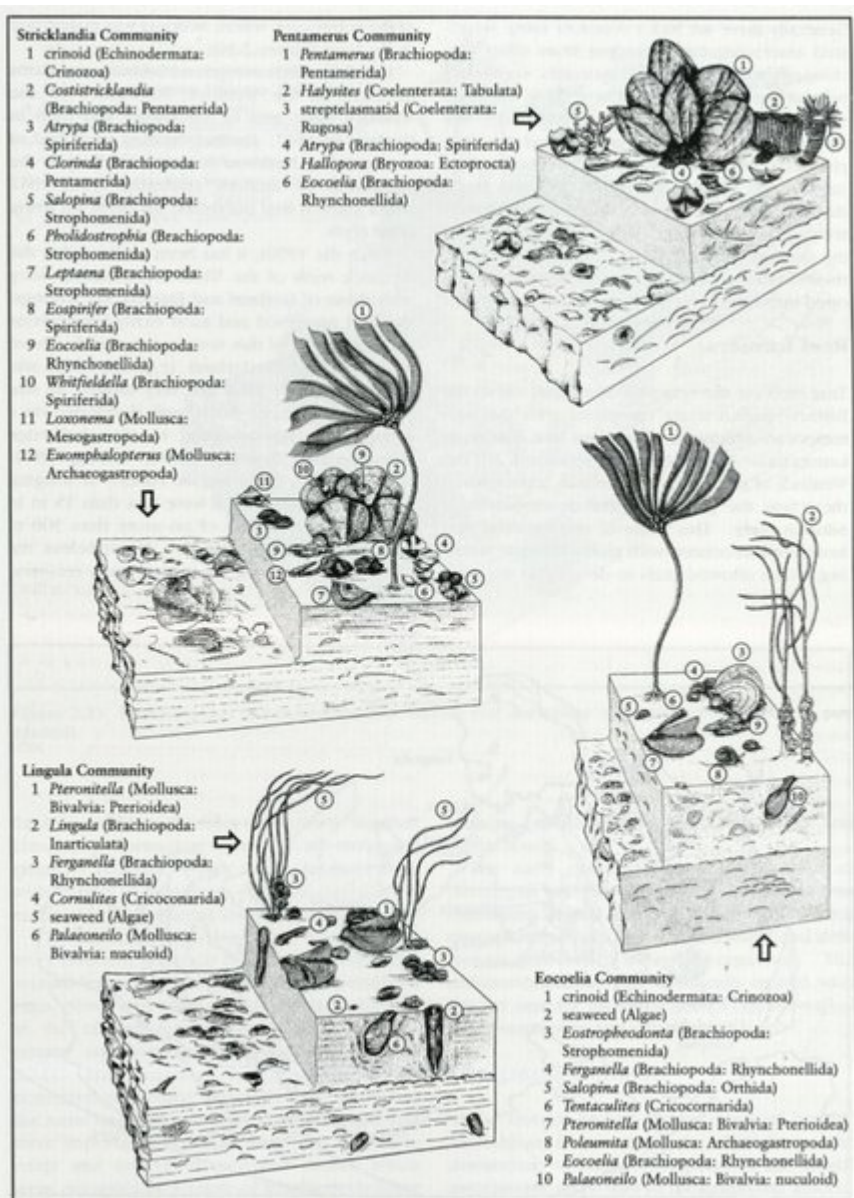
(Figure 2.17) A reconstruction of Telychian marine life with swimming squid-like nautiloids, shrimp-like phyllocarids and seabed crawling ostracods, snails and bivalves. Also shown is the selective recruitment of their hard-parts to the sediment as potential fossil remains (from Siveter et al., 1991).



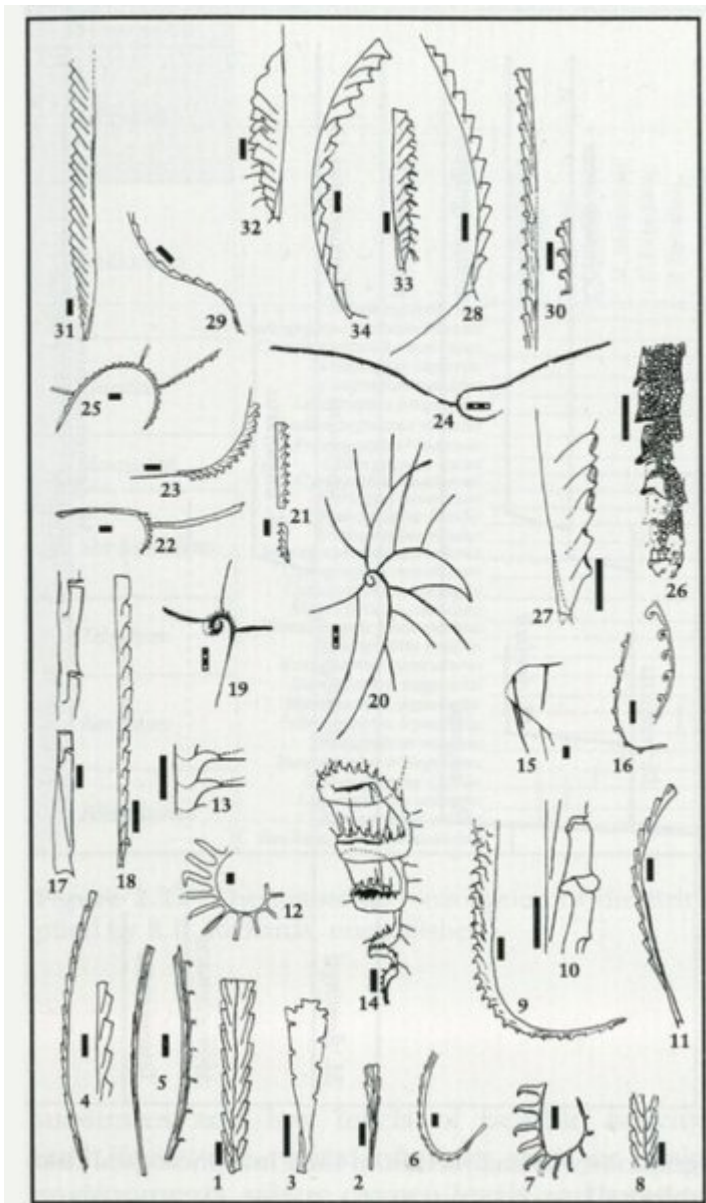
(Figure 2.18) The shift in habitats of myodocopid ostracods from benthic to pelagic through the Silurian, as reconstructed from analysis of their fossil remains in strata from Laurentia (Scotland) to Avalonia (Wales) and Gondwana (Australia and China), (from Siveter et al., 1991).



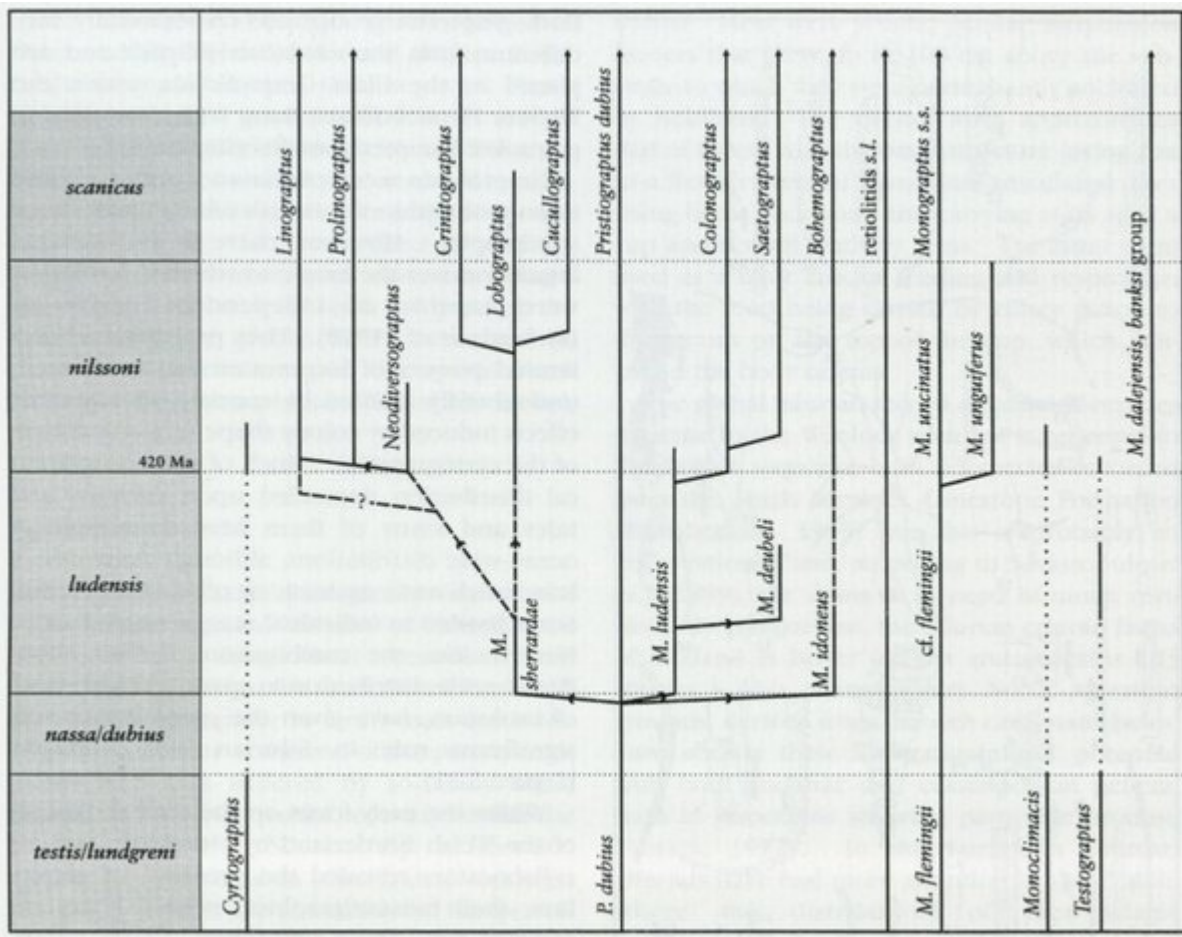
(Figure 2.19) Brachiopods. Left: *Eospirtfer radiatus*, Coalbrookdale Formation, Wenlock Series, Walsall, West Midlands; x 2. Centre: *Meristina obtusa*, Coalbrookdale Formation, Wenlock Series, Walsall, West Midlands; x 1.25. Right: *Shalleria ornatella*, Leintwardine Group, Ludlow Series, Usk district, Gwent; x 2.5. (Photos: from Siveter et al., 1989.)



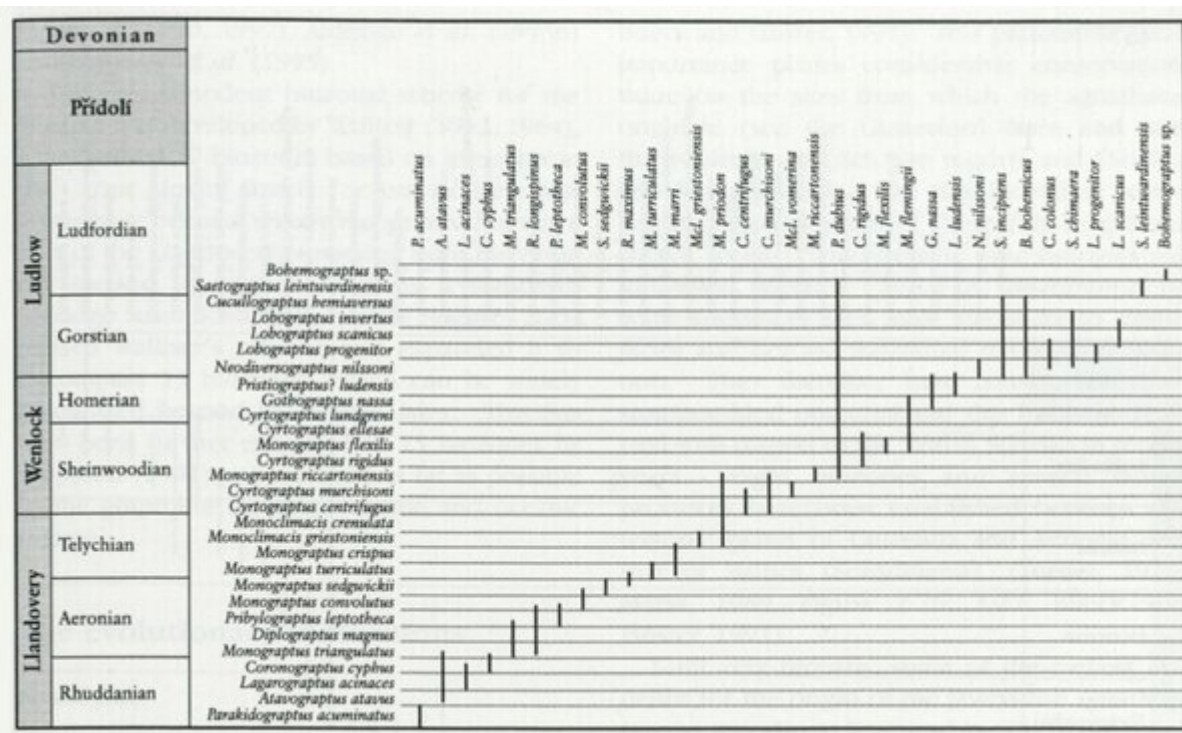
(Figure 2.29) Selected reconstructions of Silurian brachiopod dominated seabed associations from relatively shallow (*Lingula*) to deeper (*Stricklandia*) shelf seas (from McKerrow, 1978, with permission).



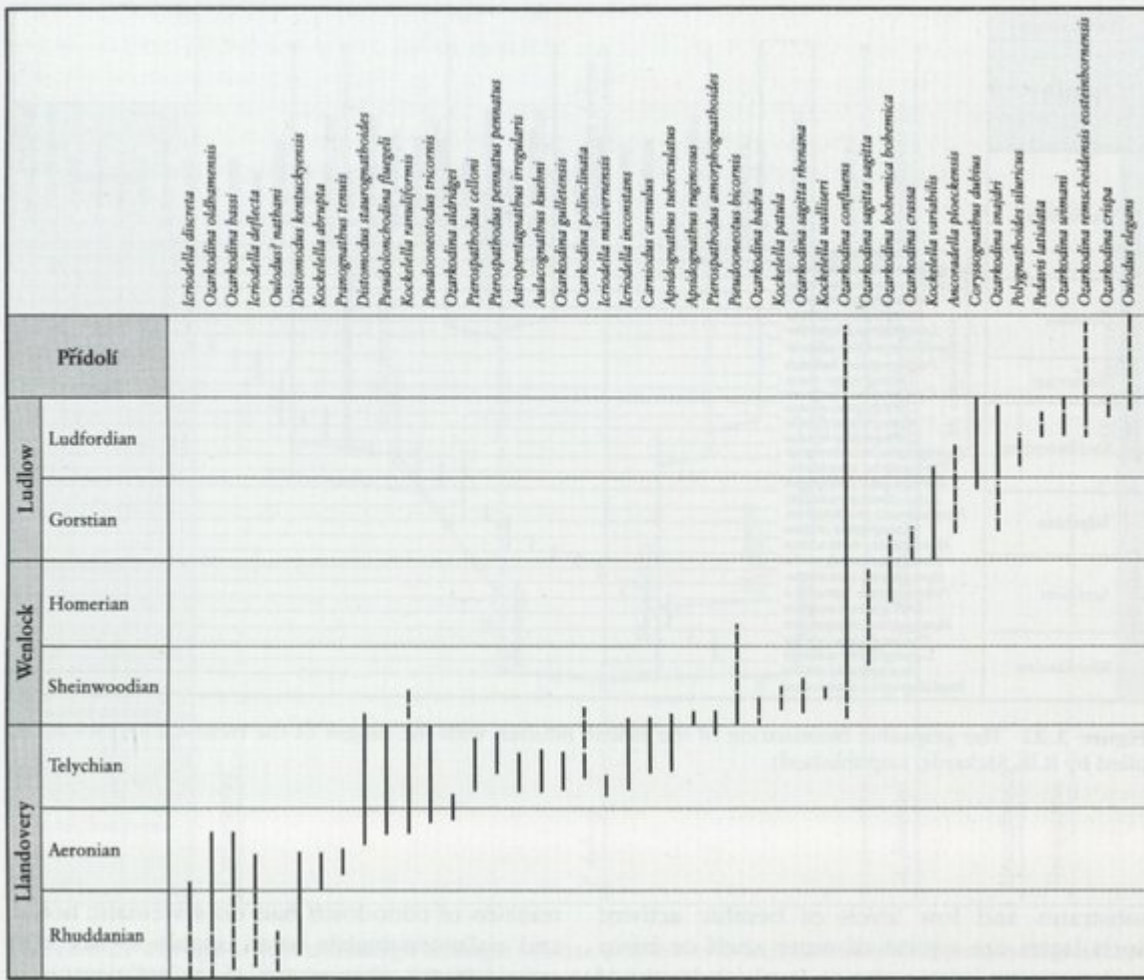
(Figure 2.20) A chronologically arranged selection (1–34) of British Silurian graptolites (broken bar 10 mm, solid bar 1 mm, open bar 0.20 mm). 1. *Glyptograptus persculptus*; 2. *Parakidograptus acuminatus*; 3. *Akidograptus ascensus*; 4. *Atavograptus atavus*; 5. *Lagarograptus acinaces*; 6. *Coronograptus cyphus*; 7. *Monograptus triangulatus*; 8. *Diplograptus magnus*; 9. *Monograptus argenteus*; 10. *Pribylograptus leptotheca*; 11. *Coronograptus gregarius*; 12. *Monograptus convolutus*; 13. *M. sedgwickii*; 14. *M. turriculatus*; 15. *Rastrites maximus*; 16. *Monograptus crispus*; 17. *Monoclimacis griestoniensis*; 18. *Monoclimacis crenulata*; 19. *Cyrtograptus centrifugus*; 20. *C. murchisoni*; 21. *Monograptus riccartonensis*; 22. *Cyrtograptus rigidus*; 23. *Monograptus flexilis*; 24. *Cyrtograptus ellesae*; 25. *C. lundgreni*; 26. *Gothograptus nassa*; 27. *Monograptus ludensis*; 28. *Neodiversograptus nilssoni*; 29. *Lobograptus progenitor*; 30. *L. scanicus*; 31. *Pristiograptus tumescens*; 32. *Saetograptus incipiens*; 33. *S. leintwardinensis*; 34. *Bohemograptus bohemicus* (after Rickards, 1989a).



(Figure 2.21) Phylogenetic relationships amongst Silurian graptolites as analysed from their morphological characteristics (from an original drawn by R.B. Rickards, unpublished).

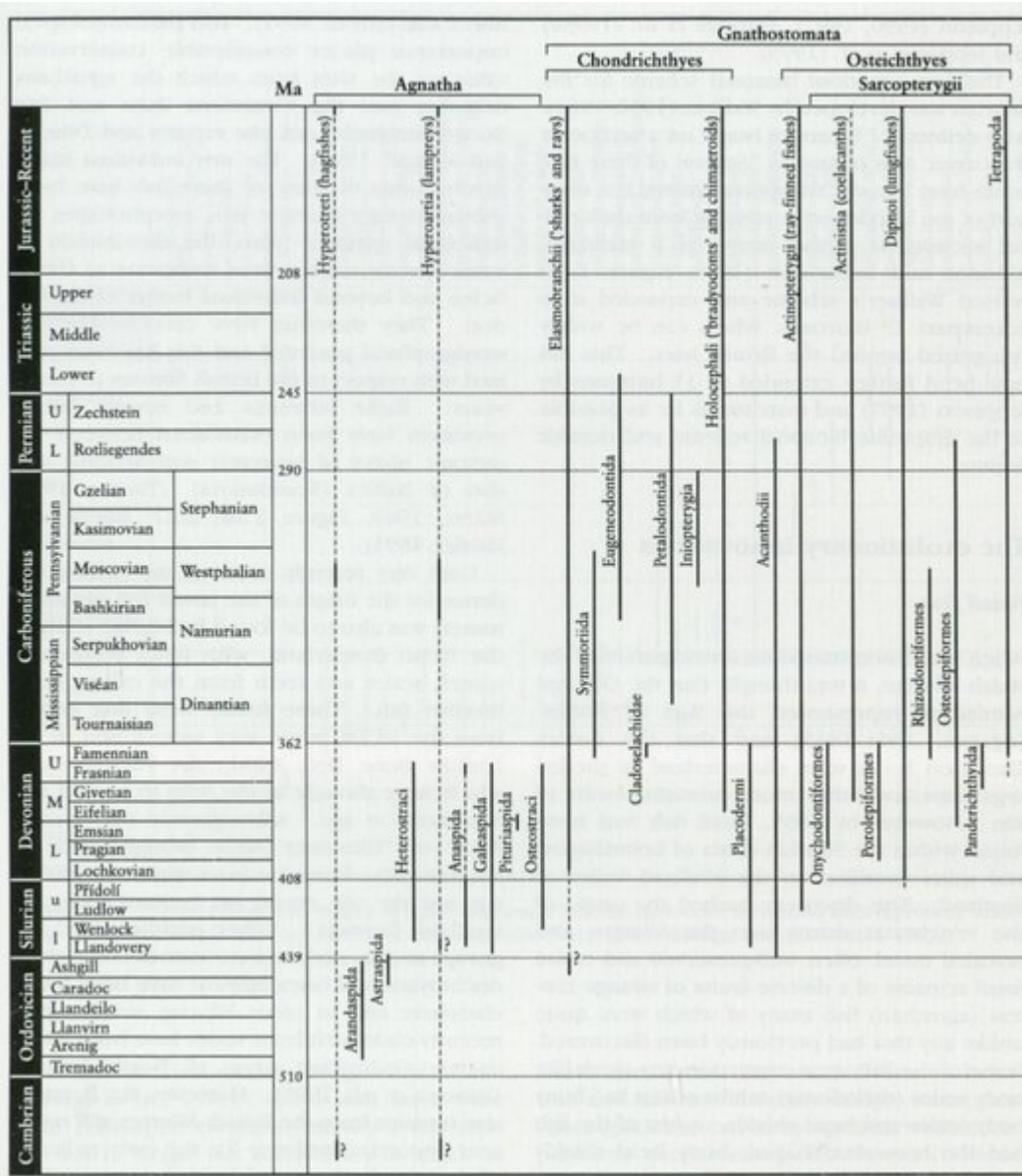


(Figure 2.22) The graptolite biozonation of the British Silurian with the ranges of the biozonal species (compiled by R.B. Rickards, unpublished).

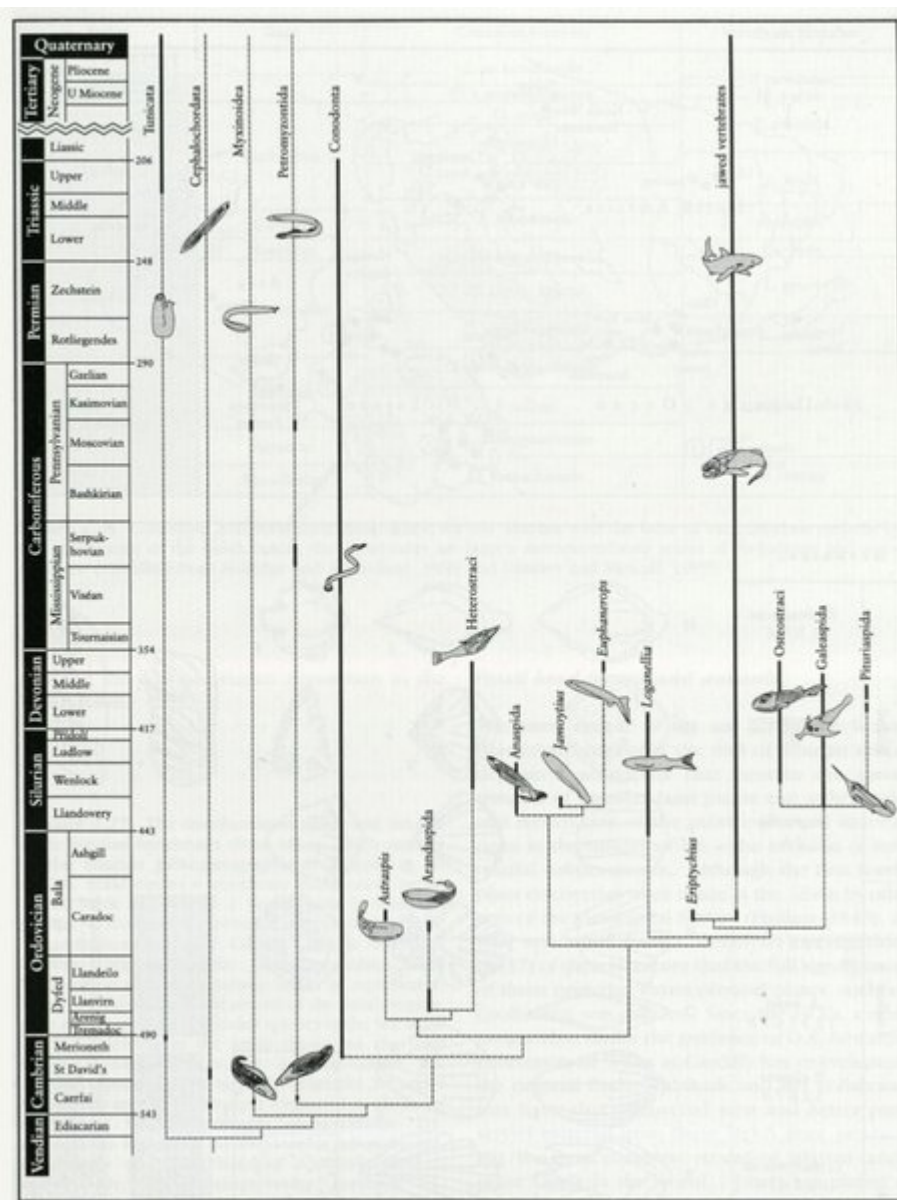


(Figure 2.23) The stratigraphical ranges of some important Silurian conodont taxa; solid bars represent British occurrences and broken bars are based on data from elsewhere (after Aldridge and Schonlaub, 1989).





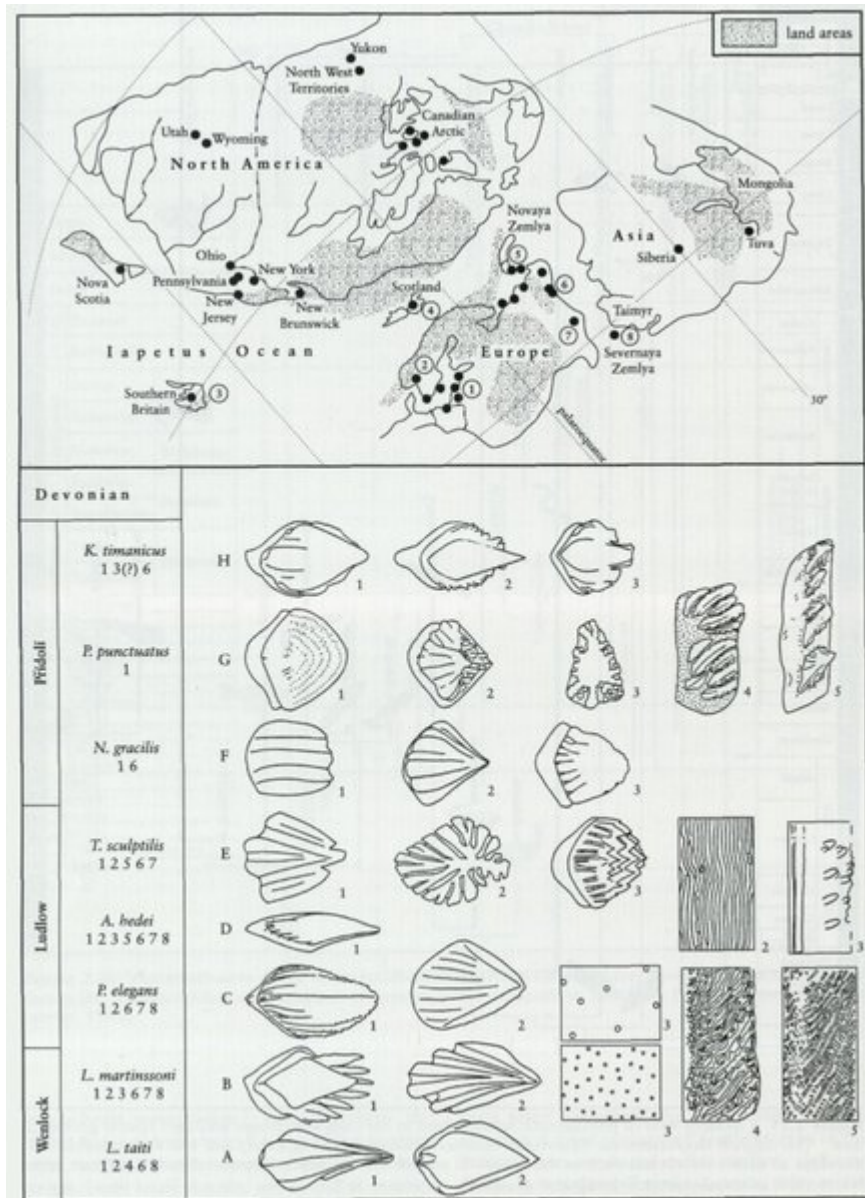
(Figure 2.24) The distribution of the major vertebrate fish groups through time, showing significant radiation during the Silurian leading to the earliest occurrence of the tetrapods in the Upper Devonian (modified from Janvier, 1996).



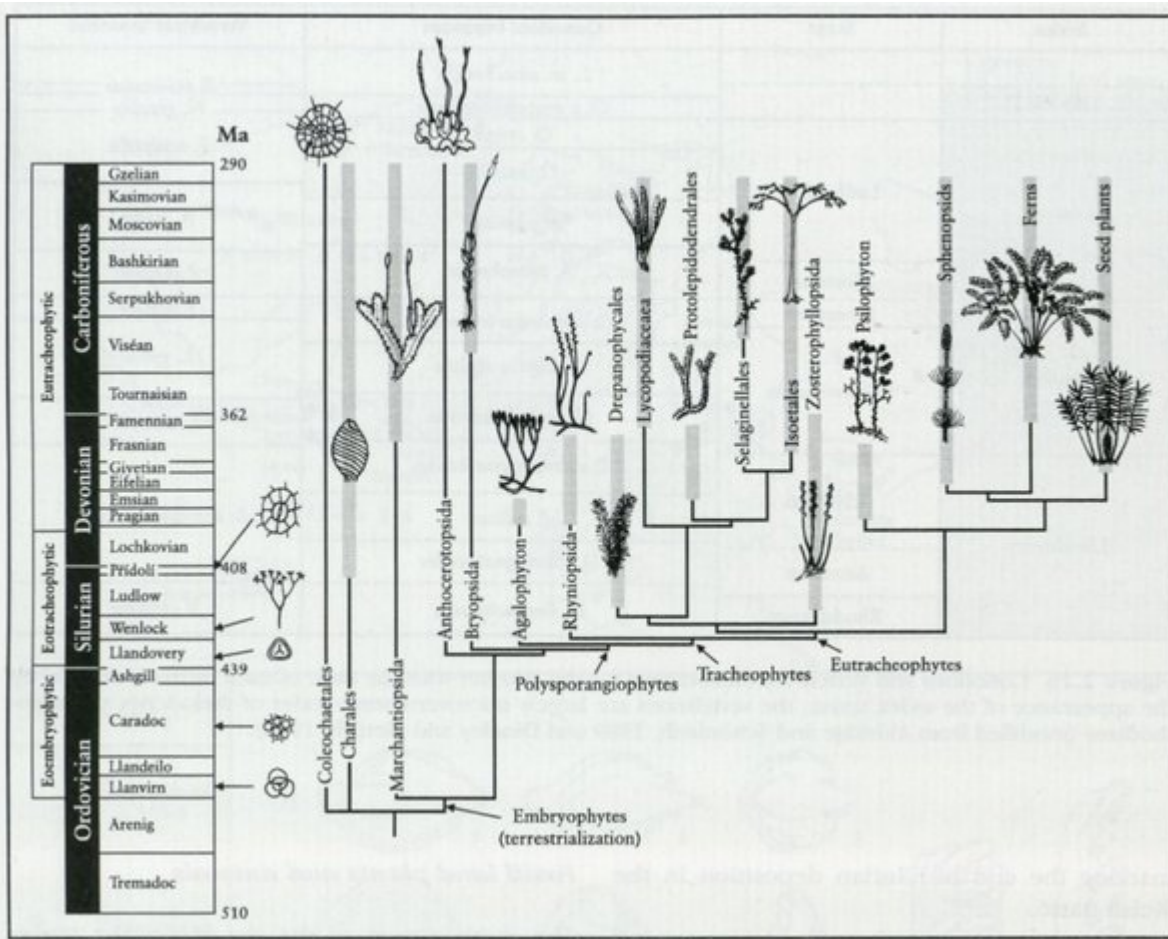
(Figure 2.25) A modern view of phylogenetic relationships in the early vertebrates arranged against geological time. The diagram emphasises the Ordovician–Silurian radiation of the agnathan fish and their possible relationships to earlier vertebrates such as the conodont animal and the newly discovered early Cambrian vertebrates (with permission from Donoghue et al., 2000).

Series	Stage	Conodont biozones	Vertebrate biozones
Pfidoli		<i>L. w. woschmidti</i>	<i>P. punctatus</i>
		<i>O. r. eosteinhornensis</i>	<i>N. gracilis</i>
Ludlow	Ludfordian	<i>O. crispa</i>	<i>T. sculptilis</i>
		<i>O. snajdri</i>	
	Gorstian Homerian	<i>P. siluricus</i>	<i>A. hedei</i>
		<i>A. ploeckensis</i>	<i>P. elegans</i>
Wenlock	Sheinwoodian	<i>O. bohemia bohemia</i>	<i>P. ornata</i>
		<i>O. sagitta sagitta</i>	<i>L. grossi</i>
		<i>O. sagitta rhenana</i>	<i>L. avonia</i>
Llandovery	Telychian	<i>P. amorphognathoides</i>	<i>L. scotica–L. sibirica</i>
		<i>P. celloni</i>	
	Aeronian Rhuddanian	<i>D. staurogathoides</i>	<i>V. cristata</i>
		<i>D. kentuckyensis</i>	

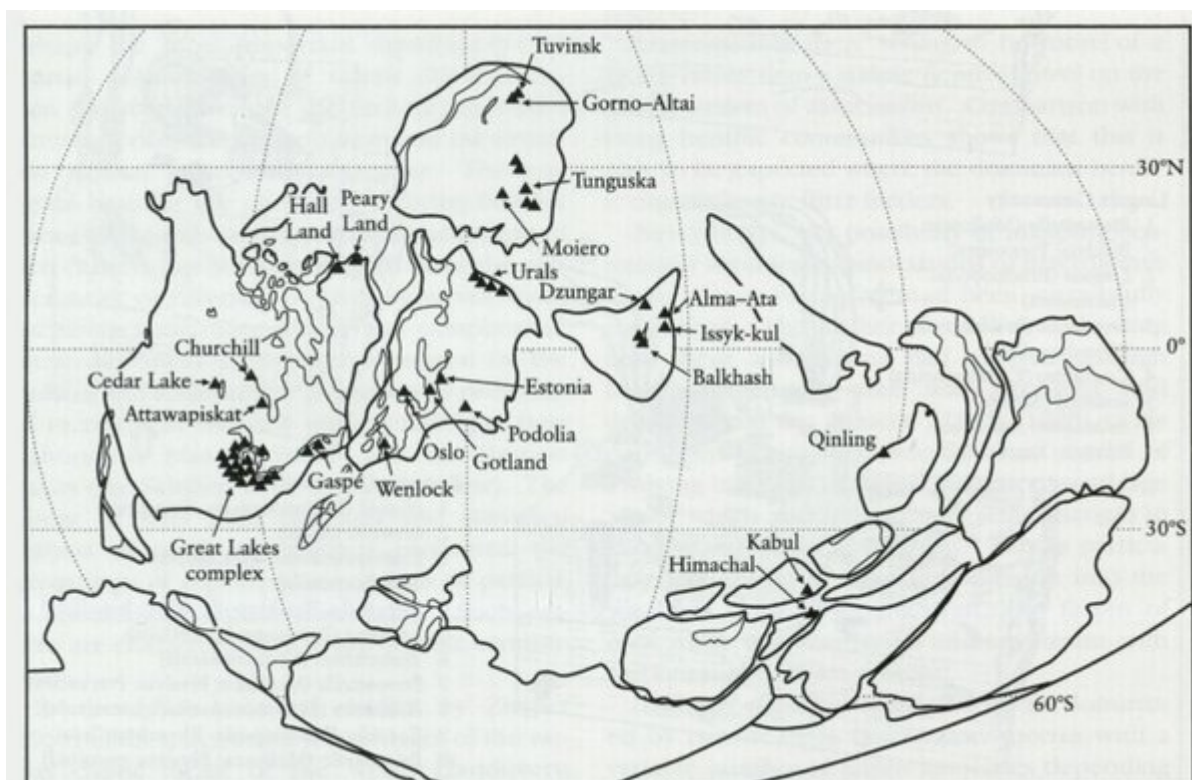
(Figure 2.26) Conodont and vertebrate biozonation for the Silurian with the base of each biozone defined by the appearance of the index taxon; the vertebrates are largely microvertebrate scales of thelodonts and acanthodians (modified from Aldridge and Schonlaub, 1989 and Dineley and Metcalf, 1999).



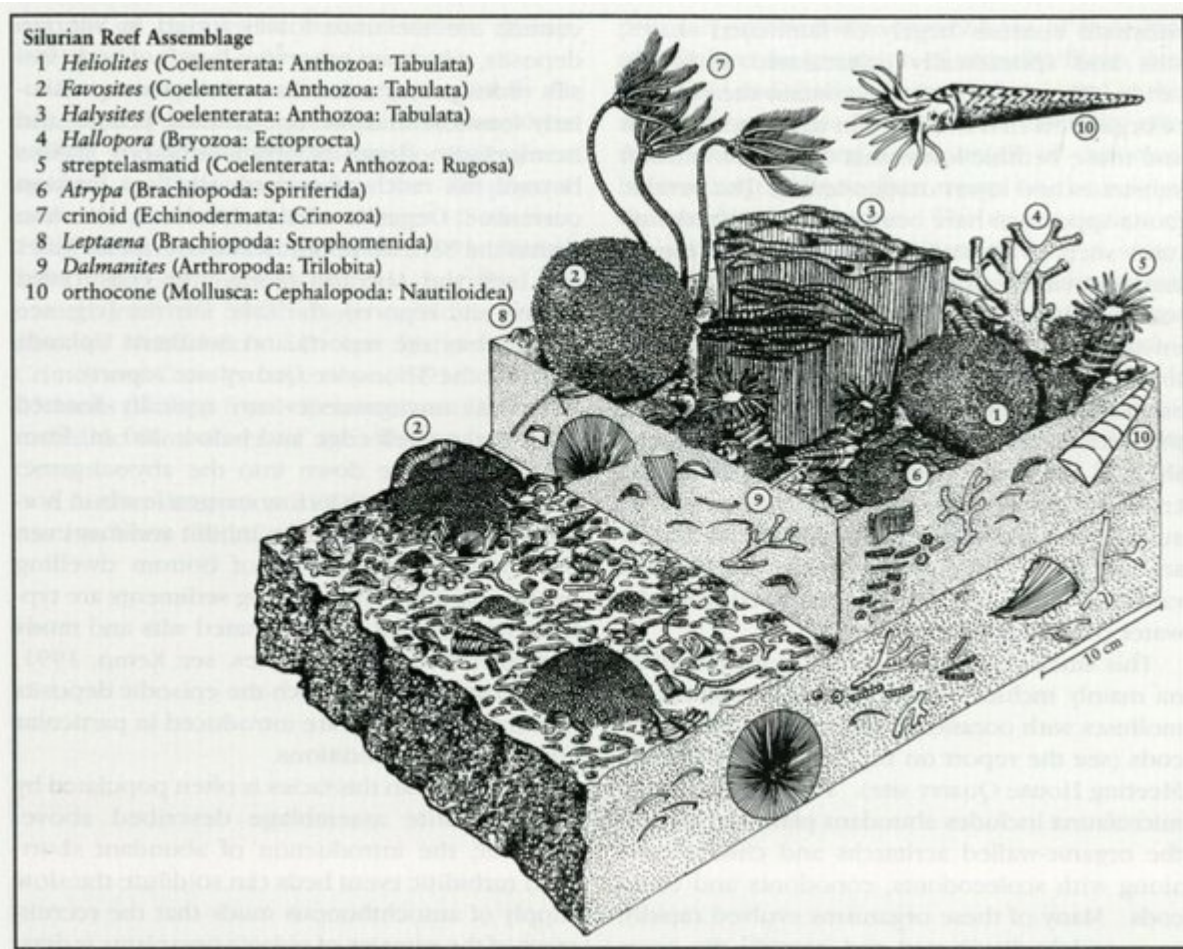
(Figure 2.27) The distribution in space and time of some Silurian vertebrates (from Märss, 1989) relative to the Silurian palaeogeography of Scotese et al. (1979). Solid circles = vertebrate distribution areas: 1. East Baltic and Poland; 2. Scandinavia; 3. Southern Britain; 4. Scotland; 5. Novaya Zemlya and Vaigach; 6. Timan–Pechora Region; 7. Central Urals; 8. Severnaya Zemlya. Stippled areas were probably land. Biozonation and characteristic scales of vertebrates, largely based on the fossil record of the Baltic region, with numbers under the index species in the left hand column referring to the areas shown on the map above. A. *Logania taiti*; B1. *L. martinssoni*; B2. *Thelodus laevis*; B3. *Tremataspis schmidtii*; B4 and 5 *Birkeniida* sp.; C1. *Phlebolepis elegans*; C2. *Thelodus carinatus*; C3. *Tremataspis mammillata*; D1. *Andreolepis hedei*; D2. *Archegonaspis schmidtii*; D3. *Birkeniida* sp.; E1. *Thelodus sculptilis*; E2. *T. admirabilis*; E3. *Poracanthodes porosus*; F1. *Nostolepis gracilis*; F2. *N. striata*; F3. *Gomphoncus sandelensis*; G1. *Poracanthodes punctatus*; G2. *Gomphoncus hoppei*; G3. *Tylodus deltoides*; G4. *Strosipherus indentatus*; G5. *Lophosteus superbus*; H1. *Katoporus timanicus*; H2. *Logania kummerowi*; H3. *Goniporus alatus*.



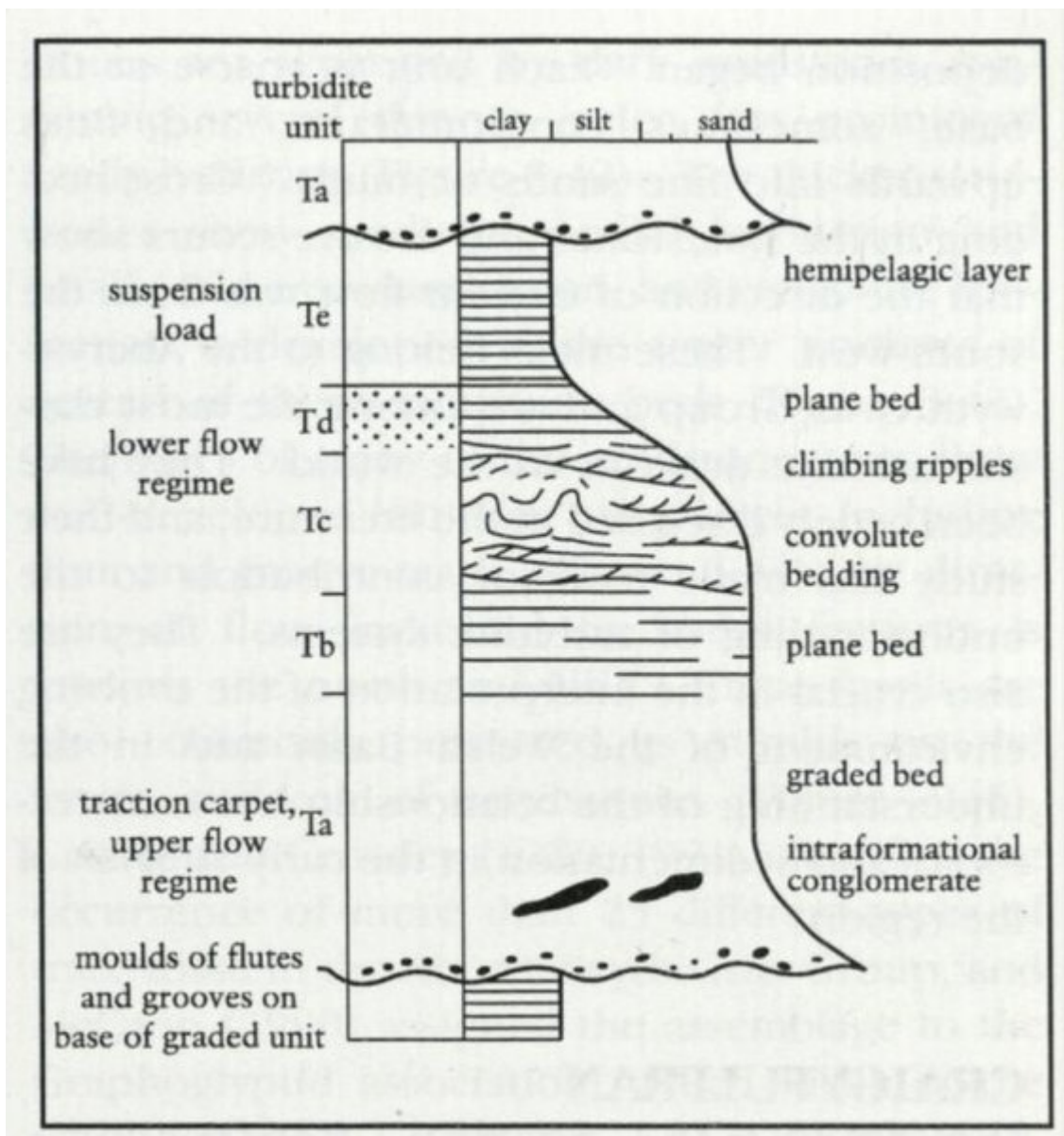
(Figure 2.28) The role of the Silurian in both the actual known and putative radiation of the Palaeozoic land plants is shown in this simplified phylogeny. The stratigraphical ranges of selected groups of land plants (thick bars) and their minimum ranges, as implied by their interrelationships, are shown (thin bars). Also illustrated are minimum age estimates for the appearance (from the bottom) of spore tetrads, cuticles, single trilete spores, megafossils and stomates (after Kenrick and Crane, 1997).



(Figure 2.30) Global distribution of Wenlock reefs related to the palaeogeography of the time (after Copper and Brunton, 1991).



(Figure 2.31) Reconstruction of a coral-dominated Silurian reef assemblage (from McKerrow, 1978, with permission).



(Figure 3.40) Idealized graphic log of the full Tabcde Bouma turbidite cycle (modified from Selley, 1978, after Bouma, 1962).