Fig. 5 Tiering history of Phanerozoic suspension-feeding echinoderms (details as in legend to Fig. 4). (From Bottjer & Ausich 1986.)

bryozoans, stelleroids, and graptolites. Much of the Ordovician radiation was among benthic epifaunal suspension feeders. During the Ordovician and through the Early Silurian the maximum level of epifaunal tiering and tiering complexity steadily increased from the low, simple tiering of the Cambrian. In the Middle Ordovician characteristic epifaunal tier subdivisions were 0 to +5, +5 to +10, and +10 to +50 cm. However, by the Middle Silurian, the maximum characteristic tier level was

one metre, and tier subdivisions were as follows: 0 to +5, +5 to +20, +20 to +50, and +50 to +100 cm. A characteristic Middle Silurian epifaunal community with maximum tiering development may have contained the following: 0 to +5 cm tier — brachiopods, bryozoans, sponges, corals, graptolites, a few bivalves, and many echinoderms; +5 to +20 cm tier — bryozoans, sponges, corals, graptolites, and many stalked echinoderms; +20 to +50 cm tier — crinoids, diploporitids, and perhaps blastoids; +50

Fig. 6 Tiering history of Phanerozoic suspension-feeding bivalves (details as in legend to Fig. 4; Actinodontoida = Modiomorphoida). (From Bottjer & Ausich 1986.)

to +100 cm tier — crinoids (see Figs 3–6) (Bottjer & Ausich 1986).

By the Middle Silurian tiering complexity stabilized and remained relatively constant until the terminal Palaeozoic extinctions. Occupation of tiers by major groups was also relatively constant until the end of the Permian. Notable exceptions were the expansion of fenestrate bryozoans during the Devonian, extinction of benthic graptolites in the Carboniferous (Fig. 4), and the gradual elimination of suspension-feeding echinoderms, except for crinoids and blastoids (Fig. 5).

Exploitation of higher tier positions is a function of growth to a larger size among individuals. However, larger size alone is not sufficient to explain the high degree of tiering complexity that characterized the epifauna of the Palaeozoic Fauna. Numerous processes were responsible for the development of

the highly structured epifaunal communities. As explained above, these include phylogenetic constraints, modes of growth, intrinsic differences between clonal and aclonal organisms, adaptation of various types of suspension feeders to life in the benthic boundary layer, and competition for food and space from which to feed (Bottjer & Ausich 1986). At the close of the Palaeozoic, tiering complexity and heights must have been drastically reduced due to mass extinction (Section 2.13.4). This presumption is based on the observed faunal reductions, although a precise morphological record of this tiering decline has not been documented.

Infaunal tiering complexity of suspension feeders developed more slowly than for epifauna. During the Cambrian −6 cm was the characteristic maximum depth, and this increased to −12 cm by at least the Early Ordovician. Consequently infaunal tier subdivisions were 0 to −6 cm and −6 to −12 cm by the Early Ordovician, and this structure persisted until the Lower Carboniferous. Bivalves and brachiopods were typical inhabitants of the 0 to −6 cm tier in the Ordovician, and trace fossil evidence forms the basis for indicating the presence of the −6 to −12 cm tier at this time (Bottjer & Ausich 1986). Bivalves began to occupy the −6 and −12 cm tier at the beginning of the Devonian, which coincides with increased levels of durophagous predation. Increased predation pressures also may have been responsible for the development of a −12 to −100 cm tier that began during the Lower Carboniferous. Both bivalves and trace fossils record the development of deep tier feeders in the Late Palaeozoic.

A detailed tiering history of post-Cambrian Palaeozoic deposit feeders is not available, therefore details of the early radiation are not known. By at least the Silurian, infaunal deposit feeding bivalves had apparently developed a tiering structure through at least the 0 to −6 cm level (Levinton & Bambach 1975). The tiering structure of Silurian deposit feeding bivalves was comparable to similar living bivalve communities (Levinton & Bambach 1975). If *Thalassinoides* in western U.S.A. Ordovician carbonate shelf deposits was made by deposit feeders, and if it can be considered to be characteristic for this time, then deposit feeder tiering in environments below fairweather wave base may have reached depths of −1 m early in the development of the Palaeozoic fauna (Bottjer and Ausich 1986).

Whereas mass extinction at the close of the Palaeozoic (Section 2.13.4) greatly affected epifaunal

organisms and the tiering structure of epifaunal suspension feeders, infaunal suspension feeders were relatively unaffected. No change in tiering structure is apparent in the record of infaunal suspension feeders between the Permian and Triassic.

Modern Fauna. The Modern Fauna, characteristic of the Mesozoic and Cenozoic, has been dominated by the following benthos: bivalves, gastropods, gymnolaemates, malacostracans, demosponges, rhizopods, and echinoids (Sepkoski 1984; Section 1.6). Immediately following the terminal Palaeozoic extinction, epifaunal suspension feeder tier levels were significantly reduced, but infaunal suspension feeder tiers were not. However, by the Middle Triassic, tier heights and complexity were restored to Middle Palaeozoic levels (see Fig. 3). Again, crinoids with 100 cm stems were present in shallow-water settings. Probably the same suite of processes and constraints that was responsible for the development of epifaunal tiering in the Palaeozoic was involved in its re-establishment during the early Mesozoic. A typical Jurassic suspension feeding community may have been composed of the following epifaunal organisms: 0 to +5 cm tier — brachiopods, bryozoans, bivalves, sponges, corals and crinoids; +5 to +20 cm tier — sponges, bryozoans, alcyonarians, and crinoids; +20 to +50 cm tier — crinoids, sponges, and alcyonarians; +50 to +100 cm tier — crinoids. Infaunal suspension feeding organisms included a variety of bivalves (Fig. 6), gastropods, and worms and crustaceans as indicated by trace fossils (Bottjer & Ausich 1986). Deposit feeders at this time apparently existed in a tiered structure (e.g. Wetzel & Aigner 1986), but in general the tiering structure for this trophic group has not been documented for the Mesozoic.

This well developed infaunal and epifaunal suspension feeder tiering complexity only lasted for approximately 100 million years. By the Cretaceous, stalked crinoids were absent from shallow-water benthic habitats, and the maximum characteristic tier height was reduced from +100 to approximately +50 cm. Displacement of stalked crinoids to deeper-water settings was a gradual process that may have been the result of increased levels of predation in the later Mesozoic (Bottjer & Ausich 1986). Since the beginning of the Cretaceous, epifaunal suspension feeders typically have not been important in soft substrata settings. Both infaunal and epifaunal suspension feeder tiering structure were relatively unaffected by the terminal Mesozoic extinction.

Post-Jurassic benthic communities in shallow-water soft substrata settings have been dominated by infauna. This basic organization has remained relatively constant for *c.* 140 million years. A characteristic Neogene community with maximum development of suspension feeder epifaunal tiering would include the following: 0 to +5 cm tier — bryozoans, bivalves, sponges and corals; +5 to +20 cm tier — bryozoans, sponges, alcyonarians; and +20 to +50 cm tier — sponges, alcyonarians. Characteristic infaunal suspension feeding organisms would include, as for the Mesozoic, a variety of bivalves (Fig. 6), gastropods, and worms and crustaceans as indicated by trace fossils (Bottjer & Ausich 1986). Deposit feeders had a tiered structure during this time in related environments (e.g. Savrda & Bottjer 1986), but, as for the Mesozoic, tiering structure for this trophic group has not been documented for the Cenozoic.

Conclusion

Examination of the fossil record for trends in tiering provides a means of tracing patterns of ecological structure independently of enumerations of taxa. Only the Phanerozoic history of suspension feeding palaeocommunities from below fairweather wave base continental shelf and epicontinental sea environments is relatively well known. However, some general contrasts between infaunal and epifaunal tiering in Vendian−Recent settings can be noted. Infaunal tiering, from the beginning, has had a history of slow but steady increase in complexity through attainment of greater burrowing depths and development of additional tiers. In contrast, if the height distinction among members of the Vendian Fauna reflects epifaunal tiering, it records the first of three periods of development of epifaunal tiering which were followed by reduction. These differences in tiering history may indicate a relatively greater resistance of the infaunal habitat to pertubations in ecological as well as evolutionary time.

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1.7.2 Plankton

R. B. RICKARDS

Introduction

The origin and early diversification of the Earth's plankton is largely shrouded in mystery, hypotheses leaning heavily upon a rather meagre fossil record and what seems like reasonable supposition. Consider briefly the two main periods to be discussed: the Vendian and the Lower Palaeozoic. Research workers dealing with Vendian fossils have been concerned, to a large extent, with establishing that they *are* fossils, and much less concerned with major ecological niches. Those organisms that give least trouble with respect to identity, such as stromatolites or trace fossils, are also the most obvious as regards mode of life. The more problematic creatures may yet have greater scope for the current objective, namely indicating the origin and defining the nature of early plankton. By contrast, the real problem in the Lower Palaeozoic lies in deducing the composition of the plankton and the relative importance

and functions of those components. Bulman (1964) gave a broad-based review of Lower Palaeozoic plankton: the improvements in our knowledge since then are considered below.

The Vendian

The general aspect of Precambrian fossil life is not today in much dispute (Sections 1.2, 1.3). Blue-green 'algae' (cyanobacteria or cyanophytes), the earliest proven life form, occurred at 3500 Ma and continue today. Grouped with early, reducing bacteria they comprise the Monera. The fossil record of the bacteria is less satisfactory, but stalked representatives may have been involved in the creation of the banded iron formations, and it seems possible that purple and green bacteria were involved with the earliest stromatolites. The question is, which prokaryotes, which Monera, could have comprised an early plankton? It is not sufficient to note that carbon isotope ratios of Precambrian black shales and dark limestones indicate an organic origin for the carbon: that merely begs the question, as well as hiding the implication that such organic carbon must be of planktic ('algal') origin. Berry & Wilde (1983) suggested that an Archaean anoxic ocean would have had similar conditions to present day deep ocean vents, and that early carbon-fixing could have been by chemautotrophic bacteria using geothermal H_2S as their primary energy source (*Anoxium*). Peripheral isolates in *Anoxium* populations probably would have evolved to take photic energy from sunlight, because they would have been disadvantaged in the competition for reduced sulphur. Berry & Wilde (1983) also support the contention that the carbon cycle was effectively stabilized by 3700 Ma (i.e. in pre-Isua time). Their first plankton would be *Anoxium* isolates at the ocean surface, developing the ability to use light as an energy source, and occupying similar ecological niches to modern purple and green bacteria.

Blue-green algae share the ability with bacteria to fix their own nitrogen. They are resistant to high and low temperatures, and to dessication, and operate best in neutral to alkaline systems. Further, phycocyanin can work in very low light (it is sensitive to blue light) and in consequence confers viability to depths of 1000 m and more. The modern blue-green *Trichodesmium* exhibits gas vacuolation, the considerable vesicular strength of which causes it to sacrifice some control of vertical mobility. In general modern blue-greens lack buoyancy control and the open ocean is considered too turbulent for

their survival. The possibility that part of the development of *Trichodesmium* occurs in a benthic environment may also be of adaptive significance. It is clear from this that *Trichodesmium*-like blue-greens in Archaean oceans would have found conditions to their liking if deductions concerning the nature of those oceans are correct; and it may partly explain the converse, that in today's oceans, despite such seeming flexibility, blue-greens are not common. (There are, however, difficulties in identifying them in plankton samples, unless epifluorescence techniques are used, when blue-greens fluoresce a distinctive orange.)

Schopf (1976) has disputed the true fossil nature of many of the claimed Archaean microfossils, but it is widely accepted that the 3200–3100 Ma *Archaeosphaeroides* (from the Onverwacht and Fig Tree Cherts) is a coccoid cyanophyte (e.g. Brasier 1979), as is *Huroniospora*. However, if these are truly chroococcales, then it should be noted that extant species do not fix nitrogen. By 2000 Ma (early Proterozoic; Aphebian) oscillatoriacids and notocacids may well be represented. Possible Riphean microfossils, which might be planktic, are almost equally contentious, but the chlorophycid *Eosphaera* from the Gunflint Chert was a *Volvox*-like green algal colony, and the prasinophycid *Tasmanites* a 100–700 μm globular form with uninucleate cells. Thus the eukaryotes were probably represented in Riphean plankton. It is generally assumed that bacteria in general preceded cyanophytes, and that some of these could have been planktic and bacillus-like.

Glaessner (1984), in his wide-ranging review of the Ediacarian fossils (Sections 1.3, 1.5), concluded that the coelomate radiation must have been pre-Ediacarian (Varangerian), and that a change from zooplankton to benthos preceded the coelomate radiation itself. This implies the existence of zooplankton in the Varangerian or earlier. Protists certainly could have been present: the Pyrrophytes begin with *Arpylorus* in the Silurian, but non-tabulate forms could have occurred in profusion in the late Precambrian. Other records of Precambrian plankton include the acritarches, some of which may have been spores of multicellular algae.

Acritarch occurrences in the upper Riphean to latest Precambrian have been widely documented (e.g. Vidal & Knoll 1983). The evidence suggests that there was a gradual rise in the number of taxa from about 1400–900 Ma, followed by a peak and decline in the late Varangerian and Valdaian: this late Precambrian extinction event was a prelude to a

spectacular Cambrian diversity increase, to at least twice that of the lowest Vendian. In terms of Vendian palaeoecology there was a recognizable division into lower diversity planktic assemblages in inshore environments, and higher diversity communities in offshore shelf regions or open shelf regions.

With the onset of Ediacarian time, in addition to the many benthic forms, there were undoubted medusoids. These included the chondrophorans, stiff-walled medusoids, floating at the surface and exploiting a phototrophic plankton. According to Glaessner (1984), their presence indicates that an ozone layer was then developed and that the ocean was of normal salinity and warmth. A lack of macrophagous predators may account for size increases in the zooplankton, with some medusae reaching 1 m. This model is apparently compatible with a progressive ventilation of the oceans (Berry and Wilde 1983), because Glaessner refers only to the surface layers, or to shallow shelf water bodies, which could be almost normal, tropical, oxygenated marine bodies.

The sequence of events in the evolution of plankton in the Precambrian was probably as follows (Fig. 1):

1 Chemautotrophic *Anoxium* at outgassing submarine geothermal vents before 3700 Ma. Such 'plankton' would have been local in distribution, above the vents?

2 *Anoxium* isolates began to use light energy, 3700–3500 Ma (and later?).

3 Late Archaean: *Archaeosphaeroides* and *Huroniospora* together with bacillus-like and other bacteria, to about 2500 Ma.

4 Early Proterozoic (Aphebian): oscillatoriacids and notocarids around 2000 Ma, with presumably more varied changes to eukaryotic microplankton.

5 Riphean: green algae well developed.

6 Varangerian: presumably development of zooplankton.

7 Ediacarian: planktic medusae, often of large size; still no macrophagous predators.

The Lower Palaeozoic

The Cambrian is typified by a dramatic diversity increase, mirroring that in the coeval benthos (Sections 1.5, 1.6). The very earliest chrysophytes may have occurred at this time, an additional phytoplankton component, though these are typically post-Palaeozoic. Radiolarians were present in the Cambrian and equatorial in their distribution.
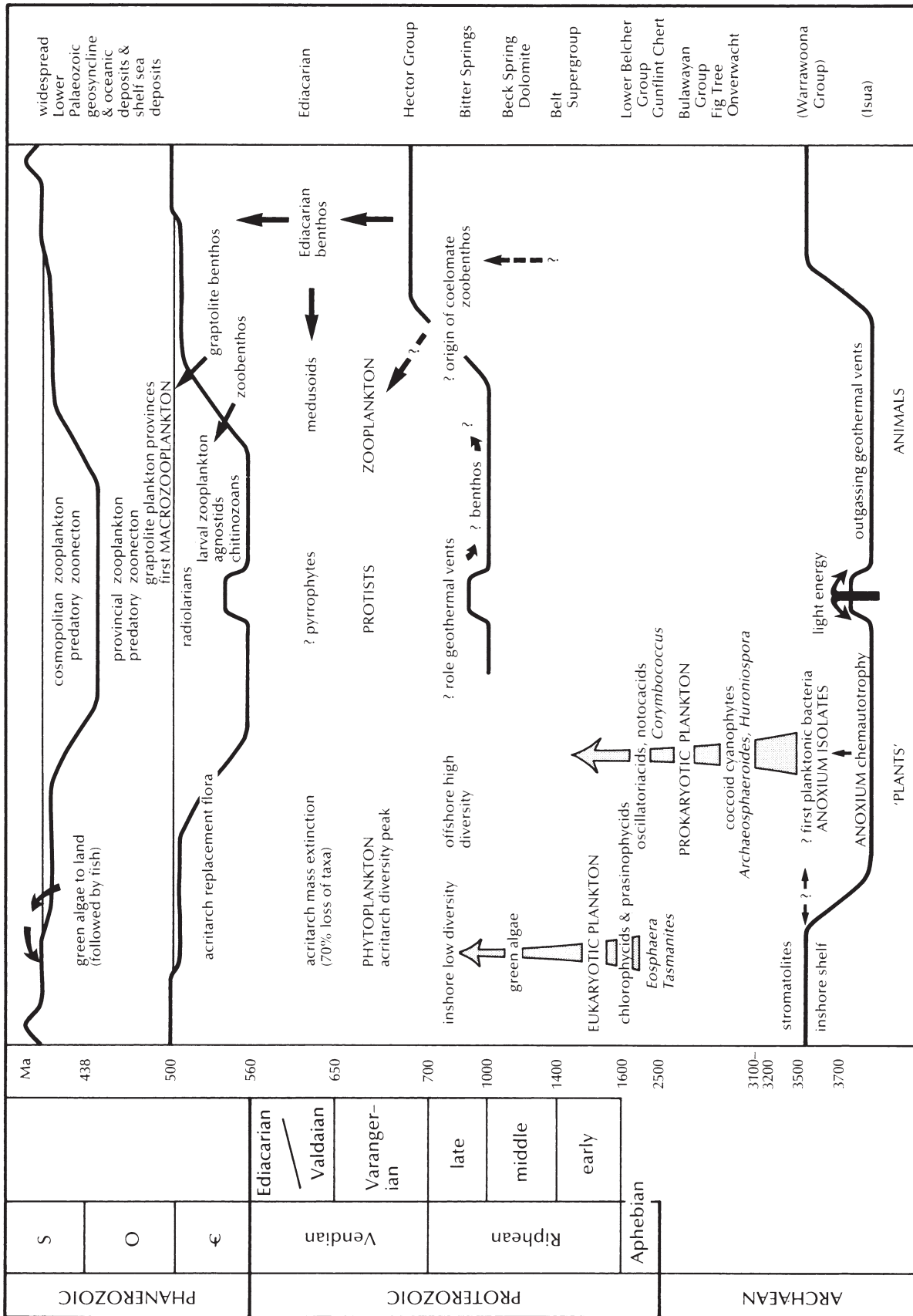
Fig. 1 Time and place in the origin and broad evolution of plankton. Inshore, shelf and slope environments are indicated diagrammatically to the left and right of the main part of the figure; narrowing oceans are suggested from the Cambrian to the Silurian; main depositories of the plankton record are shown in the right hand column and approximate time correlations to the left of the figure. The position of the Warrawoona and Isua rocks are shown in parentheses.

Foraminifera, by contrast, were almost wholly benthic throughout the Lower Palaeozoic. Larval stages (including giant larvae) of most benthic organisms were of increasing importance in the plankton, though of immeasurable proportions. One of the major components was the pelagic agnostid trilobites whose entire life cycle would have been enacted in the upper layers of the ocean. Further, there have been convincing arguments for a pelagic component in such faunas as the Burgess Shale (Section 3.11.2) indicating the presence of a soft-bodied pelagic element. In the Cambrian there is still no direct evidence of planktic macrophagous predators, and the mix must have been composed essentially of most of the above phytoplankton groups with an increasingly diverse zooplankton.

Several very major changes took place at the beginning of the Ordovician. It is clear that acritarchs became an important constituent, with a major diversity peak spanning the Ordovician–Devonian periods: in some Silurian series over 2000 species have been identified in relatively small geographical regions. Radiolarians are extremely abundant in some offshore shelf graptolitic deposits (in modern tropical planktic environments they may number in excess of 80 000 individuals per m^3). The Chitinozoa, although occurring in the Cambrian, have dramatic peaks of abundance and diversity in the Ordovician and Silurian. Their occurrence in both species diversity and facies type matches that of the graptoloids, which were undoubtedly planktic. Chitinozoans are presumed egg capsules of metazoans, which may not necessarily have been plankton themselves.

The planktic graptoloids arose from benthic forms in the earliest Ordovician, showed considerable evolutionary development, and achieved large rhabdosomal size (approaching or exceeding 1 m in several species). It is probable that they were the first abundant macrozooplankton, and their food was almost certainly minute phyto- and zooplankton. Huge numbers are preserved in black shale formations where they are often associated with sponge spicules and what may be epiplanktic bivalves and brachiopods. There is, in addition, an increasing number of nektic elements, such as cephalopods and trilobites, yet still few large predators in the *planktic* environment: orthocone cephalopods probably constituted the most important groups of (nektic) large predators. The graptoloids, associated closely with a vastly abundant algal phytoplankton (represented by the high carbon component of the black graptolitic shale), appear

to have dominated the Ordovician and Silurian planktic environment, but their large size may give a misleading impression of relative abundances and proportions within the plankton at the time. An understanding of the ecological diversity of graptoloids is still at an early stage (Rickards 1975). They may have used gas vacuoles to control their depth within the photic zone. Other specialized features such as nemata, 'floats', vanes, webs, thecal spinosity, rhabdosomal stabilizers, and overall rhabdosomal shapes may have been designed for particular hydrodynamic roles in the plankton.

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1.7.3 Reefs

C. T. SCRUTTON

Introduction

Fully diversified, large scale, shelf to shelf-edge, wave-resistant organic structures like the Great Barrier Reef represent the end member of an evolutionary continuum of ecosystems from small, simple, and local communities of benthic organisms. They are well developed when suitable constructors are available and poorly developed otherwise. Following important extinction events, re-establishment of major reef tracts lags behind the restructuring of level bottom communities, presumably

reflecting not only the availability of suitable constructors but the evolution of the more complex community structure associated with successful reef-building associations. Biostromes and bioherms are respectively sheet-like and mound-like structures dominated by skeletal organisms and either may occur in isolation or as component parts of fully differentiated reef complexes. Build-ups are any accumulations of carbonate sediment with topographic relief on the sea floor (see discussion in Heckel 1974).

The Precambrian

Reefs extend well back into the Precambrian (Copper 1974; Heckel 1974; James 1983). The earliest unquestioned stromatolites (see also Section 1.2) are from the Fig Tree Group of the Barberton Mountain Land, South Africa, 3300—3500 Ma. They are regarded as the product of a photoresponsive microbial community in a shallow, evaporitic environment, and associated microfossils include filamentous forms. There is no certainty that the microbes are true cyanobacteria but already a range of stromatolitic forms from linked domes to pseudocolumns is present. The stromatolitic carbonate ecosystem became widespread some 2500—2300 Ma (Fig. 1). Our knowledge of the evolution of the microbial communities responsible is vague but increasing. Most were probably eubacteria, but true cyanobacteria may not be very old. Eighteen morphotypes are known from the 1600—2000 Ma Gunflint Chert in Canada; most are of blue-green appearance but many are of unknown affinity. In Australia, the 1600 Ma Paradise Creek microbiota is morphologically comparable, and the 800—1000 Ma Bitter Springs community is extremely similar to that of modern stromatolite communities (Walter 1976).

Early Proterozoic stromatolites ranged from nonmarine to deeper-water environments. Extensive shelf biostromes, mainly of linked domes, grade into shelf-break bioherms with several metres relief of branching columnar morphs in the Slave Province of Canada. Individual build-ups reach 100 m diameter and 20 m thickness. They are cut by channels draining the shelf and die out rapidly down slope into the basin. Although extremely simple ecosystems, these are regarded as positionally and functionally comparable to modern reef ecosystems. Elsewhere stromatolitic masses on Proterozoic shelves < 60 m thick and 1—2 km long are reported. Precambrian stromatolites tend to be larger than
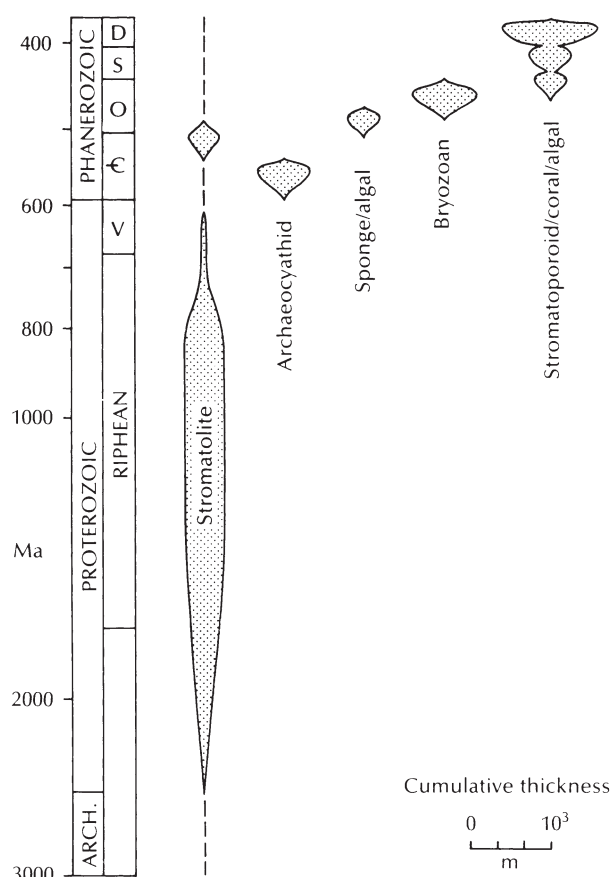

Fig. 1 Distribution in time of the major reef building biotas of the Precambrian and Early Phanerozoic.

Phanerozoic examples, and up to the early Palaeozoic, tall, narrow, erect, branched columnar morphologies dominated. This is in contrast to the broader unbranched forms which subsequently dominated. Columnar stromatolite diversity increased up to the Middle—Late Riphean but a sharp decline in abundance and diversity set in about 800 Ma.

With the earliest claimed eukaryote being from the 1200—1400 Ma Beck Springs Dolomite of California, and traces of metazoans, although poorly documented and often doubtful, known from about 1000 Ma, the decline in stromatolite build-ups seems likely to reflect the rise of grazing heterotrophs. However, Copper (1974) pointed out that the first well preserved metazoans of the Ediacara fauna (Sections 1.3, 1.5) appeared not to include algal grazers, although this fauna was not recovered from carbonate facies. He timed the decline of stromatolites as slightly later and implicated the widespread 675—570 Ma Late Precambrian glaciation.

The Cambrian

The first metazoan reefs date from the earliest Cambrian. In clastic facies, skolithid reefs are common world-wide. They form extensive masses of agglutinated sand grains, an early equivalent of modern sabellid buildups, < 80 cm thick and hundreds of kilometres long as fringing reefs in the breaker zone cut by surge channels. Accumulated thicknesses of skolithid sands often precede the first development of archaeocyathid reefs in the Lower Cambrian, the earliest of all skeletal framework reefs. Archaeocyathids, with small, usually cup-shaped, mainly solitary, porous carbonate skeletons, have been considered a distinct phylum but modern opinion tends to favour their classification as a subgroup of the Porifera. They form mainly small patch reefs, mostly < 3 m thick and 10−30 m in diameter, although larger fringing or barrier reefs are claimed in the later Lower Cambrian with accumulated thicknesses < 100 m.

Bioherms are dominated by three to four structurally different genera, some rooted and functioning principally as bafflers. *Renalcis*, *Epiphyton* and *Girvanella* are frequently associated as overgrowths and may form the bulk of the skeletal material. About 30−50% of the build-up is fine carbonate mud with some bioclastic debris, little pore space, and few cavities. There may be pockets or lenses of shelly material but generally fauna of the adjacent facies is rare. There is no evidence of biological destruction by borers or grazers.

No obvious reef zonation is reported for archaeocyathid build-ups. They are the first of a range of skeletal organisms to form patch colonizations of the sea floor with minor relief, which persist in time to form biohermal masses in the rock record. They declined at the end of the Lower Cambrian and became extinct in the early Middle Cambrian, initiating a period which, in the absence of suitable skeletal organisms, lacked significant reef growth. Algal stromatolite build-ups made a brief comeback, possibly with a decline in grazers, as gastropods are scarce in the later Cambrian (Copper 1974). Lithistid sponges occur in some of these stromatolite masses and skeletal algae are not uncommon. Stromatolite build-ups with or without a sponge contribution persist into the early Ordovician but an explosion in diversity of grazing gastropods correlates with the effective disappearance of stromatolites as major components of build-ups on open shelves.

The Ordovician

The early Ordovician sees a rise in small bioherms constructed of lithistid sponges, particularly *Archaeoscyphia* (somewhat archaeocyathid in appearance), and skeletal algae. Locally, the receptaculitid alga *Calathium*, or *Pulchrilamina* of dubious affinities but possibly a stromatoporoid, may be important biohermal components. Again, these mounds show no zonation and little relief, no borers but common burrowers, and increasingly diverse associated biotas including echinoderms, trilobites, brachiopods, crinoids, early bryozoans, and rich pockets of gastropods and cephalopods. Build-ups reach cumulative thicknesses of 20 m and lengths of 87 m. Larger examples may show simple succession (James 1983), climaxing in encrustations of *Pulchrilamina*. In addition, the early Ordovician has the earliest examples of mud mounds dominated by the cavity structure stromatactis (variously considered as of organic or purely physical origin) and lacking any (other) sign of organic framework, < 76 m thick and 300 m across. Similar structures are recorded sporadically through the rest of the Palaeozoic, whilst stromatactis is frequently a component of build-ups dominated by (other) metazoans.

There was a great expansion in benthic marine life in the early Middle Ordovician. The stromatoporoids, with doubtful Cambrian representatives, the bryozoans, and the tabulate corals had all evolved and the rugose corals appeared for the first time. These groups, including the major components of the most successful Palaeozoic reef communities, diversified rapidly and non-stromatoporoid sponges declined as reef builders. However, it was almost another 100 million years before these new components realized their full potential.

Initially, bryozoan reefs dominated, constructed of small encrusting, domed, massive, plus erect bifolial and cylindrical colonial morphologies trapping and binding lime mud. A few small sponge reefs were bound by bryozoans and stromatoporoids, with blankets of shell coquinas and pelmatozoan debris. These mainly small, unzoned build-ups may have had as much as 1 m relief and formed accumulations up to 4 m thick, but in the later Middle Ordovician, large shelf-break carbonate masses, < 250 m cumulate thickness and 60 km long, are dominated or largely constructed by bryozoans (Webby 1984). Associated faunas included crinoids, brachiopods, together with blue-green (*Girvanella*, *Sphaerocodium*) and red (*Solenopora*)

algae, some sponges and, in some of the larger build-ups, stromatactis. Tabulate coral and bryozoan build-ups coexisted briefly, with later Middle Ordovician *Labyrinthitos* patch reefs, but by this time the stromatoporoids were beginning to diversify. From the later Ordovician until the end of the Devonian, major build-ups were dominated by stromatoporoids, with corals and skeletal algae as major contributors, whilst bryozoans and other sponges were reduced to minor roles. However, corals alone and less commonly bryozoans continued to contribute patch reefs, forming bioherms and sometimes extensive biostromes, whilst sponges sometimes dominated build-ups in deeper water.

Upper Ordovician build-ups range from small patches dominated by *Tetradium*, fasciculate Rugosa, *Receptaculita* and other skeletal algae, through small algal and stromatolitic pinnacle reefs < 30 m high and 0.8 km in diameter, to zoned and unzoned coral−stromatoporoid build-ups and large stromatactis mounds < 100−140 m high and 1 km in diameter. A shelf-break complex of patch reefs, individually < 15 m high and 50 m in diameter, grades from talus flanked domical stromatoporoid mounds at the margin, through communities of laminar and domical stromatoporoids, to patches of diverse corals, algae, and ramose bryozoans in the shelf interior. By the late Ordovician, there is increasing evidence of borers and skeleton-breaking organisms at work.

The development of reef communities suffered another set-back with the late Ordovician extinctions (Section 2.13.2). Build-ups are few and small until mid Llandovery times. Thereafter, patch reef development becomes widespread, particularly in the later Llandovery and Wenlock, with individual examples developing < 5 m relief on the sea floor, < 60 m cumulative thickness, and 100 m or more in diameter. Succession may be well developed with pioneering faunas of syringoporids, favositids, spheroidal stromatoporoids, halysitids, or crinoid groves. In the diversification stage, stromatoporoids of various morphologies, colonial rugose corals, and tabulate corals (particularly heliolitids) may be prominent, with a rich associated fauna of brachiopods (often in nests), bryozoans (some cryptic), crinoids, microfauna, and stromatactis. Algae are not so prominent. Stromatoporoids, with or without tabulate corals, form the domination stage. Most build-ups show little lateral differentiation internally. However, among the hundred or more patch reefs of Middle Silurian age in the Great Lakes area, the largest structures show greater complexity. The 15 km² Marine Reef of Illinois has a core largely constructed of stromatactis, with a cen-
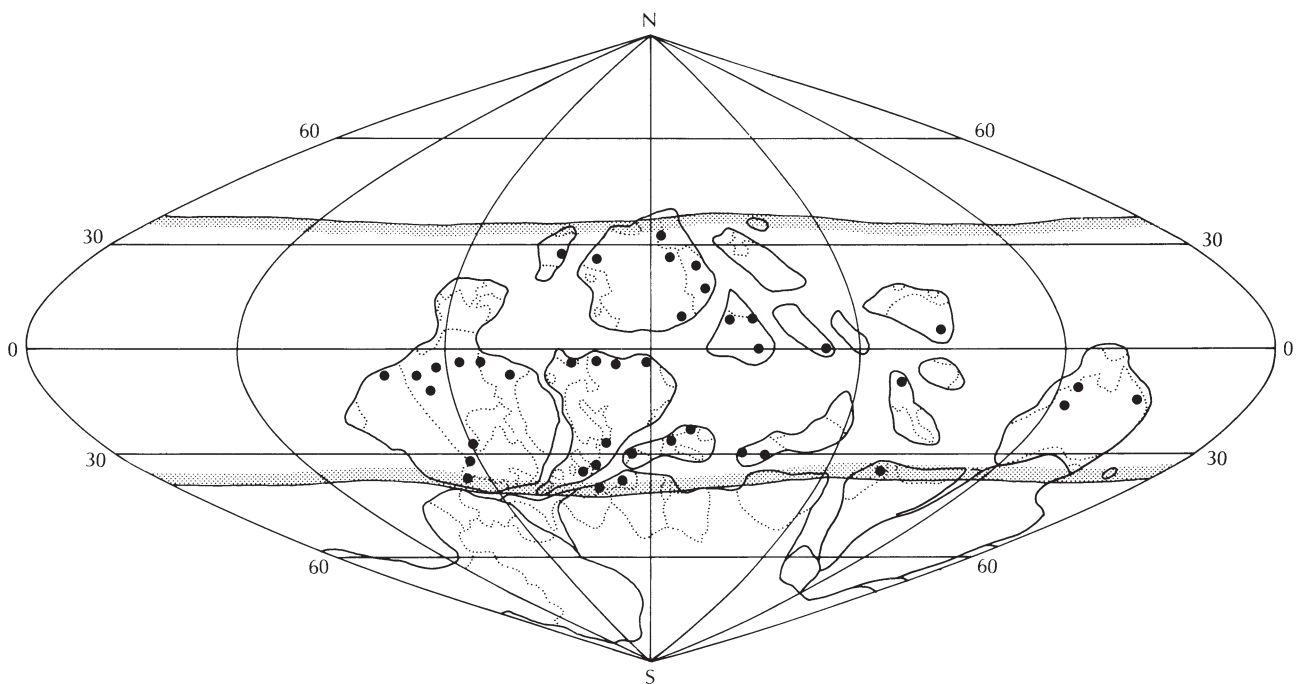

Fig. 2 Devonian continental reconstruction showing the distribution of organic build-ups (reefs and bioherms) and their latitudinal limits. (After Heckel & Witzke 1979.)

tral lagoonal facies, an externally fringing community of corals and stromatoporoids and a flanking apron composed largely of skeletal debris.

The Siluro—Devonian

These Silurian build-ups were the forerunners of the spectacular development of reef growth in the Devonian, representing the first major peak in reef diversification and possibly the all time acme for reef ecosystems (Fig. 2). Major reef complexes, persisting over tens of millions of years, resulted in cumulative thicknesses of reef and perireefal carbonates < 2 km thick and stretching for hundreds of kilometres along shelves. Fringing, barrier, and shelf based atolls (faros) are represented. Reef edge, fore reef, and back reef zones are clearly differentiated with detailed palaeoecological zonation comparable in complexity and in variation of constituent faunas and floras to modern major reef complexes. Principal constructors of the reef margin were stromatoporoids and the blue-green algae *Renalcis*. Stromatactis is often present, and corals play a subsidiary role although they were more important on the reef flat and in areas where a reef rim was poorly developed or missing. Back reef facies are characterized by distinctive lithologies and assemblages, in particular by the stromatoporoid *Amphipora*.

In some places, for example the Canning Basin of Western Australia, talus aprons and pinnacle reefs can be demonstrated on fore reef slopes descending to basinal facies < 180 m below contemporary sea level. Compared with Recent reefs, those of the Devonian show much less evidence of the activity of borers, grazers and scrapers; much of the breakdown of the rapidly cemented reef rock appears to have been physical.

This episode of reef building was terminated by the collapse of shallow-water ecosystems and the extinction or near extinction of the principal frame-building organisms near the end of the Frasnian (Section 2.13.3). In the Canning Basin, reef growth locally continued into the Famennian almost totally dominated by skeletal and non-skeletal algae. In the succeeding Carboniferous major build-ups are rare, although mud mounds are common, reflecting the relative paucity of suitable constructors among the skeletal organisms in the re-established level bottom communities. It was almost another 100 million years before large scale reef complexes were again developed, and then not on the scale of those of the Devonian.

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1.8 Terrestrialization

1.8.1 Soils

V. P. WRIGHT

Introduction

The soil is probably the most studied and best understood ecosystem on Earth, yet very little is known of its origins or the timings of each developmental stage in its evolution. This situation arises both because of the low preservation potential of soils and through a lack of study.

A variety of soils have been recognized in Precambrian sequences ranging back to over 3000 Ma. During the latter half of the Precambrian and through the Phanerozoic a gradual diversification of soil types occurred (Retallack 1986), reflecting both atmospheric evolution and biological diversification, especially since Middle Palaeozoic times.

Although many, if not most, details of the evolution of soil communities and their interactions remain conjectural, several major stages can be defined. The evidence, circumstantial at best, suggests that biologically active soils have existed since at least Middle Cambrian times (Fig. 1).

Abiotic soils

No direct evidence has been found for biologically active soils during the Precambrian, although a variety of weathering profiles and structural palaeosols have been discovered (Retallack 1986). Organic-rich palaeosols apparently occur in the 2400 Ma Blind River Formation of Ontario (Campbell 1979). High levels of radiation, adverse temperatures and atmospheric conditions must have prevented colonization of the land surface, even though microbial life existed in the contemporaneous seas. The soils which developed during the Precambrian were the products of purely physical and physico-chemical processes.

Microbial soils

Cyanobacteria were abundant in the Precambrian, including intertidal forms which were adapted to daily wetting and drying and to salinity variations. As such they were preadapted to life on land. Some silicified Precambrian forms can be compared directly to extant cyanobacteria found in subaerial settings (Campbell 1979). In present day environments, too hostile for higher plants (such as deserts or at high altitude), primitive microbial communities are dominated by cyanobacteria, both filamentous and coccoid, and chlorophytes. If such forms are capable of widely colonizing modern deserts, it would be naive to doubt their ability to colonize the ancient land surfaces. Golubic and Campbell (1979) have compared the mid-Precambrian microfossil *Eosynechococcus moorei* with the extant cyanobacterium *Gloeothece coerulea*, which is a subaerial form, providing a suggestion of the earliest terrestrial microbiota.

Biogenically influenced terrestrial to supratidal phosphates have been recorded from the Middle Cambrian of the Georgina Basin of Northern Australia (Southgate 1986). In these examples very well preserved phosphatized microbial tubes, identical to calcified fungal tubes in present day calcrete soils, occur in phosphate horizons associated with shallowing-upwards peritidal deposits. The exact setting for their formation (supratidal or fully terrestrial) is uncertain but the remarkable similarities between these phosphatic fabrics and those of present day microbial soil carbonates must place this discovery as the strongest candidate for the earliest biologically active soil.

The 'greening' of the land surface, albeit by a microbial sludge, would have begun a series of wide reaching changes in weathering and sedimentary processes. Land surfaces, lacking any biological cover, are prone to erosion by wind and runoff. Even simple microbial mats on the surface would have provided some binding of weathered materials (Campbell 1979), although roots provide a much more effective binding agent. As a result of binding, rates of erosion may have decreased and weathered materials would have had a longer residence time in the soil, allowing greater decomposition. The biological cover might also have increased levels of carbon dioxide in the soil, and would have added organic acids; both factors would have promoted chemical weathering in the soil. All these effects
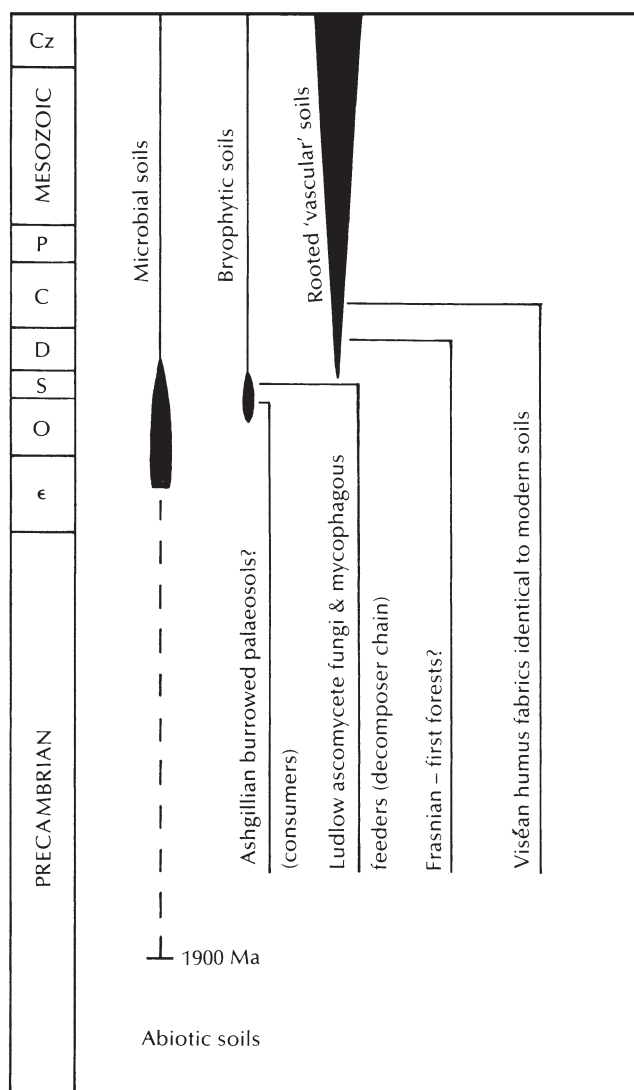
Fig. 1 Geological ranges of major soil categories and first known appearances of important soil ecosystem components.

must have increased many-fold with the advent of rooted vegetation.

On newly exposed surfaces cyanobacteria are usually the first colonizers, followed by lichens. Fungally produced oxalic acid in lichens is a major factor in rock decomposition, but the timing of the appearance of the fungal—cyanobacterial association is unclear. The vast majority of lichen-forming fungi belong to the ascomycetes, but the earliest record of these is from the Ludlow of Gotland (Sherwood-Pike & Gray 1985).

Present day microbial soils are best developed in restricted settings which do not provide guides to

the sorts of soils possible in the past. Under suitable conditions relatively thick microbial mats may have developed, especially in humid climatic regimes. Such soils must have provided suitable microclimates for the first terrestrial invertebrates (Rolfe 1985; Section 1.8.3), even if the bare landscapes were still too hostile. However, no records of such microbial soil faunas are known with confidence. Highly bioturbated palaeosols have been recorded from the Late Ordovician (Ashgillian) Juniata Formation of Pennsylvania, U.S.A. (Retallack 1986). These consist of burrows 3–16 mm in diameter, extending to depths of 50 cm in the now compacted argillaceous palaeosol. The burrows occur in fluvial overbank deposits, and it is often very difficult to determine if such burrows are truly those of soil dwellers or the result of burrowing during temporary subaqueous phases caused by flooding. As yet no attempt has been made to detect organic carbon isotope signatures in pedogenic carbonates in Lower Palaeozoic palaeosols, but this might prove a fruitful avenue of investigation.

Bryophyte soils

By the Late Ordovician bryophytic-like terrestrial vegetation had appeared (Section 1.8.2). Such a vegetation cover, although relatively thin, would again have provided opportunities for faunal colonization. The nearest possible present day analogues for such biotas are to be found associated with lichens or moss cushions. They are characterized by a community of microarthropods, such as mites and springtails, but these only have a geological record back to the Early Devonian (Siegenian) Rhynie Chert. Could it really have taken over 40 million years for invertebrates to have colonized the bryophyte 'felt' covering the land surface, a land surface which probably already had a long history of microbial cover? The earliest known terrestrial faunas of the Early Devonian (Section 1.8.3) were already diversified and contain representatives of the major soil ecosystem components.

The earliest evidence of a terrestrial biota, although tentative, consists of faecal pellet-like ovoid and cylindrical bodies of hyphal fragments from the Ludlow of Gotland (Sherwood-Pike & Gray 1985). These may provide evidence of mycophagous feeders, and the presence of associated ascomycete fungal remains indicates that the decomposer subsystem of the soil ecosystem had already evolved.

Rooted soils

The next major step was the development of a rooted plant cover. This happened progressively with the diversification of the vascular plants from Early Silurian times, with a further major step in late Devonian times when true forests first appeared. The final stage in this series of events, at least to date, was the rise of the grasses in the Tertiary (Section 1.11). The consequences of a rooted plant cover were far greater than those of a simple microbial or bryophytic one. The increased stability of the soil, and increased biomass, would have resulted in thicker soils and thicker humus. The degree of biochemical and biophysical weathering would have increased dramatically, and from Devonian times on soil-types diversified in response to these changes (Retallack 1986).

The advent of a prominent rooted zone would have been associated with the development of the rhizosphere, with its own complex biotic interactions. A critical event would have been the initiation of symbiotic fungal–root relationships (mycorrhizal associations), in which the fungal component acts as a nutrient supplier to the roots. These fungal associations occur either internally within the root (endomycorrhizae) or as sheaths around the roots (ectomycorrhizae). Occurrences of actual fungal remains with roots have been recorded from the Rhynie Chert and also abundantly from early Carboniferous soils, as calcification products of basidiomycete fungi around root tubes. In such cases, however, it is difficult to categorically establish that the fungi were not simply saprophytic forms.

Ecology

The soil is an essential component of the terrestrial ecosystem, and one of its most critical functions is to decompose organic matter, making plant nutrients available for recycling. The primary producer subsystem must, by all reasonable considerations, have been present from Cambrian times or earlier. The possible occurrence of fungal tubes in middle Cambrian terrestrial phosphorites of Australia, and the presence of ascomycete remains from the Ludlow of Gotland suggest that by the Middle Silurian, if not much earlier, the decomposer subsystem had also developed. Thus recycling became possible. Possible microarthropod faecal pellets in the Silurian suggest the presence of consumers (mycophagous forms). Some 20 million years later,

as revealed in the Siegenian Rhynie Chert, a fauna of spring-tails, mites, spiders, and trigonotarbid arachnids had appeared, representing many of the important components of the ecosystem (Section 1.8.3).

By early Carboniferous times the soil ecosystem had evolved to a point where it produced a variety of humus fabrics identical to those found in present day soils (Wright 1987), which must reflect the action of the same types of complex biogenic processes.

The evidence is frustratingly incomplete, and further work is required especially to integrate the occurrences of the early soil faunas with their associated soils. The effort needs to be made to search for evidence of biofunction in early Palaeozoic terrestrial deposits, since such soils were probably organically active. What can be said, with growing confidence, is that the first vascular plants must have colonized a land surface which already had a long history of biological activity. Studies of microbial or bryophytic soils today will provide us with some clues as to the possible forms taken by these earliest soils.

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1.8.2 Plants

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Introduction

Land plants encounter problems relating to water stress, uptake, and transport, and to aerial dispersal of propagules. Survival in such habitats is associated with three major strategies:
1 Drought avoidance via opportunism and ephemeral life cycles completed under favourable conditions.
2 Extreme desiccation tolerance involving the capacity of cytoplasm to rehydrate and then function normally (poikilohydry).
3 Maintenance of an internally hydrated environment by biochemical and anatomical modifications (homoiohydry).

Extant land vegetation includes representatives of all major groups; cyanobacteria, algae, bryophytes and tracheophytes. The last are usually considered most successful and are homoiohydric — possessing xylem (with lignin) for water transport, a waxy cuticle (cutin) for reducing evaporation, stomata and an intercellular space system for gaseous transport (Raven 1984). The poikilohydric life style of cyanobacteria, algae, and bryophytes is usually considered more primitive, is of particular significance in the colonization of unstable environments, and hence would have been important in pioneering land plants.

The *preservation potential* of land plants is linked to these strategies in that cutin and lignin are durable and may persist, albeit modified, in fossils, but in poikilohydric forms, the only parts which might be expected to be fossilized are resting stages and/or dispersal units such as spores. The latter, impregnated with sporopollenin, a complex fatty polymer, also occur in tracheophytes. Thus although there is no direct record of thallophytes (cyanobacteria and algae) colonizing moist land surfaces in the Early Palaeozoic, it seems likely that they were present. A possible limiting, physical factor may have been high ultraviolet (UV) radiation correlated with low atmospheric oxygen. Indeed it has been postulated that lignin evolved from precursors involved in UV absorbance, and that cutin and sporopollenin initially had a similar role in UV reflectance.

With regard to higher plants, attempts to demonstrate the vascular status of megafossils, thus pro-

viding unequivocal evidence for land vegetation, have traditionally dominated research. However, more recently the affinities of Ordovician and Silurian microfossils have been rigorously appraised in the search for alternative pioneering colonizers.

The first records and ranges of all fossils thought relevant to terrestrialization are documented in Fig. 1, and numbers below refer to that figure.

Sporomorphs

1, 2. Cryptospores. (lacking trilete (Y) or monolete (I) marks; after Richardson & Edwards 1989.)

Obligate permanent tetrads (1), so named because they do not split into four spores (monads) on dispersal, possess durable, smooth, unornamented walls thought to be impregnated with sporopollenin, although this has not been chemically proven. They are thus considered to derive from land plants. Those characterizing Upper Ordovician spore assemblages are smaller, smooth walled, and often lack the enveloping smooth or sculptured 'membrane' typical of most early Silurian forms. Its absence may result from poorer fossilization potential. Such tetrads increase in numbers and diversity, dominating assemblages until the end of the Llandovery. Thereafter they become relatively less common and occur only rarely in Lower Devonian sediments, where they are probably reworked. Gray (1985) has argued most persuasively that as comparable tetrahedral tetrads (sometimes membrane enclosed) occur in certain living liverworts, they thus derive from poikilohydric plants with bryophyte physiology and life histories. It is also possible that they belonged to freshwater or marine algae for which there are no modern analogues, or that they were shed by intermediate extinct forms that lived in ephemeral water bodies producing spores when these dried up. Membrane enclosed *monads* and *obligate dyads (2)* have similar ranges to tetrads and were probably of similar derivation.

3. Dyads. Habitually lacking a membrane, and believed to split into the consistently associated alete (lacking trilete or monolete marks) spores with thinner proximal faces and identical distal features, these are distally smooth walled in earliest records (Rhuddanian) and sculptured from the Homerian. They persist throughout the Silurian and are relatively common in basal Devonian assemblages. Dyads occur in *Salopella*-like sporangia in the Přídoli. The affinities of that genus remain