

from a wide variety of localities provide a seemingly impressive roster of evidence for trace fossils, in nearly every case unresolved doubts remain. Even if some pre-Ediacaran traces prove genuine, their general scarcity is difficult to explain unless extrinsic factors (e.g. oxygen levels) prohibited the wide-scale expansion of macroscopic metazoans into an effectively empty ecospace.

While these relatively large trace fossils continue, therefore, to excite scepticism, it may be that more convincing evidence could be found at a microscopic level. For example, possible faecal pellets have been reported from the *c.* 900 Ma Zilmerdak 'Series' of the Urals (Glaessner 1984), which, if confirmed, which, would indicate a grade of organization above that of the turbellarians. Clearly, a more extensive survey in suitable lithologies is required. In particular, ultrastructural studies of sediments may show features diagnostic of bioturbation. For example, documentation of grain orientation and cation concentrations (e.g. iron, aluminium) around undoubted Phanerozoic trace fossils suggests a possible approach to establishing the biogenicity of some Proterozoic examples (Harding & Risk 1986). Moreover, cherts that evidently formed at a very early stage of diagenesis, from the *c.* 700 Ma Doushantuo Formation in the Yangtze Gorges of Hubei Province, China, preserve narrow burrowlike structures that may represent the activities of a meiofauna.

While the Precambrian fossil record is dominated by stromatolites, it has long been realized that they undergo a decline in diversity during the late Precambrian (see Fig. 2). A recent reanalysis of the data (Walter & Heys 1985) indicates that, in terms of both relative abundance and diversity, stromatolites began to decline in quiet, subtidal environments (where coniform varieties were especially abundant) from about 1000 Ma. This trend was established also in intertidal environments from *c.* 800 Ma, so that stromatolites were relatively unimportant by the beginning of the Cambrian. The traditional explanation links this pattern to the rise of grazing metazoans whose activities were detrimental to the formation of the microbial mats. Thus, the initial dip in stromatolite diversity at 1000 Ma may herald the rise of primitive grazers, while the accelerating process of decline after *c.* 800 Ma could represent the widespread distribution of metazoans. However, the development of disrupted stromatolitic fabrics (a thrombolitic texture) that may be a result of extensive burrowing by metazoans, only appears in the Cambrian.

Further indirect evidence for the evolution of

metazoans at least one billion years ago comes from molecular studies. If it is demonstrated that the substitution of either nucleotides in nucleic acid chains or amino acids in polypeptides is stochastically constant and occurs at a known rate, then the differences between the sequences in any species pair should indicate their time of divergence. Using this assumption of the so-called molecular clock, existing data on haemoglobins (a group with a substitution rate that is appropriate for the time-scales involved) have been used to suggest that the metazoans evolved between *c.* 800 and 1000 Ma. A related approach utilizes 5S ribosomal RNA sequences, and such comparisons (Hori & Osawa 1987) suggest that Mesozoa might be the most primitive metazoans (if they are not derived independently from protoctists). Moreover, although the Mesozoa may have arisen before 1000 Ma, other metazoans such as the turbellarians and nematodes have divergence points at only *c.* 700 Ma.

Ediacaran faunas

The evidence for pre-Ediacaran metazoans is mounting, but the view that the fossil record indicates no metazoan older than *c.* 600 Ma is still respectable and it is the Ediacaran faunas that provide our first useful glimpse of metazoan evolution (Glaessner 1984; Conway Morris 1985; see also Section 1.3). Such faunas were described from Namibia, at that time Deutsch Sud-West Afrika, before the Second World War, and shortly afterwards in Australia. At first regarded as Cambrian, their persistent occurrence beneath abundant shelly fossils soon led them to be consigned to the Precambrian, and continuing reports from numerous localities around the world have confirmed this observation. Until recently these faunas have been dated at *c.* 620–680 Ma, with some claims of even 800 Ma. However, recent radiometric dating has cast major doubt on these estimates. High resolution uranium–lead dating of zircons from an ash fall that entombed an Ediacaran assemblage in Southeast Newfoundland (Fig. 1) yields a date of *c.* 565 Ma. Even so, the age range of the Ediacaran faunas may be considerable, and a span of *c.* 550–620 Ma may not be unrealistic.

The Ediacaran faunas are reviewed elsewhere (Section 1.3), and only a general survey in the present context is required. At present, there seem to be two broad assemblages. There are those of a shallow-water type that are superbly represented in the Flinders Ranges of South Australia, including the

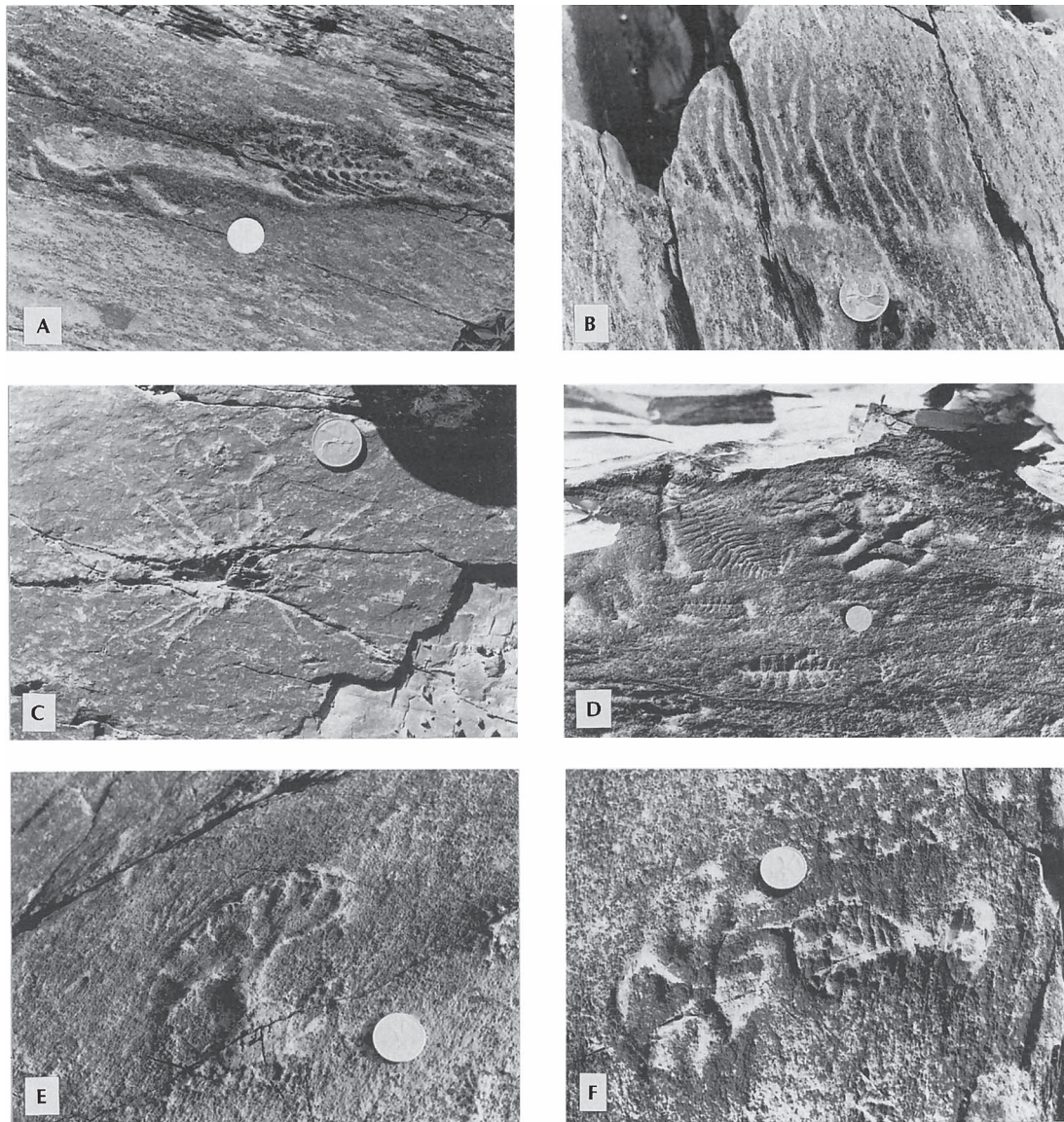


Fig. 1 Ediacaran fossils from the Mistaken Point Formation (Conception Group) of Southeast Newfoundland, Avalon Peninsula. A, Pennatuloid with hold-fast. B, Pectinate organism. C, Stellate organism. D, Bedding plane with spindle organisms and medusoids. E, Branching organism with hold-fast. F, Pennatuloid with hold-fast and medusoid. Diameter of coin 23 mm.

Ediacaran Hills, and the closely similar fauna from the White Sea of northern U.S.S.R. In contrast, the faunas of the Avalon Peninsula of southeast Newfoundland, which may be referred to as the Mistaken Point assemblage (Fig. 1), in reference to the spectacular locality near Cape Race, appear to represent a deeper-water facies. Similar occurrences in Charnwood Forest, U.K. are one of the many lines of evidence that in the early Phanerozoic this area was joined to the Avalon area on one side of the Iapetus ocean. Possibly deeper-water faunas may

also occur in the Flinders Range, but as yet only preliminary reports are available.

Despite the range of environments inhabited by these Ediacaran assemblages, they show several characters in common. Most typical are forms that the majority of workers would ascribe to the cnidarians. These include medusoids (Fig. 1D, F), some of which may be placed with reasonable confidence in cubomedusoids, chondrophores, and perhaps scyphozoans. However, other jellyfish have a highly characteristic three-fold symmetry

that finds no parallel amongst living cnidarians. Yet others lack sufficient characters to be assigned with confidence to any group. In addition, stalked forms with an expanded leaf-like body arising from a central rachis (Fig. 1A, F) invite comparisons with the pennatulaceans (the sea-pens). However, these similarities become increasingly tenuous amongst a variety of other foliate to bag-shaped organisms, and their cnidarian affinity is more questionable. Other organisms include a possible worm, the sheet-like *Dickinsonia*, a medley of arthropod-like forms, and a possible echinoderm with penta-radial symmetry (Gehling 1987).

Although the Mistaken Point assemblages evidently owe their preservation in most instances to being overwhelmed by volcanic ash, in many other cases the occurrences of these soft-bodied metazoans as sandstone impressions above siltstone intervals are difficult to explain, given the absence of such preservation in younger clastics. The problem is compounded by abundant trace fossils in some Ediacaran assemblages, most typically simple sinuous trails, that cannot be linked to the activities of any of the known body fossils. It seems necessary to invoke a contrast between entirely soft-bodied organisms, such as the trace-producing worms that were possibly largely infaunal, and those with a tougher integument, many either epifaunal or pelagic and coming to rest on the sea-floor prior to burial. It was only this latter group that was sufficiently tough to take impressions when immured by sediment. However, the explanation has not won universal approval. In a sweeping reappraisal Seilacher (1989) proposed that the Ediacaran organisms represent an entirely separate group, possibly a distinct kingdom, that owe their preservation to a unique composition consisting of a sac-like body with a tough integument. While Seilacher has highlighted the taphonomic problems posed by this preservation, his ingenious proposal seems to be oversimplified and, while perhaps applicable to some of the sac-like ernietids (see also Section 1.3) and *Pteridinium*, is difficult to reconcile with the bulk of the biota.

Whatever disagreements surround the biological affinities of the Ediacaran fauna, it is clear that they lacked hard skeletal material, the widespread appearance of which was to usher in the Cambrian some 20 Ma later. However, one notable exception demands comment. In Namibia carbonate units, intercalated with clastics containing Ediacaran fossils, yield calcareous tubes referred to as *Cloudina* (Grant 1990) (see also Section 1.4). The tubes are

double walled with connecting partitions that give a cone-in-cone appearance, although the exact mode of secretion is not clear. There is evidence that originally the walls contained substantial amounts of organic matter, and this helps to fuel the speculation that the origin of skeletal hard parts was as separate spicules or granules embedded in an organic matrix. The facies contrast in Namibia between the clastics bearing the Ediacaran fauna and the carbonates with *Cloudina* emphasizes the need for taphonomic judgements concerning original faunal distribution. However, occurrence of Ediacaran faunas in dolomites in northern Siberia demonstrates that preservation is not governed simply by lithology.

The role of the Ediacaran faunas in determining the origins of the Cambrian fauna at present is enigmatic. With the possible exception of the arthropod- and echinoderm-like forms, existing reports would indicate little continuity with either the shelly faunas or soft-bodied Burgess Shale-type assemblages. Descriptions of new finds from Siberia and Australia may go some way towards alleviating the problem, and it is likely that many of the putative ancestors are represented either by the unknown trace makers or animals too small to be preserved.

The evident demise of the Ediacaran fauna has resulted in two alternative hypotheses that are not entirely exclusive. One appeals to a change in taphonomic conditions, in particular the rise of Cambrian predators and scavengers that militated against soft part preservation. It is, however, of considerable significance that a distinct gap separates the disappearance of the Ediacaran fauna from the debut of Cambrian assemblages, an interval that contains facies that otherwise would appear suitable for preservation (Narbonne & Hofmann 1987). If indeed a substantial fraction of the Ediacaran fauna became extinct over a geologically brief period, then it may be that the subsequent Cambrian diversification was largely a response to the ecological opportunities presented. The evidence for such an end-Ediacaran mass extinction (Section 2.13.1) at present is very tenuous. It is necessary to emphasize, however, that as yet no data point to any extra-terrestrial mechanism. If comparisons were to be drawn with other mass extinctions, then there are possible similarities with the end-Permian event (Section 2.13.4) in which the formation of a super-continent and possibly development of brackish oceans because of massive evaporite deposition are invoked as significant factors.

Cambrian biotas

Whether or not there was an end-Ediacaran mass extinction, the ensuing diversifications of the Cambrian were a spectacular evolutionary event (Brasier 1979; Conway Morris 1987). Most obvious is the appearance of abundant skeletal parts (Section 1.4) composed of calcium carbonate, calcium phosphate or silica, which together provide for the first time in the history of Earth an adequate fossil record.

Given that the bulk of the fossil record consists of shelly fossils, it is not surprising that the many explanations offered for the Cambrian diversifications have focused on the origin of hard parts. While special explanations may be called for, soft-bodied organisms may have outnumbered greatly those with skeletons in the original Cambrian communities and the history of diversification of trace fossils during this interval is also an important component in documenting these adaptive radiations. Although the rise of the skeletal faunas is clear in outline, detailed resolution is hampered by uncertainties regarding inter-continental correlations, such that the exact sequence of events is still uncertain. Present evidence, however, suggests that (apart from *Cloudina*) the earliest skeletal fossils included anabaritids (elongated tubes with a highly characteristic trifoliate cross-section) and the teeth of protoconodonts, a group probably related to the modern chaetognaths (arrow-worms). Shortly afterwards they are joined by more shelly fossils, including a distinctive monoplacophoran known as *Purella*, the gastropod *Aldanella*, and primitive hyoliths. The succeeding horizons record an abundance of additional shelly fossils (Bengtson 1977), many of enigmatic affinities (see also Section 5.2.5) but also including additional monoplacophorans, the first gastropods, hyoliths, brachiopods, sponges, and, somewhat later, echinoderms. The majority of these fossils are relatively small (c. 1–2 mm), and are either composed of phosphate or are replaced secondarily by this compound. These small shelly fossils (see also Section 1.4) are the subject of active study, with special interest in the more enigmatic taxa (Bengtson 1977).

Although for many species biological relationships are entirely speculative, in others a natural classification is beginning to emerge. Three important groups include the tomotiids, which possessed a primary phosphatic skeleton, the coeloscleritophorans which comprise halkieriids, siphogonuchitids, and chancelloriids, and the cambroclaves,

the last two having calcareous skeletons. In each group the skeleton is composite, being composed of a series of sclerites that disarticulated on death. This extraordinary array of small shelly fossils persists during the early stages of the Cambrian, especially the Tommotian and Atdabanian, with some lingering into the Middle and even Upper Cambrian. It is noteworthy that the trilobites, which dominate the majority of Cambrian shelly faunas, are absent from the earliest assemblages. However, their appearance in different sections was probably not synchronous, and their debut was probably due to mineralization on pre-existing forms with only a chitinous skeleton, rather than an evolutionary event *per se*.

The rise of these skeletal faunas has been interpreted in both ecological terms, especially the rise of predators conferring the need for protective structure, and in terms of changes in the physico-chemical environment (Conway Morris 1987; see also Section 1.4). The evidence that many groups possessed either tightly interlocking sclerites that probably formed a coat over the exterior, or valves that enclosed or allowed the retraction of the soft parts, certainly supports a response to predation. In some specimens, especially tubicolous taxa, small boreholes occur. They probably represent predatory activity, but the nature of the attacker is speculative. It is also likely that the protoconodonts formed part of a predatory feeding apparatus, but in general it is necessary to infer that many of the early Cambrian predators were more or less entirely soft-bodied.

Examples of Lagerstätten that might reveal the nature of such soft-bodied organisms are not known until the Atdabanian, and of these the Burgess Shale-like Cheng-jiang fauna in Yunnan Province, South China is by far the most important. This fauna has not yet received detailed analysis, and much of our information on the role of soft-bodied organisms in the initial Cambrian diversifications must continue to rely on evidence from trace fossils (Crimes 1987). A general diversification that parallels the skeletal record is now well known. In particular, Vendian traces typically are rather small and two-dimensional. Some ichnotaxa survive into the Cambrian, but a number (e.g. *Harlaniella*) are restricted to this interval and therefore have a biostratigraphic utility. The striking increase in trace fossil diversity near the Precambrian–Cambrian boundary (Section 5.10.2) includes vertical burrows, scratch marks that generally are attributed to arthropods, and other traces that often indicate increasing behavioural complexity. It is also striking that

ichnotaxa regarded as diagnostic of either shallow- or deeper-water where they occur later in the Phanerozoic, are found together in shallow-water environments (Crimes & Anderson 1985). Indeed, it has been proposed that the deep oceans were not colonized until later in the Palaeozoic, and that the displacement of some trace makers into deeper water was a result of competitive pressure in the shallows.

While the role of ecological changes has dominated discussion on the evolution of early metazoans, it now appears that substantial alterations in the extrinsic physico-chemical environment were also taking place during this time (Conway Morris 1987). The extent to which such changes influenced or even controlled evolutionary events is far from clear, although the near synchronous nature of them is certainly suggestive.

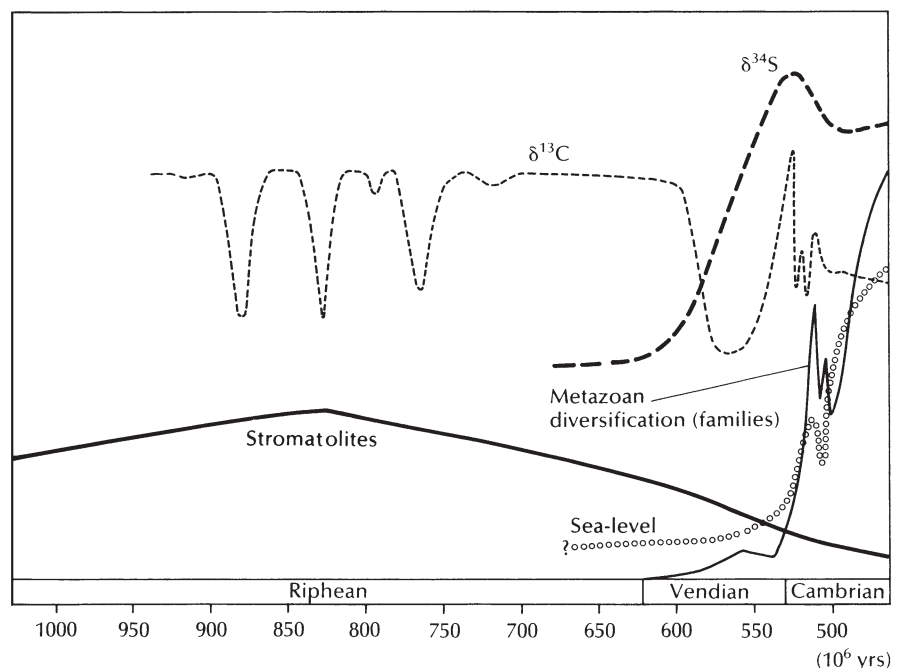
Changes in the physico-chemical environment

Extrinsic changes are registered in several ways, including: palaeocontinental distributions, sea-level curves, stable isotope variations (especially of carbon and sulphur), preference for either aragonite or calcite precipitation, and phosphate deposition. While the extent and nature of the late Precambrian super-continent is still under debate, there is clear evidence for major rifting episodes close to the Precambrian–Cambrian boundary that heralded its break-up. While the separation of continental

blocks would have encouraged the development of endemic faunas, the formation of hot, spreading ridges would have led to displacement of seawater and hence a major transgression. While the history of this Cambrian transgression is not well known in detail, it had the dual effect of increasing the habitable area for shallow-water marine life and providing an increasingly complete rock record as the facies belts migrated cratonward (Brasier 1979).

There is also evidence for substantial changes in ocean chemistry close to the Precambrian–Cambrian boundary (Fig. 2). For example, measurements of sulphur isotopes ($\delta^{34}\text{S}$) from very late Precambrian evaporites record a massive positive shift (the Yudomski event) that reflects the introduction of substantial amounts of isotopically heavy seawater into areas of evaporite formation by some sort of upwelling. The shift is so significant that it probably represents long-term storage of deep-water brines, where bacterial fractionation of sulphur led to accumulation of increasingly 'heavy' water. The sites of such storage may have been narrow 'Mediterranean-like' basins formed at an early stage of continental breakup, and the upwelling episode may also be linked to continuing evolution of the basins. It is probably no coincidence that the Yudomski event overlaps with a major episode of phosphogenesis, that is now reflected in huge economic reserves of phosphate in China and elsewhere. It has been speculated that the influx of phosphorous raised levels of productivity and

Fig. 2 Changes in ocean chemistry as registered in $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$, inferred sea-level, and diversity of metazoans and stromatolites during intervals of the Riphean, Vendian and Cambrian. (Data for stromatolites from Walter & Heys 1985; other data sources listed in Conway Morris 1987.)



helped to fuel the evolutionary radiations. Inferences on ocean productivity have also been drawn on the basis of changes in carbon isotopic ratios ($\delta^{13}\text{C}$), which show a series of substantial shifts. However, in some instances storage of organic matter (rich in photosynthetically sequestered ^{12}C), such as in anoxic basins, may be invoked as an explanation and could be linked to the formation and destruction of narrow marine basins alluded to above. Although somewhat less constrained in terms of timing, there is also evidence for a shift in inorganic precipitation (e.g. ooids) of calcium carbonate polymorphs, from aragonite in the late Precambrian to calcite in the Cambrian. The reasons for this shift are complex, but stem from processes of plate tectonics. These include hydrothermal metamorphism at spreading ridges that lower the Mg:Ca ratio of seawater, rise of partial pressure of CO_2 by volcanic exhalations, and deposition of carbonates in shallow seas versus their weathering on exposed continents. Taken together, the shift towards calcite precipitation appears to be controlled in part by continental breakup, growth of spreading ridges and subduction zones, and transgression of continental margins.

Just how important extrinsic factors, most of which seem to stem ultimately from the processes of plate tectonics, were in controlling evolutionary events is still uncertain. Metazoan diversification may have had its roots far back in the Riphean but, as yet, the possible influence of extrinsic factors on biological evolution in this interval is largely speculative. Nevertheless, the rise of skeletons near the Precambrian–Cambrian boundary can be linked with slightly more confidence to changes in ocean chemistry, and it is interesting that similar suggestions have also been made in connection with skeletal evolution during the great Permo-Trias faunal turnover. Some workers have even suggested that environmental factors may have led to sequential mineralization, from aragonite to high magnesium calcite to phosphate to low magnesium calcite (Brasier 1986). The complexity of the processes and the paucity of evidence in several critical areas, however, make this a challenging area for future palaeobiological research.

References

- Bengtson, S. 1977. Aspects of problematic fossils in the early Palaeozoic. *Acta Universitatis Upsaliensis* **415**, 1–71.
- Brasier, M.D. 1979. The Cambrian radiation event. In: M.R. House (ed.) *The origin of major invertebrate groups*. Systematics Association Special Volume 12, pp. 103–159. Academic Press, London.
- Brasier, M.D. 1986. Precambrian–Cambrian boundary biotas and events. In: O. Walliser (ed.), *Global bio-events*. Lecture Notes in Earth Sciences No. 8, pp. 109–117. Springer-Verlag, Berlin.
- Conway Morris, S. 1985. The Ediacaran biota and early metazoan evolution. *Geological Magazine* **122**, 77–81.
- Conway Morris, S. 1987. The search for the Precambrian–Cambrian boundary. *American Scientist* **75**, 156–167.
- Crimes, T.P. 1987. Trace fossils and correlation of late Precambrian and early Cambrian strata. *Geological Magazine* **124**, 97–119.
- Crimes, T.P. & Anderson, M.M. 1985. Trace fossils from later Precambrian–early Cambrian strata and environmental implications. *Journal of Paleontology* **59**, 310–343.
- Gehling, J.G. 1987. Earliest known echinoderm — a new Ediacaran fossil from the Pound Subgroup of South Australia. *Alcheringa* **11**, 337–345.
- Glaessner, M.F. 1984. *The dawn of animal life. A biohistorical study*. Cambridge University Press, Cambridge.
- Grant, S.W.F. 1990. Shell structure and distribution of *Cloudina*, a potential index fossil for the terminal Proterozoic. *American Journal of Science* **290A**, 261–294.
- Harding, S.C. & Risk, M.J. 1986. Grain orientation and electron microprobe analyses of selected Phanerozoic trace fossil margins, with a possible Proterozoic example. *Journal of Sedimentary Petrology* **56**, 684–696.
- Hori, H. & Osawa, S. 1987. Origin and evolution of organisms as deduced from 5S ribosomal RNA sequences. *Molecular Biology and Evolution* **4**, 445–472.
- Kauffman, E.G. & Steidtmann, J.R. 1981. Are these the oldest metazoan trace fossils? *Journal of Paleontology* **55**, 923–947.
- Narbonne, G.M. & Hofmann, H.J. 1987. Ediacaran biota of the Wernecke Mountains, Yukon, Canada. *Palaeontology* **30**, 647–676.
- Seilacher, A. 1984. Late Precambrian and early Cambrian Metazoa: preservational or real extinctions? In: H.D. Holland & A.F. Trendall (eds) *Patterns of change in Earth evolution*, pp. 159–168. Springer-Verlag, Berlin.
- Seilacher, A. 1989. Vendozoa: organismic construction in the Proterozoic biosphere. *Lethaia* **22**, 229–239.
- Sun Wei-guo, Wang Gui-xiang & Zhou Ben-he 1986. Macroscopic worm-like body fossils from the upper Precambrian (900–700 Ma), Huainan district, Anhui, China and their stratigraphic and evolutionary significance. *Precambrian Research* **31**, 377–403.
- Walter, M.R. & Heys, G.R. 1985. Links between the rise of the Metazoa and the decline of stromatolites. *Precambrian Research* **29**, 149–174.

1.6 Evolutionary Faunas

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Evolutionary faunas are sets of higher taxa (especially classes) that have similar histories of diversification and together dominate the biota for an extended interval of geological time. The expansion and decline of evolutionary faunas can be used to describe large-scale variations in faunal dominance and to interpret temporal changes in global taxonomic diversity in the fossil record. The concept was introduced by Sepkoski (1981), who identified three 'great evolutionary faunas' in the Phanerozoic marine record. These faunas were defined statistically in a factor analysis of familial diversity within taxonomic classes, which grouped together classes that attained their maximum diversities around the same time. The analysis permitted the histories of the aggregate faunas to be traced from initial diversification through dominance and into decline. This treatment of the faunas as units throughout their histories distinguishes the concept of evolutionary faunas from that of 'dynasties', used by some authors for assemblages of dominant taxa during specified intervals of geological time.

Marine evolutionary faunas

Characteristics. The three evolutionary faunas identified in the marine fossil record are the Cambrian Fauna, important during the Cambrian Period, the Palaeozoic Fauna, dominant from Ordovician to Permian, and the Modern, or Mesozoic–Cenozoic Fauna, dominant in the post-Palaeozoic (Fig. 1A). The classes in each fauna share a number of characteristics, or central tendencies, suggesting that they are not randomly assembled groups of taxa. The most striking characteristic is that the classes tend to diversify together, each successive fauna displaying a slower rate of diversification but higher level of maximum diversity than those preceding it. These properties lead to a sequential expansion of evolutionary faunas and a resultant step-like pattern of increase in global marine diversity (with the step between the Palaeozoic and Modern faunas disrupted by the massive Late Permian extinction event — Section 2.13.4). This pattern is present even though most marine classes originated early in the

Phanerozoic and the total number of classes has remained virtually constant since.

The expansion of each evolutionary fauna is associated with the decline of the previously dominant fauna. The declines are much slower than the initial diversifications, giving the faunas very asymmetrical histories. Such a pattern is difficult to simulate in 'random' models of diversification (Sepkoski 1981) but can be described with coupled logistic equations of the form

$$dD_i/dt = r_i D_i (1 - \Sigma D_j / \hat{D}_i),$$

where D_i is the diversity of the i th evolutionary fauna at time t , r_i is its initial diversification rate, \hat{D}_i is its maximum or 'equilibrium' diversity, and ΣD_j is the summed diversity of all faunas at time t (Sepkoski 1984; Kitchell & Carr *in* Valentine 1985). This equation states that an evolutionary fauna will diversify and replace the preceding fauna only if its initial diversification rate is lower and equilibrium diversity is higher. If r_i is higher, the evolutionary fauna will expand so rapidly that the preceding fauna will never appear to diversify; if \hat{D}_i is lower, the evolutionary fauna will never be able to expand and replace the preceding one. Thus, the coupled logistic equation suggests a certain inevitability in the sequential diversification of evolutionary faunas, although it does not specify their timing or relative differences in maximum diversity.

Classes within evolutionary faunas tend to have similar mean rates of taxonomic turnover. Classes in the Cambrian Fauna tended to have high turnover rates, those in the Palaeozoic Fauna intermediate rates, and those in the Modern Fauna comparatively low rates (with some exceptions in all cases). These differences are reflected in the responses of the faunas to mass extinctions (Sepkoski 1984): the Cambrian Fauna suffered large proportional reductions in diversity relative to the Palaeozoic fauna during mass extinctions in the Ashgillian and Frasnian, and the Palaeozoic Fauna suffered more than the Modern at all major mass extinctions of the Phanerozoic. This differential reaction seems to have led to the great change in faunal dominance associated with the Late Permian mass extinction (Section 2.13.4).

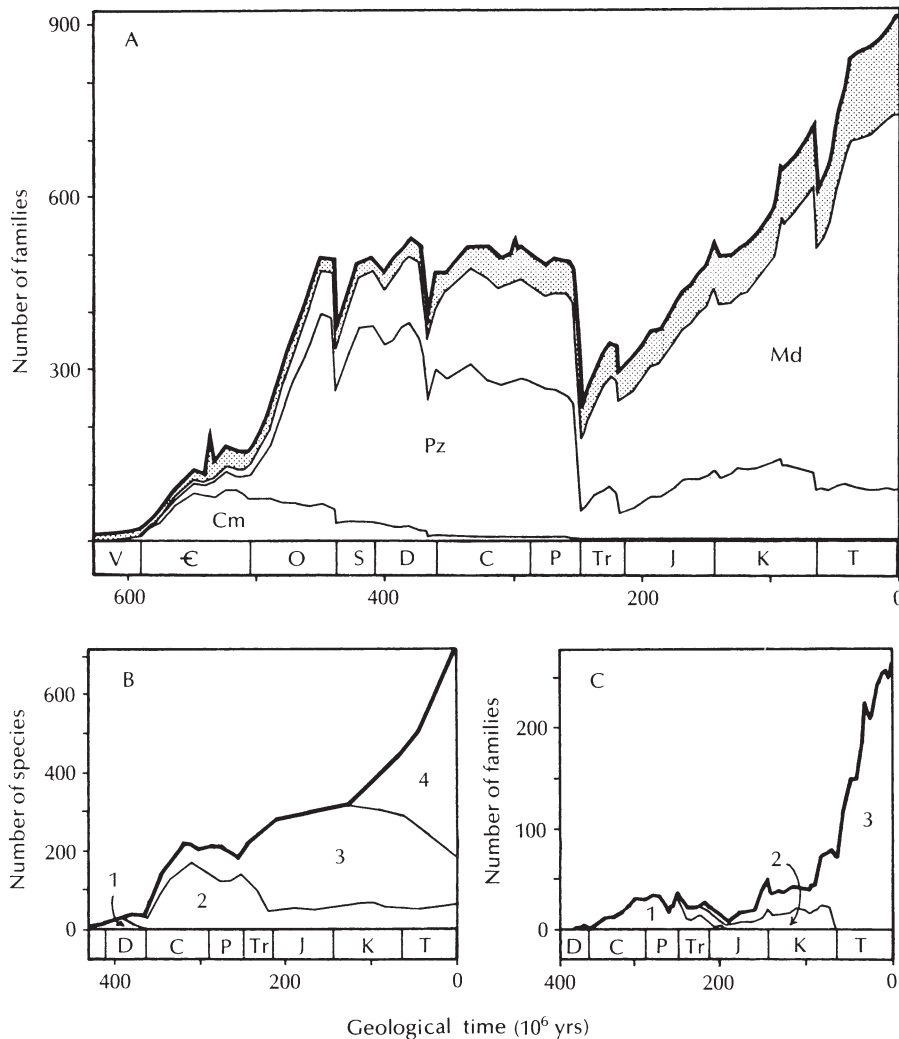


Fig 1 Diversity curves. A, Marine animal families. B, Terrestrial vascular plant species. C, Terrestrial tetrapod families. Each curve is divided into fields that illustrate the diversities of the constituent evolutionary faunas and floras. A, After Sepkoski (1984); Cm = Cambrian evolutionary fauna, Pz = Palaeozoic fauna, Md = Modern fauna; stippled field represents known diversity of families with rarely preserved members that lack heavily mineralized skeletons. B, After Niklas *et al.* (1983); numbered fields as in text. C, After Benton (1985); numbered fields as in text.

Evolutionary faunas also seem to have differing ecological characteristics. The Cambrian Fauna tended to be assembled into broadly intergrading communities that were dominated by generalized deposit feeders and grazers and had low epifaunal and infaunal tiering (Bottjer & Ausich 1986; see also Section 1.7.1). Communities of the Palaeozoic Fauna were dominated by epifaunal suspension feeders with complex tiering; many other ecological guilds were also represented so that the fauna as a whole seems to have occupied more 'ecospace' than the Cambrian Fauna (Bambach *in* Tevesz & McCall 1983). Finally, the Modern Fauna is represented by yet more guilds and is characterized by large numbers of durophagous predators (Vermeij 1987) and mobile deep infauna (Thayer *in* Tevesz & McCall 1983); epifaunal tiering is reduced in most communities.

Sepkoski and Miller *in* Valentine (1985) demon-

strated that evolutionary faunas tended to form coherent assemblages within shelf environments throughout the Palaeozoic Era. Members of the Cambrian Fauna were spread across the entire shelf early in the Palaeozoic Era but became progressively restricted to deeper-water environments during the Ordovician as members of the Palaeozoic Fauna expanded across the middle and finally outer shelf. At the same time, early members of the Modern Fauna came to dominate inner shelf environments and later, deeper, low-oxygen environments. The Late Permian mass extinction eliminated dominance of the Palaeozoic Fauna from middle and outer shelf environments and led to expansion of the Modern Fauna across the entire shelf.

It must be emphasized that none of these evolutionary and ecological differences between the faunas is absolute. In a sense, the faunas are 'fuzzy

bounded sets' with their characteristics overlapping and some members of each fauna mimicking members of others. The characteristics thus represent nodes on a continuum. Major unsolved problems are why such nodes should exist and why they seem to change so little through the Phanerozoic.

2. The Cambrian Fauna was dominated by trilobites along with inarticulate brachiopods, monoplacophorans, hyoliths, and eocrinoids; most of the problematical taxa of the so-called 'small shelly faunas' of the Tommotian are also included. Various of these classes are paraphyletic, with descendent monophyletic taxa belonging to other evolutionary faunas; however, in most cases the paraphyletic classes either declined long before their descendent

Composition and history. The individual histories of the marine evolutionary faunas are illustrated in Fig.

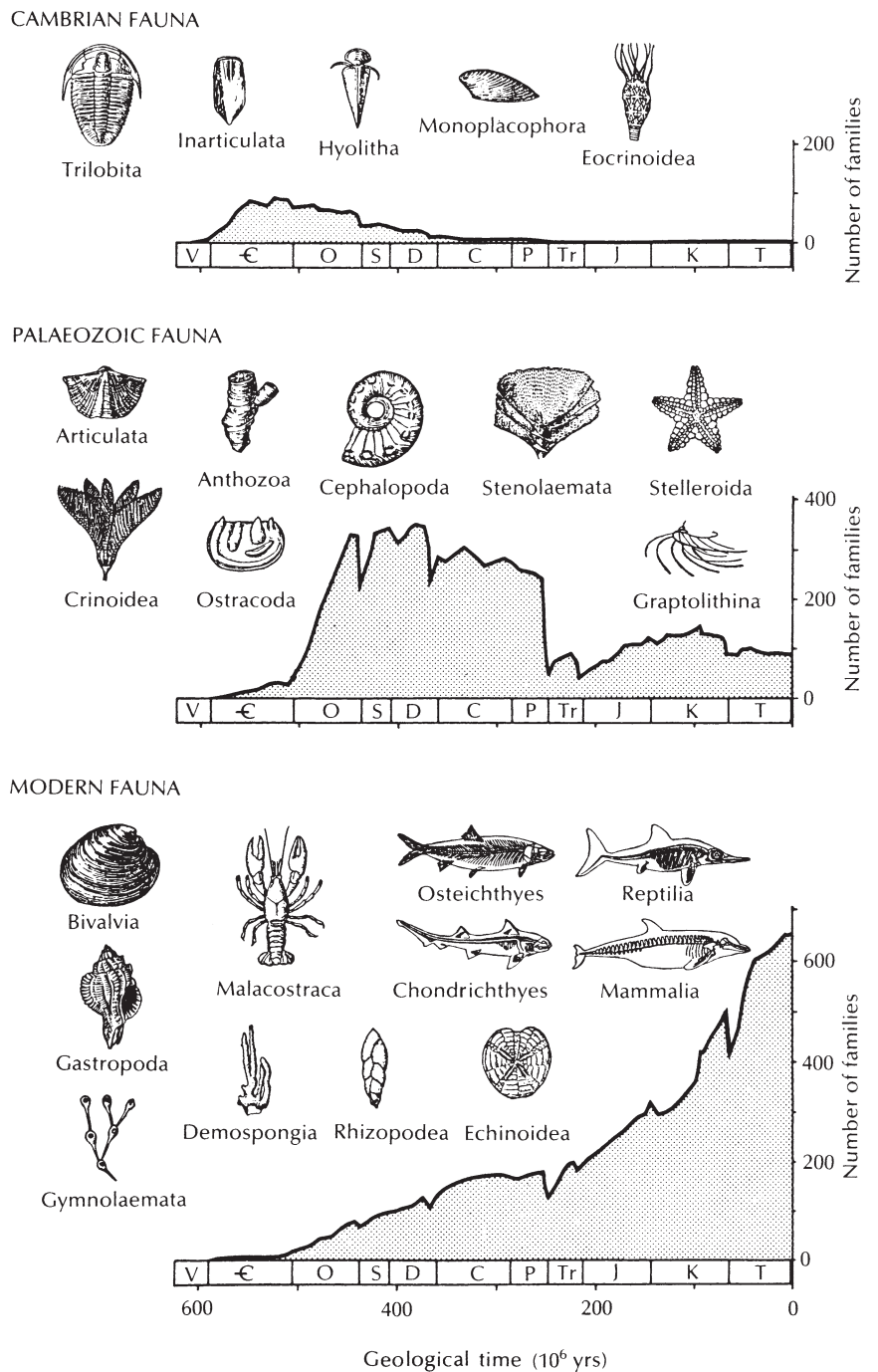


Fig 2 Histories of the three great evolutionary faunas of the marine fossil record as represented by their familial diversities through the Phanerozoic. Representatives of the important classes in each fauna are illustrated above the diversity curves. (After Sepkoski 1984.)

taxa diversified (e.g. the Monoplacophora) or contained monophyletic subtaxa that diversified in parallel with the rest of the evolutionary fauna (e.g. the Inarticulata). The Cambrian Fauna diversified very rapidly from the latest Vendian into the Early Cambrian and was the principal constituent of the 'evolutionary explosion' across the Precambrian–Cambrian Boundary (see also Section 1.5). Its maximum diversity was attained in the late Middle and early Late Cambrian. Beginning in the latest Cambrian, the fauna began a long, gradual decline, accentuated by the Ashgillian and Frasnian mass extinctions (Sections 2.13.2, 2.13.3).

The Palaeozoic Fauna initiated its expansion as the Cambrian Fauna began to decline; this combination resulted in nearly stable global diversity throughout the Late Cambrian. The Palaeozoic Fauna was dominated by articulate brachiopods with important contributions from crinoids, corals, ostracodes, cephalopods, and stenolaemate bryozoans. These groups were major components of the Ordovician radiations, which tripled global taxonomic diversity over a 50 million year interval. The Palaeozoic Fauna attained its maximum diversity from the Late Ordovician to Devonian and then began a long decline. During the Carboniferous and Permian, this decline was matched by a slow expansion of the Modern Fauna so that again global diversity remained nearly constant. The Palaeozoic Fauna was severely reduced by the Late Permian mass extinction (Section 2.13.4) but in the Mesozoic underwent two radiations: one in the Triassic, terminated by the Norian mass extinction (2.13.5), and a second, slower expansion in the Jurassic. The Jurassic expansion was reversed in the Cretaceous when global diversity exceeded Palaeozoic levels, and the remnants of the Palaeozoic fauna again went into decline.

The Modern Fauna is dominated by gastropod and bivalve molluscs, osteichthyan and chondrichthyan fishes, gymnolaemate bryozoans, malacostracans, and echinoids. Most of these classes appeared during the Cambrian and Ordovician Periods but diversified only slowly through the Palaeozoic Era. They suffered minor extinction relative to the Palaeozoic fauna during the Late Permian and became the dominant fauna in the Triassic. Through the Mesozoic and Cenozoic, the Modern Fauna continued the rather slow and steady diversification initiated earlier, producing the long post-Palaeozoic increase in global taxonomic diversity.

Throughout their histories, the three 'great' evolutionary faunas experienced considerable internal

turnover, with continuous change in ordinal and lower-level taxonomic composition. This was particularly true of the Cambrian Fauna, which underwent very rapid changes during its initial radiation. It may prove useful to subdivide this fauna and define two more evolutionary faunas: an Ediacaran Fauna, encompassing the distinctive soft-bodied animal fossils of the Vendian (Sections 1.3, 1.5), and a Tommotian Fauna, comprising the mostly problematical skeletal taxa of the earliest Cambrian (Sections 1.4, 1.5, 5.2.5). These possible faunas seem to fit into the general progression of evolutionary rates and diversity levels observed for the three great evolutionary faunas. The Ediacaran and especially Tommotian taxa appear to have had higher diversification rates and more rapid evolutionary turnover than the remainder of the Cambrian Fauna, and seem to show successive increases in diversity leading into the Cambrian Period. Further analysis of diversity patterns and faunal change in the Vendian and Early Cambrian are needed to assess whether such additional evolutionary faunas are useful for describing the early metazoan radiation.

Terrestrial biotas

The concept of evolutionary faunas has proved useful for organizing faunal turnover and diversity change in the marine record and has been extended with varying success to other evolutionary systems, specifically terrestrial vascular plants and tetrapod vertebrates. Niklas *et al.* (1983) identified four major plant groups, which can be termed evolutionary *floras*, in species-level data on tracheophyte diversity (Fig. 1B). These are: (1) an initial Silurian–Devonian flora of early vascular plants that radiated and then disappeared during the Devonian; (2) a pteridophyte-dominated flora, including ferns, lycopods, sphenopsids, and progymnosperms, that diversified in the Late Devonian and Early Carboniferous and dominated plant communities to the end of the Palaeozoic Era; (3) a gymnosperm-dominated flora of seed plants that appeared in the Late Devonian and rose to dominance in the Mesozoic; and (4) an angiosperm flora that originated in the Early Cretaceous and rapidly radiated to dominance thereafter, replacing the preceding gymnosperm flora. As in the marine system, each of these floras (excepting the angiosperms) originated early in the history of vascular plants and radiated sequentially to produce step-like increases in global tracheophyte diversity.

Three 'assemblages' of terrestrial tetrapod families

have been identified by Benton (1985) in the vertebrate fossil record (Fig. 1C). These comprise: (1) the labyrinthodonts, anaspids, and synapsids, which appeared during the Middle Palaeozoic and completely dominated the terrestrial vertebrate record to the end of the Palaeozoic; (2) the early diapsids, dinosaurs, and pterosaurs, which arose in the Triassic, attained maximum diversity in the Late Jurassic and Cretaceous, and disappeared at the terminal Cretaceous mass extinction (Section 2.13.7); and (3) the lissamphibians, turtles, crocodiles, lizards, birds, and mammals, which originated in the Triassic and Jurassic, expanded through the Cretaceous, and then diversified to very high levels in the Cenozoic. Although these assemblages have some similarities to marine evolutionary faunas, there are some important differences: the assemblages do not all appear early in the history of tetrapods and their sequential diversifications are not all associated with step-like increases in global diversity. It remains to be seen whether such patterns could be identified if more terrestrial taxa (e.g. the arthropods) were included and analyses performed at lower taxonomic levels. If so, evolutionary

faunas and floras would appear to be a general property of the development of Phanerozoic biotas.

References

- Benton, M.J. 1985. Patterns in the diversification of Mesozoic non-marine tetrapods and problems in historical diversity analysis. *Special Papers in Palaeontology* 33, 185–202.
- Bottjer, D.J. & Ausich, W.I. 1986. Phanerozoic development of tiering in soft substrata suspension-feeding communities. *Paleobiology* 12, 400–420.
- Niklas, K.J., Tiffney, B.H. & Knoll, A.H. 1983. Patterns of vascular land plant diversification. *Nature* 303, 614–616.
- Sepkoski, J.J., Jr. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7, 36–53.
- Sepkoski, J.J., Jr. 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* 10, 246–267.
- Tevesz, M.J.S. & McCall, P.L. (eds) 1983. *Biotic interactions in recent and fossil benthic communities*. Plenum Press, New York.
- Valentine, J.W. (ed.) 1986. *Phanerozoic diversity patterns: profiles in macroevolution*. American Association for the Advancement of Science and Princeton University Press, Princeton.
- Vermeij, G.J. 1987. *Evolution and escalation. An ecological history of life*. Princeton University Press, Princeton.

1.7 Early Diversification of Major Marine Habitats

1.7.1 Infauna and Epifauna

W. I. AUSICH & D. J. BOTTJER

Introduction

Benthic marine habitats and the organisms that populate them represent an intricate and diverse ensemble. Much of the initial development and diversification of metazoans was for life in this realm. Marine benthos have invaded most types of substratum at depths ranging from the supertidal to abyssal. This array of habitats, with concomitant physical and chemical limiting factors, has probably been relatively constant through most of the Phan-

erozoic. Similarly the general trophic strategies for exploitation of marine benthic habitats has been constant. Both infaunal and epifaunal organisms developed, including suspension feeders, deposit feeders, predators, scavengers, grazers, and others. However, through eustatic changes in sea-level and plate motion in the lithosphere, the habitat location has been constantly changing.

The great diversity in this benthic system is contributed by organisms. At any one time organisms

differentially adapt to a plethora of physical, chemical and biological limiting factors. The development of simple to complex ecological structuring within habitats is variable; and, of course, through evolution and extinction, the organisms populating benthic habitats have been continually in flux.

The benthic habitat

The infauna. In modern environments particulate organic material is abundant immediately above and below the sediment–water interface and decreases in quantity both up into the water column and down into the sediment (Fig. 1). Both suspension feeders and deposit feeders exploit this resource. Infaunal deposit feeders mine particulate organics within the sediment, whereas infaunal suspension feeders typically feed from the water that is immediately above. The primary physical constraints on depth of burrowing are the position of the redox boundary, and sediment stiffness, which increase with depth. Phylogenetic constraints on the development of specialized structures (e.g. fused siphons) have also been important in the history of the infauna.

Infaunal suspension feeders are largely stationary. They all feed as active suspension feeders from water immediately above the sediment surface, and particulate food in that water moves past them horizontally. In contrast, infaunal deposit feeders are mobile, and they feed on a stationary food

resource scattered through the upper part of the sediment column (Bottjer & Ausich 1986).

Durophagous predation, space competition, and adaptation to conditions in the intertidal zone are considered to have been important influences in the development of infauna and in changes in infaunal tiering structure. Increased durophagous predation pressure led to greater infaunalization of the benthos and may have also promoted the development of more complex infaunally tiered communities. Different authors have argued either that densities of infaunal bivalves are generally too low for space competition to be important, or that space competition can be important to avoid interference competition among suspension feeders which all feed from the same basic resource (Bottjer & Ausich 1986). For infaunal deposit feeders, space competition may be much more important.

The initiation of deep burrowing may have resulted from adaptations to life in the intertidal zone, where regular fluctuations in the water table are driven by the tidal cycle. Organisms in the intertidal zone track these water table changes. The ability of infauna to cope with such conditions may have preadapted them to medium- and deep-burrowing habits in the subtidal zone (Bottjer & Ausich 1986).

The epifauna. Epifaunal suspension feeders live within the benthic hydrodynamic boundary layer, i.e. the zone of diminished current velocity caused by drag across the bottom. Current velocities are

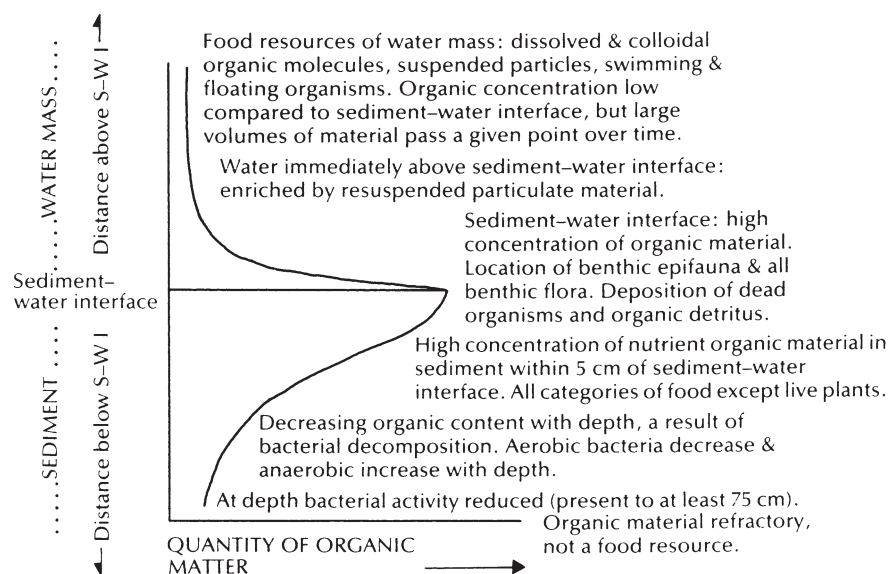


Fig. 1 Location of food resources with respect to the sediment–water interface. (From Walker & Bambach 1974.)

lowest immediately above the sea floor and increase upward into the water column (Fig. 2). The thickness of the boundary layer is a function of factors such as current velocity and substratum roughness; however, velocity always decreases toward the ocean floor. Given equal concentrations of particulate organics, more food would be available to a suspension feeder where current velocities were greater, i.e. higher within the boundary layer; however, particulate organics generally increase toward the ocean floor. In this physical setting epifaunal suspension feeders, which are largely stationary, must exploit a food resource that is moving past them horizontally at specific distances above the sediment–water interface.

Many constraints and processes are likely to have been important for the development and maintenance of epifaunal tiering (Bottjer & Ausich 1986). Phylogenetic constraints on structural materials and modes of growth, as well as the biomechanical properties of structural materials, strongly influence the height to which organisms can reach above the sea floor. The mode of growth and whether organisms are clonal or aclonal are important constraints controlling an organism's exploitation of food resources within the benthic boundary layer. Only clonal organisms (e.g. bryozoans, corals), and aclonal organisms that grow by addition of new parts (e.g. stalked echinoderms) have been able to develop medium- to high-tiered forms (Bottjer & Ausich 1986; see also Sections 4.5, 4.16).

The mode of suspension feeding also appears to be correlated with utilization of epifaunal resources. Three basic suspension feeding modes have been defined: passive, facultatively active, and active. Passive suspension feeders rely completely on ambient currents for food supply, whereas facultatively active suspension feeders rely to a large extent on ambient currents but also pump a weak current of water into the filtration apparatus. Active suspension feeders rely on pumping water. Ecological studies and documentation of the historical record (Bottjer & Ausich 1986) show that passive and facultatively active suspension feeders alone develop morphologies to become high level primary tier feeders in the epifauna. In contrast, active suspension feeders are dominant low in the boundary layer.

Competition, in conjunction with other processes and constraints, has surely played a key role in the development of ecological structure in epifaunal benthos. Space, a place from which to feed, and food competition have been important for suspen-

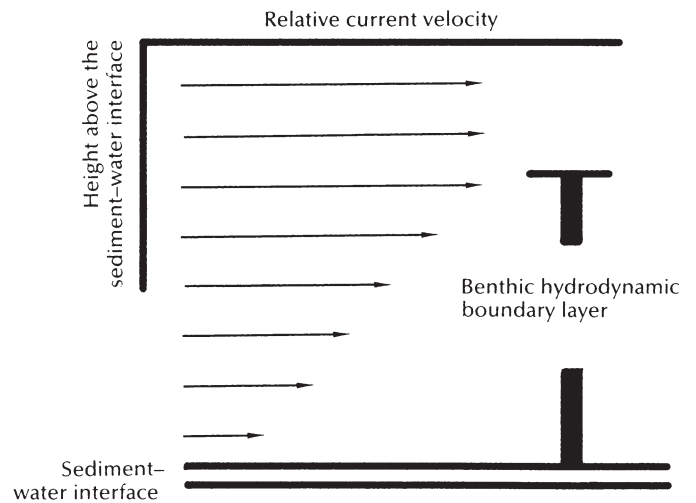


Fig. 2 Velocity profile of the benthic hydrodynamic boundary layer.

sion feeding benthos on soft substrata (Bottjer & Ausich 1986).

Tiering. Spatial separation and structuring is a common biological method of resource partitioning within communities. Vertical community structure has been documented for epifaunal and infaunal suspension feeding communities (Bottjer & Ausich 1986) and infaunal deposit feeding communities (Levinton & Bambach 1975). Bottjer & Ausich (1986) called this spatial arrangement of organisms tiering. They developed a history of tiering complexity through the Phanerozoic for suspension feeding palaeocommunities in soft substrata, deposited in subtidal shelf and epicontinental sea settings at depths greater than several metres below fair-weather wave base (Fig. 3). A comprehensive Phanerozoic history of tiering for deposit feeding palaeocommunities in these environments has yet to be compiled. Evidence for such a history, which must come primarily from studies on various features of bioturbation (cross-cutting relationships of trace fossils, burrow depths, extent of reworking) is currently being developed (e.g. Crimes & Anderson 1985; Wetzel & Aigner 1986; Droser & Bottjer 1988).

The suspension feeder tiering history (Fig. 3) displays the maximum heights and complexity of tiering in a characteristic benthic palaeocommunity at various times. Physically dominated settings are unlikely to support a biota with this maximum development of tiering complexity. The tiering history is of primary tier feeders (Bottjer & Ausich 1987), which are organisms whose body or burrow intersects the sea floor. Although detailed tiering

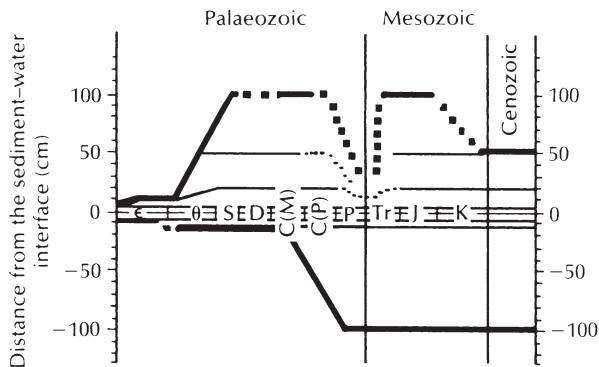


Fig. 3 Tiering in soft-substrata suspension-feeding communities through the Phanerozoic. The heaviest lines represent the maximum level of tiering above or below the substratum at any time. Other lines represent levels of tier subdivision. Solid lines represent data, and dotted lines are inferred levels. (From Bottjer & Ausich 1986.)

histories have not been compiled for other major environmental settings, such as reefs or hard-grounds, they should reflect the relative changes in suspension feeder tiering.

Faunal histories and ecological structure

Faunal diversifications and the history of benthic faunal ecological structure can be understood best in the context of temporally distinct faunas, which include the following: Vendian Fauna, Tommotian Fauna, Cambrian Fauna, Palaeozoic Fauna, and Modern Fauna. Sepkoski (1984; Section 1.6) defined the Cambrian Fauna, Palaeozoic Fauna, and Modern Fauna based on familial diversities.

Vendian Fauna. Fossils of the first benthic 'metazoans' are known from the Vendian (c. 620–570 Ma). This fauna (Sections 1.3, 1.5) was initially best described from the Ediacaran Hills in South Australia, but is now recognized world-wide (Glaessner 1984). Glaessner (1984, page 52) recognized 31 named species from the vicinity of Ediacara and assigned these fossils principally to modern metazoan groups, including Hydrozoa, Scyphozoa, Conulata, colonial Cnidaria, Polychaeta, and Arthropoda. Seilacher (1984) offered a sharply contrasting interpretation for the Vendian Fauna. He argued that many fossils interpreted as medusoids are actually trace fossils and that the non-medusoid fossils represent a clade distinct from all extant metazoans.

Clearly the zoological affinities and autecology

of Vendian taxa must be understood before community ecological structure can be reconstructed. However, whatever the trophic habit of members of the Vendian Fauna, it is apparent that Vendian communities displayed some ecological structure. *Charniodiscus* and *Glaessnerina* species apparently attained variable heights above the sea floor. Maximum preserved heights of individuals include the following: *G. grandis*, 16 cm; *C. longus*, 25 cm; *C. arboreous*, 60 cm. Other organisms lived directly on the bottom. It is possible that this height distinction among members of the Vendian Fauna may represent an ecological structuring analogous to epifaunal tiering.

The widely distributed Vendian Fauna apparently suffered major extinction (if not total extinction; Seilacher 1984) at the end of the Proterozoic (Section 2.13.1). The Phanerozoic record of benthic faunas has always been significantly different from that present during the Vendian.

Trace fossils from the Vendian are Palaeozoic in affinity and indicate that a worm-like fauna of shallow-burrowing deposit feeders existed during this time (Glaessner 1984). Vertical dwelling burrows are generally lacking, indicating that infaunal suspension feeders were rare or had not yet developed. Thus, at most a shallow infaunal tier of deposit feeders existed, up to several centimetres below the sediment–water interface, in soft substrata Vendian environments.

Tommotian Fauna. The first major occurrence of fossilized metazoan hard parts was during the Tommotian at the base of the Cambrian (c. 570 Ma). The Tommotian Fauna preceded the first occurrence of trilobites, which was approximately at the base of the Atdabanian (c. 560 Ma) (Conway Morris 1987). This fauna (Sections 1.4, 1.5) is recorded by a variety of very small, principally phosphatic skeletons. Characteristic taxa include small conical shells such as *Protohertzina* and *Anabarites*, inarticulate brachiopods, the sclerites of *Lapworthella*, archaeocyathids, and trace fossils (e.g. McMenamin 1987). Like the Vendian Fauna, the Tommotian Fauna has recently been documented to occur worldwide.

More autecological study on elements of the Tommotian Fauna is necessary before the palaeoecological structure of these early Phanerozoic communities can be fully understood. Problems include (1) which of the component taxa are skeletal remains of single organisms and which are sclerites of some larger creature (for example *Halkieria*; Conway Morris 1987); and (2) the autecology and

functional morphology of Tommotian organisms that have no clear living counterpart.

Regardless of shortcomings in the detailed understanding of the Tommotian Fauna, it is clear that it represents the initial establishment of the basic benthic ecological structure, albeit simple and composed of small organisms, that would characterize the remainder of the Phanerozoic. The Tommotian Fauna includes sessile and mobile forms, simple suspension feeders such as *Sinotubulites*, more complex suspension feeders such as archaeocyathids and inarticulate brachiopods, and predators such as *Protohertzina* (McMenamin 1987).

Tommotian skeletons and skeletal elements are typically smaller than one centimetre. Epifaunal suspension feeders were confined to the lowest levels within the benthic boundary layer and were probably characteristically within the 0 to +5 cm tier of Bottjer & Ausich (1986). Trace fossils associated with Tommotian faunas indicate that the initial appearance of vertical burrows 4–5 cm deep occurred during this time (McMenamin 1987) in near-shore settings above fairweather wave base. In general, though, trace fossils formed in soft substrata settings below normal wave base appear to penetrate depths no greater than several centimetres in the substrate (e.g. Crimes & Anderson 1985); thus the 0 to –6 cm tier of Bottjer & Ausich (1986) was present for both suspension and deposit feeders.

Cambrian Fauna. Whether driven by ecological processes, general laws of size increase, or intrinsic diversification after approximately 10 million years, the Tommotian Fauna was replaced by the Cambrian Fauna. The Cambrian Fauna represents a diversification of metazoans and an increase in body size of benthos, both of which resulted in more complex benthic communities. From analysis of familial diversities, dominant faunal elements in the Cambrian Fauna include trilobites, inarticulate brachiopods, hyolithids, monoplacophoran molluscs, eocrinoid echinoderms, and archaeocyathids. The Cambrian Fauna dominated the benthic habitat for approximately 55 million years.

Typical preservation of a Cambrian benthic community reveals a simple tiering structure; a relatively simple structure is also evident in the Burgess Shale fauna despite preservation of the soft-bodied faunal component (Section 3.11.2). Tiering levels for both epifaunal and infaunal suspension feeders remained quite low (Bottjer & Ausich 1986). Two tier levels are defined for epifaunal suspension feeders: 0 to

+5 cm, and +5 to +10 cm (see Fig. 4). The +5 to +10 cm Cambrian tier included eocrinoids, edrioasteroids, crinoids, archaeocyathids, and sponges (Figs 4, 5). The 0 to +5 cm suspension feeders included, among others, a variety of echinoderms, sponges, archaeocyathids, and inarticulate brachiopods.

Infaunal suspension feeders were also close to the sediment–water interface during the Cambrian. Only the –6 cm tier was occupied in environments below fairweather wave base (Bottjer & Ausich 1986). Droser & Bottjer (1988) reported that in Cambrian inner and middle shelf carbonate deposits of western U.S.A. bioturbation occurs at depths no greater than 6 cm. If these results are typical for such Cambrian environments, they indicate the continued presence of the 0 to –6 cm tier for both deposit and suspension feeders through the Cambrian. In contrast, deeper *Skolithos*, possibly made by deposit feeders, is abundant in Cambrian strata deposited in nearshore settings above fairweather wave base, forming the typical pipe-rock.

Palaeozoic Fauna. The Palaeozoic Fauna (Sepkoski 1984; Section 1.6) characterized benthic habitats from the Ordovician to the Permian and was dominated by articulate brachiopods, crinoids, anthozoans, ostracodes, cephalopods, stenolaemate

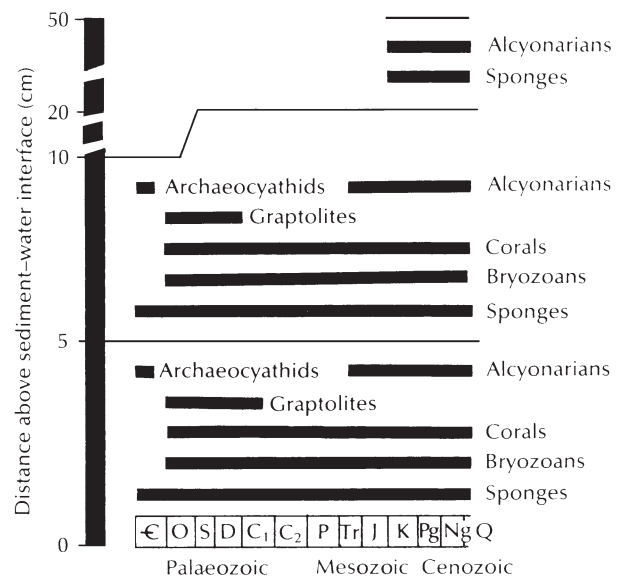


Fig. 4 Tiering history of Phanerozoic colonial suspension feeders on soft substrata from non-reef, shallow subtidal shelf, and epicontinental sea settings. Vertical distribution within each tier is arbitrary and only implies occupation in a tier for the duration indicated. (From Bottjer & Ausich 1986.)