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Ediacaran biota: The dawn of animal life in the shadow of giant protists

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Abstract. Functional, constructional, and preservational criteria led to a reinterpretation of seemingly complex trace fossils and the majority of assumed metazoan body fossils from Vendian lagerstatten. In the new scenario, Ediacaran biota were dominated by procaryote biomats and giant protozoa (Xenophyophoria and Vendobionta), which developed a great variety of shapes and lifestyles in the climatically controlled "golden age" that followed the Marinoan snowball earth. Contemporary metazoans (sponges; polyps; soft-bodied mollusks; possible echinoderms; worm-like burrowers) were adapted to this non-uniformitarian environment, but they remained scarce and relatively small. Some phyla (arthropods, brachiopods) appear to have still been absent. Our study also accentuates the Cambrian Explosion, which put an end to the peaceful "Garden of Ediacara". Not only did the former rulers become extinct or restricted to less favorable environments, but the radiation of metazoan phyla was also accompanied by an ecological revolution that established a new and more dangerous world, which persists to the present day.

Key words: Cambrian explosion, Ediacaran fossils, macroevolution

Introduction

"The Dawn of Animal Life" was the title of Martin Glaessner's (1984) fundamental book, in which he summarized the knowledge of his time about Precambrian fossils. In the meantime, much new material has come to light in Ediacara-type lagerstätten all over the world. Yet, Glaessner's view still prevails: that, however strange, the large and "complex" Ediacaran fossils must in some way represent the stem groups of later metazoans (Fedonkin, 1987; Gehling, 1991; Jenkins, 1992; Runnegar, 1995).

In the present overview we show how this scenario may have to be changed in the light of ecological and taxonomic reinterpretations.

Metazoa

There is no doubt that animal phyla had already a long history when they appeared almost instantaneously in the Lower Cambrian fossil record. This is shown by molecular evidence (Conway Morris, 2000), trace fossils, fecal pellets, metazoan embryos (Xiao and Knoll, 2000) and a number of body fossils of the Late Proterozoic that can be directly compared to later occurrences—not only with regard to general morphology, but also in a functional sense. The following list of Vendian Metazoa excludes the Xenophyophoria and Vendobionta (see below) and reinterprets a number of other Ediacaran fossils.

Porifera

By their low degree of organismic integration, sponges are to be expected early in evolution. Certain "death masks" (Gehling, 1999) from Ediacaran localities show poriferan features, while differing from later sponges by their discoid shapes and a possibly sandy skeleton.

Palaeophragmodictya from the Flinders Ranges (Gehling and Rigby, 1996) reaches 10 cm in diameter. It has a single osculum in the center and root-like radial extensions around the margin. Only in the largest specimens a quadrangular network of presumably hexactinellid spicules can be seen on the top surface. Lateral deformation during storm burial suggests that the body of *Palaeophragmodictya* was soft.

Members of another group, the Trilobozoa (Fedonkin,

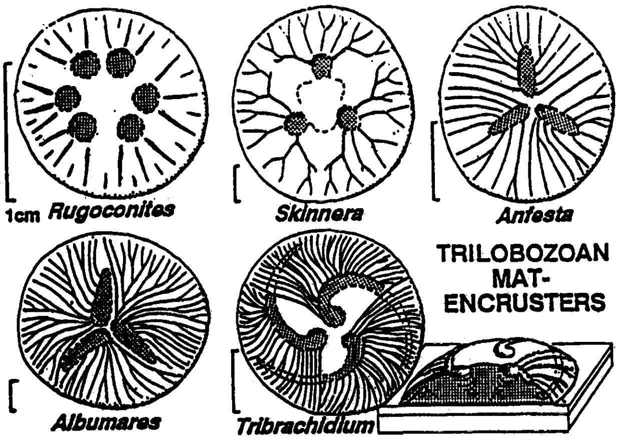


Figure 1. While the shield shape of Trilobozoa reflects their life style as mat encrusters, finer canals for inhalation and wider ones for exhalation correspond to the irrigation system of sponges. (From Seilacher, 1999).

1987), are too small for a spicular skeleton to be recognized. Instead, they show groove patterns that correspond to typical poriferan circulation systems (Figure 1). In this interpretation, the narrow canals merging towards the center would have transported the water to the flagellate chambers. In contrast, the wider canals would have drained the water towards the oscula, whose position around the top facilitated evacuation by the chimney effect. The fact that Trilobozoa are neither deformed by currents nor compactionally collapsed suggests a rigid and possibly sandy baseskeleton.

On the other hand, the shield shapes of *Palaeophragmodictya* and the Trilobozoa can be explained by attachment to resistant biomats that sealed the otherwise soft sediments in Precambrian times (Seilacher, 1999).

Coelenterata

Because diploblastic animals are to be expected early on and because Vendian lagerstatten were considered as beach deposits, medusae ranked high in early faunal lists. With one possible exception (D.G., in preparation) these round "medusoids" are now considered either as pseudofossils (*Pseudorhizostomites*), as attachment discs (*Aspidella*; Gehling *et al.*, 2000), or as other sessile organisms with concentric growth.

In contrast to medusae, solitary polyps are fairly well established. Assumed resting traces of actinians (*Bergaueria*; Narbonne and Hofmann, 1987, figure 5b) show not only the round outline of the body bag, but also its active lateral displacemant (Figure 2) within the sediment. Similar structures from earlier deposits in Namibia (Glaessner, 1988), however, are probably pot casts of

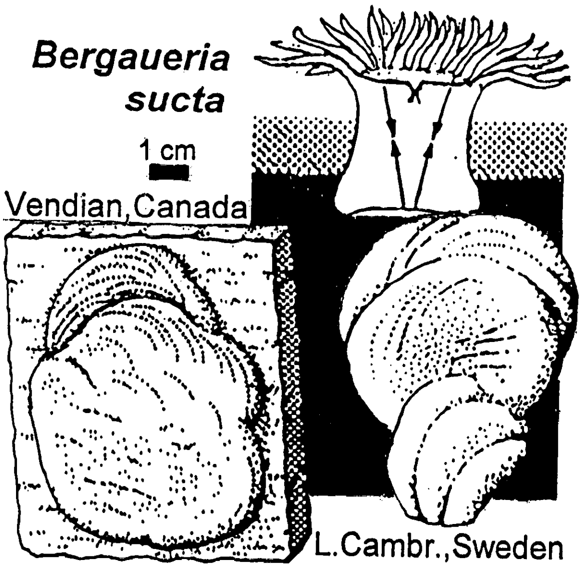


Figure 2. The interpretation of *Bergaueria* as the burrow of an actinian-grade animal is particularly convincing when there are traces of active lateral displacement. (After Narbonne and Hofmann, 1987, and a specimen in the Stockholm museum).

physical origin. Other soft, actinian-grade animals (*Inaria*, Gehling, 1988 ; Grazhdankin, 2000), are preserved as current-deformed death masks. They were attached to, or shallowly buried within, biomats. A third group, interpreted as passively implanting actinians with a massive mesogloeal sand skeleton (Psammocorallia; Seilacher and Goldring, 1996), is well represented in the Lower Cambrian. However, similar Vendian occurrences (*Nemiana*; Fedonkin, 1987) could also be microbially bound sand balls, i.e. rolling equivalents of biomats. A rare conulariid from the White Sea region (Ivantsov and Fedonkin, 2002), whose phosphatic pyramidal cup is three-dimensionally preserved, can be directly compared to Paleozoic members of this extinct coelenterate group.

Mollusks

Mineralized shells, which characterize mollusks in the Phanerozoic, are unknown before the Cambrian explosion. Nevertheless, the preservational conditions of Ediacaran mat grounds provide us with a unique record of soft-bodied ancestors. In *Kimberella* from the White Sea region (Figure 3), death masks of the ventral side show a flat foot with a ring of segmental muscles, whose contraction upon death produced equidistant wrinkles. Also impressed is the edge of a dorsal shield, which was soft enough to become deformed during burial (Fedonkin and Waggoner, 1997; Seilacher, 1999). In addition, associated radula scratches (*Radulichnus*), tell us that *Kimberella* grazed the

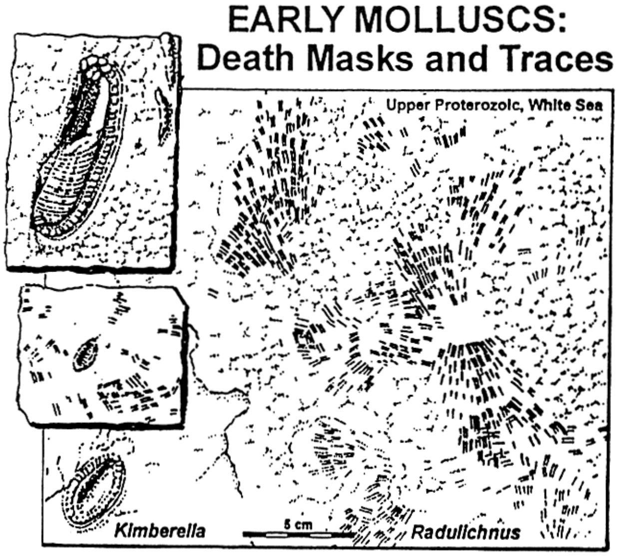


Figure 3. The molluscan nature of *Kimberella* is expressed by impressions of the flat foot and the margin of a soft dorsal shield seen in ventral deathmasks of the bodies. Associated conical scratch patterns (*Radulichnus*) show that the animal systematically grazed biomats with a long proboscis from a central station. Note that there are neither trails of the body nor scratches of smaller individuals. This is because they did not penetrate deep enough to produce undertracks at the base of the biomat, which is marked by elephant-skin structure. (After cast of a White Sea specimen in Tübingen collection).

microbial mats, which sealed otherwise soft sediments prior to the bioturbational revolution (Seilacher and Pflüger, 1994). These biomats were obviously soft enough to be scratched by radular teeth in stationary feeding with a long proboscis, but too tough for the heavy body to leave a trail. The fact that only the raspings of adult individuals are preserved confirms this view: juveniles did not scratch deep enough to produce a preservable undertrace at the base of the mucus-bound veneer. Ecologically, *Kimberella* can be interpreted as a "soft limpet" (Seilacher, 1999). Today this guild is restricted to rocky substrates, but it makes sense also on a tough Precambrian biomat.

Arthropoda

Ediacaran body fossils (*Spriggina, Parvancorina, Mialsemia, Vendia, Vendomia* etc.), commonly thought to be stem-group arthropods, are here interpreted as bilateral Vendobionts that grew by serial addition of new quilts at only one pole. In fact, none of them shows any appendages. Even more telling is the complete absence of arthropod trackways or burrows in Ediacaran deposits, because they do not require a hard skeleton to be formed and would be easy to recognize.

Figure 4. On a sole face from South Australia, the irregular hypichnial grooves made by worm-like undermat miners avoid *Tribrachidium* that was attached to the mat in the center of the picture. (Photo by Jim Gehling).

Echinodermata

The only candidate so far is *Arkarua*, which Gehling (1987) has described as an echinoderm because of its five-rayed symmetry. On the other hand, it resembles trilobozoans by its shield shape. In any case it expresses convergent evolution towards the Vendian lifestyle of mat encrusters, analogous to the skeletonized edrioasteroids that encrusted hard substrates in later times.

Worm burrows

After removal of the more complex forms (see below) there remains only a small number of relatively simple burrows that can be referred to the activity of worm-like animals (Figure 4). Their diversity becomes increased, if one interprets "*Aulozoon*" (Figure 5) as the actively backfilled burrow of a large flatworm. If the radiate *Mawsonites* is also a trace fossil, this would be the only form with a systematic search pattern.

In addition to their behavioral simplicity, all Precambrian

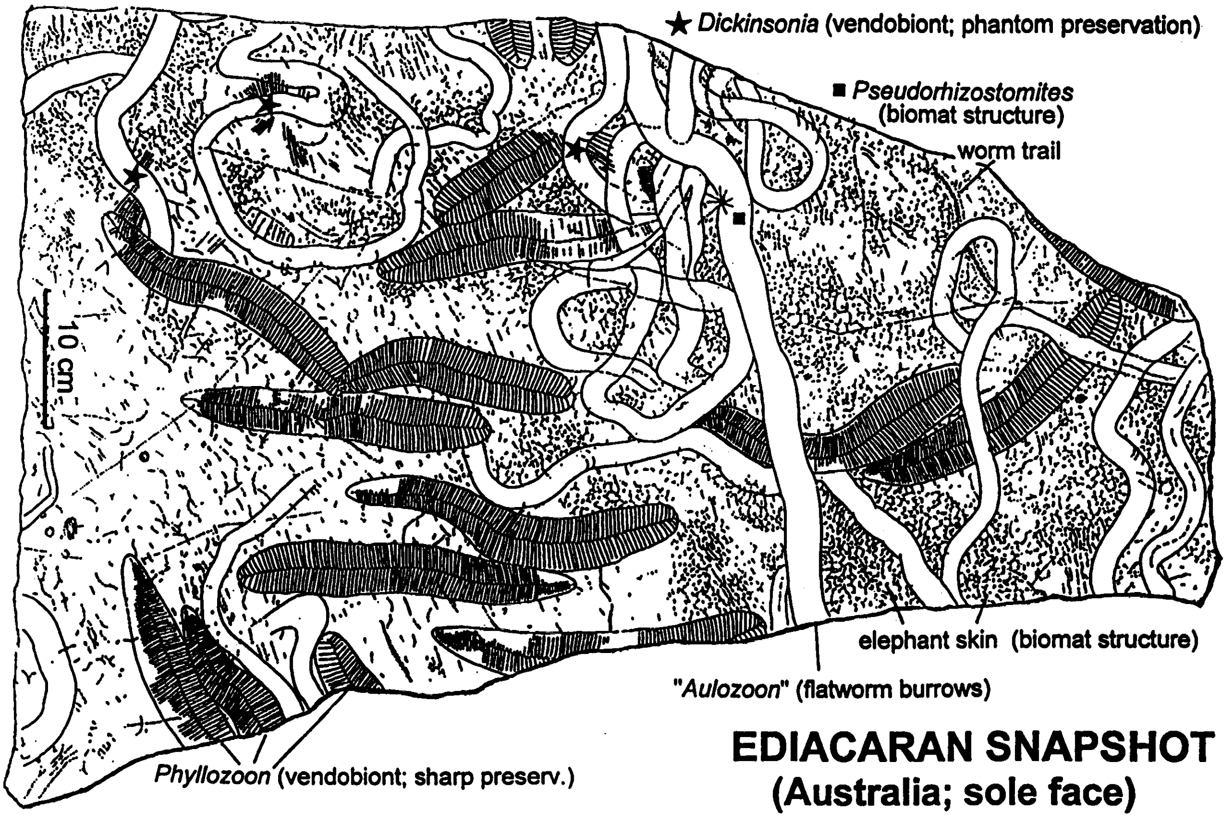


Figure 5. Sole surface from South Australia with nonoverlapping death masks of *Phyllozoon* and a few faint phantoms of *Dickinsonia*. The latter were presumably lying on top of the biomat, the former presence of which is indicated by elephant-skin structures. Note the more pointed growing ends and the uniform sizes in all individuals of *Phyllozoon*, which obviously belonged to the same generation. Associated sand-filled ribbons ("*Aulozoon*") either contour the stationary vendobionts or pass above and below them. They are interpreted as backstuffed burrows of large flatworms. (After cast of a slab analyzed by Jim Gehling and figured by Runnegar, 1994, fig. 3)

worm traces are restricted to single bedding planes. This does not mean that their makers crawled on the sediment surface. More likely they were undermat miners (Seilacher, 1999) eating the dead lower parts of the biomats and perhaps using the living upper part as an oxygen mask.

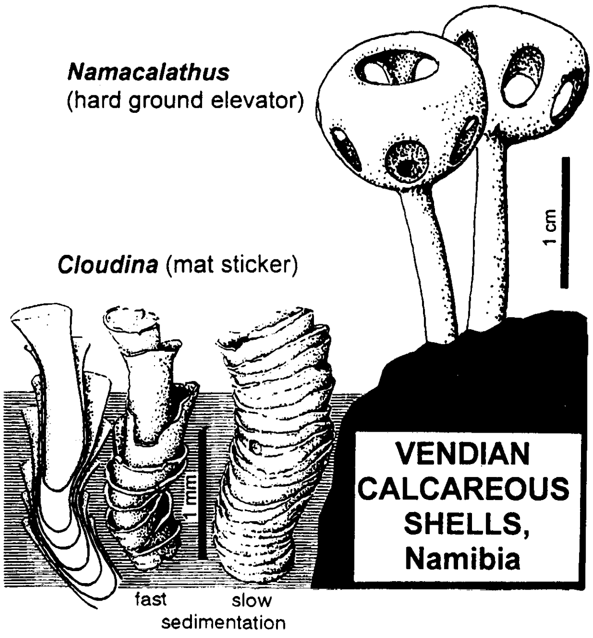
In summary, metazoans were certainly present in Vendian biota. Yet, their diversity becomes much reduced after the Vendobionta and Xenophyophoria have been removed (see below). They are also rare. After having studied hundreds of fossils on an excursion to the Newfoundland lagerstatten, a participating biologist stated that he had not seen a single clear metazoan body or trace fossil.

Protozoa

The statement that biomineralization emerged in the Cambrian Explosion applies only to metazoan phyla. Recent studies in Vendian carbonates (Grotzinger *et al.* 2000) have revealed millimetric calcareous skeletons of distinctive morphologies. The goblet-shaped *Namacalathus* (Figure 6) has been identified as a metazoan; but its shell does not fit the morphospace of accretionary growth and its affiliation remains problematic. Similarly unresolved is the taxonomic position of *Cloudina*, whose conical shell consists of stacked cones (Figure 6). In contrast, Porter and Knoll (2000) could show that vase-shaped microfossils from the Chuar Limestone and other localities are testate amoebae similar to the ones living today in freshwater environments. With familiar rhizopods being thus documented in Vendian times, our affiliation of much larger Vendian fossils with this group is perhaps more acceptable.

Requirements for unicellular gigantism

For physiological reasons, single cells are size-limited at a micrometric scale. Metazoans bypass this limit by cell division. Larger foraminifera of different clades (Figure 7) show us the tricks, by which excessive size can be reached in single cells.



(a) *Multinuclearity.* Multiplication of nuclei and their equal distribution in the protoplasm allows plasmodial organisms to manage larger volumes.

(b) *Cell Shape.* Since diffusion also limits the distance between any point in the protoplasm and the cell wall, protists cannot exceed a certain volume if they maintain a globular shape. This limit can be stretched by making the cell sausage-shaped.

(c) *Compartmentation.* Another trick to increase cell volume without exceeding the critical diameter is segmentation of the protoplasm. By the rhythmic growth of their chambered shells, foraminifers are preconditioned for this strategy. What changes in giant forms is the

← **Figure 6.** The irregular cone shape of *Cloudina* suggests that it lived as a mat-sticker. Note that growth of the minute calcareous shells proceeded not by marginal accretion, but by stacking of instant cups. In contrast, *Namacalathus* grew on hard substrates and could not secondarily enlarge its shell. (From Seilacher, 1999 and Grotzinger *et al.*, 2000).

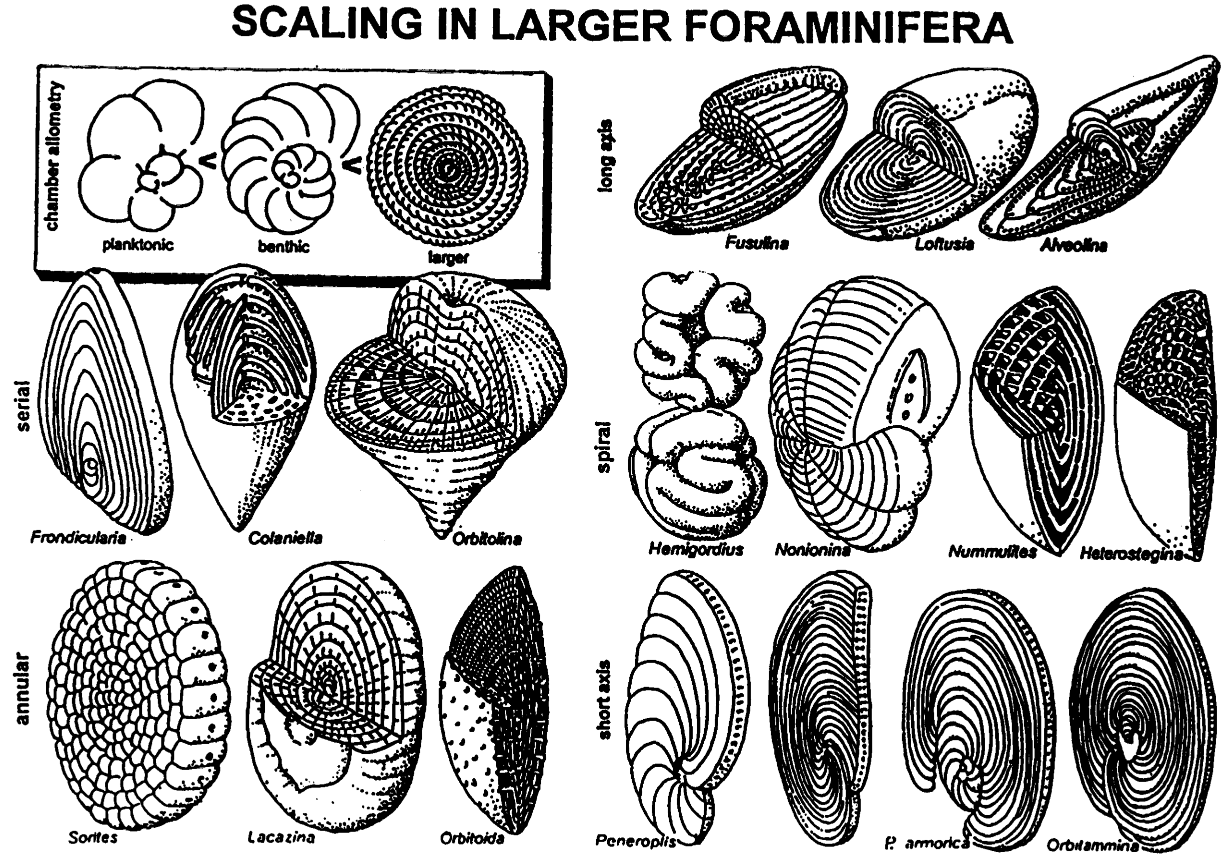


Figure 7. While subsequent chambers increase in size during shell growth of small Foraminifera, they maintain the same diameter in oversized ones (diagrams in upper left corner). All other examples illustrate how the limitation of chamber diameter is bypassed in various clades of larger forams.

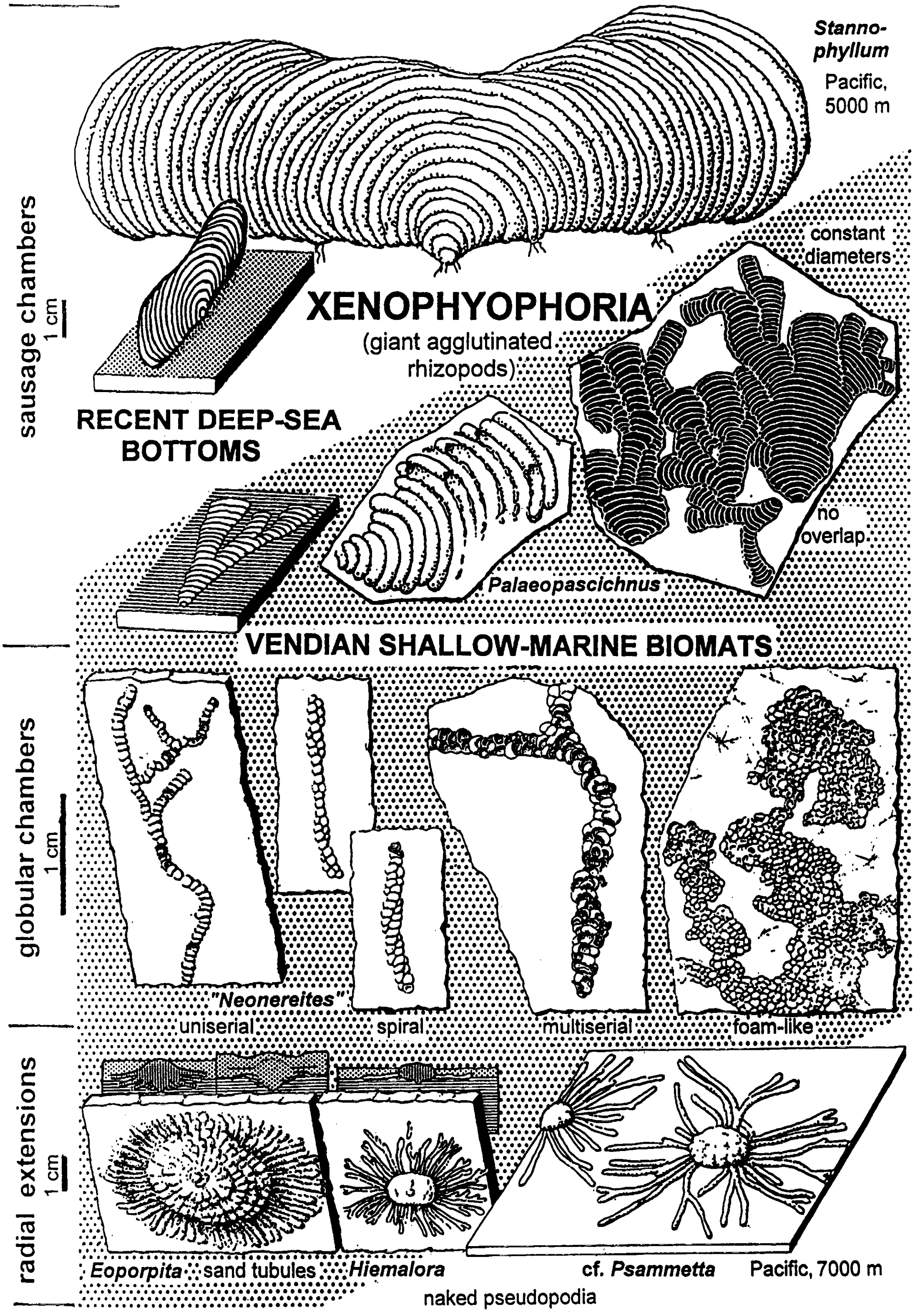


Figure 8. In modern xenophyophores, giant size is reached by allometric chambered growth (e.g. *Stannophyllum*); but chamber diameters can be much larger than in Foraminifera (Figure 7), because the actual compartmentalization of the protoplasm is effected by a fill skeleton (stercomare) of finer fecal sediment inside the chambers. Vendian representatives from the White Sea region (and elsewhere) lived embedded in biomats, so that the lower parts of their agglutinated tests could be preserved as hyporeliefs on the elephant-skinned base of the mat. Star-shaped fossils in the same preservation can be compared to modern xenophyophores, in which the protoplasm radiates either in the form of agglutinated tubules or of naked pseudopodia leaving traces in the sediment (After Tendal, 1972 and material in the Palaeontological Institute, Moscow).

transition from isometric to negatively allometric growth; *i.e.*, chamber diameters remain the same in all growth steps.

(d) *Fill Skeletons.* In addition, the spaces inside the sausage-shaped chambers of larger foraminifera are subdivided by secondary walls or pillars into still smaller units (chamberlets). The same effect could probably be reached by enclosing foreign material, such as sand, into the chambers.

(e) *Endosymbiosis.* Larger foraminifera of present times are restricted to shallow tropical seas, where they can employ photosynthetic symbionts for additional food supply. This appears to have been true also for fossil forms.

The same constraints apply, with modifications, to other oversized cells, such as deep-sea foraminifers with tubular tests (Komokiacea; Tendal and Hessler, 1977; Tendal, 1979), the quilted umbrella of the green alga *Acetabularia* (Serikawa and Mandoli, 1998; Dumais and Harrison, 2000) and the stroma cells forming echinoderm ossicles. So it is reasonable to use these criteria also in the interpretation of the problematic Vendian fossils discussed in the following sections.

Xenophyophoria

Xenophyophores are a group of marine rhizopodan protists that today are restricted to abyssal depths greater than 500 m down to more than 7,000 m (Tendal, 1972). Consequently, little is known about their biology (Levin *et al.*, 1986). It is well established, however, that their protoplasm contains *multiple nuclei.*

The leathery, agglutinated walls of xenophyophores also grow in a chambered (i.e. compartmented) fashion, but the diameters of their chambers and tubules are so big that they can be seen with the naked eye (Gooday and Tendal, 1988; Figure 8). The explanation for this difference in scale can be found in the xenophyophore's internal structure. As shown by Tendal (1972), their chambers do not only contain protoplasm, but also a kind of fill skeleton. Firstly, there are the *stercomata* consisting of fine sediment. They originate as fecal pellets during extracellular digestion and—in addition to their possible function as fermentation chambers (Tendal, 1979) — subdivide the protoplasm into narrow strands. Secondly, the protoplasm itself contains *granellae* of the insoluble mineral barite; they may act as a kind of fill skeleton that makes the plasma more consistent.

It is only due to their unusual chamber size that xenophyophoran tests can be recognized as fossils. On the other hand, they may easily be mistaken for trace fossils (Glaessner, 1969; Crimes, 1992, 1994; Fedonkin, 1977, 1990), because their agglutinated walls consist of the same material as the sediment surrounding them. In the case of Vendian forms (Figure 8; including *Neonereites*, *Intrites*, *Yelovichnus* etc.), the similarity with traces is further enhanced by the fact that they were enclosed in biomats and are therefore spread on bedding planes (Seilacher, 2000; Seilacher *et al.*, submitted). This habit also favored the preservation, as positive hyporeliefs on the base of the mat, of tests that in modern forms are so delicate that they hardly survive the mechanical stress of dredging: just as trace makers deform the interface between sand and mud layers, mat-inhabiting xenophyophores deform it by agglutinating the chamber walls with sand from above (Figure 9).

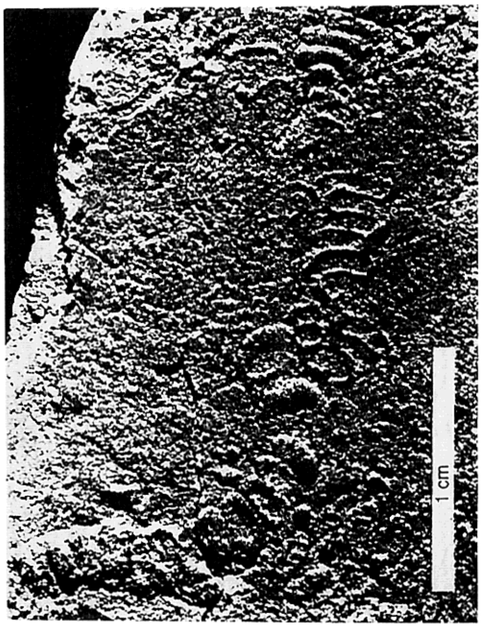


Figure 9. Xenophyophore (*Intrites*) on sole of a biomat with elephant-skin structures. Where the chamber bottoms are incompletely agglutinated or broken away, the remnants of the walls resemble meandering trails. White Sea, Winter Coast; scale 1cm (Palaeontological Institute, Moscow).

It had already been suspected that the Vendian forms in question are a kind of body fossils rather than trace fossils (Gehling *et al.*, 2000). The new claim that they are xenophyophores provides not only another example of onshore-offshore migration (Sepkoski and Sheehan, 1983); xenophyophore construction also sheds new light on the nature of the controversial Vendobionta.

Vendobionta

Typical Ediacaran biota are dominated in numbers, body size, and morphological diversity, by strange organisms whose regular and seemingly complex structure invites comparison with animals of various phyla (coelenterates;

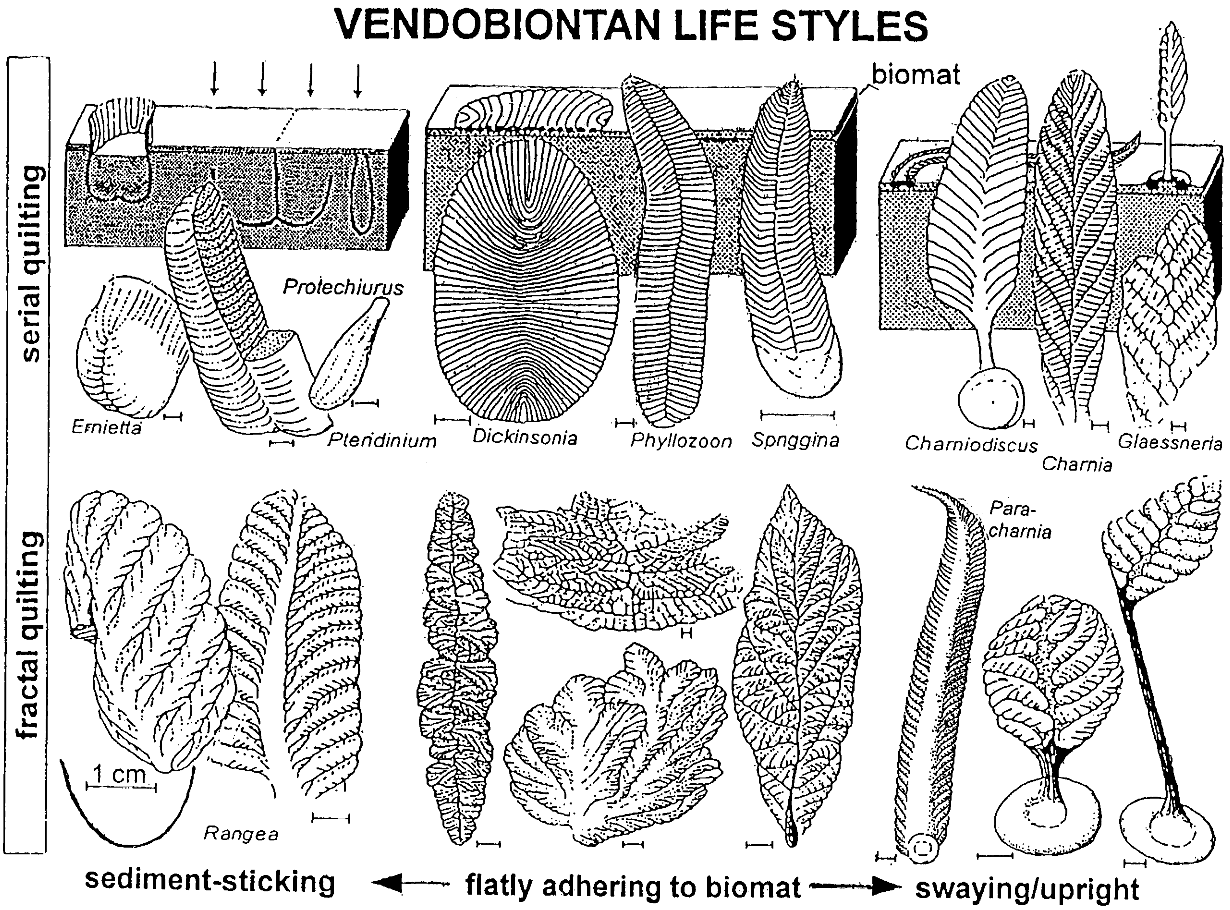


Figure 10. Both groups of vendobionts, the ones that grew by serially adding sausage-shaped chambers of fixed diameters and the ones expanding and fractally subdividing established quilts, developed different life styles in the Precambrian matground world (modified from Seilacher, 1992).

annelids; arthropods; Fedonkin, 1987). In detail, however, neither preservational features nor functional considerations fit metazoans of similar morphologies (Seilacher, 1989). On the other hand, all these "Vendobionta" (Seilacher, 1992; = Petalonamae Pflug, 1972) share a foliate and quilted construction with chambers being strongly allometric, so that they maintain the same diameters in bodies growing to many times their original size. Therefore it has been claimed (Seilacher, 1992) that we deal with giant unicellulars compartmenting their protoplasm by quilting a flexible organic wall. With this basic construction, vendobionts managed to explore a wide spectrum of ecological strategies (Figure 10). Most forms adhered flatly to biomats, while others developed a discoidal holdfast, on which they could elevate themselves in a plantlike fashion into the water column (Seilacher, 1999). Series of impressions discovered by Ivantsov (1999) even suggest that some carpet-like species had some mobility that allowed them to digest new areas of the underlying microbial mat. In a third group, the organism was completely immersed in sand (Grazhdankin and Seilacher, 2002), where chemosymbiosis might have been adopted as an alternative metabolism .

While detailed studies of the infaunal Namibian forms (Grazhdankin and Seilacher, 2002) confirmed the vendobiont hypothesis, the phyletic affiliation of these strange organisms remained in limbo. An earlier suggestion to consider them as a lost kingdom, or phylum (Seilacher, 1992), was only an unsatisfactory escape out of a taxonomic dilemma. What, exactly, are their closest living relatives? Comparison of the vendobionts with xenophyophores now brings us closer to an answer.

In principle, the allometric compartmentation of vendobiontan fronds was a valid argument for unicellularity (Figure 10); but it had one weakness: the quilts are much larger in diameter than the chambers of larger foraminifera. If maximum diameters are constrained by the physiology of

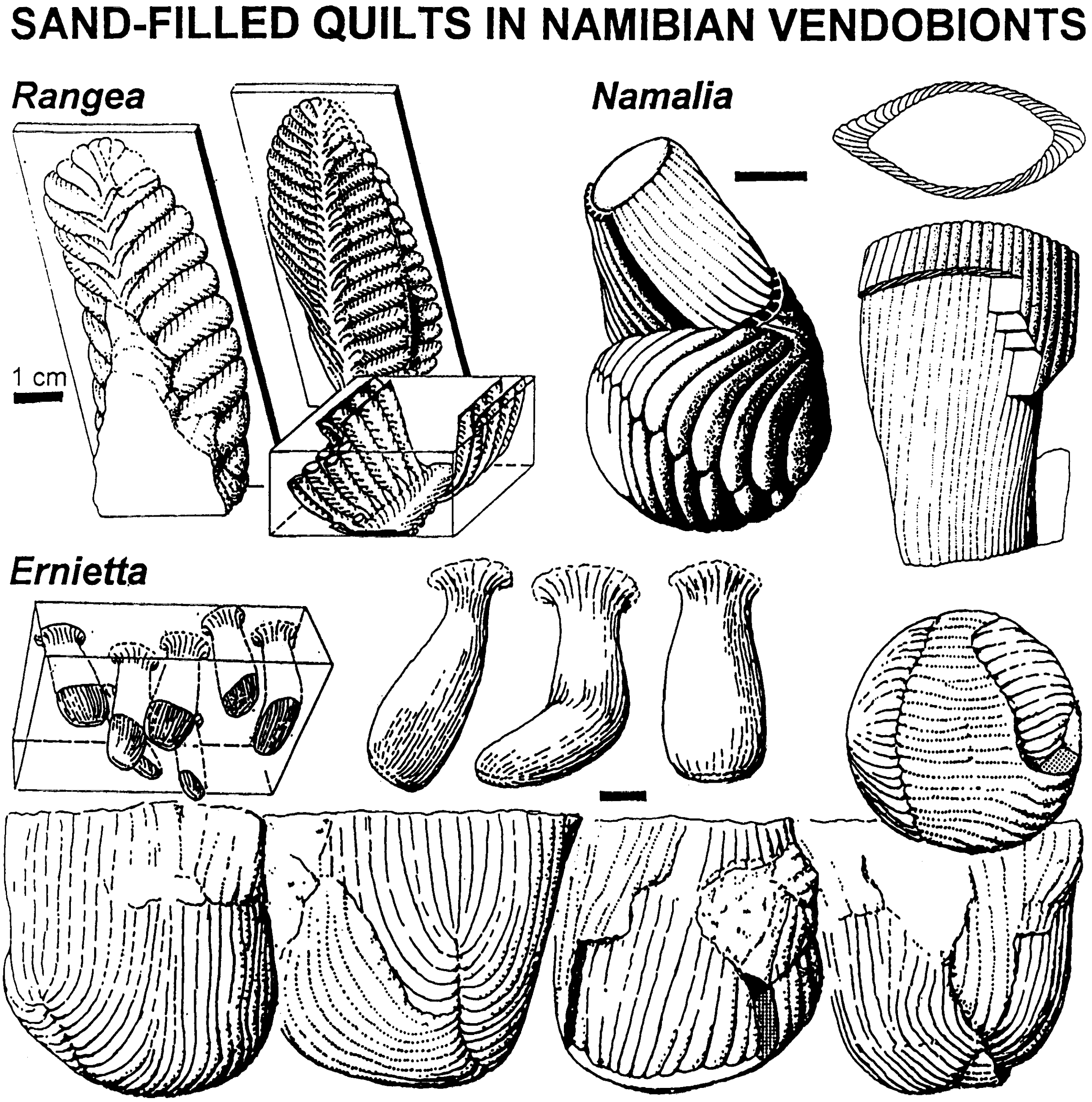


Figure 11. In the vertical vanes of infaunal vendobionts from Namibia, sand sank into the lower parts of the quilts after death and kept them from collapsing. In life it probably functioned as a fill skeleton that further compartmentalized the protoplasm like the stercomare of xenophyophores.

the plasma, they should be approximately the same in different groups of unicellular organisms. But in a fabricational sense, chambers reflect primarily growth steps, while the real compartmentation of the protoplasm is defined by smaller-scale internal structures. These are chamberlets and pillars in larger forams and the stercomare in Xenophyophoria. No such structures are known in vendobionts, whose quilts tended to collapse after death. Yet, the collapse was commonly incomplete due to loose sand inside the quilts. This is most evident in the lower portions of upright sand stickers, such as *Ernietta*, *Namalia* and *Rangea* (Figure 11). Earlier we thought that the sand somehow entered the quilts after death, which would pose a mechanical problem in hydrostatically supported structures (Grazhdankin and Seilacher, 2002). It makes much more sense that this sand was already there in life. It could have been loosely bound into trabecular structures that disintegrated soon after death (as the xenophyophoran stercomare). Alternatively, the sand grains may have floated in the protoplasm. In any case the internal sand could have had the required compartmentalizing effect.

Consequently we now consider the vendobionts as an extinct class of giant rhizopods. Like large foraminifers and xenophyophores they subdivided the protoplasm by chambered growth and internal structures; but instead of making more or less rigid outer walls by biomineralization or by agglutinating foreign particles, they had a flexible organic cuticle supported by hydrostatic pressure. Together with the xenophyophores they dominated benthic communities in the Late Proterozoic.

Conclusions

If one accepts the interpretations here proposed, our traditional view of Late Precambrian benthic communities has to be modified.

The climatically favorable "golden age" (Seilacher, 1998) that followed the Marinoan snowball earth led to an evolutionary climax of rhizopod protists. In the shadow of these giants, and constrained by ubiquitous matground conditions, metazoan phyla also diversified. Yet, they remained a minor element and in the absence of macropredation their evolution appears to have proceeded at a relatively slow rate. These conditions changed dramatically in the Cambrian Explosion, the importance of which is accentuated by our studies.

In our interpretation, the Vendian record of metazoans (in the form of body and trace fossils) becomes reduced to few and relatively simple forms constituting only a minor part of the thanatocoenoses. Except for some problematic organisms with small calcareous shells (Figure 6), Vendian Metazoa were soft-bodied. They are represented by stem-group sponges, coelenterate polyps, possible echinoderms, and burrows of worm-like burrowers, while molluscs are documented by death masks of *Kimberella* together with its radular scratches. There is neither a clear record of carnivory, nor of arthropod tracks and burrows. The metaphor of the "Garden of Ediacara" (McMenamin, 1986) therefore adequately describes a world in which the trophic pyramid appears to have been largely restricted to primary producers and decomposers.

As suggested earlier (Seilacher and Pflüger, 1994), bacteria were also important in Precambrian times. Not only did they act as sinks for carbonate (in the form of stromatolites), but they also sealed otherwise soft clastic sediments. In Precambrian biomats, mucous binding was not restricted to a superficial film, but extended into the upper millimeters of the sediment. Contemporary organisms adapted to these tough matgrounds by becoming either limpet-shaped mat scratchers (*Kimberella*), flat or elevating mat encrusters (most vendobionts and trilobozoan sponges), mat stickers (e.g., *Cloudina*), mat inclusions (xenophyophores), and undermat miners (worm-like animals producing horizontal burrows).

Next to the mat-forming bacteria (and probably fungi), rhizopod protists constituted the major part of the standing Vendian biomass. Large xenophyophores were probably enclosed in the biomats. Vendobionta reached even larger sizes and radiated into a variety of self-organizational shapes and ecologic niches. They were the rulers in shallow marine communities. Thanks to a special preservational process ("death masks"; Gehling, 1999), they also dominate the fossil record in clastic sediments. The revised Precambrian history of metazoans thus resembles that of the mammals, which originated about 200 million years ago and had a "slow burn" before they could radiate after the demise of the ruling dinosaurs only 65 million years ago.

The reorganization of the biosphere in the Precambrian/Cambrian transition appears to have been driven mainly by biological feedback rather than by extrinsic triggers. One critical event was that the protistan rulers of Vendian shallow-marine biota became either extinct or reduced to refugees in less favorable environments (Conway Morris, 1993; xenophyophores on deep-sea bottoms). The new guild of carnivorous animals may have been instrumental in their demise. On the other hand, this extinction was not followed by an extended period of recovery. Instead there was an immediate diversification of animal phyla, which from then on became the rulers. The acquisition of hard parts was another crucial event, because it started the evolutionary arms race between predator and prey species and expanded the trophic chain, as documented by a rich record of body fossils. At the same time, intensified and deeper-tier bioturbation put an end to matgrounds except in hostile environments. This "Agronomic Revolution" (Seilacher and Pflüger, 1994) was accompanied by an equally explosive radiation of behavioral programs in burrowers devoid of mineralized skeletons; i.e., the "Cambrian Explosion" is not a preservational artifact.

On a more general line, it appears that at the level of populations Darwinian evolution proceeds continuously (even if punctuated), while ecological power structures are more resilient. Therefore macroevolutionary turnovers are tied to revolutionary events, the biggest and most consequential of which has been the Cambrian Explosion.

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