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Appearance and Evolution of Marine Benthic Communities in the Early Palaeozoic

S. V. Rozhnov

Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia
e-mail: Rozhnov@paleo.ru

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Abstract—The development of marine benthic communities in the Early Palaeozoic occurred mainly in the shallow water epicontinental seas. It included those stages of the Cambrian and Ordovician evolutionary radiations that were dominated by a high rate of morphogenesis, when new food and territory resources were not limited. This provided many opportunities for coadaptation of emerging organisms. At the time of the Cambrian radiation, the body plans of all animals were formed, while in the Ordovician, the maximum rank of emerging taxa did not exceed the level of class. The beginning of each radiation was explosive. Vendian benthic communities developed in cold seas and in the shallowest areas of warm seas, where organic matter from the surface layers was available at the bottom because of the absence of a thermocline. The Cambrian radiation began with the appearance of pelagic suspension feeders, because of which much of the primary production could penetrate the thermocline and settle at the bottom. This allowed the occupation of warmer seas and greater depths. At the same time, the productivity of the pelagic region sharply increased because of the emergence of positive feedback between the producers and consumers in the water, leading to increased water transparency and elongation of trophic chains. Arthropods, the first suspension feeders, were the launch group of the Cambrian radiation. Cambrian benthic suspension feeders could seize only the smallest particles, mostly bacteria, and dissolved organic matter. This food resource was contained in the thin bottom water layer. Therefore, the food grasping structures of all the Cambrian suspension feeders were near the bottom, without forming tiers. The Ordovician evolutionary radiation began with the launch of the Pelmatozoan echinoderms, which were the first benthic suspension feeders to begin feeding on plankton. The exploitation of this resource led to the creation of a 1-m tier above the bottom and an increase in their calcite productivity. Positive feedback emerged between the grounds and the community of its inhabitants and considerably changed the composition and diversity of grounds, which sharply increased the diversity of benthos. The appearance of positive feedback between different components of ecosystems resulted in explosive evolution in both the Cambrian and Ordovician.

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Key words: Marine benthic communities, evolutionary radiation, Early Palaeozoic.

INTRODUCTION

Of all the biological sciences, palaeontology has the least opportunity to study organisms, because it deals with their fragments, imprints, and skeletons, with no detailed information on their soft parts, and no possibility for direct biological experiments.

At the same time, palaeontology has a certain advantage over other sciences: it provides an opportunity to study all the observed facts and all processes of the development of biodiversity against actual geological time. This opportunity alone can produce interesting results.

The well-known Sepkoski's curve (Fig. 1), a graph of the total number of marine fossil genera in the Phanerozoic, shows a sharp increase in the number of genera in the Early Cambrian, while in the Middle and Upper Cambrian their number was stabilized somewhat at a moderate level (Sepkoski, 1995, 1996). The curve shows that maximum diversity was reached at the end of the Ordovician. At the Ordovician–Silurian boundary, the number of genera sharply decreased, but, then, increased rapidly, approximately reaching the previous level. Throughout the entire Palaeozoic, the number of genera remained more or less the same at each point, excluding short extinction events. The graph portrays this situation as a so-called *Palaeozoic Plateau.* At the Permian–Triassic boundary, the number of genera decreased sharply, but, then, gradually increased to reach the modern level, which greatly exceeds that of the Palaeozoic.

Hence, the early evolution of Palaeozoic biodiversity happened in two stages, Cambrian and Ordovician; these stages were not separated by a mass extinction, or massive depletion in the generic biodiversity, like the one separating the Ordovician and Silurian evolutionary radiations (Alekseev et al., 2001; Sepkoski, 1996). This time was evidently a period of initial development and saturation of ecological niches.

The early evolution of benthic communities in the Early Palaeozoic seas was one of the first steps in the

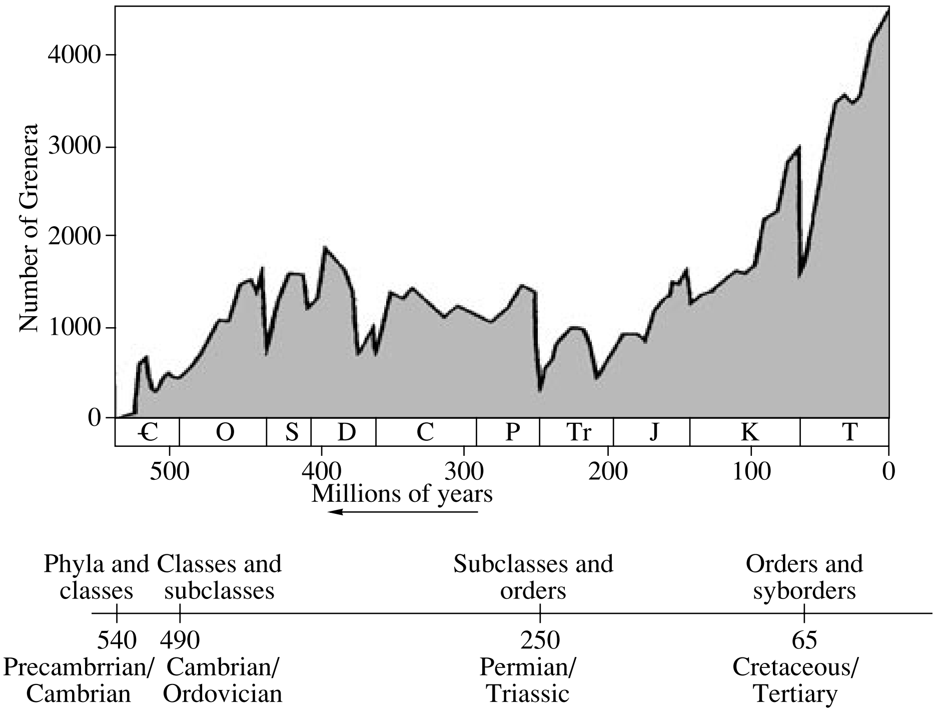

Fig. 1. Phanerozoic taxonomic diversity of marine animal genera (after Sepkoski, 1995, modified) and maximum taxonomic level of the evolutionary radiation of marine animals at the major boundaries (modified after Rozhnov, 2002). Abbreviations: (Є) Cambrian, (O) Ordovician, (S) Silurian, (D) Devonian, (C) Carboniferous, (P) Permian, (Tr) Triassic, (J) Jurassic, (K) Cretaceous, and (T) Tertiary.

development of the modern ecological structure of the marine biota. This development occurred in place of the previously existing prokaryotic and eukaryotic biotas (Zavarzin, 2003). Metazoans, known from the Vendian, differ strongly from the Cambrian metazoans, and the more so from their modern counterparts. This profound difference is related not only to different preservation of Cambrian and Vendian organisms, but mostly to a very rapid increase in biodiversity at the beginning of the Cambrian. This *Cambrian Explosion* was marked by the appearance of the first organisms with a mineralized skeleton. This so-called small-shelled fauna, so much characteristic of the Tommotian of Siberia, was rapidly supplemented by many other skeletal organisms. It is difficult to assign Vendian organisms to any particular type of modern animal not only because of the incomplete preservation of these soft-bodied animals and, hence, difficulties in the interpretation of their morphology, but also because of the similarity of characteristic characters, unusual combinations of these characters, and an indistinct archetype. This evolutionary explosion led to the appearance of the so-called Sepkoski's Cambrian evolutionary fauna, which existed for about 50 m.y. (Sepkoski, 1981). Its gradual evolution in the Cambrian was replaced in the Ordovician by the explosive appearance of many new taxa of higher rank, as a result of which the Cambrian fauna was replaced by the Palaeozoic fauna, which had relatively stable composition of its higher taxa for the next 240 m.y., until the end of the Permian. The process of the replacement of these two faunas is referred to as the Great Ordovician Biodiversification Event (Webby, 2004). This radiation is easier to study because many Ordovician groups were rooted in the Cambrian among skeletal forms. Evolutionary radiations on a smaller scale later occurred repeatedly. However, in contrast to the Cambrian and Ordovician evolutionary reorganizations, they were preceded by more or less distinct biotic crises, which led to the sharp impoverishment of the biota, extinction of many taxa, and the clearing of a large ecological space. The crisis that terminated the Ordovician was exactly of such nature, being followed by the Silurian innovation of the marine biota. Comparison of these three evolutionary events allows the revelation of the mechanisms of the explosive evolution, which led to sharp changes in the benthic communities and enables the evaluation of the role of environmental factors. For this, it is first of all important to estimate the time and nature of the appearance of higher taxa of Metazoa.

THE TIME OF THE APPEARANCE OF HIGHER TAXA OF METAZOA

The most popular way to estimate the time of the appearance of higher taxa is based on the hypothesis of gradual and successive development of their archetype. According to this hypothesis, the divergence of any groups begins with small differences first in one character, whereas later the number of these different characters increases. Hence, the rank of the diverging taxa also gradually increases. Thus, it is suggested, although often vaguely, that the differences between closely related phyla once began in the Precambrian from the differences between two closely related species.

Paleontological evidence contradicts this hypothesis. At present, there is enough data accumulated to show that all presently surviving phyla were formed in the latest Precambrian and Cambrian, while the majority appeared in the Early Cambrian (Valentine, 1995, 2004).

This fact raises two questions: (1) What were the metazoans prior to the appearance of modern phyla? (2) Why did no more new phyla appear after the Cambrian? While the first problem is traditionally not discussed, for the second problem the so-called genome and ecospace hypotheses were proposed as possible explanations as to why no radiations similar to one in the Cambrian occurred in the post-Cambrian epochs (Valentine, 1995, 2004).

Both these problems can be combined in one: How and under which conditions new plans of body structure of higher taxa were formed? Below a possible explanation of this problem is discussed.

Each taxon is characterized by a certain body plan, i.e., to simplify it, by a certain number of key characters, tied to each other. Each phylum has its own body plan. However, each class in a phylum also has its own body plan, which is superimposed on, or more precisely, explicates the body plan of the phylum. Classes contain orders with their own body plans, and so on, up to the families, or possibly to the genera inclusive. Hence, there is a certain hierarchy of body plans, which corresponds to that of the taxonomic position of a taxon. Body plans appear suddenly in the fossil record, rather than evolve gradually. Ancestral taxa have characters which would become parts of the body plans of descendent taxa, but these are scattered, occurring in combinations with other characters. The origin of the characters, constituting a body plan of descendants in different lineages of the ancestral taxon in a form of numerous parallel appearances was noted by Tatarinov (1976) in synapsid reptiles, and was referred to as mammalization. Later, similar processes were found to be characteristic of many groups of various ranks. For instance, I described such a process in crinoids (Rozhnov, 2002). Ponomarenko (1993, 2004) referred to a similar process occurring in the early evolution of arthropods in the Cambrian as arthropodization.

At the same time, paleontological data show that all large changes in the organic world in the Phanerozoic occurred at certain levels (Fig. 1), each of which was characterized by the maximum ranks of the emerging taxa (Rozhnov, 2001, 2002). For instance, all animal phyla appeared at the time of the Cambrian evolutionary radiation (Fig. 1). No more new phyla appeared after the Cambrian. Many classes appeared at the time of the great Ordovician evolutionary radiation. No more new classes appeared later. The Palaeozoic–Mesozoic boundary was marked by an even lower taxonomic level of evolutionary radiation of the marine biota, when emerging taxa were not above subclass or order level. At the Cretaceous–Tertiary boundary, emerging taxa were at the level of superfamilies and suborders. Some rare exceptions only prove the general rule.

High-rank taxa apparently appear only under certain conditions allowing the appearance of a new body plan. A new body plan is always a combination of characters rather than a single character. In addition, the ancestral taxon is morphogenetically and, hence, typologically always taxonomically higher than the descendent taxon because it has a greater morphogenetic and evolutionary potential. The morphogenesis and its variability in the ancestral taxon define the possibility of morphological innovations in the emerging new taxon. However, their actual realization requires firstly a certain maturity of the ancestral taxon and, secondly, the presence of an appropriate environment. The maturity of a taxon means a stabilization of the combination of characters defining the body plan, while the less important characters are highly variable.

An appropriate environment is one which facilitates fast and superfast growth in quantity, so that morphological innovations may rapidly appear, become widespread and diversify. For benthic animals such environment in the geological history appeared during strong marine transgressions, when after a regression, sea again floods large areas of land to form new epicontinental marine basins. Mass occupation of new biotopes during a short time may lead to various heterochronies in the ontogeny of many immigrants, which is a powerful morphogenetic factor.

I developed these ideas while studying the evolution of Paleozoic echinoderms (Rozhnov, 2002). When such an approach is used, the phylogenetic scheme of classes of Echinodermata resembles a meadow rather than a tree. A generalization of these data allows the conclusion that the early evolution of higher echinoderm taxa followed the route of combination of characters of various ranks, the mechanism of which was defined by various heterochronies, i.e., by changes in the relative time of the appearance of structures. Here, one should imagine a pattern of the alternation of the superimpositions of the ontogenetic stages in organisms, related to the increase in size and its subsequent subsidence, i.e., shifting to the earlier ontogenetic stages and reduction in longevity due to the improvement of morphogenetic processes. The unevenness of the subsidence led to various heterochronies. The best constructively and morphogenetically fitted combinations of characters determined the appearance of new higher taxa, which occurred at certain boundaries in the evolution of the marine biota defined by rapid changes in the environment. From the point of view of the possibility of combination of characters of different taxonomic ranks, all classes of echinoderms that appeared in the Cambrian, including the so-called small classes, would be regarded based on the level of organization of their structural plans as monotypic subphyla rather than classes. This is reflected in their archaic diversity, with combinations of characters of the highest rank, i.e., chordates and echinoderms. Classes that appeared in the Ordovician, including the small classes, have the level of organization of true classes, which is reflected in the combinatorics of characters.

Thus, the above discussion suggests that the evolution of echinoderms was directed from the development of an archetype, or general body plan, to the appearance of the smaller details, mainly based on combinatorics and defined by the heterochronies. Such a taxonomic differentiation in the phylogeny may be imagined as a periodically branching inclined channel, similar to Waddington's (1957) interpretation of the epigenetic landscape to illustrate the channelled morphogenetic processes in the ontogeny. A ball illustrating the evolution of a taxon, descending in the channel, may roll from side to side due to the curvature of the bottom. This illustrates the possibilities of variability of the taxon. When the channel branches, the ball may get into a narrower channel, hence, the range of variability will be narrower, and will be altogether different. This portrays the decrease in rank of taxa, which can emerge after the ball gets in a new channel after the branching point. If the data received on the higher taxa of echinoderms are extrapolated onto earlier metazoan faunas, the Precambrian (Vendian) metazoans are true superphyla or groups of a similar rank, and they cannot be assigned to later phyla, or classes, although many characters of the later groups were already present. In this case, a parallel and almost synchronous appearance of the mineralized skeleton in many groups indicates only a closeness of the appearances of these groups in time.

The appearance of new taxa requires the presence of the necessary free resources, primarily, food, in the environment. A total amount of trophic resources available to marine Metazoa possibly did not change much throughout the Phanerozoic, but their diversity increased proportionally to the increase in biodiversity.

FOOD RESOURCES OF THE PROTEROZOIC BOTTOM-DWELLING COMMUNITIES

To live, bottom-dwelling animals require the supply of nutrients and oxygen from the upper photic, well lit, zone. It is in this zone, especially in its upper layer, where the phototrophs produce vast amounts of primary organic matter. Dying cells slowly descend to the depths, being destroyed by bacteria on their way. Because of their small weight, these decaying remains cannot pass through the thermocline (the zone separating water warmed by the sun and cold deep water). Therefore, in these cases, nutrients freed through the activity of the reducing bacteria return to the circulation of the photic zone, while producers again develop on their basis. This is a so-called microbial loop (Zavarsin, 2003).

In modern seas, the thermocline occurs at various depths, depending on many factors, primarily, on the climate. In the places where the upper layer gets considerably warmed up, the thermocline may occur a few meters from the surface. In the places with a cooler climate, the thermocline is much deeper. The same situation was present in ancient epochs. In the Phanerozoic marine basins, a considerable amount of organic matter was transported through the thermocline due to the zooplankton, which filtered the phytoplankton, packed the indigested organic matter in pellets, whereas these pellets (enlarged aggregates of organic matter) settled through the thermocline and reached the bottom. The rich bottom-dwelling fauna presently thriving at all depths of the oceans was developed based on these nutrients.

No filtrators (at least pelagic) existed in the Vendian. There was no pelletization. Therefore, decaying remains of phototrophs could not penetrate through the thermocline and reach the bottom in places where the thermocline was well developed. Considering that the Vendian climate was cool, the thermocline could be altogether absent in the shallow epicontinental seas, a situation enabling decaying plankton along with the bacteria feeding on it to reach the bottom. The cold climate in the Vendian provided a supply of organic particles to the bottom of shallow seas and encouraged the development of benthic communities. This probably explains the mass development of benthos in the cold Vendian seas that allowed Fedonkin (1995, 2000) to formulate his hypothesis of the *Cold Cradle of Animal Life.*

The warming at the beginning of the Cambrian could have brought the entire bottom-dwelling life to the end because of the appearance of the thermocline even in shallow seas. The bottom life could have remained only in the shallowest coastal waters, well lit and therefore, saturated with phytoplankton. However, in these littoral and sublittoral zones, strong water turbulence precluded the occupation by animals lacking special defensive structures. Therefore, this niche was rapidly occupied by the small-shelled fauna of mollusks and other animals, which quickly became very diverse. This niche was suitable for sponges that acquired a skeleton, and following the small-shelled fauna, it was occupied by diverse archaeocyaths, similar in their biology to the sponges. However, the greatest significance for the occupation of large bottom areas of the Early Cambrian shallow epicontinental seas was the appearance of arthropods during the process of the so-called arthropodization (Ponomarenko, 1993, 2004). A rapid distribution of these organisms at the beginning of the Cambrian over the coastal shallow water biotope free from competitors and a superfast increase in their numbers led to their high diversity. Very quickly, literally in a few million years, this process led to a sharp change in the marine biota in the very beginning of the Cambrian and stimulated its evolution throughout the Phanerozoic.

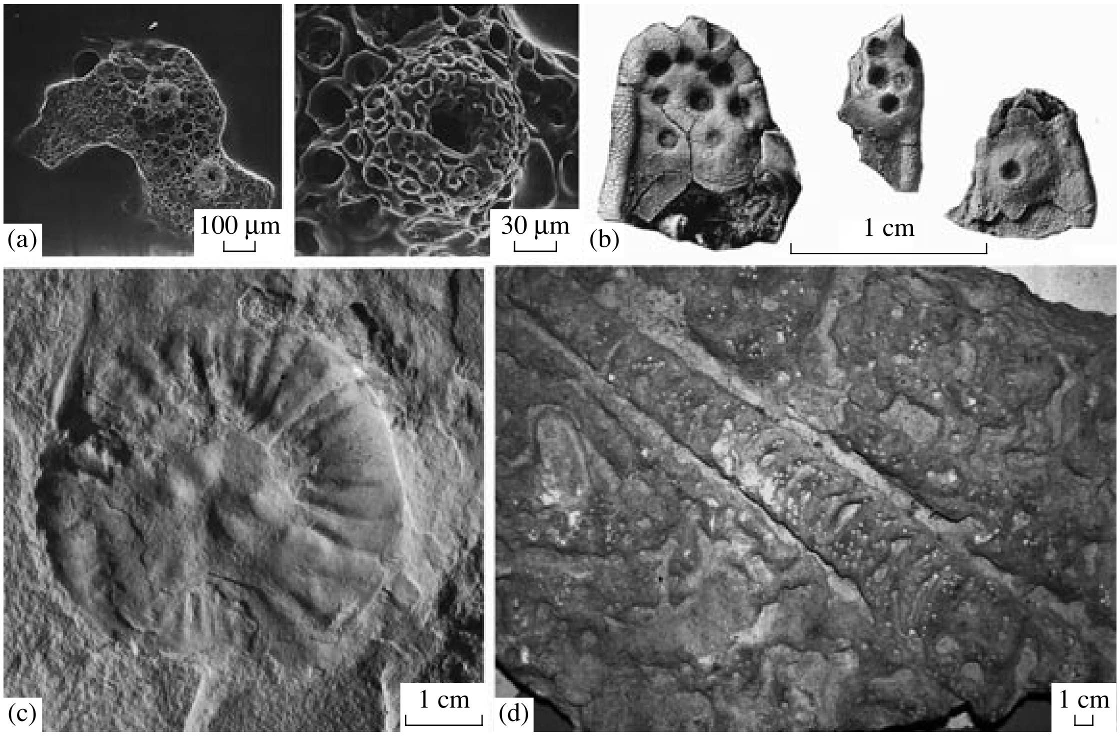

Fig. 2. Some Cambrian and Ordovician animals: (a) cysts of mysostomid-like parasites on the plate of the eocrinoid *Gogia* (Middle Cambrian of Australia), (b) cysts of mysostomid-like parasites on the theca of the eocrinoid *Rhipidocystis* (Middle Ordovician of the Baltic Region), (c) imprint of the mouth apparatus of *Anomalocaris* (Middle Cambrian of Siberia), and (d) hardground with a mold of endoceratid shell, borings of *Trypanites*, and a crinoid holdfast (Middle Ordovician of the Baltic Region).

PHANEROZOIC FOOD RESOURCES AND THEIR STABILIZATION

As a result of arthropodization, the first pelagic suspension feeders appeared in the Early Cambrian. These were small arthropods with legs possessing setae similar to those in the most advanced modern filtrators. A few genera of possible filtrators have been already described from the Lower Cambrian (Butterfield, 2001; Ponomarenko, 2004). Pelagic filtrators became the launching group of the Cambrian evolutionary radiation, because collecting organic matter in the subsurface water layer facilitated its fast transport to the bottom through the thermocline. The pellets of these arthropods contained a lot of organic matter, and easily penetrated the thermocline and enriched the sea bottom with nutrients over large areas and at various depths of both warm and cold epicontinental seas. This allowed benthic animals to quickly occupy vast unexploited areas of the sea bottom. The latter caused a chain reaction of increase in complexity of food chains, since each appearing benthic organism represented a new food resource, available to other organisms, at least after its death.

Mesoplanktonic and macroplanktonic filtrators sharply increased the productivity of the photic zone by removing the large mass of phytoplankton, which prevented the oversaturation and increased the rate of the renewal of the phytoplankton. In addition, small clay particles were filtered and settled at the bottom together with the plankton. This considerably increased transparency and expanded the highly productive part of the photic zone.

Benthic filtrators received both the organic particles arriving from the top, and muddled bottom organic matter. Archaeocyaths, sponges, brachiopods, and many echinoderms in the Cambrian were main benthic filtrators among skeletal animals. Most annelids and arthropods were apparently debris feeders, although many of them were active macrobenthic scavengers and, when possible, fed on living organisms. However, there were probably few active specialized predators. For instance, Anomalocarida (Fig. 2c), which are considered to be the largest predators of their time (they had a frightening appearance and were over a meter long), could hardly have been active predators because the sizes of an active predator and its prey should be comparable, and there were no contemporary prey of a suitable size. Most likely these animals were scavengers, scavenging on variously sized corpses, although occasionally capable of swallowing (more precisely sucking up) live organisms with their peculiar mouth. Healed bite marks on trilobites also indicate that the predators were not very sophisticated, better adapted to feeding on corpses. Descending food particles were apparently filled with bacteria, which constituted a large proportion of the available nutrients. Therefore, many suspension feeders were adapted to feed on bacteria. Because the early evolution of metazoans in the Cambrian was related to the appearance of morphological and physiological innovations, it is quite likely that the organic matter that could be digested by the first metazoans was previously partially reduced by bacteria to create digestible structures. Hence, suspension feeders, debris feeders, and scavengers originally had mainly intracellular digestion, whereas physiology of their feeding could originally be very similar (only decayed organic matter and bacteria could be digested). Feeding on living organisms required a considerable change in digestion, for example, the presence of symbiotic bacteria in the digestive system or appearance of the extracellular digestion in addition to intracellular digestion. This is another fact supporting the hypothesis that predators appeared later compared to debris feeders or suspension feeders.

In the Cambrian, debris feeders inhabited only the uppermost layer of the sediment (Droser and Xing Li, 2001). However, gradually they occupied the lower horizons. This is related to the fact that the organic material supplied to the bottom was a feeding resource not only for the benthic animals, but also for sediment-dwelling bacterial communities. This combination of bacterial activity and bioturbation led to a change in the chemistry of the sea water. The saturation of the sediment by oxygen as a result of bioturbation allowed an increase in the tiering depth by the anaerobic bacteria and ichnofauna.

Pelletization of the organic matter not only facilitated its more efficient transport to the bottom, but also more even distribution, stabilization of its supply, and stabilization of benthic communities. The advent of food chains stabilized the communities even more efficiently. However, it was important for suspension feeders to survive periods of lower productivity of phototrophs and episodic depletions of nutrients. With the exploitation of new feeding resources, the role of the dissolved finely dispersed and bacterial organic matter remained high and was sharply increased in the periods of depletion in productivity of phototrophs. Many groups of echinoderms acquired specific adaptations (such as pores) to improve the use of such organic matter by the external body parts.

The Cambrian evolutionary radiation was accompanied by a rapid exploitation of abundant food resources and the filling of the vast empty space on the bottom of epicontinental seas with life. Hence, the resulting high rate of morphogenesis provided broad possibilities of coadaptation of emerging forms and gradually led to the development of stable communities. Competition was less important. Stabilization of communities and disappearance of the surplus feeding and territorial resources resulted in a slowing down of the formation of new life forms in the second half of the Cambrian, since it became much more difficult for new taxa to intrude into a stable community. Carbonate productivity of the macrobenthos increased throughout the Cambrian, and by the beginning of the Ordovician, it reached a level which profoundly changed the composition of properties of the grounds. Therefore, at the beginning of the Ordovician, the character of the sea bottom rapidly changed because the ground was enriched by calcite debris supplied by the skeletons of dead animals, which again led to explosive biodiversification and the beginning of the great Ordovician evolutionary radiation.

MECHANISM OF THE ORDOVICIAN EVOLUTIONARY RADIATION

The Ordovician evolutionary radiation, like the Cambrian radiation, began with the appearance of the possibility of exploitation of a new excessive resource, i.e., large areas of the sea bottom with grounds enriched by calcite debris (Rozhnov, 2001, 2002). However, in contrast to the Cambrian radiation, when newly occupied spaces were not previously used by animals, in the Ordovician the new type of grounds firstly replaced the previously existing grounds exploited by the previous fauna. Secondly, this new biotope emerged and was supported through the metabolism of the fauna inhabiting it. Thus, a positive feedback developed between the distributions of the ground enriched by the debris and the community with calcite skeletons living on it. This led to the appearance of a rapidly expanding self-reproducing ecosystem. Fast and superfast growth of the quantity of benthos during some periods resulted in explosive diversification that determined the beginning of the Ordovician radiation.

These consequences were manifested especially clearly and sharply because of the wide distribution of specialized hard carbonate grounds that were lithified simultaneously with sedimentation (Wilson and Palmer, 1992). The hardgrounds first appeared as early as the Cambrian, but became truly widespread only in the Ordovician (Fig. 2d). This was related not only to the change in the character of the marine water at the end of the Cambrian–beginning of the Ordovician, but also to the sharp change in the morphology of echinoderms, which, from the beginning of the Ordovician, increased carbonate productivity and became capable of using a water column of one meter high over the bottom (in the Cambrian, they used only the first 10–20 cm) (Bottjer and Ausich, 1986; Rozhnov, 1993). The Ordovician hardground was formed due to the supply of the calcite debris from the community of animals inhabiting this ground, primarily, pelmatozoan echinoderms (Fig. 3). In the Cambrian, there was not sufficient debris, a hardground appearing in an unsuitable environment did not grow, but declined. For comparison, in the Cretaceous, hardgrounds were formed due to the supply of debris by the dead plankton, primarily, coccolitophorids, the life of which is not directly connected to the type of the bottom.

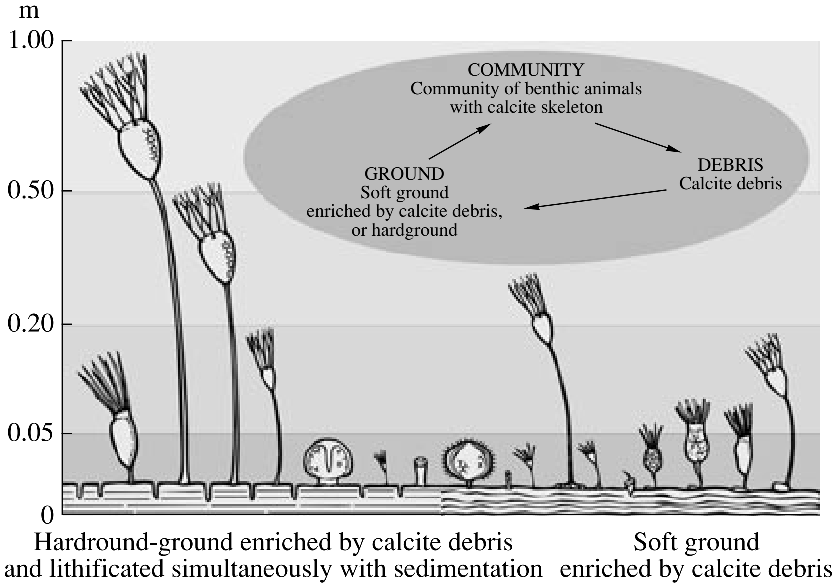

Fig. 3. The tiering of echinoderm communities of the hardgrounds and soft grounds in the Middle Ordovician of the Baltic Region; scheme showing positive feedback between the increase of the calcite productivity of the community and the increased area of ground enriched by calcite debris.

Thus, the Ordovician hardgrounds were able to expand due to the community inhabiting them (see Rozhnov, 2001, 2002). In other words, a hardground and a community on it were parts of a self-reproducing ecosystem capable of rapid expansion.

While arthropods were the launching group of the Cambrian radiation, in the Ordovician, this role belonged to echinoderms, because originally they were major suppliers of calcite debris. Debris supplied by dying echinoderms was a good material for hardgrounds, because each plate of echinoderms is a monocrystal and could rapidly amalgamate in the ground with other plates by calcite cement. The more hardgrounds expanded, the more echinoderms inhabited them and more material for the expansion of the hardgrounds was supplied (Fig. 3).

An established positive feedback between the increase in the area of hardgrounds and increase in the biomass of echinoderms in the shallow Ordovician seas in a suitable sedimentary environment (the rate of the supply of sediment was equal or smaller than the rate of lithification of the ground) led to a very fast distribution of hardgrounds over large territories and to the fast and superfast growth in numbers of echinoderms and other benthic fauna. Indeed, the self-reproducing hardgrounds in the Ordovician were a new, unexploited system of ecological niches, quite favorable for the existence of many benthic groups of fauna, primarily, echinoderms (Sprinkle and Guensburg, 1995). A competition for free space on the bottom suitable for inhabitancy sharply decreased until the expansion of the changing grounds reached its natural limits, and the community inhabiting it became stabilized. It is far more difficult to replace a member of the already formed community than to invade the same niche earlier than it was occupied. Therefore, natural selection favored early sexual maturity and through pedomorphism resulted in the preservation of juvenile ancestral characters in descendent adults (Smirnov, 1991; McKinney and McNamara, 1991). Pedomorphosis, which was a strong mechanism of biodiversification in that time led to the appearance of many diverse morphs, coadaptation of which resulted in the appearance of new communities made of new members.

A FEW WORDS ON PARASITISM

Traces of parasitism are difficult to find among extinct organisms, although parasitism was undoubtedly common. It is noteworthy to mention Myzostomida, which were parasitic on echinoderms, forming small pits on the skeleton of fossil echinoderms, surrounded by a rim of stereome. In the Ordovician, their settlements are found on the stems of crinoids, on the theca of the eocrinoid *Rhipidocystis*, and on the thecae of Soluta, Carpozoan echinoderms. Sometimes, they are solitary, but quite frequently are found in large numbers. Infestation by these parasites could be quite serious, e.g., about 10% among Baltic *Rhipidocystis* (Fig. 2b). These traces of settlements were about 2–3 mm in size (Rozhnov, 1989). I observed traces of such settlements on the plates of Cambrian eocrinoids (Fig. 2a). Some plates had more than one settlement. Cambrian eocrinoids were ten times smaller than their Ordovician counterparts, whereas their myzostomid parasites were also ten times smaller, which is an interesting case of coevolution of sizes.

ROLE OF ACTIVE PREDATORS IN THE EARLY PALAEOZOIC

The role of predators in the Early Palaeozoic food chains is considered to be high (Bengtson, 2002; Vannier and Chen Junyuan, 2005). This may be not entirely true, even the predation is understood as such in a broad sense, as killing of one organism by another in order to feed. But if the predators are considered in a narrow sense, as animals actively attacking and killing other animals, their role was very insignificant. There were only few such predators in the Early Palaeozoic.

As noted above, Cambrian Anomalocarida (Fig. 2c) were unlikely to have been active predators. Their huge size and scary looks adds to the confusion. Among the Ordovician predators, huge endoceratoids are usually considered as such (Fig. 2d). Their skeleton occasionally reached 9 m in length. In my view, their size contradicts the hypothesis of their active predation, because there was no prey of a suitable size. Most likely endoceratids were suspension feeders, in which tentacles were transformed into a grasping net. It would have been energetically unprofitable for such huge animals to pursue small prey, e.g., trilobites.

However, some active predators did exist. This is suggested by scarcely found healed damages on trilobites, brachiopods, and echinoderms interpreted as traces of predatory attacks. The ability of trilobites to curl perceived in some groups is also related to the defensive strategy against predators. However, most likely the attackers were not specialized predators, but scavengers, occasionally picking on live organisms. In any case, the population pressure of active predators was not strong. Therefore, we do not have sufficient evidence suggesting that the explosive character of the Cambrian and Ordovician radiations was connected to the appearance and evolution of active predators.

FILLING OF ECOLOGICAL NICHES BY THE END OF THE ORDOVICIAN AND THEIR CLEARANCE AS A RESULT OF EXTINCTION

By the end of the Ordovician, all benthic ecological niches became occupied as a result of the intensive evolutionary radiation, whereas almost all elements of the Palaeozoic fauna were already present. However, ecologically these communities contained many animals as though imitating those of the Cambrian fauna. For instance, among echinoderms, Rhombifera and Diploporita, which did appear in the Ordovician, ecologically were hypertrophic elements of the Cambrian fauna. Like Cambrian eocrinoids, many representatives of these two classes fed on (judging from the diameter of the food-collecting structures) bacteria and small particles of decayed organic matter. Their skeleton was penetrated by a system of numerous pores, which probably served primarily for feeding on dissolved and finely dispersed organic matter using external phagotrophy (Rozhnov and Kushlina, 2001; Rozhnov, 2002). Using this strategy, they provided tight competition for crinoid juveniles, the most characteristic group of the Palaeozoic fauna. Significant cooling at the end of the Ordovician led to a glaciation and strong marine regression. The withdrawal of seas resulted in the disappearance or decrease of many shallow water biotopes and in the extinction of many groups, including cystoids. During the Early Silurian transgression, vast spaces of the shallow epicontinental seas, the environment favorable for benthic organisms, re-appeared. The remains of the Ordovician fauna, which survived in the refuges, rapidly occupied this new space; however, this happened in the environment of competition between the already formed major ecological types of animals. This led to the situation, when the place of cystoids was quickly taken by small crinoids, which evolved by pedomorphosis. Thus, the Silurian evolutionary radiation was the first to be preceded by a significant extinction of marine organisms, which cleared large ecological spaces.

COMPETITION VERSUS EXCESSIVE ECOLOGICAL RESOURCES

The appearance of the Vendian diversity of the benthic biota and increase in the morphological and taxonomic diversity of the marine biota during the Cambrian and Ordovician evolutionary radiations were related to a sharp increase of free ecological niches, their size and range. This increase in available niches was related to the appearance of positive feedback between the increase in biodiversity and the diversity of ecological niches, between the increase in number, morphological diversity, and possibility of coadaptation. A rapid increase in numbers at the time of the sharp increase of the food resource in the Early Cambrian and of the size of hard and coarsely detrital grounds in the Ordovician, while the initial competition was low, led to a wide morphological diversity, rapidly developing coadaptation of the members of the community, and subsequent development of body plans of phyla and classes on this basis. The large diversity of morphotypes of various animals, which appeared at the time of a superfast growth in number of the biota, resulted in rapid and well-calibrated coadaptation of all members of the community. Interactions between those resulted in complete occupation of the ecological space. Therefore, periods of explosive evolution were replaced by periods of slow, gradual evolution, because in these periods it was difficult for new immigrants to enter established communities.

The Cambrian and Ordovician radiations occurred at the times when the ecological space was not completely filled by other animals. In the Cambrian, these were large areas with excessive food resources, while in the Ordovician, these spaces represented unexploited new types of grounds. In both cases, these new spaces were organized very rapidly, based on a principle of positive feedback between the resource and the community using it.

Thus, the mechanisms of the Cambrian and Ordovician evolutionary radiations were dominated by a high rate of biodiversification against the background of excessive food and spatial resource. This opened a wide possibility of coadaptation of appearing forms. A competition was less important. The Silurian radiation began after a large extinction at the end of the Ordovician, in the time of transgression, when new areas of epicontinental seas appeared and were populated by slightly changed remains of the Ordovician benthic fauna under the pressure of strong competition.

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