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Precambrian Metazoans: The Problems of Preservation, Systematics and Evolution [and Discussion]

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Precambrian metazoans: the problems of preservation, systematics and evolution

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The unique appearance of Vendian metazoans in the Precambrian fossil record is controlled not only by taphonomic and ecological factors, but also by the level of morphological and physiological organization of these animals. The peculiar nature of these factors means that the Vendian represents an important stage in metazoan evolution. This notion is supported by the Bauplan analysis of Vendian forms, many of which have a bodyplan (architectonics) that is most unusual in comparison with animals from later periods. This new information allows a revision of the systematics of Precambrian metazoans at a high taxonomic level. The new classes Cyclozoa, Inordozoa, and Trilobozoa are recognized among Vendian Coelenterata. The phylum Proarticulata, with classes Dipleurozoa and Vendiamorpha, represents the most primitive Vendian Bilateria. These, the oldest faunas on Earth, provide indication of the earliest modes of metazoan evolution that have not been part of the theoretical predictions of neontologists, and they also serve as a tool to check certain phylogenetic models.

1. Introduction

The world-wide distribution of Precambrian non-skeletal metazoans, their similarity in aspects of ecology and level of organization as well as the co-occurrence of species in the localities situated far from each other, even in palaeogeographic reconstructions, indicates that these animals represent a global fauna and a special stage in metazoan evolution.

The study of the late Precambrian invertebrates known as Ediacaran fauna is of great importance because they actually are the earliest known page of the metazoan fossil record. The important peculiarity of the fauna is an absolute dominance of soft-bodied animals. This peculiarity made all megascopic organisms more or less equal with respect to preservation potential, and the study of the soft tissue imprints allows us to use some methods of comparative anatomy in a broader manner than in the traditional study of skeletal remains. In this paper I shall touch on both preservational and morphological questions concerning the Precambrian metazoans.

In the type area of the Vendian, which is considered as the terminal system of the Precambrian (Sokolov & Fedonkin 1984) the oldest fossil metazoans appear stratigraphically close above the tillites of the Varangian glaciation. Their abundance and morphological diversity in the lowest normal marine deposits of the Vendian are indirect but strong evidence for the existence of a Pre-Vendian stage of metazoan history.

It is interesting that fossil invertebrates occur in abundance in the lower half of the Vendian, but in the upper part of the sequence the occurrence of Ediacaran-type fauna is sporadic, though trace fossils do exist in this stratigraphic interval. A good example of such a phenomenon is the distribution of the fossils in the reference sequence of the Vendian in the Dniester River Valley in Podolia, Ukraine (Fedonkin 1983*b*; Sokolov & Fedonkin 1984).

This prominent gap in the palaeontological record of megascopic metazoans in the upper part of the Vendian suggests a mass extinction of many groups of invertebrates long before the beginning of the Cambrian period (Fedonkin 1983*a*). This extinction is most apparent in the taxa that flourished in the Vendian and thus constitute the most characteristic elements of the Ediacaran-type fauna. One of the causes of this mass extinction may have been ecological events; they could be related to the competition for food resources and habitat partitioning with the more progressive lines of Metazoa which extended into the Phanerozoic.

Despite the fact that soft-bodied animals always comprised an essential if not the major part of the animal kingdom in later geological periods, their fossil record was greatly reduced owing to the influence of various factors, for example, the activity of predators and other necrophagous animals, progressive colonization with time of the sea bottom by metazoans and the destructive effect of bioturbation on potential fossils and the sediments as a whole. The study of the Vendian fauna provides us with a unique opportunity to delineate adequately the general panorama of the animal world at one of its earliest stages of development.

2. Some questions regarding the taphonomy of the Vendian soft-bodied metazoans

The fact that the majority of the Precambrian invertebrates did not have mineralized skeletal parts resulted in certain important taphonomic phenomena: (i) all megascopic animals had a more or less equal preservational potential though some factors could change the original proportions among different groups of organisms; (ii) soft tissues are easily affected by bacterial decay and mechanical destruction. That is why all occurrences of fossil non-skeletal metazoans represent associations of animals which lived contemporaneously and not far from their burial place; (iii) the same factors must have excluded the possibility of protracted transport of the dead organisms and allows us to assume a rapid process of burial in the majority of cases; (iv) the nature of fossils, for example, imprints and moulds of soft-bodied animals suggests that all the fossils were formed *in situ* and the redeposition of the fossils was practically impossible. The factors mentioned here should be taken into account in the course of palaeoecological reconstructions and biostratigraphic investigations.

Typically, the most numerous Precambrian fossils occur in finely laminated clastic rocks represented by alternating beds of relatively coarse-grained sediment and fine-grained pelitic ones, for example, siltstone and clay. Imprints of animals in negative and positive relief are usually preserved on the bottom of coarse grained beds. This is indicative of relatively rapid and sudden sedimentation events which lead to the burial of living or recently dead animals. A large number of Vendian fossils are also known from homogeneous non-laminated clayey siltstone of presumably proximal turbiditic origin, such as those in the Ust–Pinega Formation in the Suzma River Valley of the northern Russian Platform (Keller & Fedonkin 1977; Fedonkin 1981*a*) and thin-bedded bituminous dolomites of the Khatyspyt Formation in the Khorbusuonka River valley of the northern Siberian Platform (Sokolov & Fedonkin 1984). Almost all known localities with Precambrian metazoans are found in deposits accumulated in a shallow water environment. Rare finds of metazoan imprints in relatively deep water deposits, and a small number of associated trace fossils show that the Vendian invertebrates were living mainly in the shallow waters of the subtidal zone.

The processes of burial and fossilization of these marine animals must have been controlled by a number of factors (figure 1): (i) the size and the form of the body and its internal structure; (ii) density of the tissues and specific weight of the body; (iii) resistance of the tissues to mechanical and biochemical agents of destruction; (iv) presence or absence of special organs that chemically or mechanically protected the body from the predators and scavengers; (v) density of population; (vi) position of the species in the trophic chain; (vii) mode of life and character of the habitat; (viii) hydrodynamic régime; (ix) rate of sedimentation; (x) structure of the sediment in which the body was buried; (xi) temperature and degree of oxygenation at the bottom near the burial place; (xii) intensity of biological processing of the sediment by mudeaters (bioturbation).

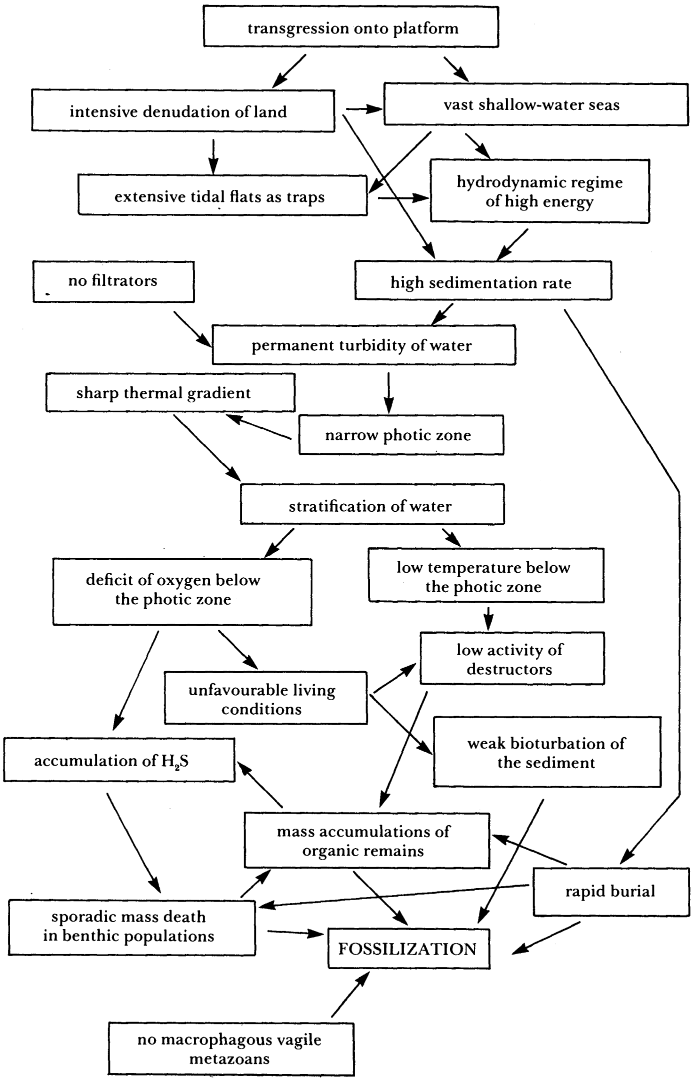

Figure 1. Some factors controlling and promoting the preservation of soft-bodied metazoans in the Vendian.

One of the numerous enigmas concerning Precambrian metazoans is related to the question as to why these soft-bodied animals have been preserved in such abundance, in a way that is not typical of the later fossil record. The unique preservation of non-skeletal invertebrates was obviously determined by the environment and the biota peculiar to the Vendian. Among abiotic factors which promoted the preservation in abundance of the fauna we may suppose the following: (i) the post-glacial transgression onto the continents resulted in vast epicratonal seas with a predominance of shallow water conditions favourable to the wide adaptive radiation of metazoans. During this time there existed very extensive tidal flats which could serve as natural traps for a great number of organisms. Such enormous tidal flats were a result of long-term transgression and intensive coastal denudation; (ii) the same causes induced a high rate of sedimentation promoting rapid burial of animals. Occasionally the burial could have had a catastrophic character because of high energy conditions in the shallow-water environment; (iii) intensive denudation of the land and a high sedimentation rate in wide littoral and sublittoral zones with unstable bottom conditions produced strong turbidity of the water. This phenomenon (especially combined with the absence of active filtrators that would have cleared the water) resulted in the narrow photic zone in the sea. This zone was relatively warm and well aerated because of the photosynthetic activity of algae. A sharp thermal gradient which should exist in such a situation, prevented the mixing of the warm and cold waters and did not permit homogenization of the oxygen content in the pelagic zone. This could lead to an oxygen deficiency below the photic zone and thus make the relatively deep-water environment unfavourable for metazoan life. Limited destruction of organic material by bacteria in the conditions of low temperature and low oxygen concentrations in the water near the sea floor could result in accumulation of large masses of organic remains on the sea bed. Part of them could have been buried by sediment during storm events and thus become potential fossils. A low rate of biotic destruction allowed the carcasses to stay unimpaired for a long enough time to be buried and then to be fossilized in effectively a perfect preservation. A slow decay of organic matter could lead to an anoxic or reducing environment even in the shallow water sublittoral zone, particularly in the depressions of the sea floor. This occasionally could cause mass death in benthic populations, especially in the case of the change in hydrodynamic regime and thus promote mass burial. Among other factors one might expect a high population density of sessile benthic forms including a large number of large-sized animals, which deformed the sediment in their life position and thus produced structures that potentially could be preserved. It has been suggested that there was a rarity and a restricted activity of macrophagous predators and necrophagous metazoans in the late Precambrian (Davitashvili 1969; Glaessner 1979, 1984), but I would stress also the low degree of biological processing of the sediment by mudeaters and other infaunal representatives of benthic metazoans in the Vendian period. The structures produced by living or dead animals in soft sediment were mainly preserved undisturbed. The situation changed abruptly when bioturbation of the sediment increased rapidly at the very end of the Vendian, when the two-dimensional colonization of the bottom surface was followed by the three-dimensional colonization into deeper layers of the sediment (Fedonkin 1977, 1981*a*).

3. The problems of classification of the Precambrian metazoans

The great evolutionary distance of the Vendian soft-bodied animals from Recent metazoans, as well as long gaps in the fossil record of non-skeletal fauna as a whole, make the elucidation of the systematic position and the phylogenetic relations of the Precambrian metazoans rather difficult. Attempts to place the Vendian animals within taxonomic schemes of post-Vendian, living taxa are usually contrived.

Body plan analysis, especially study of symmetry or promorphology, is one of the methods of comparative anatomy, and can be very useful for the classification of the Vendian fossils. The main reasons are the following: (i) in lower metazoans symmetrical features vary widely and thus allow us to recognize the low rank taxa; (ii) the number of characteristic morphological features that can be used for assumptions concerning the systematic position of the Vendian metazoans is small; and (iii) the vast majority of Precambrian fossils cannot be placed in the existing classificatory system of Metazoa. Below I shall consider and compare the main body plans of the Precambrian soft-bodied metazoans; this will be based on the concept of symmetry as the most precise and developed method of comparative anatomy (Beklemishev 1964).

3.1. *Radiata*

In the fossil associations of the Precambrian metazoans radial symmetry is dominant. Coelenterates constitute up to 67% of 1500 specimens of soft-bodied Metazoa collected in the Flinders Range near Ediacara in South Australia (Glaessner 1972, 1979). Various coelenterates account for 70% or more of the total number of the described species from the White Sea biota of the Vendian (Fedonkin 1981 *a*, *b*, 1982). Even higher percentages of coelenterates are found in the Vendian of the Ukraine (Palij *et al.* 1979; Fedonkin 1981 *a*, 1983 *b*). In some other localities no fossils other than coelenterates have been discovered, for example, Avalon fauna of southeastern Newfoundland (Anderson & Misra 1968; Anderson 1976, 1978; Anderson & Conway Morris 1982), and among the abundant metazoans in the Precambrian Khatyspyt Formation of Oleniok Uplift in northern Yakutia (Sokolov & Fedonkin 1984).

The prevalence of coelenterates in the Vendian metazoans can be considered to some extent as an artefact. In comparison with other soft-bodied organisms the coelenterates may have had a higher preservation potential for a number of reasons (Fedonkin 1983 *a*). The Vendian coelenterates, especially the most primitive solitary and colonial forms, usually have a greater body size. Some of those forms had a very thick mesogloea which was resistant enough to produce a prominent structure in the sediment after burial. A great number of the Vendian medusoids were benthic sessile forms attached to the soft bottom by means of a short extension of the aboral side of the disc-like body. These forms as well as other solitary and colonial polyps deformed the sediment while still in life position, thus producing structures capable of preservation and fossilization. It is quite possible that the Vendian coelenterates may have been already cnidarians, for example, they may have had cnidoblasts which protected them from carnivores during life and even for some time after death, so allowing them to be buried in the sediment without any damage. And finally, like Recent representatives of the phylum, the Vendian coelenterates occupied a position at the end of trophic chains, which seem to have been very short in this period.

On the basis of symmetry all Enterozoa (animals with a gut) are united into the division Bilateria, and all coelenterates into the division Radiata. The diversity of various kinds of radial symmetry in coelenterates may indicate that evolution of this phylum led to the attainment of various forms of radial symmetry. Precambrian radial animals also show a high diversity, but this diversity differs from living and later fossil Radiata in important features of symmetry. On the basis of the symmetry Vendian Radiata can be subdivided into three main groups: first, those numerous forms with a concentric organization and with the axis of symmetry of an infinitely high order; second, consisting mainly of radially arranged forms but with axis of radial symmetry of variable order; and third, including forms with a constant order of symmetry. In general these three levels of symmetry, the concepts of which are discussed by Beklemishev (1964), correspond to definite levels of organization of Precambrian Radiata, and can be considered within a framework based on the early phylogeny of metazoans.

3.1.1. *Radiata with a concentric body plan*

The Vendian coelenterates with a monaxial heteropolar symmetry (that is, the main axis of the organism shows differentiation of either pole) of infinitely high order are the most primitive group, yet the most flourishing of Precambrian megascopic metazoans. Representatives of this group share common characteristics such as type of symmetry, concentric body plan resulting from additive growth, the absence of well developed radial elements in the wide gastral cavity, the absence of radially arranged branching canals of a gastrovascular system, and presence of different modes of asexual reproduction, particularly simple longitudinal fission. All these traits suggest a primitive and archaic character for the group as a whole, and a monophyletic origin of its representatives. This group of the Vendian Radiata is considered as the class Cyclozoa within the Coelenterata (Fedonkin 1983*a*, 1984). Three taxa of lower rank within this class are recognized, and these differ in structure, character of growth, peculiarities of reproduction and ecology. The first group consists of sedentary organisms with, or even without, irregular concentric structure, such as in *Nemiana* (Palij 1976; Palij *et al.* 1979). The second group includes medusoids with a prominent, regular concentric body plan, in which the number of concentric zones increases during ontogeny. Oligomerous forms (that is, with few parts, in this case concentric ones) in this group usually show either very few wide concentric rings embracing the entire disc-like body (*Cyclomedusa davidi* Sprigg), or its central parts only (*Cyclomedusa plana* Glaessner & Wade). The combination of concentric and radial organization can be seen as numerous radial furrows in *Cyclomedusa davidi* or as irregular bosses that increase in size outwardly and form radially elongated lobes in *Mawsonites spriggi* (Glaessner & Wade 1966).

Polymerous cycloidal Radiata demonstrate numerous, relatively narrow, concentric rings which are particularly narrow in the centre and wide in the outer zones of the disc (for example, *Kullingia*, *Eoporpita* and *Kaisalia*). Certain polymerous cycloidal Radiata combine a concentric and radial organization, for example, *Eoporpita medusa* with several concentric series of radially oriented polypides (Wade 1972*a*) or tentacles; others are concentric with a bilateral body plan, for example, *Ovatoscutum concentricum* and *Chondroplon bilobatum* (Glaessner & Wade 1966; Wade 1971). This phenomenon allows the derivation of bilaterally segmented animals from the forms with concentric body plan (figure 2); for example from *Kullingia* to *Ovatoscutum* to *Chondroplon*

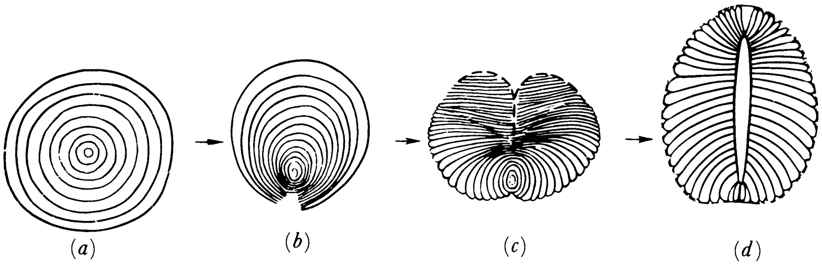

FIGURE 2. Transformation of the body plans of *Kullingia* (*a*), through *Ovatoscutum* (*b*) and *Chondroplon* (*c*) to *Dickinsonia* (*d*) showing the theoretical possibility of morphological derivation of bilaterally segmented forms from Radiata with a concentric body plan.

to *Dickinsonia* (Fedonkin 1983*a*, *b*). The discovery of this pattern, which follows from the analysis of the body plan, had not been predicted theoretically, and it stresses the great importance of a knowledge of the Vendian fauna for addressing fundamental problems of comparative anatomy of invertebrates. The speculative transformation from a polymerous concentric to bilaterally segmented polymerous body plan may also indicate the relatively low level of organization of Dickinsoniidae, they may be morphologically closer to coelenterates than to annelids, as many authors suggest (Glaessner & Wade 1966; Wade 1972*b*; Glaessner 1979, 1984; Runnegar 1982). We can assume that the Dickinsoniidae, a member of phylum Proarticulata, may represent a branch of metazoan evolution somewhere between Radiata and Bilateria (Fedonkin 1983*a*).

The third group of the Precambrian Radiata with a concentrically arranged body plan represents forms with a constant but small number of concentric rings. Most typical of these are: *Medusinites asteroides* Glaessner & Wade, *Paliella patelliformis* Fedonkin, *Nimbia occlusa* Fedonkin, *N. dniesteri* Fedonkin, *Irridinitus multiradiatus* Fedonkin, etc., with two concentric zones and *Ediacaria flindersi* Sprigg and *Tirasiana disciformis* Palij with three concentric zones. Many representatives of oligomerous cycloidal forms with a constant number of concentric rings tend to combine the concentric organization with prominent radial elements; for example, with numerous and fine radial furrows in the outer ring in *Ediacaria* and *Irridinitus*, or with numerous marginal tentacles in *Ediacaria* and *Nimbia* (Fedonkin 1983*c*).

3.1.2. *Radiata with essentially radial body plan*

(*a*) *Forms with the radial symmetry of variable order.* Radiata with monaxial heteropolar symmetry and with an axis of variable but finite order comprise a large and diverse group among the Vendian coelenterates that have a radially arranged body plan. Radial symmetry of a variable order is reflected in the whole organism as well as in different organs, for example, marginal tentacles (*Hiemalora stellaris* Fedonkin), the channels of the gastrovascular system (*Rugoconites enigmaticus* Sprigg), gonads (*Hallidaya brueri* Wade, *Armillifera parva* Fedonkin, *Elasenia aseevae* Fedonkin), gastral cavity (*Bonata septata* Fedonkin), etc. (for illustrations see Glaessner 1979, 1984; Fedonkin 1981*a*, 1983*a*, 1984).

The main peculiarity of the representatives of this group is an increase of the order of radial symmetry during ontogeny, that is, new antimeres (symmetrically corresponding parts, anatomically identical (Hyman 1940)) are added while the organism is growing but no order or succession in their formation have been observed; furthermore the number of antimeres is not related to any particular value. Forms with this type of symmetry were, in the Vendian, more widespread than now or in the Palaeozoic. In living cnidarians this type of symmetry is believed to be one of the lowest types (Beklemishev 1964).

Despite the primitive mode of formation of antimeres this group is, on the whole, of a higher organization than Radiata which are characterized by an axis of symmetry of infinitely high order (Cyclozoa). The members of the group with variable radial symmetry usually have a well arranged system of tentacles and different and complicated systems of gastrovascular canals which branch several times toward the periphery and sometimes form a plexus-like network. The system of reproductive organs (gonads) in many forms of this group indicates the prevalence of sexual reproduction; asexual reproduction in this group of Radiata is, however, rare. This seems to indicate that in the level of organization the Vendian coelenterates with radial symmetry of variable order are more closely related to later cnidarians than to the representatives of the class Cyclozoa. Such a fundamental promorphological feature as the variable radial symmetry in the group of coelenterates described above, makes it necessary to consider this group as a separate class, the Inordozoa.

(*b*) *Forms with the radial symmetry of stable order*. Coelenterates with a stable order of radial symmetry are not as numerous among the Vendian Radiata as representatives of other groups with a more primitive organization and archaic symmetry. This is opposite to the situation found in recent Cnidaria. This may indicate that the regulation of radial symmetry resulting from the stabilization of a number of antimeres was a relatively late development representing a specific and main trend in the evolution of Coelenterata. The Vendian Radiata with axes of radial symmetry of a stable order are more similar to living forms of Cnidaria than to other Precambrian coelenterates. Nevertheless, in this group we observe characters which are neither typical of the coelenterates nor of the recent metazoans in general.

One such peculiarity is a threefold symmetry. This order of symmetry occurs only exceptionally in recent cnidarians and in other groups of Metazoa it is rare and always a secondary phenomenon. This symmetry was, however, widespread in the Vendian medusae, for example, *Skinnera brooksi* Wade, *Tribrachidium heraldicum* Glaessner, *Albumares brunsae* Fedonkin and *Anfesta stankovskii* Fedonkin (Glaessner & Wade 1966; Wade 1969; Keller & Fedonkin 1977; Fedonkin 1981*a*, 1983*a*). A unique threefold radial symmetry makes the above group sufficiently homogenous in the phylogenetic sense, and allows us to consider it as a taxon of high rank (Fedonkin 1983*a*). It is possible to recognize it as a coelenterate class, the Trilobozoa. I consider that this class includes also the oldest skeletal organisms known as the Augustiochreidae (Valkov & Sysoyev 1970) or as Anabaritidae (Missarzhevski 1974; Glaessner 1979) which appeared at the end of Vendian and became widespread in the Early Cambrian. The relation of these organisms united in the subclass Angustiomedusae (Valkov 1982) to the class Scyphozoa is not evident because a three-fold symmetry is not characteristic of this class of cnidarians. A four-fold symmetry prevails in Scyphozoa. This seems to suggest that the Trilobozoa is a separate class of Coelenterata with an organization similar to the class Scyphozoa but with a different symmetry; with respect to their symmetry this makes it as coherent a group as the scyphozoans.

The forms with the four-fold symmetry comprise an integral part of the Precambrian Radiata with a stable order of radial symmetry, for example, *Comomedusites lobatus* Glaessner & Wade, *Kimberella quadrata* (Glaessner & Wade), *Ichnusina cocozzi* Debrenne & Naud, *Persimedusites chahgasensis* Hahn & Pflug, *Staurinidia crucicula* Fedonkin (Glaessner & Wade 1966; Wade 1972*a*; Hahn & Pflug 1980; Debrenne & Naud 1981; Fedonkin 1983*a*, 1984). A high degree of organization, as well as their symmetry typical of scyphozoans, make it possible to consider these small jellyfishes as members of the class Scyphozoa. The indirect evidence for such a supposition is the presence of the only form with a theca (*Conomedusites*) among the fourfold coelenterates. Glaessner (1979) placed this genus in the class Conulata but the subclass Conulata was originally considered to belong to the class Scyphozoa (Moore & Harrington 1956).

The forms with a stable order of radial symmetry are relatively rare among the Vendian Radiata and they show considerable diversity in their body plan. The threefold and fourfold forms are the most widespread, and are characterized by great variation in the gastrovascular system (single and paired; branching and non-branching radial channels). In some forms an umbrella is divided into narrow branching lobes, in which channels are probably present

(*Anfesta*). Such organization can be considered as primitive and early in an evolutionary sense: thin branching channels in the gastrovascular system could be developed from such hollow lobes.

Unlike the forms with a symmetry of infinitely high and variable order, the Vendian coelenterates with the stable order of symmetry do not show any sign of asexual reproduction. Their reproductive organs demonstrate a certain diversity in shape and position.

3.1.3 *Precambrian Radiata and the early phylogeny of the coelenterates*

The study of the body plan of the Vendian Radiata opens the possibility of understanding the earliest stages of the morphological evolution of Coelenterata. The symmetry of infinitely high order and concentric body plan of the class Cyclozoa allows us to consider this group as an independent, major phylogenetic branch of early coelenterates. I assume that in an earlier evolutionary stage of Radiata the symmetry typical of the class Cyclozoa was dominant. The symmetry and the body plan of the simplest forms in this group are strikingly similar to the hypothetical gastrula-like ancestor of all multicellular organisms conventionally placed at the base of the phylogenetic tree of Metazoa. This structure is the most primitive among the Vendian coelenterates and possibly the earliest in the history of the phylum. Comparable symmetry is rare in recent cnidarians and occurs only in the larval stage or in adults of *Protohydra*. In the Vendian, however, we already see other tendencies in the evolution of Coelenterata, which were later to prevail in the Phanerozoic, for example, the development of radial organization. The Precambrian Radiata demonstrate simultaneous presence of concentric and radial symmetry and this suggests historical links between the concentric and radial body plan. The combination of concentric and radial types of symmetry may be indicative of the phylogenetic relation of Cyclozoa to those later and more advanced Coelenterata which have the radial body plan. On the other hand the combination of these features may characterize very primitive forms such as those described above.

Among organisms with a concentric body plan the sedentary forms are the most common; pleustonic and planktonic animals are rarer. This predominance of one ecological type in the group of the most primitive Precambrian Coelenterata may be considered evidence for the primary nature of a polypoid stage in the evolution of the metagenesis (alternation of sexual and asexual generations) of Cnidaria. An anisotropic environment on the sea floor and a spectrum of various habitats that was wider than in the pelagic zone could have promoted such a diversity of forms.

The Vendian coelenterates with the symmetry of infinitely high order and with an essentially concentric body plan represent a way of attaining diversity within this type of symmetry. This results in the concentric zonation of the body. It is followed by the polymerization of concentric rings, then by oligomerization and by strong regulation of their number in combination with the radial symmetry of uncertain order or with bilateral symmetry.

A variable order of radial symmetry is very rare in living cnidarians and is considered a primitive feature. But in the Vendian Coelenterata this symmetry prevailed in many groups of relatively high organization. We can suppose that the radial symmetry of uncertain variable order represents an important and possibly a necessary stage in the early evolution of many phyletic lines of Coelenterata (Fedonkin 1983*a*). Many structures and many systems of organs characteristic of recent Cnidaria appear to have been formed in the Precambrian Radiata at the stage of radial symmetry of variable order. It is logical to consider the Vendian Coelenterata with such a specific type of the symmetry as a special class Inordozoa. On the other hand the variable order of radial symmetry could have evolved independently in different phylogenetic lines of Coelenterata.

This analysis of the body plan of the Precambrian Radiata indicates that in the Precambrian the path of evolution of Coelenterata was from the concentric to radial body plan and from a variable to a stable order of radial symmetry.

3.2. *Bilateria*

A large diversity of body plans exists among the Vendian Bilateria, in which a wide range of types of organization shows highly advanced and separate branches of this large group. This was discussed in detail earlier (Fedonkin 1983*a*), therefore only general remarks are now necessary. An overwhelming majority of known Vendian bilateral metazoans are flat-bodied. Various segmented animals dominate among them, including polymerous and oligomerous forms with signs of homonomous and heteronomous (respectively, development of similar and dissimilar segments) metamerism as well as with the characteristic feature of imperfect segmentation and the symmetry of glide reflection (that is, segments alternate rather than being opposed).

A strong prevalence of segmented forms among Vendian Bilateria supports the idea that in many branches of Metazoa the process of formation of bilateral symmetry and of segmentation (metamerism) are related (Fedonkin 1983*a*).

The large majority of Vendian Bilateria is characterized by peculiarities not observed in many later multicellular animals; the most important being the plane of symmetry of glide reflection. This is characteristic of very primitive Bilateria, in particular of polymerous forms with homonomous metamerism (Dickinsoniidae) and of oligomerous Bilateria with evident signs of cephalization (Vendomiidae).

The thin, sheet-shaped Dickinsoniidae have the lowest level of organization among segmented forms. Initially they were consideed Coelenterata of the class Dipleurozoa (Harrington & Moore 1956), later annelids (see, for example, Glaessner & Wade 1966; Wade 1972; Runnegar 1982) and finally flat worms (Fedonkin 1981). The analysis of symmetry of this family and the comparison of their body plan with the architectonics of Coelenterata, Turbellaria and Annelida suggests that the Dickinsoniidae is an independent branch of the oldest Bilateria (Fedonkin 1983*a*). The derivation of the symmetry of Dickinsoniidae from the most archaic Radiata with an axis of rotation of infinitely high order and with concentric organization, (*Kullingia–Ovatoscutum–Chondroplon–Dickinsonia*) or with an axis of variable order and with radial organization (*Irridinitus–Dickinsonia*), indicate that this group is very primitive (figures 2 and 3). It is possible that the Dickinsoniidae represent one of the branches of Bilateria that separated from Radiata earlier than others. It is very difficult to determine whether this was successful, but since in addition to the Dickinsoniidae other more highly organized Bilateria existed in the Vendian, the Dickinsoniidae seem to have developed as a blind alley which possibly became extinct in the Vendian (true Dickinsoniida or similar forms are neither found in the late Vendian nor in the Cambrian). Thus Dickinsoniidae can be assigned to a specific class Dipleurozoa, but not as Coelenterata but within primitive Bilateria of the phylum Proarticulata (Fedonkin 1983*a*).

Animals with a flat, oval body, a large cephalic area with an axial lobe, and postcephalic segments are an independent and specific group of the Vendian Bilateria. The left and right segments are either placed opposite each other or they alternate. This group, represented by the family Vendomiidae Keller (Keller & Fedonkin 1977) tends to develop a large cephalic area, apparently a progressive development. However, the plane of symmetry of gliding reflection in *Vendia sokolovi* Keller (Keller 1969), and the flat oval body in those animals without lateral appendages surely indicate an extremely archaic character. It represents a blind branch, one of the 'experiments of Nature' on its way towards true Articulata and possibly a class Vendiamorpha of the phylum Proarticulata.

Some rather specific groups of Vendian Bilateria, including the above, are difficult to place within the existing classification of Metazoa. Representatives of these are often characterized by a complex of features, which separately are typical of widely separated later phyla. An example is the presence in the families Sprigginidae Glaessner and Bomakellidae Fedonkin of shoe-shaped heads resembling the head shields of trilobites and bodies of annelids. Such forms may be transitional or ancestral to groups that separated in the course of evolution. The specific characters of Sprigginidae and Bomakellidae suggests that these groups belong to a class Paratrilobita possibly of the phylum Arthropoda. With this in mind certain groups of the Vendian Bilateria can be considered to continue to the Phanerozoic, for example, among Arthropoda Parvancorinidae Glaessner 1969, and among Sabelliditidae Sokolov 1965, which may be compared with recent Pogonophora (Sokolov 1972).

3.2.1. *The problem of metamerism in the light of the Vendian fossil record*

The prevalence of segmentation among the oldest Bilateria forces us to rethink the problems of the origin of bilateral symmetry and metamerism. Many workers are preoccupied with these fundamental problems of comparative anatomy and zoology, and these problems remain acute.

Certain authors who accept the protaxonia (gastrular axis preserved as oral–aboral axis, blastopore becomes mouth) of all Bilateria (Hyman 1940; Ivanov 1968, 1976) actually consider problems of the origin of bilateral symmetry and metamerism separately: according to them, non-segmented Scolecida appeared first, and segmented Articulata second. A similar view is supported by Clark (1964).

The Vendian fossil record does not support these concepts. Non-segmented forms are very rare among the Vendian Bilateria (Glaessner 1979; Fedonkin 1983*a*), and their nature is questioned; while a transition from these non-segmented animals to the Vendian Articulata appears practically impossible.

Other concepts derive Bilateria from Radialia through transformation of an oral to a ventral side and by accepting the plagiaxonia (that is, gastrular axis does not persist as adult axis). In this case metamerism could have been derived from cyclomerism (antimerism, see below) of Coelenterata (Sedgwick 1884; Melnikov 1971, 1977), or could have appeared independently due to the metamerization of the metacoel (that is, the third pair of coelomes of the archicoelom of the primitive ancestor) (Masterman 1898; Remane 1950, 1952).

In my opinion the diversity and morphology of the Vendian Bilateria reflects to a great extent the concept of simultaneous appearance of bilateral symmetry and metamerism. This concept is supported by at least three very clear tendencies: (i) the prevalence of segmented over non-segmented forms; (ii) the presence of primitive animals with a large number of metameres and with preserved traces of the radial arrangement of metameres; and (iii) the presence among polymerous and oligomerous forms of alternating segments, which can be considered a result of the peculiar structure of zones of growth that 'shifted' or 'glided' relatively to each other.

There are three major theories explaining the origin of metamerism in annelids: (i) origin of metamerism by metamerized differentiation and the regulation of the position of organs; (ii) origin by suppressing transverse division (strobilar theory); (iii) origin of metamerism derived from the antimerism of Coelenterata. The new data on the Vendian fauna allows us to consider in detail the third theory of the origin of metamerism in annelids from 'cyclomerism' (antimerism) of Coelenterata. This theory, proposed by Sedgwick in 1884, has since been supported by many other workers.

Sedgwick thought that annelids originated from ancestors similar to corals (Anthozoa). He accepted the origin of the mouth and anus of annelids from the siphonoglyphs of the closed slit mouth and therefore according to him the ventral part of annelids is homologous with the oral side of Anthozoa. The nerve plexus of the oral disc of the polyp, having become compact, developed into the nerve ring, which formed many cross commissures after the primary slit-shaped mouth became closed. A part of the ring anterior to the definitive mouth developed into a ganglion. The body became elongated, the radial chambers of the gastral cavity became closed and developed into coelomic pouches. The tentacles of polyps produced extremities. The posterior growth zone in annelids is homologous to the only growth zone of such corals as Ceriantharia.

This simple theory has a paradoxical element, which in the opinion of Beklemishev (1964), is the result of an attempt to derive annelids not from primitive, but from highly specialized forms such as higher corals.

Analysing the theory of metamerism Beklemishev (1964) considers that the ideas of Sedgwick can be partly applied to the ectodermal metamerism of the larval body, but not to the metamerism of the coelome and its derivatives associated with the postlarval body. The differences in the organization of coelenterates and of coelomates are great.

Remane (1950, 1952) possibly avoided the difficulties of directly deriving coelomates from Coelenterata because he derived them from Cnidaria with four gastral pouches, a number that does not correspond to the number of coelome pouches in segmented organisms. According to the version of Remane an unpaired front gastral pouch and two lateral pouches become protocoels and mesocoels respectively. This is preserved in oligomere animals (hemicordates, echinoderms and pogonophores), though neither protocoel, nor mesocoel is preserved in adults.

Remane considers the tetramerous polyp as a prototype of all Bilateria. While crawling on the oral side the polyp stretches the gullet and thus a new longitudinal axis of the body appears perpendicular to the primary axis (Remane 1950). When the architectonics of Enteropneusta are derived from this protoype it is assumed that the anterior gastral pouch forms an unpaired proboscis coelome, that the lateral pouches produce collar coelomes, and that a posterior pouch divides into two parts and produces thoracic coelomes. According to Beklemishev (1964) the theory of Remane cannot be applied to Deuterostomia, but can be applied to trochophorous animals. The major defect of the theory is an attempt to derive all Bilateria from a single root by using one method while the major stems of Bilateria can be derived from at least three different prototypes at different levels of organization and with the use of different reconstructions of these prototypes (Beklemishev 1964).

The third version of the cyclomerism theory has been put forward by Lemche (1959, 1960). It is similar to the theory of Sedgwick in that the organisms with metameric segmentation are derived from corals, but although Lemche accepts the enterocoel theory it differs from other versions of the cyclomerism theory in that the segmented subdivision of the coelome is not considered an important characteristic of metamerism. Lemche homologizes the crown of outer tentacles of the polyp with the ctenidia of molluscs (primitively arranged around the foot as in Neopilina), with parapodia of polychaetes, with the branchiae of trilobites, and with the limb of Arthropoda. The aboral gland of molluscs which secretes a shell corresponds to the aboral pedal disc of Cnidaria which secretes a theca.

The fourth variant of this theory was suggested by Melnikov (1977). In his opinion the metamerization of cyclomerism during the evolution of Arthropoda (which originated from the previously pelagic coelenterate ancestors which began crawling on the blastoporal side of their body) was accompanied by formation of pairs of metamerized cyclomeres of completely segmented rings. While the blastoporal body became large, this process proceeded in such a way that segmented rings closed behind the aboral part.

The analysis of the promorphology of the Vendian Metazoa offers us palaeontological arguments supporting the cyclomere theory of Sedgwick. And at the same time it removes the major contradiction, or the paradox, of this theory. The Vendian segmented Bilateria with irregular metamerism, which is characterized by the plane of gliding reflection, serves as one such argument. This type of symmetry is quite natural and even a necessary step for certain polymerous, as well as oligomerous, Vendian Bilateria which lie at the starting point in the phylogenetic process of the formation of true metamerism. It is derived, not from higher corals, but from less specialized and more primitive forms of Radiata which have an axis of symmetry of variable order and which were widespread in the Vendian. If the supposition that Radialia with an axis of rotation of infinitely high or variable order were dominant at earlier stages of the evolution of multicellular animals (a conclusion drawn from the analysis of the Vendian material) then deriving of the metamerism of Articulata leads to the forms with an irregular arrangement of metameres similar to *Vendia*, *Dickinsonia*, etc.

The plane of symmetry of glide reflection can be considered of important and fundamental significance, reflecting a necessary stage in the evolution of metamerism in various branches of Metazoa. This symmetry, atypical of the majority of the Phanerozoic multicellular solitary animals, is one of the evidences from palaeontology supporting the hypothesis which derives the metamerism of segmented forms (Articulata) from the radially symmetrical organisms. But we must emphasize that the plane of symmetry of glide reflection of the Vendian Bilateria may indicate the possibility of the early origin of bilateral segmented forms from radially symmetrical animals in which an axis of rotation is of variable order (figure 3).

Consequently the stage of irregular metamerism (the plane of glide reflection) can take place in various lines of Bilateria, but it cannot be protracted. The alternating arrangement of metameres is not advantageous for actively moving animals. To a lesser extent it was not convenient for the forms that moved with peristaltic waves along the ventral side of the body, but even more so for organisms with appendages. Flat-bodied shapes and the absence of lateral appendages in certain Vendian Bilateria suggest the peristaltic mode of crawling. It is noteworthy that trace fossils of the Vendian invertebrates reflect mainly this style of locomotion. Traces of crawling by appendages are extremely rare in the Vendian ichnocoenoses (Fedonkin 1981*a*).

Thus the data obtained from the analysis of the promorphology of the Precambrian multicellular animals support theories which derive bilateral animals directly from radial animals. New palaeontological data seem to indicate that the process of the formation of bilateral symmetry and that of metamerism are closely related at least in some branches of Metazoa.

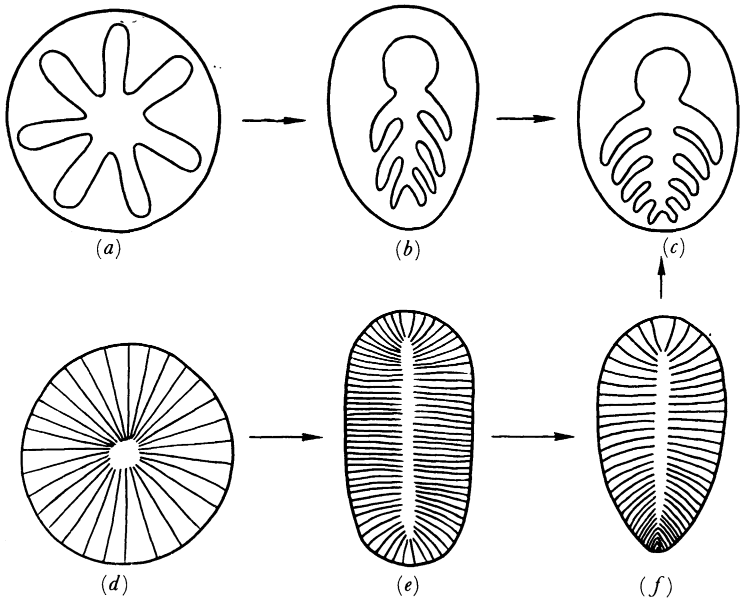

FIGURE 3. Transformation of the body plans of Radiata with variable order of the symmetry (upper line, oligomerous forms; lower line, polymerous forms) to the bilaterally segmented architectonics as illustrated by some Precambrian metazoans: (*a*) *Bonata*, (*b*) *Vendia*, (*c*) *Praecambridium*, (*d*) *Irridinitus*, (*e*) intermediate form, (*f*) *Dickinsonia*.

4. DISCUSSION

Among recent metazoans the bilaterally symmetrical animals are more numerous and more diverse than the radially symmetrical forms. But such was not always the case: among megascopic Vendian multicellular animals the ratio of abundance of Bilateria and Radiata was quite different. Palaeontological data indicates the prevalence of Radiata in the Vendian (Glaessner 1979; Fedonkin 1981*a*, 1983*a*, *b*). This important palaeontological observation supports the idea that the most primitive groups of Bilateria are related to Coelenterata (Beklemishev 1964). The abundance, diversity and large dimensions of Vendian coelenterates strongly suggest that they were the oldest group of Metazoa. The animal world of the Vendian dominated by Radiata supports the idea that during the earliest, possibly short stage of evolution of multicellular animals, radially symmetrical organisms completely dominated, and that the animal world consisted only of Radiata (figure 4). This apparently fantastic supposition is based on the retrospective extrapolation, but it is palaeontologically supported by the Vendian fossil record.

It is important to note that comparative anatomists widely accept the thesis of the primary nature of radial symmetry in the ontogeny and phylogeny of Eumetazoa. However, various authors discuss only how bilateral organisms could have evolved from the radially symmetrical forms (see, for example, Beklemishev 1964; Clark 1964 and references therein). The only exception is the concept of bilaterogastrea of Jägersten (Jägersten 1955, 1959, 1972) in which recent Radiata are derived from bilaterally symmetrical forms, and the concept of J. Hadži (Hadži 1944, 1963) which postulates the origin of Turbellaria from the protists due to cellularization, and the origin of Coelenterata from Turbellaria. The prevalence of Radiata in the Vendian fauna thus support this existing idea from comparative anatomy about the primary nature of radial symmetry.

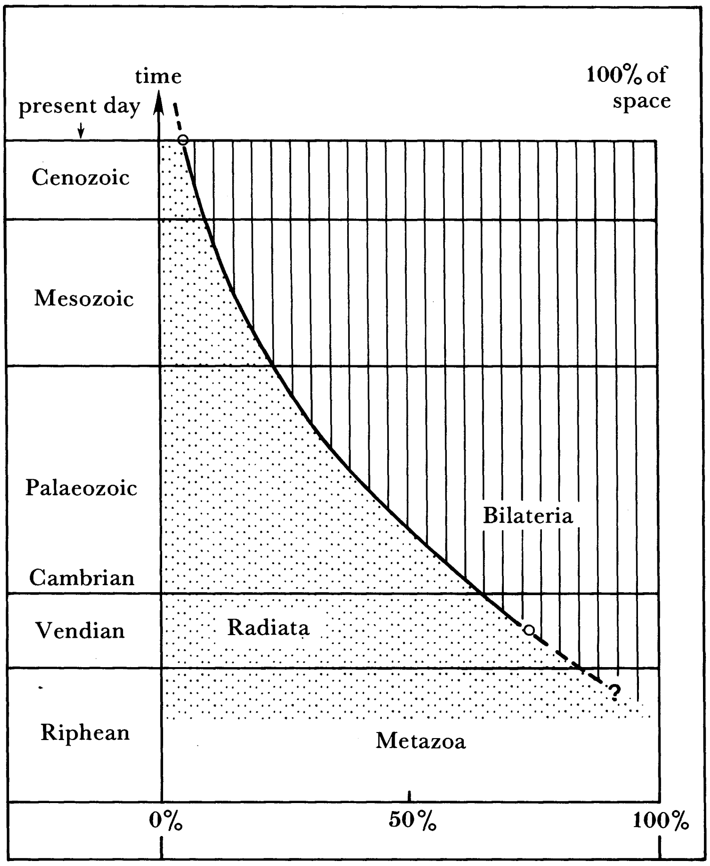

FIGURE 4. Comparison of the abundance of Radiata and Bilateria at the present day and in the Precambrian fossil record, allows us to make a retrospective extrapolation which supports the idea of the primary nature of radial symmetry and of the coelenterates as the oldest group of Metazoa.

If we assume that the palaeontological record of the Vendian Metazoa adequately reflects the ratio of major groups in the late Precambrian animal world, then during the Vendian, in comparison with the radially symmetrical, the bilaterally symmetrical animals were in the minority. This is partly explained by ecological and taphonomic peculiarities of the above-mentioned groups of the fauna. However, the main reason for such a disproportion may be the diversification of Radiata earlier than Bilateria and the priority of radial symmetry in the metazoan evolution.

Studies of the promorphology of Vendian multicellular animals allows us to see the peculiarities of the Precambrian history of Metazoa including the most important trends of morphological evolution so far known. The new data are of great significance for the development of ideas on some fundamental problems of the comparative anatomy of invertebrates and for the general theory of morphological evolution as well. In particular we can state that the earliest radiation of multicellular organisms followed the path of the realization of symmetrical diversity. Various body plans appeared in the course of this radiation, some of which were inherited during the evolution of Metazoa and became fixed features of higher taxa.

The most archaic is monaxic heteropolar symmetry of infinitely high order, usually related to concentric body plan which is characteristic of many primitive forms of Vendian

Coelenterata. Those Radiata that increase an order of radial symmetry in ontogeny are characterized by a higher organization. A variable order of radial symmetry characteristic of many forms of Vendian Coelenterata is here considered a necessary stage in the evolution of many lines of Radiata, particularly those on the way towards the symmetry of stable order so typical of Phanerozoic Cnidaria. The stable order of symmetry of the Vendian Radiata is represented by forms with a threefold and fourfold radial symmetry which in turn are characterized by the highest level of organization. The analysis of architectonics of Vendian Coelenterata allows us to suppose that the evolution of Radiata proceeded from those forms with symmetry of infinitely high order, through the forms with variable multirayed symmetry to those with stable order of symmetry; and from the animals with concentric organization to the forms with a mainly radial body plan.

In comparison with radial forms, the remains of Vendian Bilateria constitute the minority. Many of the Precambrian bilateral animals are characterized by a flat segmented or metamerized body. The large variety of their body plans in this large group reflects a wide range of types of organization. Strong prevalence of segmented forms among Vendian Bilateria suggests that in many branches of Metazoa the evolutionary development of bilateral symmetry and metamerism were related processes, which did not however, always lead to coelomates. One of the most important peculiarities of segmented forms is the imperfect symmetry or the symmetry of glide reflection characteristic of the most primitive Bilateria. This symmetry, atypical of the latest bilaterally symmetrical Metazoa, can be indicative of very early origin of metamerized Bilateria from radially symmetrical Metazoa with an axis of rotation of variable order. It is possible that imperfect metamerism, or the symmetry of glide reflection, was a very important stage in the evolution of some groups of Metazoa evolving towards true Articulata. Some groups of Vendian Bilateria are not yet assigned to any classes or phyla of Metazoa. The representatives of this group have either an unusual body plan or are characterized by a combination of features typical of different phyla later widely separated in the palaeontological record.

Studies of the Vendian fauna indicate that at the end of the Vendian many groups of Metazoa became extinct. This extinction occurred first in taxa that flourished in the Vendian and that constituted the most characteristic elements of Vendian–Ediacarian fauna. These include the main groups of Radiata particularly those with a symmetry of infinitely high order and with concentric organization; many Bilateria, especially forms with imperfect metamerism; and also other specific groups such as Petalonamae. One of the causes of this mass extinction may have been ecological events; these may have been related to competition for food resources and habitat partitioning with the more progressive lines of Metazoa which continued into the Phanerozoic.

The level of organization of many groups of Precambrian Metazoa, their very problematic character and their uniqueness together with the peculiarities of ecology of the Vendian biota, all support the status of the Vendian as an independent stratigraphic system. A sharp difference between the Vendian and the Cambrian (and the Palaeozoic as a whole) biotas is a sign that the Vendian–Cambrian boundary is not only the boundary between systems but also a boundary between the Palaeozoic and pre-Palaeozoic erathems. In other words, the Vendian is a terminal period of the pre-Palaeozoic era, this era is comparable in importance and in the peculiarities of its evolutionary events to any other era. Many of the Precambrian fossils represent a new group of organisms, that became extinct at the end of the Vendian period.

A high level of differentiation of the animal world at the beginning of the Vendian, and the abundance of invertebrates of different levels of organization may have been a result of the pre-Vendian development of Metazoa. This forces us to search for multicellular animals in even older periods. The future discovery of the earliest metazoan history coupled to the palaeozoological criteria may change our definition of the lower boundary of the terminal Precambrian system.

The cosmopolitan nature and great abundance of many Vendian metazoans that existed during the gigantic postglacial transgression in the first half of the Vendian, allows us to use the remains of soft-bodied faunas and trace fossils for broad stratigraphic correlations. The differences in taxonomic composition and in the levels of organization of multicellular organisms from various localities may indicate their different age and the potential for biostratigraphic studies of the Precambrian Metazoa and their related ichnological developments.

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Discussion

J. C. W. Cope (*Department of Geology, University College of Swansea, Swansea SA2 8PP, U.K.*). My experience with the Vendian faunas of the Carmarthen area, South Wales, supports the view of Dr Fedonkin that the lack of burrowing organisms within the sediment was a key factor in the preservation of Ediacaran faunas. The sediments in the South Wales Vendian are very finely laminated; frequently as many as 20 laminations per centimetre thickness of sediment have been encountered. Although I have examined large numbers of cut slabs of these sediments, all have appeared free from the sort of disturbance that would be caused by bioturbation. The faunas of the area includes a significant trace fossil element but this is confined to surface traces, feeding trails, etc., and lacks any form that penetrated into the sediment. Thus here, as in the White Sea area from which Dr Fedonkin had obtained his extensive fauna, burrowing traces are unknown.

M. A. Fedonkin. Traces of burrowing organisms do occur in extremely shallow-water facies. Diverse horizontal burrow systems are met rather often but vertical burrows are very rare. The latter ones are usually not deep. In general, biological processing of sediment by metazoans is always small in the Precambrian.