1976

THE EDIACARIAN FAUNA AND ANIMAL EVOLUTION

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ABSTRACT: The period that preceded the appearance of animals with a carbonate or phosphate skeleton (the period known as the Wendian in Eurasia) gave rise to a fauna that has been preserved in several regions of the globe. The best known site of such a fauna at the present time is Ediacara in South Australia (Glaessner and Wade, 1966). The present authors have therefore called the fauna "Ediacarian" (Termier and Termier, 1960). This, the first zone of stratigraphic paleontology, has a duration of a hundred million years. It is deep within it that we should seek an answer to the question of the origin of the animals that were to replace it.

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ORIGIN OF THE METAZOA

The establishment of animal life evidently entailed great difficulties. The traces of life in the Precambrian, which are known from deposits more than three billion years old, are mainly of schizophytes, and eukaryotic plants have been in existence for more than one billion years. However, the first animals are known from deposits no more than 700 million years old. There are probably causes for such a lag, two at least of which seem obvious:

1) the need for a fairly high content of free oxygen in any environment, a gas which could have been released only as a result of photosynthesis over the course of several hundred million years;

2) the preexistence of food, since animals are incapable of synthesizing organic matter from inorganic elements, as can plants. Such food must have become abundant in the seas from the Riphean onwards, thanks to the development of phytoplankton. It must also be stressed that the symbiosis between numerous marine invertebrates and microscopic plant flagellates and zooxanthellae today successfully resolves both problems. It is highly probable that the appearance of symbioses of this type was one of the most important events in animal evolution.

Logic requires animal evolution to have proceeded progressively from the simple to the more complex, i. e. initially from the Protozoa to the Metazoa, and then from two-layered to three-layered Metazoa and finally to the Coelomata. At the same time it is difficult to find the phylum that could have given rise to the Metazoa among the extant Protozoa. Their organization is, in fact, too complex. Thus, for example, the intracellular organelles of the Protozoa have all the most important functions. At the same time each of the Metazoa passes through an original unicellular stage. They originate either from plasmatic protistans [this hypothesis was rejected by Brien (1969)], or from colonial protistans which, however, might not be Protozoa.

New elements have been introduced into the solution of this problem by recent discoveries in histology at the ultrastructural level. We would recall that the similarity between the choanocytes of sponges and colonies of choanoflagellates confirms the second hypothesis (James-Clark, 1868; Bütschli, 1884). Choanocytes were later noted among the ciliated epithelial cells of various phyla of the Metazoa: echinoderms, bivalves, annelids and acranians. Investigation of the ultrastructure of these different types of cells has shown that it is not instances of simple convergence that are concerned, but close connections; the research has also led to the discovery of choanocytes in the Enteropneusta and in cnidarians (Norrevang and Wingstrand, 1970; Bilbaut and Pavans de Ceccaty, 1971, etc.). The monophyletic origin of the Metazoa has been inferred by the authors concerned from this important fact. This deduction is applicable at all events to the diploblastic Metazoa, i. e. to sponges and cnidarians.

The members of the diploblastic Metazoa in the Ediacarian fauna were mainly jellyfishes (Trachylina and Scyphozoa) and Pennatulida, with which the Rangeidae may also be converged. Choanocytes have also been established in such of the Pennatulida as Veretilles.

The presence of pennatulids in the Ediacarian fauna is, therefore, an extremely interesting transitional stage. However, no connection is established between the Cnidaria and Spongiaria at

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Translated from Ediakarskaya fauna i evolyutsiya zhivotnogo mira, Paleont. Zhur., 1976, no. 3, p. 22-29.
Paleont. Jour. 1976, no. 3

this level, since sponges are unknown in the Ediacarian fauna. Archaic groups of organisms having a mineralized skeleton, among which we may seek to discover divergence between the Spongiaria and the Cnidaria, are found in a slightly later epoch corresponding to the Early Cambrian, including the Tommotian Age (fig. 1). We refer to the Archaeocyatha and the Radiocyatha (Debrenne, Termier and Termier, 1970, 1971). The Archaeocyatha are very primitive creatures in which, in the opinion of Zhuravleva, Konyushkov and Rozanov (1964) the living matter was multicellular "lactoplasm" intermediate between the cytoplasm of the Protozoa and the tissues of the Metazoa. It may be thought that this "lactoplasm" had extensive potential for evolution. Archaeocyathan skeletons are reminiscent in shape of a gastrae (Capsulocyathus), or of a sponge or a cnidarian. Radiocyathan skeletons sometimes have only one wall, in which case they are on a lower level than a gastraea; when they have two walls they exhibit some similarity to sponges (Uranosphaeridae) or echinoderms (Radiocyathidae). We can imagine the living matter of these ancient groups: cells of choanocytic type in combination with plasmoidal masses could have corresponded to the first stage of development of the tissues in the Metazoa. We are thus coming closer to the hypothesis that the Volvocaceae are similar to the "original Metazoa". These presentday protistans which, however, belong to the vegetable kingdom, since their cells have cellulose walls and contain chlorophyll, also exhibit embryonic rudiments and inversion of the surfaces similar to that to be observed in sponges. This "overturning of layers" occurring in the metamorphosis of the larva - the parenchymula in sponges, may be compared with the "excurvation" of the blastula in Volvox; it is now regarded as true gastrulation (Brien, 1969).

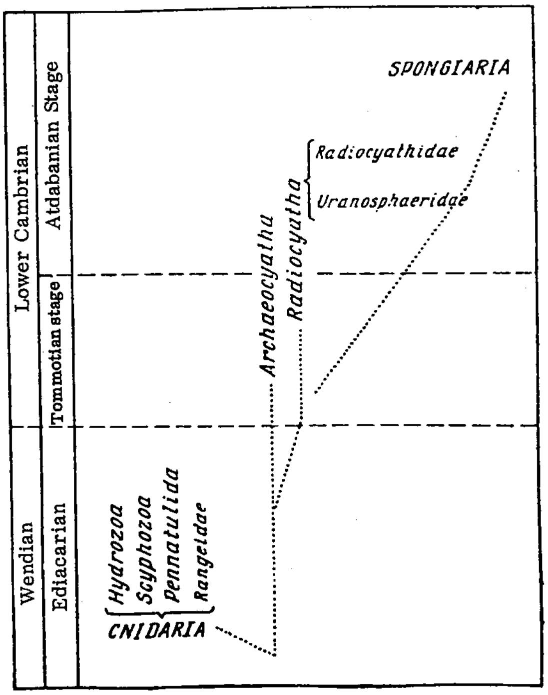

FIGURE 1. Phylogeny of the Archaeocyatha, Radiocyatha and Spongiaria.

The convergence of these primitive Metazoa with the Volvocaceae is of interest in that it incorporates them in biokinesis (Termier and Termier, 1968) at the level of a coordinated grouping of individual cells (such a definition seems more suitable than the concept of a "protozoan colony"). This as yet weakly differentiated stage, corresponds to the hypothetical blastaea of Haeckel and to the level (stegia*) which we refer to as monoblastic (Termier and Termier, 1968). Among the Lower Cambrian Radiocyatha some genera evidently still correspond to the blastaea stage (Gonamisphaera, Kuraya). The gastraea stage is manifested in the Archaeocyatha (Capsulocyathus) and in some of the Radiocyatha (Girphanovella). It is present in the Spongiaria and Cnidaria.

It is logical to suppose that the members of these Monoblastica, a considerable proportion of which lacked a mineralized skeleton, like the Volvocaceae, were present in the Ediacarian fauna.

The connections between the Monoblastica and the difference between the animal and plant kingdoms remain open questions. In fact, although the presentday Volvocaceae are definitely plants, loss of chlorophyll pigment is combined in many other unicellular flagellates, as is known, with characters transitional to animals. It may be hypothesized that a similar phenomenon may have occurred at the beginning of the Phanerozoic, and that some of the Monoblastica possessing chlorophyll consequently deviated toward plants (fig. 2).

ORIGIN OF THE COELOMATA

The other Metazoa of the Ediacarian fauna are the subject of lively discussion, since they may be converged only in part with the presentday groups of the Coelomata by virtue of the absence of a mineralized skeleton. This lack of mineralization does not exclude the existence of firm teguments composed of organic matter, which was subsequently destroyed, but which may have left clear impressions. Spriggina, an organism of a metamerized type classified as belonging to the

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*Translator's note. Not traced.

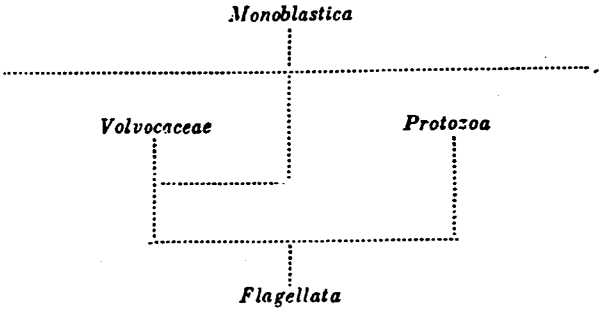

FIGURE 2. Diagram showing the possible relations between the plant and animal kingdoms.

Annelida, indicates an anterior-posterior orientation connected with motion and exhibits cephalization already comparable with that to be seen in primitive trilobites.

It is possible that Dickinsonia is closer to the Triploblastica, while still not being of the Coelomata, like turbellarians. For example, it has an alimentary canal with lateral processes, but its dorsal tegument seems metamerized.

Parvancorina is highly reminiscent of a trilobite larva in the Protaspis stage, but there are, in addition to small individuals, others whose length exceeds 2 cm and which are distinguished from the small ones only in having an elongated and pointed tail part. Praecambridium, with which Glaessner (Glaessner and Wade, 1971) converges Vendia from the Wendian of the Russian Platform, is also, in Glaessner's opinion, to some extent similar to Protaspis. We have also suggested that it is similar to the nymphoid stages of mollusks, crustaceans and onychophorans (Termier and Termier, 1968). Finally, Tribrachidium, a discoidal organism with three bending arms bearing tentacles, was similar to echinoderms in the nature of its symmetry. Its arms undoubtedly resemble lophophores, but the lack of a skeleton, which is here a very greatly complicating factor, makes it impossible to include it with any confidence in any particular group of organisms.

It is highly probable that the Pogonophora or related forms existed at the same time as the Ediacarian fauna, but in different facies. Sokolov (1972) interprets the Sabellitida of Eurasia as organisms belonging to this group, many of the characters of which are highly archaic.

We have suggested (Termier and Termier, 1966, 1968) that all Metazoa in which the adult form does not pass beyond the stage known under other circumstances as a larval stage should be united in a special category under the name nymphoids. In accordance with this definition the Ediacarian Parvancorina is a nymphoid. Other typical examples could also be given in the Cambrian and at later times.

The total or almost total absence of a mineralized skeleton is one of the characters of larval invertebrates. The same feature is to be observed throughout the Ediacarian fauna. At the same time a mineralized skeleton is one of the main factors stabilizing morphology. From the evolutionary standpoint it is a fairly simple matter to compare aquatic coelomates when they are in the larval state. Thus, the trochophore larva typical of annelids is constructed in accordance with the same plan as the phoronid actinotrocha and the molluscan veliger. There are only minor differences between the actinotrocha and the tornaria of Balanoglossus or similar pelagic larvae of echinoderms. The characters of adult organisms that are typical of each phylum of the Coelomata are established only in the concluding stages of larval development.

We tend to assume that the Ediacarian fauna was rich in nymphoids, i. e. in adult organisms whose shape was similar in type to the larvae of the later Metazoa known to us. If this hypothesis is accepted, the evolution of the Coelomata may be depicted as having unfolded by the selection of mutations, the amplitude of which was no greater than is to be seen in presentday processes. However, these were mutations of an allometric type, i. e. affecting the proportions of the various parts of the body. By affecting parts of the larva, each of which corresponded to a series of organs, they could have determined the general orientation of each phylum, both morphologically and physiologically (fig. 3).

It should be noted that neoteny is most often fundamental to the appearance of phyla which it has been possible to establish in the course of biokinesis, or in other words that the morphology of the larval, rather than of the adult form is the starting point of mutations. Not wishing to extend the number of examples, we would note that this phenomenon has been established in brachiopods and trilobites. A similar, but irreversible process probably occurred beginning with nymphoids.

The process whose course we have attempted to reconstruct here emphasizes the common structural plan of coelomates, while at the same time explaining the lack of lateral connections between the various phyla, since divergence was fanlike, beginning with nymphoids, which belonged to an earlier stage of evolution. As early as the Early Cambrian the Coelomata were divided into a series of similar groups which may, however, have been of different origin. Logically, their links should be sought at the more primitive levels of biokinesis, probably in the epoch of the Ediacarian fauna, in which of course only a small proportion of the first faunas of the Metazoa was represented.

THE INDICATIONS PROVIDED BY THE TYPE OF SKELETON

If we give overall consideration to the mineralized skeleton, which appeared, roughly speaking, in Tommotian times, i. e. immediately after the Ediacarian, we may immediately note two major categories: 1) skeletons associated with the mesenchyme, including the mesogloea of the Diploblastica, and the mesoskeletons of echinoderms and vertebrates and 2) cuticular skeletons formed at the epithelial level, including, in the general sense, all shells and a large proportion of carapaces (fig. 4). Mesenchymes are known in the Diploblastica: the mesogloea of sponges, cnidarians and ctenarians (the latter essentially attain stages of the Triploblastica); the mesoderm in coelomates also gives rise to the mesenchyme. However, not all these organisms were equally provided with a mineralized mesoskeleton. The category includes the spicular skeletons of sponges, alcyonarians and echinoderms, on the one hand, and the vertebrate skeleton, on the other.

Cuticular skeletons are far more prevalent. Large numbers are known in cnidarians, annelids, mollusks and arthropods, quite apart from the groups in which they coexist with mesoskeletons, e. g. in the Lophophora (brachiopods and bryozoans - ectoprocts).

Most mesoskeletons are permeable to water. They let through moving cells, either in isolation or connected with the circulation of fluid. Thus, amoebocytes pass through the spicules of sponges, and amoeboid coelomocytes through the skeletal loops of echinoderms.

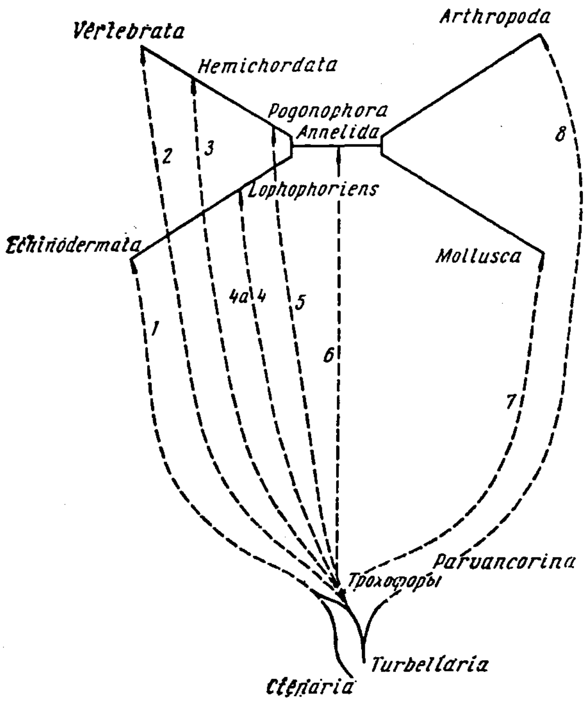

FIGURE 3. Diagram of the differentiation of nymphoids:

1 - asymmetry → atrophy of right coelom; 2 - atrophy of protosoma and mesosoma, metamerization of metasoma; 3 - protosoma not atrophied, delayed metamerization of mesosoma; 4 - regression of protosoma, attachment by means of metasoma (4a - mesosoma → lophophore); 5 - protosoma strongly developed, alimentary canal wanting; 6 - early metamerism of metasoma; 7 - commencement of metamerization of metasoma; 8 - early metamerism of metasoma, cephalization of postoral segments.

Although the archaeocyathan skeleton is not made up of spicules, it is extremely porous and behaves like a mesoskeleton, since it is so constructed as to let through cell elements through all the open-work walls. In the Radiocyatha the walls are made up of intricate skeletal elements of stellate structure - nezastrae ("nezastry") (Debrenne, Termier and Termier, 1971), which are known in the Uranosphaeridae and Girphanovellidae; nezastrae are not genuine spicules. In the Radiocyathidae they give way to true stellate plates, which are to some extent similar to the plates of echinoderms (Debrenne, Termier and Termier, 1970). However, each echinoderm plate consists of true spicular tissue, the elements of which are trabeculae.

The role of these primitive mesoskeletons is primarily that they provide a sort of armature for the sieve, and since this armature is incorporated in the mesenchyme it supports the whole body, thus strengthening its morphology. In addition, they outline and consolidate the irrigation channels in the broad sense, which are sometimes paths for the assimilation of nutrients. For example, a function of this type is performed by the vibratory baskets of sponges, the chambers of which are lined with choanocytes that have mainly sensory functions. In echinoderms the mesoskeleton retains all these advantages in their entirety, since its close connection with the coelom affords the possibility of combining all these roles; the development of a sinusoidal duct carrying the intracoelomic fluid is added to them (Termier and Termier, 1971).

In general, development of the motor functions of the body gives new refinement to the skeleton. Segmented elements are formed in which the mineralized skeleton is combined with collagenous fibers, to form hard, waterproof assemblages.

New research is now in progress on the analogy between the skeleton of primitive vertebrates (the subaponeurotic system of dermal plates in cephalaspids) and the skeleton of echinoderms.

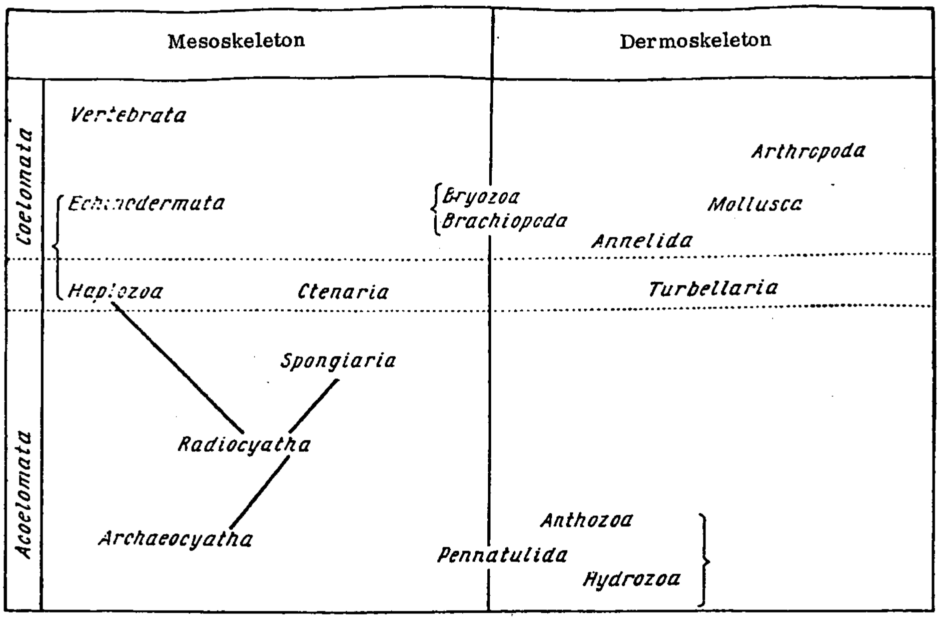

FIGURE 4. Skeletal types in different groups of organisms.

Without considering this intricate matter here, we may emphasize that a considerable proportion of the vertebrate skeleton is also mesoskeleton permeated with canals linked with circulatory functions.

We have demonstrated the close connections existing between the skeletons of Paleozoic tubular bryozoans and collolophid brachiopods (Termier and Termier, 1959, 1970) such as strophomenids and productids. The exoskeleton of these brachiopods, which is cuticular in origin (fibrolamellate) includes elements made up of calcite, namely taleolae, which often form projections in the inner part of the shell or a punctate lattice on the surface. The acanthopores of tubular bryozoans are elements connected with the coelomic zone. They should be regarded as a residual mesoskeleton, which may have served for attachment of the mantle by means of small bundles of muscle fibers.

Many authors have drawn attention to the systematic position of two Australian genera found at the boundary between the Lower and Middle Cambrian, namely Cymbionites and Peridionites. The morphology of Peridionites resembles that of ctenarians of the family Platyctenidae, which are benthic, unlike other ctenarians. However, whereas all the ctenarians known at the present time have an exceptionally soft and even a spreading body, Peridionites and Cymbionites have a dense and extremely hard theca consisting of calcitic trabeculae, practically identical in the structure of the calcite to its structure in echinoderms. Furthermore, those trabeculae of Cymbionites that we have been able to study are more or less normally elongated, slightly resembling the structure of the larval skeleton of Pluteus. The existence of these forms known only from far more recent deposits than those which contain the first echinoderms (Lower Cambrian of California, genera Helicoplacus and Gogia), is at least suggestive of a connection between them and the Diploblastica through the Ctenaria.

CONCLUSIONS

The way in which the main lines of biokinesis took shape may be arrived at by evaluating data on the comparative histology of cells and living tissues, data on presentday and fossil skeletons and, on the other hand, the important data already obtained on the Ediacarian fauna and the fauna of the Tommotian Stage, and by making use of general data on comparative histology, the conclusions from which may be carried over to the phenomena to be observed at the beginning of the evolution of the animal kingdom.

From our point of view, the sources of the Metazoa should not be sought among groups of already fairly specialized Protozoa, but among colonial Protista similar to the Volvocaceae, even if we have to assume that some of these Monoblastica still had chlorophyll. It was probably only gradually that gastrulation, which is a feature of the Diploblastica, began to be accompanied by specialization of the sensory ectoderm directed toward perception of the environment, and of the endoderm, which was increasingly adapted to the assimilation of living food. The Archaeocyatha and Radiocyatha of the Lower Cambrian provide a good indication of how this gastrulation must have been established, but the preceding Ediacarian fauna provides evidence that these phenomena occurred before the formation of mineralized skeletons, which increased the changes of fossilization. Most of the Diploblastica and large groups of the Coelomata were already in existence from the Ediacarian onward. It seems probable that the divergence of phyla that are now very clearly segregated occurred by weak mutations in soft larval forms which never reached the morphology of adult organisms, i. e. in nymphoids. A fairly accurate idea of nymphoids is now provided by the larvae of coelomates, which all originate from the trochophore.

The various phyla must have taken shape fairly rapidly at the beginning of the Phanerozoic. The subsequent changes, as a result of which the animal kingdom became what it now is, occurred mainly by means of larval mutations similar to those to which we referred when considering nymphoids; evolution by neoteny has been repeatedly demonstrated factually.

The influence of the environment mediated by the physico-chemical modifications to which the genome was subjected, must have played a decisive role in the completion of biokinesis.

French to Russian translation by M. Ye. Raaben

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