Is fossil evidence consistent with traditional views of the early metazoan phylogeny?

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Abstract

The best known of the alleged Cambrian medusoids, *Velumbrella*, is a skeletal fossil. It is proposed to be a relative of *Eldonia* and *Dinomischus*, and is placed together with them in a separate new class Eldonioidea of the lophophorates. The supposed Cambrian coral *Tabulaconus* is probably a successor of the Tommotian *Cysticyathus*, which does not show features that could substantiate such a taxonomic placement. Ordovician *Conchopeltis* is closely related to scenellids and, having a bilaterally symmetrical, probably aragonitic shell with radially arranged muscle scars cannot be interpreted as a chondrophoran pneumatophore. The small size of ancestral conchiferan molluscs, assumed on fossil evidence, is a preservational artifact that resulted from very slow rate of sedimentation connected with phosphatization in the most fossiliferous strata of the earliest Cambrian. Adult specimens occurring rarely in the same strata do not differ in size from later molluscs. Relatively large size is also characteristic of the most primitive articulate, *Xenusion* from the basal Cambrian of the Baltic region. It is suggested that major evolutionary transformations between phyla operated between organisms of centimetre sizes, so their record is potentially recognizable in the fossil evidence.

Introduction

To derive a phylogenetic tree from morphologic data an assumption is necessary: that there is some correspondence between time that has passed since separation of lineages under consideration and the present morphologic distance between them. If such a correspondence really exists, one may expect that going back in time the morphologic differences within any monophyletic unit should generally decrease. It follows also that, however incomplete is the fossil record of evolution, the morphologic differences between oldest known representatives of any taxon and its ancestor should be smaller than between any Recent forms and the ancestor, simply because the time interval is shorter.

When this way of reasoning is accepted, it becomes somewhat surprising that the tremendous increase in knowledge of Vendian and Early Palaeozoic fossils in the last few decades has influenced so little our understanding of the early evolution of the metazoans. Usually we tend to blame incompleteness of the fossil evidence, but another possibility has also to be considered, namely that something is wrong with basic hypotheses that we are attempting to test. Virtually all interpretations of the early phylogeny of the Metazoa, which are based on analyses of the anatomy and biochemistry of Recent organisms, place the coelenterates and flatworms at the base of the tree (see Bergström 1986) and/or declare that the earliest representatives of the major groups were microscopic in size (see Nielsen 1985). In this review I intend to examine, on the basis of a few examples, whether these two features of the metazoan phylogeny necessarily result from the available evidence or perhaps they are unnecessary assumptions that we tend to fit with an obviously incomplete fossil data.

How ancient are coelenterates?

A remarkable feature of the Ediacarian assemblages of supposed jelly-fishes is an apparent lack of tetraradially organized forms. This does not allow us to consider them reasonable ancestors of later scyphozoans. The only fossil declared to show this kind of radial symmetry in the Vendian is *Conomedusites* from Ediacara (Glaessner, 1971) but its morphology is far for being convincingly scyphozoan. Its conical body seems to be split into four lobes which were movable in relation to each other allowing various arrangements (see Glaessner 1971; Pl. 1 9-10). It has been compared with allegedly the most primitive, widely conical "conulariid" *Conchopeltis* from the Trenton (Late Caradoc) of New York. However, it has been already shown by Oliver (1984) that *Conchopeltis* is not a radial organism but shows clear bilateral symmetry. It has little to do with conulariids, as already pointed out by Kozlowski (1960), and supposed tentacles represent rather a cuticular fringe along the shell margin.

This interpretation may find support in a new finding of a *Conchopeltis*-like fossil in the Baltic Caradoc (Fig. 1). Morphologically it is transitional between Cambrian *Scenella* and *Conchopeltis*. It is of interest to find radially arranged riblets on its interior that are interpreted as bordering muscle scars resembling those in *Scenella* (Rasetti, 1954). The shell was probably aragonitic as it is preserved in the same manner as associated snails, in contrast to trilobites and brachiopods cooccurring in the same block. It lacks any remnants of organic matter, despite good preservation of graptoliths and other organic fossils in the rock. To establish definitely the nature of the fossil it would be necessary to know either the shell microstructure or its early ontogeny. That is not possible in the case of the specimen under consideration, but in another boulder of similar age a minute plate has been found which somewhat resembles it in outline and presence of inconspicuous radial ribs on its interior (Fig. 2). Like in associated snail conchs an original shell matrix is replaced with an iron mineral, which is not the case regarding trilobites and brachiopods in this kind of rock. Its external side is tubercular and the shell is bent transversely in a way resembling polyplacophorans, so it may actually be an anal plate of a chiton. The apex is not preserved well enough to prove conchiferan or polyplacophoran affinities but definitely shows that it is not a coelenterate.

Because of inferred aragonitic wall composition,

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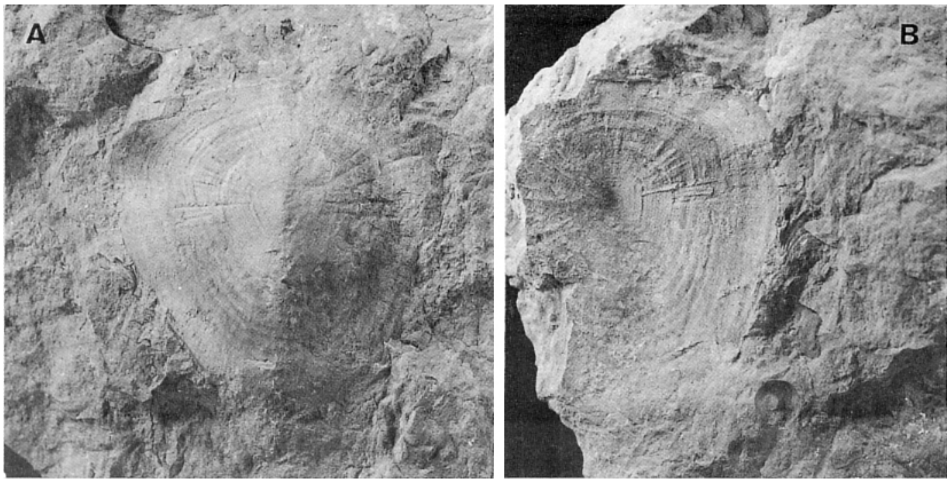

Fig. 1. *Conchopeltis*-like fossil from Chasmopskalk erratic boulder (late Caradoc) of Baltic origin, Jóźwin near Konin, Poland. A. Part. B. Counterpart, Both x 1.

apparent growth lines and structures interpreted as muscle attachments in both these fossils any possibility that they are chondrophorans can be rejected and I extend this also to morphologically close *Conchopeltis* and *Scenella*-like fossils. In some of them original mineralization is apparent (see Yochelson & Stanley, 1981; Fig. 1E for imprints of calcite prisms of external shell layer) which is hardly compatible with the notion of the chondrophoran pneumatophore. Shells of *Plectodiscus* are known to be overgrown with cementing organisms (Yochelson *et al.*, 1983), which require they were stiff and resistant for decay, features unlikely to develop if they were not mineralized. Horný (1985) found clearly bellerophontid larval shell in a Silurian fossil morphologically undistinguishable from *Palaeolophacmaea*.

Among the most controversial Early Palaeozoic fossils assigned to the Chondrophora by Stanley (1986) is the Middle Cambrian *Velumbrella*, originally described by Stasińska (1960) as a jelly-fish (see also Bednarczyk, 1970). It has been already pointed out by Fedonkin (1987) that actually *Velumbrella* is a skeletal fossil. It is known from numerous specimens. (Stasińska, 1960) lists 110 imprints (and more can be traced in private collections) which are not preserved on the bedding plane, as is usual for fossil jelly-fishes, but well within an unbedded coarse somewhat conglomeratic sandstone with small quartz pebbles. The *Velumbrella* discs are variably oriented, sometimes bent, and many small fragments of crushed specimens cooccur (see Fig. 3). This indicates high energy and shallow water conditions of sedimentation. It was

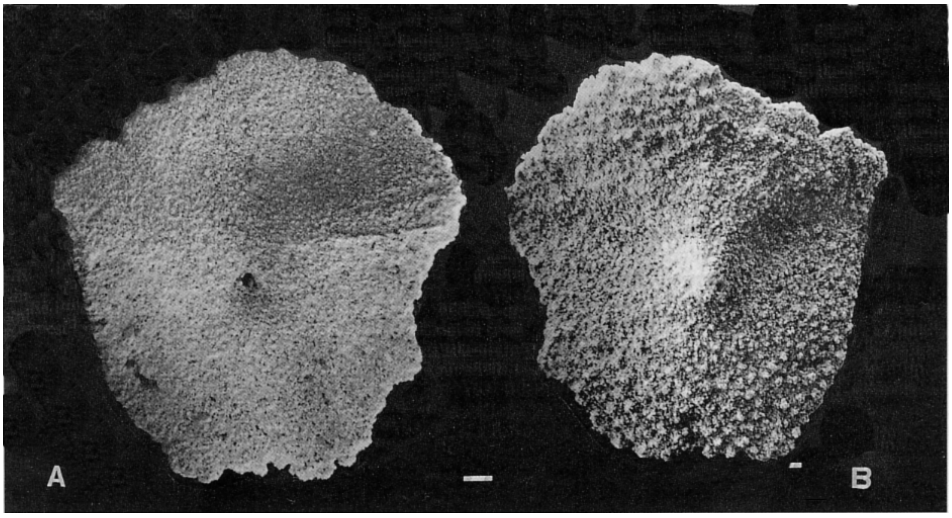

Fig. 2. Juvenile specimen of a species possibly related to that in Fig. 1 with original shell matrix replaced with an iron mineral; erratic boulder of pink micritic limestone (probably Vasalemma Baltic stage; late Caradoc), Orłowo near Gdynia, Poland. A. Inner side, note radial riblets. B. External view. Both x 32.

definitely not an environment appriopriate for preservation of jelly-fishes or organic chondrophoran pneumatophores. Discs of *Velumbrella* were clearly stiff, possibly mineralized, although still somewhat flexible, so indicating some organic matter.

Together with *Velumbrella czarnockii* Stasińska, 1960 another, probably related, species occurs, represented in the collection by two fragmentary specimens. These are labelled *Brzechowia* sp. by Jan Czarnocki, who assembled the whole collection. Specimens of "Brzechowia" are apparently two-walled. A space between the walls is filled with sand which requires, as long as the margins of both valves are not displaced despite their breakage prior to burial, a firm connection between them, presumably in the centre of valves. Another possibility, that the discs had been bent in half prior to their burial is less likely; at least it is not supported by any signs of bending in proximity of the breakage margin. It seems likely that *Velumbrella* was also bivalved, although all specimens are disarticulated and only in two cases (Stasińska, 1960: Pl. II; here Fig. 3A) paired valves occur in partial overlap.

In both *Velumbrella* and "Brzechowia" the valves grew by marginal accretion. In the *Velumbrella* discs the central area (8 mm in diameter) does not show radial ornamentation and may represent an attachment area for both valves. "Brzechowia" differs from it in lacking a concentric depression in about half of the disc radius as well as radial ribs (both features occurring also in the Cambrian parapsonematid described by Popov 1967), although radial organization is clearly noticeable close to the margin. Concentration of growth lines close to the margin in "Brzechowia" and almost uniform size of all well preserved specimens of *Velumbrella* indicate that their mature size was determined ontogenetically.

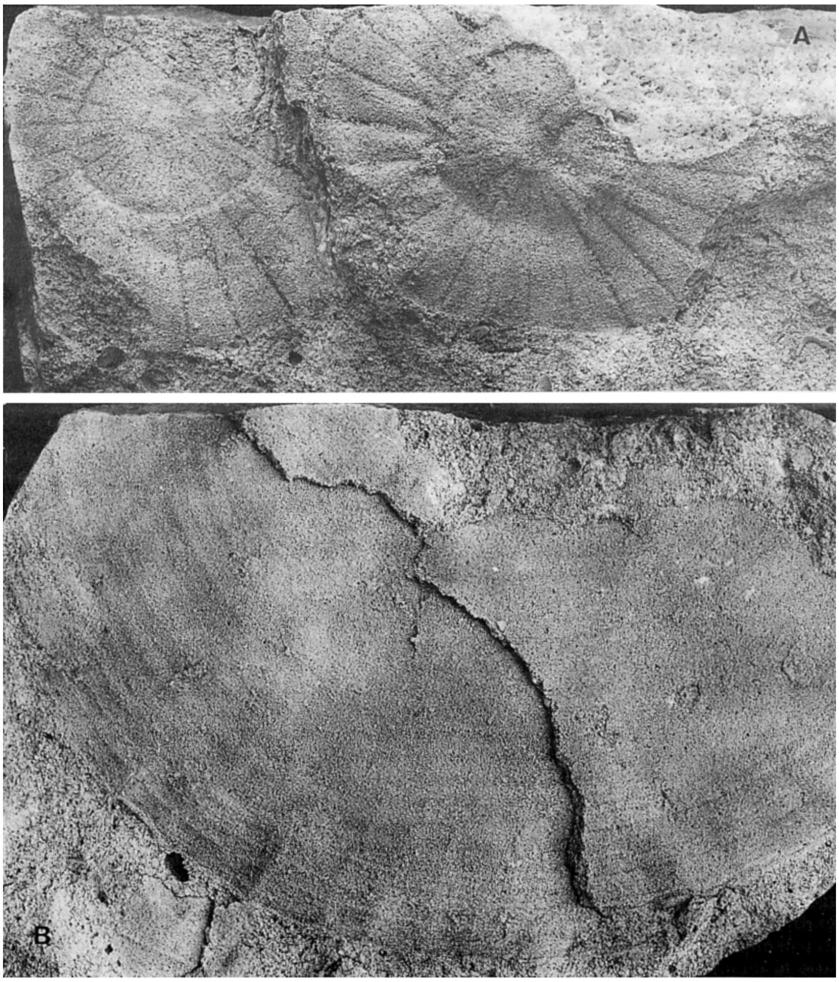

Fig. 3. *Velumbrella czarnockii* Stasińska, 1960, earliest Middle Cambrian (Bednarczyk 1970) of Brzechów, Holy Cross Mts, Poland: two associated discs possibly belonging to a single specimen. B. "Brzechowia" sp. from the same locality with both valves still in articulation, note detritus of *Velumbrella* disks below. Both x 1.

The morphologic data listed above do not allow by themselves to establish the systematic position of these fossils. They show, however, that they definitely were not scyphozoans and give little support for their interpretation as chondrophorans. Supposedly near-shore, shallow water environment of fossilization, two-walled organization with walls connected (and attached to the substrate?) in the centre, scleritized (mineralized?) externally except for growing margin, suggest rather a benthonic mode of life of these organisms.

The Cambrian skeletal fossil morphologically closest to *Velumbrella* is *Yunnanomedusa* from the Chiungchussu fauna of Yunnan, China (Sun & Hou, 1987). The degree of scleritization of its disc was somewhat lower than in *Velumbrella* and radial ribs, being more numerous (about 44 instead of 20) are also less distinct. Even less scleritized is *Stellostomites* from the same strata, with about 60 radial striae. Conway Morris & Robison (1988) consider these Chinese genera synonymous with *Eldonia*. At the end of a morphocline of these Chinese discoidal fossils can be placed *Rotadiscus*, unless soft parts studied recently by Conway Morris (personal communication) will counterevidence this. It has a strongly scleritized disc without any prominent radial ornamentation but, instead, with distinct concentric growth lines and rugae. In all these fossils can be identified a central attachment area (interpreted as a mouth by Sun & Hou, 1987). The opposite end of the morphocline can be supplemented by the disc of "Brzechowia", *Eldonia* from the Middle Cambrian Burgess Shale of British Columbia (Durham, 1974) and the Spence Shale and Marjum Formation of Utah (Conway Morris & Robison, 1988) as well as a Siberian Late Cambrian fossil (perhaps assignable to *Parapsonema* but erroneously described under the name of the echinoderm genus *Camptostroma* by Popov, 1967; see Conway Morris & Robison, 1982) which have the margin of discs lobate. Within the central area of discs of *Eldonia* (Durham, 1974) and *Stellostomites* (Sun & Hou, 1987; p. 265) is preserved a helically coiled structure, interpreted as a gut by Durham (1974), that indicate that the morphocline represents a monophyletic group (Conway Morris & Robison, 1988). Assuming that the Durham's reconstruction of *Eldonia* is correct, in searching for affinities for this group one has to look for organisms with an U-shaped intestine and a conical body with radially lobate margins.

Transversely striated scleritized lobes around the margin of a conical cup and a U-shaped intestinum located in the centre of the cup are shared with the velumbrellids by another problematic fossil of the Cambrian, *Dinomischus*. The cup of *Dinomischus*, having a radius of about 2 cm, is thus much smaller than most of the velumbrellids. It bears approximately 10 scleritized "bracts" (Chen *et al.*, 1989: p. 69) and is attached to a long stalk. The structure interpreted by Chen *et al.* (1989) as an anal tube was actually the basal part of the stalk, strongly bent and partially hidden under the cup (Conway Morris, 1989: p. 270). I propose to homologize the stalk of *Dinomischus* with the attachment area in discs of the velumbrellids and the radial lobes of *Eldonia* with "bracts" of *Dinomischus*.

I conclude thus that the velumbrellids and *Dinomischus* form a monophyletic group. Unlike other problematic Vendian and Cambrian fossils enough anatomical data are available to characterize it in zoological terms and to propose its placement, at least provisionally, in the classification scheme of the Metazoa. The U-shaped intestine, mouth armed with two branched tentacles (known in *Eldonia*) strongly suggest

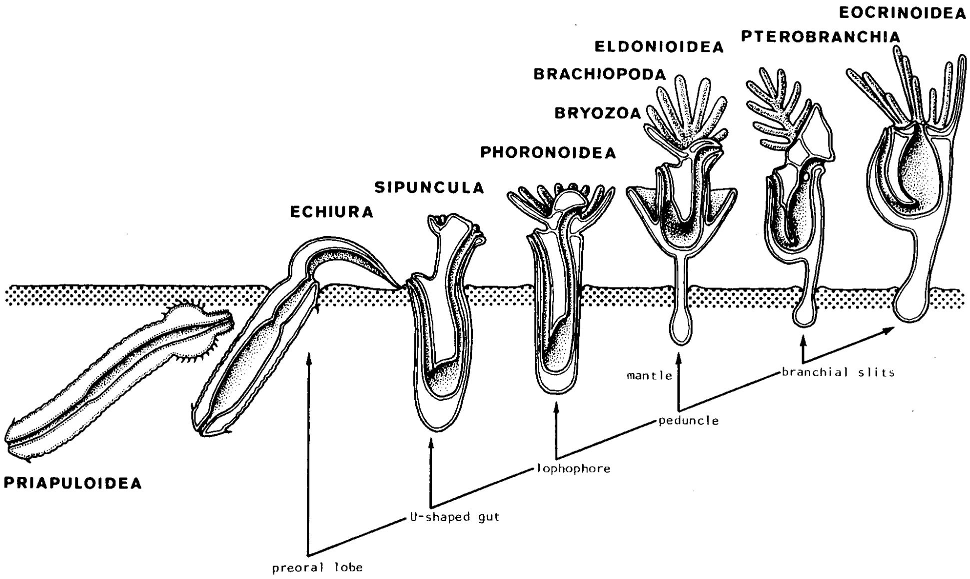

Fig. 4. Interpretation of relationships of sedentary coelomates derived from an assumption that the priapulids represent their basal stock. According to the proposed scenario there was a shift from active predatory life, with hydraulic locomotion, through detritophagy of the echiurids and sipunculids, to filtratory feeding of the lophophorates (from Dzik, in press b).

their placement among the lophophorates (phylum Tentaculata) (Fig. 4). Homology of the scleritized disc, surrounding both the anus and mouth, to organs of other lophophorates is the crucial point in the interpretation of the anatomy and relationships of the group. Conway Morris (1977b) discussed and rejected possible entoproct relationships of *Dinomischus*. It seems thus unlikely that these are giant solitary entoprocts. Instead, I propose to homologize the disc secreting organ with the mantle of the brachiopods and the bryozoans. The presence of a bryozoan-type protoecium in Ordovician *Cornulites*-like fossils suggests that at least in the evolution of the Bryozoa development of a skeleton, secreted by the mantle had preceded the origin of coloniality (Dzik, in press a). I propose, therefore, to classify the velumbrellids and *Dinomischus* in a new class, Eldonioidea, characterized by a conical, lobate mantle instead of cylindrical (as in the Bryozoa) or bivalved (as in the Brachiopoda) ones. This implies that the mantle is a shared derived character of the advanced Tentaculata (lacking in, although possibly secondarily lost by, the Phoronoidea). Two distinct groups of ordinal rank can be distinguished within the class: the Dinomischida, new order, characterized by a long pedicle and deeply lobate mantle, and the Velumbrellida, new order, with a circular, disc shaped body with reduced peduncle. Within the latter group at least two branches, both showing diverse modes of scleritization of the disc, can be discerned: the Eldoniidae Walcott, 1911, with radial ribs [including *Eldonia* Walcott, 1911, *Velumbrella* Stasińska, 1960, and *Yunnanomedusa* Sun & Hou, 1987 (= *Stellostomites* Sun & Hou, 1987)] and the Rotadiscidae, new family, with almost smooth discs ornamented only by growth lines (*Rotadiscus* Sun & Hou, 1987).

With *Velumbrella* and other alleged chondrophorans removed from considerations, little remains in the whole Early Palaeozoic, which can be reasonably compared with planktonic coelenterates. The oldest known undoubted coelenterates are thus sedentary polyps, well recognized from the beginning of the Early Ordovician when both the conulariids (see also Babcock, van Iten, this volume) and corals appear. Supposed Cambrian conulariids await thorough redescription and their presence among the oldest known, Vendian and Early Cambrian, metazoans is rather doubtful, although some tubular middle Early Cambrian fossils seem to show a conulariid-like tetraradial symmetry (Qian & Bengtson, 1989). The coelenterate nature of alleged Vendian pennatulaceans, Petalonamae, has been already soundly questioned by Seilacher (1984) and the new reconstructions proposed by Jenkins (1985) present creatures with petaloids attached to imperforate membranes, which are more likely to be photosynthesizers rather than sessile predators or even filter-feeders.

There are some fossils in the Early Cambrian that resemble corals in having a conical calcareous exoskeleton filled with tabulae. *Tabulaconus* from the late Early Cambrian of Alaska is the best known among them (Debrenne *et al.*, 1987), but the oldest one remains *Cysticyathus*. This genus frequently occurs in archaeocyathid buildups in the Tommotian of the Lena River, Yakutia. The wall microstructure of the fossil is definitely not of the archaeocyathan type, lamellar with tabulae of meniscal shape continuously passing into the wall layers (Fig. 5). Although unlike associated archaeocyathids, *Cysticyathus*, as well as its probable successors *Tabulaconus* and *Bacatocyathus*, do not necessarily need to be interpreted as corals. The calyx is somewhat too irregular in shape and its wall, lacking any radial septa or septal spines, shows at least in distal parts structures suggestive of porosity secondarily covered from inside with laminar calcitic layers (Fig. 5B) This makes its attribution to corals and coelenterates most unlikely. It could well be of sponge origin.

I do not pretend to state that coelenterates are completely lacking in the Vendian and Early Cambrian. Afte̍r closer examination some problematic fossils may prove to belong to the phylum. Especially worthy reconsideration in this respect is *Parapsonema*, ranging from the Late Cambrian (see Popov, 1967) until the Late Devonian, and the Middle Cambrian *Fasciculus* (Simonetta & Delle Cave, 1978, Collins *et al.*, 1983). In any case it remains clear that at the beginning of the Phanerozoic coelenterates were much less important than one would expect, keeping in mind their role in most interpretations of the early phylogeny of the Metazoa. This is not unreasonable, however, from a purely ecological point of view. Until pelagic environments became really rich in nektonic and planktonic metazoans, the organization of benthic or planktonic predators, more or less passively waiting for freely living prey, did not make much sense.

Body size of the oldest metazoans

In Recent organisms anatomical simplicity is usually connected with small size. It is understandable thus that in most of neontologically biased interpretations of the phylogeny the smallest of Recent organisms or early ontogenetic stages of others are the main source of information on the anatomy of hypothetical ancestral forms. The resulting expectation that the oldest known organisms should also be small in size, however, is not met by fossil evidence. Size distribution of Middle Cambrian Burgess Shale fossils shows clear predominance of macroscopic sizes (Briggs & Whittington, 1985), although a taphonomic bias cannot be excluded (Conway Morris, personal communication). There are also arguments to the contrary from neontology itself. Cladistic analysis of Recent microscopic worms shows that "pseudocoelomates have evolved from relatively large ancestors with body sizes measured in centimeters rather than millimeters" (Lorenzen, 1985: p. 210). Locomotory mechanisms predominating among the metazoans, especially the development of gait, require also macroscopic sizes of ancestral forms developing particular method of locomotion (see Clark, 1979; Elder, 1980).

The most elaborated attempt to prove, on the basis of fossil data, that the oldest members of a large branch of evolutionary tree, which is now represented by organisms of wide range of sizes, were initially of millimetre size refers to the earliest molluscs. It is generally assumed as proven that until the Ordovician they were of microscopic sizes. Runnegar & Jell (1976; Fig. 5; also Runnegar, 1983: Fig. 30) computed then available data on shell size of Early Palaeozoic molluscs, which seemingly showed almost exponential increase in size starting from not more than a couple of millimetres in the earliest Cambrian.

Considering this particular problem it is necessary to refer to the geological background of data used in

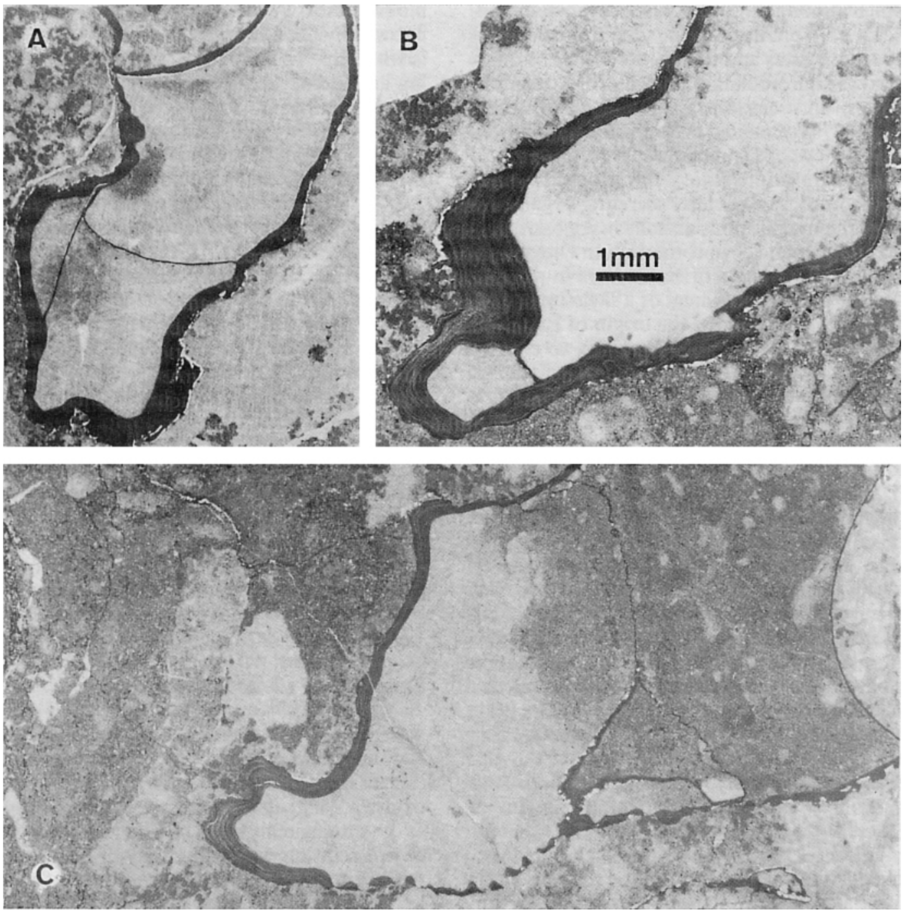

Fig. 5. *Cysticyathus tunicatus* Zhuravleva, 1956 from an archaeocyathid bioherm, Tommotian (loose block), Tiktirikteech on the Lena River, Yakutia. All x 10. A. Specimen with irregularly distributed tabulae. B. Another specimen with well visible laminated wall structure and continuity between wall and tabula. C. Specimen with wall structure suggestive of original porosity subsequently covered from inside by lamellar calcitic tissue.

the computation. Their basic source is the Siberian sections of the Tommotian and Atdabanian. Virtually all published materials concerning Tommotian molluscs were derived from rocks disaggregated by chemical means. They are usually phosphatic steinkerns of conch apices, juveniles or larval shells. The most fossiliferous Tommotian limestone sections are more or less stratigraphically condensed, abound in sedimentary discontinuities, with numerous hard-grounds and pockets filled with glauconitic limestones enriched in phosphatic debris (Fig. 6A, C). In such a conditions of reduced rates of sedimentation, with winnowing and reworking of the sediment, it would be difficult for any macroscopic mollusc shell to be preserved completely. As a result only microscopic shells can be found in residues, exactly as occurs in similar lithologically sections of the Baltic Ordovician where thousands of juvenile and larval shells can be found in a single sample while adult specimens are found in other beds.

In the Tommotian sections at the Lena River abundant assemblages of adult mollusc occur in the surroundings of archaeocyathid buildups, where locally rate of sedimentation was higher (Fig. 6B). At least in two such buildups, in localities Tiktirikteech and Bydjangaia, I was able to recognize such assemblages represented by the same species as are present in acid-resistant residues. Undoubtedly adult, with concentrations of growth lines at their apertures, specimens of *Bemella* (Fig. 7A-D) reach 25 mm in length. This is hardly different from sizes typical for Ordovician molluscs. The supposed small size of the earliest molluscs is thus a preservational artefact.

Another even more persuasive example of relatively large size of ancestral forms is provided by the oldest known lobopodian *Xenusion* (Fig. 8). The second specimen of the Geiseltalmuseum, Halle supplemented earlier interpretations with some new data enabling a tentative reconstruction of the entire body (Dzik & Krumbiegel, 1989). There are two remarkable points in its morphology: (1) An unbelievably simple organization, with a gradient in development of segmentation but without any signs of specialization in homonomous appendages arming the tubular body with terminal mouth. (2) A large size of the animal, counting at least twenty centimetres in length. The organization of the body of *Xenusion*, with pairs of dorsally located

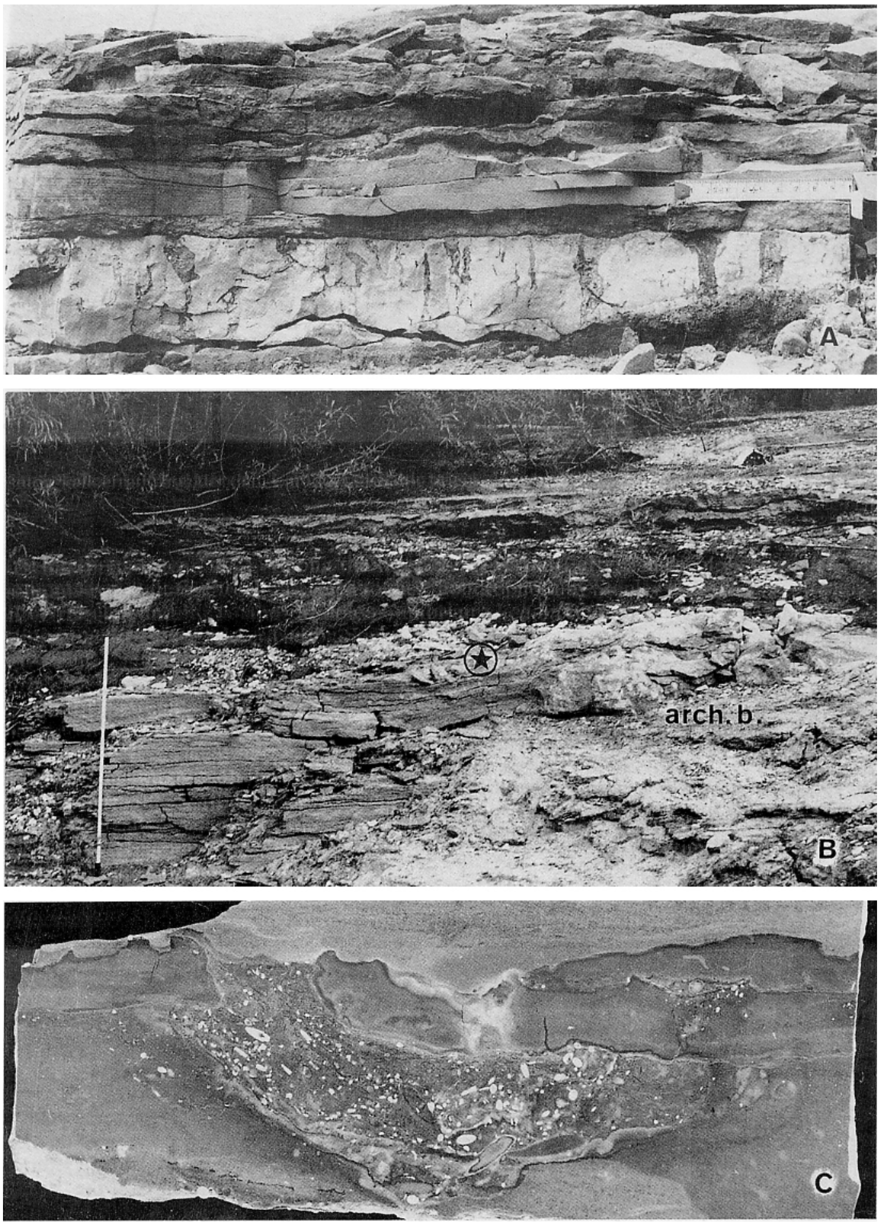

Fig. 6. Source strata for earliest Tommotian molluscs in Yakutia. A. Sedimentary discontinuity covered by a layer enriched in small shelly fossils which fill also burrows below (note laminated limestone above, which is almost barren palaeontologically), Tiktirikteech, shore of the river. B. Archaeocyathid bioherm (at right) flanked by limestone beds with large mollusk shells (marked with asterisk), Tiktirikteech, mouth of the creek. C. Polished section across a discontinuity surface with burrow filled with sediment enriched in phosphatic fossils, Isyt'; x 2.

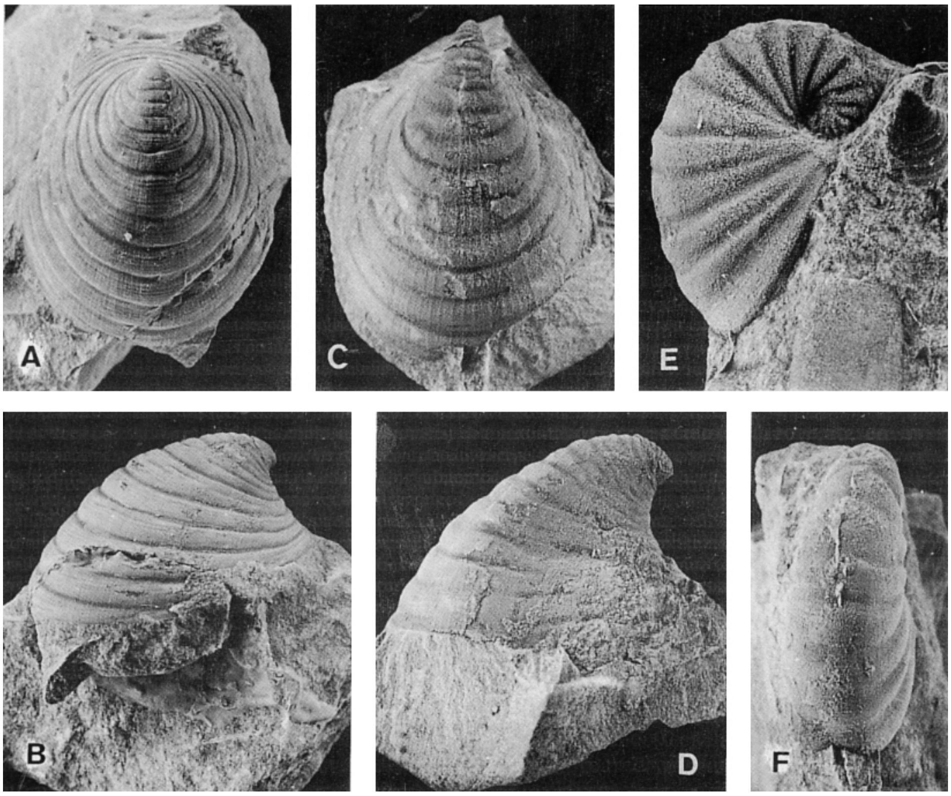

Fig. 7. Mollusc shells from a glauconitic limestone bordering an archaeocyathid buildup at the locality Bydjangaia (near Isyt'), Yakutia. A-D. Two subadult specimens of *Bemella jacutica* (Missarzhevsky, 1966); adults are 25 mm in diameter; x 2. E-F. Probably adult *Latouchella korobkovi* (Vostokova, 1962); x 3.

spiniferous "humps" and ventrolateral appendages in each segment, is suggestive of being derived from an original tetraradial arrangement. If taken together with the cylindrical shape, annulation of the cuticle, and terminal location of the mouth it reminds the organization of the nemathelminthan worms (Dzik & Krumbiegel 1989). This seems noteworthy as it has been already shown by Conway Morris (1977a) that in the Cambrian the priapulids were much more diverse than today and from their morphological organization all other groups of Nemathelminthes can be derived. It is now clear that anatomical (not necessarily physiological) simplification and reduction in size were the predominant feature in the phylogeny of the phylum (Lorenzen, 1985). The Priapuloidea may thus appear to be close to the roots of the metazoan phylogenetic tree. This implies that transitions between phyla took place at the level of relatively large, hydraulically propelled animals. Such a conclusion is optimistic for palaeontologists, giving fossils a chance not only to contribute to our understanding of details of phylogeny in some groups but also to help us in solving the basic problems of the phylogeny.

Conclusions

Complete lack of fossil flatworms (Conway Morris, 1985) and at best a low diversity of Cambrian coelenterates suggest that traditional phylogenetic trees placing the coelenterates and flatworms at the base should be critically reevaluated. At present, it is only possible to offer little more than a very provisional review on the ancestral anatomical organization for major groups of the Metazoa known from the Early Palaeozoic. It is clear that already by the Vendian two basic branches of free-living metazoans were established. The first one was represented by animals crawling over the sediment surface, ancestors of the molluscs and nemertineans (perhaps also flatworms). The second was represented by burrowers in the sediment, ancestors of the priapulids. Members of the first branch were propelled either directly by direct waves of muscular contraction in the foot or used hydraulic mechanisms (see Clark, 1979; Elder, 1980) with retrograde waves passing along vacuolized (filled with haemolymph in lacunae) foot, while in the second branch direct waves of muscle contraction pumped fluids through an unsegmented body cavity (Hunter *et al.*, 1983). This was used to propel the body in, as well as above, the sediment. Probably by secondary adaptation of the latter mechanism to active life on the surface of the sediment, gait of the onychophoran type developed. This resulted in development of appendages and increasingly deep segmentation of internal organs (Dzik & Krumbiegel, 1989). Sedentary life with adaptations to collect detritus from the sediment surface resulted perhaps in development of a preoral lobe of the echiurid type, and

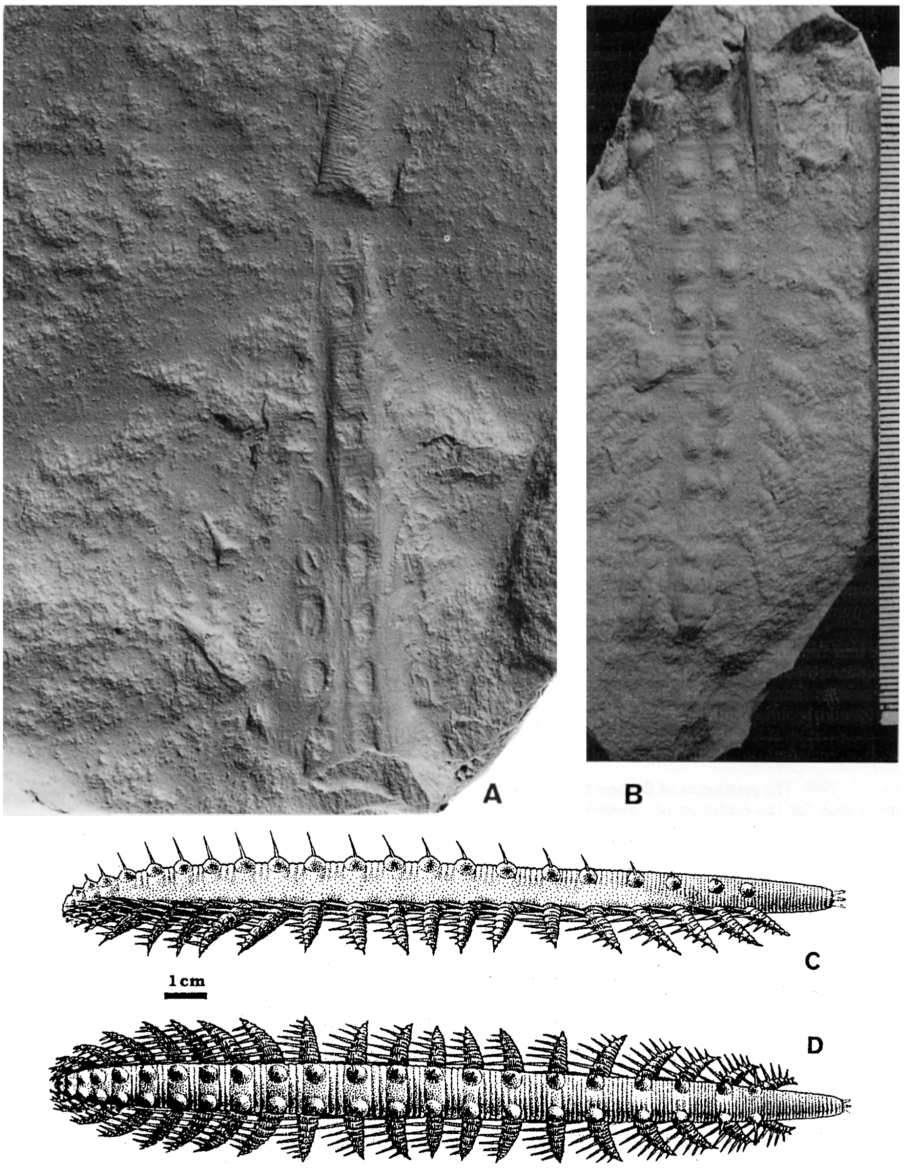

Fig. 8. *Xenusion auerswaldae* Pompeckj, 1927 from erratic boulders of the Kalmarsund Sandstone, basal Cambrian of the Baltic region; latex casts, both x 1. A. Specimen housed at Geiseltalmuseum, Halle (see Dzik & Krumbiegel 1989), three-dimensionally preserved exuvium probably representing anterior part of the body. B. Holotype housed at the Museum für Naturkunde, Berlin; probably posterior end of the body. C-D. Reconstruction of the body in dorsal and lateral views.

U-shaped digestive tract and tentacles of the sipunculid type, which further might have allowed development of a lophophore leading, finally, to the echinoderm organization level (Nichols, 1967). In this highly speculative scenario (Fig. 4) the flatworms and coelenterates are not included and their position in the phylogenetic tree remains mysterious. A possibility that they represent secondarily simplified successors of more anatomically complicated forms should not be excluded.

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