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Anatomical Information Content in the Ediacaran Fossils and Their Possible Zoological Affinities[1]

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SYNOPSIS. **Various modes of preservation of Ediacaran fossils in different sediments, quartz sand at Zimnie Gory in northern Russia and lime mud at Khorbusuonka in northern Yakutia, show that the sediment was liquid long after formation of the imprints and that its mineralogy did not matter. A laminated 2 mm thick microbial mat is preserved intact at Zimnie Gory. It stabilized the sediment surface allowing formation of imprints on it. The soft body impressions on the under surface of the sand bed and within it developed owing to formation of a less than 1 mm thin "death mask" by precipitation of iron sulfide in the sediment. Fossils of the same species or even parts of the same organism may be preserved differently. Internal organs either collapsed, their cavities being filled with sediment from above, or resisted compression more effectively than the rest of the body. This allows restoration of the original internal anatomy of Ediacaran organisms. At Zimnie Gory numerous series of imprints of *Yorgia* on the clay bottom surface with the collapsed body at their end represent death tracks. The environment of formation of the Ediacaran fossils was thus inhospitable to most organisms. Those adapted to it, namely the radially organized frondose Petalonamae (of possible ctenophoran affinities), anchored in the mat with their basal bulbs. They evolved towards sessile life possibly in symbiosis with photo- or chemoautotrophic microorganisms. Vagile Ediacaran organisms belong mostly to the Dipleurozoa (somewhat resembling chordates and nemerteans), characterized by a segmented dorsal hydraulic skeleton, intestine with metameric caeca, and serial gonads. Only a fraction of the actual Precambrian faunal diversity is represented in the Ediacaran biota.**

INTRODUCTION

There is no doubt that the oldest fossil remnants of metazoan animals are of crucial importance in deciphering their phylogeny. In the same sense ancient written documents are important to historians, whatever are their material deficiencies and incompleteness of the information they contain. To be valuable, such documents need to be readable. Unfortunately, we meet great difficulties with reading the messages left to us from the time of the initial diversification of the animal world. To decipher the true meaning of the oldest fossils one first has to understand the way they formed. Only then can the extracted information be used to restore the anatomy and to compare it to the body plans of better known organisms from later geological epochs, including the present.

The latest Precambrian fossils of soft bodied organisms, famous owing to their South Australian locality Ediacara, are the main source of information on the evolution of earliest multicellular animals. Although numerous and diverse, they remain controversial both in respect to their original anatomy and relationships. There is a variety of opinions on them, even regarding the most basic aspects of their body plan. The dominant view is that the bodies of Ediacaran organisms were extremely flat and lying on the sea bottom (*e.g.*, Runnegar, 1991) or immersed in the sediment (*e.g.*, Seilacher, 1999). Few authors support the earlier popular view that these were organisms directly related to Recent phyla (*e.g.*, Gehling, 1991). The main cause of these problems with interpretation is the non-uniformitarian Ediacaran taphonomy: these soft-bodied, evidently easily disintegrating organisms were imprinted in coarse sandstone in a way that appears basically different from the fossilization processes acting in younger epochs. Their preservation is difficult to repeat experimentally, even in laboratory conditions.

The recent discovery of a new locality with extraordinarily well preserved Ediacaran fossils in the White Sea cliff in northern Russia (Grazhdankin and Ivantsov, 1996) may help in understanding their origination and the anatomy of organisms they represent. In the present paper this new taphonomic evidence will be reviewed. On this basis a restoration of the original three-dimensional organisation of the most common Ediacaran organisms will be attempted. Finally, some preliminary evolutionary interpretations will be proposed.

TAPHONOMY OF THE EDIACARAN FOSSILS

The style of preservation of soft organs typical for the Ediacaran fossils could not be possible in the present conditions of sedimentation. Any inference on the internal anatomy requires thus understanding the process of its formation (taphonomy) of such fossil material. Examination of various modes of preservation within different sediments may help in this. Of special importance from this point of view are exquisitely preserved fossils occurring in sandstone of the Yorga Beds of the Mezen Formation at Zimnie Gory and those preserved in limestone of the Khatyspyt Formation on the Khorbusuonka river in northern Yakutia. These are the main sources of information presented below.

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Shroud of Ediacara

Two highly fossiliferous horizons are exposed in the cliff of the White Sea 4–5 km south of Zimnie Gory lighthouse, within the strata representing the Redkino stage of the Vendian (radiometrically dated as 555.3 ± 0.3 Ma; Martin *et al.*, 2000). They are about 3 m apart in the rock column. The upper one is a 10 cm thick sandstone bed that extends for at least 200 m without any significant change in thickness. This is a fine-grained quartz sandstone with clayish matrix. Quartz grains are angular, suggestive of eolian origin. The bed yielded a fossil assemblage with both sole casts (positive imprints on the lower sandstone bed surface, that is convex hyporelief) and external molds (negative imprints as concave hyporelief). The dominating large, up to 23 cm long, specimens of *Yorgia* and single specimen of very large *Dickinsonia* are represented by both kinds of preservation (Dzik and Ivantsov, 1999). The feathery organism *Epibaion* (about 30 cm in length; Ivantsov and Malakhovskaya, 2002) is known only from imprints on the clay surface cast in sandstone. A small unnamed dickinsoniid, a tongue-like relative of *Chondroplon* (*Andiva* of Fedonkin, 1998, 2002), and *Kimberella* (Fedonkin and Waggoner, 1997) are known only from external molds of their bodies. The sole casts show external morphology of the organism ventral surface, the external molds show its dorsal morphology at various stages of decomposition.

The most striking aspect of the sole casts is that in the case of *Yorgia* and large *Dickinsonia* their series end with an external mold representing the same specimen that left the imprints on the sea bottom (Figs. 1, 2A). For such a series to originate it was necessary to have the surface of the clay exposed, not covered with sand, as is usually the case with trace fossils. The surface also had to be stabilized to protect the clay against turbulence unavoidably occurring while the body moves or is elevated by current. The mucus from a cyanobacterial mat was invoked as a stabilizing agent (Dzik and Ivantsov, 1999). The presence of microbial mats in the Ediacaran environment can be inferred on the basis of other indirect evidence (Seilacher, 1999; Gehling, 1999). At Zimnie Gory microbial mats can be observed directly, especially in the lower fossiliferous horizon.

There, numerous *Kimberella*, *Parvancorina*, *Tribrachidium*, *Dickinsonia costata*, and "*Dickinsonia*" *lissa* occur, represented by external molds (Grazhdankin and Ivantsov, 1996; Fedonkin and Waggoner, 1997). Unlike the *Yorgia* bed, the lower horizon is not uniform in thickness but split into lentiform sandstone bodies. They were originally interpreted as sand fills of erosional channels (Grazhdankin and Ivantsov, 1996). These lenses cannot be channel fills because the bedding is parallel to their bases, with the first layer being of uniform thickness, similar to that of the *Yorgia* bed. Thus, the lenses originated as an effect of plastic deformation of layered sand under load. Normally, such plastic deformations result in developing smooth or gently wrinkled boundary surfaces. In this particular case, however, an extensional tension acting at the basal surface resulted in formation of numerous transverse ruptures ("stretch marks" covering the lenses). Thus a firmly flexible, but not elastic, sheet separated the clay substrate from the sand load. Through the ruptures liquidized sand penetrated to the underlying clay (Fig. 3A). The stretch marks frequently pass across fossils. This clearly shows that both the sand above and clay below the intersurface were loaded with water long after formation of sole casts and external molds. The same conclusion was reached, based on microfaults, by Gehling (1999, p. 48) in respect to the Ediacara fossils.

A network of pyritized filaments can be frequently observed at Zimnie Gory, adhering to the sandstone sole even after the soft clay is washed out. This alone documents the presence of a microbial community preceding the sand deposition, but does not allow one to estimate its thickness and mechanical properties. This can be seen at margins of stretch marks. The sand injection expanded below the mat removing the hydrated mud but the mat margin remained intact, locked between the sand layer above and its tongue below. It appears that the mat was about 2 mm thick, and laminated like a stromatolite. The laminae became more and more densely distributed towards the upper surface and the quartz grains gradually disappear, being completely replaced with clay minerals. Apparently sedimentation ceased. A couple of millimeters apart from the rupture, the mat thins to about two thirds of its thickness at the margin (Fig. 3A), its compaction was thus only slightly greater than the surrounding sandstone. There is virtually no pyrite or any other mineralization within the mat—just clay minerals. Its mechanical resistance was thus probably due to impregnation with an organic matter virtually lacking sulfur, thus presumably with mucopolysaccharides.

Contrary to earlier interpretation of the Zimnie Gory imprints (sole casts) of *Yorgia* (Dzik and Ivantsov, 1999) the real problem is posed not by too soft surface of the clayish bottom but, instead, by the stiffness of the mat. The mat appears to be a kind of firm shroud on which bodies of the Ediacaran organisms were imprinted. To leave imprints, a body had to impose a significant pressure on the mat, which seems unlikely in the case of probably strongly hydrated bodies of unskeletonized Ediacaran organisms, or stay on it long enough to hamper its growth locally.

Most interestingly, the sand injections behaved in a specific way while crossing external casts (Fig. 4). The cast, instead of rupturing, shows its normal ornamentation at the stretch mark, which is expressed only as a prominent elevation on the sandstone surface. Apparently, the soft tissue of the fossilizing organism was still intact at the moment of formation of stretch marks. It was elastic, allowing the sand to penetrate down to some depth. This closely resembles the situation observed, on a different scale, in the Namibian

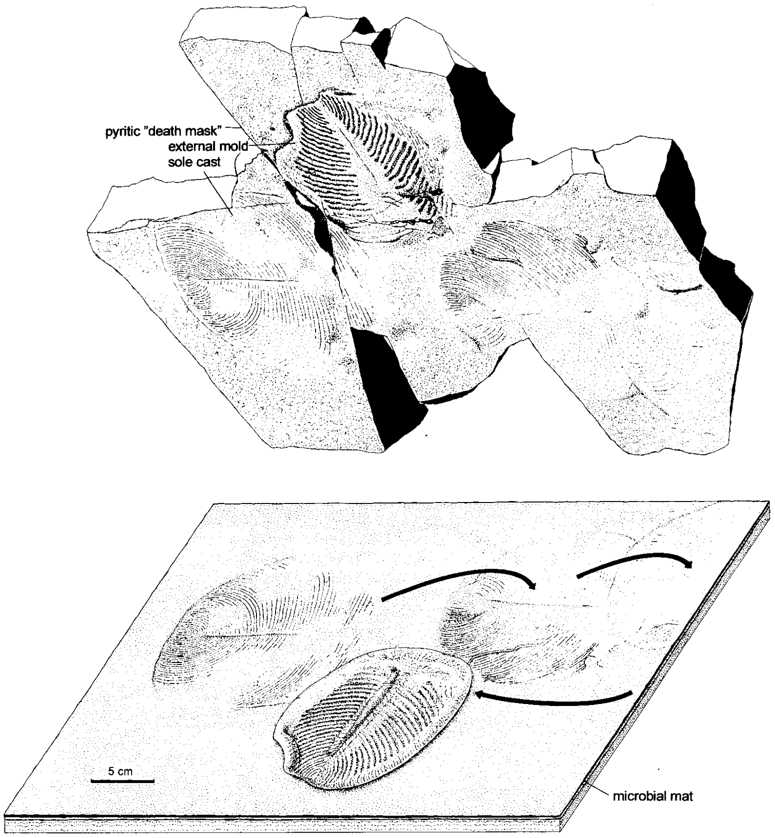

FIG. 1. Interpretation of the origin of positive (sole casts) and negative (external molds) imprints of *Yorgia* on the under surface of a slab from Zimnie Gory on the White Sea shore, Russia, as death tracks (modified after Dzik and Ivantsov, 1999, fig. 2). Series of imprints were left on the microbial mat by dying animal periodically changing its position and finally buried under sand. The shape of the dorsal surface of the body was fixed owing to cementation of the sand layer near its basal surface with pyrite.

Ernietta (Dzik, 1999*a*). It appears thus that in both cases the fossils were fixed not only before diagenesis of the sediment, but even before decomposition of the soft tissues!

This introduces additional complexity into the scenario for origination of the Ediacaran fossils. Nevertheless, there can be no doubt that the presence of a microbial mat is necessary to explain formation of imprints on the clay bottom surface (sole). The cyanobacterial mucus apparently stabilized the surface to be replicated by the base of the overlying sand bed (Dzik and Ivantsov, 1999). However, the mat does not help much to understand formation of the most common kinds of Ediacaran fossils, that is the external molds of soft bodies on the under surface of the sand bed. In fact, sole casts are represented also at Ediacara (*e.g.*, Fig. 7A) but in the coarse sandstone they are difficult to notice.

Ediacaran death mask

Gehling (1999) concluded that the external molds required a "death mask" to form; that is stabilization of the sand layer near its under surface. He proposed amorphous iron monosulfide to be the stabilizing agent. Actually, the Zimnie Gory fossiliferous sandstone beds owe their smooth under surface to cementation with pyrite (Dzik and Ivantsov, 1999, p. 258). Thin sections across the base of both *Yorgia* and *Kimberella* beds at the Zimnie Gory locality invariably show dark iron sulfides impregnating the rock near the under surface in proximity to fossils (Fig. 3B). After gentle etching with hydrofluoric acid, framboids about

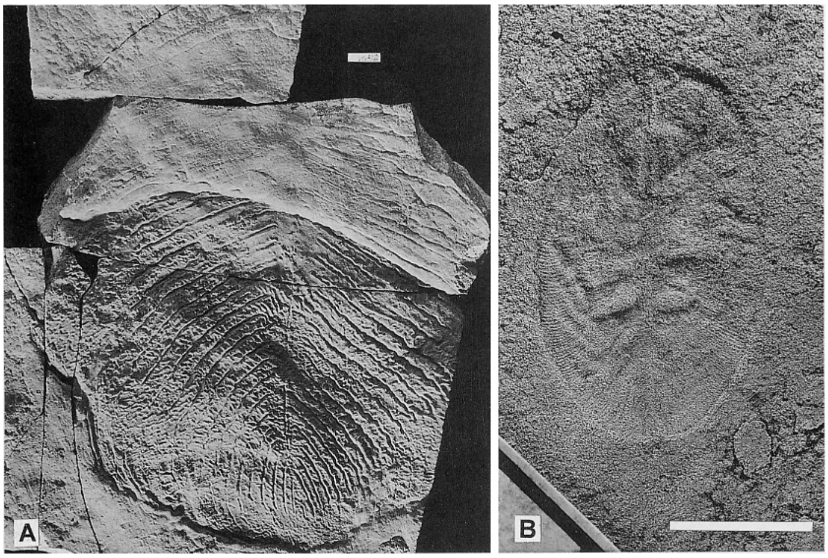

FIG. 2. Preservation of Ediacaran fossils in the *Yorgia* bed at Zimnie Gory. Specimens housed at the Paleontological Institute, Moscow (PIN). A. *Yorgia waggoneri*, specimen PIN 3993/5018 (illustrated also in Dzik and Ivantsov, 1999, fig. 1B) showing anterior part preserved as sole cast (presumably sediment penetrated interior of the body in this area) and as partially collapsed external mold of the rest of the body. Resistant internal organs attached to the septa of the "quilt" are preserved as furrows. B. Unnamed dickinsoniid of the "*D.*" *lissa* group (see also Fig. 8 and Dzik and Ivantsov, 2002), external mold PIN 3993/5067 showing imprints of internal organs. Resistant tubular organs are represented by depressions on the under surface of the sandstone bed; collapsed oval cavities filled by sediment migrating from above form elevations. Bar scales equal 1 cm.

5 μm in diameter, crusts over filaments, and loose crystals 1 μm large with poorly defined octoedral shapes can be seen in SEM (Fig. 3C). The EDAX analysis confirms the presence of iron sulfates that in X-ray analysis appear to represent pyrite. Framboids may have originated in the water column (Wilkin *et al.*, 1996) but in this case the abundant presence of tubular aggregates around filamentous bacteria indicates precipitation at the sea bottom. Framboids thus probably formed from aggregates of amorphous sulfide precipitating within the sediment (Herbert *et al.*, 1998, fig. 1). Steiner and Reitner (1999) reported a heavy sulfur isotope value for the framboidal pyrite from Zimnie Gory ($\delta^{34}S = +37{,}8‰$) that, according to them, indicates origin from sulfate reduction. Because of the apparent connection of the pyrite crust with fossilized bodies, the primary source of sulfur is likely decomposition of proteins. As there was no pyrite precipitation within the underlying microbial mat, obviously rich in organics, deficiency of iron was possibly the limiting factor. The eolian provenience of the sand grains also makes it likely that iron, which enabled pyrite formation in the sandstone, was of such origin.

It thus appears that originally the early cement at the fossil-bearing sandstone surface was truly composed of amorphous iron monosulfide. Its slimy appearence and subsequent gradual crystallization into pyrite was probably the factor giving the basal surface of the bed some mechanical resistance. In Recent seas poorly crystalline iron sulfides form primarily as a result of bacterial reduction of sulfate. They eventually transform to well crystallized mackinawite Fe_9S_8, the full transformation taking up to two years at 25°C (Herbert *et al.*, 1998). Ferrimagnetic greigite Fe_3S_4 is the subsequent precursor to marcasite or pyrite (both FeS_2), which are stable components in the rock. Marcasite forms predominantly below pH 4 (Schoonen and Barnes, 1991) and oxidizes more easily while weathering, an effect of different crystal structure (Uhlig *et al.*, 2001). It is lacking at Zimnie Gory; the sedimentary environment was thus not necessarily acidic, although rich in decomposing organic matter. The occurrence of Ediacaran fossils in limy environment of the Khatyspyt Formation (with high bituminosity) suggests neutral or even weakly alkaline conditions of the "death mask" formation. Although potentially the microbial mat offered source of organic matter for the whole surface of the fossiliferous bed, the pyrite formation seems to be restricted to external molds and their proximities. The decaying body was thus more important.

This is nicely shown by specimens of *Dickinsonia* and *Yorgia* preserved partially as external molds and partially within the sandstone bed (Fig. 5). Probably, while the sand bed was deposited, the bodies lying over the surface of the microbial mat were partially

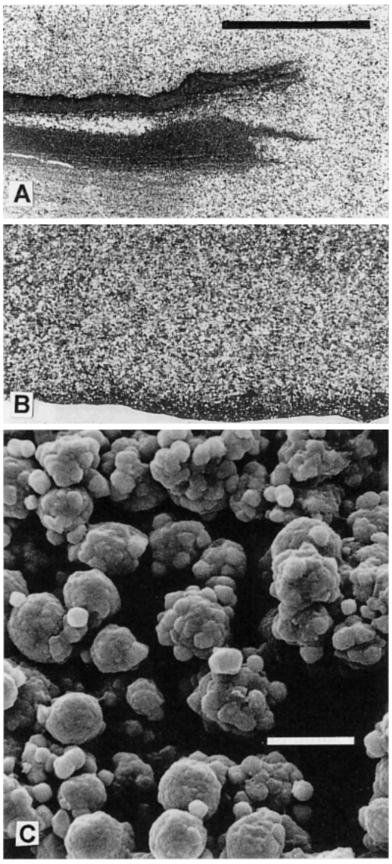

FIG. 3. Structure of the microbial mat and pyritic cementation of the sandstone sole in the *Kimberella* horizon at Zimnie Gory. A. Thin section across ruptured microbial mat at the margin of a stretch mark. Note laminated structure of the mat and pattern of its breakage; the mud below shows also lamination or even stromatolitic structure but low resistance. Bar scale equals 5 mm. B. Thin section across the base of the *Kimberella* bed in proximity of an external mold. Note dark zone close to the bed sole cemented with pyrite. Same magnification. C. SEM photograph of the surface of the bed gently etched with hydrofluoric acid. Note framboids and isolated crystals of pyrite. Scale bar equals 10 μm.

displaced, sucked up by the turbulence and then compressed under the sand load. There is no difference in preservation between parts originally being in proximity to the microbial mat and those distant from it. Parts of the body preserved inside the sandstone collapsed almost completely, with anatomical structures shown in low relief. Specimens quarried at Zimnie Gory freshly from the exposure are covered with pyrite, which easily oxidizes. Iron sulfide precipitated there directly on the soft tissue of the cadaver. Although not so well preserved, the Namibian Kuibis Quarzite fossils also probably originated in such way. Such fossils would include *Rangea* bodies collapsed within the sand, *Pteridinium* organic sheets preserved within suddenly deposited sediment or loaded *Ernietta* sheets migrating to the underlying bed. The mat was thus of no importance in formation of three-dimensional fossils. All this provides a strong, if not conclusive, support to Gehling's (1999) idea of "death mask," even if the "mask" did not form any separate veneer over the sandstone sole.

FIG. 4. Rupture of the microbial mat crossing an external mold of "*Dickinsonia*" *lissa* from the *Kimberella* horizon at Zimnie Gory (plaster cast). Note ornamentation of the "quilt" crossing the surface of the stretch mark—the quilt was thus intact and formed a kind of bag for the liquidized sand. Similar mechanism, although on a larger scale, produced fossils of *Ernietta* in Namibia (Dzik, 1999*a*).

The preservation of Ediacaran fossils in limestone in the Khatyspyt Formation at Khorbusuonka is virtually identical with the preservation at typical Ediacaran localities. The sediment mineralogy does not matter, except that there was a cyanobacterial mat at the interface between layers where the body of the organism was deposited. There is an asymmetry in cementation between the beds above and below the fossiliferous surfaces at Ediacara, as noticed already by

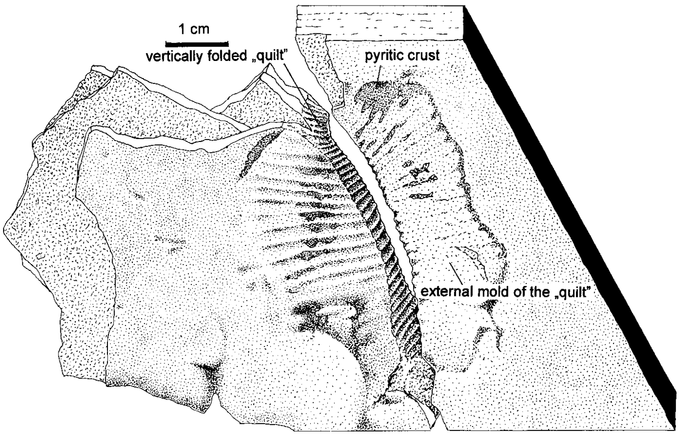

FIG. 5. Diagrammatic presentation of three-dimensionally preserved *Dickinsonia costata*, based on actual specimen from Zimnie Gory. Note that the admedial part of the quilt was sucked into sand during its deposition. Originally the entire specimen was covered with a thin pyritic crust, which exfoliates while weathering.

Wade (1968). The soft sediment from below filled the cavities of external molds, but this does not necessarily have anything to do with the difference in grain size (Gehling, 1999, p. 47), although it is usually finer in the mat. Perhaps the mucus blocked iron oxide migration from the sand above, thus protecting the mat against early cementation.

In the following chapter, this recent progress in understanding the origin of Ediacaran fossils is used to restore their original anatomical structure.

INFERRED ANATOMICAL STRUCTURES

The Ediacaran fossils may differ more in effect of disparity in their modes of formation than in their original anatomies. In many cases different parts of the same organism are preserved differently, either under direct contact with the mat, or distant from it, as well documented at the Zimnie Gory locality, but also by some Australian and Namibian fossils. This allows us to extract reasonable information on the (1) original body surface, (2) shape and distribution of internal cavities, (3) collapsed internal organs, (4) organs resistant to collapse, and (5) organic sheets of the basement membrane.

Remarkably, external molds representing evidently the same species and preserved at the same bedding plane may substantially differ in the depth of impression (Gehling, 1999) and pattern of preserved structures. The latter is especially impressive in the case of *Yorgia* (Dzik and Ivantsov, 1999) and an unnamed oval dickinsoniid. In small specimens of *Yorgia* organs attached to the septa of the "quilt" are preserved as elevated areas. In larger undeformed specimens the same organs are preserved as depressions (Fig. 2A). Apparently, in juveniles these organs collapsed more easily than the rest of the body—they were empty. In adults their infill was more resistant than the quilt chambers. On this basis and their topographic position it was proposed that these were serial gonads (Dzik and Ivantsov, 1999).

In the unnamed oval dickinsoniid from the same fossil assemblage the probably homologous organs are oval in appearance, much less numerous than the quilt segments, and not connected with septa at their length (Figs. 2B, 6; Dzik and Ivantsov, 2002). As in *Yorgia* specimens of similar size, they easily collapsed. In several specimens some other internal organs are imprinted as furrows passing obliquely across the "quilt" segments. They were apparently rather resistant to collapse. Because of this and their connection with the similar axial furrow they were interpreted as intestinal caeca filled with gut contents (Dzik and Ivantsov, 2002). Most likely it was purely organic in this species and in closely related "*Dickinsonia*" *lissa*. Similar, but more numerous caeca filled with sediment, occur in the very large *Dickinsonia* (Ivantsov and Malakhovskaya, 2002) and in rare small specimens of *Dickinsonia costata* from Ediacara (reviewed in Dzik, 2000). In these cases the number of caeca seems to correspond to the number of the "quilt" segments but the caeca moved freely within the body cavity, as shown by their irregular disposition. The rarity of such preservation suggests that sediment was normally not present in the gut of these animals. The sole marks of *Dickinsonia* and *Yorgia* show that their venter was flat with fine segmentation which strictly follows that of the dorsal quilt.

In the unnamed Zimnie Gory dickinsoniid the rare strongly concave external molds bear weak impressions of the proposed caeca. The quality of their impression increases with compression of the specimens, and the most informative of them have their marginal

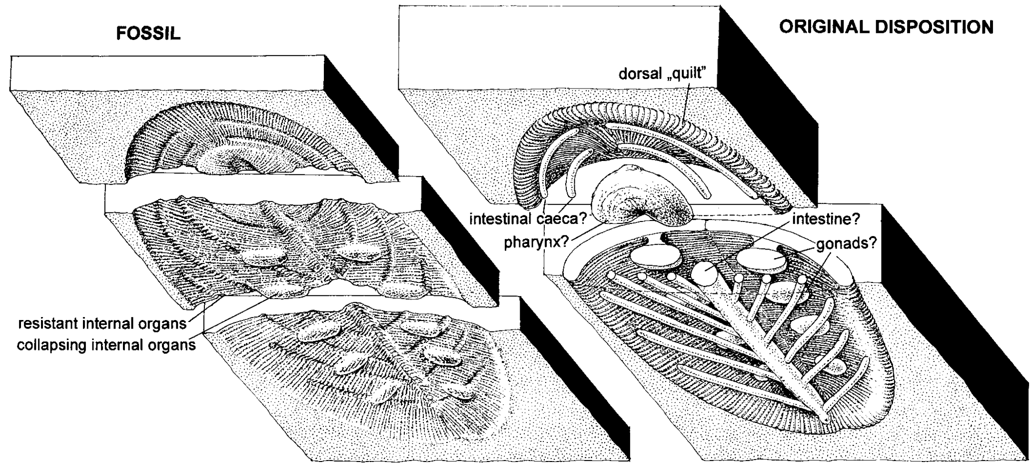

FIG. 6. Diagrammatic presentation of processes leading to formation of internal organ imprints on external molds of Ediacaran organisms at Zimnie Gory (compare with Fig. 2B). Organs with resistant fill preserve as depressions on the sandstone bed sole, those empty or with a soft content form elevations.

parts almost completely collapsed. The most common kinds of preservation of this species, as well as of *Dickinsonia costata*, are flat, but in a basically different sense. The whole body surface is planar except for the margin, which is very steep. This was interpreted as preservation of an isolated "quilt" with the rest of the soft tissues being decayed. The "quilt" itself was probably the collagenous basement membrane of a dorsal unit acting both as a hydraulic skeleton and muscular locomotory organ perhaps analogous to the set of myomeres in chordates (Dzik, 1999*b*, 2000).

The same type of analysis can be applied to other Ediacaran organisms preserved as collapsed bodies on a microbial mat, partially infilled with sediment, or three-dimensionally within sandstone.

The fossil evidence enabling restoration of internal anatomy of the Precambrian sea-pens has been reviewed elsewhere (Dzik, 2002). It ranges from rare sole marks through external molds to three-dimensional specimens stuffed with sand in various ways.

DIVERSITY OF EDIACARAN BODYPLANS

Two anatomically distinct groups dominate in the Ediacaran biota. The Dipleurozoa were bilaterally organized vagile organisms characterized by a segmented dorsal hydraulic skeleton, intestine with metameric caeca, and serial gonads (Dzik and Ivantsov, 1999; Dzik, 2000). The Petalonamae were radially organized sessile organisms characterized by a basal anchoring bulb extending into the axial cavity and radially organized frond with pinnate organs (Dzik, 2002). At Zimnie Gory specimens of *Charniodiscus*-like petalonameans have been found three-dimensionally preserved within the sandstone bed and anchored in the underlying microbial mat (Steiner and Reitner, 2001). The picture of anatomical diversity of Ediacaran organisms presented below is a result of studies on the new fossils from Zimnie Gory and reinterpretation of earlier findings based on increased understanding of their fossilization stories.

Dipleurozoans

The most completely known Zimnie Gory dipleurozoans are *Yorgia*, the unnamed dickinsoniid reviewed above, and *Dickinsonia costata* (Fig. 7). They have close relatives in this and other Ediacaran faunas. Thus, *Marywadea* and *Spriggina* show asymmetry of the quilt, bifurcations of probable caeca in the frontal area, and transverse ridges in the adaxial part of the body resembling probable gonads in *Yorgia*. The asymmetric disposition of the first chamber of the quilt is shared also by *Praecambridium*, *Vendia*, a trilobite-like metameric organism figured by Gehling, 1991 (pl. 4, fig. 4) (*Archaeaspis* of Ivantsov, 2001*c*, preoccupied by *Archaeaspis* Repina, 1965 in Khomentovskii and Repina, 1965), and several other poorly known minute organisms (Fig. 8). A probably asymmetric quilt, but with very narrow, densely arranged chambers, characterizes the Australian *Chondroplon* and its close relative *Andiva* from Zimnie Gory (Fedonkin, 2002).

The dipleurozoan body plans shows surprising similarity to the hypothetical ancestor of chordates invented by Bjerring (1984) mostly on the basis of embryonic development of amphioxus. He presented an organism with dorsoventrally compressed oval body, dorsally located metameric muscular chambers and intestine with lateral caeca (subsequently transformed into the branchial openings). Notably, the oldest known Early Cambrian chordate *Yunnanozoon* had its metameric muscular units located dorsally of the no-

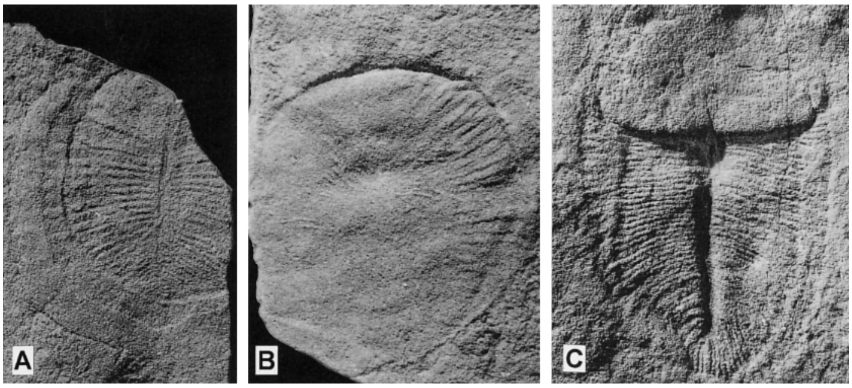

FIG. 7. Various modes of preservation of *Dickinsonia costata* in the Pound Quartzite at Ediacara in the Flinders Range, South Australia, resembling fossils from Zimnie Gory. Specimens housed at the South Australian Museum, Adelaide (SAM); natural size. A. Sole cast and two stages of collapse (possibly constriction) of the body preserved as external mold SAM F 173331. B. External mold with infill of intestinal caeca SAM T 61-2051 (illustrated also in Glaessner and Wade, 1966, pl. 101:4). C. Specimen SAM P 14387 anteriorly preserved as sole cast with interior filled with sand (compare with similar preservation of *Yorgia* on Fig. 2A) and the rest of the body as external mold, partially collapsed and showing resistant medial tubular organ (intestine) and narrow zones on resistant organs on both its sides (gonads?).

tochord, although its body was laterally compressed (Dzik, 1995). Perhaps this functional anomaly has a historical explanation. Some aspects of the dipleurozoan anatomy, especially the presence of serial lateral caeca and gonads, can be also compared with the nemerteans; the dorsal quilt would then be a homologue of the rhynchocoel (Dzik, 2000). Such rather bizarre combination of characters in the body plan of these Ediacaran animals seems to indicate a relatively complex anatomy of the ancestors of Recent metazoan phyla and a high contribution of secondary simplification to their subsequent phylogeny.

Petalonamaeans

The diversity of Petalonamae is poorly recognized. The best known *Rangea* and *Charniodiscus* show well differentiated stalk and wide tetraradial frond (Fig. 9B–C), but the stalk was probably weakly developed in related *Bomakellia* (Dzik, 2002). If the possible homology between the axial canal in the Petalonamae and the gut of Dipleurozoa (Dzik, 2002) is true, the stalk elongation or its complete lack would represent extreme derived states. The Cambrian ctenophores *Fasciculus* and *Maotianoascus* seem to share some features of their body plans with the enigmatic alleged Cambrian petalonamaean *Thaumaptilon* and true Vendian Petalonamae but the pattern of relationships and scenario of transformation is hard to resolve (Dzik, 2002). Possibly, the irregularly distributed dark spots on the fusiform units of *Thaumaptilon* represent macrocilia, a transitional stage in formation of comb organs from uniformly distributed ciliated cells. The frond-like appearance of the body, with feathery distribution of comb organs, would then be inherited by the earliest pelagic ctenophores after their sedentary ancestors. Even if this hypothesis is true, most of the known petalonameans seem to be too derived anatomically and ecologically to have any direct relationships to the ctenophores.

The bizarre *Ventagyrus* from Syuzma in northern Russia (Fig. 9A) shares some aspects of its anatomy with petalonamaeans, but was of triradial organization (Ivantsov, 2001*a*). Membraneous skeleton of its ovoid body tends to split post mortem into separate units closely resembling those of *Pteridinium*. These petalonameans do not occur in connection with microbial mats and could have been pelagic.

Possible ecdysozoans

Some Ediacaran organisms are difficult to fit in the Dipleurozoa-Petalonamae dichotomy despite possible relationship between these clades. Among them is another triradial organism—*Tribrachidium*. Seilacher (1999) applied sponge model to *Tribrachidium* envisioning system of "inhaling and exhaling canals." This is not supported by the Zimnie Gory material.

Instead, the *Tribrachidium* body surface shows bifurcating concave areas separated by sharp ridges, thus opposite to the imprints left by the chambered "quilt" of *Dickinsonia*, and resembling rather stiff cuticular structures than elastic internal membranes (Fig. 8). Inside there were three bodies obliquely radiating from the center. They were resistant, but may correspond to collapsing chambers in the related trilobozoans *Albumares* and *Anfesta*. In *Tribrachidium* sediment penetrated from above only in areas between these organs, close to the center of the body. Such differences in preservation parallel those of probable gonads in *Yorgia* and the unnamed dickinsoniid. The spiral orientation of the internal bodies in the trilobozoans is suggestive of their being a modification of originally longitudinal to the axis dispo-

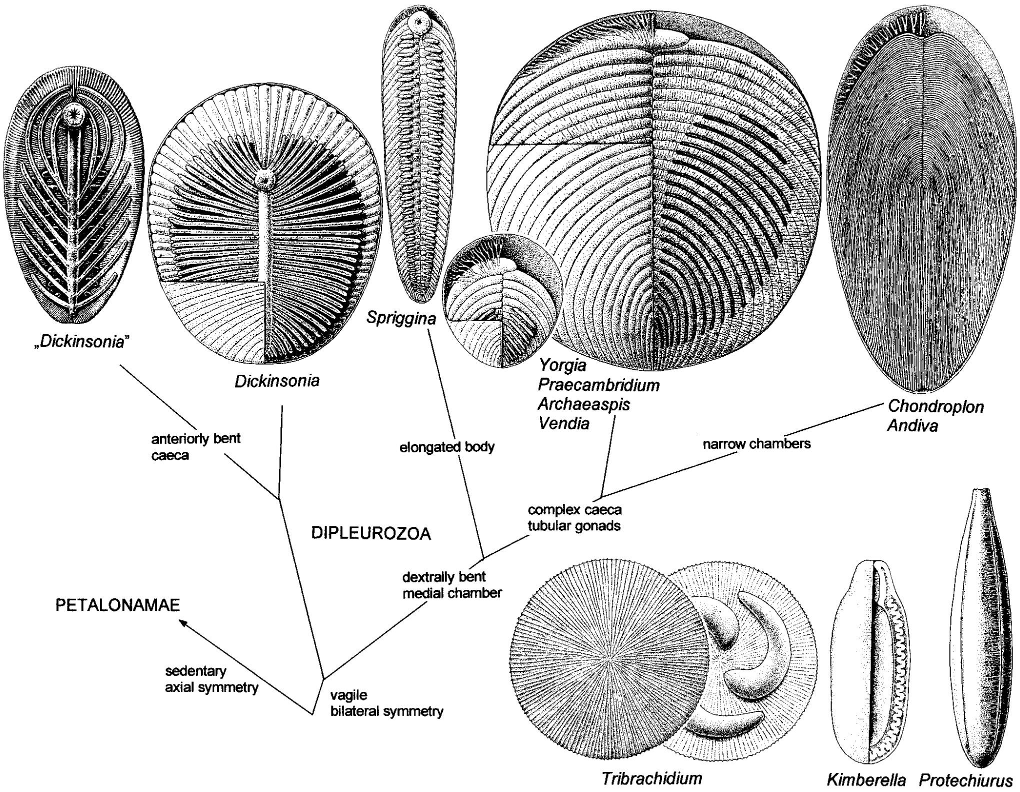

FIG. 8. Possible relationships among the best-known members of the Dipleurozoa. Note that within the Dipleurozoa two clades can be distinguished. They differ in the disposition of the medial chamber of the dorsal quilt, oriented either medially forward or bent laterally. In both groups the quilt segments vary being rather voluminous, filled with liquid, to narrow and compact. Possibly, the petalonamean basal bulb and axial canal are homologues of the dipleurozoan pharynx and intestine, respectively (Dzik, 2002). Restorations of even more controversial and enigmatic Ediacaran fossils are added. *Tribrachidium* was a discoidal organism lacking any appendages (Seilacher, 1999), but with three voluminous, easily collapsing organs inside, covered with radially ribbed body covers. In its three-radial symmetry it is similar to *Ventagyrus* (Fig. 9) and *Protechiurus* (*Vendoconularia* of Ivantsov and Fedonkin, 2002). The latter shares its sac-like body with *Kimberella*, which shows an internal muscular, pharynx-like organ in many specimens, among others also on the slab with the largest specimen illustrated by Fedonkin and Waggoner (1997).

sition of the organs. This is an additional hint that these were organisms with abilities to secrete cuticle—relatives of round worms.

The Namibian *Protechiurus* may also belong here, as it shows signs of hexa- or perhaps rather triradial symmetry. This is a kind of bag filled with sand through an opening at one end, similarly preserved as *Ernietta*. The opposite tip is blunt. Sharp, low ridges delimit fusiform areas along the body surface with fine transverse striation recognizable in places (Glaessner, 1979). I had occasion to examine a cast of the only known specimen (its depository is unknown; personal communication, J. Gehling), which shows rather clearly that there were six ridges, not eight as suggested by Glaessner (1979; his incomplete ridges 4 and 7 seem to be artifacts of deformation).

Possible "coelenterates"

Another Ediacaran organism of controversial affinities is *Kimberella*. It is represented by hundreds of specimens from the lower fossiliferous horizon at Zimnie Gory. Fedonkin and Waggoner (1997) and Seilacher (1999) compared these fossils with artificially produced cast of the polyplacophoran sole. However, they do not represent sole casts but, instead, external molds of the collapsed upper surface of the body. The similarity to limpet soles is thus quite superficial. The main argument for the molluscan nature of *Kimberella*

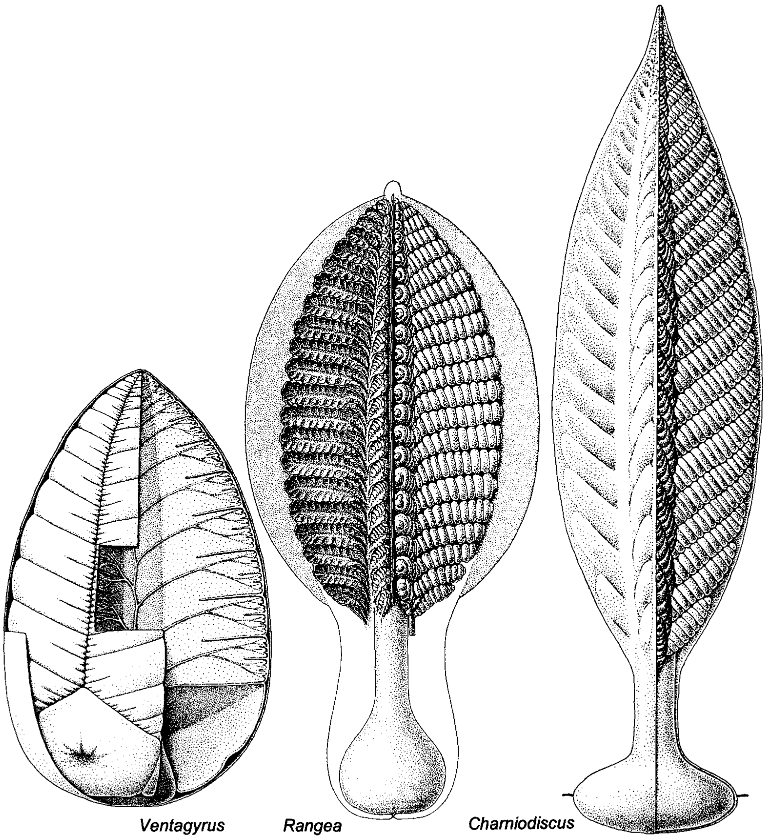

FIG. 9. Restorations of the internal body organization of the best-known members of the Petalonamae. *Ventagyrus* based on Ivantsov (2001*a*), *Rangea* and *Charniodiscus* on data and interpretations in Dzik (2002); approximately natural size.

remains thus its association with putative radular marks proposed by Seilacher (1999). However, it is unclear what these structures truly represent.

The most prominent aspect of *Kimberella* fossils is a voluminous depression in their center. In many specimens it is somewhat asymmetric, deformed in a way suggestive of a lateral displacing of the content of this cavity. The most likely interpretation is that this was a gut content. It was probably of purely organic composition. This is shown by specimens with a fine network of pyritized algae covering the surface of the cavity. It leaves no space for sediment between the mat and the dorsal surface of the cavity. Thus the animal was probably not a mud eater.

In all well preserved specimens of *Kimberella* there is a distinctly delimited narrower part of the proposed gut, perhaps representing a muscular oesophagus or even evertible proboscis. Transverse depressions on both sides of the body are irregularly distributed, suggestive of contraction of concentric muscles. There are also specimens with very short and wide bodies in effect of longitudinal muscular contraction.

The feature of *Kimberella* that may be of much phylogenetic importance is the stable width of the area between the gut wall and the body surface. This suggests that the space between was filled with tissue, thus with a kind of mesoglea. If the transverse wrinkles on this area are truly muscles (thus mesogleal muscles) this would point to ctenophoran affinities of *Kimberella*.

The diversity of the Ediacaran anatomies thus includes organisms with bilaterally symmetric, partially asymmetric, and radial body plans. A significant part of them have a lot in common, and the monophyly of the "Vendobionta" cannot be excluded. This scenario does not need to be in conflict with their possible relationship to various Phanerozoic phyla. Hardly the whole spectrum of the Precambrian animal life is represented in the Ediacaran biota, however. Missing, at least, are makers of traces of locomotory activity found elsewhere (*e.g.*, Jensen *et al.*, 2000) in rocks of latest Precambrian (Vendian) and earliest Cambrian (Manykaian) ages.

EDIACARAN BIOTA ENVIRONMENT

Identification of the internal structure of the microbial mat underlying the *Yorgia* bed at Zimnie Gory removes the most troublesome aspect of preservation of sole casts there. Namely, the problem with series of up to eight imprints on the mat ending with the collapsed body of the same organism molded in the overlaying sand (Ivantsov, 1999, 2001*b*; Ivantsov and Malakhovskaya, 2002). There are no signs of movement over the mat surface, neither dragging nor peristaltic waves. An *ad hoc* explanation was proposed that formation of water vortices was repeatedly taking the body in suspension moving it a little forward (Dzik and Ivantsov, 1999). This is no longer necessary. The real problem is rather how to produce imprints on the relatively rigid surface of the mat.

The laminated structure of the mat documents its prolonged growth. The mat corresponds to an episode of nondeposition of possibly seasonal nature, as suggested by rhythmic occurrences of microbial mats in other parts of the Mezen Formation at Zimnie Gory. The sole marks developed either in effect of long enough pressure (but the load of the unskeletonized body in water was no doubt very small) or in effect of inhibition of the growth at the covered mat surface. The latter required prolonged stay of the body at the mat surface: the lamination offers evidence for required time.

The numerous series of sole marks with the cadaver at their end occurring in the *Yorgia* horizon at Zimnie Gory are thus not only superficially similar to the famous spiral death tracks of Solnhofen (*e.g.,* Barthel *et al.*, 1990, fig. 5.5; Röper *et al.*, 1999). In the Jurassic of Bavaria, the beds with death tracks and exquisite imprints of jellyfishes intefinger with horizons with mass occurence of the bivalve *Solemya*, known to have symbiotic chemoautotrophic bacteria in its gills, feeding on H_2S. Imprints of microbial mats are also known from there (Röper et al., 1999, figs. 44–46). As in the stagnant waters of the Jurassic Solnhofen basin, the Zimnie Gory dipleurozoans made their last crawl before collapsing at the end of their tracks. This is also why trace fossils are practically missing in the Zimnie Gory fossiliferous horizons.

According to Gehling (1999, p. 43) the Ediacaran biota are confined in south Australia to relatively deeper-water facies. This situation is similar to that observed in carbonates of the Khatyspyt Formation. The black bituminous limestone with Ediacaran fossils is there underlain and overlain by stromatolitic facies. The thin limestone beds intercalate with shale. The mud was originally strongly hydrated and compaction reduced it to thin films. The mud layers were originally many times thicker, as shown by the pattern of deformation around stromatolitic columns penetrating the black limestone unit at its base. At Zimnie Gory both the *Yorgia* and *Kimberella* horizons may represent terminations of deepening events, with a sudden sand deposition, as suggested by the unusally fine grain of the clay (compared with the rest of the section) underlying the microbial mat in both cases.

Probably most of the discoidal Vendian "medusoids" represent casts of the petalonamaean's basal bulbs (Gehling *et al.*, 2000). Many of them show finger-like protuberances penetrating the mat (Fig. 10). These resemble the foot of some specialized bivalves (*Solemya* or *Lucina*) used to penetrate putrid sediment to release H_2S consumed by symbiotic chemoautotrophic bacteria. Especially elaborate are such protrusions on bulbs of *Hiemalora* abundantly occurring in the stinking limestone of the Khatyspyt Formation.

The Ediacaran biota not only offer an incomplete representation of the latest Precambrian life—they were not representative for it at all. It was not a "garden" but, instead, an inhospitably extreme environment for most organisms. Some of the Ediacaran fossils apparently represent organisms foreign to that environment. To find their grave there they had to fall into it. In the case of the dipleurozoans, they were probably swimming by waving their bodies, as suggested by the presence of a dorsal metameric muscular organ. If correctly interpreted above, *Kimberella* was also a freely swimming animal. All dipleurozoans probably were trapped accidentally by lethal bottom waters. This may be why they are represented in only some of Ediacaran localities, being missing *e.g.,* in the Khatyspyt Formation, where only basal discs and fronds of petalonameans are represented among several hundred specimens collected (Fedonkin, 1985; Vodanjuk, 1989). Those Ediacaran organisms that were able to survive in such severe conditions developed special adaptations. Most were sessile, either passively lying over the microbial mat surface (Trilobozoa) or standing erect, anchored in the mat with a basal bulb (Petalonamae). For a more complete documentation of the life in the Vendian we have thus to look elsewhere.

CONCLUSIONS

The microbial mat formed during nondeposition events is preserved virtually intact at the Zimnie Gory fossiliferous horizons with Ediacaran fossils. It was of stromatolitic appearance, with a significant mechanical resistance. Ruptures originating at plastic deformations of loaded sand bed formed stretch marks with sand penetrating through them to the clay. The mucus stabilized the clay surface to such a degree that movement by animals over its surface did not leave any recognizable marks. However, as shown by the lamination, the surface of the mat not covered with sediment was exposed to seawater long enough to allow bodies lying on it to leave impressions. The mat provided a kind of shroud on which animal bodies were printed as sole marks.

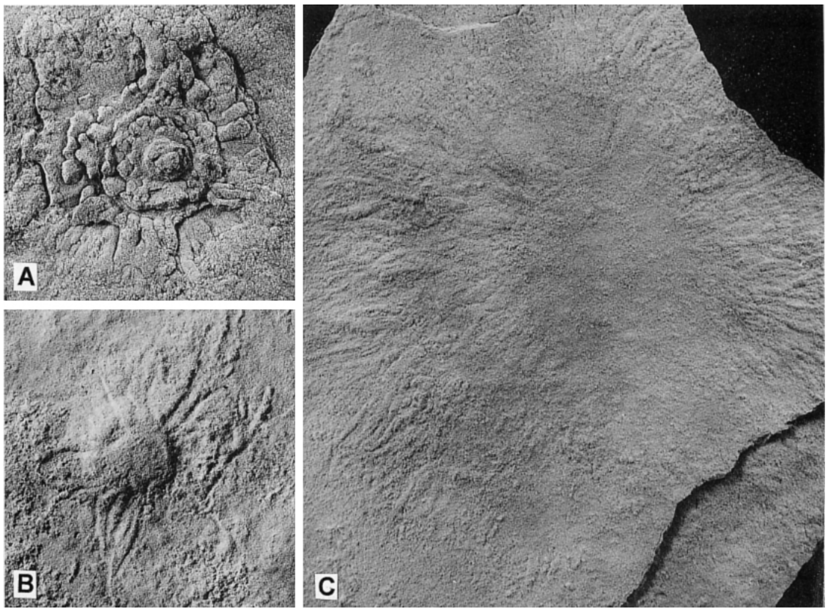

FIG. 10. Basal discs of petalonamaeans or related organisms with finger-like protrusions functioning as roots or, possibly, as penetrating organs releasing hydrogen sulfide from the microbial mat. Specimens housed at the Institute of Paleobiology, Warsaw (ZPAL); all natural size. A. *Mawsonites*? sp. from Zimnie Gory. B–C. *Hiemalora pleiomorpha* Vodanjuk, 1989 from black limestone of the Khatyspyt Formation, Khorbusuonka River section, northern Yakutia; juvenile specimen preserved as external mold and adult preserved as sole cast.

After the deposition of a sand bed on the mat, soft tissues specifically collapsed under the sediment load. Their upper surfaces were stabilized by iron sulfide precipitation near the sand layer sole, forming the Ediacaran death mask of Gehling (1999). Both the clay beneath the mat and sand above it were liquid long after fossilization. Mineralogy of the sand did not matter, as fossils preserved in limestone are closely similar to those in sandstone. The mat was not necessary for external molds to originate.

In the *Yorgia* horizon at Zimnie Gory series of circularly arranged sole marks frequently end with an external mold of the dead animal body, mimicking the spiral death tracks known from the Jurassic of Solnhofen. Similarly as at Solnhofen, the Ediacaran environment was also inhospitable to most organisms. Few of them were able to adapt to it. These were mostly petalonamaeans with radially organized frond anchored in the mat. They may be distantly related to ctenophores. To the dipleurozoans, with the body plan resembling chordates and nemerteans, the Ediacaran environment was probably lethal.

The *Yorgia* death tracks offer a kind of the Rosetta stone, which allows us to break the Ediacaran code and decipher the nature of the biota. They appear to be extreme examples, not representative of the animal life in the terminal Precambrian. The main stream of the evolution towards Phanerozoic phyla was flowing elsewhere. In a sense this provides support to Seilacher's (1989, 1994) idea of "Vendobionta," as a blind road of Precambrian evolution. The organisms specific for the Ediacaran environment (Petalonamae) may have been truly chemoautotrophic, although ironically the flattest of them (Dipleurozoa) tended to be killed by that environment so are unlikely to use such a physiology. However, the anatomy of the Ediacaran organism does not seem to be as fundamentally distinct from that of Recent phyla, as it was earlier assumed.

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