

# Skeletal Nets of the Ediacaran Fronds<sup>1</sup>

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**Abstract**—The Ediacara fauna is traditionally regarded as the first complex, diverse and widespread macroscopic life. The uncertainty of systematic position of its members has led to very different views on the early evolution of metazoans. In part, this may be due to a lack of data on sclerotization: a hard skeleton is a part of the archetype of the most taxa known from the fossil record, whereas the Ediacara fauna as a whole is most often considered soft-bodied, which complicates comparison. Here we report the Late Precambrian frond-like fossils (Petalonamae) from the Vendian assemblage of the Southeastern White Sea area (~555.3 Ma), which show evidence of elaborate skeleton composed of a regular meshwork reinforced by dense longitudinal and circular bands. Judging from the nature of preservation and the dynamics of the environment Ediacaran fronds secreted a relatively rigid but flexible skeleton. The fact that frond-like Petalonamae had a supporting structure similar to that of sponges and cnidarians seems to be a powerful argument in favor of their metazoan affinity. The new observations indicated also that the widespread skeletonization had occurred long before the “Cambrian skeletal revolution”.

**Keywords:** Precambrian, Vendian, Ediacara fauna, Lower Metazoans, skeletogenesis

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The appearance of the abundant skeletal fossils at the beginning of the Cambrian period seems to be a mysterious phenomenon. Was this event really an “explosive occurrence” as many have believed or had it been preceded by a long history as was assumed by Lowenstam and Margulis, 1980; Knoll, 2003 and others. The Late Precambrian fossil record will allow a deeper insight into the knowledge of skeletogenesis and tracked evolutionary patterns of Metazoa.

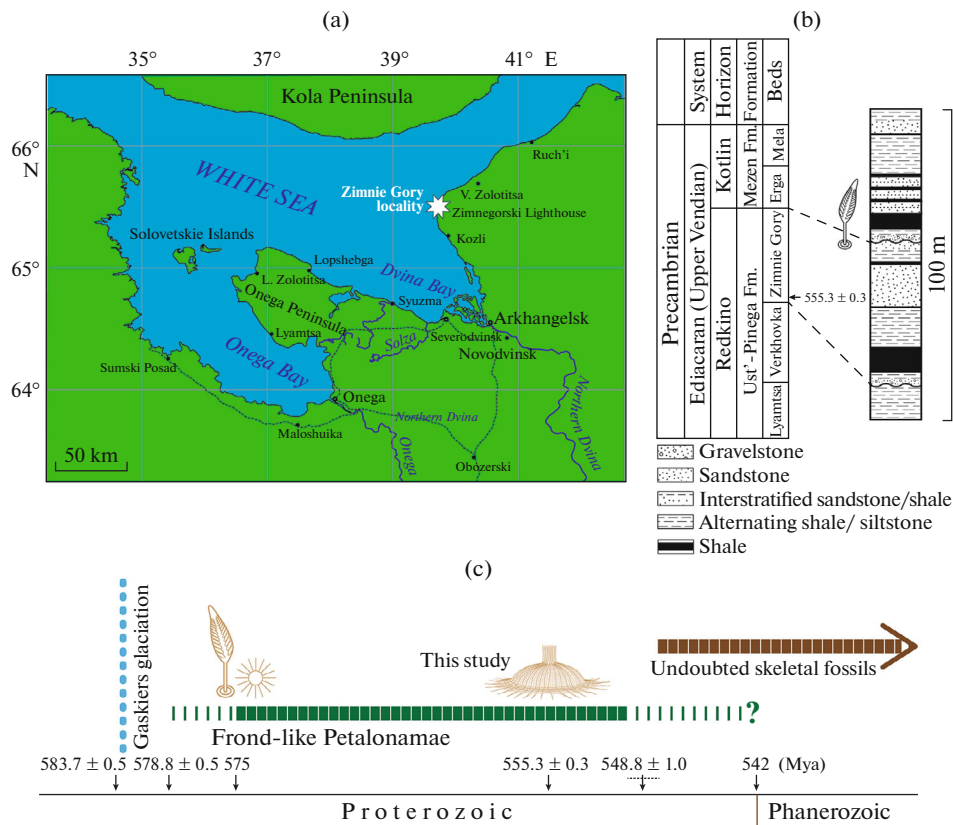
Despite a long history of research, the nature of the Ediacara fauna continues to be a matter of controversy (see Glaessner, 1962; Pflug, 1974; Fedonkin, 1985; Seilacher et al., 2003; Xiao and Laflamme, 2009; Grazhdankin, 2014; Dunn et al., 2017 and others). Perhaps its phylogeny has remained problematic due to the Ediacaran fossils have been traditionally thought to be “soft-bodied” or “non-skeletal”. A skeleton is regarded as a part of the archetype of many Phanerozoic taxa; and in most cases, it is the skeleton that is the basis of comparison of fossil and modern creatures. However, to the beginning of the 21st century, new data on morphology, taphonomy, and ecology of the Ediacaran fossils cast doubt on the concept of their being entirely soft-bodied (see review by Kouchinsky et al., 2012; Serezhnikova, 2014).

More than half a century ago, Glaessner, 1962 described skeletal remains in the Ediacaran fronds: he interpreted long linear impressions in stalks and branches in some specimens of *Rangea* and *Charnia* as imprints of spicules and based on that and on the external morphology compared them with Pennatulacea. It should be noted that frond-like fossils are now recognized as most widespread and most common Precambrian body fossils, but more often only their attachment discs are known from fossil sites worldwide (see Gehling et al., 2000).

The study of internal structures in the fronds went more detail by examining the material from the Southeastern White Sea area where the organic style of preservation is common in some localities. Steiner and Reitner, 2001 interpreted thin linear pyritized remains as “extremely thin organic walls” rather than pennatulacean spicules but later these remains were re-interpreted as “monaxonic spicule bundles” (Reitner and Wörheide, 2002). These data, coupled with new data on morphology, taphonomy, and modes of growth of Ediacaran fronds (see Seilacher, 1989) raise questions about their being Pennatulacea or even Metazoa, though their possible assignment to the stem group of poriferans had also been discussed (Steiner and Reitner, 2001).

The phylogenetic affinities of the frond-like Petalonamae are not considered now pennatulacean.

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**Fig. 1.** (a) Sketch map showing the location of the collection site in the Southeastern White Sea area. (b) Schematic stratigraphic column of the Upper Vendian (Ediacaran) sequence, Zimnie Gory locality (modified after Stankovsky et al., 1981, Grazhdankin, 2003, Ivantsov et al., 2005). (c) The fossil record of the frond-like *Petalonamae* (with U–Pb zircon dates, Grazhdankin, 2014 and with the dates of the origin and diversification of animals, Erwin et al., 2011).

Unlike the frond-like *Petalonamae* interpreted as firmly attached benthos which having occupied peculiar Precambrian hard-grounds (e.g. Serezhnikova, 2005) in dynamic shallow and deep-water marine environments (Gehling, 1999; Grazhdankin, 2003), most pennatulaceans are actively burrowing animals anchored in the soft muddy or sandy substrate by a muscular peduncle. Precambrian fronds have very different morphology, the symmetry type, and the growth mode compared to modern Pennatulacea (see Seilacher, 1989; Antcliffe and Brasier, 2008); in addition to this, the oldest undisputed fossil pennatulaceans are known only from the early Maastrichtian (see Reich and Kutscher, 2011). Nevertheless, frond-like *Petalonamae* can be assigned to Lower Metazoa and this is not in conflict with the latest paleontological and molecular genetic evidence obtained by Erwin et al., 2011, that support a hypothesis of Precambrian diversification of metazoan phyla suggested by Glaesner, 1962, 1984; Sokolov, 1972, 2012; Fedonkin, 1985; Valentine et al., 1996 and others.

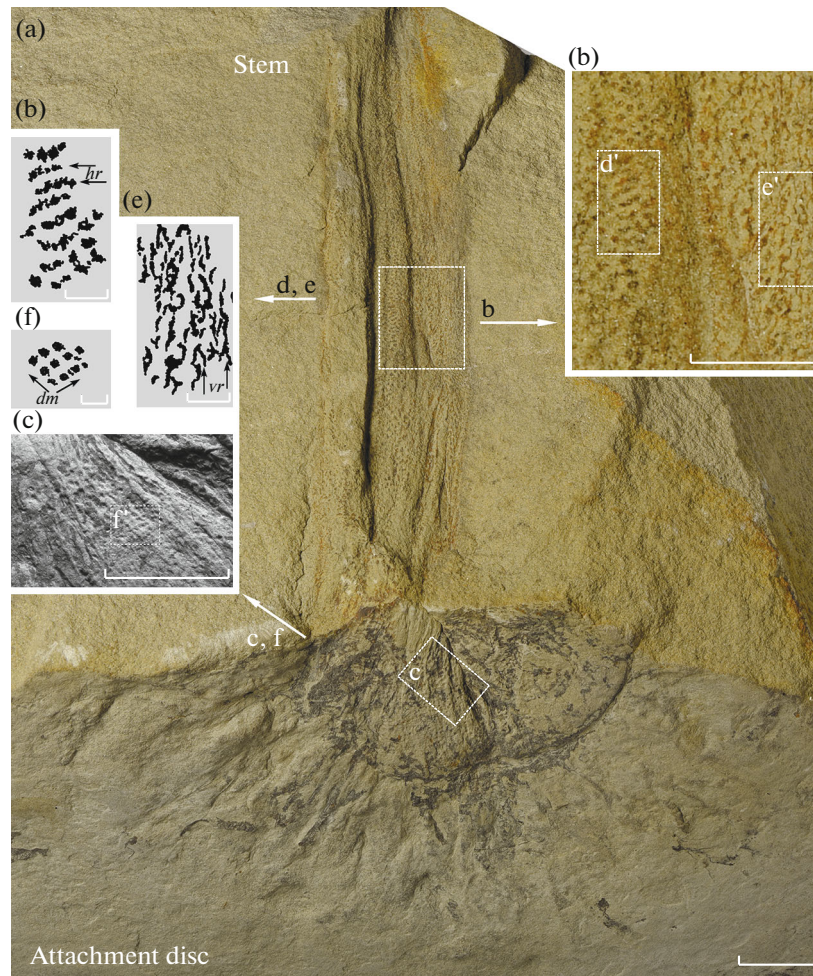
The new finds presented here and reinterpretation of previously published data on the skeletal structures of various frond-like *Petalonamae* from the Vendian of the Southeastern White Sea area may be very

important for understanding the morphology and evolutionary relationships of these most widespread and abundant macrofossils of the Late Precambrian.

### ZIMNIE GORY LOCALITY, THE VENDIAN OF THE SOUTHEASTERN WHITE SEA AREA

The most diverse assemblages of the Ediacara fauna in the Southeastern White Sea area occur in the upper Vendian strata of Zimnie Gory locality (Figs. 1a, 1b). The Late Proterozoic deposits of the region reach up to 550 m in thickness and lie almost horizontally on the crystalline basement of the platform and on the Upper Riphean sediments filling the grabens and deep depressions of the basement; toward the northeast, east, and southeast, the Vendian strata submerge deeply under Paleozoic deposits of the Mezen syncline (see Stankovsky et al., 1981; Aksenov, 1990).

According to Grazhdankin (2003), the Vendian complex of the Southeastern White Sea area is a regressive sequence that was formed in the estuary sea-shore under conditions of progressive northeast progradation of the delta distribution system from the Kanin-Timan fold-and-thrust belt.



**Fig. 2.** *Hiemalora stellaris* (Fedonkin, 1980), specimen PIN, no. 3993/9627; Arkhangelsk Region, Winter Coast of the White Sea; Upper Vendian, Mezen Formation, Lower part of the Erga Beds. (a) Complex imprint of the attachment disc with a stalk. (b, c) Enlarged photographs of the skeletal mesh. (d, e, f) Schematic drawings based on the photographs of the fragments (d; e; f) (*hr*—horizontal rows, *vr*—vertical rows, *dm*—dictyonal mesh). Scale bars, 10 mm (a), 5 mm (b, c), 1 mm (d, e, f).

The main part of the Zimnie Gory section is represented by green-colored and variegated terrigenous marine sediments of the Late Vendian, gently falling south along the coastline. The richest fossiliferous strata (Fig. 1b) dated at about 555.3 Ma (Martin et al., 2000). In general, the strata are quite monotonous, represented by interbedded fine-grained, greenish-gray sandstone, siltstone, and mudstone. There are strata of cross-bedded siltstones and large lenses of sandstone which contain abundant fossils, including frond-like Petalonamae of varying degrees of preservation (Ivantsov, 2016) (Fig. 1b); the assemblage was dominated by *Andiva ivantsovi*, *Arborea arborea*, *Charniodiscus yorgensis*, *Dickinsonia costata*, *D. lissa*, *Kimberella quadrata*, *Tribrachidium heraldicum*, *Yorgia waggoneri*.

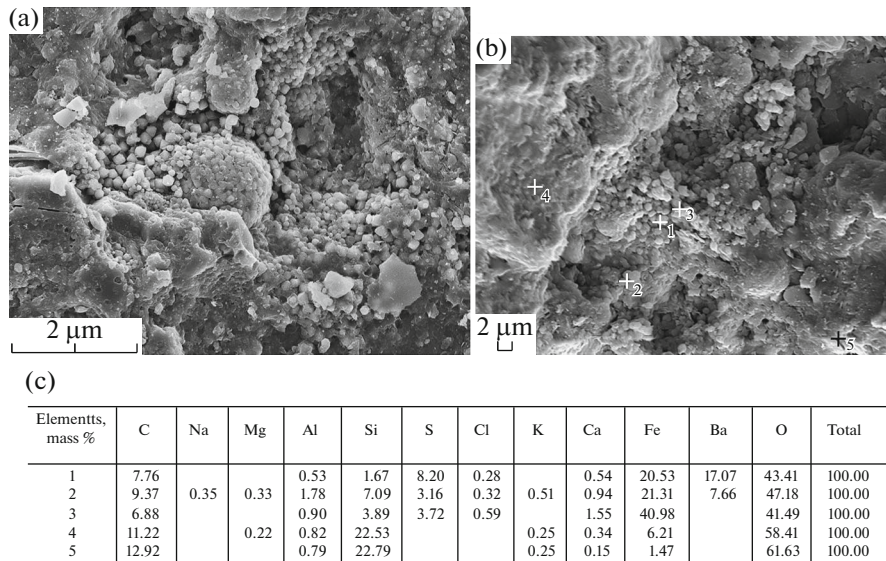
The material was collected by A. Ivantsov and staff of Belomorian field group, Precambrian Laboratory, PIN RAS during several field trips in the 2000s. The collection is housed at the Paleontological Institute RAS (PIN, no. 3993).

#### SKELETAL ELEMENTS OF THE FROND-LIKE PETALONAMAE FROM ZIMNIE GORY LOCALITY

##### *Organisms Possessing Root-Like Basal Discs of Hiemalora stellaris (Fedonkin, 1980)*

**Morphology of the fossils.** The specimen is preserved as a composite imprint of both the attachment disc on the bedding plane and the vertical stem within a massive medium-grained sandstone; the remains of the stem consist of cast and counterpart on the cross section perpendicular to the bedding planes; the fossil and sediment surface is locally covered with thin pyritic crust (Fig. 2).

The lower part of the attachment disc is differentiated into two zones. The central zone is rounded (about 45 mm in diameter) and has a negative relief; its margin is bordered by a shallow furrow about 1–2 mm wide. Numerous radial offshoots up to 40 mm in length spread out evenly around the central zone,



**Fig. 3.** *Hiemalora stellaris* (Fedonkin, 1980), specimen PIN, no. 3993/9627; Arkhangelsk Region, Winter Coast of the White Sea; Upper Vendian, Mezen Formation, Lower part of the Erga Beds. (a, b) Stalk microstructure, scanning electron microscope (SEM) images (Tescan Vega SEM (a), Leiss EVOSO with the microprobe Oxford INCA (Energy 350) (b), figures show microprobe sites). (c) Element composition of the stalk fragment.

occasionally crossing each other; the offshoots are gently curved and become very narrow at the ends (maximum width 1 mm).

The stem is generally straight, 160 mm long with an average width 20 mm. A remarkable feature of the stem is a set of delicate linear stripes (<0.1 mm broad) along its surface consisting of dark organic matter completely replaced by framboidal pyrite with rough outlines or hair-like in appearance; the distance between adjacent stripes is about 0.2 mm (Figs. 2b, 2c, 2e). The surface of the stem and the central disc is densely covered with minute depressions some of which are marked by thin pyrite crusts (Figs. 2c, 2d, 2f); in the low-relief parts, on the contrary, the pyrite crusts are preserved as small arcs around light spots (Figs. 2b, 2e). There are rare areas where the dark or light depressions are rather regularly arranged forming a fine network of longitudinal and transverse rows (Figs. 2c, 2f). The shape of the depressions ranges from near round and oval to square and rectangular, obviously, depending on the degree of deformation; their diameter may vary from 0.2 to 0.4 mm. The depressions are separated from each other by flat areas; the distance between the centers of the adjacent ones may be up to 0.5–0.7 mm or less, so that some depressions seem to be merged.

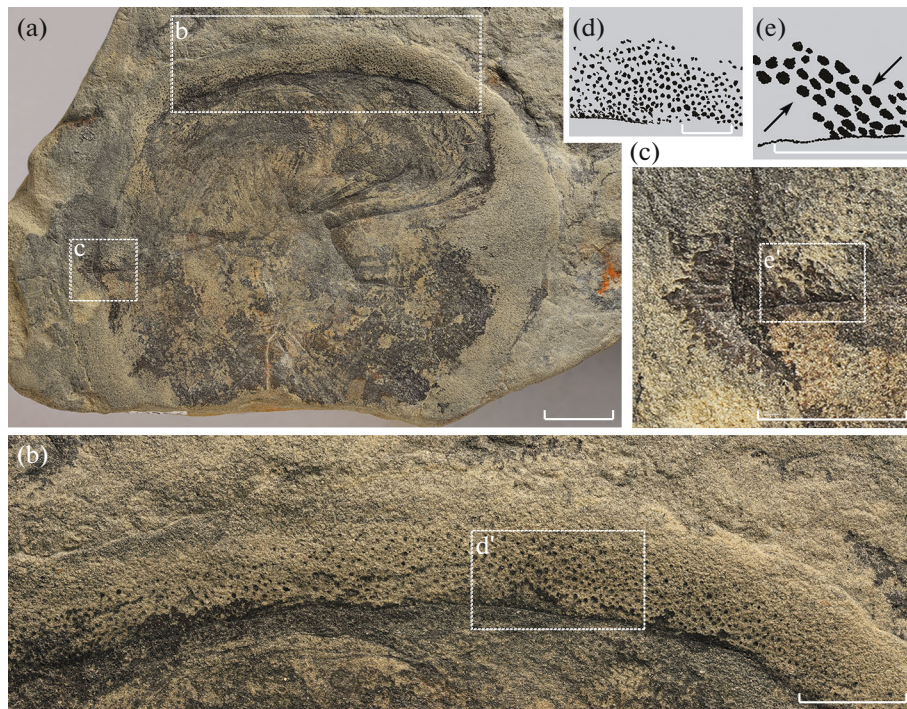
**Microstructure and chemical composition.** No evidence of original organic or mineral matter was found using scanning electron microscopy and X-ray chemical microanalysis. An examination of the least weathered part of the specimens, a stalk fragment extending from the attachment disc, shows that it is composed of small globules of iron oxide combined with rather large spheroidal aggregates (framboids) of pyrite up to

10 µm in size (Figs. 3a–3c). The examination was performed by L.V. Zaitseva using SEM Leiss EVO50 with an Oxford INCA (Energy 350) microprobe and E.A. Zhegalov using SEM Tescan Vega (PIN RAS).

*Organisms Possessing Discoid Basal Discs  
of Genera Protodipleurosoma Sprigg, 1949  
and Ediacaria Sprigg, 1947*

**Morphology of the fossils.** The specimens are preserved on the bedding plane of a massive medium-grained sandstone as composite imprints of the attachment discs with relatively low relief; the surface of the fossils and sediment are partly covered with iron oxides and sulphate incrustations.

***Protodipleurosoma wardi* Sprigg, 1949**, specimen PIN, no. 3993/6566, is oval in shape with two concentric zones and has biradial symmetry; the imprint is slightly concave in the center and convex on the periphery; the maximum dimension is about 75 × 60 mm (a small fragment of the fossil is lost); the outer zone is about 7–10 mm in width (Fig. 4a). Within the central part of the imprint, there are many thin radial wrinkles and a few larger ones, which are irregularly located and curved towards the outer zone; the distance between the adjacent thin wrinkles is about 0.2 mm or less. Some parts of the surface of the specimen bears numerous small round or oval depressions 0.2 mm in diameter (Figs. 4b, 4d) which sometimes form a rather regular pattern (Figs. 4c, 4e); all the structures are accentuated by the presence of the pyritic crust which covers the most part of the central area of the specimen. The outer zone is, on the contrary, of a light



**Fig. 4.** *Protodipleurosoma wardi* Sprigg, 1949, specimen PIN, no. 3993/6566; Arkhangelsk Region, Winter Coast of the White Sea; Upper Vendian, Mezen Formation. (a) Attachment disc. (b, c) Enlarged photographs of the skeletal mesh, (d, e) Schematic drawings based on the photographs of the fragments d' and e' (*dr*—rows of dimples). Scale bars, 10 (a), 5 (b, c), 2.5 mm (d, e).

color, and the dark pyritic crusts are commonly located in the depressions.

***Ediacaria flindersi* Sprigg, 1947**, specimen PIN, no. 3993/9680 is bizonal with rounded outlines; its inner zone is biradially symmetrical and more concave (especially in the center) than the outer one which has radial symmetry; the whole imprint is about 90 mm in diameter, the outer zone is up to 20 mm in width; the surface is locally encrusted with iron oxides, especially in the center of the imprint (Fig. 5). The surface of the fossil is covered with various radial structures of low relief; they are almost straight in the middle of the central part where they are not abundant and not evenly spaced (Figs. 5a, 5c), whilst toward the periphery the structures become denser (up to 3–4 per cm) and thinner, sometimes forming an irregular mesh of cells with the size of 0.2–0.5 mm (Fig. 5b). The outer zone possess some rough concentric ridges (0.1–0.5 mm in thickness) covered with thick pyritic crust; they are unevenly spaced on the surface commonly occurring in groups with a minimum distance of 0.2 mm between adjacent ones (Fig. 5d).

#### A COMPARATIVE MORPHOLOGY OF THE SKELETON

The body plans of frond-like Petalonamae are difficult to compare with Phanerozoic archetypes, but since the observations of their morphology and ecology

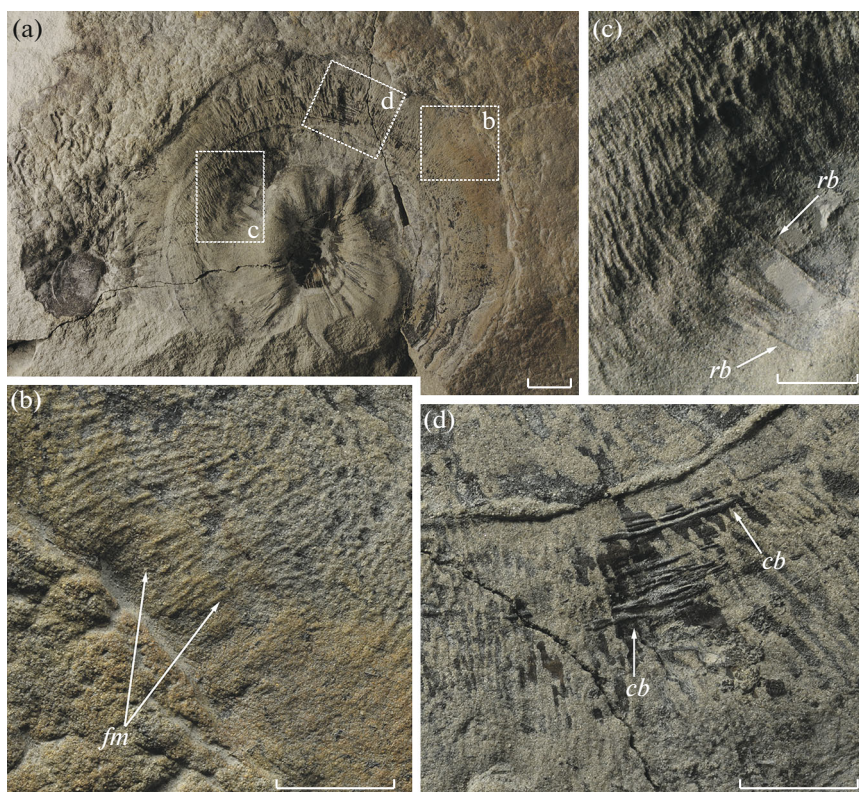
rather support the interpretation of their affinity with animals we will find comparison among Metazoa.

#### *Structure of the Skeleton*

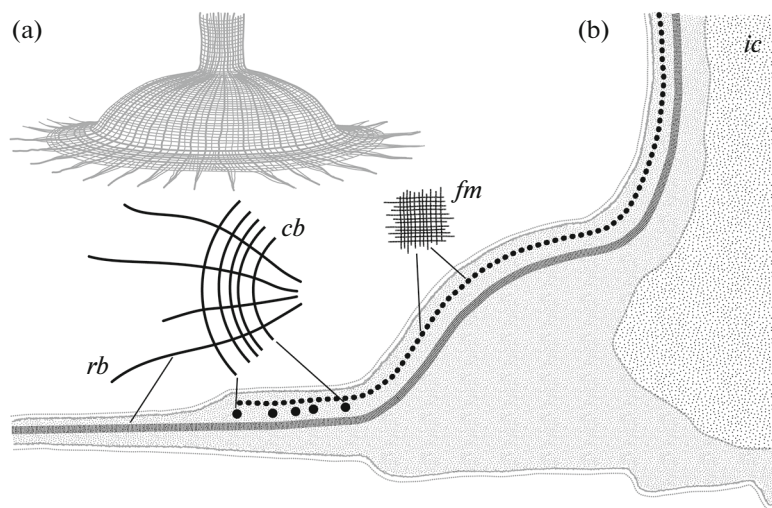
Generally, the frond-like Petalonamae show evidence of various skeletal elements including delicate nets and relatively dense concentric and radial bands (Fig. 6). The skeleton of a stem of the frond-like Petalonamae can be reconstructed as a thin-walled hollow cylinder. The surface of the cylinder consists of a regular meshwork composed of a series of tiny vertical and horizontal bundles, which were reinforced by relatively dense longitudinal bands (restored based on the specimen of *Hiemalora*; the stems of *Protodipleurosoma* and *Ediacaria* seem to have the same structure, judging from the similarities in the appearance of their basal discs). The discoid basal discs are additionally strengthened by rough concentric bands, which are sometimes zonally arranged.

It should be noted, that Jenkins and Gehling, 1978 have reconstructed a “spicular supportive devices in the polyp-leaves” in the holotype of *Charniodiscus oppositus*.

Supporting structures including netlike meshes and long spicules and bands are quite common for the skeletons of Parazoa, but such a combination of skeletal elements, as were described in the frond-like Petalonamae are not typical of the Phanerozoic Lower Metazoa.



**Fig. 5.** *Ediacaria flindersi* Sprigg, 1947; specimen PIN, no. 3993/9680; Arkhangelsk Region, Winter Coast of the White Sea; Upper Vendian, Mezen Formation, Lower part of the Erga Beds. (a) Attachment disc. (b, c, d) Enlarged photographs of the skeletal elements (*rb*—radial bands, *cb*—concentric bands, *fm*—filamentous mesh). Scale bars, 10 (a), 5 mm (b, c, d).



**Fig. 6.** Sketch reconstruction of the supporting structure of the frond-like Petalonamae. (a) General view (based on the reconstruction of *Palaeophragmodictya reticulata* Gehling, Rigby, 1996). (b) Anatomical drawing of the attachment disc, skeletal elements are enlarged (*ic*—internal cavity; other acronyms are the same as in Fig. 5).

#### *Composition of the Skeleton*

Neither organic nor mineral structures that can be of biochemical origin are observed in the imprints of the fossils. The original tissues are lost or replaced by framboidal pyrite and iron oxides, even in the best-

preserved specimens. Judging from the nature of post-mortem deformations and the dynamics of the environment, the frond-like Petalonamae had a relatively rigid but flexible skeletal matter that allowed these organisms to create delicate and elaborate structures.

Based on these observations it can be argued that the skeleton of fronds could be made of spongin, opaline silica, calcium carbonate, chitin, each of which occurs commonly in Lower Metazoa. A presence of mineral matter appears probable but the hard components could have been dissolved during early diagenesis, in the same way as suggested earlier by Gehling and Rigby (1998, after Steiner 1993), Clites et al. (2012) and others. It is noteworthy that in anoxic environments such as that reconstructed for the Late Proterozoic (Schröder and Grotzinger, 2007), mineral components dissolve particularly quickly (see Yanin, 1983 for references).

#### *Reticulation*

The stems and attachment discs of frond-like *Petalonamae* show fine structures with a lattice-like pattern of longitudinal and transverse bundles (the regularity is not observed in some cases, which may be due to post-mortem deformation). There is no direct evidence of reticulation in the frond-like extensions, but it should be noted that the “cells” (or “pustules”) of much the same size sometimes arranged in rows (“linear arrays”) are described on the branches of *Thaumaptilon* from the Middle Cambrian Burgess Shales of Canada; these structures were considered to represent zooids although with no evidence for tentacles or other substructure (see Conway-Morris, 1993). According to our reconstruction, the skeleton of frond-like *Petalonamae* could probably be porous; the appearance of their skeletal mesh is very similar to that of some sponges; the size and pattern of the “cells” also resemble those of some archaeocyathids. The porosity is a common feature in many taxa of Lower Metazoa including colonial ones. Porous structure and the ability to a suspension feed have been suggested for a few Ediacaran taxa (e.g. Gehling and Rigby, 1996; Fedonkin et al., 2012; Sperling et al., 2011). A porosity in frond-like *Petalonamae* appears probable and it is suggested that these organisms may be suspension feeders. It is not possible, however, to conclusively determine their feeding strategy.

#### *Internal Cavity*

The stem of the fronds was likely to have been hollow so that the cavity has become filled with sand either during life or immediately after death (see Serezhnikova, 2005; Vickers-Rich et al., 2013 and others). The organically cemented sand may serve as “anchor” for increased stability as has been suggested for *Psammodorallia*, which is a mixed group of problematical fossils from the Vendian, Lower Cambrian and Upper Ordovician (see Seilacher, 1992).

In any case, the presence of perforations in the walls of *Petalonamae* could have allowed sand to penetrate into the cavity of their bodies. The internal (paragastral, gastral) cavity is a characteristic feature

of sponges and coelenterates (e.g. Dogel', 1975). The exact biology and physical properties of the cavity in *Petalonamae* remain unclear as yet.

#### *Growth Form*

As the largest specimens exhibit the most number of the skeletal elements, both radial and concentric (the growth pattern of discs was described by Serezhnikova (2005, 2007), there is a strong possibility that the frond-like *Petalonamae* grew by adding new skeletal units at the base. The arrangement of the concentric structures shows zones of different kinds, which could represent life rhythms of the organisms, in some cases possibly responses to environmental fluctuations; these zones grew outward from a center of the attachment disc and increased in width with age (for plots, see above-cited references). Due to the paucity of data, it is not possible as yet, to determine the growth pattern of the netlike mesh (the large specimens are the only ones where the meshes are clearly preserved). It should be noted, that the upper parts of the fronds grew by inserting new branches at the apex, while existing branches continued to grow (Antcliffe and Brasier, 2008; for a review of new data on fronds branching see Hoyal Cuthill and Conway Morris, 2014. An apical position of the generative zone is typical of a variety of colonial animals (see Marfenin, 1993); concentric zones, denser and clearer bands alternating with one another are common in coelenterates but similar concentric striation is seen in other groups of organisms too.

### NOTES ON THE SYSTEMATIC POSITION OF EDIACARAN FRONDS AND SCLEROTIZATION DURING THE PRECAMBRIAN

In general, based on the observation of supporting structures of frond-like *Petalonamae* we are tempted to assign them to a basal group of Sponges, Lower Metazoa. However, the elaborate construction of the attachment discs and fronds suggests a level of organization higher than that in modern Sponges. It has led to the conclusion that frond-like *Petalonamae* combine features of Parazoa and colonial coelenterates. It has something in common with Pflug's opinion that “*Petalonamae* organisms of the Lower Vendian” may be considered “as an evolutionary stage preceding the separation of Metazoa and Metaphyta” (Pflug 1974, p. 328). But according to recent data, this happened much earlier (Knoll, 2003).

It is intriguing, that according to data from genomics and proteomics, supposed Precambrian ancestral metazoans should have had a complex genetic toolkit (Müller, 2007). Recent studies have revealed that the last common ancestor of sponges had to possess a much more diverse repertoire of DTFs (Developmental transcription factors) than extant sponges (Fortu-

nato et al., 2015). It may support the idea that morphological complexity of modern Lower Metazoans appeared to decrease as compared to the last common ancestor of all animals. The authors cited above found also that their study confirmed the hypothesis of Ernst Haeckel who proposed a direct relationship between body plans of calcareous sponges and cnidarian polyps. Interestingly, these groups would once have been united in the taxon of higher rank, Cladus Bush-animals (Haeckel, 1870). Perhaps frond-like Petalonamae would be recognized as members of this “Cladus” if they could be known at that time.

Recent fossil finds help to confirm a hypothetical complexity of ancient Lower Metazoa: ctenophores described from the Chengjiang biota (Lower Cambrian of South China) are “sclerotized and armored” (Ou et al., 2015), whereas modern ctenophores are exclusively soft-bodied organisms. In classical zoology, keratinous and soft-bodied taxa of sponges, for example, are considered as secondary (Dogel', 1975), but their exact phylogenetic position is still being controversial (see Wörheide et al., 2012 and others) and need to be tested by paleontological records.

It is remarkable that frond-like Petalonamae had a support structure similar to that of sponges and cnidarians. These problematic fossils can, therefore, be confidently assigned to Lower Metazoa (which agrees with Glaessner (1984), Fedonkin (1985) and many others).

The theory of “initial morphological diversity” suggested by Mamkaev (1986) may help to explain the enigmatic “blurred” body plan of some Ediacaran groups, which show features of superphyla; such a scenario is suggested for periods of the early evolution of higher rank taxa. We can draw a parallel with problematic short-lived groups: archaeocyaths, radiocyathids, anabaritids, and many others, which can be as difficult to compare with modern taxa as the members of Ediacara fauna.

Revisiting the morphology of the Ediacaran fronds we have shown that the widespread occurrence of skeletonization was long before the “Cambrian skeletal revolution” (Fig. 1c). Whether the skeletonized fossil Lower Metazoans were evolutionarily primitive or derived remains a question for the future.

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#### REFERENCES

- Aksenov, E.M., Vendian of the East European Platform, *The Vendian System*, Vol. 1: *Regional Geology*, Sokolov, B.S. and Fedonkin, M.A., Eds., Berlin: Springer, 1990, pp. 1–37.
- Antcliffe, J.B. and Brasier, M.D., *Charnia* at 50: Developmental models for Ediacaran fronds, *Palaeontology*, vol. 51, pp. 11–26.
- Clites, E.C., Droser, M.L., and Gehling, J.G., The advent of hard-part structural support among the Ediacara biota: Ediacaran harbinger of a Cambrian mode of body construction, *Geology*, 2012, vol. 40, no. 4, pp. 307–310.
- Conway Morris, S., Ediacaran-like fossils in Cambrian Burgess Shale-type faunas of North America, *Palaeontology*, 1993, vol. 36, Pt. 3, pp. 593–635.
- Dogel', V.A., *Zoologiya bespozvonochnykh* (Invertebrate Zoology), Moskva: Vysshaya shkola, 1975 (in Russian).
- Dunn, F.S. and Liu, A.G., and Donoghue, Ph.C.J., Ediacaran developmental biology, *Biol. Rev.*, 2018, vol. 93, pp. 914–932.
- Erwin, D.H., LaFlamme, M., Tweedt, S.M., Sperling, E.A., Pisani, D., and Peterson, K.J., The Cambrian Conundrum: Early divergence and later ecological success in the early history of animals, *Science*, 2011, vol. 334, pp. 1091–1097.
- Fedonkin, M.A., Sistematischeskoe opisaniye vendskikh Metazoa, in *Vendskaya Sistema. Istoriko-Geologicheskoe i Paleontologicheskoe Obosnovanie*, Tom 1: *Paleontologiya*, Sokolov, B.S. and Ivanovskii, A.B., Eds., Moskva: Nauka, 1985, pp. 70–106 (in Russian).
- Fedonkin, M.A., Gehling, J.G., Grey, K., Narbonne, G.M., and Vickers-Rich, P., *The Rise of Animals: Evolution and Diversification of the Kingdom Animalia*, Baltimore: Johns Hopkins Univ. Press, 2007.
- Fedonkin, M.A., Vickers-Rich, P., Swalla, B.J., Trusler, P., and Hall, M., A New Metazoan from the Vendian of the White Sea, Russia, with possible affinities to the ascidians, *Paleontol. J.*, 2012, vol. 46, pp. 1–11.
- Fortunato, S.A.V., Adamski, M., and Adamska, M., Comparative analyses of developmental transcription factor repertoires in sponges reveal unexpected complexity of the earliest animals, *Mar. Genomics*, 2015, vol. 24, pp. 121–129.
- Gehling, J.G. and Rigby, J.K., Long expected sponges from the neoproterozoic Ediacara fauna of South Australia, *J. Paleontol.*, 1996, vol. 70, pp. 185–195.
- Gehling, J.G., Microbial mats in terminal proterozoic siliciclastics: Ediacaran death masks, *Palaios*, 1999, vol. 14, pp. 40–57.
- Gehling, J.G., Narbonne, G.M., and Anderson, M.M., The first named Ediacaran body fossil, *Aspidella teranovica*, *Palaeontology*, 2000, vol. 43, pp. 427–456.
- Glaessner, M.F., Precambrian fossils, *Biol. Rev.*, 1962, vol. 37, pp. 467–494.



- Glaessner, M.F., *The Dawn of Animal Life*, Cambridge: Cambridge Univ. Press, 1984.
- Grazhdankin, D., Patterns of evolution of the Ediacaran soft-bodied biota, *J. Paleontol.*, 2014, vol. 88, pp. 269–283.
- Grazhdankin, D.V., Structure and depositional environment of the Vendian complex in the southeastern White Sea Area, *Stratigr. Geol. Correl.*, 2003, vol. 11, pp. 313–331.
- Haeckel, E., On the organization of sponges and their relationship to the corals, *Ann. Mag. Nat. Hist.*, 1870, vol. 5, no. 25, pp. 1–13; vol. 5, no. 26, pp. 107–120.
- Hoyal Cuthill, J.F. and Conway Morris, S., Fractal branching organizations of Ediacaran rangeomorph fronds reveal a lost proterozoic body plan, *Proc. Natl. Acad. Sci. U. S. A.*, 2014, vol. 111, pp. 13122–13126.
- Ivantsov, A.Yu., Reconstruction of Charniodiscus yorgensis (macrobiota from the Vendian of the White Sea), *Paleontol. J.*, 2016, vol. 50, no. 1, pp. 1–12.
- Ivantsov, A.Yu., Leonov, M.V., Serezhnikova, E.A., and Malakhovskaya, Ya.E., Localities of imprints of Late Vendian Metazoa in southeastern White Sea area (Arkhangelsk region), *Technical Report*, 2005 (in Russian).
- Jenkins, R.J.F. and Gehling, J.G., A review of the frond-like fossils of the Ediacara assemblage, *Records of the South Australian Museum*, 1978, vol. 17, pp. 347–359.
- Knoll, A.H., Biomineralization and evolutionary history, *Rev. Mineral. Geochem.*, 2003, vol. 54, pp. 329–356.
- Kouchinsky, A., Bengtson, S., Runnegar, B., Skovsted, C., Steiner, M., and Vendrasco, M., Chronology of Early Cambrian biomineralization, *Geol. Mag.*, 2012, vol. 149, pp. 221–251.
- Lowenstam, H.A. and Margulis, L., Evolutionary prerequisites for early Phanerozoic calcareous skeletons, *BioSystems*, 1980, vol. 12, pp. 27–41.
- Mamkaev, Yu.V., Initial morphological diversity as a criterion in deciphering turbellarian phylogeny, *Hydrobiologia*, 1986, vol. 132, pp. 31–33.
- Marfenin, N.N., *Phenomen kolonial'nosti* (The Phenomenon of Coloniality), Moskva: Izdatel'stvo Moskovskogo Universiteta (MGU), 1993 (in Russian).
- Martin, M.W., Grazhdankin, D.V., Bowering, S.A., Evans, D.A.D., Fedonkin, M.A., and Kirshvink, J.L., Age of Neoproterozoic bilaterian body and trace fossils, White Sea, Russia: Implications for Metazoan evolution, *Science*, 2000, vol. 288, pp. 841–845.
- Müller, W.E.G., Li, J., Schröder, H.C., Qiao, L., and Wang, X., The unique skeleton of siliceous sponges (Porifera; Hexactinellida and Demospongiae) that evolved first from the Urmethozoa during the Proterozoic: A review, *Bio-geosciences*, 2007, vol. 4, pp. 219–232.
- Ou, Q., Xiao, S., Han, J., Sun, G., Zhang, F., Zhang, Z., and Shu, D., A vanished history of skeletonization in Cambrian comb jellies, *Sci. Adv.*, 2015, vol. 1, e1500092.
- Pflug, H.D., Vor- und Frühgeschichte der Metazoen, *Neues Jahrb. Geol. Palaeontol., Abh.*, 1974, Bd. 145, pp. 328–374.
- Reich, M. and Kutscher, M., Sea Pens (Octocorallia: Penatulacea) from the Late Cretaceous of Northern Germany, *J. Paleontol.*, 2011, vol. 85, pp. 1042–1051.
- Reitner, J. and Wörheide, G., Non-Lithistid fossil Demospongiae—Origins of their palaeobiodiversity and highlights in history of preservation, *Systema Porifera: A Guide to the Classification of Sponges*, Hooper, J.N.A. and Van Soest, R.W.M., Eds., Dordrecht: Kluwer Acad. Plenum Publ., 2002, pp. 52–68.
- Schröder, S. and Grotzinger, J.P., Evidence for anoxia at the Ediacaran–Cambrian boundary: the record of redox-sensitive trace elements and rare earth elements in Oman, *J. Geol. Soc.*, 2007, vol. 164, pp. 175–187.
- Seilacher, A., Vendozoa: organismic constructions in the Proterozoic biosphere, *Lethaia*, 1989, vol. 22, pp. 229–239.
- Seilacher, A., Grazhdankin, D., and Legouta, A., Ediacaran biota: the dawn of animal life in the shadow of giant protists, *Paleontol. Res.*, 2003, vol. 7, pp. 43–54.
- Seilacher, A., Vendobionta and Psammocorallia: lost construction of Precambrian evolution, *J. Geol. Soc. (London, U. K.)*, 1992, vol. 149, pp. 607–613.
- Serezhnikova, E.A., *Palaeophragmodictya spinosa* sp. nov., a bilateral benthic organism from the Vendian of the southeastern White Sea region, *Paleontol. J.*, 2007, vol. 41, pp. 360–369.
- Serezhnikova, E.A., Skeletogenesis in Problematic Late Proterozoic Lower Metazoa, *Paleontol. J.*, 2014, vol. 48, pp. 1457–1472.
- Serezhnikova, E.A., Vendian *Ediacaria* from the Zimnii Bereg Locality of the White Sea: New records and new reconstructions, *Paleontol. J.*, 2005, vol. 39, pp. 386–394.
- Sokolov, B.S., *Vendskii etap v evolyutsii zemli, Mezhdunarodnyi Geologicheskii Kongress, 24 Sessiya, Doklady Sovetskikh Geologov. Problema 7, Paleontologiya*, Moskva: Nauka, 1972, pp. 114–124 (in Russian).
- Sokolov, B.S., Precambrian paleontology and acrochrons of the biosphere evolution: On the theory of the expanding biosphere, *Stratigr. Geol. Correl.*, 2012, vol. 20, no. 2, pp. 115–124.
- Sperling, E.A., Peterson, K.J., and LaFlamme, M., Rangeomorphs, Thectardis (Porifera?) and dissolved organic carbon in the Ediacaran oceans, *Geobiology*, 2011, vol. 9, pp. 24–33.
- Stankovsky, A.F., Verichev, E.M., Grib, V.P., and Dobenko, I.P., Vend yugo-vostochnogo Belomor'ya, *Izvestiya Akademii Nauk SSSR, Seriya Geologicheskaya*, 1981, vol. 2, pp. 78–87.
- Steiner, M. and Reitner, J., Evidence of organic structures in Ediacara-type fossils and associated microbial mats, *Geology*, 2001, vol. 29, pp. 1119–1122.
- Steiner, M., Mehl, D., Reitner, J., and Erdtman, B.-D., Oldest entirely preserved sponges and other fossils from the lowermost Cambrian and a new facies reconstruction for the Yangtze platform (China), *Berl. Geowiss. Abh. (E)*, 1993, vol. 9, pp. 293–329.
- Valentine, J.W., Erwin, D.H., and Jablonski, D., Developmental evolution of metazoan bodyplan: The fossil evidence, *Develop. Biol.*, 1996, vol. 173, pp. 373–381.
- Vickers-Rich, P., Ivantsov, A.Yu., Trusler, P.W., Narbonne, G.M., Hall, M., Wilson, S.A., Greentree, C., Fedonkin, M.A., Elliott, D.A., Hoffmann, K.H., and Schneider, G.I.C., Reconstructing Rangea: New discoveries from the Ediacaran of southern Namibia, *J. Paleontol.*, 2013, vol. 87, pp. 1–15.
- Wörheide, G., Dohrmann, M., Erpenbeck, D., Larroux, C., Maldonado, M., Voigt, O., Borchellini, C., and Lavrov, D.V., Deep phylogeny and evolution of sponges (phylum Porifera), *Adv. Mar. Biol.*, 2012, vol. 61, pp. 1–78.
- Xiao, S. and Laflamme, M., On the eve of animal radiation: phylogeny, ecology and evolution of the Ediacara biota, *Trends Ecol. Evol.*, 2009, vol. 24, pp. 31–40.
- Yanin, B.T., *Osnovy tafonomii* (Fundamentals of Taphonomy), Moskva: Nedra, 1983.