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The last jellyfish of the Precambrian

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ABSTRACT: The late Precambrian is traditionally considered the time of the flourishing of coelenterates *sensu lato*. Many dozens of fossil taxa from late Ediacaran (Vendian) deposits were interpreted as morphologically diverse jellyfishes. However, a progress in paleontological studies of the Precambrian biota allows us to short significantly the list of presumable cnidarians. Firstly, a number of them is recognized as various taphonomic variations. Secondly, intact attachments of these so-called jellyfishes to the substratum and their associations with stems of frond-like petalonamids are established. At present, *Staurinidia crucicula* Fedonkin, 1985 is suggested to be the only jellyfish of the late Precambrian. Here, we analyze in details morphological features of *Staurinidia*. This observation allows us to affiliate this fossil to cnidarians due to presence of elongated tentacles surrounding massive body and a radially branching gastrovascular system with a single central oral opening. In turn, a presence of the tetraradial symmetry, rounded, low and wide body shape and a branched, relatively small gastric cavity as well as the absence of a stem and theca hint to the affinities of this fossil with the scyphomedusae. The restriction of the fossil itself to a burial event horizon of the Flinders-Belomorian style indicates a benthic lifestyle of this Precambrian jellyfish.
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KEY WORDS: Late Precambrian, Ediacaran, Vendian, southeastern White Sea, Cnidaria, Scyphozoa, *Staurinidia*.

Последняя медуза докембрия

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РЕЗЮМЕ: Поздний докембрий традиционно считался временем расцвета кишечнополостных организмов. Многие десятки ископаемых таксонов из отложений позднего эдиакария (венда) интерпретировались как разнообразные по морфологии медузы. Однако прогресс в палеонтологических исследованиях докембрийских биот позволил кардинально сократить списки потенциальных книдарий. Во-первых, выявлено, что многие их них являются тафономическими вариациями. Во-вторых, установлено прикрепленное прижизненное положение таких «медуз» и их принадлежность к прикрепительным дискам у стеблей перовидных петалонам. В итоге, к настоящему времени единственной вероятной медузой позднего докембрия осталась *Staurinidia crucicula* Fedonkin, 1985. Здесь мы подробно анализируем морфологические особенности *Staurinidia*. Совокупность наблюдаемых морфологических признаков

Devoted to memory of Claus Nielsen.

ставринидии, включая массивное тело, окруженное венчиком вытянутых щупалец, внутреннюю разветвленную радиально-симметричную гастроваскулярную систему и центральное ротовое отверстие, позволяет отнести этот ископаемый организм к книдариями. Более того, четырехлучевая радиальная симметрия, округлое, низкое и широкое тело и разветвленная, сравнительно небольшая по объему гастральная полость при отсутствии стебелька и теки предполагает ее принадлежность к сцифомедузам. Приуроченность ископаемых остатков ставринидии к событийным захоронениям флиндерско-беломорского стиля свидетельствует о бентосном образе жизни этой докембрийской медузы.

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КЛЮЧЕВЫЕ СЛОВА: поздний докембрий, эдиакарий, венд, Юго-Восточное Беломорье, Cnidaria, Scyphozoa, *Staurinidia*.

Introduction

According to molecular clock data, cnidarians had a common ancestor with bilaterians and diverged from them in the late Precambrian. Estimated time of this event varies, mostly ranging from the Cryogenian to the early Ediacaran (Vendian) (Peterson, Butterfield, 2005; Peterson *et al*., 2008; Erwin *et al*. 2011; Van Iten *et al*., 2014; dos Reis *et al*. 2015). The first diversification of cnidocytes probably occurred in the Ediacaran period (Sierra and Gold, 2024). However, in the fossil record, macroscopic remains of putative crown-group cnidarians appear only in the late Ediacaran, about 560 million years ago (Ma) (Liu *et al*., 2014; Dunn *et al*., 2022; McIllroy *et al*., 2024). Such a significant delay is explained by both the incompleteness of the fossil record and the difficulty of recognition of stem taxa. It was traditionally suggested that the end of the Ediacaran was the time of the flourishing of coelenterates *sensu lato* as some of the simplest metazoans (e.g., Fedonkin, 1985). Both early publications and general reconstructions of Ediacaran biotas of the second half of the 20th century showed a lot of different jellyfishes (e.g., Sprigg, 1949; Jenkins, 1992, fig. 10). They also show a large number of organisms with a frond-like body, which were interpreted as colonial polyps similar to modern pennatularians (Glaessner, Wade, 1966), or as peculiar sessile ctenophores (Dzik, 2002). However, by the end of the 20th century it became clear that almost all jellyfish-like fossils of the Precambrian are attachment discs of frond-like petalonamids. Moreover, almost all the diversity of round discs with smooth margins can be reduced to one formal genus *Aspidella* (Gehling *et al*., 2000). The scale of the forthcoming revision is demonstrated by Table 1, which contains probable synonyms of *Aspidella terranovica* (Fig. 1). Less numerous discs with marginal outgrowths (*Hiemalora*, *Eoporpita*, *Palaeophragmodictya*, etc.) can also be reduced to several genera and correlated to the petalonamids as well (Figs 2, 3). For example, it was established that *Hiemalora*, the disc with “tentacles”, was an attachment structure of a complex branched tree-like structure called *Primocandelabrum hiemaloranum* (Hofmann *et al*., 2008).

Petalonamids themselves (Petalonamae Pflug, 1972) constitute a large extinct taxon of high rank (phylum?), the position of which in the system of Metazoa is not determined. These are radially symmetrical organisms, but their body plan is peculiar. The body organization of petalonamae is chartracterized by axes of radial symmetry of the 3rd or 6th order and planes of sliding reflection (Ivantsov, Zakrevskaya, 2021). In fossil remains of petalonamids, it is impossible to identify the presence of individual zooids, a gastric cavity, tentacles, and even more so, cilia and cnidas. Therefore, it is not possible to classify them as cnidarians, ctenophores or any other extinct phylum of coelenterates *sensu lato*, i.e. animals that have a gastric cavity.

However, among minor groups in fossil communities of Ediacaran macroorganisms, probable remains of cnidarians have recently been identified. And quite a few such finds have already been made. Some of these fossils (*Auroralumina*, *Haootia*, *Mamsetia*) are interpreted as body impressions of medusozoan polyps and staurozoans (Liu *et al*., 2014; Dunn *et al*., 2022;

Table 1. List of fossil species of “jellyfishes”, probable synonyms of the attachment structure, *Aspidella terranovica* Billings, 1872.

1. *Askinica dimerus* Bekker, 1996
2. *Aspidella costata* Vodanjuk, 1989
3. *Aspidella hatyspytia* Vodanjuk, 1989
4. *Barmia lobatus* Bekker, 1996
5. *Beltanella gilesi* Sprigg, 1947
6. *Beltanella velikania* Menasova, 2003
7. *Bonata septata* Fedonkin, 1980
8. *Brachina delicata* Wade, 1972
9. *Charniodiscus concentricus* Ford, 1958
10. *Charniodiscus planus* Sokolov, 1972
11. *Cocardia valerii* Grytsenko, 2016
12. *Cyclomedusa davidi* Sprigg, 1947
13. *Cyclomedusa delicata* Fedonkin, 1981
14. *Cyclomedusa gigantea* Sprigg, 1949
15. *Cyclomedusa leonidi* Grytsenko, 2016
16. *Cyclomedusa minuta* Fedonkin, 1981
17. *Cyclomedusa radiata* Sprigg, 1947
18. *Cyclomedusa plana* Glaessner et Wade, 1966
19. *Cyclomedusa serebrina* Palij, 1969
20. *Ediacaria flindersi* Sprigg, 1947
21. *Elasenia uralica* Bekker, 1996
22. *Elasenia zhuravlevae* Gureev, 1988
23. *Evmiaksia aksionovi* Fedonkin, 1984
24. *Garania petali* Bekker, 1996
25. *Glaessneria imperfecta* Gureev, 1987
26. *Gritcenia nana* Menasova, 2003
27. *Gureevella elliptica* Menasova, 2003
28. *Inaria karli* Gehling, 1988
29. *Irridinitus multiradiatus* Fedonkin, 1983
30. *Jurtia paliji* Bekker, 1996
31. *Kaisalia levis* Gureev, 1987
32. *Kaisalia mensae* Fedonkin, 1984
33. *Madigania annulata* Sprigg, 1949
34. *Majaella verkhojanica* Vologdin et Maslov, 1960
35. *Mawsonites randellensis* Sun, 1986
36. *Medusina mawsoni* Sprigg, 1949
37. *Medusinites asteroides* (Sprigg, 1949)
38. *Nimbia dniesteri* Fedonkin, 1983
39. *Nimbia occlusa* Fedonkin, 1980
40. *Olgerdina einori* Grytsenko, 2016
41. *Paliella pateliformis* Fedonkin, 1980
42. *Pollukia shulgae* Gureev, 1987
43. *Protodipleurosoma asymmetrica* Bekker, 1996
44. *Protodipleurosoma paulus* Bekker , 1989
45. *Protodipleurosoma rugulosum* Fedonkin, 1980
46. *Protodipleurosoma wardi* Sprigg, 1949
47. *Protoniobia wadea* Sprigg, 1949
48. *Spriggia annulata* (Sprigg, 1949)
49. *Spriggia wadea* Sun, 1986
50. *Suvorovella aldanica* Vologdin et Maslov, 1960
51. *Tateana inflata* Sprigg, 1949
52. *Tirasiana cocarda* Bekker, 1985
53. *Tirasiana concentralis* Bekker, 1977
54. *Tirasiana coniformis* Palij, 1976
55. *Tirasiana disciformis* Palij, 1976
56. *Vendella haelenicae* Gureev, 1987

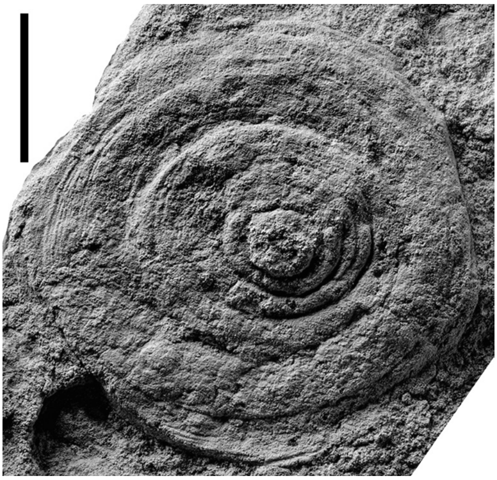

Fig. 1. One of the forms of the attachment structure of petalonamids; characterized by a smooth outer edge; “*Ediacaria flindersi*” (a preservational form of *Aspidella terranovica* Billings; 1872); bottom view; specimen PIN; No. 4564/1080; natural cast. Scale bar 1 cm.

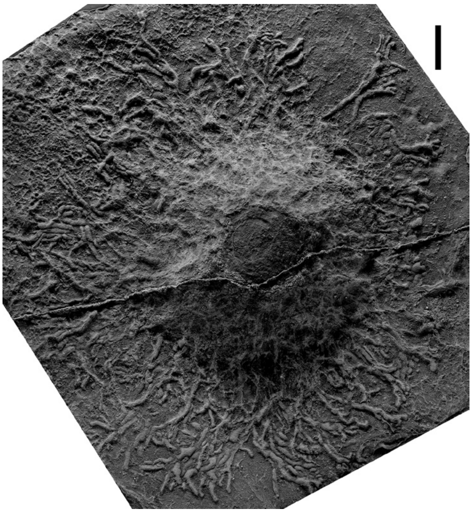

Fig. 2. *Hiemalora stellaris* (Fedonkin; 1980) — another form of the attachment structure of petalonamids; equipped with root-like branching outgrowths; top view; the smooth area in the center corresponds to the base of the stem; specimen PIN; No. 3993/9966; latex cast from a natural imprint. Scale bar 1 cm.

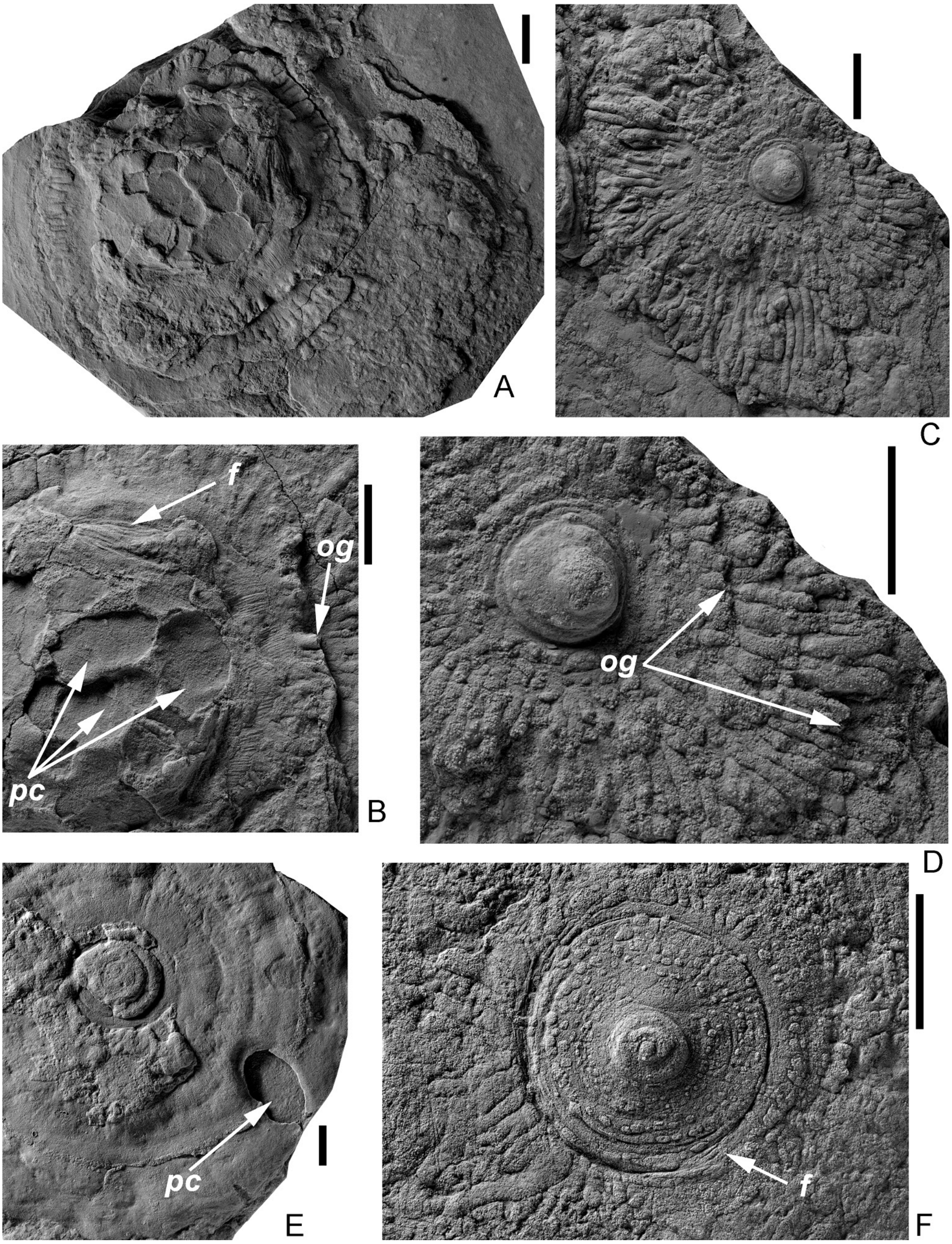

Fig. 3. Characteristic features of *Bjarmia* and their expression in natural casts of attachment structures of petalonamids: A; B — *Bjarmia cycloplerusa* Grazhdankin; 2016; holotype PIN; No. 3993/10247 (A — general view; B — a fragment of the central part of the specimen); C; D; F — *Eoporpita medusa* Wade; 1972 (C; D — specimen PIN; No. 3993/6445; C — general view; D — a fragment of the central part; F — specimen PIN; No. 3993/8880); E — "*Ediacaria flindersi*"; specimen PIN; No. 3993/5618.

Abbreviations: f — thin concentric folds; og — root-like outgrowths which were partially broken off and arranged in tiers; pc — cavities from mudstone pebbles. Scale bar 1 cm.

McIllroy *et al*., 2024), while various tubular forms, initially organic or mineral in composition (*Corumbella*, *Crassitubus*, *Paraconularia*, *Quadratitubus*, *Sinocyclocyclicus*, and *Ramitubus*), are considered to be thecae of Anthozoa, Scyphozoa, or indeterminate cnidarians (Liu *et al*., 2008; Vinn, Zaton, 2012; Van Iten *et al*., 2014; Leme *et al*., 2022).

At the same time, there are no confirmed fossil remains of Ediacaran pelagic jellyfish (Young, Hagadorn 2010; Han *et al*., 2016). It seems that early coelenterates were represented only by polyps. Even ctenophores could have started their evolutionary path with a polyp-like body plan, and there seems to be paleontological evidence for it (Zhao *et al*., 2019). Perhaps the polyp-like body form was the original state for many early animals, not only for cnidarians and ctenophores (Zhao *et al*., 2019). And the jellyfish life form could have been derived from polyps later, independently in different classes of Medusozoa (Collins, 2002; Kayal *et al*., 2013; Han *et al*., 2016).

The total absence of pelagic organisms in fossil communities of Precambrian metazoans may be determined by taphonomic processes. Three main assemblages of Ediacaran macrofossils are known: Avalon, White Sea, and Nama. Each of them is characterized by its own preservation style (Narbonne, 2005; Ivantsov, Zakrevskaya, 2018). Avalon and White Sea fossils were formed as a result of burial of the bottom community under the covers of volcanoclastic or terrigenous sandy-clayey material. Nama fossils were preserved during the transfer of bodies captured by shifting flows of deconsolidated sandy sediments. Thus, all macrofossils originating from these localities are related exclusively to benthic, mainly sessile organisms. Sandy shores, muddy lagoons, and, less commonly, deeper parts of the sublittoral with a predominance of muddy sediments are environments favourable for the preservation of pelagic invertebrates, especially jellyfish, based on the study of Phanerozoic localities (Young, Hagadorn, 2020). Such environments were apparently quite common in the shallow Ediacaran basins of South Australia, Eastern Europe, and Namibia. However, nothing even remotely resembling, for example, the jellyfish-rich sandy shores of the Cambrian (Young, Hagadorn, 2020) is observed here. This fact strongly supports the idea of the initial absence of pelagic macro-sized life forms among the Ediacaran metazoan biotas.

Precambrian jellyfish-like organisms

It seems that the affiliation with pelagic jellyfish has not been disputed, only for two monospecific genera of Ediacaran organisms, the remains of which were found in the Erga Beds of the late Vendian of the southeastern White Sea area: *Bjarmia* Grazhdankin and *Staurinidia* Fedonkin. Although, the Vendian deposits of the White Sea were not included in the list of "thirteen confirmed deposits containing jellyfish" by Young & Hagadorn (2020), but there were no explanation.

Bjarmia

This monospecific genus with the species, *Bjarmia cycloplerusa* Grazhdankin, 2016 was described from a single, heavily damaged cast, the central part of which is occupied by a cluster of cavities left by destroyed mudstone pebbles (Fig. 3A, B). The fact that the body of this hypothetical jellyfish (which obviously had practically zero buoyancy) makes it up to the burial event horizon can be explained by its loading with denser mineral pebbles during the taphonomic process, which is possible when the body is transferred within a flow of mineral suspension (Grazhdankin, 2016). However, in the case of *Bjarmia*, the appearance of pebbles within the cast could have occurred as a result of them getting into a depression on the bottom formed after the decomposition of an organic body which was partially submerged in the ground (Fig. 4). The insertion of pebbles into a depression left by an attachment structure is a fairly common phenomenon in the White Sea burial event horizons (Fig. 3E). The fossil fragment represented the holotype of *Bjarmia* differs very little from *Eoporpita*, a common attachment structure in the White Sea region, with thick, non-branching, root-like outgrowths (Fig. 3C, F). The imprints of the muscle cords, described in *Bjarmia,* correspond to the crumple folds characteristic of the deformation of three-dimensional soft bodies (Fig. 3B, F). The tentacles *Bjarmia* also correspond to the bases of the root-like outgrowths of *Eoporpita*, usually arranged in several stepped circles (Fig. 3B, D). Thus, we can conclude with certainty that the

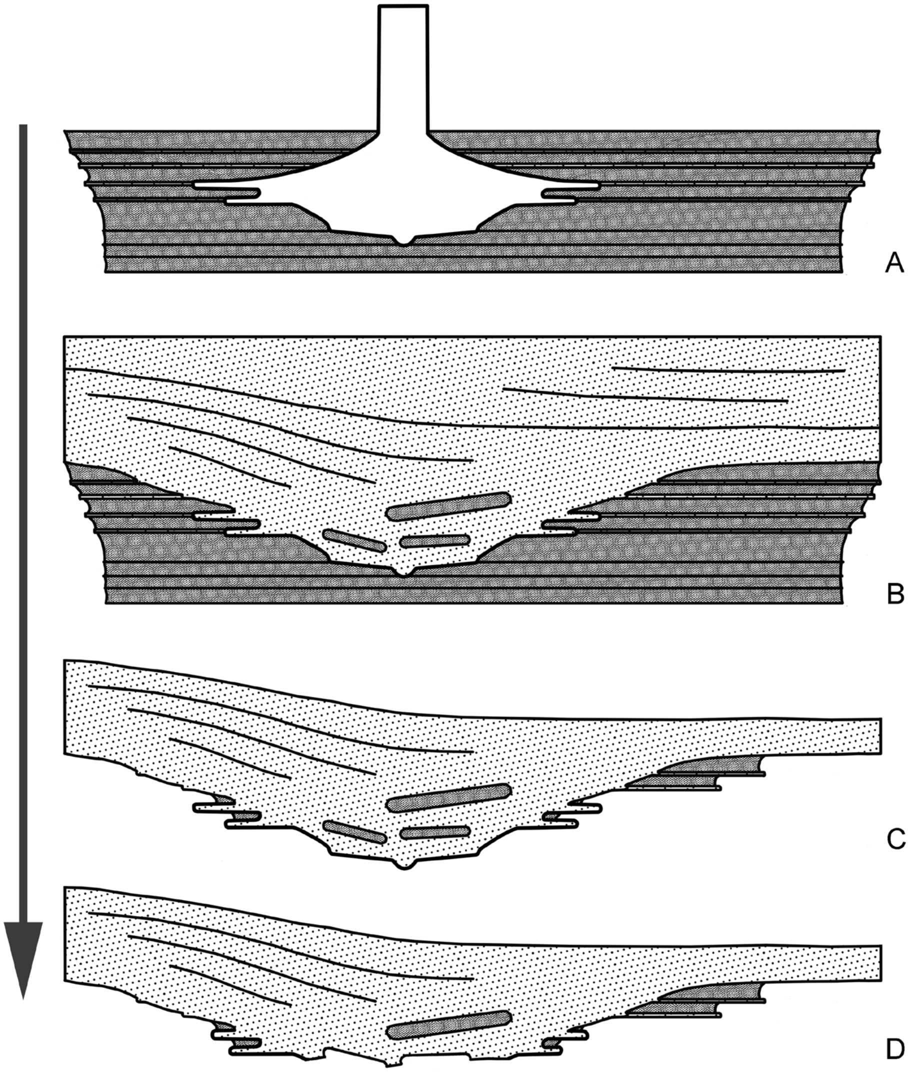

Fig. 4. Proposed scenario of the formation of the holotype of *Bjarmia cycloplerusa* Grazhdankin; 2016 (the arrow on the left indicates the sequence of events): A — the initial position of the attachment structure; *Eoporpita*; in silty-clayey ground with thin sand layers; B — formation of the fossil remains in the following sequence: death of the organism with subsequent decomposition of the organic matter — exposure of the remaining cavity in the ground by a water flow — deposition of coarse sandy sediment with clay pellets — formation of a cast of the lower side of the attachment structure; C — fragmentation of the rock slab during modern weathering; D — separation of the central part of the sand cast along a cluster of mudstone pebbles. Scale bar 1 cm.

Bjarmia "jellyfish" is an incompletely preserved remnant of *Eoporpita* representing an attachment structure of an unknown petalonamid.

Staurinidia

This genus is also monospecific, and its type species, *Staurinidia crucicula* Fedonkin, 1985 is known by a single sample, which contains four undamaged, albeit small, disc-shaped impressions (Fig. 5A). Within each of them, there is a regular cruciform structure with a massive swelling at the tip of each branch. The fossil was directly compared with hydromedusae similar to extant *Obelia*. The main part of the cruciform

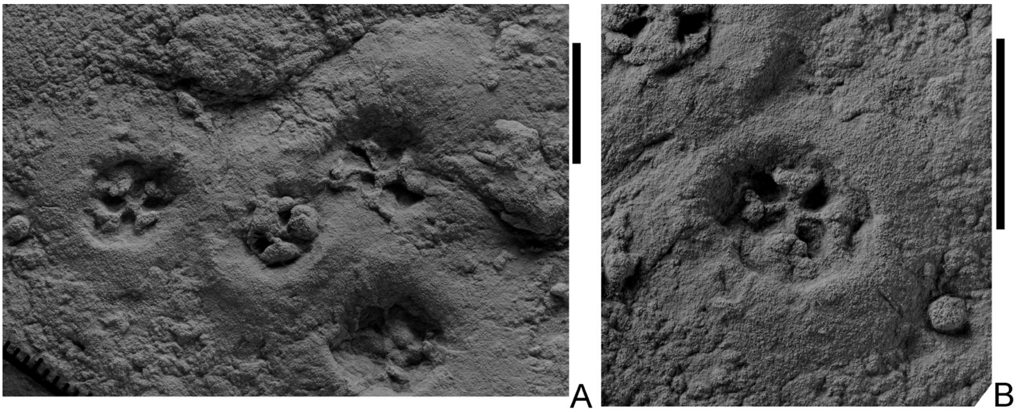

Fig. 5. *Staurinidia crucicula* Fedonkin; 1985; type series; specimen PIN; No. 3993/392: A — general view of a group of imprints (top right — holotype); B — paratype PIN; No. 3993/392B. Scale bar 1 cm.

structure was interpreted as radial canals of the gastric system, while the terminal swellings were interpreted as gonads (Fedonkin, 1985).

In the 40 years since the description of this form, not a single impression was found that closely resembled the small specimens of the type series. However, we have collected several larger specimens with a pronounced cruciform positive structure similar to that found inside the imprint of *Staurinidia*. The new material was collected in the same Zimnie Gory locality and in the same Erga Beds as the type series, but at a slightly higher stratigraphic level (Figs. 6, 7). A size difference suggests that new specimens represent a later ontogenetic stage of the same species. New additions to the type collection represented by significantly larger specimens demonstrate further morphological features allowing us to modify the diagnosis of *Staurinidia*.

PRESERVATION. All known fossils of *Staurinidia* are located on the bottom of event sandstone beds and are represented by imprints of the body upper side. This is a typical preservation of benthic macroscopic body remains in the burial event horizons of the Flinders-Belomorian style. This is how the bodies of benthic organisms, which were fixed to the bottom of the basin at the time of the taphonomic event, are preserved (Ivantsov, Zakrevskaya, 2018).

Noteworthy, that large specimens of *Staurinidia* are comparatively less prominent than small ones, and in some of their imprints, the margins of the central body completely lack a relief (Figs 6F, 7). This allows us to assume that the substance that made up most of the organism was relatively unstable and was easily subjected to compression and biochemical degradation. The extreme case of such a preservation, in which the organic matter is completely decayed and only volumetric sand fillings of the internal cavity of an individual are preserved, has been recorded for jellyfishes (Young, Hagadorn, 2020).

CENTRAL BODY. The main part of the imprint is a rounded depression (central body). In small specimens from the type series, its depth is relatively pronounced (1.5–2 mm for an average diameter of 6–7 mm) (Fig. 5). In larger specimens, it is significantly shallower. Moreover, the external borders of the central body are poorly expressed, and the depression itself breaks up into 4 depressions separated by four radial branches forming a cruciform structure (Fig. 6A, B). The central body is not observed in the largest specimen at all (PIN, No. 3993/5225). This specimen is diagnosed as *Staurinidia* only by the characteristic outline of the internal structure (Fig. 7). The tendency for a relatively positive relief of the central body to decrease while the linear dimensions increase reflects a low-density of the body organic substance, which is easily decomposed, similar to the jellyfish mesoglea.

INTERNAL STRUCTURE. The most striking and main diagnostic feature of *Staurinidia* is its central convex, equilateral cruciform structure filled with sandstone. The center of this structure coincides with the center of the body itself. The structure is composed of the material from the layer bearing the imprint, which means it was formed directly during the taphonomic event. The cruciform structure could be formed in two ways: either by filling of a depression that existed on the upper surface of the body (for example, by pressing the surface with sediment over some internal cavities); or by penetration of sediment into the internal cavities of the organism. The second scenario seems more likely. This is evident by the variability in the quality of the expression of details of the structure (if, for example, the specimens of the type series are compared, Fig. 5A). A small amount of sand penetrated into the cavity of the cruciform structure in the specimen PIN, No. 3993/5225, explains the resulted low relief of the branches, the discontinuity of the ridges and transitions from convex relief to almost flat and even slightly concave one (Fig. 7). Apparently, the filling process started in an upward-facing opening at the center of the cruciform structure and continued towards its margins. As a result, the distal tips of the branches were filled by sediment less evenly and not completely.

Abrupt expansions of the distal tips of the branches of the cruciform structure (“heart-shaped swellings” described by M.A. Fedonkin) are interpreted here as bundles of numerous secondary order branches. They were at an incipient stage in small specimens.

The internal structure of *Staurinidia*, resembling a complexly bifurcated cruciform structure and connected to the external environment by a single opening, is interpreted by us, following Fedonkin, as a digestive-distribution (gastrovascular) system.

TENTACLES. The presence of thin, “short and sparse” tentacles was noted in the original description of *Staurinidia crucicula* (Fedonkin, 1985). However, their exact appearance on the imprints was not indicated. We interpret the sinuous, irregularly oriented ridges surrounding the impression of the central body in several specimens as tentacle remains (Fig. 6B, C). An uncertainty in the orientation of the ridges, as opposed to the strict radial arrangement of the branches of the cruciform structure, indicates a relative free position and intial flexibility of these ridges. This feature can justify the interpretation of the ridges as tentacles (Norris, 1989).

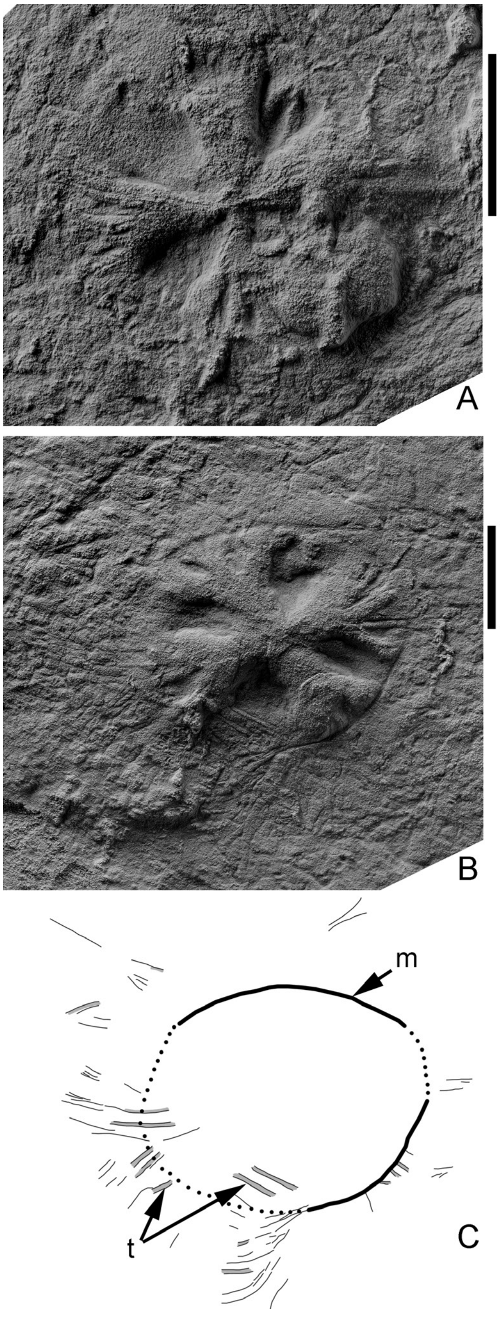

Fig. 6. *Staurinidia crucicula* Fedonkin; 1985; large specimens: A — specimen PIN; No. 3993/9714; B — specimen PIN; No. 3993/9713; C — same specimen as B; schematic drawing.

Abbreviations: m — margin of the central body; t — tentacles. Scale bar 1 cm.

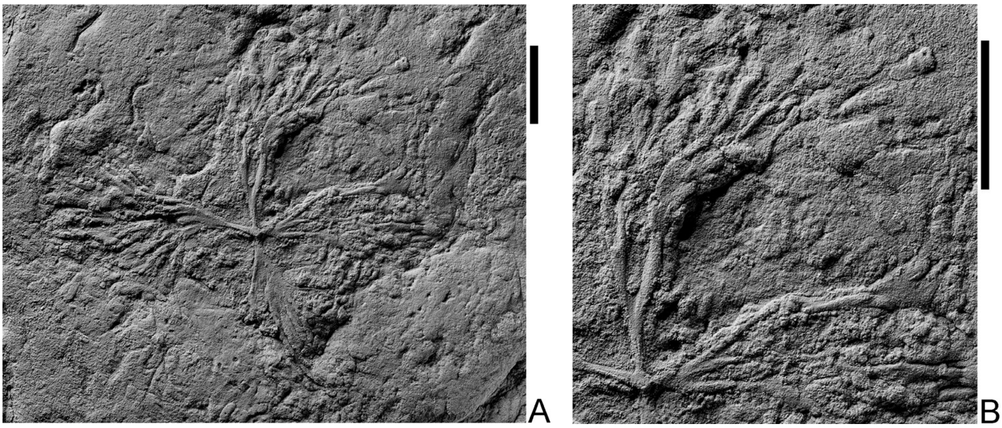

Fig. 7. *Staurinidia crucicula* Fedonkin; 1985; specimen PIN; No. 3993/5225: A — general view of the internal structure; B — fragment. Scale bar 1 cm.

Discussion

The morphological features observed in the imprints of *Staurinidia* allow us to confidently affiliate this Ediacaran organism to scyphomedusans. The volumetric body surrounded by thin flexible tentacles and the internal cavity with a central opening fully correspond to the cnidarian archetype. Although cruciform shape of its internal branching structure resembles the morphology of an early Cambrian presumable alga from the Qingjiang biota of South China (Fu *et al*., 2019, fig. 2D), the overall morphology of *Staurinidia*, especially the presence of a massive body differs it from this alga. Tetraradial symmetry is a characteristic feature of the Medusozoa (e.g., Ruppert *et al*., 2004). Most medusozoans usually have two stages in their life cycle: asexual (polyp) and sexual (medusa) (e.g., Collins, 2002). However, the morphological differences between the stages are rather vague. For example, jellyfish have a wide disc-shaped body, most of which is occupied by mesoglea. In contrast, polyps are elongated in height, have a relatively large and less differentiated gastric cavity, and are often covered by a theca with an attachment structure at the base. That said, these differences are largely attributable to the lifestyle of the organism at the corresponding stage of its ontogenesis. In the case of the absence of one of the life cycle stages, it is quite difficult to establish properly if the adult organism is a polyp or a jellyfish. The imprints of *Staurinidia* do not show signs of a theca and an attachment structure, and the canals of the supposed gastrovascular system are separated by a vast, seemingly structureless space (mesoglea?). Such features most likely confirm the primary interpretation of *Staurinidia* as a jellyfish suggested by Fedonkin (1985). However, we do not find remains of gonads even in the largest specimens of the collection. In the first description, apparently the swellings of the gastrovascular canals preceding their branching were recognized as gonads. A comparatively large size of *Staurinidia* as well as the branched gastrovascular cavity is not typical for hydromedusae; the disc-shaped body and the absence of a stalk distinguish it from the Stauromedusae, and its rounded shape distinguishes it from typical box jellyfishes. Thus, *Staurinidia* can be reasonably ascribed to scyphomedusae. At the same time, it led a benthic lifestyle, attaching itself (possibly temporarily) to the bottom with the aboral end of its body (Fig. 8).

Systematics

Genus *Staurinidia* Fedonkin, 1985

Staurinidia (nomen nudum): Fedonkin, 1983: 59, 1984: 53.

Staurinidia: Fedonkin, 1985: 89; Fedonkin, 1990: 96.

ORIGINAL DIAGNOSIS (Fedonkin, 1985). A small jellyfish, characterized by a simply arranged gastrovascular system in the form of four radial canals extending from a small gastric cavity in the center of the bell. Heart-shaped swellings of the distal parts of the radial canals probably correspond to the gonads.

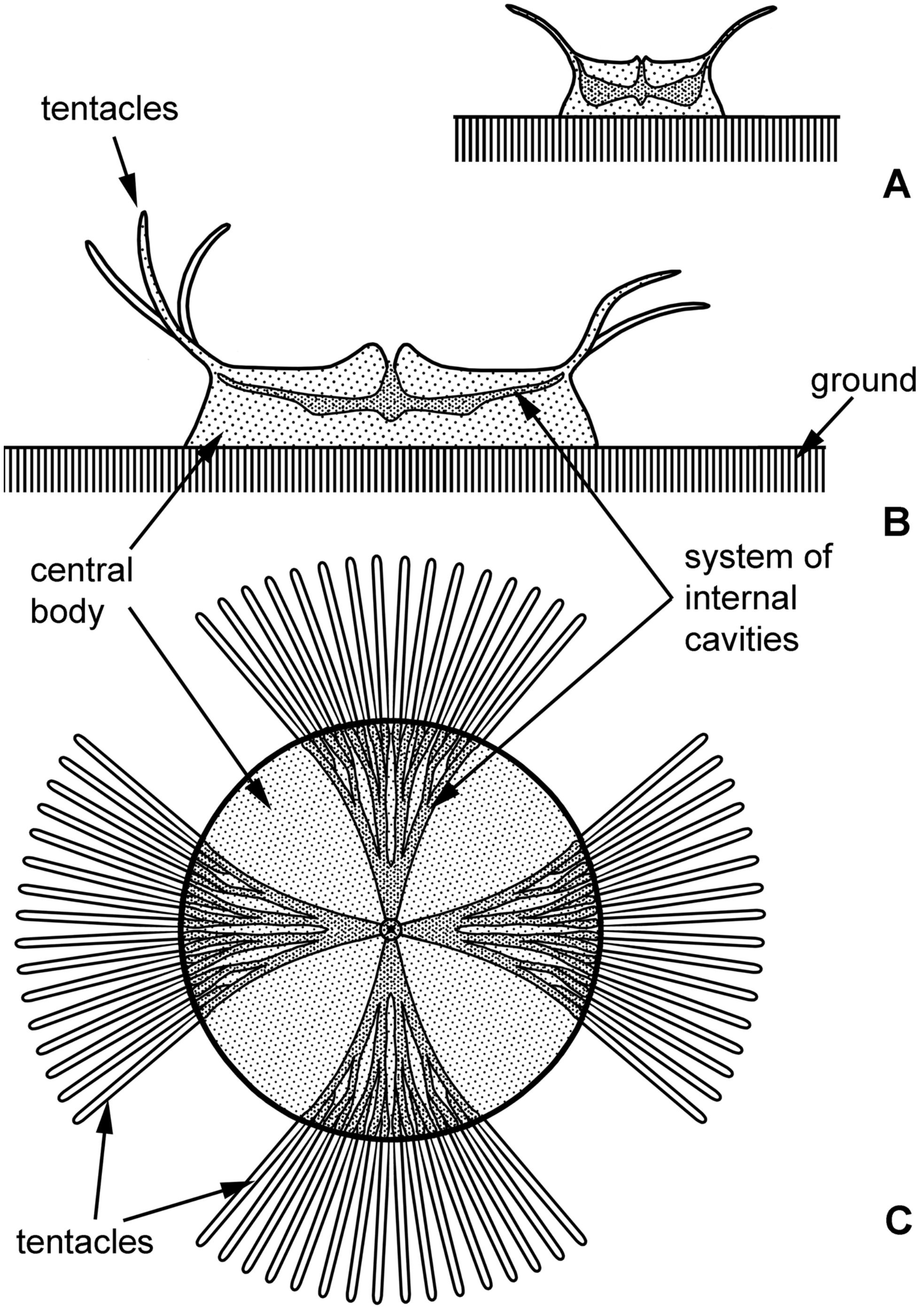

Fig. 8. *Staurinidia crucicula* Fedonkin; 1985; schematic reconstruction: A; B — life position; cross-section (A — young specimen); C — top view. The arrangement of the tentacles in groups and the four-rayed oral opening are shown as an assumption; not supported by the factual material.

The marginal tentacles are thin and sparse, and are not always preserved.

MODIFIED DIAGNOSIS. A benthic sessile organism with a round, low, disc-shaped central body. There is a branched system of cavities with a general cruciform structure (gastrovascular system?) inside the body. Each of the four branches of the cross sharply expands towards the margins of the disc and it bifurcates several times. There are numerous unbranched outgrowths (tentacles?) on the external side of the body.

COMPOSITION. The genus is monospecific.

Staurinidia crucicula Fedonkin, 1985
Fig. 5–8.

Staurinidia crucicula (nomen nudum): Fedonkin, 1983: 59, fig. 19;

Staurinidia crucicula: Fedonkin, 1985: 89, Pl. IV, figs 1, 5; Fedonkin, 1990: 97, Pl. 4, figs 1, 5.

TYPE MATERIAL. Holotype. PIN, No. 3993/392A (Fig. 5A); Fedonkin, 1985: Pl. IV, fig. 1; Fedonkin, 1990: Pl. 4, fig. 1; Fedonkin *et al.*, 2007: 287. Vendian, Mezen Formation, Erga Beds; Winter Coast of the White Sea, mouth of the Medvezhy stream.

DIAGNOSIS. As for genus by monotypy.

DESCRIPTION. The central body is best expressed on small imprints of the type series, where it looks like a deep depression (Fig. 5). In large specimens, its presence may be noticeable by the bend in the general relief of the imprint or by the groove surrounding the internal cruciform structure, or by the depressions separating the branches of the internal structure, slightly sunken in relative to the bearing surface of the layer (Fig. 6A, B). The internal structure with its four branches of equal size resembles form of a Templar cross. The branches of the cross, thin near its center, increase their width several times towards its ends. The expansion of each branch is caused by its multiple, bundle-like bifurcation. In specimens of the typical series, this expansion seems very abrupt (Fig. 5). In larger specimens it appears smoother, leveling out due to an increase in the relative size of the bifurcating part (Fig. 6A, B). The morphology of the branches is best visible in the specimen PIN, No. 3993/5225 (Fig. 7). It is evident that each of the four branches is narrow and unitary near the center of the cross, and then it significantly widens and divides several times into separate smaller branches. In the center of the cruciform structure there is a small bulge. Presumably, the entrance to the cavity of the structure (oral opening), through which sand sediment got inside, was located here, on the side of the bearing surface. The rather strict mutual arrangement of the main branches and all their divisions, in contrast to the freely lying tentacles, is characteristic of the cruciform structure. This arrangement is explained by the fixation of the cavities by the substance of the disc during the taphonomic event. The finest radial grooves and ridges, laterally bounded by such grooves, which diverge radially from the depression of the central body, may be the remains of tentacles on specimens of the type series (Fig. 5A). The grooves and the fine ridges surround the central body of the specimen PIN, No. 3993/9713; most of them are oriented in one direction, possibly reflecting the direction of paleocurrent at the time of burial (Fig. 6B, C).

DIMENSIONS. The maximum distance between the ends of the opposite branches of the cruciform structure (approximately corresponds to the diameter of the central body): holotype — 7 mm; specimen PIN, No. 3993/9714 — 20 mm; specimen PIN, No. 3993/9713 — 27 mm; specimen PIN, No. 3993/5225 — 50 mm.

LOCATION AND MATERIAL. Russia, southeastern White Sea area, Zimnie Gory locality; late Ediacaran (Vendian), Mezen Formation, Erga Beds; undefined part of member No.5 according to the scheme by Fedonkin (1981) (holotype PIN, No. 3993/392A and paratypes PIN, No. 3993/392B-D), as well as Z1(I) burial event horizon (specimen PIN, No. 3993/5228, 5825, 9713, 9714) and Z2(III) burial event horizon, specimen PIN, No. 3993/5225.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

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