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Hydraulic sediment penetration and seasonal growth of petalonamean basal discs from the Vendian of Ukraine

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ABSTRACT

Around the Ediacaran-Cambrian transition, about 540 million years ago, marine organisms began to dig in the sediment that has resulted in its better ventilation and further expansion of infaunal life. Few vertical infaunal burrows are known from the Precambrian and they are usually attributed to sea anemones. Here we show that the enigmatic Ediacaran petalonamean 'sea pens' were able to penetrate sediment for more than one centimetre depth while anchoring the body in the microbial mat. Their growth, as evidenced by numerous well-preserved basal discs from the late Ediacaran Lomoziv Member of the Mohyliv Formation in Podolia, Ukraine, was under control of rhythmic sedimentation events and periodic microbial mat development. Size frequency distribution in classes of both the final disc size and growth retention stages show that their size increase was stepwise. Each discrete stage corresponds to deposition of a thin sediment layer and development of the microbial mat at its top. Podolia was located near the South Pole in the Ediacaran (Vendian) and such rhythmic sedimentation was probably connected with the local climate seasonality.

1. Introduction

Exposures of the latest Precambrian strata in the Dniester River valley in Podolia, Ukraine, are among world localities richest in discoidal body fossils (Fedonkin, 1985; Fedonkin and Vickers-Rich, 2007; Ivantsov et al., 2015). Most of these fossils represent either attachment discs of the frond-bearing petalonameans or more or less compressed spherical microbial colonies (Narbonne and Hofmann, 1987, p. 666; Ivantsov et al., 2014). The microbial balls can be easily distinguished from metazoan body fossils owing to the pattern of their folding in result of the sediment compaction. The Podolian discs presumably representing petalonameans show neither chaotic oblique folding, typical for the microbial balls, nor finely distributed concentric increments characterizing some discoidal fossils from other Ediacaran localities. Their surface is smooth except for the concentric circular rings apparently corresponding to retentions in their growth. The first such ring marks the end of a juvenile stage in development of the disc that was of a finger-like appearance and deeply penetrated the sediment. These penetration marks resemble mysterious traces of short horizontal movements and vertical penetration of sediment attributed to cnidarians polyps that were reported from Podolia by Fedonkin (in Velikanov, 1985, p. 161, pl. 31:6). Similar structures are associated with minute discoidal fossils in the Fermeuse Formation in the Avalon Peninsula of Newfoundland (Menon et al., 2013). Longer trails have been described from the slightly older Mistaken Point Formation in the same region (Liu et al., 2010). Their relationship to the petalonameans was rejected and a cnidarian affinity was preferred by these authors, but the new Podolian material described here shows that the Ediacaran alleged 'sea pens' (see Antcliffe and Brasier, 2008) were truly able to penetrate sediment to a significant depth. This introduces a new aspect to the process of 'Agronomic Revolution' near the Precambrian-Cambrian transition (Seilacher et al., 2005; Dzik, 2005, 2007; Mángano and Buatois, 2014).

2. Material and methods

The studied specimens have been collected by the junior author in the quarry that operated for about 15 years, until 2015, on the northern bank of the Dniester River below the Novodnistrovs'k dam. There are several fossiliferous horizons in the Lomoziv Member of the Ediacaran Mohyliv Formation exposed in the quarry, represented by intercalations of sandy siltstone and thin arkosic sandstone lenses, as well as the

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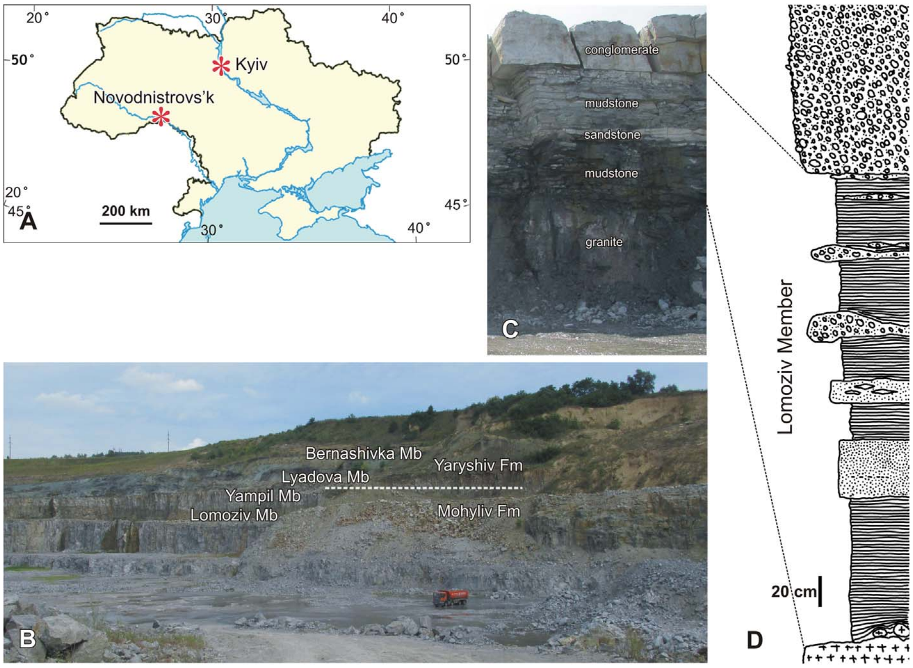

Fig. 1. Late Vendian strata exposed in the Novodnistrovs'k quarry, Podolia, Ukraine (modified after Dzik and Martyshyn (2015)). A. Location of the Novodnistrovs'k electric plant dam on the map of Ukraine. B. General view of the eastern wall of the quarry. C. View of the section exposed in the south-western corner of the quarry. D. Rock column of the fossiliferous lower Lomoziv Member of the Mohyliv Formation.

Yampil Member of the same Formation, consisting mostly thick-bedded sandstone (Fig. 1; Martyshyn, 2012; Dzik and Martyshyn, 2015). The bedding is horizontal and there is no tectonic deformation or metamorphism of the strata.

The fossiliferous thin-bedded mudstone of the Lomoziv Member occurs immediately above, and in continuity with, the basal conglomerate at the weathered granite surface. Conglomerate beds intercalate with the mudstone and cover the fossiliferous unit. No doubt that the environment was shallow marine water (Paliy et al., 1979; Fedonkin and Vickers-Rich, 2007; Tarhan et al., 2015). In this respect the conditions of life of petalonameans in Podolia contrasted with those in Newfoundland, interpreted as relatively deep-water (e.g., Laflamme et al., 2004).

The 'elephant skin' surfaces indicate profuse development of microbial mats in the Lomoziv Member, on which metazoan fossils are frequently encountered, mostly the petalonamean basal discs. The rock between such surfaces is irregularly laminated, as visible in thin sections (Dzik and Martyshyn, 2015, Fig. 2B). To some degree this is an aspect of the rock compaction but many of these laminae seem to have resulted from mineral grains trapping on the microbial slime. In result of compaction of the mudstone, the fossils are usually preserved in a low relief and mostly as replicas of imprints left by collapsed animal bodies on the microbial mat.

The countless fossils covering the sandstone slabs in the upper part of the Yampil Member represent more or less compacted moulds of spherical microbial (cyanobacterial?) colonies classified in *Beltanelliformis* (Leonov, 2007; Ivantsov et al., 2014). Occasionally also metazoan fossils, including petalonamean 'sea pens' holdfasts and fronds, occur among them providing closer approximation to their original three-dimensional geometry.

719 best-preserved specimens of the petalonamean basal discs have been selected, measured and photographed for the purpose of the present study. The illustrated specimens are stored in the Department of General and Historical Geology, Taras Shevchenko National University of Kyiv, Ukraine (abbreviated KSU).

3. Taphonomy

To explain fossilization of soft-bodied organisms one has to assume deposition of their dead bodies in an environment protecting them against decomposition. Either by steady sinking of such bodies in a toxic fluidised sediment blocking access to scavengers (which is unlikely to be the case with the Ediacaran fossil assemblages) or by a catastrophic sudden entombment under a burden of sand. The latter was apparently the case with the Ediacaran organisms at the Mistaken Point in Newfoundland, which were preserved after being smothered by volcanic ash, later covered by microbial mats. This preserves fossils on the upper surface of the beds that represent the seafloor before arrival of the entombing materials ("Conception-style" of Narbonne, 2005). In Australia, the "death mask" of Gehling (1999) preserved specimens at the bases of the entombing siliciclastic event beds, which were later sealed off supposedly by microbial mats or cementation with iron sulphates ("Flinders-style" of Narbonne, 2005; Dzik, 2003). Cementation with pyrite may preserve organic membranes three-dimensionally also within the sandstone bed. Such are preserved the stalks emerging from the basal discs attached to three-dimensionally entrained, current-aligned stalks illustrated by Tarhan et al. (2015, fig. 5B) from Ediacara. Their contours and the centrally located circular structure are preserved on the lower surface of the rock slab in positive relief (as a replica of depression in the microbial mat) but the margin represented by a narrow furrow may continue with the stem, three-dimensionally preserved within the sandstone. According to Tarhan et al. (2010, 2015) this results from a force from the current of suspended sediment drawing the frond and deforming the disc as well as the mat below, to which it was attached. As shown by Grazhdankin (2000) the pattern of deformation shows that the stalk was connected with the disc by randomly distributed fibres within the external wall of the disc but mostly with the central region of its base. In result, its middle was the first to be elevated together with the microbial mat (Grazhdankin, 2000). This is consistent with information offered by the three-dimensionally preserved specimen from the White Sea Ust-Pinega Formation illustrated by Steiner and Reitner (2001, fig. 4). This means that many fossil assemblages of sedentary Ediacaran organisms represent community structures frozen at the moment of a catastrophe. The termination of a community could have been caused by a sudden deposition of the sediment layer too thick to allow subsequent unearthing of the fronds. In such cases the bed above the microbial mat and the infill of imprints of the discs are of the same composition and of equal degree of compaction (Figs. 2D, 4).

Most of the discs from the Lomoziv Member and other localities are

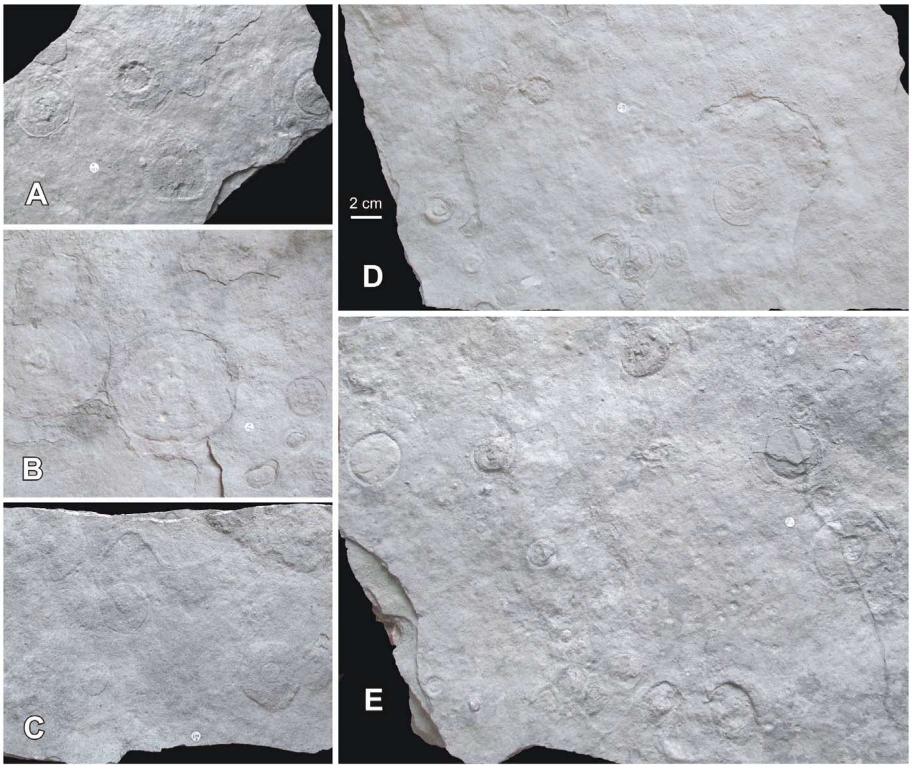

Fig. 2. Slabs of mudstone with *Charniodiscus*-like discs from the Lomoziv Member of the Mohyliv Formation exposed in the Novodnistrovs'k quarry (all specimens in the same magnification). A. Upper surface of slab KSU K 283 with depressions after discs filled with coarse sediment. B. Sole of slab KSU K 200 showing discs at various growth stages. C. Sole of slab 007 with growth of discs terminated after the second stage. D. Sole of slab KSU K 187 with mostly juvenile discs. E. Upper surface of slab KSU K 264 with discs at various stages of development.

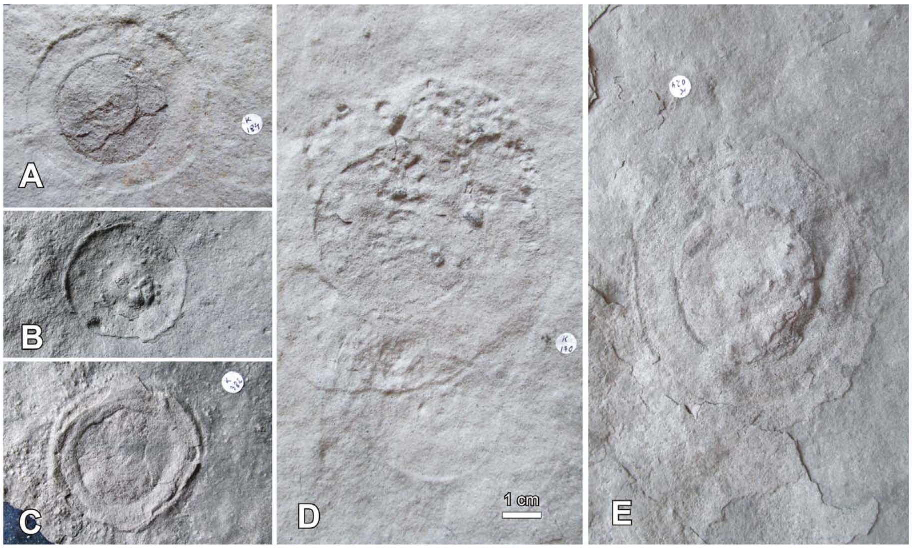

Fig. 3. Depressions after *Charniodiscus*-like discs filled with mineral grains or sand preserved on the upper surface (A) or sole (B-E) of mudstone slabs from the Lomoziv Member in the Novodnistrovs'k quarry (all specimens in the same magnification). A. Specimen from slab KSU K 184 with all stages of growth filled with sand except for the last one. B. Specimen from slab K-213 with sand concentrated at vertical walls and gravel randomly distributed over the disc impression. C. Specimen from slab 382 with a wide marginal band of sand. D. Specimen from slab KSU K 170 with gravel accumulated on one side of the disc imprint. E. Specimen from slab KSU K 24 with gravel in the middle deepest part of the disc imprint.

preserved owing to properties of the microbial mat covering the upper surface of the sediment layer. The mat stabilised depressions on its surface acting as the 'Ediacaran shroud' (Steiner and Reitner, 2001; Dzik, 2003). In many specimens the disc margin and marks of its growth retentions are delimited by a thickening. It consists of a sediment somewhat coarser that in the surroundings. Its rope-like appearance may have resulted from a post-diagenetic compaction, which affected its sandy contents less than the mudstone around (Fig. 3B). In some specimens such sandy margin forms a wider belt around the disc (Fig. 3C). The nature of this structure remains enigmatic. Perhaps the slime produced by the disc and keeping it at the mat surface incorporated sand grains. In some cases the sand may have accumulated *post mortem* along the steep margins of the disc imprint in result of winnowing (Fig. 3D).

The positive replica in the sole of the overlying bed may have originated long after the depression in the microbial mat originated. Frequently, the deepest part of depression is filled with a coarse-grained sediment different from that forming the overlying bed (like discs studied by Laflamme et al., 2011 but unlike those of Mapstone and McIlroy, 2006). Angular grains of quartz or feldspar may gather within the shallower part of the depression. Apparently, it was the winnowing that concentrated coarse grains there (Figs. 2A, 3B, D). Such pattern of preservation requires that the depressions were empty and the winnowing segregated mineral grains filling them before the final burial under sand or mud from suspension. It seems that the morphology of the lower disc surface is replicated with the same fidelity irrespective of whether they originated in a sudden catastrophic event or as a result of prolonged, biphasic sedimentation process. The event of burial was not the main cause of the petalonamean community cessation. A factor of mortality other than a sudden burial was in action. One may speculate

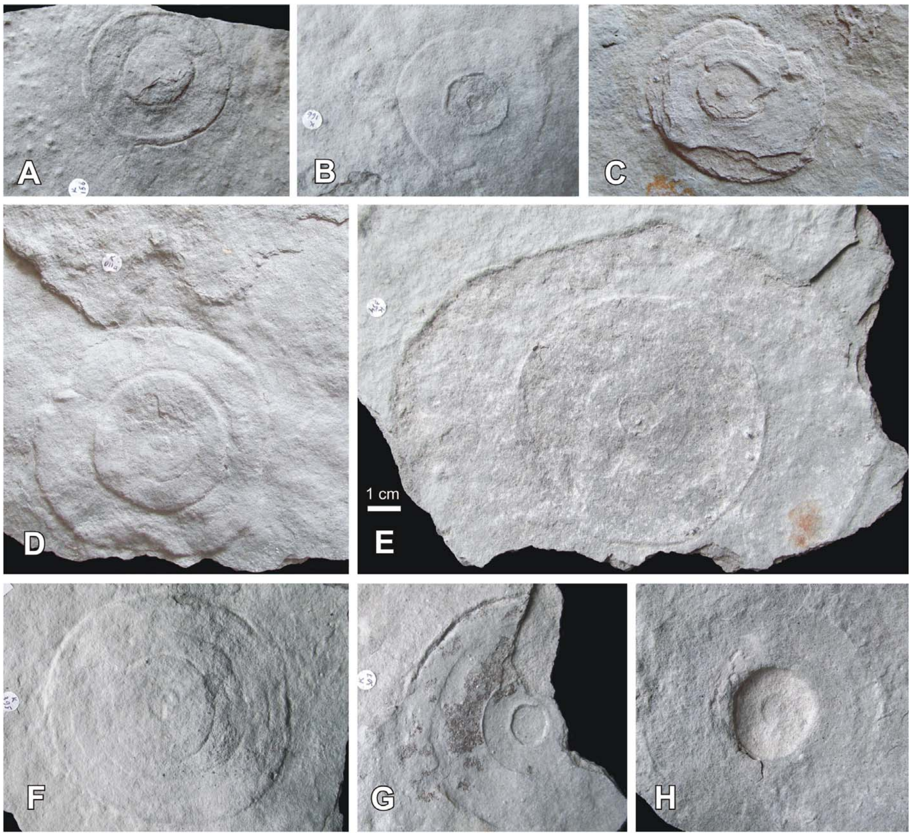

Fig. 4. Imprints of *Charniodiscus*-like discs on the sole (A-D, F) and upper surface of mudstone slabs (E, G, H) from the Lomoziv Member in the Novodnistrovs'k quarry showing various elevation of relief (all specimens in the same magnification). A. Strongly compacted specimen from slab KSU K 156 with the central part and the disc margin filled with sand. B. Specimen from slab KSU K 166 with sand concentrated only at vertical walls demarcating early growth stages. C. Similarly preserved specimen from slab KSU K 013 showing partially preserved laminae of the basal bed, in which it was rooted. D. Larger specimen from slab KSU K 011 with four growth stages delimitated by a rope-like concentration of sand. E. Strongly compressed large specimen with irregular margin from slab KSU K 354, originally the disc imprint was filled with a thin layer of sand. F. Specimen from slab KSU K 395 with six growth stages. G. Specimen from slab KSU K 307 showing relatively high relief. H. Larger specimen from slab KSU K 245 with first two growth stages originally filled with a sediment of low compaction.

that this could have been a seasonal temperature rise or drop exceeding the tolerance of these organisms, or a too low food supply. A period of time long enough to enable complete decay of the petalonamean bodies separated their death from burial.

4. *Charniodiscus*-like basal discs

The surface of the Podolian discs under study is smooth, without any apparent growth increments. Similar fossils from Ukraine were earlier attributed to genera *Cyclomedusa*, *Mawsonites*, *Marnium*, and others (Ivantsov et al., 2015). Majority of the discs show concentric rings expressed as both elevation above the microbial mat and furrows in it. The first such ring usually delimits a central area filled with a more coarse material than that above and below. In most cases it is hard to determine nature of the concentric folds because of the sediment compaction. Only few specimens from the Lomoziv Member are preserved in a more sandy sediment less prone to compaction, exposing then the original geometry of the central part of the disc (Fig. 4G, H). Especially instructive specimen KSU K 181 is preserved as a depression in a relatively coarse grained substrate covered and underlined by microbial mats (Fig. 5A–C). Each concentric ring corresponds to a microbial mat surface separated by a set of few sediment laminae. Sedimentation was apparently rhythmic and after each event of deposition a new microbial mat developed. The disc accommodated to the elevated surface while increasing its size until the next sedimentation event. The disc was attached to the sediment surface, not imbedded in it, as proposed by Grazhdankin (2000) for similar structures from the White Sea.

The actual correspondence between the early stages of growth is preserved on the slab of sandstone from the Yampil Member of the Mohyliv Formation (Fig. 5D, E). In this case the event frozen in the sandstone bed was apparently catastrophic. Deposition of sand uniformly filled the depression emptied by the decayed discs. The sandstone is not as prone to compaction as the mudstone and exposes obtuse conical tips of the discs that penetrated the mudstone further below the microbial mat. Irrespective of the disc diameter, its initial part was deeply submerged in the mudstone whereas the expanding disc margin 'crawled' over the microbial surface during its subsequent growth. The present elevation of the finger-like mould of the initial disc portion (plug) is about 6 mm. The associated sandstone moulds of originally spherical *Beltanelliformis* microbial balls offer estimate of the original depth of penetration by the disc. Their compaction is usually two- to threefold. The penetration by the petalonameans was thus more than one centimetre deep.

The rhythmic development of growth retentions in specimens from the Lomoziv Member of Mohyliv Formation strongly contrasts with preservation of discs in fine-grained tuffite of specimens on slabs KSU K 205 and 206 from the Bronnycia beds (strata located immediately above those exposed in the Novodnistrovs'k quarry) at the Borshchiv Jar site in Mohyliw Podilski. They lack any marks of growth retention on the discs. The animals were apparently killed by deposition of a more coarsely grained tuff that makes a layer of about 1 cm thickness. Subsequent compaction of the tuffite preserved the conical appearance of the disc moulded in the coarse-grained tuffite and deformed the underlying fine-grained sediment. The course of rock laminae within the bed follows more or less precisely the disc conical shape until it disappears about 43 mm below the disc base.

The taxonomic identity of discs with smooth margins of the concentric units is partially disclosed by rare findings of their associated elevated parts. The most complete but poorly preserved is the imprint on the sole of coarse sandstone slab KSU K 422 (Fig. 6A). It shows a disc with at least two concentric units and probable short stem with a small frond (or just its basal part). It is hard to tell, which genus this fossil represents except for that its probable nature is petalonamean. Another specimen, KSU K 419, seems to represent an initial stage of the disc development with a poorly preserved basal part of a very long stem (Fig. 6B). The best preserved of available specimens KSU K 201 represents a long stem widened at contact with its basal disc (Fig. 6C, D). The disc is preserved as a depression penetrating two relatively thick

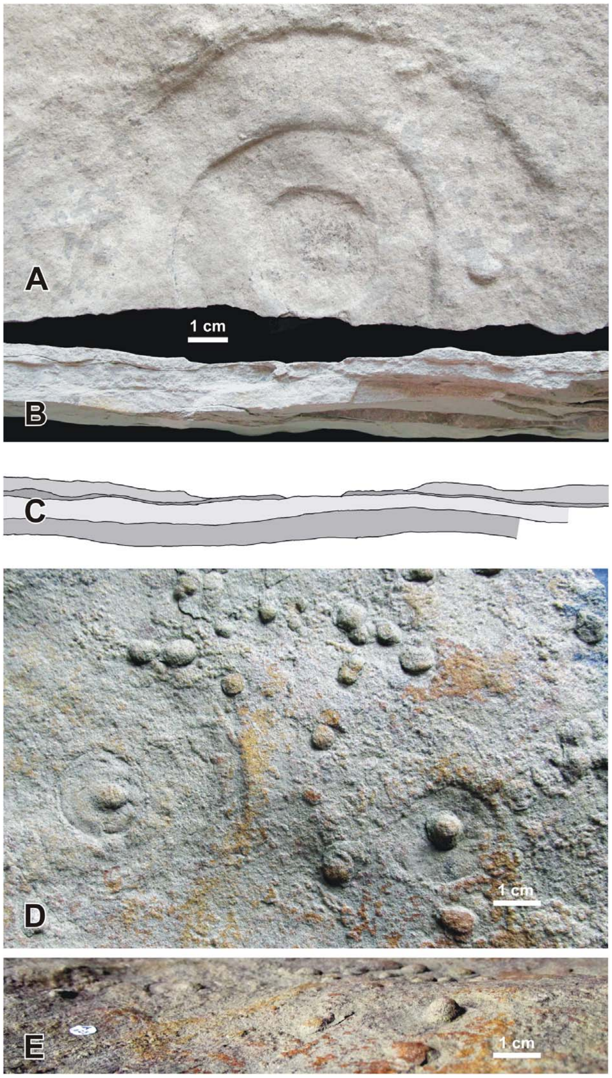

Fig. 5. A-C. An imprint of a *Charniodiscus*-like disc on the upper surface of the Lomoziv Member mudstone slab KSU K 181 showing correspondence of its stadial growth to the succession of sediment layers; basal view of the imprint (A) and transverse breakage of the slab and its interpretive drawing (B, C). D, E. Basal surface of sandstone slab KSU K 123 from the Yampil Member of Mohyliv Formation in the Novodnistrovs'k quarry with a relatively low compaction of the *Charniodiscus*-like discs imprints with two discs showing a deep initial penetration and subsequent growth at the microbial mat surface associated with numerous termination of growth of other individuals at the 'probings' stage; basal (D) and oblique (E) views showing elevation of the 'probings' replicas; two- to threefold compaction of spherical *Beltanelliformis* sandstone moulds in the same strata indicate that the actual penetration was proportionally deeper.

and coarse-grained laminae. The rope-like thickening at its margin forms an elevation above the microbial mat and is slightly imbedded in it (Fig. 6E). The stem is preserved in the layer above this microbial mat partially as a depression in it or, in its distal part, as a slightly elevated fill of a coarse-grained material. At the sole of the overlying bed (represented in the counterpart) only an impression of the fossil in negative relief can be traced. The stem is fractured some distance from the disc and its distal portion is displaced. This means that there was a period of non-deposition prolonged enough to enable partial decay and fragmentation of the cadaver. The length of the stem makes this fossil similar to the Newfoundland species *Charniodiscus procerus* Laflamme et al., 2004 and to *Flavostratum incrustatum* Serezhnikova, 2013 from the White Sea, both different in this respect from other charniid petalonameans (Laflamme et al., 2004; Serezhnikova, 2013). Other species from the White Sea (Ivantsov, 2016) and (Grazhdankin, 2014) had the frond elements developing immediately above the discs, actually

Fig. 6. *Charniodiscus*-like discs with attached stems from the Lomoziv Member in the Novodnistrovs'k quarry (all specimens in the same magnification). A. Juvenile specimen on slab 422 sole with a long stem and hardly discernible base of the frond (petaloid). B. Juvenile disc with poorly preserved short stem and frond on the slab KSU K 419 sole. C, D. Poorly preserved disc on upper surface of slab KSU K 201 with long stem torn out and displaced some distance from the disc; a rope-like sandy thickening along the disc margin in oblique view. E. A thin section across the slab showing relatively thick claystone laminae representing microbial mats at the base and top and a less apparent lamination within it marking the surface on which the disc and the stem are preserved.

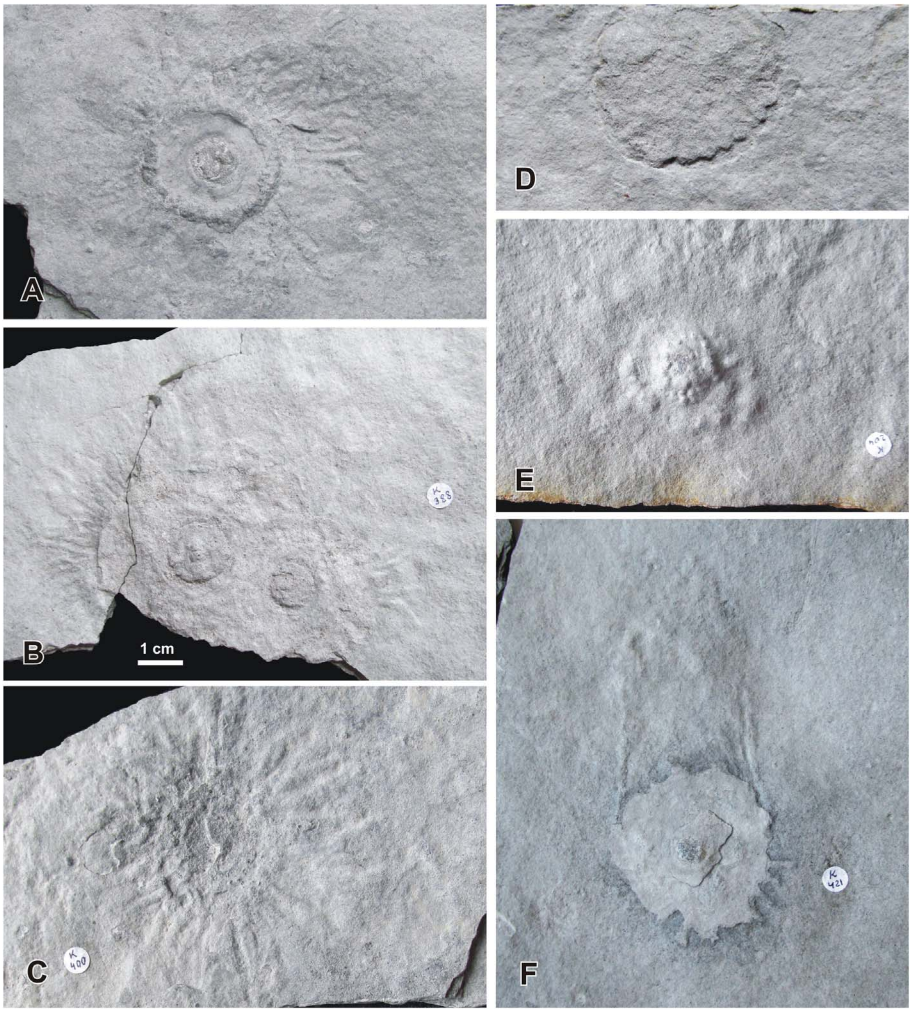

Fig. 7. *Eoporpita*-like discs from the Lomoziv Member in the Novodnistrovs'k quarry (specimens A–F in the same magnification). A. Slab KSU K 401 sole with a disc showing truncated initial part penetrating the sediment lamina with an imprint of the smooth discs and imprints of rays at the next microbial mat-bearing lamina. B. Slab KSU K 388 sole showing stages in development of two associated discs. C. Slab KSU K 400 upper surface with imprints of rays. D. Slab E 202 sole with a discs at the stage of developing marginal rays. E. Slab KSU K 204 sole with almost not compacted vertically oriented rays of the juvenile stage filled with coarse sand. F. Slab KSU K 421 sole with a juvenile disc vertically penetrating two partially preserved laminae of underlying bed and partially preserved imprint of the elevated portion of the body with the diameter similar to that of the disc.

lacking the stem. Several incomplete fronds of *Charnia* or *Charniodiscus* morphology are known from both the Lomoziv and Yampil Members of the Mohyliv Formation but their relationship to the discs remains unsolved.

5. *Eoporpita*-like basal discs

Associated with *Charniodiscus*-like discs but less common are discs, which show whorls of numerous thin protrusions instead of a single centrally located finger-like plug (Fig. 7). As shown by specimen KSU K 204 with first few circles of rays filled with coarser sediment (Fig. 7E), initially they penetrated the sediment vertically to attain a more radial disposition thereafter. The appendages do not branch and their diameter (about 2 mm) does not seem to change significantly during growth of the disc, although preservation precludes precise measurements. Their bases almost touch each other at the disc margin, which means that their number is proportional to the disc diameter. The pattern of growth of probably most of the Podolian specimens was similar to that of associated *Charniodiscus*-like discs. That is, the lower surface of the disc was smooth and it adhered to the surface of the microbial mat until reaching certain size. Then, as suggested by specimen KSU K 204 (Fig. 7D) with incipient rays along the margin, they penetrated the newly deposited sediment probably without crossing the underlying microbial mat. This pattern was repeated with each subsequent portion of the mud and a microbial mat at its top.

Specimen KSU K 418 preserved in the weakly compacted sandstone of the Yampil Member shows that in absence of a periodic microbial mat the circles of rays could develop in a less rhythmic way, although details of their morphology are poorly visible in the coarse rock matrix. This suggests the species level identity of the Podolian material with the White Sea specimens three-dimensionally preserved within sandstone, identified as *Eoporpita* or *Hiemalora* by Fedonkin (1985), but not necessarily with the rather indifferent holotype of *Hiemalora stellaris* Fedonkin, 1980, the species characterized, according to Grazhdankin (2014), by pinnately branching rays. There is no evidence of ray branching in the Podolian specimens and in this respect they resemble the northern Siberian *Hiemalora pleiomorpha* Voanyuk, 1989 (transferred to *Mawsonites* by Grazhdankin, 2014) preserved in strongly compacted bituminous muddy limestone of the Khataspyt Formation of northern Siberia (Dzik, 2003; Serezhnikova, 2007; Nagovitsin et al., 2015). The problem of taxonomic identity of this species is out of scope of this paper and for convenience we provisionally refer to it as being similar to *Eoporpita* of Wade (1972).

One specimen of the appendage-bearing disc from the Lomoziv Member, KSU K 421 (Fig. 7F), is associated with a wide structure that may represent the erect part of the body. It terminates with an acute triangular margin showing series of thickenings of unknown nature. This seems consistent with data on *Primocandelabrum* occurring in several formations of the Ediacaran in the Bonavista Peninsula, Newfoundland (Hofmann et al., 2008). A frond with radially expanding branches characterizes also *Haootia* from the Fermeuse Formation of the Bonavista Peninsula of Newfoundland. A small structure in the centre of its disc was interpreted as the base of a narrow stalk (Liu et al., 2014) but it is similar rather to the finger-like plug in the Podolian discs.

The strict connection of the Podolian discs with the underlying

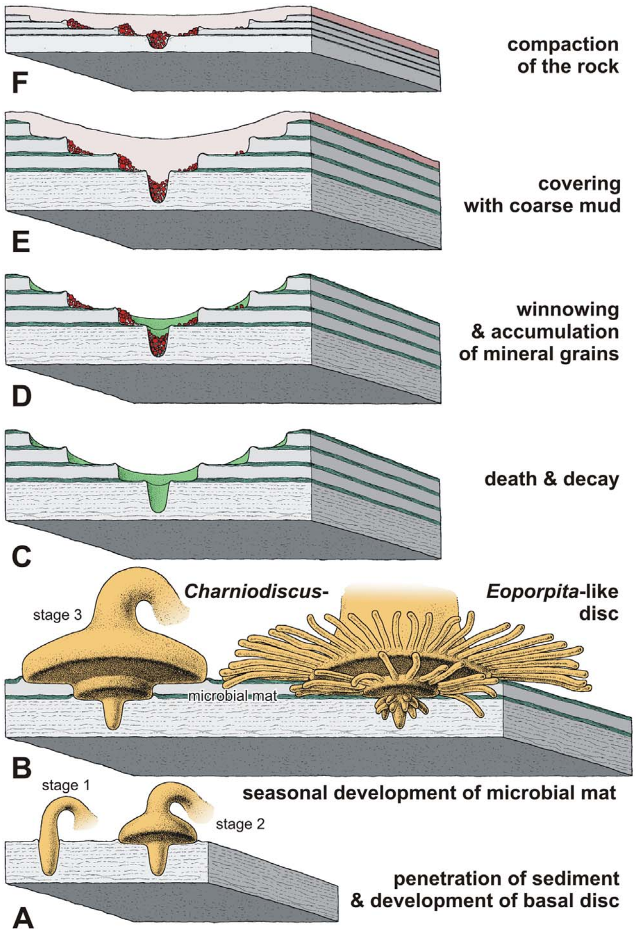

Fig. 8. Proposed scenario of *Charniodiscus*- and *Eoporpita*-like discs growth and their taphonomic history in the Lomoziv Member. A. Penetration of sediment (stage 1) and subsequent formation of the disc morphology (stage 2). B. Accommodation to seasonal sediment supply and growth of microbial mat on its surface (stage 3). C. Death and decay of the disc. D. Partial filling of the depression with mineral grains by winnowing. E. Covering with sediment. F. Differential compaction of the beds.

microbial mats and their stadial growth (Fig. 8) may have resulted from either intrinsic physiological or external environmental factors. Potentially, one may disclose their nature based on the pattern of their population dynamics and its possible connection with sedimentary processes. Assuming that the diameter of discs and stages of retention in their growth correspond to their ontogenetic age one may approach the population dynamics of these petalonameans.

6. Population dynamics of the disc-bearing petalonameans

The quarrying at Novodnistrovs'k with use of explosives prevented studies of large rock surfaces but some slabs show abundant occurrences of discoidal fossils. Their number is too small to make the study statistically significant but there is no doubt that the discs' assemblages on most slabs represent specimens of different ontogenetic age (Fig. 2). This means that there was no single event of recruitment of a new population after emergence of an environment suitable for colonization. Such conditions continued long enough to enable some discs to reach almost half a metre in diameter, as shown by fragmentary specimens. Darroch et al. (2013) offered evidence that at least in case of the rangeomorph petalonameans from the Mistaken Point, Newfoundland, their populations colonized the sea bottom continuously. They did not represent opportunistic 'blooms' exploiting new substrate emerging with development of a new microbial mat. The association of discs of different size in the Podolian fossil assemblage indicates that there were prolonged episodes of conditions suitable to growth of the petalonameans rarely punctuated by probable catastrophic event of their extermination or burial. This does not necessarily mean that meanwhile the Podolian petalonameans grew and died steadily, like those living in the deep-water environment of the Newfoundland Fermeuse Formation. The size frequency distribution of discs from there is smooth, showing a peak at 6 mm with relatively rare specimens of large size (Gehling et al., 2000, text-fig. 16). A similar distribution is shown by discs from Argentina (Arrouy et al., 2016). A less smooth size frequency distribution characterizes specimens from the Bonavista area (Hofmann et al., 2008, Fig. 8) with peaks at 14 and 45 mm, although the number of measured specimens (84) was rather low.

In contrast, the Podolian specimens exhibit a clearly multimodal size frequency distribution. The peak of frequency at about 4.5 mm is followed by a rhythmic series of peaks in frequency of the final disc diameter, both in the discs similar to *Charniodiscus* and those similar to *Eoporpita* (Fig. 9A, B). It appears that their mortality was controlled by an environmental factor of a rhythmic nature. The size frequency distribution of successive retentions in their growth exposes the rhythmic pattern even more clearly (Fig. 9C). It has been already shown above that the disc retention stages correspond to a periodic deposition of the sediment layer and development of a microbial mat (Fig. 5). This makes likely that the main factor responsible for the stadial growth and death of the petalonameans during sedimentation of the Lomoziv Member was a seasonality of climate in the Vendian of Podolia. The continent of Baltica, with Podolia at its southern tip was that time located near the South Pole (Chumakov, 2007). The near-shore and shallow-water environment at the crystalline basement elevation near Novodnistrovs'k strongly depended on supply of various kinds of sediment from the land during wet seasons and cessation of its transport and development of microbial mats in dry periods.

The first increase of mortality of the Lomoziv Member petalonameans corresponds to the end of the first stage in the development of discs (Fig. 9C). The body base had not yet developed discoidal shape and had a finger like appearance, being able to penetrate sediment with hydraulic force. Although the diameter of this part of the disc is highly variable, the size frequency distribution is unimodal, with the modal value about 4.5 mm (Fig. 10). There is either only a single species of *Charniodiscus*-like petalonamean in the Lomoziv Member, or this character is too general to enable species determination. In some other petalonamean species the high conical shape of their base probably retained to the maturity (Grazhdankin, 2014, Fig. 2:3, 4). This may be a trait of phylogenetic importance.

7. Petalonamean taxonomic identity

Discoidal imprints significantly contribute to many soft-bodied organisms' fossil assemblages of the latest Precambrian (Gehling et al., 2000; MacGabhann, 2007; Serezhnikova, 2013). At the time of their discovery, the paradigm of phylogeny of invertebrates was that medusozoan cnidarians are among the most primitive animals and, accordingly, these Ediacaran fossils had been initially interpreted as medusae (e.g., Glaessner and Wade, 1966; Wade, 1969, 1972; Sun, 1986) or at least problematic cnidarians (e.g., Wade, 1969, 1972; Sun, 1986). With better understanding of the ways these fossils originated it has become apparent that many of them are actually holdfast structures of frond-like organisms (Gehling, 1988; Grazhdankin, 2000; Serezhnikova, 2007, 2013; Tarhan et al., 2010, 2015). Their exact affinities remain controversial but most likely they had little to do with the extant cnidarians (Dzik, 2002; Antcliffe and Brasier, 2008). However, knowledge of their biology and anatomy is too incomplete to determine their exact position on the phylogenetic tree of organisms.

All fragmentary petalonamean fronds found in the Lomoziv and Yampil Members of Mohyliv Formation in the Novodnistrovs'k quarry are of the charniid morphology, which suggests that the Podolian petalonamean community was of low taxonomic diversity, unlike those of

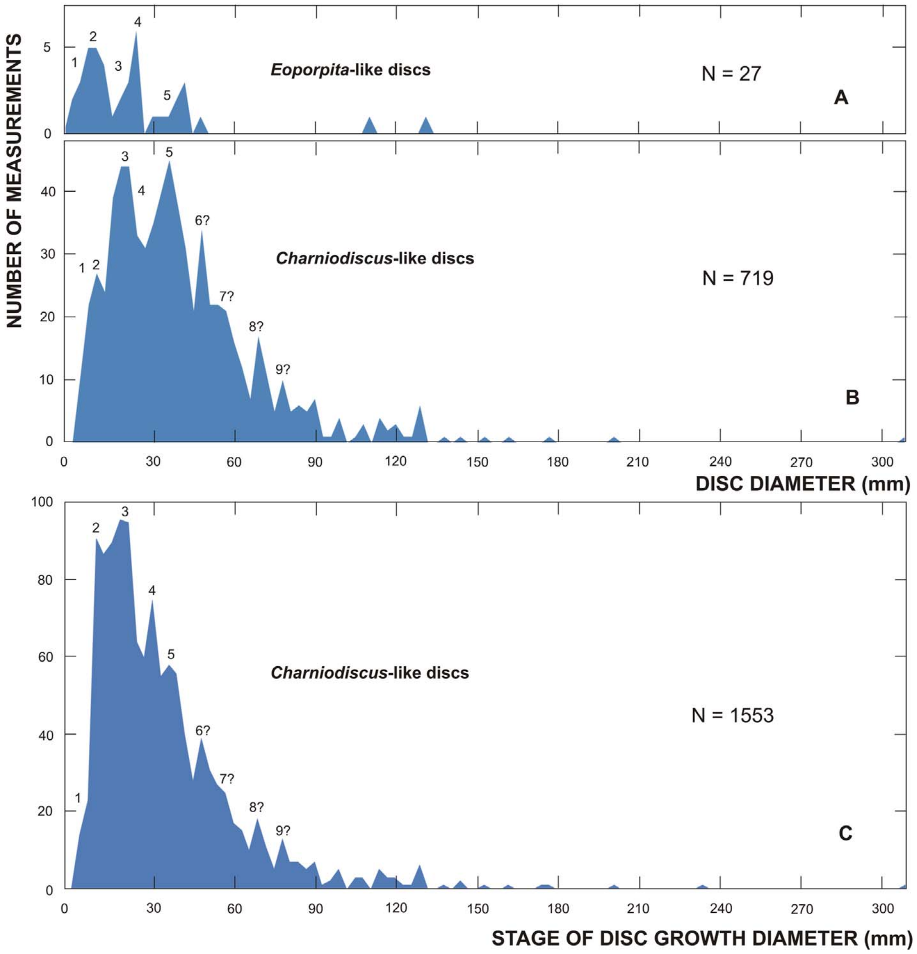

Fig. 9. Size frequency distribution of the basal discs size from the Lomoziv Member in the Novodnistrovs'k quarry (in 3 mm classes; successive growth stages marked with numerals). A. Final size of *Eoporpita*-like disc. B. Final size of *Charniodiscus*-like disc. C. Size of both final *Charniodiscus*-like discs and their growth retention stages.

Newfoundland. The discs with attached stalks and fronds discussed above are not especially informative and it remains unsettled whether the discs lacking appendages are conspecific with the isolated fronds or not. The only source of information on the elevated part of the body of the rays-bearing discs is the specimen with the wide stalk terminating with a triangular crenulated structure (Fig. 7F). Our new data do not enlarge the spectrum of morphologic diversity of the petalonameans known from other regions of the world (e.g., Hofmann et al., 2008; Liu et al., 2014; Burzynski and Narbonne, 2015). A new aspect of their anatomy is the finger-like stage in development of the Podolian species, with hydraulic function, the presence of which may be probably extended to other petalonameans. This is one more of their enigmatic traits.

Among the remarkable aspects of the charniid frond is the ease with which the secondary units were filled with sand during fossilisation. There are at least two explanations of this phenomenon possible: either the internal structures of the frond collapsed easily while being adpressed to the microbial mat under the load of sand or tuff, or the secondary units did not represent closed chambers but had wide openings enabling the sediment to enter. The former scenario applies

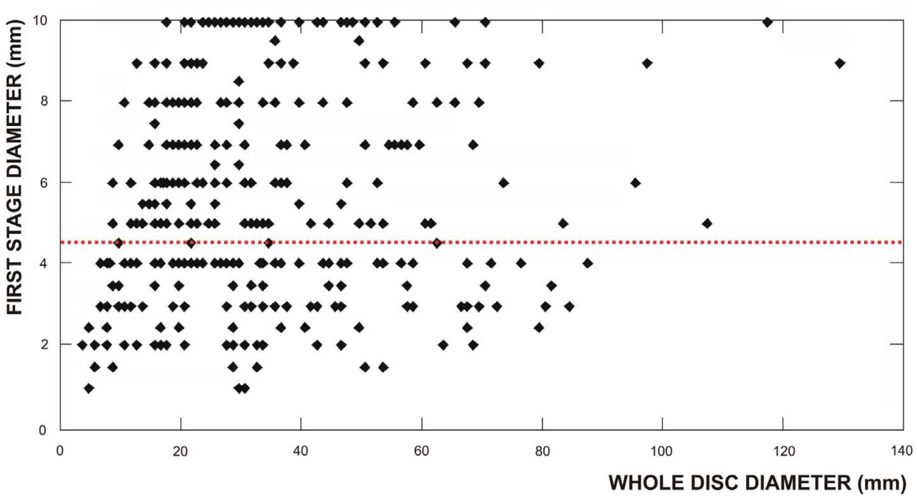

Fig. 10. Relationship between complete size of *Charniodiscus*-like discs from the Lomoziv Member of the Mohyliv Formation and their smallest development stage marked by a retention of growth (shown only for those of diameter below 10 mm; dashed line shows the modal value).

well to intact specimens catastrophically killed by volcanic ash or by a suspended sand deposition. Specimens of this kind usually show only some of the units in full relief of anatomical details. The latter scenario refers to partially disintegrated specimens, with their smooth external membrane probably torn out. The frond anatomy would be then similar to that of the pteridiniid *Ventagyrus*, with tri-radially arranged series of chambers precisely reproduced by the sand fill (Fedonkin and Ivantsov, 2007), as well as to *Pambikalbae* from Ediacara (Jenkins, 2007) and *Siphusauctum*, their triradial possible relative in the Mid Cambrian Burgess Shale biota (O'Brien and Caron, 2012).

According to Laflamme et al. (2007), based on the Charnwood Forest original specimen, the secondary transverse units of the frond of *Charnia* had a tertiary rangeomorph complex structure. This is not confirmed by much better preserved specimens from the White Sea fossil assemblage (Ivantsov, 2016), in which (and in the best preserved fragmentary Podolian fronds as well) the oblique folds on the surface of secondary units are artefacts originating during compaction of specimens. This makes extremely elongate fronds of '*Charnia*' *wardi* Laflamme et al., 2007, with petals of the rangeid complexity, rather unrelated to *Charnia*. It is a matter of dispute, what the complex rangeid structure of the frond, exhibited by many Newfoundland petalonameans, represents.

As shown by the Australian specimens of *Charniodiscus* (*Arborea*) *arboreus* (Glaessner, 1959) at different stages of decomposition and decay (Dzik, 2002, fig. 4), the external surface of the frond was smooth and internally located secondary transverse units emerge only after the external surface-covering membrane is pressed to them or removed. A smooth surface imprint (interpreted as obverse) has been illustrated also for *Charniodiscus oppositus* Jenkins and Gehling, 1977 (Jenkins and Gehling, 1977, fig. 6). This means that there were no polyps on the frond and no mouth opening, neither on the frond tip (Antcliffe and Brasier, 2008), nor in its base. This seriously hampers search for relatives of the petalonameans. The smooth external surface, as well as resistant fibres and membranes inside, suggest the presence of epithelium and collagenous basement membrane (Dzik, 1999, 2003). Most likely these were animals being at least on the cnidarian (Antcliffe and Brasier, 2008) or ctenophore (Dzik, 2002) body plan level.

Loss of the mouth opening, as exemplified by the siboglinid polychaetes, may be connected with chemoautotrophic symbiosis but this, in the lack of mouth, requires increase of contact surface with the source of energy (hydrogen sulphide?), which is not the case with the petalonameans. But a lot of energy was necessary to penetrate hydraulically the sediment. One may ask for what purpose was this expenditure of energy? One possible answer is that it was for hydrogen sulphide uptake, like in present-day siboglinid polychaetes and bivalves (Julian et al., 1999; Dzik, 2002). This may also offer explanation for the very complex internal anatomy of the rangeid petalonameans. The high oxygen demand of the thioautotrophic symbionts requires circulatory organs for efficient distribution of oxygen carrying pigments (Childress and Girguis, 2011). If true, an explanation how substrates to chemoautotrophy entered the interior of the frond has to be found (Dufour and McIlroy, 2017).

8. Conclusions

The newly collected fossil Ediacarans from the Lomoziv Member of Mohyliv Formation show that at early ontogenetic stages these passive benthic organisms were active sediment burrowers. There is no need to invoke presence of cnidarians similar to the present-day sea anemones to explain traces of locomotion in the Ediacaran (Dzik et al., 2017). This may make the fossil record more consistent with molecular phylogenetic interpretations. In their further growth, the Podolian petalonameans depended on a periodic sediment deposition and on development of the microbial mat. Their growth was stadial and under control of rhythmic environmental factors. Location of the area near the South Pole in the Vendian suggests that climatic seasonality was the controlling factor. Co-occurrence of individuals of various ages indicates that there were prolonged episodes of conditions enabling development of microbial mat and its colonization by the petalonameans. In many cases death of the petalonameans communities significantly preceded deposition of the sediment layer, on the sole of which the discs' imprints are preserved.

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