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Intravital damage to the body of *Dickinsonia* (Metazoa of the late Ediacaran)

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Abstract.—Several specimens of *Dickinsonia* cf. *D. menneri*, originating from a single burial event at the Lyamtsa locality of the late Ediacaran (Vendian) in the southeastern White Sea area, Russia, represent deviations from normal morphology: a reduction in the total length of the body; the loss of portions of the body; various deformations of the transverse elements, called isomers; and splitting of the longitudinal axis with the formation of two posterior ends. It is assumed that these deformations were formed as a result of non-lethal damage, which occurred long before the burial event, and the response of *Dickinsonia* to them. The progress of the regeneration process at the damaged areas, and especially its deviations, indicates that the growth zone was located at the posterior end of the *Dickinsonia* body. The cause of non-lethal damage to *Dickinsonia* could not be established, but the local distribution of deformed specimens preserved in the same burial event alongside cyanobacterial colonies, and the presence of weak deformations, expressed only in shortening of the length of some isomers, lead to the conclusion that damage resulted from short episodes of physicochemical impact, rather than occasional attacks by a hypothetical macrophage.

Introduction

The famous romantic notion of the “Garden of Ediacara” proposed by Mark McMenamin is based on the assumption that the late Ediacaran involved the proliferation of “peaceful” immobile, macroscopic organisms feeding by photosymbiosis, chemosymbiosis, and osmotrophy (McMenamin, 1998; Seilacher, 1999; Laflamme et al., 2004, 2009; Laflamme and Narbonne, 2008). However, studies over the last two decades have shown the presence of mobile Metazoa with more advanced feeding methods in benthic communities of shallow marine waters of the late Ediacaran of Russia and Australia in the interval of ca. 558–550 Ma (Narbonne et al., 2012). Several species of the genus *Dickinsonia*, along with the genus *Yorgia*, closely related to it, destroyed the upper layer of microbial mats, leaving deep and wide depressions arranged in chains (Ivantsov and Malakhovskaya, 2002; Gehling et al., 2005; Ivantsov, 2011; Evans et al., 2019a, b). The small organisms that left *Helminthoidichnites* traces apparently fed on the substance of buried mats and dead bodies of macroorganisms, including those belonging to such relatively highly organized creatures as *Dickinsonia* and *Spriggina* (Gehling and Droser, 2018; Evans et al., 2020). The unique bilateral animal *Kimberella* had sharp “teeth,” by which it left scratches on the microbial mat and tore out large pieces of it (Ivantsov, 2013; Gehling et al., 2014). And it seems that the microbial substrate was not alone in experiencing aggression from this animal. There are various discoidal imprints belonging to the composite species *Aspidella terranovica* Billings, 1872 in the majority of Ediacaran localities. This species also includes discs that sometimes are identified as several species of *Cyclomedusa* (Gehling et al., 2000). These fossils are considered to be holdfast structures of the frond-like macroorganisms. Fossil remains of such holdfast structures that have been crossed by *Kimberella* traces were found in one locality in the southeastern White Sea area (north of European Russia) (Fig. 1). The fossil disc is represented by a negative imprint of the upper side of the body. The trace is equally distinct both on the disc and outside its boundaries, which indicates that it is the trace that superimposes the disc, and not vice versa. However, with such fossils, it is still not clear if the damage was caused to a living organism rather than to its carcass.

Evidence of intravital damage (i.e., damage that did not immediately lead to death) in fossil remains of Ediacaran macroorganisms is extremely rare and probably known only in some multifoliate rangeomorphs (Kenchington et al., 2018). This fact makes the discovery of a whole group of *Dickinsonia* specimens with such damage in the White Sea area highly interesting. We have previously published a small number of images of individual specimens of this group (Ivantsov et al., 2019b, c), but the entire known sample collection is described here for the first time. All found specimens belong to a single species of the classic Ediacaran genus *Dickinsonia*. The species is close to *Dickinsonia menneri* Keller in Keller and Fedonkin, 1976.

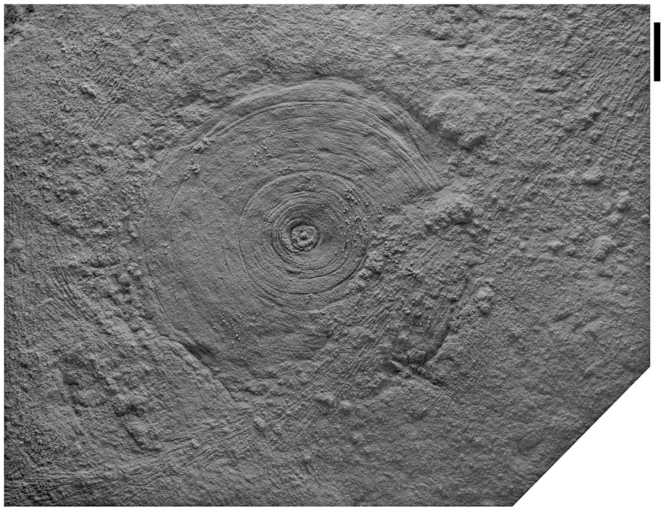

Figure 1. The feeding trace of *Kimberella* (*Kimberichnus teruzzii* Ivantsov, 2013) crossing the imprint of *Cyclomedusa* sp.; specimen PIN, No. 4853/1122; Late Vendian, the Ust-Pinega Formation, the uppermost part of the Syuzma Beds; Southeastern White Sea area, Solza locality, burial SL1(VII). The scale bars represent 1 cm.

A large array of information on *Dickinsonia* has accumulated over 70 years of research, including data on the body morphology, analysis of the molecular composition of the preserved organic matter, the structure, and the spatial distribution of the traces. These data allow us to consider these Ediacaran macroorganisms as specific early Metazoa similar to Placozoa (Rozhnov, 2009; Sperling and Vinther, 2010; Bobrovskiy et al., 2018a, 2019) or Eumetazoa and even Bilateria, with anteroposterior and dorso-ventral differentiation of a body that was capable of active movement (Fedonkin, 1990; Ivantsov and Malakhovskaya, 2002; Gehling et al., 2005; Ivantsov, 2011; Gold et al., 2015; Evans et al., 2017, 2019a, b; Ivantsov et al., 2019a, b). However, there are other interpretations that describe *Dickinsonia* as syncytial protists (Zhuravlev, 1993; Seilacher et al., 2003), “coelenterates” (Sprigg, 1949; Harrington and Moore, 1956; Valentine, 1992; Zhang and Reitner, 2006; Brasier and Antcliffe, 2008), and polychaetes (Glaessner and Wade, 1966; Wade, 1972; Conway Morris, 1989), along with a number of other, more exotic hypotheses.

Similar to the majority of other representatives of *Dickinsonia*, the body of *D.* cf. *D. menneri* was flattened and ovate-elongated (Fig. 3.1, 3.6). The usual imprint of the *D.* cf. *D. menneri* body clearly shows a transverse division into two rows of right- and left-handed elements (isomers) that extended from the body axis in an alternating order (Fig. 3.2). But in our view, this structure represents only a part of the organism’s body. It was a thin-walled structure that enveloped the internal parts of the body from above and below (Ivantsov et al., 2019b) and consisted of a substance more dense and resistant to decomposition than other materials that made up the *Dickinsonia* body (Bobrovskiy et al., 2019). The ventral and dorsal sections of this structure are preserved as two layers on some imprints of *Dickinsonia*. This structure seems to represent a basement membrane, and was covered externally with an ectodermal tissue (Ivantsov et al., 2019b). An unpaired lobe was located at one end of the body. It has a subtriangular outline in small specimens of *D.* cf. *D. menneri*, and a pear-shaped outline in large specimens (Figs. 3.3, 3.6, 4.1). Judging from associated chains of feeding traces found alongside body imprints of *Dickinsonia costata* Sprigg, 1947, the section bearing this unpaired lobe was likely the anterior end of the *Dickinsonia* body, judging from the direction of its movement (Gehling et al., 2005, 2014; Evans et al., 2019a). There is a shallow longitudinal depression (Figs. 3.1, 3.3, 3.7, 3.8, 4.4, 4.8), which is likely a reflection of internal axial structure of an unclear nature, possibly the digestive canal, on the surface of many imprints (Wade, 1972; Jenkins, 1992). The growth during ontogeny of *Dickinsonia* involved an increase in the number of isomers, as well as their linear dimensions. This process was accompanied by a transformation of the shape of the anterior lobe, and a reduction in its relative area (Runnegar, 1982; Hoekzema et al., 2017).

Materials

Macrofossils exhibiting evidence of damage were found in the Lyamtsa locality, located on the south coast of the Onega Peninsula, where the sediments of the Lyamtsa and Arkhangelsk Beds of the Ust-Pinega Formation of the Late Vendian are exposed (Fig. 2). The locality is characterized by the so-called Flinders- or Flinders-Belomorian-style preservation of fossil remains, in which the body imprints are located on the soles of sand layers (Narbonne, 2005; Ivantsov and Zakrevskaya, 2018). In this case, the bodies of a variety of benthic organisms were buried in life position (Seilacher, 1999; Grazhdankin, 2003, 2004; Narbonne, 2005; Droser et al., 2006; Ivantsov, 2012). *Dickinsonia menneri* is the only species of this genus distributed in the lowest part of the Vendian of the White Sea section in the interval up to the upper half of the Syuzma Beds (Fig. 2) (Ivantsov, 2007). The studied material originates from the Lyamtsa Beds from a single bedding plane of the local burial event, marked as bed L2(XII).

Repository and institutional abbreviation.—Type, figured, and other specimens examined in this study are deposited in the Paleontological Institute of the Russian Academy of Sciences (PIN RAS), Moscow, Russia (collection number 4716).

Results

The sole of a cross-bedded sandstone of variable thickness (3–17 cm) serves as the fossiliferous surface of the L2(XII) burial event. The surface is even and has a microbially induced texture in the form of low, flat-topped tubercles separated by curving grooves (Fig. 5.2). In places, this surface bears the casts of shallow (up to 1 cm in depth) erosion channels (Fig. 5.3). The diversity of the assemblage of macrofossils on this bed is extremely poor. In addition to *D.* cf. D. *menneri* it contains *Beltanelliformis brunsae* Menner in Keller et al., 1974, *Parvancorina minchami* Glaessner, 1958, fragments of ribbon-like algae, small palaeopascichnids, rare traces of *Epibaion axiferus* Ivantsov in Ivantsov and Malakhovskaya, 2002, and another two or three poorly diagnosed taxa. The deformed specimens of *Dickinsonia* and the specimens without visible damage are located together, without sorting by size.

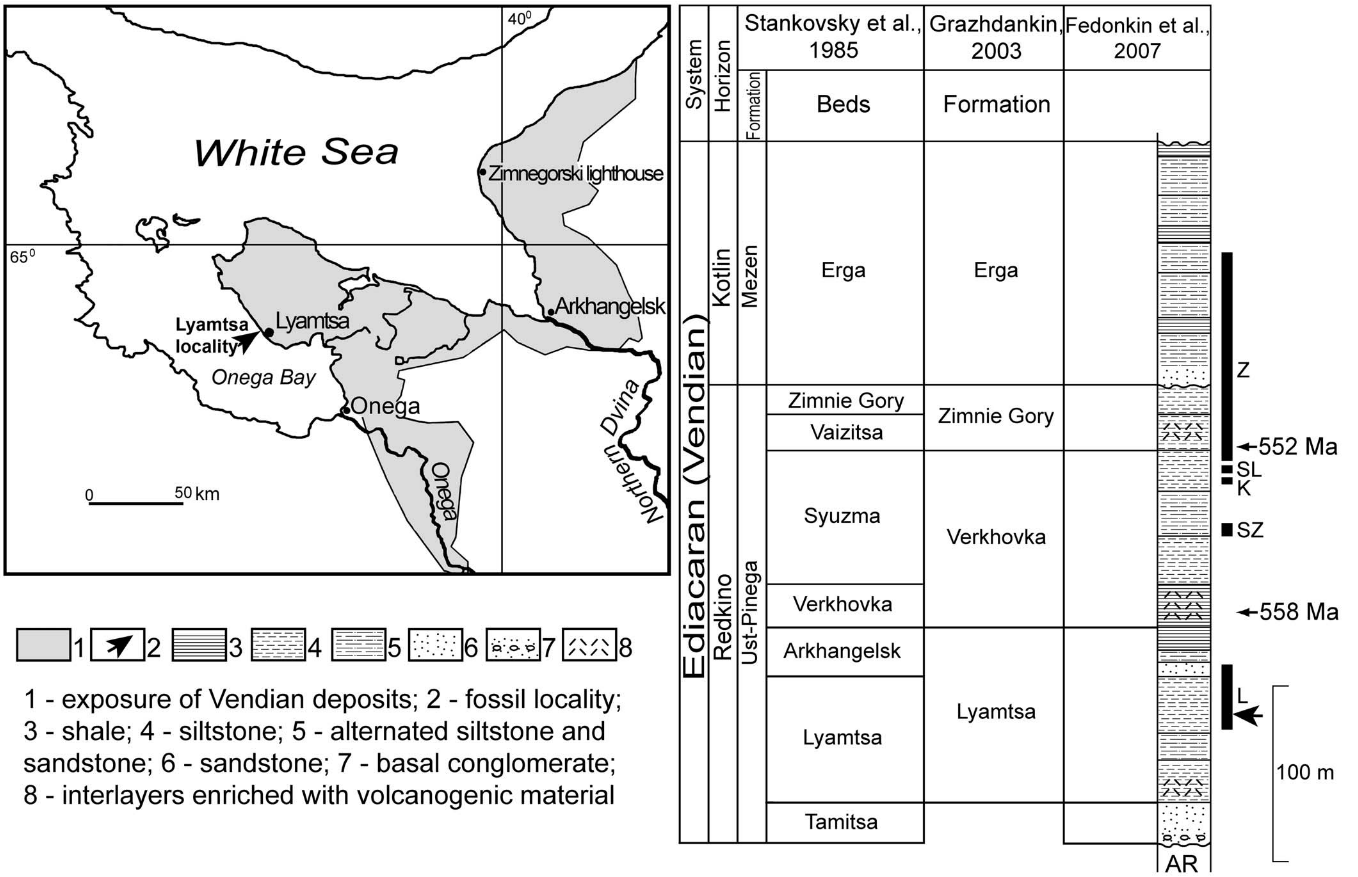

Figure 2. Geographical and stratigraphic position of the Lyamtsa locality, burial L2(XII) (arrow); black vertical stripes on the right correspond to the intervals of the localities: L = Lyamtsa, SZ = Suyzma, K = Karakhta, SL = Solza, Z = Zimnie Gory.

In total, 146 specimens of *Dickinsonia* of various sizes and with different numbers of isomers were discovered in the local burial L2(XII) (Figs. 3.1, 3.5, 3.6, 8). The exact number of the isomers often cannot be calculated because their thickness is greatly reduced towards the posterior end of the body, and they become indistinguishable against the background of a granular rock. However, this indistinct zone is rather small; its area is ~0.5 mm^2 and does not depend on the size of the specimen. Therefore, we consider it negligible when estimating the relative number of isomers.

Bayesian Information Criterion (BIC) analysis was used to determine the likely number of size groupings for distributions of *Dickinsonia* using the MCLUST package in R (Fraley and Raftery, 2007; Darroch et al., 2013; Zakrevskaya, 2014). As a result, the set of measured samples falls into two groups according to both univariate and multivariate analyses for logged data (Figs. 6, 7): (1) individuals of small size with body length 4.1–13.2 mm with the number of visible isomers from 15 to 38 in one row (106 specimens); and (2) medium and large individuals with length 18.3–122.0 mm with the number of visible isomers from 70 to 173 in one row in non-deformed individuals (40 specimens) (Fig. 6). Based on our observations of the communities of Ediacaran (Vendian) organisms of the White Sea region (Zakrevskaya, 2014), such a division indicates the existence of two or more different generations of *Dickinsonia* in this locality. Clear deformations were found in only 23 specimens of large and medium sizes and in one specimen of small size. A significant reduction in the relative length of the body is typical for these deformed specimens, so that the length of the body approximates to the width or becomes even smaller (Figs. 3.3, 4.1, 4.4). Meanwhile, the undamaged specimens are comparatively elongated, and the degree of their elongation increases with addition in the number of isomers (Fig. 3.1, 3.6).

According to the nature of their development, the deformations observed on the imprints can be divided into two-sided and one-sided deformations. The two-sided deformations affect the isomers of both rows, with the affected isomers being more or less symmetrical about the axis of the body. The area of two-sided deformations itself is located in the posterior half of the body in all studied specimens. The one-sided deformations involve the isomers of only one row, and such changes can be found at any point along the body axis, except for the posterior end.

The area of two-sided deformations is enclosed between the anterior and posterior regions of unaltered isomers in all studied imprints (Fig. 9). Its boundary with the posterior region is here called the "break line," which demonstrates a sharp transition from the most-deformed isomers to the isomers of normal shape. By contrast, the transition to the anterior region is continuous and accompanied by a gradual decrease in the intensity of deformation (Figs. 3.3, 4.1). We do not mean that there is an actual break in the integrity of the *Dickinsonia* body along this

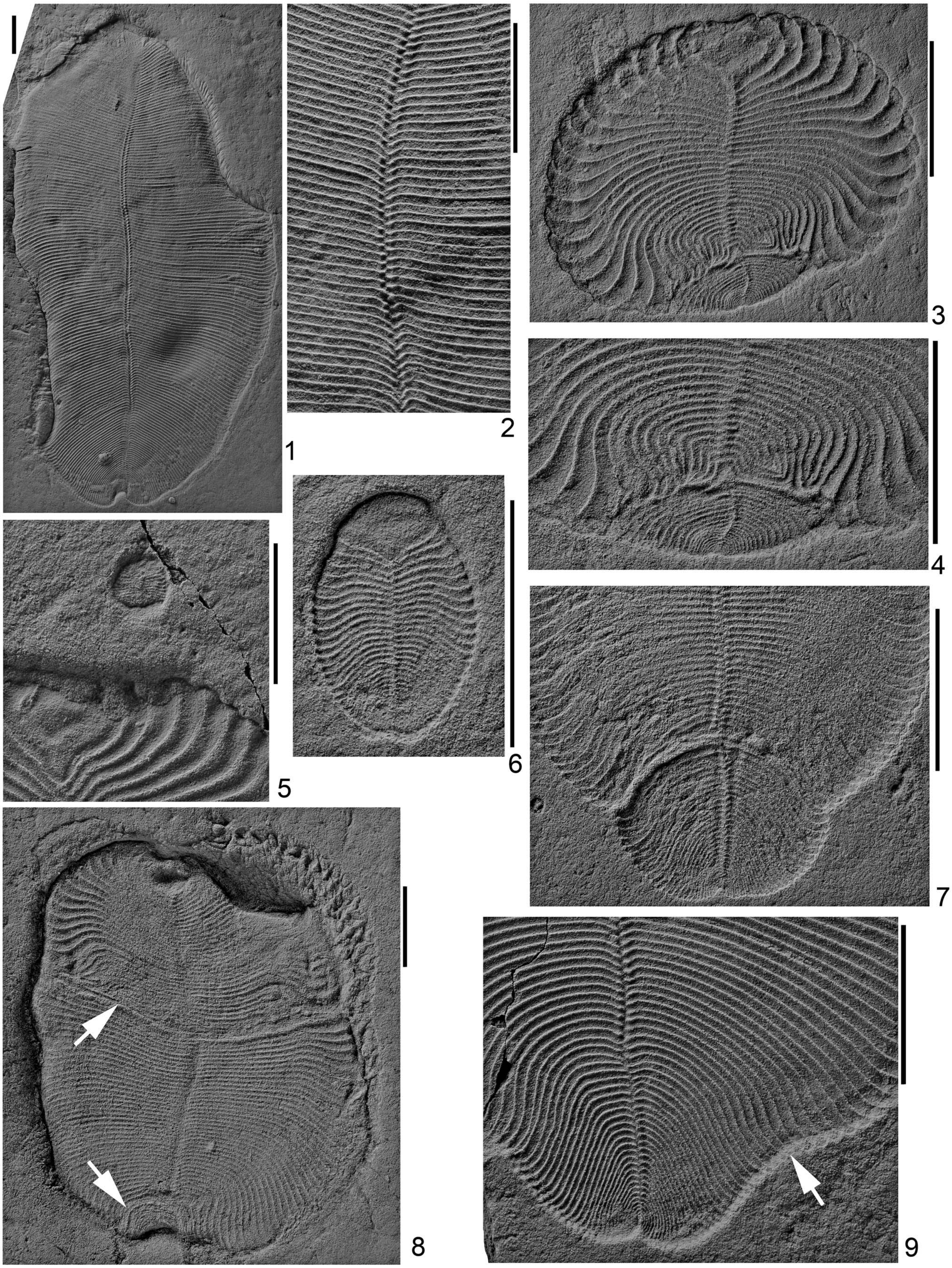
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Figure 3. *Dickinsonia* cf. *D. menneri* from the sediments of the Ust-Pinega Formation, late Vendian, southeastern White Sea area, Lyamtsa locality, burial L2(XII). (**1**) Specimen PIN, No. 4716/5165, one of the largest undamaged specimens of the species; the left (on the imprint) margin of the body is completely, and the right one is partially, turned up into the overlaying layer; a cross-overlapping of the dorsal and ventral parts of the dissected structure is observed at the top left of the imprint, plan view; (**2**) same as (**1**), fragment showing an alternating arrangement of isomers; (**3**) highly deformed specimen PIN, No. 4716/5187, plan view; (**4**) same as (**3**), posterior end; (**5**) specimen PIN, No. 4716/5149 (upper part of the figure), one of the smallest known specimens of *Dickinsonia* from Lyamtsa; its posterior end is turned up; the length of the visible fragment is 3.5 mm; (**6**) small, normally developed specimen without damage, specimen PIN, No. 4716/5150; (**7**) deformed specimen with lateral displacement of the axial structure along the break line, specimen PIN, No. 4716/5177; (**8**) specimen PIN, No. 4716/5282, experienced non-lethal damage twice; arrows indicate break lines; the anterior (upper in the figure) end of the body has been slightly bent and compressed during the taphonomic event, resulting in the formation of a band of scratches on the host rock surface; (**9**) specimen PIN, No. 4716/5181, exhibiting minor deformation, expressed as a reduction in the length of several isomers (arrow). The scale bars represent 1 cm.

line, but we observe a break in the normal sequence of the isomers' articulation. Only a few pairs of isomers are usually subjected to sharp deformations. The posterior region is mostly small (Fig. 9); its length varies from 3.7 to 17.1 mm, making up from 1/20 to 1/2 of the total body length of *Dickinsonia*. The number of isomers that can be distinguished in the posterior region varies from 10 to 35 in one row (Fig. 5.2). The peculiar specimen PIN, No. 4716/5282 has two zones of two-sided deformations (Fig. 3.8); the first one is located near the posterior end of the body, and the second one in the middle. The 20 mm long section enclosed between the two break lines contains ∼40 pairs of isomers.

The tiniest observed changes (specimen PIN, No. 4716/5181) involve a small reduction in the length (the distance between the proximal and distal ends) of several isomers, causing shallow invaginations on the lateral edges of the body, along with a slight curvature of the proximal ends of these isomers (Fig. 3.9). However, often the reduction in the length of the isomers is significant and progresses towards the posterior end of the body, as in specimen PIN, No. 4716/5187 (Fig. 3.3). On the same specimen, typical fan-shaped bends of normally developed isomers are seen, which in this way cover the deformed area from the sides. Sometimes wavy and zigzag-shaped bends of isomers can be observed. They are especially distinct near the axis of the body, as in specimen PIN, No. 4716/5170 (Fig. 4.2), and increase in magnitude in the posterior isomers. In this specimen, the proximal parts of several pairs of isomers are partially destroyed and partially crumpled. These "clumps" press on the isomers of the anterior region (some harder, the others weaker), causing them to bend sharply. This bend is transmitted to the following pairs of isomers, gradually diminishing towards the anterior end of the body. Some specimens show a rupture of the axial structure and a slight displacement of the ends of the separated parts along the rupture line relative to the vertically oriented "sagittal" plane (Fig. 3.7).

We also attribute a splitting of the axis and dividing of the posterior end of the body in two (into two series of isomers) to the two-sided deformations. In specimen PIN, No. 4716/5146, the second series, consisting of small isomers, was formed on the right (in the imprint) side of the body. The symmetry axis of this secondary series is directed sideways at a large angle to the axis of the main body (Figs. 4.6, 4.7, 10). In specimen PIN, No. 4716/5188, both series of isomers have similar dimensions and are more or less symmetrical (Figs. 4.4, 4.5, 11). However, their inner rows are suppressed and partially upturned (passing into the host sandstone). Therefore, the posterior end of this specimen has the form of a two-horned tail with the tips of the "horns" facing each other.

One-sided deformations were recognized only in two specimens of medium size. In specimen PIN, No. 4716/5179 (28 mm in length), the distal ends of two dozen isomers of the left row (in the imprint) are lost in the posterior part of the body (Fig. 4.3). The proximal ends of the majority of these isomers are completely normal. The sample also displays two-sided deformation. The posterior end and the lateral margin of the organism's body were affected. Almost the entire left (in the imprint) side of the body is deformed in specimen PIN, No. 4716/5182 (23 mm in length) (Fig. 4.8). No fewer than a dozen anterior isomers are absent on the left side of the body, compared to the right one, and the lengths of the remaining ones are significantly reduced. A part of the axial structure and, possibly, the proximal ends of the isomers of the right row are also lost in this case. As a result, the body of *Dickinsonia* was curved to the left and the axial structure is arcuate. The collection also contains one very small specimen (specimen PIN, No. 4716/5226), the left (in the imprint) side of which is arcuate, and the entire right side is crumpled so intensely that the isomers on it are hardly visible. However, whether this may be connected with intravital damage cannot be established due to the small size of the specimen (its length is 4.8 mm).

Therefore, the following suite of deformations is observed in *Dickinsonia* specimens of the Lyamtsa locality: (1) a change in the body proportions with a reduction in length relative to width; (2) shortening of the isomers' lengths with the formation of the invagination of the lateral edge of the body; (3) sharp nontypical bends of the isomers close to the midline; (4) a disappearance of the distal and proximal ends of the isomers and even entire isomers; (5) a fan-shaped bend of the distal ends of the isomers; (6) curvature of the body axis; (7) a rupture of the axial structure followed by a shifting of a part of it towards the "sagittal" plane; and (8) splitting of the body axis with the formation of an additional series of isomers.

Discussion

Many well-known imprints from Ediacara and the White Sea region show deviations from the ideal morphology of *Dickinsonia*, expressed as compression, stretching, curvature, wrinkling and various folding of the body, overlapping of some parts of the body with each other, intersecting of the inner layers, longitudinal wrinkling, pinch-out, and bifurcation of individual isomers. Sometimes the imprint shows the disappearance of a part of the body or its fragmentation. The occurrence of these deformations is explained by the folding, twisting, stretching, and rupture of the body during burial (Seilacher, 1989; Gehling et al., 2005; Brasier and Antcliffe, 2008; Evans et al., 2019b), by

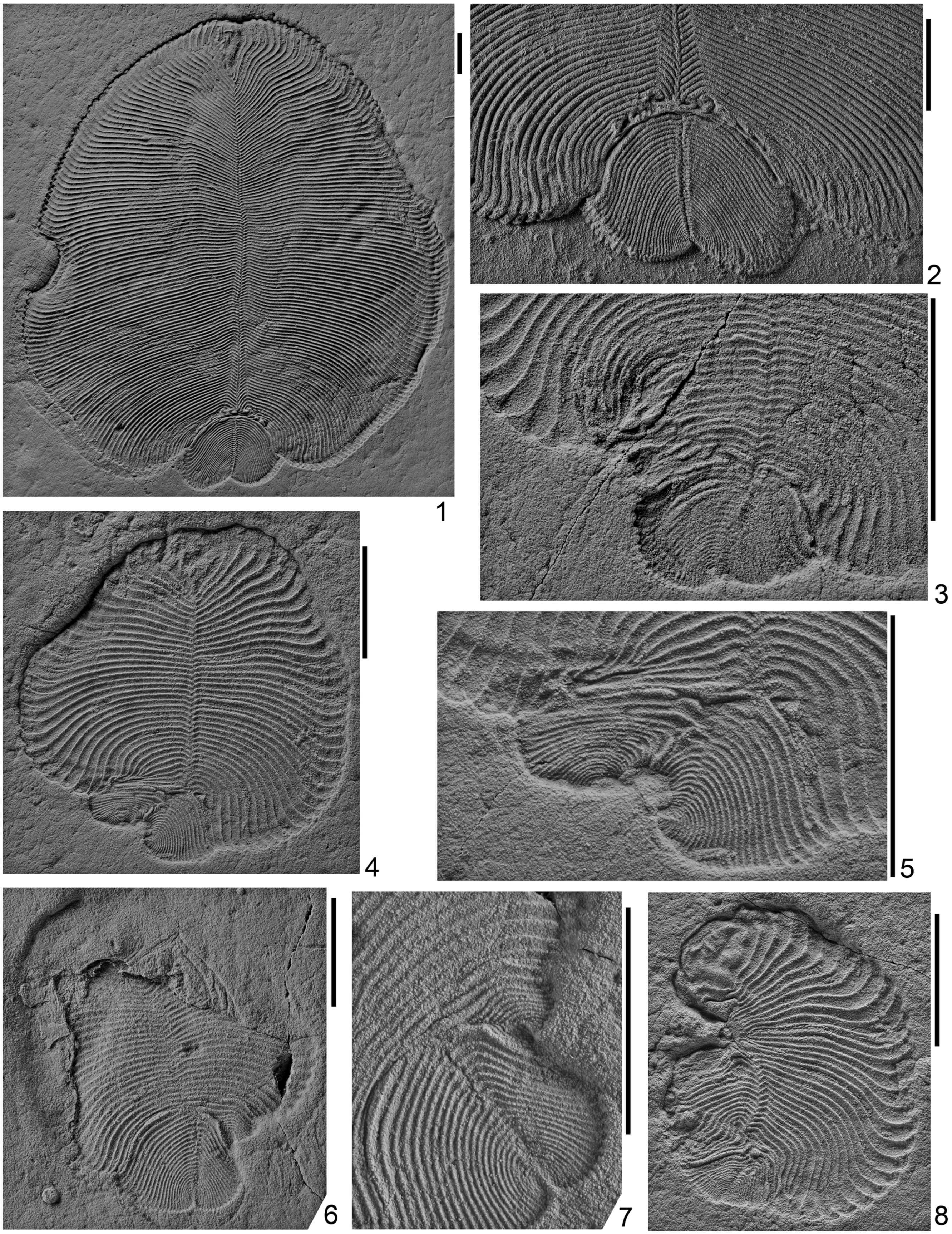
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Figure 4. Deformed specimens of *Dickinsonia* cf. *D. menneri* from the Ust-Pinega Formation, Late Vendian, Southeastern White Sea area, Lyamtsa locality: (**1**) specimen PIN, No. 4716/5170, plan view, one can clearly see a gradual reduction of the curvature of the bends of the isomers' inner ends in the anterior direction starting from the deformation zone; (**2**) same as (**1**), posterior end, latex cast from a natural mold; (**3**) specimen PIN, No. 4716/517, posterior end; (**4**) specimen PIN, No. 4716/5188, plan view; (**5**) same as (**4**), posterior end; (**6**) specimen PIN, No. 4716/5146, with intravital damage to the posterior end of the body, leading to splitting of the body axis and subsequent growth in two directions, plan view; (**7**) same as (**6**), fragment, the anterior part of the body was raised and located within the overlapping layer, the boundaries of the body are indicated by a sharp bend of the relief; (**8**) specimen PIN, No. 4716/5182, showing deep one-sided and two-sided deformations—loss of the several anterior isomers and a significant reduction in the length of the isomers of the left (in the figure) half of the body; loss of the front section of the axial structure and, possibly, the proximal ends of the adjacent isomers of the right row; lateral displacement of the posterior section of the axial structure and wave-like bending of the adjacent isomers; general curvature of the body. All scale bars represent 1 cm.

the lifting of some of its parts from the bottom surface (Evans et al., 2015), by shifting the structures of the upper and lower sides of the body relative to each other (Ivantsov et al., 2019b), or by penetration of the sediment into the body (Dzik, 2003). Concentric folds and a decrease in the body surface area relative to the feeding trace are interpreted as the result of muscle contraction preceding the death of the organism or postmortem contraction (Glaessner and Wade, 1966; Wade, 1972; Runnegar, 1982; Seilacher, 1989; Gehling, 1991; Jenkins, 1992; Gehling et al., 2005; Evans et al., 2019b). The pinch-out and the bifurcation of the isomers still require explanation (Brasier and Antcliffe, 2008). Folding, disappearance of parts, reduction in the body area during the taphonomic event, and separation into layers were also found on the fossil remains of *Dickinsonia* from the burial L2(XII) (Bobrovskiy et al., 2019; Ivantsov et al., 2019b, c). In the samples presented in this article, we can observe curling of the body margins and their shift along the bedding plane (Figs. 3.1, 3.5, 3.8, 4.1), lifting of a part of the body into the overlying sediment (Fig. 4.6), and overlapping of the dorsal and ventral parts of the dissected structure (Figs. 3.1, 4.4, 11).

The deformations studied here differ from those previously described in displaying a group of shortened isomers sharply "cut" from both margins. These isomers are surrounded on all sides by curved isomers of normal length. Only in cases of weak deformation do the shortened isomers have no other pronounced defects (Fig. 3.9). The attribution of this case to the studied phenomenon is determined by the symmetric arrangement of the groups of the shortened isomers on both sides of the body, and by some curvature of the corresponding section of the axial structure. Alternatively, it can be assumed that lateral compression of the *Dickinsonia* body in this area was the result of contraction of hypothetical muscles. However, there are no other possible signs of compression, such as the development of transverse folds in the isomers or the appearance of grooves on the surface of the host sandstone due to the displacement of the body margin (Evans et al., 2019a).

In some cases of deformation, it is possible to suspect folding and extrusion of the distal sections of the folds upwards into the overlapping sediment (Figs. 3.7, 4.5 [upper left quarter]). Here the difference in width and orientation of the isomers on both sides of the fold, although sharp, is nevertheless consistent with the observations of the degree of possible stretching of *Dickinsonia* body (Evans et al., 2019b). However, many of the described deformations (for example, Fig. 3.3, 3.4) cannot be explained by folding.

We must also consider the assumption that structures that appear to be two-sided deformations are, in fact, a consequence of the process of a vegetative reproduction, possibly present in *Dickinsonia*. In this case, the posterior region of normal isomers may represent a future juvenile, and the break line may be the place of its contact with the original organism. A similar mechanism of vegetative reproduction, called paratomy, occurs in some modern invertebrates, such as flatworms and polychaetes (Ruppert et al., 2004), which are groups to which *Dickinsonia* previously has been allied (Glaessner and Wade, 1966; Termier and Termier, 1968). This observation is supported by the similarity in the number of isomers visible in the small specimens (15–38 in one row) and in the posterior region of the deformed specimens (10–35 in one row). However, the pair of maternal and daughter individuals must exceed the non-divided organism in length or at least be equal to it. Meanwhile, as was noted above, the relative length of the deformed specimens is less than that of undeformed specimens (Fig. 8.1). The size of the young specimens present on the same bed is substantially smaller than the size of a hypothetical "not yet detached outgrowth." While the length is quite similar (4–13 mm), the body width of free individuals reaches 11 mm, and the width of the posterior region in the non-deformed isomers is almost twice as large and reaches 18.5 mm (Fig. 8.2). In one large specimen (PIN No. 4716/5170), the length of the posterior region is 17.1 mm, and its width is 23.5 mm (Fig. 4.1, 4.2). And finally, the described structure was found only in a few *Dickinsonia* specimens of the same species, originating from a single local burial, whereas hundreds of specimens of different *Dickinsonia* species from the numerous local burials of Eastern Europe and South Australia have never shown anything like a "daughter individual."

It seems to us that the most probable explanation is that the considered deformations are the result of damage to some parts of *Dickinsonia* body, and the body's reaction to this damage, as well as, possibly, the result of some short-term depressing effect on the growth of the isomers. In the case of mild deformations (Fig. 3.9), it was probably only temporary inhibition of growth. In the cases of two-sided deformations, the damage was caused to the posterior end of the body. In addition, the organism lost its growth zone (see below), probably along with some isomers. Some of the isomers closest to the axis on both sides exhibit damage to their distal ends (Fig. 3.3). Sometimes the isomers closest to the damaged region retain their distal sections, but lose the proximal ends adjacent to the body axis (Fig. 4.2). The *Dickinsonia* body responded to damage by surrounding the damaged areas with normal isomers (Figs. 3.3, 3.4, 3.8, 4.2, 4.5), and through curvature of the body to compensate for the loss of part of the flesh (Fig. 4.8). This indicates the intravital, non-lethal nature of the negative impact. Traces of locomotory activity found in association with damaged specimens (Ivantsov et al., 2019a) show that these deformed individuals did not lose the ability to move independently.

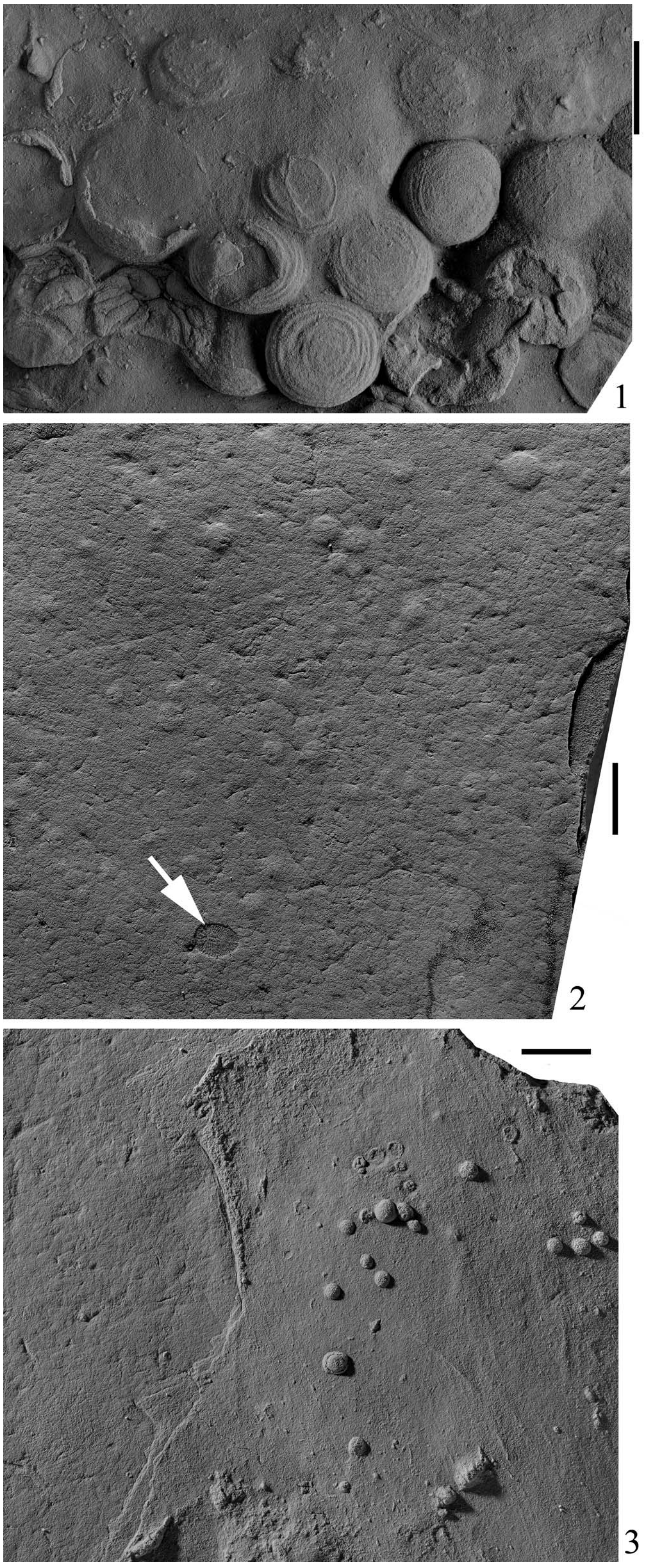

Figure 5. Cyanobacterial colonies *Beltanelliformis brunsae* Menner in Keller et al., 1974 from the Lyamtsa locality. (**1**) Medium-sized specimens from talus in the lower part of the Lyamtsa outcrop; (**2**) small specimens from burial L2(XII), casts of depressions formed over collapsing colonies lying inside or immediately below the microbial mat and "translucent" through the structure of its surface (arrow indicates the imprint of a small *Dickinsonia* cf. *D. menneri* lying on the mat); (**3**) small specimens from burial L2(XII), imprint of the microbial mat's surface (left third of the figure) and cast of an erosive cutting that removed the mat and revealed a cluster of the *Beltanelliformis* colonies (right side of the figure). All scale bars represent 1 cm.

Based on the available samples, it appears that the damaged ends of the isomers were not restored, but the isomers retained the possibility of their own growth and continued to increase in length. As a result of this growth, the damaged parts of the isomers gradually moved away from the axis to the lateral margins of the body (Fig. 3.8). The organism did not completely lose its ability to form new isomers—the growth zone was re-stored after the negative factor was removed and growth of the isomers was resumed in the usual manner. Regeneration of the growth zone was sometimes accompanied by defects. For example, a small lateral displacement of the axial structure is observed on the break line in many specimens (Fig. 3.7, 3.9). Their growth zone probably was recovered slightly away from the "sagittal" plane of the body. Two specimens show bifurcation of the body axis with the formation of an additional series of isomers (Figs. 4.4, 4.5, 4.6, 4.7, 9, 11). The process of divergence of the two newly formed growth zones could be gradual. For instance, the additional right (on the imprint) series of the isomers was formed in the specimen PIN, No. 4716/5146 (Fig. 4.6, 4.7). In this case, we can see that at first, after the resumption of the formation of the isomers, isomers of the left series appeared only on the left side, while in the case of the right series they appeared only on the right side (Fig. 10).

The specimen PIN, No. 4716/5282 (Fig. 3.8) shows two episodes of restoration of the growth zone, separated by a significant period of time during which at least 40 pairs of normally developed isomers were formed. Thus, *Dickinsonia* from Lyamtsa was a rather resilient animal, and could survive the loss of significant areas of the body and even parts of the axial structure. They could relatively easily restore the growth zone if it was lost.

Implications for understanding anatomy and developmental processes, and the position of *Dickinsonia* within the Metazoa

In many deformed specimens of *Dickinsonia* from Lyamtsa, the distal ends of the isomers of the damaged zone are truncated by the isomers of the first pair of the posterior unchanged area, and even stand perpendicular to them (Fig. 3.3). However, the body does not break along this junction. If there was a break, then the posterior area would be practically free, and would connect with the rest of the body only in a very limited area near the axis. In this case, the posterior part is expected to be unconstrained and would easily move relative to the rest of the body. So, we would see an overlapping of the edges of the anterior and posterior areas on each other on one side of the body, and the divergence of the areas with a gap on the other. In reality, this never happens. Something prevented the areas of normal isomers from diverging. This may be a confirmation of the authors' conclusion about the presence of an ectodermal integument, which covered the body with a continuous shield from the dorsal side, in *Dickinsonia* and related organisms (Ivantsov et al., 2019b).

It is thought that an increase in the number of transverse elements of *Dickinsonia* was achieved by terminal addition of new ones at the posterior end of the body (Runnegar, 1982; Gold et al., 2015). As a result, the body was extended in the posterior direction (Fig. 3.1, 3.6), while the previously formed elements moved away from the posterior end (Fig. 12.1). According to

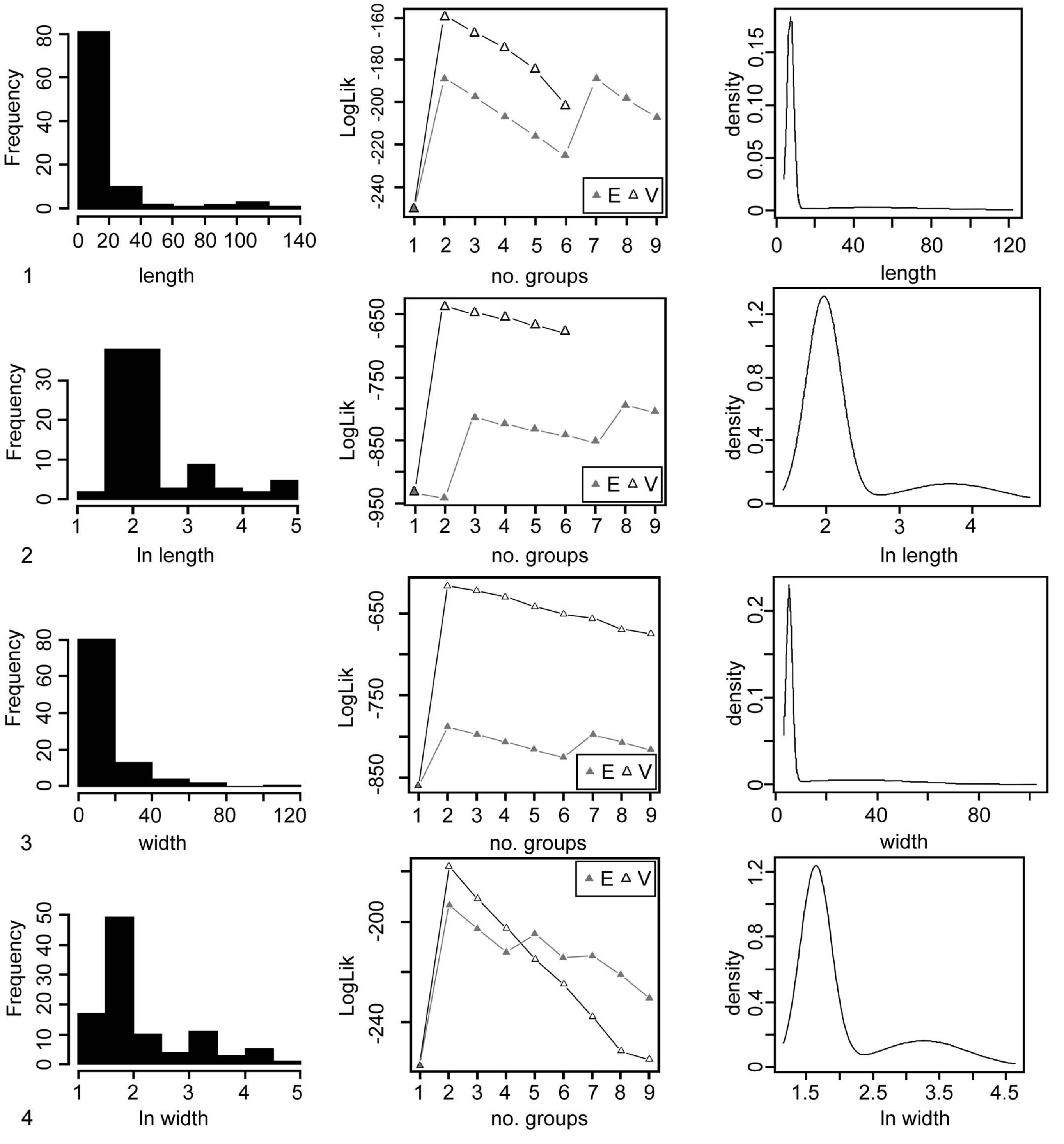

Figure 6. Statistical histograms showing size-frequency distributions, univariate BIC curves (E = equal variance, V = unequal variance, LogLik = log likelihood value), and density distribution plots for *Dickinsonia* from the Lyamtsa locality. (**1**) Length in mm; (**2**) logged length; (**3**) width in mm; (**4**) logged width.

the hypothesis of the isomeric structure of the *Dickinsonia* body, each new isomer probably appeared in the space between its two predecessors and alternately shifted to the right and to the left side of the longitudinal axis (Ivantsov, 2008). This resembles the formation process of germ leaves in the apical meristem of plants. However, an alternative hypothesis was recently made, suggesting that growth occurred near the opposite end of the body of *Dickinsonia* (Hoekzema et al., 2017; Dunn et al., 2018). According to this hypothesis, a pair of new isomers (constituting a whole segment, rather than separated) was formed on the edge of the triangular lobe and expanded the body. In this case, the growth of *Dickinsonia* resembled the growth of articulate animals (Fig. 12.2). The appearance of the deformed White Sea specimens of *Dickinsonia* with a posterior region distinctly

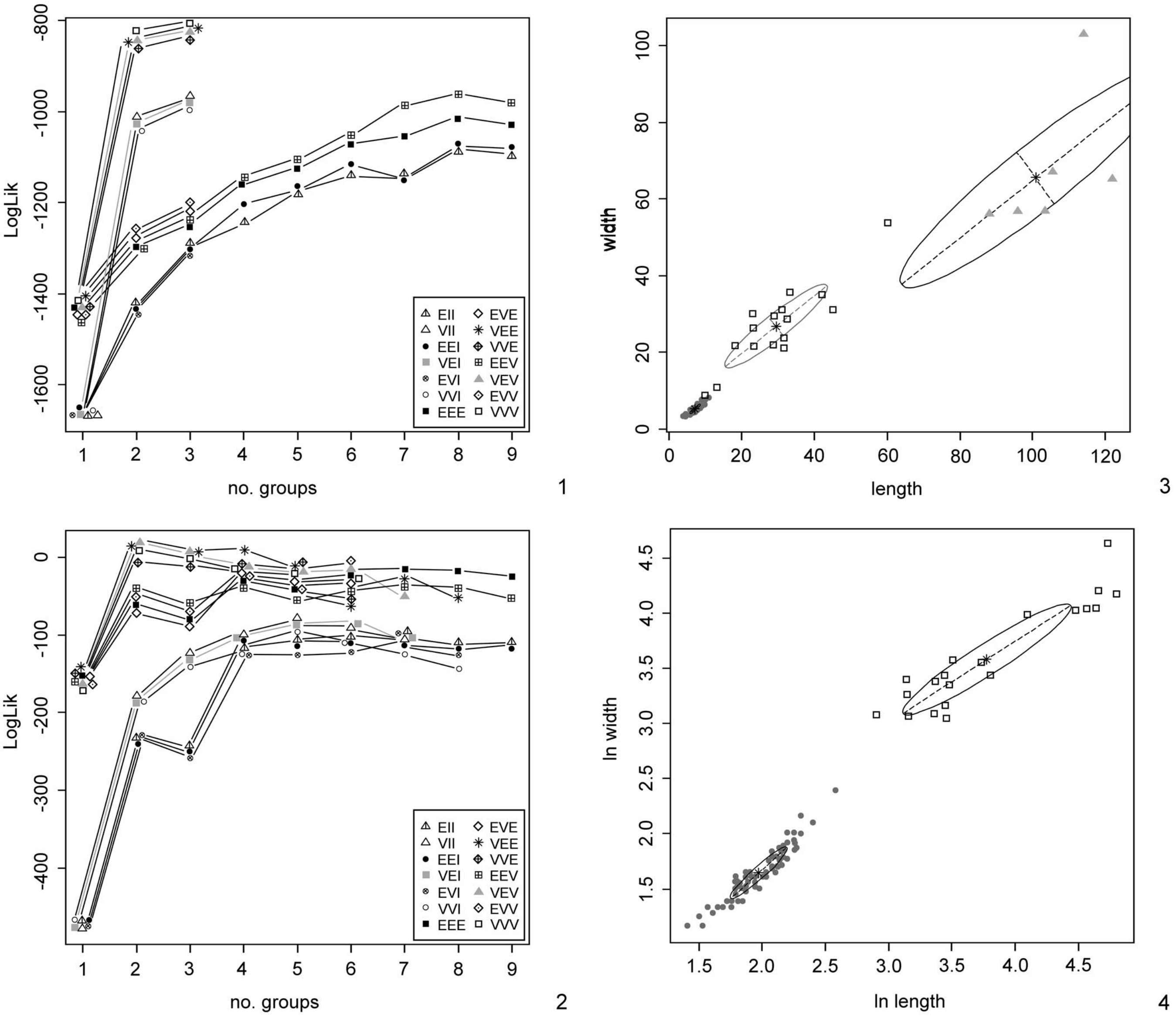

Figure 7. Multivariate BIC plots and classifications. (**1**) Length and width, best BIC models are VEE, VEV, VVV with 3 clusters; (**2**) logged length and width, best BIC models are VEV, VVV, VEE with 2 clusters; (**3**) classification for length and width, the ellipses superimposed on the classification plots correspond to the covariances of the components; (**4**) classification for logged length and width. The BIC plot shows each BIC value for each profile in which line graphs illustrate the different types of multivariate normal distributions integrated into the model per cluster. Each model is illustrated with a different icon and a three-letter sequence. The letter sequence is a code for the geometric characteristics of volume, shape, and orientation (E = equal, V = varying, I = shape, or orientation). Models: EII = spherical, equal volume; VII = spherical, unequal volume; EEI = diagonal, equal volume and shape; VEI = diagonal, varying volume, equal shape; EVI = diagonal, equal volume, varying shape; VVI–= diagonal, varying volume and shape; EEE = ellipsoidal, equal volume, shape, and orientation; EVE = ellipsoidal, equal volume and orientation, varying shape; VEE = ellipsoidal, varying volume, equal shape and orientation; VVE = ellipsoidal, varying volume and shape, equal orientation; EEV = ellipsoidal, equal volume and shape, varying orientation; VEV = ellipsoidal, equal shape, varying volume, and orientation; EVV = ellipsoidal, equal volume, varying shape, and orientation; VVV = ellipsoidal, varying volume, shape, and orientation. For a detailed description, see Fraley and Raftery, 2007; Darroch et al., 2013.

separated from the rest of the body along the break line and resembling, for example, the trilobite pygidium suggests the possibility of a third hypothetical variant of the formation of new isomers: insertion of new isomers somewhere within the middle of the organism, in front of some primary group of isomers (Fig. 12.3), formed behind the triangular lobe at the earliest stages of individual development. This variant can be supported by our conclusion concerning the existence of a dissected larval stage in the ontogenesis of *Dickinsonia* (Zakrevskaya and Ivantsov, 2017).

The validity of the second and third hypotheses is contradicted by the existence of the specimens with a split axis and an additional series of isomers in the posterior region of the body of *Dickinsonia*. The presence of such a series is possible only with a posterior terminal location of the growth zone. Also, the last two hypotheses cannot explain the formation of the symmetry of the gliding reflection typical for *D.* cf. *D. menneri* from Lyamtsa. Thus, the most valid hypothesis is that the growth zone is located at the posterior end of the body of *Dickinsonia*.

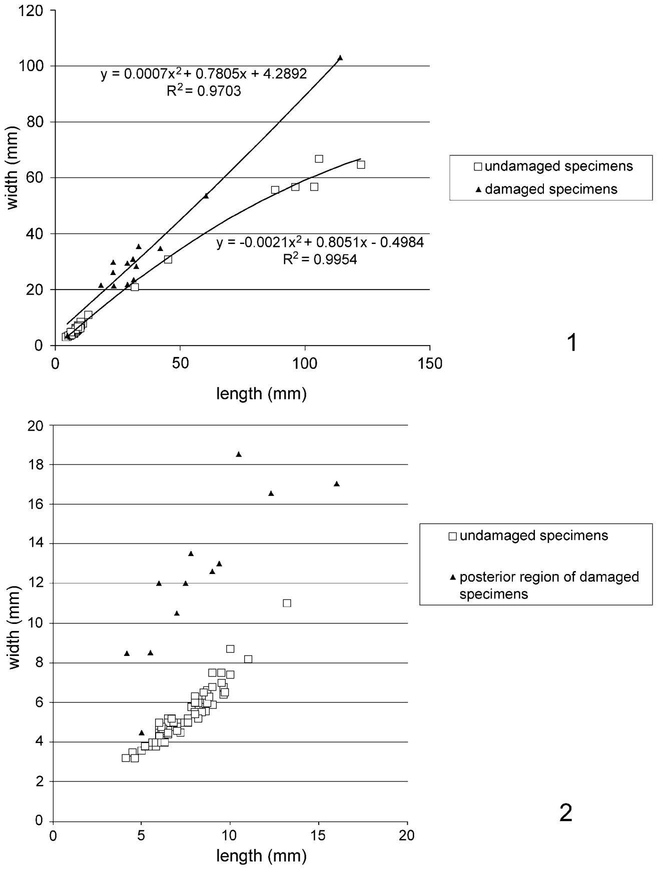

Figure 8. The ratio of length to width in *Dickinsonia* from Lyamtsa. (**1**) Damaged (14 specimens) and undamaged specimens (78 specimens); (**2**) small undamaged specimens (71 specimens) and a posterior region of damaged specimens with two-sided deformations (12 specimens).

The discovered ability of *Dickinsonia* to regenerate cannot alone be an argument in the discussion about the position of these creatures in the Metazoa system. However, the conclusion about the terminal location of the growth zone, made on the basis of the recognition of splitting of the axis of the regenerated area of the body, is very important in this regard. The posterior terminal location of the growth zone, along with the isomeric structure of *D.* cf. *D. menneri*, makes the position of *Dickinsonia* among the currently known branches of Bilateria unclear (see also Dunn et al., 2018).

The nature of the damaging factor

The cause of the damage to *Dickinsonia* from the Lyamtsa locality is mysterious. In the body of *Dickinsonia*, the defects of the margins and posterior end resemble healed injuries of different genesis known in fossil invertebrates. Such damage of the shields of trilobites were described by many researchers (see modern review by Bicknell and Pates, 2020), including one of the authors of the present article (Ivantsov, 2003). The injuries of trilobites associated with the attacks are concentrated at the margins of the pleura of the thorax and pygidium, mainly in the posterior part of the body (Babcock, 1993). This localization is explained by the behavior of a predator chasing its prey from behind and the reaction of the victim to an attack, expressed as turns in one direction or another. In addition, the pleural damage was less dangerous for trilobites than damage to the head shield and rachis, where their main vital organs were located. Therefore the individuals with such injuries were more likely to survive (Babcock, 1993).

In *Dickinsonia*, as well as in trilobites, the deformations tend toward the posterior half of the body. Most of them are more likely to represent a loss of body part rather than to be a result of inhibition of the development. It is possible that *Dickinsonia* was attacked by an unknown predatory animal, whose remains for some reason are not preserved in the burials of the Flinders-Belomorian style. However, the damage to the *Dickinsonia* body does not show any consistent shape at the margins that could be associated with the morphology of offensive weapons of a predator. In addition, the predominant posterior localization of their deformations could be caused by increased vulnerability of the growth zone. It is difficult to explain the weak deformations, expressed as a small reduction in the length of the isomers, by direct physical action. Also, we cannot ignore the above-noted fact that the peculiar deformed individuals of *Dickinsonia* were found only in one out of many local burials known in Eastern Europe and South Australia. This information, combined with the observation that only medium-sized or large individuals were affected, inclines us to think about the formation of the damage as a result of one or two short episodes of a physicochemical, microbial, or some other similar effect, rather than occasional macrophage actions.

The following hypothesis can explain the occurrence of conditions that could have damaged *Dickinsonia* individuals. Large, initially spherical remains of *Beltanelliformis brunsae* are widely distributed in the Lyamtsa locality in general (Fig. 5.1). Their relationship to benthic colonial cyanobacteria was established by several independent methods (Steiner, 1996; Ivantsov et al., 2014; Bobrovskiy et al., 2018b). The average diameter of the colonies is 1–2 cm, although specimens with a diameter of up to 9 cm are known from the White Sea region (Ivantsov et al., 2014). These three-dimensional aggregates of photosynthesizing cells were enclosed in a dense matrix, and at the same time were partially submerged into the substrate. Apparently, these organisms could exist only in environments of extremely shallow waters (Ivantsov et al., 2014).

To the authors' knowledge, the local assemblage L2(XII) represents the only case of joint in situ burial of *Dickinsonia* and *Beltanelliformis* anywhere in the world. At the beginning of the taphonomic event, the bodies of the *Dickinsonia* were located on the upper, final surface of the microbial mat. The small (2–5 mm in diameter) collapsed colonies of *Beltanelliformis* were located below this surface, as evidenced by the inexpressive relief of the casts and the occurrence of microbially induced textures on them (Fig. 5.2). The erosive incisions that accompanied the taphonomic event removed the small areas of the mat and exposed the remains of these colonies (Fig. 5.3).

The absence of mineral sediment between the top of the mat and the colonies of *Beltanelliformis* implies the joint growth of these objects at some point, after which the colonies were inhibited and died. Perhaps here we have a record of seasonal changes in the mixed microbial community. Based on the small size of the colonies, the time favorable for their formation did not last

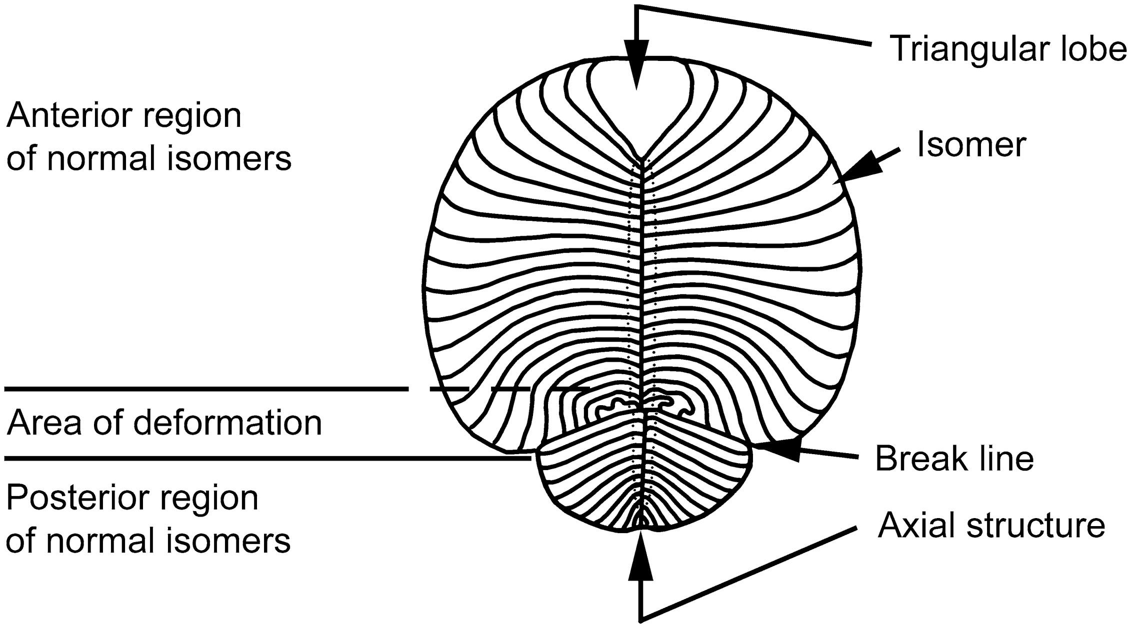

Figure 9. Elements of the structure of a deformed specimen of *Dickinsonia* cf. *D. menneri* of medium size (the number of the isomers is reduced).

long. It is impossible to determine the moment of the appearance of colonies, whether it was before, at the same time, or after the beginning of the microbial mat's formation and the expansion of the assemblage of macroorganisms associated with it. But, if we assume that one generation of *Dickinsonia* (represented by medium and large individuals in the burial) and the *Beltanelliformis* colonies existed together for some time, this could possibly lead us to a source of the damaging effects. The general background for the occurrence of the damage could be a temporary change of the physicochemical environmental conditions (temperature, salinity, light intensity, oxygen, or cyanotoxin concentrations, etc.), which had become less

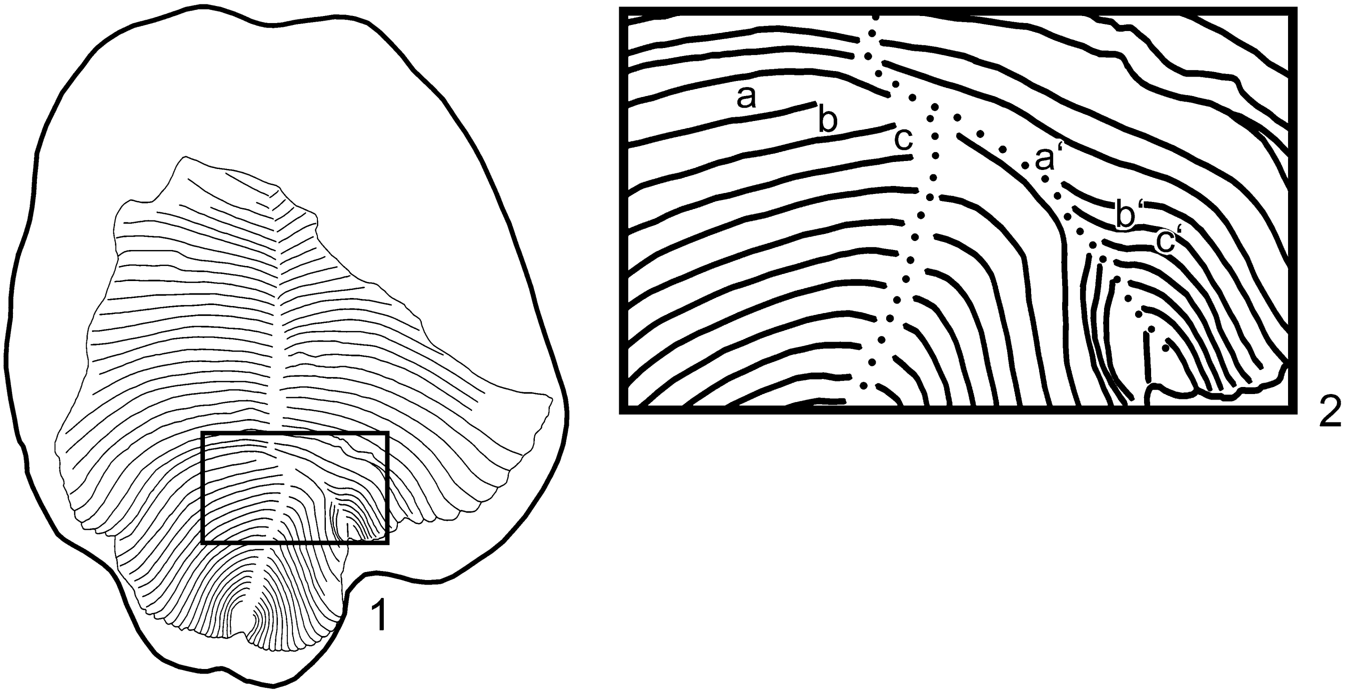

Figure 10. Schematic drawing of the deformed specimen of *Dickinsonia* cf. *D. menneri*, PIN, No. 4716/5146 from a photograph (Fig. 4.6, 4.7). (**1**) Plan view; (**2**) fragment, the dotted line shows the splitting axis (a-c and a'-c' = successively formed isomers of the left and right rows in the initial stage of the growth zone division); the specimen demonstrates the gradual process of divergence of two newly formed growth zones; it can be seen that at first, after resumption of the formation of the isomers, the isomers of the left series appeared only on the left side (a-c), while the isomers of the right series appeared only on the right side (a'-c').

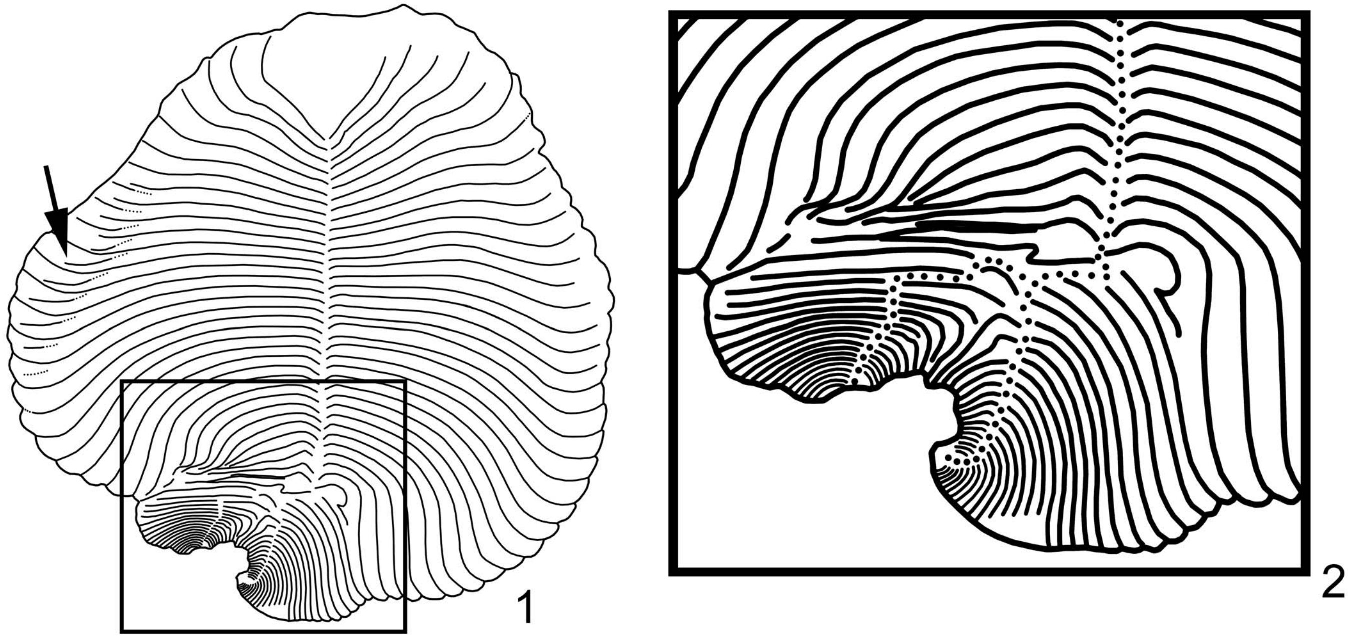

Figure 11. Schematic drawing of the deformed specimen of *Dickinsonia* cf. *D. menneri*, PIN, No. 4716/5188 from a photograph (Fig. 4.4, 4.5). (**1**) Plan view, the arrow indicates an overlapping section of the dorsal and ventral parts of the dissected structure; (**2**) fragment, the dotted line shows the splitting axis.

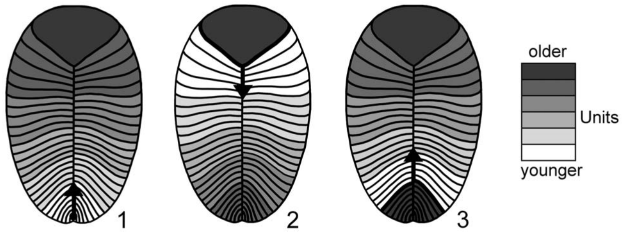

Figure 12. Hypothetical variants of the location of the formation point of new isomers in a young specimen of *Dickinsonia* (marked by a dot or a bold line). (**1**) At the posterior end of the body (Runnegar, 1982; Ivantsov, 2008; Gold et al., 2015); (**2**) on the sides of the triangular lobe (Hoekzema et al., 2017; Dunn et al., 2018); (**3**) at the front margin of some primary group of isomers; the arrow indicates the direction of apparent movement of the isomers along the axis of the growing organism.

favorable for *Dickinsonia*, in the given part of the seabed. After death of the *Beltanelliformis* colonies, presumably, the conditions optimal for *Dickinsonia*'s life were restored and their normal growth resumed. Therefore, the small individuals that likely appeared in the area after these events don't have any damage. However, at this stage it remains impossible to identify the direct factor that led to the non-lethal damage of *Dickinsonia*.

Summarizing our research, it should be noted that, despite the discovery of damaged individuals in the "Garden of Ediacara," the reliable presence of macrophages in the late Precambrian has not yet been established.

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