Body plan of *Dickinsonia*, the oldest mobile animals

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ABSTRACT: Materials collected on the territory of the southeastern White Sea area, including diversely preserved body imprints, combined body-trace fossils, specimens with signs of intravital damage and regeneration, and extended ontogenetic series, make it possible to significantly widen the data on the body plan and biology of *Dickinsonia*, the oldest known mobile animal, included in the Late Precambrian taxon of high rank, Proarticulata. A number of reconstructed anatomical features were added to the obvious directly observed features of *Dickinsonia*, such as a consistent body shape lacking lateral appendages and temporary outgrowths, transverse differentiation, and anterior–posterior polarity. These reconstructed features include dorsoventral polarity, ciliated mucus-secreting epithelium underlain by a basal lamina, two rows of blind food-gathering pockets, absence of a through-gut, nervous system of diffusive type, axial support band and muscle fibres. Such a set of features indicates the affinity of *Dickinsonia* and Proarticulata as a whole (the only known Ediacaran Metazoa) to Urbilateria, a hypothetical ancestor of bilaterally symmetrical animals.

KEY WORDS: anatomy, Bilateria, Ediacaran biota, Eumetazoa, Late Precambrian, Proarticulata, southeastern White Sea area, Urbilateria.

Mobility, the ability of an individual organism or its parts to actively move through space, is one of the fundamental features characteristic of animals. In the fossil record, this feature is recorded to the extent that organisms were able to disturb the natural texture of bedding surfaces and the stratification of sediments. Sedimentological structures resembling traces are already known from the Paleoproterozoic (Albani *et al*. 2014), but undisputed locomotion traces appear only in the Late Ediacaran (Mangano & Buatois 2020). In addition to trace chains, combined fossils are found in the deposits of this age, consisting not only of a trace fossil but also of the remains of the body of the trace maker. Such finds directly indicate the ability of a certain extinct organism to move and also provide the basis for well-grounded opinions about its anatomy, functional morphology, and ethology. This fact is especially important for understanding the nature of peculiar Ediacaran organisms. To date, six genera of Ediacaran presumable animals, preserved as combined remains, are known: *Dickinsonia*, *Ikaria*, *Kimberella*, *Tribrachidium*, *Yilingia*, and *Yorgia* (Ivantsov 2011, 2013; Chen *et al*. 2019; Evans *et al*. 2019a, 2020; Ivantsov *et al*. 2019b; Ivantsov & Zakrevskaya 2021b). Among them, the most studied is *Dickinsonia*, which is emblematic of the macrobiota of the entire Late Precambrian, although its distribution is limited by a rather narrow spatial and time frame. Fossil remains of several species of *Dickinsonia* occur in the Late Ediacaran deposits of South Australia (Flinders Ranges, Nilpena, Ediacara) (Sprigg 1947, 1949; Glaessner & Wade 1966; Wade 1972; Runnegar 1982; Seilacher 1989; Jenkins 1992; Gehling *et al*. 2005; Brasier & Antcliffe 2008; Evans *et al*. 2017, 2018, 2019a, 2019b, 2021a; Reid *et al*. 2018) and Eastern Europe (southeastern White Sea area, Middle Urals, Podolia) (Fedonkin 1983, 1990; Ivantsov & Malakhovskaya 2002; Ivantsov 2008, 2011, 2013; Zakrevskaya & Ivantsov 2017; Bobrovskiy *et al*. 2018, 2019; Bobkov *et al*. 2019; Ivantsov *et al*. 2019b, 2019c, 2020a; Ivantsov & Zakrevskaya 2021a). One

single fragmented specimen of *Dickinsonia* sp. was found in China (Wang *et al*. 2021), while problematic *Dickinsonia*-like structures were described from India (Retallack *et al*. 2021). It seems that the earliest combined remains of *Dickinsonia* originate from the southeastern White Sea area, where they begin to appear from the base of the part of the section characterised by macrobiota (Ivantsov & Zakrevskaya 2021a), located at least 50 metres below the level dated to 557.3 Ma. (Grazhdankin 2004; Yang *et al*. 2021). *Kimberella* remains, numerous in the White Sea area, are much younger. Their imprints begin to appear in sandstones stratigraphically located approximately 75 metres above the mentioned level. *Yilingia* is also younger (551–539 Ma, Chen *et al*. 2019). The same apparently goes for *Ikaria*. The site in Nilpena marked 1 T, from where the combined fossils of *Ikaria* originate (Evans *et al*. 2020), contains an advanced macrofossil assemblage, including *Dickinsonia costata*, *Parvancorina minchami*, and *Tribrachidium heraldicum* (Droser *et al*. 2019). In the White Sea area, these species are included in the assemblages crowning the sequence of Ediacaran oryctocenoses. The deposits of the Mistaken Point Formation of Newfoundland, about 565 Ma old, contain combined fossils consisting of trace-like horizontal and vertical structures and rounded attachment discs of the genus *Aspidella* (Menon *et al*. 2013; Buatois & Mangano 2016; Mangano & Buatois 2020). However, these are morphologically the simplest varieties of *Aspidella*, which cannot be associated with any particular taxon of Ediacaran organisms. Thus, *Dickinsonia* is apparently the oldest known animal, mobility of which is confirmed by fossil remains.

A great amount of the examined fossil material and a diversity of forms of preservation of the remains made it possible to identify a whole series of presumable anatomical structures in *Dickinsonia* (Glaessner & Wade 1966; Wade 1972; Runnegar 1982; Seilacher 1989; Jenkins 1992; Dzik & Ivantsov 2002; Ivantsov

2008, 2011; Reid *et al*. 2018). Although in most cases *Dickinsonia* fossils are represented by imprints of isolated bodies, sometimes they are found surrounded by their own trace fossils. Among the trace fossils, we know chains of imprints of the ventral surface, initially 'engraved' on a microbial mat by feeding animals, named *Epibaion axiferus* and *E. costatus* (Ivantsov & Malakhovskaya 2002; Gehling *et al*. 2005; Ivantsov 2011, 2013; Evans *et al*. 2019a; Ivantsov & Zakrevskaya 2022). Mucous-mineral pathways associated with sliding along the substrate and silt-sandy rings resulting from temporary attachment to the substrate were also identified (Ivantsov *et al*. 2019b; Ivantsov & Zakrevskaya 2021a). In *Dickinsonia*, intravital damage (loss of a significant part of the body, tumour-like expansions?) and signs of successful regeneration were revealed for the first time in the animal record (Ivantsov *et al*. 2020a, 2020b). It should also be taken into account that *Dickinsonia* is not a separate group, but is included in a large taxon, Proarticulata (Fedonkin 1990), or Dickinsoniomorpha plus Bilaterialomorpha of a later classification (Erwin *et al*. 2011), which includes at least 17 genera of Precambrian organisms (Ivantsov *et al*. 2019a). The body plan of all proarticulates is quite similar. Their body consists of two rows of unbranched transverse elements, with their generation zone located at a slightly pointed end. The opposite blunt end of the body is characterised by the presence of a more or less developed isolated lobe or a pair of strongly expanded transverse elements. In small-sized specimens or at early ontogenetic stages, this lobe or pair of elements widely or completely envelops the body along its margins (Ivantsov *et al*. 2019a). Those anatomical structures that are diagnosed in *Dickinsonia* are common in varying degrees in representatives of other genera of this group. However, the interpretation of the peculiar morphological features of the fossils, all possible anatomical structures of *Dickinsonia* and other proarticulates, the mechanism of trace formation, as well as the assumptions about the affinities of these organisms are the subjects of ongoing discussion. Nevertheless, a consensus on these issues may be reached in the near future. The opinion of *Dickinsonia* belonging to annelids that was widespread at the early stage of the study (Glaessner 1959; Glaessner & Wade 1966; Wade 1972; Runnegar 1982; Conway Morris 1989; Jenkins 1992) is currently not supported. In the publications of the last two decades, it appears as a peculiar primitive animal located near the base of a number of metazoan clades (but see Seilacher *et al*. 2003; Retallack 2007, 2013; for example, Evans *et al*. 2017; Hoekzema *et al*. 2017; Dunn *et al*. 2018). In the course of perceptions of the body complexity, it was progressively compared with placozoans (Rozhnov 2009; Sperling & Vinther 2010), ctenophores (Zhang & Reitner 2006), coelenterates (Brasier & Antcliffe 2008; Ivantsov & Zakrevskaya 2021c), and early bilaterians (Gehling *et al*. 2005; Gold *et al*. 2015; Evans *et al*. 2019b; Ivantsov *et al*. 2019c). In this article, we propose a refined reconstruction of the body plan of *Dickinsonia* and substantiate its definition as stem Eumetazoa close to Urbilateria, the hypothetical ancestors of Bilateria.

The unique diversity of forms of preservation of the White Sea area fossils illuminates the biological features of *Dickinsonia* that are unknown or poorly represented in other regions. It makes it possible to reconstruct the structural plan of these organisms with the greatest possible completeness to date.

1. Material

Fossil remains of *Dickinsonia* are found in abundance in all main localities of macrofossils of the southeastern White Sea area, distributed in the Ust-Pinega and Mezen Formations (Lyamtsa-Erga Formations according to a different scheme) of the local section of the Ediacaran (Vendian) deposits (Ivantsov & Zakrevskaya 2021a). The interval of distribution of fossils reaches

about 250–300 metres with refined inner dates of an absolute age of 557.3 ± 0.6 and 553 ± 0.7 Ma (Yang *et al*. 2021). At the same time, the first levels with combined body-trace remains of *Dickinsonia* are located in the section several tens of metres below the tuffaceous horizon with the earliest of the specified dates (Ivantsov & Zakrevskaya 2021a).

Our collection contains more than 1,250 specimens of body imprints of *Dickinsonia* belonging to four species, *D. costata*, *D. tenuis*, *D. lissa*, and *D. menneri*, as well as the individual trace fossils and their groups, *Epibaion axiferus* and *E. costatus* (34 specimens). Fossils were preserved in various forms, including imprints and casts of the upper and lower sides of the body in various stages of compression and decomposition, as well as combined remains composed of a body imprint and trace fossils of various genesis, three-dimensional casts, and mineral pseudomorphs of internal structures. We studied both the natural casts and imprints themselves and the latex casts from them. Mineral (iron sulfides and hydroxides) pseudomorphs after an organic matter were studied at the Paleontological Institute of the Russian Academy of Sciences using a NEOSCAN N80 X-ray microtomograph (source voltage (kV) = 92, source current (µA) = 174, filter = Cu 0.25 mm, rotation 180°, rotation step 0.3°, image pixel size (µm) = 7.5).

2. Morphological features of *Dickinsonia*

2.1. Body shape and dimensions
Dickinsonia had an oval shape with slightly different ends: one a little blunt and the other a little narrowed (Fig. 1d). *Dickinsonia* lacked any permanent appendages or temporary outgrowths, similar to the other proarticulates, with the exception of *Cephalonega*, on the dorsal side of which long filamentous outgrowths are distinguishable (Ivantsov *et al*. 2019a).

The smallest distinguishable specimens of *Dickinsonia* are 1–2 mm long (Ivantsov & Zakrevskaya 2022). The average length of their body is a few centimetres, although there are known specimens that reach 1 metre in length (Gehling 1991; Jenkins 1992; Gehling *et al*. 2005) and possibly even bigger ones, reconstructed from fragments (Jenkins 1996). The length of the largest White Sea specimen of *D. tenuis*, which is not completely visible on the surface of the bearing layer, exceeds 55 cm. The width of *Dickinsonia* varies over a wide range, ranging from about the full length in *D. costata* to one-fifth of the length in *D. lissa*.

The characteristic imprints of *Dickinsonia* show differentiation into many narrow transverse elements, usually reaching a maximum length (here measured across the longitudinal axis of the body) in the middle part of the body and decreasing towards the ends (Fig. 1d, h). A special lobe is distinguished at the blunt end of the body. In juvenile individuals, it has a semicircular shape and makes up more than half of the body area; then, in the course of ontogeny, it elongates, becoming round-triangular, and then almost ribbon-shaped (Fig. 1f). Its relative size decreases many times (Ivantsov & Zakrevskaya 2022). Based on the orientation relative to a trace chain, this lobe was located at the anterior end of the body of *Dickinsonia* (Ivantsov 2001a, 2001b, 2011, 2013; Gehling *et al*. 2005; Evans *et al*. 2019a). At the opposite posterior end, the elements can be tiny, and so close in size to grains of the bearing rock that they become almost indistinguishable (Fig. 1g). Evidently, there was a zone of their formation here (Runnegar 1982; Gold *et al*. 2015), which is confirmed by the observation of the dynamics of 'normal' growth and deviations during the regeneration of *Dickinsonia* (Ivantsov *et al*. 2020b; Evans *et al*. 2021a).

2.1.1. Discussion. The widespread idea of the extreme thinness of the body of *Dickinsonia* needs to be clarified. The depth of most imprints is really small. For example, in the largest
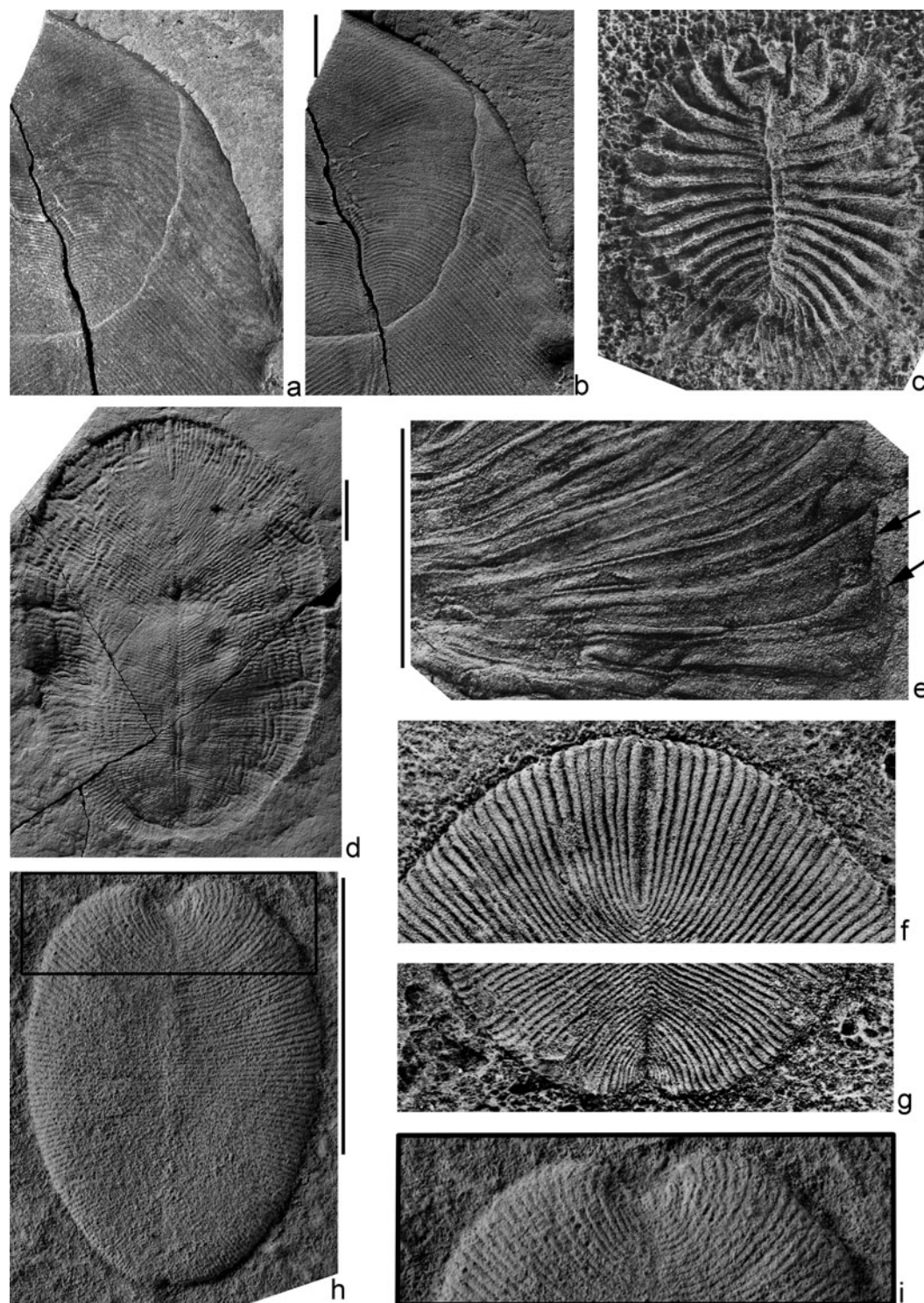
Figure 1 (a, b) *D.* cf. *menneri*, specimen PIN, no. 4716/5175. (c) *D. costata*, specimen PIN, no. 3993/5231, a specimen with an extreme degree of decomposition before fossilisation, when practically only the differentiated structure remained from the body. (d) *D. tenuis*, specimen PIN, no. 3993/9967, a specimen that supposedly experienced radial compression, as indicated by numerous concentric folds. (e) *D. costata*, specimen PIN, no. 3993/5247, arrows indicate the upper and lower plates of the differentiated structure, belonging to the same isomer, separated during the taphonomic process. (f–g) *D. tenuis*, specimen PIN, no. 4852/14 (f, anterior end; g, posterior end). (h, i) *D. tenuis*, specimen PIN, no. 4852/64 (h, plan view; i, anterior end with high magnification). (a, b), (d, e) are natural imprints, (f–i) are latex casts from natural imprints; (b), (c), (e–i) were taken with the coating with ammonium chloride; the scale bar is 1 cm.

specimen of the *D. costata* from the White Sea, the depth is no more than 3.5 mm with an imprint's width of 350 mm (the ratio is 1:100) (Ivantsov & Zakrevskaya 2022). However, in small specimens of *D. tenuis* from the Zimnie Gory locality, which experienced extreme compression, the relative depth of the imprint is much bigger (see also Dzik & Ivantsov 2002; Zhang & Reitner 2006) and reaches 1:5. This parameter is comparable to or even exceeds the limit values of imprints of such

well-known Ediacaran organisms as *Kimberella* and *Tribrachidium* (Ivantsov & Zakrevskaya 2021b), which are not considered thin-bodied. It is evident that the body thickness of *Dickinsonia* widely varied depending on the state of the organism. However, an accurate determination of its value is impossible in the absence of data on the degree of collapse of the tissues of these animals at the time of lithification of the sandstone forming the imprints.

2.2. Differentiated structure

Most of the known body imprints of *Dickinsonia* are formed by some kind of differentiated structure. It presumably had the shape of a sack (Fig. 2), which, in the course of fossilisation and decomposition of the organic matter enclosed within it, collapsed to a double-layer compression (Ivantsov *et al.* 2019c). An analysis of taphonomic features shows that the differentiated structure of *Dickinsonia* consisted of a rather tenacious material that was resistant to biochemical destruction (Fig. 1c), and which could contain biopolymers like collagen, keratin, or elastin (Bobrovskiy *et al.* 2019; Evans *et al.* 2019b). The contacts between the upper and lower layers of the differentiated structure were very weak, and during the collapse the layers could shift relative to each other. Therefore, on samples with both layers preserved simultaneously, for example when the upper layer is in the form of an imprint and the lower one is preserved only in the form of a smear of organic matter, one can often observe a sharp discrepancy in the orientation of the boundaries of their transverse elements (Fig. 1a, b; Ivantsov *et al.* 2019c).

According to E. Dzik, the differentiated structure was a separate organ located on the dorsal side of the body of *Dickinsonia*. Its collagenous basement membrane bounded the muscle blocks homologous to chordate myomeres (Dzik 1999, 2000, 2003). We follow a similar interpretation, comparing the differentiated structure of *Dickinsonia* and proarticulates in general with the basal lamina, but we assume that it surrounded the body from all sides. On top of it, there was an epithelial integument (Ivantsov *et al.* 2019c, 2020b).

2.2.1. New observations and discussion.
Additional evidence of the high elasticity of the material composing the differentiated structure can be the prominent local swellings (expansions?) of sections of the transverse elements (Fig. 3e). In the specimen shown in this figure (one out of six available specimens), two of the elements experienced a local threefold increase in width. At the same time, there are no obvious signs of rupture of the material of the differentiated structure.

The layers of the differentiated structure apparently consisted of transverse plates separated by narrow folds. Depending on the nuances of taphonomy, folds can be reflected in different ways in the imprints, sometimes in the form of furrows, sometimes ridges (Fig. 4b). They can also be represented by furrows sandwiched between thin ridges (the central part of Fig. 1e). One plate from the upper and lower layers corresponded to each transverse element. It can be clearly seen in the sample (Fig. 1e), in which the plates belonging to the same transverse element are separated and displaced relative to each other.

The strength of the horizontal bonds between the transverse elements in each of the layers of the differentiated structure varied. In the lower layer, these connections were rather weak. Therefore, on many specimens, we can see bends, overlapping of transverse elements, and their fragmentation (marked by arrows in Fig. 4a). In contrast, in the upper layer, the bonds were significantly stronger. Here, splits between the transverse elements are never observed. However, a furrow extends along the longitudinal axis of the body, dividing the transverse elements in two with the formation of two rows of 'half-segments', which we call isomers (Ivantsov 2001b). Along the axis of the body, the shift of the rows of the isomers relative to each other was possible along with the overlap of the rows over each other in the transverse direction. In the example of the imprints of *D.* cf. *menneri*, it can be seen that the arrangement of ridges, representing the isomer boundaries, can change from alternating to opposite as a result of the longitudinal shift, creating the appearance of continuity of isomer boundaries on the body axis (Fig. 5a, b, e, f). A slight transverse overlap of one row over another results in a zigzag pattern, while a bigger overlap creates a lattice pattern (Fig. 5c, d, g, h). This feature of fossil remains has led to an ongoing debate about the presence of true segments in the body of *Dickinsonia*. According to M. A. Fedonkin's opinion (Fedonkin 1990), which we share, the initial order of isomers was alternating. However, examples of opposite arrangements of isomers are numerous, especially for small specimens of *D. costata*. They are illustrated in detail in publications and used as proof of the primary reflective symmetry of all *Dickinsonia* in general (for example, Glaessner & Wade 1966; Wade 1972; Runnegar 1982; Gehling *et al.* 2005; Gold *et al.* 2015; Evans *et al.* 2017; Hoekzema *et al.* 2017; Dunn *et al.* 2018; Reid *et al.* 2018). But it is precisely the inconstancy of the mutual arrangement of the halves of the 'segments' that makes the hypothesis of complete bilaterality of *Dickinsonia* untenable (Ivantsov *et al.* 2019a).

2.3. External epithelial integument

According to our interpretation, the differentiated structure forming the standard *Dickinsonia* imprint was located deeper inside the body at some distance from the body surface (Ivantsov *et al.* 2019c) (Fig. 2). Indirect evidence of the presence of a certain isomer-binding structure in a living organism is provided by specimens with extensive intravital damage. Despite the fact that their bodies were divided almost in half so that the isomers of the anterior part stuck their ends into the sides of the isomers of the posterior part (Fig. 6a), it did not lead to any freedom in the relative position of the parts (Ivantsov *et al.* 2020b). The conclusion about the presence of a certain 'membrane' that held together the transverse elements of *Dickinsonia*'s body was also made by Evans *et al.* (2017). Imprints on which the isomeric structure disappears under the undifferentiated tubercle-bearing surface are a direct indication of the presence of a special outer integument (Fig. 6b, c). A similar integument is more clearly expressed on the imprints of other species of proarticulates, and this fact gave reason to assume that the integument on the upper side of the body of proarticulates (including *Dickinsonia*) was not differentiated, and its outer surface bore numerous closely spaced tubercles (Ivantsov *et al.* 2019a, 2019c). There is much more data on the structure of the lower side of *Dickinsonia*. It is supplied by feeding traces created by animals in a calm environment (Ivantsov & Malakhovskaya 2002; Gehling *et al.* 2005; Ivantsov 2011, 2013; Evans *et al.* 2019a). The fully developed trace is, in fact, a direct imprint of the ventral surface of *Dickinsonia*. Based on it, the lower side of the body of *Dickinsonia* was divided into transverse elements in the same way as the differentiated structure lying deeper inside the body.

2.3.1. New observations and discussion.
However, there is one significant difference. The trace fossil, *E. axiferus*, which corresponds to *D.* cf. *menneri* (Ivantsov & Zakrevskaya 2021a) and *D. tenuis* shows that these species had a wide axial undivided lobe on the lower side (Fig. 6d, e) (Ivantsov & Malakhovskaya 2002; Ivantsov 2011). This fact contrasts not only with the morphology of the upper surface of the body of *Dickinsonia* but also with the structure of the upper side of the differentiated structure, where, in all *Dickinsonia*, the isomers converge with each other directly on the longitudinal axis. Another important observation from the structure of the feeding trace of both species (*E. axiferus* and *E. costatus*) is confirmation of the widespread idea that *Dickinsonia* lack ventrally oriented mouth and anal openings, which was once assumed for Australian *Dickinsonia* and *D. tenuis* from the Zimnie Gory locality (e.g., Wade 1972; Dzik & Ivantsov 2002).

Some details of the morphology of the trace fossils provide insight into the way they were created. Thus, the trace-forming grooves and ridges are usually very distinct, even if the body isomers of the animal were narrow. When traces are superimposed on each other, the clarity of their expression does not decrease, as
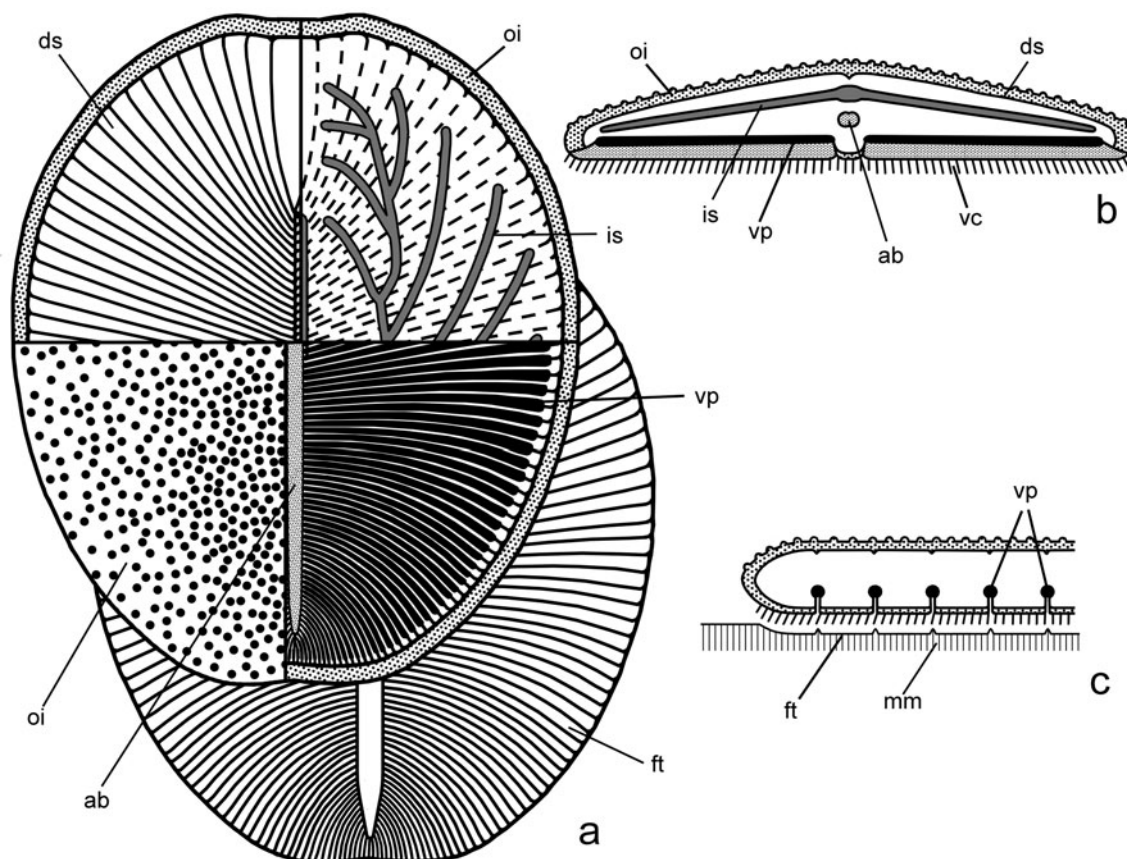
Figure 2 Generalised diagram of the body plan of *Dickinsonia*: (a) plan view, (b) cross section, (c) longitudinal-tangential section. Abbreviations: oi = outer integument; ab = axial band; ds = differentiated structure; vp = ventral pockets; is = internal structure of *D. tenuis*; vc = ventral ciliary field; mm = microbial mat; ft = feeding trace (imprint of the ventral side).

a result of which a reticulate pattern is created (Fig. 6f). It would have been impossible if the trace fossil was formed due to a solution of digestive ferments, i.e., the animal released them into the external environment and then absorbed nutrients with the ventral sole (Sperling & Vinther 2010). It is more probable that the trace fossil was formed mechanically by phagocytosis by the cells of the lower side of the *Dickinsonia*'s body or by scratching the upper layer of the microbial mat with cilia. Phagocytosis seems to be easier to explain the composition of the relict organic matter preserved on the imprints of the White Sea *Dickinsonia* (Bobrovskiy *et al*. 2018; Runnegar 2021). Nevertheless, the ciliary scratching with the transportation of extracted particles into special food-gathering/digestive cavities (Ivantsov & Malakhovskaya 2002; Ivantsov 2008, 2011, 2013) is more consistent with the presence of ventral pockets. The summarising assumption is that the phagocytosis occurred within the ventral pockets. The recently described traces of locomotion of *Dickinsonia* and the areas of temporary adhesion cleared of silt can also be more simply explained as a result of the effect of mucus secretions and ciliary movements on the substrate (Ivantsov *et al*. 2019b; Ivantsov & Zakrevskaya 2021a). Thus, we reconstruct the presence of an integumentary epithelium in *Dickinsonia* which was capable of secreting mucus and bearing cilia, at least on the ventral side of the body.

2.4. Ventral pockets

Elongated sand ridges are occasionally found on the imprints of *Dickinsonia*. They are interpreted as casts of some internal cavities (Glaessner & Wade 1966; Wade 1972; Jenkins 1992). At least two such imprints from South Australia and three from the White Sea area are depicted in literature (Ivantsov 2008, 2011, 2013; Ivantsov & Zakrevskaya 2022). In reality, such ridges

in varying stages of development can be seen on many imprints (for example, Ivantsov & Zakrevskaya 2021a, Figs 5d, 6a, 7c, 8c). The ridges can have variable width and length, occur in small groups or cover half or more of the imprint area, fall into chains of fragments and separate from the imprint in the form of sand cores (Ivantsov 2008, 2011, 2013). The distance separating the axes of neighbouring ridges corresponds to the width of the isomers (Fig. 4d). However, the direction of their strike does not coincide with the position of the isomers' boundaries of the upper plate of the differentiated structure but correlates with the isomers' boundaries of the shifted lower plate. Therefore it was concluded that the structure is confined to the ventral side of the body of *Dickinsonia* (Ivantsov 2011). It is assumed that the rods and ridges were formed as a result of sandy sediment getting into certain elongated cavities during the taphonomic event. At the same time, the uniform distribution of sand in thin and long cavities is taken as evidence of the connection of these cavities, called ventral pockets, with the external environment along their entire length (Ivantsov 2011).

2.4.1. New observations and discussion. Like fossils of the Nama-style preservation, the ventral pockets of *Dickinsonia* are fossilised as sandstone casts (ridges or rods, Fig. 4d) or as ferruginous, originally pyrite incrustations (Fig. 4e). CT images show that the ferruginous pockets look like tubes extending along the ventral side of the body (Fig. 4g). Each tube was connected to the external environment by a slit-like opening on the ventral side. On the casts of the lower side of *Dickinsonia*, pyrite-encrusted walls of the slit sometimes protrude in grooves between the isomers in the form of low dykes (Fig. 4c, e, f). The weakness of bonds between isomers on the lower side of a decomposing body can be explained by the presence of deep gaps separating them. All tubes are oriented across the body of *Dickinsonia*. We did not find
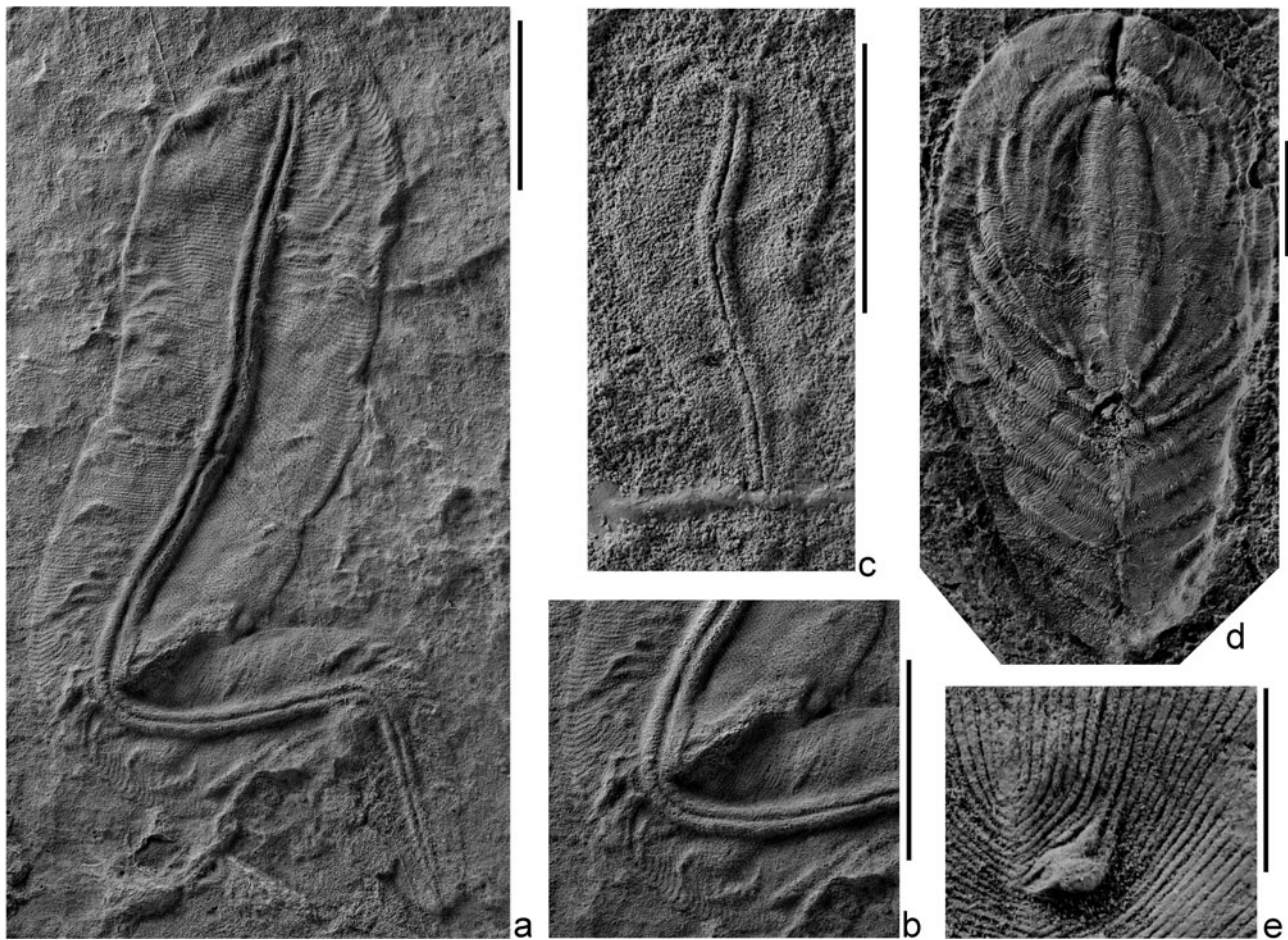
Figure 3 (a) *D. lissa*, medium-sized specimen PIN, no. 3993/9468. (b) Same fragment with higher magnification. (c) *D. lissa*, small specimen PIN, no. 3993/9438. (d) *D. tenuis*, specimen PIN, no. 3993/5173. (e) *D. tenuis*, specimen PIN, no. 3993/5172; local expansion (swelling?) of two adjacent isomers. All photographs were taken with the coating with ammonium chloride; scale bars represent 1 cm (a–d) and 0.5 cm (e).

longitudinal tubes in the area of the body axis, nor any structures that could connect the tubes to each other.

There are at least three hypotheses regarding the functional purpose of the internal transversely oriented cavities of the proarticulates. In *Dickinsonia*, they are recognised as lateral branches of the digestive system (Glaessner & Wade 1966; Wade 1972; Jenkins 1992; Dzik 1999, 2003). Similar structures of *Yorgia* were interpreted by Dzik (1999, 2003) as gonads. According to one of the authors of this article, these were accumulative (digestive) pockets, and the food particles did not get into them through the central gut, but directly from the external environment, through extended slits opened to the lower side (Ivantsov 2008, 2011, 2013). However, contrary to our earlier assumption, we did not find a common longitudinal cavity that could connect the pockets into a single system, at least in *Dickinsonia*. Accordingly, we cannot confirm the presence of a straight intestinal tract, which was once reconstructed for *Dickinsonia* (Jenkins 1992; Dzik 1999, 2003). The probable absence of rather closed intestinal tract with a special microflora in *Dickinsonia* is also indicated by the latest biomarker study (Bobrovskiy *et al*. 2022).

In the fossil remains of *Dickinsonia*, there are no structures that can be compared with gonads and copulatory organs. Also, we do not find signs of structured excretory organs. Solid waste may have simply fallen out through the slits of the ventral pocket. Such coarse material disintegrated into individual 'sausages' can be seen on the imprint of a giant specimen of *D. tenuis* PIN, no. 3993/5195 (Ivantsov 2011, pl. 1, Fig. 3). Thinner waste could be removed by diffusion through the body wall, which was favoured by the small thickness of *Dickinsonia*.

2.5. Axial band

On the upper surface of the collapsed body of *Dickinsonia*, there is often a phantom trace of some axial structure, expressed as a ridge (groove on the imprint) of a uniform width that tapers or flattens at the ends (Fig. 1d, h). On the small specimens of *Dickinsonia* from the White Sea it is usually not visible, and begins to appear at a centimetre length of the individual; it is most often clearly pronounced on the specimens of medium and large size (Ivantsov & Zakrevskaya 2022). The structure extends along the axis of the body along the inner ends of the isomers and, consequently, it does not reach either the posterior or anterior ends of the body (Fig. 2). In wide specimens of *D. costata*, the relative width of the structure is very small. For example, in the large imprint PIN, no. 3993/6192, the width of the groove is 1.2 mm with a body width of 172 mm (ratio 1:143). And in one species of *Dickinsonia* from the White Sea, traditionally defined as *D. lissa*, which has a very narrow body, it is much larger (Fig. 3a–c). The medium-sized specimen (no. 3993/5512) has a groove with a width of 2.5 mm and a body with a width of 23 mm (ratio 1:9) (Ivantsov & Zakrevskaya 2022). The structure as a whole can stand out rather sharply in the relief of imprints (Fig. 3a, c), but it disappears at a high degree of tissue decomposition (Fig. 1c). Apparently, it represented some kind of a band that lay inside the body of *Dickinsonia* (Wade 1972; Runnegar 1982; ; Gehling 1991; Jenkins 1992; Evans *et al*. 2019a; Ivantsov & Zakrevskaya 2022).

2.5.1. New observations and discussion. The material of which the axial band was composed was flexible and behaved differently during fossilisation from the substance of the
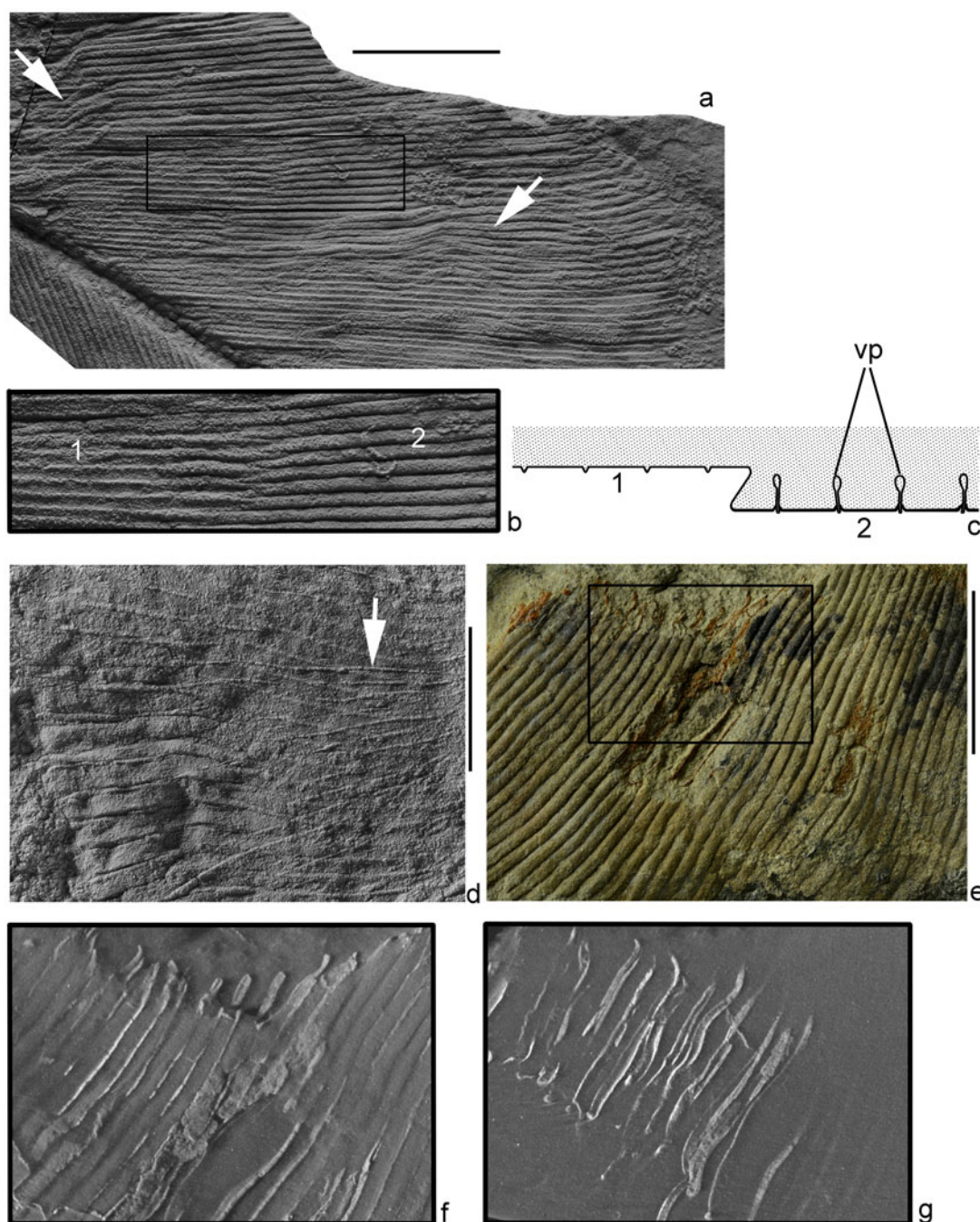
Figure 4 (a) Specimen PIN, no. 3993/9913, a fragment of a large individual of *D. tenuis* (linear depression from the axial structure extends obliquely in the lower-left corner of the image). (b) Fragment of the same specimen with higher magnification; consists partly of an imprint of the upper side of a differentiated structure (1, isomers look like grooves, and the boundaries between them look like ridges), and partly of an indirect cast of its lower side (2, isomers are ridges, interisomer boundaries are furrows). On the indirect cast of the lower side, one can observe wavy bends, overlapping of isomers on each other, elbow bends, and breakage of isomers (arrows); in the strata above it, there are ferruginous remains of ventral pockets. (c) Diagram explaining the difference between preservational variants 1 and 2 (vp = ventral pockets). (d) *D. costata*, specimen PIN, no. 3993/8875, sand filling of the cavities of the ventral pockets on the imprint of the upper side of the body (arrow). (e–g) *D. tenuis*, specimen PIN, no. 3993/9878, a fragment of an imprint with three-dimensionally preserved ferruginous ventral pockets (e, plan view; f, g, fragment with high magnification, marked with a rectangular frame in (e), virtual plane sections made using an X-ray microtomograph (f, at the level of supply slits; g, at the level of tubular cavities). (a), (b), and (d) were taken with the coating with ammonium chloride; all scale bars represent 1 cm.

surrounding areas of the body. It was denser but less resistant to biochemical decomposition than the substance of the differentiated structure. The band is not equally manifested in the relief of collapsed bodies of different species of *Dickinsonia*. In *D.* cf. *menneri*, it is very weak, noticeable on the imprints only by the curvature of the ends of the isomers (Fig. 5a, c). In *D. costata* and *D. tenuis*, it can be high and appears single, although in some specimens it begins to be divided into two parts by a longitudinal groove (Fig. 1d, bottom of the image). In *D. lissa* of the

White Sea, it appears very high and clearly double. On casts of specimens of this species, it consists of two parallel ridges spaced at some distance from each other (Fig. 3a, c). The structures corresponding to the ridges responded to deformations independently to some extent. Thus, in the shown zigzag specimen, the left portion of the axial band remained unchanged in the area raised by a steep fold, while the right portion is slightly expanded and flattened (Fig. 3b). A double band is present in all specimens of *D. lissa* from the White Sea and, it seems, it was the band that
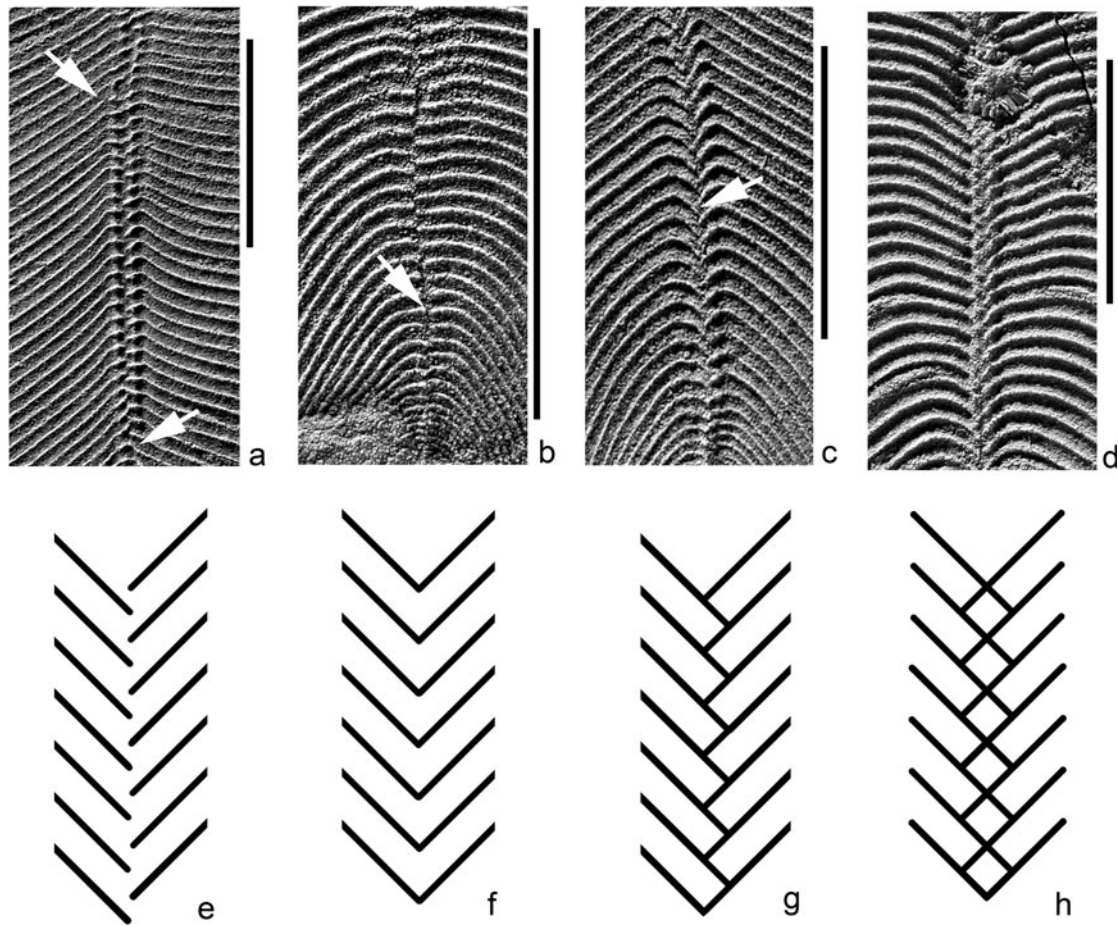
Figure 5 *D.* cf. *menneri*, variants of the mutual arrangement of the right and left rows of isomers. (a), (e) Alternating arrangement (a, specimen PIN, no. 4716/5272); in some areas, the appearance of continuous segmentation is created (arrows); however, at the same time the isomers combine randomly, as a result of which 'extra' isomers that do not have a pair appear on the right side. (b), (f) Opposite arrangement with the appearance of 'segments' (arrow), specimen PIN, no. 4716/5191. (c), (g) Small transverse overlap (arrow), specimen PIN, no. 4716/5271. (d), (h) Bigger transverse overlap, same specimen. All photographs were taken with the coating with ammonium chloride; all scale bars represent 1 cm.

ensured the smoothness of the curves of the narrow and thin body of this species. It is unclear whether the band was segmented; perhaps not, since the notches visible on its imprints seem to be a continuation of the grooves separating the isomers of the lateral areas of the body. On all specimens of *Dickinsonia,* both from our collection and published ones, the axial band has clearly pronounced even lateral boundaries. Obviously, it did not have lateral outgrowths and visible connections with ventral pockets. The fact that the axial band and ventral pockets do not form a single structure is also indicated by the different taphonomic fate of these structures: the band is never preserved as a sandy cast or pyrite incrustations.

The axial band on the imprints resembles the axial lobe of the trace fossil, *E. axiferus*. However, there are significant differences. Despite variations in the degree of manifestation on fossil remains, the axial band looks like an elevation above the more or less even surface of the collapsed body and is bounded at the margins by a surface bend. The boundaries of the isomers pass through this elevation from its margins to the very axis of the body. The lobe of the trace fossil, *E. axiferus,* resembling this band, is uniformly expressed in all specimens and is limited at the margins by a furrow. The groove-boundaries of meta isomers of the trace bump into this groove and do not pass through it. In other words, the ridge on the dorsal side is the result of the printing of some internal structure through the integuments, while the lobe on the ventral side is the structure of the body surface. In addition, the lobe of the trace is never doubled. And it is completely absent in the traces of *E. costatus* belonging to

D. costata, even though the hollow from the axial band is usually clearly expressed on medium and large-sized body imprints of this species (Ivantsov 2011; Ivantsov & Zakrevskaya 2022).

The nature of the linear axial structure of *Dickinsonia* is discussed here. It is hypothesised that the food-filled gut could have been preserved in this form (Wade 1972; Runnegar 1982; Gehling 1991; Jenkins 1992), but it is also believed that it was a mechanical artefact that arose during the process of fossilisation (Brasier & Antcliffe 2008) or that the axial structure, 'midline', was like a dense membrane to which the transverse elements were attached (Gehling *et al.* 2005; Evans *et al.* 2017). In one of their papers, Evans *et al.* (2019a) suggest that the 'midline' was filled with fluid and acted as a hydrostatic skeleton during the work of various muscles of *Dickinsonia*. The White Sea specimens clearly show that it was a real anatomical structure. However, the integrity of the axial band was not critical for the functioning of the body. Indirect evidence of this observation is given by the *D.* cf. *menneri* individual, which experienced very serious intravital damage (Ivantsov *et al.* 2020b; Ivantsov & Zakrevskaya 2021a). Eventually, at the stage of growth with approximately 30–35 pairs of isomers, it lost the generation zone, as well as more than 30 % of the body, including about half of the axial region (Fig. 7). However, it retained viability, restored the generation zone, and built up another 17–20 pairs of isomers before dying in the main taphonomic event. At the same time, the rest of the lost fragments, including the section of the axial band, did not regenerate, which is why afterwards the body was strongly bent to the right during uneven growth.
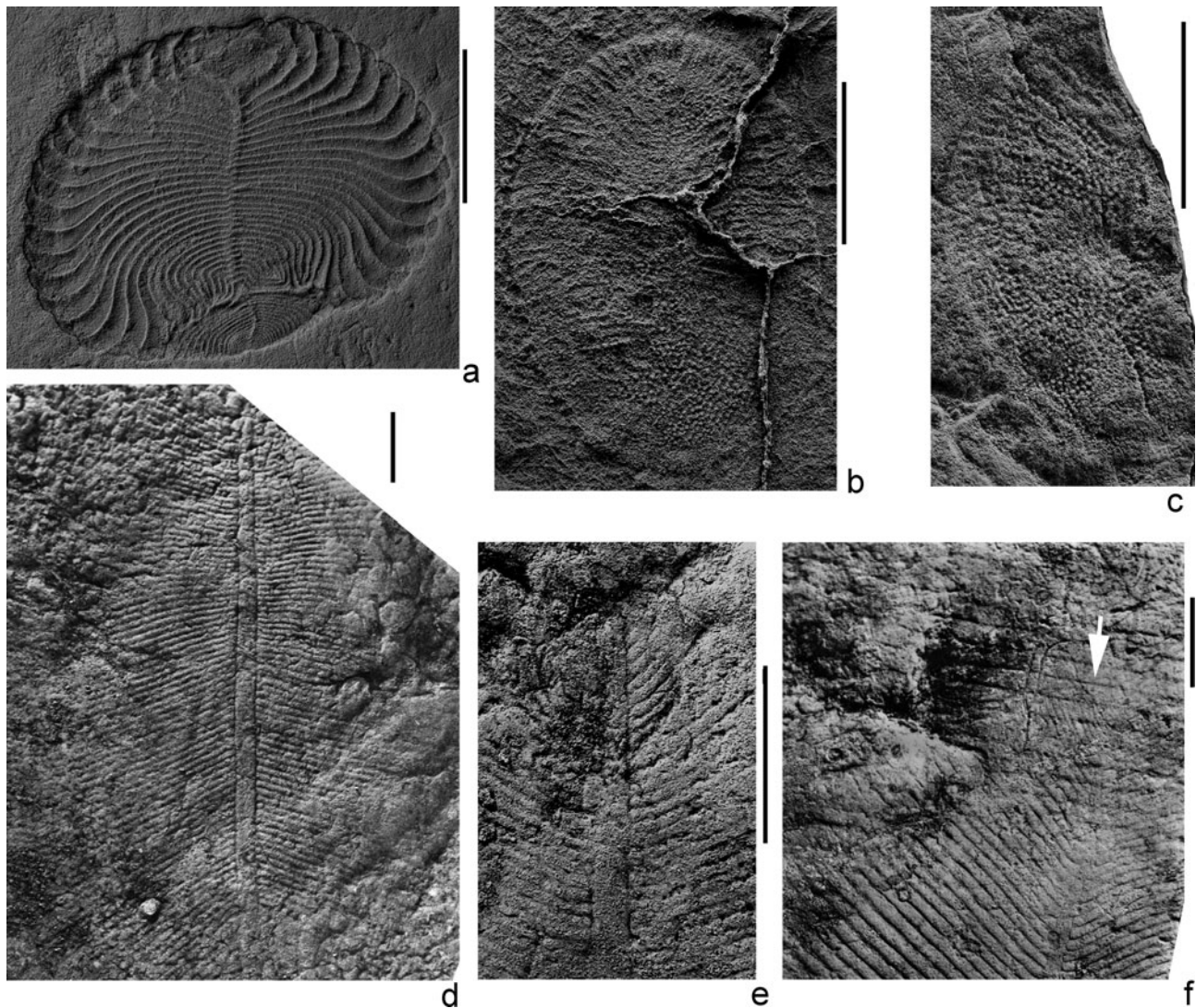
Figure 6 (a) *D.* cf. *menneri*, severely deformed specimen PIN, no. 4716/5187. (b), (c) *D. tenuis*, specimen PIN, no. 3993/8500 and 3993/6414. (d–f) Feeding traces of *Epibaion axiferus* (d, e, specimen PIN, no. 3993/5199; (f) holotype PIN, no. 3993/5199, overlapping of two traces with the formation of a distinct reticulate pattern (arrow)). All photographs were taken with the coating with ammonium chloride; all scale bars represent 1 cm.

Based on this fact, it can be assumed that the axial band performed a function that was not essential for the life of *Dickinsonia* or only a particular species, *D.* cf. *menneri*. The most likely purpose of the axial band was internal support during muscle-induced movement. The difference in the degree of its development in different species of *Dickinsonia* may be due to the predominance of either ciliary or muscular mode of movement. The strong resistance to bending during life and compression during fossilisation suggests that the substance of the axial band of *Dickinsonia* in terms of density and elasticity approached the vacuolated cells of the chordate notochord. At the same time, the duality of the structure brings it closer to an axochord of protostomes, in which muscle bands also form a pair (Lauri *et al.* 2014; Brunet *et al.* 2015).

By extension of the conclusion about the importance of the paraxial region, we can draw an interesting generalising conclusion: *Dickinsonia* did not have any vitally important organs extended along the axis. In other words, *Dickinsonia* clearly did not have a thorough intestinal tract, and their nervous system was not centralised.

2.6. The implication of the anterior lobe

2.6.1. New observations and discussion. In the above-mentioned highly curved specimen of *D.* cf. *menneri*, the position of the anterior end transferred from the anterior lobe to the arched left side of the body based on the trajectory of the traces left (Fig. 7). This observation makes one think about the significance of the anterior lobe in the life of *Dickinsonia*.

The growth of *Dickinsonia* was coordinated so that the longest transverse elements kept their location approximately in the middle of the body; and, in general, the shape of the organism remained unchanged (Evans *et al.* 2017). At the same time, in the course of ontogenesis, the anterior lobe decreased in relative size and shape, became elongated, but continued to grow at approximately the same rate as adjacent isomers. Nevertheless, the anterior isomers quite often outran the anterior lobe in growth and even enveloped it. As a result, a small notch appears in front, resembling the one present at the posterior end of the body (Fig. 1g). In one specimen of *D. tenuis* from the White Sea collection, the anterior lobe is completely absent, and the isomers closest to the anterior lobe are extremely short. A very deep notch appeared in place of the vacated volume (Fig. 1h, i). The specimen became almost biradial (with the vertically oriented axis), retaining only a slight asymmetry in the proportions of the anterior and posterior ends. The anterior lobe in this individual could not be absent initially, since the ontogenetic process begins from it (see above); apparently, it disappeared as a result of some damage or developmental disorder. The minimum size of the anterior isomers also needs to be considered. The broad possibilities of *Dickinsonia*'s regeneration described earlier (Ivantsov *et al.*
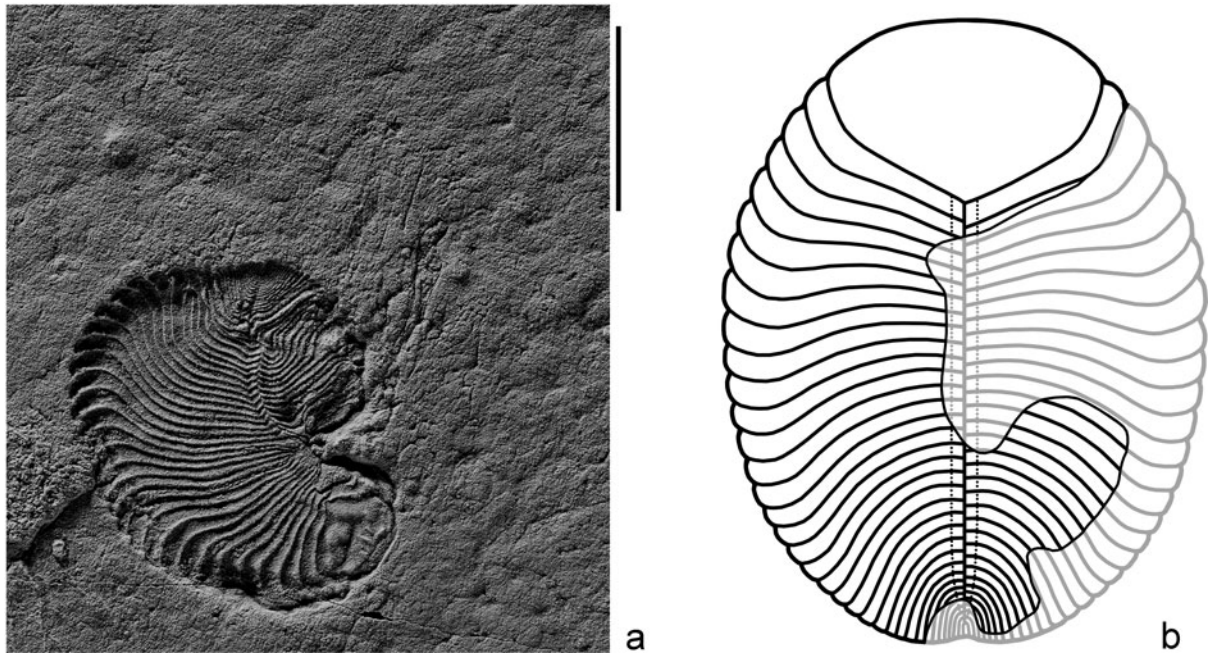
Figure 7 *D.* cf. *menneri*, a specimen with strong damages, specimen PIN, no. 4716/5182. (a) Plan view of the imprint, taken with the coating with ammonium chloride; scale bar represents 1 cm. (b) Schematic reconstruction of the specimen at the damaging moment; the missing part of the body is lightened.

2020a, 2020b) suggest that this specimen could have an additional zone of isomer formation not at the posterior, but at the anterior end. Yet it does not look like regeneration after damage, since there are no discontinuities characteristic of places that have undergone damage and subsequent recovery (Ivantsov *et al*. 2020a, 2020b). As an alternative hypothesis, it can be proposed that the anterior isomers experienced a secondary decrease in size following the disappearance of the anterior lobe. The specimen does not show any other changes, which indicates the continuation of a normal life activity by the organism up to the moment of the taphonomic event.

The analysis of deformed specimens gives grounds to conclude that the anterior lobe of *Dickinsonia*, despite some sort of morphological isolation and a certain position during the movement of the animal, did not contain any vital organs and sensory structures responsible for orientation in space and the choice of food objects.

2.7. Internal structure of *D. tenuis* from the Zimnie Gory locality

At several levels of the Zimnie Gory locality, peculiar imprints of *D. tenuis* are found, which are distinguished by a strongly reduced width, increased depth, and undulating surface relief. The visible pattern of the curves of this relief is formed into a single structure of a well-defined morphology (Fig. 3d) (Dzik & Ivantsov 2002). This structure has a linearly elongated paraxial canal and numerous lateral branches. The anterior half of the paraxial canal is wide (it is approximately twice the width of the axial band of *D. tenuis* of the corresponding size), while the posterior one is narrow, and it is this canal from which the branches alternately extend in both directions. The first two pairs of branches split several times, resulting in the structure uniformly covering the entire space of the body, with the exception of a narrow marginal strip. All lateral branches are directed approximately perpendicular to the isomer boundaries. The number of branches of the internal structure is several times less than the number of isomers. This structure appears only in extremely narrow specimens of *D. tenuis* and is apparently due to a sharp spasmodic lateral compression of their bodies before burial. Presumably, in this way, a certain internal structure, which

was located below the upper layer of the differentiated structure, manifested itself (Dzik & Ivantsov 2002; Ivantsov 2004, 2008; Zhang & Reitner 2006).

2.7.1. New observations and discussion. On the imprints with the internal structure, the narrower axial band is absent, and vice versa. Such antagonism of manifestation indicates the location of the internal structure above the axial band (Fig. 2). A sharp discrepancy between the number of branches of the internal structure and the number of isomers of the differentiated structure, as well as the discrepancy in the direction of their extension, may be evidence of a difference in the nature of the differentiation of the internal areas of the body of *Dickinsonia* and its integuments.

The structure was interpreted as a digestive tract with diverticula (Dzik & Ivantsov 2002), a digestive distribution system (Ivantsov 2004, 2008), and a gastrovascular system of ctenophores (Zhang & Reitner 2006). However, it has no visible openings to the external environment either in front or behind. The purpose of the internal structure of *D. tenuis* from the Zimnie Gory remains uncertain. Its architecture determines the range of possible functions in the body by the accumulation and distribution or collection and excretion of some substances. However, the apparent absence of openings to the external environment limits it to the internal regions of the body. The structure is absent in other *Dickinsonia* species, but also in *D. tenuis* outside the Zimnie Gory locality. The manifestation of the structure in only one species and within one region shows that it is a private acquisition of one of the *Dickinsonia* populations.

2.8. Muscles

The body of *Dickinsonia* was able to expand and contract over a wide range (Wade 1972; Runnegar 1982; Evans *et al*. 2019a, 2019b). Although the remains of muscle fibres are not recorded on the imprints of *Dickinsonia*, the ability to contract the body and sometimes observed concentric folds (Fig. 1d) may represent indirect indicators suggesting the presence of a muscular system in these organisms (Glaessner & Wade 1966; Wade 1972; Runnegar 1982; Gehling 1991; Jenkins 1992; Gehling *et al*. 2005). Hypothetically, *Dickinsonia* should have had a system of multidirectional muscle fibres, including longitudinal, transverse,

Box 1 Key features of *Dickinsonia*, based on the results of the study of body imprints and complex body-trace fossils. In the upper part of the box, there are features that are directly observed or obtained by interpreting visible structures, while the reconstructed ones are placed in the lower part.

Consistent body shape, absence of lateral appendages and temporary outgrowths;
   Anterior–posterior polarisation and dorsoventral differentiation;
   Quasi-segmental (isomeric) differentiation, which may not have completely affected the internal areas of the body;
   Axial support structure;
   Lack of mouth, anus, and axial gut in general;
   Unique digestive? system in the form of two rows of transversely elongated, unconnected ventral pockets;
   Muscles;
   High level of regenerative ability;
   Development is direct, but the juvenile seems to have been devoid of isomers.

   Complex internal structure (probably tissue level of organisation);
   The presence of epithelium and a dense basal lamina;
   Ciliated mucus-secreting integumentary epithelium on the ventral side of the body; participation of cilia in locomotion and food capture;
   Terminal posterior addition of transverse elements;
   Mechanical way of capturing food objects (scratching the microbial mat with cilia, transporting and accumulating food particles inside specialised cavities, ventral pockets) with their subsequent phagocytosis or extracellular digestion;
   Lack of excretory organs, copulatory organs, and gonads (there is no direct evidence of their presence);
   Nervous system, most likely diffuse type;
   The supposed mode of locomotion is cilia gliding, plus muscle contractions;
   Ability to orientate in space is typical but there are no pronounced receptors and organs of orientation in space;
   Lack of sexual dimorphism (not detected);
   Sexual reproduction (no evidence of vegetative division was found);

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circular, and possibly diagonal ones (Runnegar 1982; Gehling 1991; Jenkins 1992). The often-observed slight variability in midline orientation and the asymmetry of the right and left sides of the body in length and width may indicate that muscles were used by *Dickinsonia* during movement (Evans *et al.* 2019a; Ivantsov & Zakrevskaya 2021a). Other indicators include the discontinuity of the traces and the ability to push through the sandy sediment (Ivantsov & Zakrevskaya 2021a).

2.8.1. New observations and discussion. The body of *Dickinsonia* was able to contract not only as a whole, but also in its individual parts. It is clearly seen in the bends recorded on the imprints. For example, in the shown specimen of *D. lissa* (Fig. 3a, b), the width of the isomers located on the outer side of the bend is at least twice as large as that of the ones on the inner side. This list also includes the revealed ability to push through the sediment (Ivantsov & Zakrevskaya 2021a). Sharp serpentine bends of *D. lissa*, accompanied by contraction and expansion of the isomers, are best explained by alternating muscle-driven contractions of the right and left sides of the body. The extraordinary height of the narrow specimens of *D. tenuis* from the Zimnie Gory was also presumably caused by a sharp muscular contraction. The branching internal structure seen in these imprints appears to be revealed due to being enveloped in a layer of tissue containing spasmodically contracted muscle fibres.

2.9. Reproduction and development

Dickinsonia had high viability and the possibility of regeneration. The loss of a body part could lead to a change in the proportions characteristic of the species, but did not end in death. The regenerated area was not separated, and the defects gradually smoothed out (Ivantsov *et al.* 2020b). And although failures could occur in the process of restoring the growth zone, even including a bifurcation of the body axis, no signs of asexual reproduction were found in these organisms. With a high probability, the reproduction of *Dickinsonia* was sexual. As far as it is seen from the fossil material, development was direct, and growth was due to an addition of the isomers terminally at the posterior end of the body, followed by their expansion (Runnegar 1982; Ivantsov 2008; Gold *et al.* 2015; Evans *et al.* 2017, 2021a; Ivantsov *et al.* 2020b; Ivantsov & Zakrevskaya 2022).

2.9.1. Discussion. The abundant studied fossil material on *Dickinsonia* does not give any signs of the vegetative reproduction of these animals. It can be concluded that the reproduction

of *Dickinsonia* was most likely sexual. But no signs of sexual dimorphism have been identified in *Dickinsonia*. With a length of less than 1 mm (in *D. costata* with a length of about 0.4 mm), the body of *Dickinsonia* might not have been differentiated yet. And at such size, they presumably led a planktonic lifestyle (Ivantsov 2007; Ivantsov & Zakrevskaya 2022). Individuals that did not form isomers also did not have ventral pockets since the latter is directly connected with the grooves separating the isomers. Such individuals probably fed differently from differentiated individuals, perhaps not fed at all. Based on this observation, we can assume that *Dickinsonia* had a planktonic, possibly non-feeding larva.

3. Conclusion of the position of *Dickinsonia* in the animal system

Based on the results of observations of fossils from the White Sea area, we reconstruct the following set of key features of *Dickinsonia* (Box 1). These were mobile marine benthic animals with the upper (photosynthetic) layer of microbial mats as their food object.

This set allows us to test the main hypotheses of the affinities of *Dickinsonia*.

Placozoan hypothesis. The comparison of *Dickinsonia* with *Trichoplax* (Sperling & Vinther 2010) is based, among other things, on only one observation of fossil material, or rather on one assumption that the feeding trace is formed by the action of the digestive sole. According to our conclusion, the proarticulates already had specialised digestive cavities, although they were open throughout their length to the external environment (Ivantsov & Malakhovskaya 2002; Ivantsov 2008, 2011, 2013). Of course, it cannot be ruled out that various anatomical structures of the ancient ancestor underwent a total reduction in *Trichoplax*. Then the big problem will be to identify the apomorphies that unite them. It seems quite unjustified to extend the features of a recent species to rather randomly chosen fossil taxa.

Ctenophora hypothesis. Comparison of *Dickinsonia* with ctenophores (Zhang & Reitner 2006) is based on the author's idea of the biradiality (with the axis oriented horizontally) of their bodies and on one specimen of *D. tenuis* from the Zimnie Gory, the fragmentary preserved internal structure of which was interpreted in a peculiar way. Since this specimen had only four pairs of lateral branches of the internal structure, they were homologised with the meridian canals of the gastrovascular system of ctenophores (Zhang & Reitner 2006). However,

specimens with a more fully preserved structure show a significantly larger number of lateral outgrowths, multiple branching of the anterior ones, and an alternating arrangement relative to the longitudinal canal. This observation clearly does not correspond to the organisation of ctenophores.

Hypothesis of polypoid Cnidaria. Valentine (1992) considers *Dickinsonia* to be radially symmetrical with a dorsal oral slit leading into the enteron, and interprets its isomers as diverticula, suggesting the skeleton of the modern scleractinian, *Fungia scutaria*, as a model for comparison. None of the points of this interpretation is supported by fossil material. Only in a very rough approximation can the skeleton of scleractinian resemble *Dickinsonia*. In addition, the growth of *Dickinsonia*, which is carried out by the addition of isomers, is opposite to the growth of corals through the addition of concentric rings (Gold *et al.* 2015).

Hypothesis of uncertain 'Coelenterata'. The traditional view of the axial band as an intestine filled with food, extended by the assumption of its joint with ventral pockets and observation of the mechanism of formation of feeding traces, allows us to interpret this structure as a branched gastric cavity, open throughout its entire length to the bottom side of the body (Ivantsov 2008, 2011). In this form, *Dickinsonia* can be compared with some polypoid animal, lacking tentacles, but able to crawl along the sea bottom on its oral side. Since the time of A. Sedgwick, such an organism has been recognised as a possible ancestor of the Phanerozoic Bilaterians (see, for example, Malakhov 2004). The hypothesis falls apart with the reinterpretation of the axial band as a dense non-hollow structure, of a different nature from the ventral pockets.

Hypothesis of segmented Bilateria with a coelomic level of organisation. According to Gehling (1991), *Dickinsonia* were normally segmented bilateral animals with muscles and a through-gut. However, even if *Dickinsonia*'s isomers are considered to be connected in pairs, it is hardly right to compare them with true segments (Evans *et al.* 2017, 2021a, 2021b), and the double axial band of *D. lissa* bears little resemblance to the intestine.

Xenacoelomorpha hypothesis (sister group to all remaining Bilateria (= Nephrozoa)). The set of xenacoelomorph features, the presence of which can be in some way identified on fossil remains, includes bilateral symmetry (including right–left differentiation, detected by the direction of movement), a blind gut (or its absence), a reticular nervous system, circular and longitudinal muscles, absence of nephridia, feeding by phagocytosis, locomotion mode by muco-ciliary gliding, and direct development (Cannon *et al.* 2016; Haszprunar 2016; Hejnol & Pang 2016). We find all these features in *Dickinsonia*. Particularly noteworthy is the blind gut of xenacoelomorphs, lined with phagocytic cells, with a different position of the oral opening on the body. Here we can find homology with the ventral pockets of *Dickinsonia*. The obvious difference between *Dickinsonia* and xenacoelomorphs is that the former has a transverse differentiation and an axial support band, features common in Nephrozoa. Such an 'intermediate' position between the two main branches of Bilateria provides a basis for comparing *Dickinsonia* with Urbilateria (the hypothetical closest common ancestor of Bilateria; De Robertis & Sasai 1996).

Urbilateria hypothesis. According to neonatologists, the common ancestor of bilaterians was probably a benthic, apparently bilateral, mobile ciliated flatworm with a single opening in the epithelial gut and a diffuse nerve net (Cannon *et al.* 2016; Hejnol & Pang 2016). Below the epidermis, it had a fibromuscular system; ultrafiltration cells and excretory organs were completely absent; the movement was performed by the method of muco-ciliary gliding; Urbilateria had a highly developed ability to regenerate, and development was direct without a true larval stage (Haszprunar 2016). The urbilaterians already had an axochord-like structure (Brunet *et al.* 2015). It is obvious that the set of features of *Dickinsonia* (and subsequently of all other proarticulates) that we have identified coincides with the characteristics of urbilaterians. And they are the only Ediacaran Metazoa known to us with such characteristics. Even the quasi-segmentation (isomerism) of the proarticulates does not contradict this fact, since the urbilaterians could already be segmented to some extent (Balavoine & Adoutte 2003). A significant discrepancy is the gigantic size and epifaunal lifestyle of *Dickinsonia*, while Urbilateria seems to be a very small, probably interstitial organism (Hejnol & Pang 2016). Gigantism involves the development of an excretory system in *Dickinsonia*; there were probably other differences, which also cannot be established from fossil remains.

The appearance of *Dickinsonia* in the fossil record occurred in the Late Ediacaran, about 557 million years ago. Simultaneously with *Dickinsonia*, other bilaterally symmetrical animals (for example, *Parvancorina*) appeared, that were morphologically far from both proarticulates, as far as one can judge from fossil remains, and Urbilateria. At the same time, or somewhat earlier, locomotion traces appeared, probably belonging to bilaterians (Buatois & Mangano 2016; Evans *et al.* 2020). Meanwhile, the moment of separation of cnidarians and bilaterians, primarily calculated on the basis of molecular data, refers to the Cryogenian (Erwin *et al.* 2011). It could mean that the proarticulates were an extremely conservative group, retaining in their body plan a number of basic features of the common ancestor of bilaterians for several tens of millions of years.

4. Acknowledgements

5. Competing interests

The authors declare none.

6. References

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