Trace Fossils of Precambrian Metazoans "Vendobionta" and "Mollusks"

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Abstract—Metazoan trace fossils from the Upper Vendian are preserved together with remains of corresponding organisms. The traces belong to "Vendobionta", representing the Precambrian phylum Proarticulata and to a presumably trochophoran animal *Kimberella quadrata*. These organisms fed on microbial mats, which preserved fossil traces. Impressions of the mat surface structures, traces, and bodies of animals are preserved in marine terrigenous sediments on the basal surfaces of sandstone beds. Proarticulata grazing traces are represented by groups and chains of impressions left by the ventral side of a body or its central and posterior parts. *Kimberella* traces are represented by long ridges united into bundles, fans, and chains of fans. All these traces were largely formed mechanically, i.e., by mat scratching with cilia (Proarticulata) or teeth (*Kimberella*). Proarticulata representatives destroyed only a thin upper layer of the mat, while *Kimberella* could possibly scratch the mat through its entire thickness or even tear off pieces from it.

Keywords: Vendian, trace fossils, Vendobionta, Metazoa, Trochozoa, Proarticulata, *Kimberella*

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INTRODUCTION

The taxonomic affinity of several groups of Late Precambrian organisms, relatively large fossil remains of which are found in localities of Australia (Ediacara), Europe (Arkhangel'sk region), Africa (Namibia), North America (Newfoundland), and other regions remains debatable. A. Seilacher, who considered them to belong to a single group of extinct organisms, suggested the term Vendobionta. At the same time, he gradually reduced in his successive publications the scope of this taxon ranking it as a separate extinct kingdom (Seilacher, 1992), animal phylum (Leo and Seilacher, 1994), and a class of protists (Seilacher et al., 2003).This name is usually currently used for all the Vendian megascopic organisms. In the existing reconstructions, Vendobionta are interpreted as organisms with a multichambered occasionally fractal body and external surface area significantly prevailing over its volume. At the same time, three-dimensional impressions preserved in sandy lenses in a seemingly lifetime position, as well as a visible lack of the oral aperture and digestive tract suggest that some species dwelt inside sediments and were symbiotrophic or osmotrophic feeders (Burzin, 1996; Seilacher, 1989, 1992, 2008; Grazhdankin and Seilacher, 2002; Seilacher et al., 2003). *Dickinsonia costata* Sprigg, 1947 is considered as one of the typical members of Vendobionta and a model object for describing their body structure (Seilacher et al., 1989). *Dickinsonia* is the most diverse genus of Vendian animals with eight or nine fossil species belonging to the phylum Proarticulata Fedonkin, 1985, the largest group of Precambrian metazoans. Despite their extremely high taxonomic diversity, Proarticulata were apparently relatively restricted geographically since their fossil remains are still only known in Ediacaran sections of the Flinders Ranges of southern Australia and Vendian sequences of the East European Platform. *D. costata*, which is now sufficiently well studied, was the first Proarticulata to be discovered. However, this species is not the most informative representative of this group. Extensive data on anatomy and life style of Proarticulata were obtained from studying fossil remains belonging to *Yorgia waggoneri* Ivantsov, 1999, a close relative of *Dickinsonia*. Some elements of the internal structure (most likely shared with Proarticulata), are preserved only in other, relatively rare species. All the Proarticulata forms had a transversely segmented body and, in some of them had a distinctly developed cephalic lobe, which suggested their affinity to annelids, or even arthropods (Menner, 1963, Glaessner and Wade, 1966, 1971; Wade, 1972a, Glaessner, 1976, 1979; Jenkins, 1992). However, other anatomical features of Proarticuata, primarily the absence of truly complete segmentation, articulate limbs, and any other lateral processes do not agree with this interpretation. The body of these organisms consisted of two rows of right- and left-side identical "half-segments" (isomers) located along its longitudinal axis in line with the principle of glide reflection

symmetry (Fedonkin, 1985), not of a series of segments as in most Articulata. This type of symmetry, also observed in other Vendobionta apart from Proarticulata, is not typical of solitary Phanerozoic Metazoa, although it occurs in Protista, multicellular colonies and, frequently, plants. Nevertheless, this does not stop supporters of the hypothesis of Metazoan affinity of Vendobionta. A discovery of long trails served as a decisive argument for attributing at least Proarticulata species to Metazoa (Ivantsov and Fedonkin, 2001a, 2001b).

First traces of the impact of Proarticulata on the substrate together with impressions of trace-maker bodies were discovered in the Vendian sections of the Arkhangel'sk region (Ivantsov, 2001a, 2004; Ivantsov and Fedonkin, 2001a; Ivantsov and Malakhovskaya, 2002). Subsequently, similar trace fossils were found in Ediacaran rocks of southern Australia (Gehling, 2005). These regions also yielded similar assemblages of traces and body remains of *Kimberella quadrata* (Glaessner and Wade, 1966), a representative of another Metazoa group (Fedonkin, 2001; Seilacher et al., 2003; Seilacher, 2007; Fedonkin et al., 2007b; Ivantsov, 2009).

PROARTICULATA TRACES

In the Arkhangel'sk region, many localities of fossil remains belonging to Vendian uni- and multicellular organisms are found in the southeastern White Sea (the so-called Belomor'e) region. In the latter, benthic animals were buried in their habitat sites in the shallow-water sea basin with terrigenous sedimentation, where high-energy hydrodynamics frequently resulted in sediment roiling and reworking of fine detrital material (Grazhdankin and Ivantsov, 1996; Grazhdankin, 2003, 2004). Depositional environments in burial sites of these traces are interpreted as being prodeltaic (Grazhdankin, 2003, 2004). The local accumulation of impressions, the so-called Yorgia Bed of the Zimnie Gory locality (Z2(III)) is characterized by perfect preservation of Proarticulata remains (Ivantsov, 1999, 2001b, 2008, 2011; Ivantsov and Malakhovskaya, 2002). In this locality, all the impressions are confined to a single bedding surface, i.e., to the base of an extensive bed of fine-grained sandstone approximately 7 cm thick. The bed is underlain by mudstone that includes thin sandy lenses. The base of the bed exhibits areas with structures of two types. The surface of the first type is smoothed, grained, and complicated by chattermarks, while the surface of the second type is finely to moderately hummocky with large isometric depressions. The contact of areas with different surface types is distinct. As compared with the smoothed surface, the hummocky one is slightly impressed into the bed and its margins are usually bended and locally submerged into sediments for a few centimeters, where it grades into a jointing surface. Locally, trace impressions are submerged into the

bed with such a surface retaining trace patterns also at the jointing surface. Abundant fossil traces occur only on surfaces of the second type. Their accumulations include remains of the bodies of seven Proarticulata species (*Andiva ivantsovi, Cyanorus singularis, Dickinsonia costata, D. tenuis, Lossinia lissetskii, Paravendia janae, Yorgia waggoneri*) and several other typically Vendian organisms (*Cyclomedusa* sp., *Kimberella quadrata, Parvancorina minchami, Tribrachidium heraldicum, Vaveliksia vana*, and others). All these remains are represented by impressions, which is typical of Vendian localities. The Yorgia Bed locality was formed during the rapid burial of a sandy–muddy bottom area with living organisms and some traces of their life activity. Areas with the smoothed surface reflect bottom erosion, which immediately preceded this event. To the contrary, the hummocky surface was formed by a flat object, which covered bottom and was able to break, bend, and take impressions. This object was most likely a microbial mat that was subsequently entirely destroyed. In the burial state, only cast of its upper side with peculiar microornamentation and trace impressions are preserved. The microbial mat was relatively compact and thick to retain Proarticulata traces, which changed, in case of deformation, together with the latter as a single object (Ivantsov and Malakhovskaya, 2002; Ivantsov, 2008, 2011). This locality yielded three Proarticulata species including a very long fragment of *Yorgia waggoneri* trace chain 4.3 m long left by a specimen 19 cm long (Ivantsov and Malakhovskaya, 2002).

The typical Proarticulata trace consists of several elementary impressions (trace platforms) each representing a cast of the ventral animal side, although isolated platforms are also observable. The relatively large surface area shows that most trace platforms are grouped into continuous or discrete trails sometime very long and consisting of many impressions. In such groups, trace platforms are characterized by equal sizes that are uniform through the every observed fragment. Within the trace platform, the hummocky patterns of the mat surface disappear being replaced by smooth and almost flat impression of the ventral side of the Proarticulata body with thin grooves left by zones separating isomers. Unlike body impressions with negative high-amplitude relief, traces are displayed as positive and relatively low structures. The lack of a sharp contact with host rocks along the entire contour or its separate areas represents another peculiar feature of the trace platform (Plate I, figs. 1, 2 (below)). Frequently, impressions are left only by the central (relative to the longitudinal axis) or posterior parts of the body. The anterior area never leaves separate impressions. The frequent intersection of different traces is an additional feature of trace fossils. When two trace platforms are overlapped, the last of them is better expressed usually masking the younger one. Locally, relief of both platforms is preserved in the overlapping area to provide distinct reticulate patterns
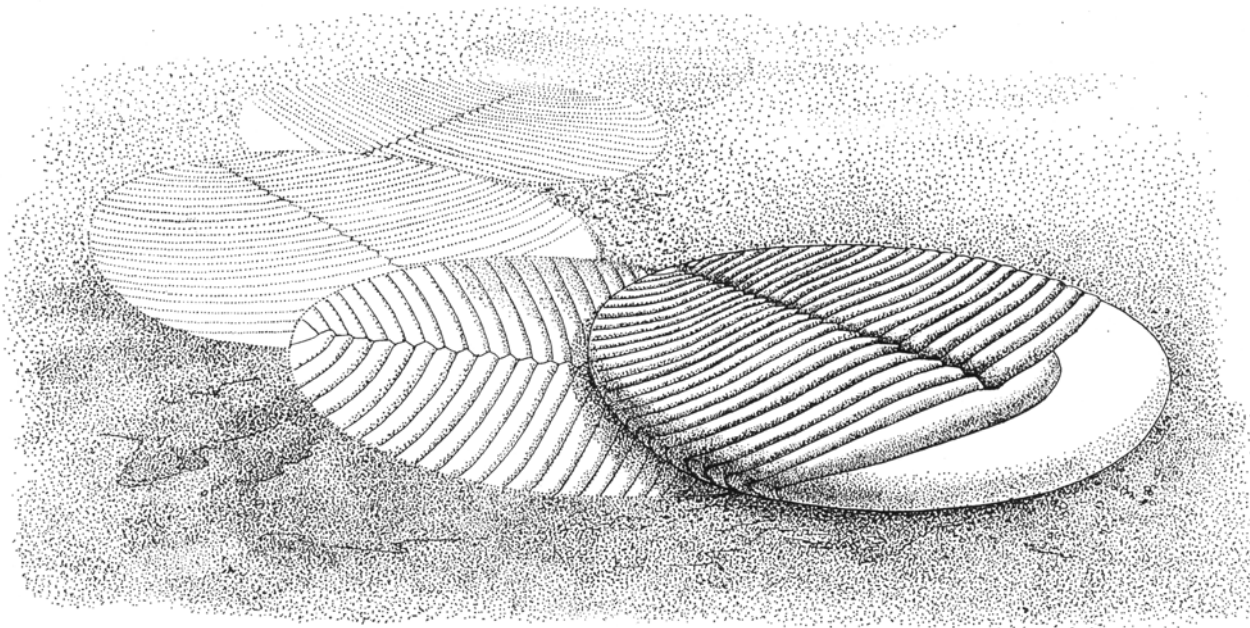
Fig. 1. *Yorgia waggoneri* Ivantsov, 1999 with grazing traces of *Epibaion waggoneris* Ivantsov, 2011 (my reconstruction, drawing by A.A. Besedina).

(Plate I, fig. 1). Contrary to traces, body impressions of Vendian organisms buried on the microbial mat are rarely found overprinted by each other; moreover, *Dickinsonia* traces and body impressions demonstrate an antagonistic distribution (Gehling, 2005). The remarkable feature of Proarticulata traces is also a lack of features indicating body motion along the substrate surface: impressions resemble accurately made reprints with a body serving as a punch (Plate I, fig. 2).

The trace platform was left by an animal that somehow destroyed the upper layer of its habitat substrate (microbial mat). Sprawling along the mat surface, a Proarticulata specimen "etched" it to an insignificant depth and then moved to a new place (Fig. 1). In doing so, it disintegrated only the upper layer of the mat, which remained elastic to preserve traces even during breakage and movement within the host sediments. In

my opinion, the impact of Proarticulata on the mat was a result of grazing (Ivantsov and Malakhovskaya, 2002; Ivantsov, 2004, 2008a, 2008b, 2011). Dzik (2003) assumed that *Yorgia* staying at the same place for a long time shaded and restrained the growth of the mat. According to (Gehling, 2005), suppressing the mat, *Dickinsonia* caused atrophy of the mat's upper layer and then sucked in decomposition products via its ventral surface. Gehling (2005) thought that degradation of the first impression in each group of trace platforms of *D. costata*, observable in Australian trace fossils, may serve as indirect evidence for significant duration of this process. Poor preservation of some trace platforms is interpreted as resulting from regeneration of the upper mat layer destroyed by Proarticulata organisms (Ivantsov and Malakhovskaya, 2002). At the same time, no regeneration of the upper layer of

Plate I. Body impressions and grazing traces of Proarticulata from the Upper Vendian sections of the Arkhangel'sk region (Zimnie Gory locality, (1−3) Erga Formation, accumulation of impressions Z2(III) "Yorgia Bed", (4, 5) Zimnie Gory Formation; (1−3, 5) natural impressions; (4) latex cast of the natural impression.
Fig. 1. Fragments of two superposed *Epibaion axiferus* Ivantsov, 2002 trace platforms; holotype PIN, specimen no. 3993/5199 (×1.5); the subsequent platform (below) partly obliterates the preceding one.
**Fig. 2.** Chain of race platforms (specimen nos. 3993/5149−3993/5152) and body impression of small trace-making *Yorgia waggoneri* Ivantsov, 1999 specimen (in the upper part of the image, specimen PIN, no. 3993/5058 (×2). Occupying a smaller area compared with the trace platform, the body impression is characterized by uneven contours and covered by rough folds; these deformations presumably reflect attempts of the animal to escape from sediments.
Fig. 3. The fragment of the *Yorgia waggoneri* trace platform, specimen PIN, no. 3993/5147 (×2). Isomer impressions exhibit V-shaped striation presumably formed by scratching movements of cilia; cylindrical swellings on boundaries between isomers are impressions of deep grooves of unknown genesis on the microbial mat, which were located beneath food-accumulating cavities.
Fig. 4. Fragment of the *Dickinsonia* sp. body impression; specimen PIN, no. 3993/8874 (×2.5); lumpy content of food-accumulating cavities observable through collapsed tissues.
Fig. 5. The posterior part of the *Dickinsonia costata* Sprigg, 1947 body impression; specimen PIN, no. 3993/8875 (×1.5); replicas of food-accumulating cavities located at large angles relative to isomers and filled with sandy material.

Plate I
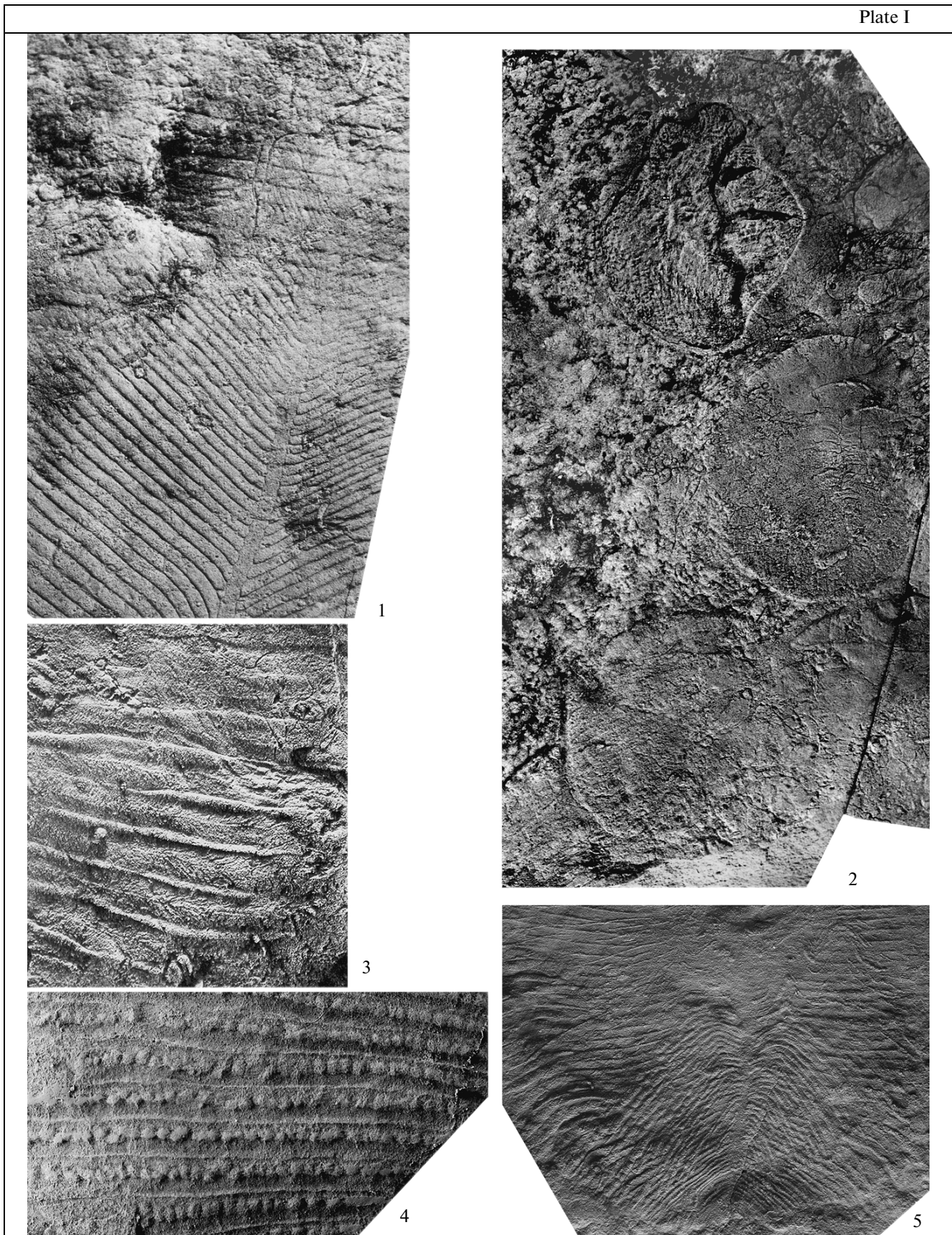
mat destroyed by Proarticulata is observed in large fragments even of the longest trails in the Yorgia Bed locality. This means that both grazing and locomotion of these animal organisms along the bottom could be relatively quick. In addition, a tendency to form reduced platforms corresponding only to the central and posterior parts of the body without participation of margins and anterior end is inconsistent with the hypothesis of the long immobile stay on the mat. This also makes an idea of secretion of digestive enzymes immediately onto the mat surface with the subsequent absorption of digested particles by the ventral side hardly probable: this process requires a large area and maximal physical contact of the body with the digested substrate. The surface of *Y. waggoneri* traces is locally covered by a thin V-shaped striation (Plate I, fig. 3). It is conceivable that the ventral side of the Proarticulata body was covered by cilia, which captured and transferred food particles. In *Yorgia* representatives, these cilia probably formed groups, which were responsible for the formation of the above-mentioned striation (Ivantsov, 2004, 2008a, 2008b, 2011). Judging from orientation of striae, hypothetical cilia moved from the isomer axis toward its nearest edges: half of them toward the anterior end and another half, toward the posterior end. According to this hypothesis, food particles were collected at sites located between isomers. Indeed, several known impressions of the *Dickinsonia costata* body exhibit additional thin radial ridges composed of sandstone (Glaessner and Wade, 1966, pl. 101, fig. 4). One excellent such specimen originates from the Zimnie Gory locality (Plate I, fig. 5). The photo illustrating a fragment of the *D. costata* impression shows that ridges near its posterior end adhere to the surface and diverge from the latter in the middle part of the body being replaced by thin grooves. Such patterns are determined by preservation of some elongated cavities located near the ventral side of the animal body. Inasmuch as the impression was left by the upper side of the body, the space between the latter and cavities was initially occupied by soft tissues. As these tissues became decomposed, sand overlying the body and that filling cavities gradually approached each other to be partly joined by the lithification onset remaining locally separated by a thin lamina of organic matter. During rock sampling, free sandy rods were broken away leaving grooves on the impression. The crisscross arrangement of ridges and isomer impressions is also observable in other *Dickinsonia* species (Ivantsov, 2008, 2011). Chains of tubercles located in the isomer from a single *Dickinsonia* sp. sample may also represent impressions of filled cavities. In this situation, no filling material was preserved; instead it formed ridges elevated against the background of the collapsed body (Plate I, fig. 4). Similar cavities filled by compact subsequently vanished material could likely be responsible for the formation of additional deep depressions on impressions left by many Proarticulata species. They are represented by two grooves extending along the longitudinal axis of the impression in *Dickinsonia lissa* or transverse twisting deeps confined to isomer boundaries in *Yorgia waggoneri*. These structures on Proarticulata impressions are interpreted as representing remains of internal body cavities: usually as a main channel of the digestive tract and its lateral apophyses (Glaessner and Wade, 1966; Wade, 1972a; Jenkins, 1992). In the opinion of E. Dzik, structures separating isomers in *Yorgia* represent gonads (Dzik and Ivantsov, 1999; Dzik, 2003). With regard to depressions, one can suggest that internal body cavities were filled with organic matter or its decomposed products. In case of sandy impressions, the occurrence of sediment and its regular distribution in cavities, which were isolated from environments and frequently narrow, are difficult to explain. When cavities were open or, moreover, had connection with environments along the entire body length, they could easily be filled with sediment. For example, incidental penetration of sand into hollow cavities could occur during body burial. Another scenario also cannot be ruled out: gradual accumulation of mineral grains representing a normal component of the microbial mat proper, which were randomly consumed by animals. In these cavities opened toward the ventral side through its entire length, particles from the microbial mat were subjected to fermentative decomposition with the subsequent consumption of released nutrients (Ivantsov, 2008, 2011). With such a digestive system, it was unnecessary for Proarticulata specimens to stay for a long time at the same site and closely adhere to the mat. To the contrary, it was sufficient just to touch it briefly by some segment of its ventral surface. Certainly, the mechanical mode of food collecting does not exclude biochemical or any other influence of the animal on the mat, although it was likely dominant.

Grazing traces yield little information on the mode of Proarticulata locomotion, since the microbial mat only the final result of deep impact, which destroyed the structure of its upper layers. During grazing, the animal remained immobile leaving no indications of its sliding along the substrate or repulsion from the latter onto the trace platform (Ivantsov and Malakhovskaya, 2002; Ivantsov, 2004, 2008a, 2008b, 2011; Brasie and Anticliffe, 2008). Although the animal undoubtedly moved between platforms corresponding to different grazing sites, no features indicating this movement are observable since the continuity of the mat remained undisturbed. This movement was deliberate, as is evident from the regular orientation of impressions in trails by the blunt end (corresponding in some Proarticulata species to the nonsegmented cephalic lobe) in its direction (Plate I, fig. 2). Occurrence of trace systems, solitary platforms, body impressions separately from traces, and groups of traces separately from corresponding bodies is explainable, if we assume that the animal could move

for a relatively long period between feeding or, probably, rise above the bottom and float.

The analysis of *Yorgia* remains reveals that this animal left the complex positive−negative impressions, when it was buried immediately on its own trace platform (Ivantsov, 1999). In this situation, its negative part corresponding to the body is surrounded by the positive rim of traces since the surface of the contracted body is always smaller as compared with the latter (Plate I, fig. 2, upper impression). This resembles very much impressions of *D. costata* from Australian localities with contraction indications, which presumably resulted from postmortem shortening of the decomposing body (Wade, 1968). In fact, they are similar phenomena, although in the case of the trace platform its positive impression could be left by the animate being, not a dead body compressed under the sediment load, as it is assumed for *Dicksonia*; moreover, body contraction occurred following the animal's death, not in the postmortem state. It is obvious that no contraction features may occur without body impressions, while solitary platforms are frequently observable.

By now, three types of Proarticulata traces are described. They are united into a single ichnogenus *Epibaion: E. axiferus* Ivantsov, 2002, *E. waggoneris* Ivantsov, 2011, and *E. costatus* Ivantsov, 2011. From the most simple trace platform of *E. costatus*, others differ by development of nonsegmented lobes: axial in *E. axiferus* and cephalic in *E. waggoneris* (Ivantsov and Malakhovskaya, 2002; Ivantsov, 2011).

GRAZING TRACES OF *KIMBERELLA*

Kimberella is another Vendian metazoan, which left preserved traces on the microbial mat. This organism was first considered to represent a cubomedusa (Wade, 1972b; Jenkins, 1992) and, then, shelly mollusk, the oldest one in the geological record (Fedonkin and Waggoner, 1997; Fedonkin, 2001, 2003, Fedonkin et al., 2007b). In my opinion, *Kimberella* had little to do with mollusks, although it was probably a primitive trochophoran animal (Trochozoa). It was characterized by a worm-shaped body, large head, which could be pulled in, and strong dorsal musculature (Ivantsov, 2009, 2010a, 2010b). The conclusion on belonging of traces precisely to this being was derived, similar to Proarticulata traces, from its complex fossil remains (aggregation of traces and body impression). The trace, which is typically fan-shaped and consists of thin ridges, was known for a long time from the Ediacaran section of Australia, although it has never been formally described. It is conceivable that M. Glaessner interpreted precisely this fossil as a bundle of straight sponge spicules (Gehling and Rigby, 1966). Subsequently, it was reinterpreted as a trace left by chelate limbs of unknown Arthropoda form close to the genus *Monomorphichnus* Crimes, 1970 (Gehling, 1991; Jenkins, 1995). A. Seilacher considered this fossil similar to traces left by radula and attributed it to *Kimberella*, body impressions of which occur on the same bedding surfaces (Seilacher, 1999, 2007, 2008; Seilacher et al., 2003). The first complex impression consisting of several fans of ridges and a *Kimberella* body impression was revealed by M.A. Fedonkin in the collection of the Museum of Natural History in Milan. This sample, originating from the Zimnie Gory section of the White Sea coast, was illegally collected and exported by private fossil collectors, and then returned to Russia through the courtesy of G. Teruzzi, the director of this museum (Fedonkin, 2001; Fedonkin and Vickers-Rich, 2007b). Analyzing features of this trace, Fedonkin interpreted it as a trace left by a solitary conjugate pair of teeth located at the end of a long proboscis that stretched far forward beyond the main body (Fedonkin, 2003; Fedonkin and Vickers-Rich, 2007b; Fedonkin et al., 2007b).

The locality SL1(VII) in the upper part of the Verkhovka Formation at the Solza River yielded abundant aggregations consisting of traces and body impressions of *Kimberella*. In this locality, fossils occur at the base of a bed composed of fine-grained flatly cross-bedded sandstone 17 cm thick. The productive surface is smoothed, frequently with deep (1−3 cm) and wide (10−20 cm) isometric flat-bottomed depressions, grooves, and small tubercles. The locality includes diverse Metazoa remains such as *Armillifera parva, Cyanorus singularis, Dickinsonia costata, Dickinsonia* sp., *Fedomia mikhaili, Lossinia lissetskii, Onega stepanovi, Palaeophragmodictya spinosa, Parvancorina sagitta, Solza margarita, Temnoxa molliuscula, Tribrachidium heraldicum*, and *Vendia rachiata*, in addition to *Kimberella* traces (Ivantsov, 2007). The *Kimberella* traces in this locality are represented by narrow (approximately centimeter-wide) uncertainly long low eminences consisting of uniform successive fans of fine ridges. They are closely spaced and being left by small specimens are of little interest. The larger and more freely spaced traces are found at the base of the Zimnie Gory Formation cropping out in the Zimnie Gory area. In this locality, fossils cover the basal surface of a fine-grained sandstone bed 2 cm thick (Plate II, figs. 3−5). The burial is monospecific: despite the large area of the exposed surface no other Metazoa remains including *Kimberella* bodies were found in this locality.

The *Kimberella* traces are usually united into large groups locally covering the entire observable bed surface. Each fan in a trace is composed of a system of converging ridges or vague bundles. The fans are juxtaposed upon each other and form chains, where all of them are oriented in a single direction, while the narrow end of each fan is overlapped and masked by the wide end of the neighboring one. In aggregations, the *Kimberella* body impressions are located at convergence points of ridges or at the ends of fan chains, which provides good evidence for their belonging to this animal. No isolated ridges are observable. A single
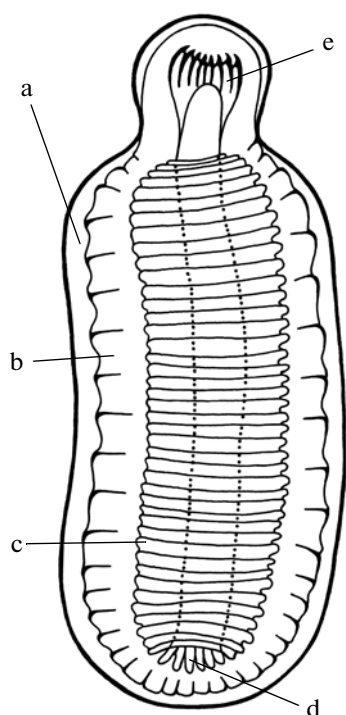
Fig. 2. Schematic structure of *Kimberella quadrata* (Glaessner et Wade, 1966) (reconstruction from typical impression): (a) lateral and lower parts of the body (leg?); (b) scalloped part of the dorsal covering structure; (c) transverse muscular bundles; (d) longitudinal muscular strand; (e) teeth.

fan lacks also transverse ridges. Long ribbons, which consist of hundreds of ridges left by a moving animal, demonstrate bundles or successive fans, but never steps of ridges. The mobile animal with a long, flexible proboscis freely bending in all directions should leave more chaotic traces. This implies that the animal got deeper into the mat using a larger structure with several teeth and limited ability for lateral bending, rather than separate teeth located at the end of the flexible proboscis. Such a structure was most likely represented by the entire anterior part of the *Kimberella* body together with a large head, which was able to extend and widen (Ivantsov, 2009, 2010, 2011). In order to cut narrow and deep grooves, teeth should be thin and hard (sclerotized). Similar to the sclerites of dorsal covers defined in *Kimberella* forms, they included some mineral component, which was unstable in H_2S-saturated environments of sandy sediment and, therefore, and they were not preserved in the fos-

sil record. It is conceivable that crescent grooves (ridges in the latex mould) occasionally observable in the central part of the head represent their impressions (Plate II, figs. 1, 2). This internal area is reflected in the high relief, which points to its relatively higher density as compared with surrounding organs. Its shape changes depending on the position of the head. In presented images of specimens, the head is located in the intermediate position, when the area which connects it with the main body, was strongly, although incompletely contracted. In such a position, the internal area resembles a bulb. It is similar to an arrow tip with large lateral limbs in the head pulled into a body and horseshoe or crescent in maximally forward-pushed head (Ivantsov, 2009, 2010a, 2010b). The variability of shapes may point to different positions of the tooth battery, usually folded in two groups on both sides of the pharynx and unfolded in a half-circle manner along the lateral and frontal parts of the mouth aperture during food capture (Fig. 2). The unfolded teeth were used for mechanical impact of the mat. Contracting the anterior part of a body and head, the animal scratched the substrate using its teeth leaving a bundle of converging grooves and then ingested a lump of food particles collected in such a manner. Staying in the stable position, it usually made several scratches in different directions to leave a fan-shaped trace. Moving further with a forward-oriented posterior end, *Kimberella* formed the next fan at the site, where it stayed before (Fig. 3).
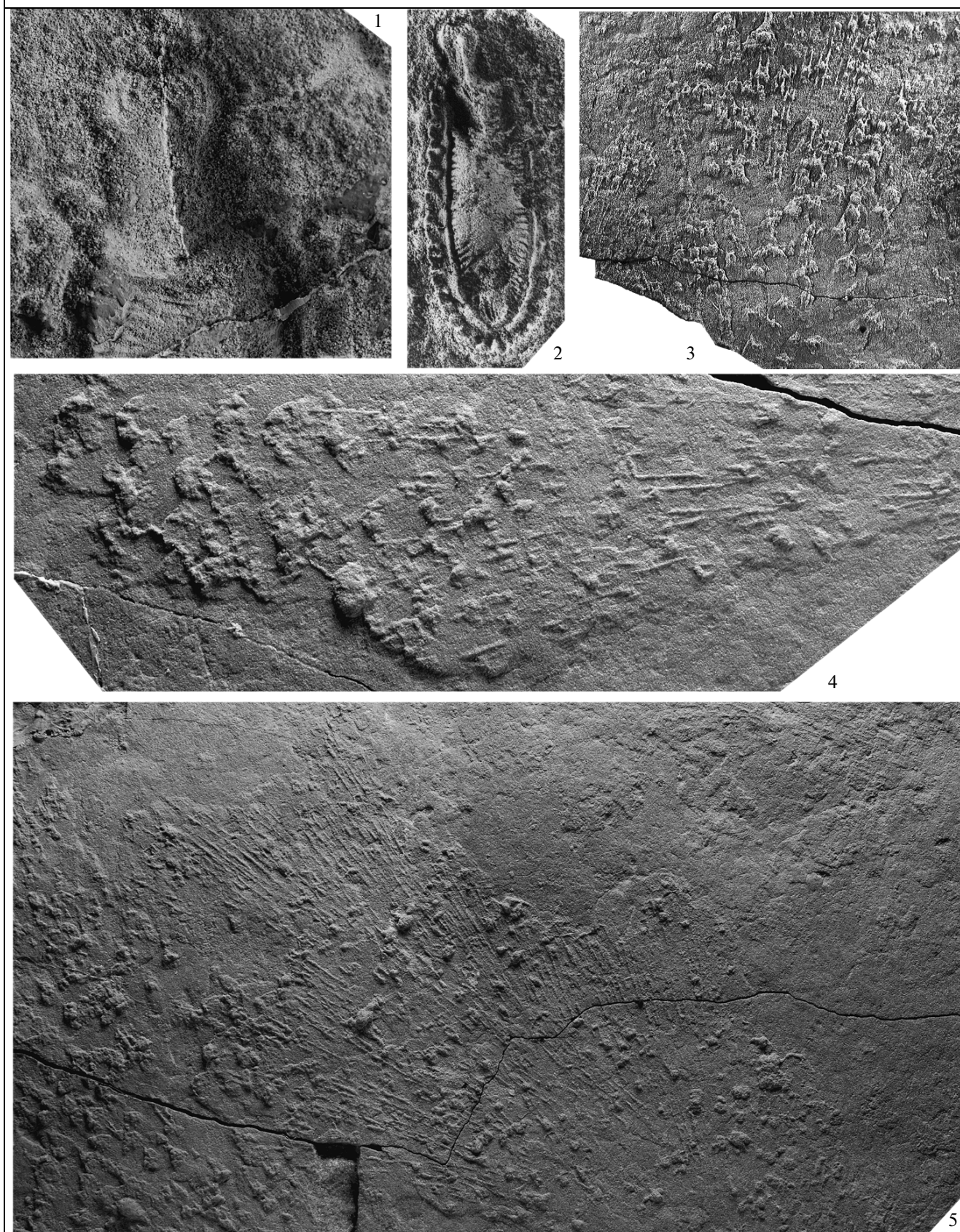
This hypothesis cannot explain, however, a peculiar feature of the *Kimberella* trace: the tendency of ridges to form relatively distinct pairs (Plate II, fig. 3). It is conceivable that teeth could occasionally converge in pairs, although acted as a single group. Ridges are frequently characterized by discrete patterns since the mat surface was uneven. Such fans of fragmented paired ridges resemble impressions of arcuate scratch traces left by radula of the mollusk *Radulichnus* Voigt, 1977 (Seilacher, 1999, 2007, 2008; Seilacher et al., 2003). At the same time, ridges in *Kimberella* traces are readily traceable, despite their discrete patterns, over significant distance and exhibit usually fragments disproportionately long for radula traces. For example, in large fans up to 7 cm wide from the Zimnie Gory locality, continuous fragments of ridges are 1.5–2.0 cm long with distances between paired ridges being equal to 3.5 mm. The complete ridge was probably at least 5 cm long. It means that the *Kimberella* scratch was 5–15 times longer than the distance between paired grooves in the latter, while the length of molluscan
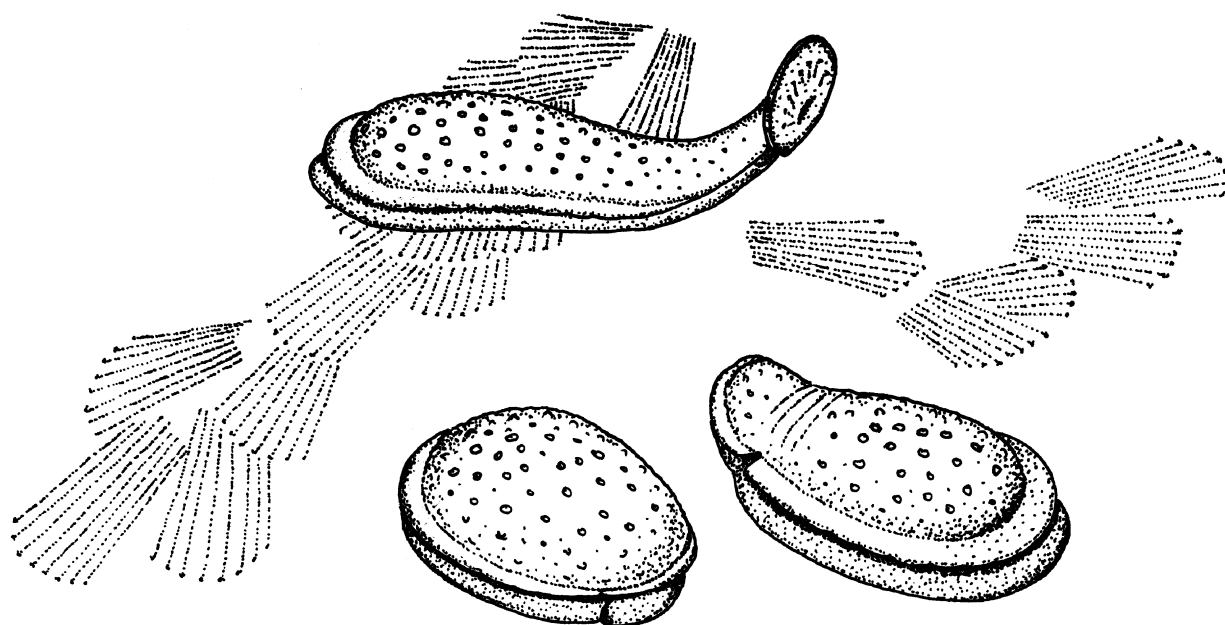
Plate II

Fig. 3. Reconstruction of *Kimberella* with grazing traces of *Kimberichnus teruzzii*, isp. nov. (from Ivantsov, 2009).

radula traces exceeds their widths at maximum three times, as follows from images in (Voigt, 1977).

In many samples of traces collected from the base of the Zimnie Gory section, fans of ridges are accompanied by groups of tubercles with the variable (locally, large) height. The tubercles are isometric or slightly elongated; some of them are triangular. Their sizes range from 1.5 to 5.0 mm, sometimes the specimens up to 1 cm in length occur. The image in (Plate II, fig. 4) shows that tubercles are confined to a wide fan margin remote from the body. They never occur beyond fans representing traces of *Kimberella*, not structures of the mat (Plate II, fig. 5). Tubercles are also not impressions of some food particles since their impressions should be reflected in another (negative) relief and also would extend beyond fans. The diversity of shapes and sizes of tubercles and their positive relief are inconsistent with the assumption that they were left by *Kimberella* victims (Fedonkin et al., 2007b). These structures most probably represent scratches on the mat resulting from the mechanical impact of *Kimberella* teeth. In some bottom areas, the mat was probably thin so that the animal could tear off pieces from it. Short crests, in the shape of an overturned V, which begin some ridges, may also be explained by local breaks in the mat (Fedonkin, 2003, fig. 15, upper group of traces). The peak of the crest is located at the ridge with its limbs facing toward the convergence point of the fan ridges. This means that the animal scratched the mat toward itself (Ivantsov, 2010). The distal arrangement of tubercles also implies that the impact on the substrate was maximal away from, and minimal close to, the body, respectively. Such patterns make traces left by *Kimberella* igen. nov. cardinally different from radula traces, since using the latter mollusk directs it away from itself (Ruppert et al., 2004). Another difference consists in selection of a site for new grooves. Eating up the substrate, the mollusk moves with its head oriented forward; therefore, new scratches were formed on the external side relative to the animal body. To the contrary, *Kimberella* moved backward; therefore, a new bundle of scratches appeared near the internal end of their preceding group.

DISTRIBUTION OF PROARTICULATA AND *Kimberella* GRAZING TRACES

The *Epibaion* and *Kimberichnus* traces are usual ichnofossils occurred in the middle part of the Upper Vendian section in the southeastern White Sea region. The representatives of the first genus appear at different levels: *E. axiferus* in the Lyamtsa Formation; *E. costatus* in the upper part of the Verkhovka Formation; *E. waggoneris* slightly above. All these species disappear simultaneously in the basal part of the Erga Formation (Fig. 4). Beyond the White Sea region, only *E. costatus* is known from the Ediacara Member of the Ransley Quartzite in southern Australia (Gehling, 2005; Ivantsov, 2011). The first specimen of the isolated trace platform of this species was illustrated in (Sprigg, 1949, plate XX, fig. 1), where it was identified as body imprint of *Dickinsonia costata*. The Ediacara Member yielded *Phyllozoon hanseni* as well, which is also considered to represent body remains (Jenkins and Gehling, 1978). In its main features (positive relief, tendency for the formation of compact palimpsests, lack of sharp lateral boundaries), *Phyllo-*
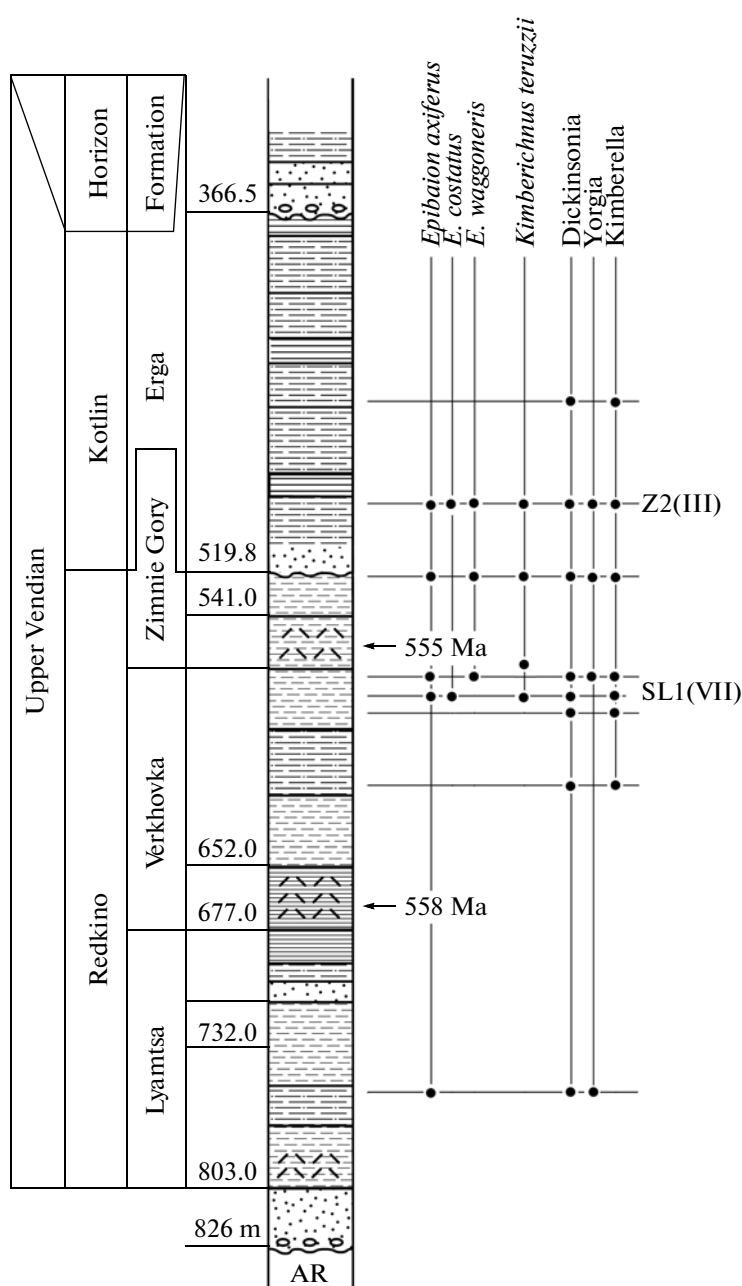
Fig. 4. Distribution of grazing traces and hypothetical trace-making organisms in the Upper Vendian sections of the southeastern White Sea region (correlated with the section of the Borehole Ust'-Pinega (from Fedonkin et al., 2007a, modified)).

zoon belongs to the group of fossils under consideration also likely representing the Proarticulata grazing trace (Ivantsov, 2008, 2011). The third Australian fossil from this group was found in the upper part of the Uratanna Formation dated by "traditional" traces of benthic animals back to the Early Cambrian (Jensen et al., 1998). Jensen et al. (1998) identified this fossil as a "frond-shaped organism similar to *Swartpuntia*." At the same time, some of its features such as low relief and obscure contours, as well as preservation in form of negative impressions on the upper surface of a bed allow it to be interpreted as a Proarticulata trace. If the

hypothetical axial structure (which is unobservable in images from the last work) is excluded, this fossil is identical to *E. waggoneris*.

Both the *Kimberichnus* and *Epibaion* traces are most abundant in the upper fourth of the Verkhovka Formation, Zimnie Gory Formation, and in the basal part of the Erga Formation. The distribution of body remains of potential trace-makers is wider (Fig. 4). Noteworthy is the spatial antagonism of Proarticulata and *Kimberella* grazing traces: despite their abundant finds, they have never been met together at the same

bedding surface. The sole probable exception is the "Yorgia Bed" burial traceable over several hundreds of meters along the strike. In addition to abundant and diverse Proarticulata traces, this locality yields also plates found in talus with the *Kimberichnus* traces preserved at the surface with the structure of the microbial mat. The limited number of finds of these fossils prevent the relationships between the two ichnogenera from being clarified. It is conceivable that feeding preferences of these trace-making animals were different and they used mat areas with different prevailing groups of microorganisms.

Observations show that development of structures of the microbial mat at some surfaces by no means guarantees the discovery of grazing traces on the latter. And to the contrary, mass accumulations of *Kimberichnus* traces are not necessary accompanied by *Kimberella* remains. It means that preservation condition of traces and bodies were different. The ability of the mat to preserve damage left by grazing metazoans was probably the main factor determining these differences. The latter could depend on many still poorly known causes such as, for example, age of the particular microbial community and season, when traces were left (Zakrevskaya, 2011).

According to the ethological classification (Seilacher, 1953), *Epibaion* and *Kimberichnus* should be attributed to grazing traces (*Pascihnia*). Some researchers (Palii, 1976) also include *Paleopascichnus delicatus* Palij, 1976 and *Harlaniella podolica* Sokolov, 1972, which occur locally together with *Epibaion* representatives on the same bedding surfaces, into this category of traces. At the same time, *Paleopascichnus* and *Harlaniella* representatives can be preserved in both positive and negative relief. Changes in the relief are frequently observed even in the same impression. There are also other features, which allow *Harlaniella* finds to be interpreted as body fossils rather than traces (Jensen, 2003). *Paleopascichnus* might appear to be shells of giant Protista (Seilacher et al., 2003). Thus, the fossils described in this work still remain the sole reliable grazing traces on microbial mats.

PALEONTOLOGICAL DESCRIPTION

***Kimberichnus teruzzii* Ivantsov, igen. et isp. nov.**

Plate II, figs. 3–5; Fig. 3

Traces of Arthropoda limbs: Gehling, 1991, p. 215, pl. 6, fig. 3; Jenkins, 1992, p. 168, fig. 10; 1995, p. 57, pl. 1, fig. c.

Radulichnus (part): Seilacher, 2007, p. 182, pl. 63; 2008, p. 30, fig. 15; Seilacher et al., 2003, p. 44, fig. 3.

Scratch marks and grazing tracks of *Kimberella quadrata*: Fedonkin, 2003, p. 29, figs. 15, 16; Fedonkin et al., 2007b, p. 174, figs. 19, 20, 22; Fedonkin and Vickers-Rich, 2007a, pp. 141, 142, fig. 265; Fedonkin and Vickers-Rich, 2007b, p. 215, figs. 397, 416–418; Ivantsov, 2009, p. 4, pl. II, figs. 5–7, 9.

N a m e. From *Kimberella* and in honor of prof. G. Teruzzi.

H o l o t y p e. PIN, no. 3993/5619; Arkhangel'sk region, Zimnii Bereg, White Sea; Upper Vendian, Zimnie Gory Formation (Plate II, fig. 4).

D e s c r i p t i o n. Thin ridges reflecting moulds of grooves on the primary substrate. The ridges slightly converge in the same direction, occasionally paired and grouped into bundles. Converged and partly fused bundles form wide fans. The latter may constitute unbounded in extent trails, where the subsequent fan is located near (or instead of) narrow internal end of the preceding fan.

S i z e s. Length of ridges and width of fans are highly variable, although both of them never exceed 10 cm. The distance between paired ridges ranges from 0.5 to 3.5 mm.

R e m a r k s. The fossil under consideration differs from *Radulichnus* Voigt, 1977 (trace of the molluscan radula activity) by the opposite teeth movement when making grooves, substantially larger length, and opposite site of initiation of new grooves: on the internal not external margin of its area. Traces are preserved only at the base of sandstone beds being accompanied by microbial mat structures.

D i s t r i b u t i o n. Arkhangel'sk region, Upper Vendian, Redkino Horizon, Verkhovka, Zimnie Gory, and Erga (basal part) formations; southern Australia, Flinders Ranges, Ediacaran, Ransley Quartzite.

M a t e r i a l. Holotype and specimens PIN nos. 3993/5137, 5549, and 6170 (Zimnie Gory Formation; Zimnie Gory locality), specimens PIN nos. 3993/9461, 9463, and 9464 (Erga Formation; Zimnie Gory locality), specimens nos. 4853/176, 318, 380, 1037−1041, 1068, 1103, and 1104 (Verkhovka Formation; Solza locality).

CONCLUSIONS

This work concludes for now our investigation of grazing traces left by enigmatic Precambrian metazoans. The described traces are usual fossils from Vendian sections of southern Australia and northern European Russia. Although the first representatives of this group were found in the mid-20th century, only the recent discovery of complex remains consisting of traces and body impressions of corresponding animals made it possible to both reliably interpret these fossils as grazing traces and attribute them to particular organisms. This allowed, in turn, the behaviour features of some Vendian animals to be clarified and the anatomical structure of their food collecting organs and digestive system to be specified.

All the examined remains are housed at the Borissiak Paleontological Institute, Russian Academy of Sciences (collection nos. 3993 and 4853).

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