

Paleontological Evidence for the Supposed Precambrian Occurrence of Mollusks

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Abstract—The paper discusses a group of the Late Vendian fossils supposedly related to mollusks. The fossils include imprints with some anatomical characteristics of mollusks, traces resembling scratch marks left by radula, and structures resembling soft shells. *Kimberella quadrata*, which is represented by all the above kinds of fossils was most likely a trochophore animal of a pre-molluscan evolutionary stage. Remains of *Armillifera parva* and *Solza margarita* only slightly resemble shells, and in the absence of the knowledge on the soft body of these animals there are no enough evidences affiliate them with mollusks.

Keywords: Precambrian, Vendian, mollusks, *Radulichnus*, *Kimberella*, *Armillifera*, *Solza*.

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INTRODUCTION

One of the most interesting questions in Precambrian paleozoology is the origin and early evolution of the phyla of Metazoan animals, especially those (like arthropods and mollusks) that are successful in the modern biosphere. Judging from the “SSF”, the remains of true mollusks, at least gastropods, monoplacophorans, and polyplacophorans, appear seemingly suddenly in the fossil record near the base of the Cambrian (Parkhaev, 2008). The phylum had probably appeared earlier, in the Vendian, but mineral shells and sclerites are absent among the Vendian fossils represented by imprints of soft bodies and trace fossils. It is possible that the early mollusks lacked a shell, or had a soft, weakly mineralized shell. Examination of the collection of Vendian fossils at the Paleontological Institute, Russian Academy of Sciences allowed the recognition of a group of fossils provisionally assigned to mollusks and resembling soft saucerlike shells, trace fossils resembling the scratch marks left by radula, and imprints with anatomical characteristics resembling those of mollusks. It has recently been shown that most of these fossils represent variously preserved remains of the metazoan animal *Kimberella* (Fedonkin et al., 2007).

MATERIAL

All specimens are housed in the Paleontological Institute, Russian Academy of Sciences (PIN), collection nos. 3993 and 4853.

SOFT BODY IMPRINTS

Kimberella (*Kimberella quadrata* (Glaessner and Wade, 1966)) is a relatively common fossil from the Upper Vendian of the Arkhangelsk Region. Remains of *Kimberella* come from the Verkhovka, Zimnegory, and Yorga formations (as interpreted by Grazhdankin, 2003), which together constitute about half of the section containing Vendian macrofauna. However, they are only found in one type of deposits, i.e., at the bases of lenses and strata resulting from short episodes of turbulence and redeposition of sandy sediments. The assemblages with *Kimberella* in the same localities contain typical Vendian fossils, e.g., *Tribrachidium*, various species of *Dickinsonia* and *Parvancorina*. All fossils are represented by low relief imprints of the upper surface of the dead organisms (Ivantsov, 2009).

Kimberella has frequently been studied by Vendian paleontologists. However, reconstructions of animals based on different material at different times are significantly different. In the mid-20th century, when *Kimberella* was known only from a few poorly preserved imprints of compressed bodies from the Ediacaran beds of South Australia, it was assigned to siphonophores, or chirodropid cubozoans (Glaessner and Daily, 1959; Wade, 1972; Jenkins, 1992). Only by the end of the 1990s, after the first excavations in the Arkhangelsk Region (Zimnegory locality), resulting in several dozen excellently preserved specimens, it became possible to establish that this was a complex benthic organism, similar in its organization to triploblastic animals, possibly to shelled mollusks (Fedonkin and Waggoner, 1997). As a result of further large-scale excavations in Zimnegory and on the Solza River, several hundred imprints were collected, and at

least three types of body preservation were discovered (Pl. 2, figs. 1–7). *Kimberella* showed the presence of dense, possibly mineralized covers, muscles, and intestines, traces of its movement were discovered, and specific feeding traces were confirmed as belonging to these animals (Ivantsov and Fedonkin, 2001a; 2001b; Seilacher et al., 2003; Fedonkin and Vickers-Rich, 2007). Thus, the hypothesis of the molluscan affinity of *Kimberella* has been fixed in the literature (Fedonkin, 2003; Fedonkin et al., 2007; Seilacher, 2007; Trusler et al., 2007). The discovery at the beginning of the 21st century of strongly elongated specimens of *Kimberella* allowed the reinterpretation of previously collected material (Pl. 1, figs. 1–3). According to new interpretations, this animal had a worm-like body and head, and a compressible, possibly retractable ante-head region (Ivantsov, 2009).

TRACE FOSSILS

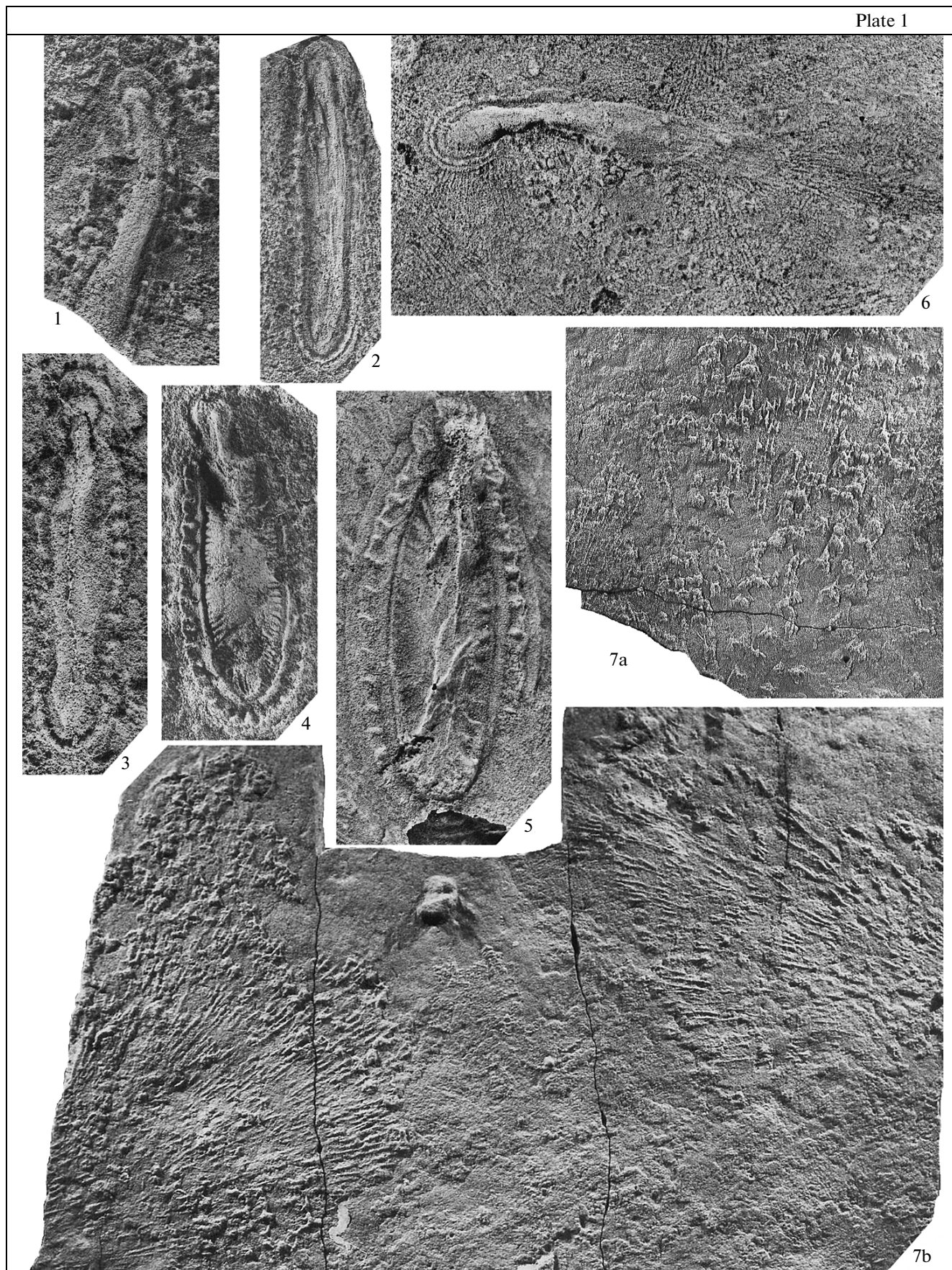
Kimberella was one of few metazoan animals that produced trace fossils. The fact that the trace fossil trails belonged to this particular organism was established based on aggregate imprints (a combined imprint of a trace fossil trail and that of a soft body). Two kinds of traces are recognized: (1) flat bands, weakly raised over the edge of the trail and (2) fan-shaped groups of thin grooves (the description of the relief is based on a latex cast; on the rock matrix the former kind of traces appear as elongated depressions, and the latter as narrow ridges (Pl. 1, figs. 6, 7)). It is suggested that these traces were left by *Kimberella* on the substrate it inhabited (Ivantsov and Fedonkin, 2001a; 2001b). What kind of substrate was that? Judging from the lithology of the host rock, the mineral component of the bottom sediment was composed mainly of clayey or silty particles. However, the texture of the base of the sandstone overlying the fossiliferous surface suggests that the upper layer of the substrate was of biogenic origin and was probably a microbial mat. The substance of the mat decayed as the mat was buried in the siliciclastic sediment, and the only cast of its upper surface can be preserved. Fossil trails of *Kimberella*, and Proarticulata (other Vendian actively moving animals) were found on this very surface (Ivantsov, 2008; Ivantsov and Malakhovskaya, 2002).

The first type of traces found in association with the soft body imprints of *Kimberella* was found by the present author together with Ya.E. Malakhovskaya in the Verkhovka beds on the Solza River (Ivantsov and Fedonkin, 2001a; 2001b). Band-trails usually form aggregates with soft body imprints and bunches of grooves. One end of such a band is in contact with the head side of the soft body imprint, as if continuing or “flowing” from the body; while the other end levels and becomes obsolete above the narrow side of the bunch of grooves (Pl. 1, fig. 6). We had previously suggested that the trail was originally a burrow in a sandy sediment that the animal made before it was dead

(Ivantsov and Fedonkin 2001a; 2001b; Fedonkin et al., 2007). Moving along the boundary between the mat and overlying sediment, *Kimberella* moved the sediment and inevitably should have disturbed the texture of the surface of the mat. However, it can be observed in places where the height of the band was at minimum that the surface of the mat was not deformed. The “burrow” hypothesis is not consistent with the generally sharp and irregular changes in the width of the band. It is more likely that the mucous sheath was preserved, as a large amount of mucous was apparently secreted by a distressed animal, i.e., suddenly surrounded by a cloud of perturbed, oxygen-deprived sediment. The mucous could be made denser (which increased its volume on the imprint) by the sediment particles from the cloud stuck to it and engulfed by it. The length of the band is definitive, similar to the length of the stretched out body of *Kimberella*. It is suggested that the animal was covered by the sediment while stretched out, and became compressed and secreted mucous after it was covered (Ivantsov, 2009).

The second type of trace fossil has been long known from Australia, where it was interpreted as spicules of sponges (see references in Fedonkin and Vickers-Rich, 2007) or casts of scratch marks left by claws of an unknown arthropod (Gehling, 1991; Jenkins, 1992; 1995). Seilacher (1999; 2007) and Seilacher et al. (2003) interpreted them as resembling scratch marks left by radulae and assigned them to *Kimberella*, whose imprints are occasionally found on the same bedding planes (Seilacher, 1999; 2007; Seilacher et al., 2003). The first aggregate imprint consisting of a fan of grooves and a body imprint of *Kimberella* was discovered by M.A. Fedonkin in university museum in Western Europe. That specimen, originally from the Winter Coast of the White Sea, was illegally excavated and exported out of Russia by private collectors and was returned to Russia due to the gracious decision of the director of that museum (Fedonkin, 2001; Fedonkin and Vickers-Rich, 2007). When analyzing the trace fossil, Fedonkin interpreted it as having been left by a single articulated pair of teeth located at the end of a long protracted proboscis (Fedonkin, 2003; Fedonkin et al., 2007). Massive collections of aggregates of both types of trace fossils were collected by the present author and Yana Malakhovskaya on the Solza in 2000–2006.

Traces, fanlike grooves, are always found in large accumulations, sometimes covering the entire visible surface of the bed. Each fan consists of several indistinctly separated and convergent bunches of grooves rather than an isolated groove or pairs of grooves. Grooves in a bunch are almost parallel or clearly converge to one of the ends (Pl. 1, fig. 7b). The fans often overlie each other to form series, in which they are all directed, with the narrow end of each overlain and smoothed by the wide end of the next bunch. In case of aggregates, the imprint of *Kimberella* lies in the



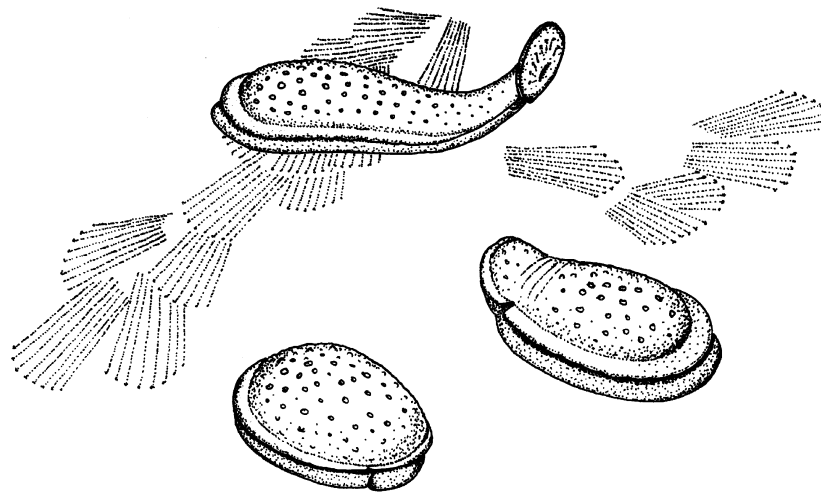


Fig. 1. A reconstruction of *Kimberella* (Ivantsov, 2009).

point of convergence of grooves or on the end of a series of fans. These trace fossils of *Kimberella* lack isolated pairs of grooves, and pairs intersecting the general radial directions of the grooves in the fan. In long bands consisting of hundreds of grooves left by a moving animal, it is possible to observe bunches of grooves following one another and fans consisting of bunches, but never a diagonal series of grooves. A moving animal with a long, flexible proboscis should have left more chaotic traces. In addition, the bunch in general was usually slightly submerged in the sediment, and hence appears as a low projection on the imprint. All this may suggest that the deepening in the mat was achieved not by using isolated teeth but by a larger structure composed of several teeth. Such a structure could be the whole anterior part of the body of *Kimberella* with a large expandable head (Ivantsov, 2009). The morphology of the lower surface of the head is still unknown. It probably possessed a mouth equipped with teeth. They did not constitute an even row as it is shown on my graphic reconstruction (Ivantsov, 2009; text-fig. 1, and this paper), but were not arranged totally irregularly because although the external margin of the bunch appears uneven, the distance between the grooves or their pairs in one bunch is more or less the same. By retracting the body and head, the animal dragged the teeth along the substrate leaving the traces

of convergent grooves, and then swallowed the lump of nutrient particles collected. It stayed on the same spot while making a few grasps in various directions; hence the resulting trace was fan-shaped. Moving forward with its aboral end, *Kimberella* formed a new fan in the place where it had been a moment earlier.

The surface of the mat was not even, which may explain the frequently observed interrupted dashed appearance of the grooves. Groups of fragmented paired grooves resemble archlike scratch marks of a radula, "*Radulichnus*" (Seilacher, 1999; 2007; Seilacher et al., 2003). However, in the case of *Kimberella* the groove, despite being interrupted can easily be followed over a large distance and demonstrates fragments of a length inconsistent with radula's tracks. For instance, on the large fans from the base of the Zimnegory section, up to 7 cm in width, continuous fragments of grooves reached a length of 1.5–2.0 cm (Pl. 1, fig. 7b). Numerous specimens collected in this locality possess series of deep pits (looking like nodes on a matrix) connected with fans of grooves. The pits are isometric or slightly elongated, sometimes triangular or arrow-shaped (Pl. 1, figs. 7a, 7b); their usual size varies from 1.5 to 5 mm, but occasionally there can be found specimens up to 1 cm long. The pits tend to be more abundant toward the wider end of the fan, which is more distant from the animal. The long axis of the

Explanation of Plate 1

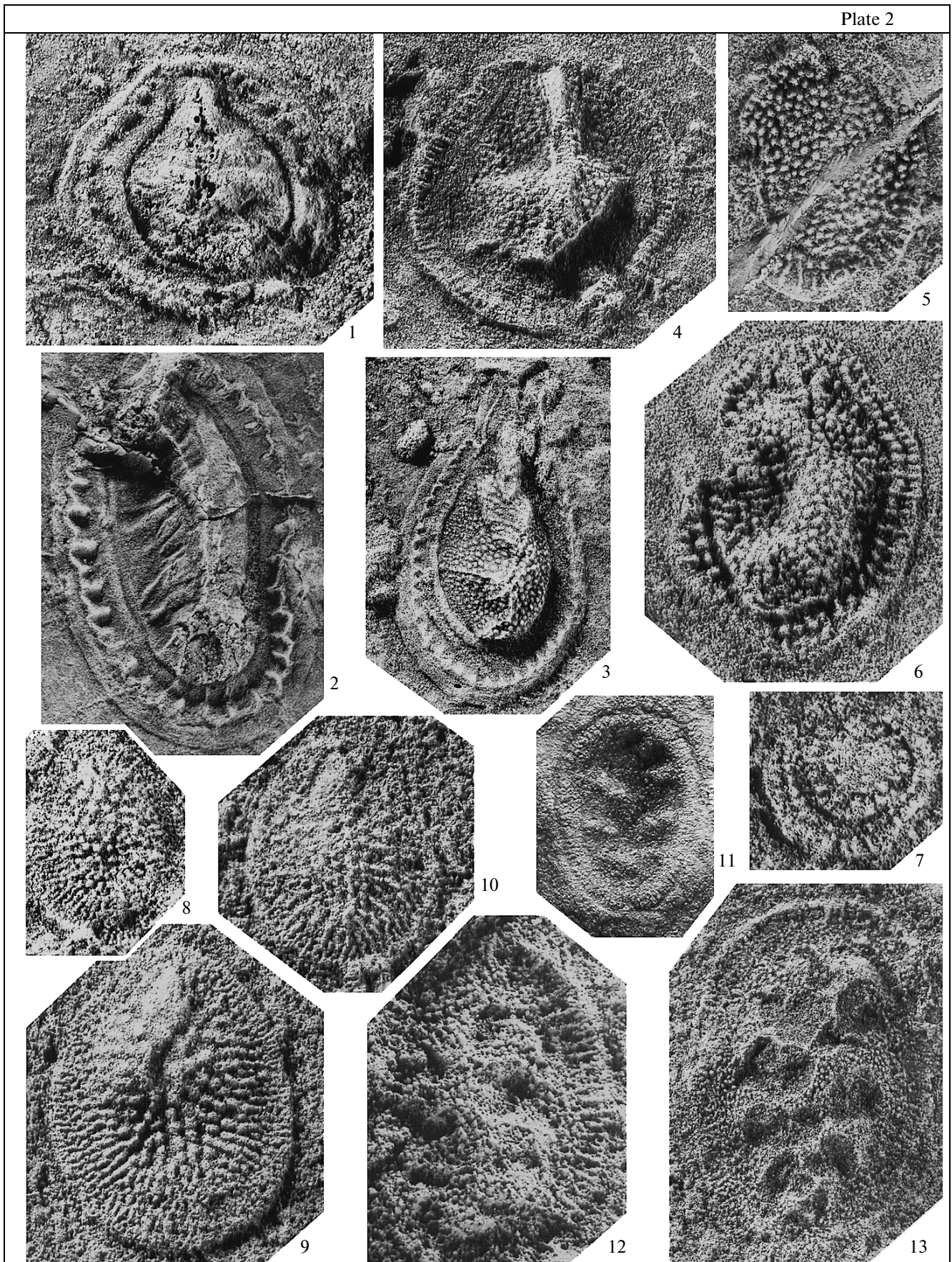
Imprints and feeding traces of *Kimberella quadrata* (Glaessner and Wade, 1966) from the Late Vendian of the Arkhangelsk Region; (1–6) latex casts of natural imprints, (7a, 7b) natural imprint.

Figs. 1–3. Imprints of bodies in the maximum stretched state; Solza locality: (1) specimen PIN, no. 4853/336, $\times 2.5$, (2) specimen PIN, no. 4853/360, $\times 2$, (3) specimen PIN, no. 4853/337, $\times 3$.

Figs. 4–5. Specimens with shortened (retracted?) ante-head region; thin ridges in the anterior part of the head possibly correspond to teeth occurring closer to the lower part of the body: (4) specimen PIN, no. 3993/5565, $\times 3$, (5) specimen PIN, no. 3993/5600, $\times 3$.

Fig. 6. An aggregate composed of a retracted imprint, a bunch of feeding grooves on the surface of a microbial mat, and a mucous band containing mineral particles, extending from the anterior end of the animal; Solza locality, specimen PIN, no. 4853/318, $\times 2$.

Figs. 7a and 7b. Two fragments of the same surface with feeding traces; Zimnegory locality; specimen PIN, no. 3993/5619, $\times 1$.



oval pits is perpendicular to the nearest grooves. They are not the common structures of the mat, because they are not found outside the fans. Nor are they imprints of nutrient particles because the casts of any additional particles lying on the seafloor should have preserved in a different (negative) relief. The diversity of sizes, and characteristic orientation of pits across the grooves contradicts the hypothesis that they are remains of the prey of *Kimberella* (Fedonkin et al., 2007). These traces most likely resulted from physical damage to the mat produced by the teeth of *Kimberella*. Apparently, the animal did not simply scratch the mat, but occasionally pulled pieces off it. The most numerous small pits do not always cover one groove, but a pair of grooves, hence apparently the teeth indeed worked in pairs (Pl. 1, fig. 7a, top). Local discontinuities of a mat can also explain short crevices in an upside down V-shape, which are observed at the beginning of some grooves (Pl. 1, fig. 7b, left). The apex of the crevice lies on a groove, whereas its wings extend toward the meeting point of the grooves. This means that while scratching the mat the animal scratched toward the body. The distal arrangement of the pits also suggests that the substrate was most strongly affected further from the body and weakest near the body. This is a fundamental difference between the traces left by *Kimberella* and those of a radula, since when using the radula, mollusks move it in an outward direction (Rupert et al., 2004).

“SHELLS”

As suggested by Fedonkin, *Kimberella* possessed a dense shell (Fedonkin and Waggoner, 1997; Fedonkin, 2001; Fedonkin, 2003; Fedonkin et al., 2007). A structure very similar to a nodular shell, with festooned edges can be observed in the center of the body of *Kimberella* in one of the varieties of its preservation types (Pl. 2, fig. 3). However, many characters of the imprints contradict the hypothesis of a single shell. It also displays a wide variety of outlines, from elliptical to circular, strongly elongated and sometimes bent almost in half. The absence of growth lines is also not typical of a shell (Fedonkin et al., 2007). Imprints of all sizes typically lack heads. Judging from the curved fold of the rear part of the body, it was upright, extend-

ing into the overlying sandy sediment (Pl. 2, fig. 2). The fossils with a well-preserved head show that it possessed tubercles similar to those on the body, and that it was not separated from it by a seam (Pl. 2, fig. 3). It is clear that the covers could be easily bent. These considerations leave no doubt that the body of *Kimberella* contained no large dense structures. On the other hand, specimens with tubercles are clearly more simply organized and possess fewer fine details than specimens with folds. Apparently their covers were denser. The alternative appearance on the imprints of tubercles and coarse folds can be explained if it is suggested that the cores of the tubercles were made of lumps of a hard material that did not preserve well. Aragonite could be such a material, and there were no chance for it to be preserved in the siliciclastic sediment, saturated with hydrogen sulfide (Gehling, 2005). When the fixation of an imprint preceded the dissolution of mineral sclerites, only elements of the outer covers were preserved in it. The dissolution of sclerites revealed other structures of *Kimberella* normally lying deeper in the body (Pl. 2, figs. 1, 2) (Ivantsov, 2009). The teeth of *Kimberella* were hard and thin, as they left deep, narrow grooves with smooth edges. However, no traces of the teeth are found on the imprints. Only two imprints in the anterior part of the head possess thin ridges, which were probably casts of teeth (Pl. 1, figs. 4, 5). Apparently the teeth were mainly composed of some mineral similar to aragonite. Some specimens of *Kimberella* resemble shells, free from the soft tissue and lying separately. (Pl. 2, figs. 4–7). However, the burial of single shells in such a taphonomic environment could hardly be possible because all light object unattached to the mat were washed out to areas with less turbulent waters. Apparently this was the reason that the preserved bodies were buried compressed, with a head folded under the body and retracted edges of the foot. Therefore, these specimens are always wide, and sometimes almost circular (Ivantsov, 2009). The Vendian beds of the Arkhangelsk Region also contain fossils resembling shells and similar to *Kimberella*. *Solza* (*Solza margarita* Ivantsov, 2004) is found in the Verkhnovka and Zimnegory formations on the Solza River and Zimnii Bereg (Winter Coast). The fossil is the shape of a low oblique cone with a base oval in plan and slightly pointed to one side (Pl. 2, figs. 8–10). The

Explanation of Plate 2

Some Precambrian fossils, one of the preservation forms resembling a soft shell; Late Vendian, Arkhangelsk Region. All specimens, except fig. 11 are latex casts from natural imprints.

Figs. 1–7. *Kimberella quadrata* (Glaessner and Wade, 1966); (1–6) Zimnegory locality, (7) Karakhta locality: (1, 2) specimens with demineralized covers: (1) specimen PIN, no. 3993/5590, $\times 6$; (2) specimen PIN, no. 3993/4006, $\times 3$; (3) specimen PIN, no. 3993/5604, which contained mineral sclerites (tubercles on the cast) in the dorsal covers at the time when the imprint was formed, $\times 3$; (4–7) strongly retracted specimens suggesting primary presence of mineral sclerites in the covers; “shells”: (4) specimen PIN, no. 3993/5553, $\times 5$; (5) specimen PIN, no. 3993/5599, $\times 5$; (6) specimen PIN, no. 3993/5609, $\times 5$; (7) specimen PIN, no. 4852/94, $\times 7$.

Figs. 8–10. *Solza margarita* Ivantsov, 2004; Solza locality: (8) specimen PIN, no. 4853/61, $\times 6$; (9) specimen PIN, no. 4853/60, $\times 6$; (10) specimen PIN, no. 4853/56, $\times 6$.

Figs. 11–13. *Armillifera parva* Fedonkin, 1980; (11, 13) Zimnegory locality, (12) Solza locality: (11) specimen PIN, no. 3993/5130, $\times 6$; (12) specimen PIN, no. 4853/62, $\times 8$; (13) specimen PIN, no. 3993/6387, $\times 4$.

upper side of the fossil is covered by the meshwork of grooves, wide at the apex of the cone, and tapering and branching towards its margins (Ivantsov et al., 2004). Because the grooves anastomize, spaces separating them are transformed into variously shaped nodes and ridges. In contrast to *Solza*, the “shell” of *Kimberella* is convex in the center with flattened flanks. Its surface is covered by rounded tubercles, which only occasionally and only on the flanks fuse to form short rounded ridges. *Armillifera* (*Armillifera parva* Fedonkin, 1980) is restricted to almost the same stratigraphic range as *Kimberella*, but is very rarely found. *Armillifera* was described from one specimen and was interpreted as a medusa preserved in a distorted state but with a fringe of tentacles (Fendonkin, 1990). About one and a half dozen new specimens collected from the *Solza* and Zimnegory localities suggest that the oval shape was usual for these fossils, rather than being a product of postmortem distortion. Like the “shell” of *Kimberella*, *Armillifera* is convex in the center with a flattened surrounding band, and its surface is covered by numerous tubercles fused on the band to form rounded ridges. Both these fossils are very similar, although tubercles in *Armillifera* are considerably smaller, and most importantly, the surface of its central region possesses deep hook-shaped depressions (Pl. 2, figs. 11–13). The fact that these depressions are arranged according to glide reflection symmetry allows the comparison of *Armillifera* with Proarticulata. Apparently, the depressions were produced by the collapse of large metameric inner cavities, typically found in Proarticulata (Dzik and Ivantsov, 2002; Ivantsov, 2004, 2008). Nothing similar has been found in *Kimberella*.

DISCUSSION

The reason that fossil remains of *Solza* and *Armillifera* are not imprints of empty sheaths or fragments of bodies lying freely on the seafloor is the same as for *Kimberella*. As in *Kimberella*, “shells” of *Solza* and *Armillifera* lack growth lines, nor have they signs of primary mineralization. Bilateral symmetry of the fossils suggests that these were likely to have been actively moving organisms. However, the resemblance of the fossils to shells should not be treated as ultimate evidence, and it is still unclear to which phylum of the animal kingdom they belonged. Zoologists suggest that primary traits of mollusks include a mantle, the dorsal area of which can secrete a chitinous cuticle and calcareous spicules, a radula, a foot, paired pedal retractor muscles, paired featherlike gills, and a four-cord nervous system (Nielsen, 2001; Ruppert et al., 2004). According to our observations, the flexible and stretchable dorsal covers of *Kimberella* were armored with numerous hard sclerites, possibly aragonitic, whereas its head with a ventrally positioned mouth was equipped with teeth. It is also suggested that this animal had a wide foot adapted for crawling. This is sufficient to assume a molluscan affinity of *Kimberella*.

However, its teeth, located in front of the mouth orifice and not rigidly articulated to one another are not homologous to a radula. The developed dorsal muscles also distinguish this animal from shelled mollusks. I consider the position of the anterior and posterior ends of the body of *Kimberella* inconsistent with the direction of the movement of the animal, and the absence of any sensor processes as an important character. Probably, *Kimberella* is only closely related to mollusks, but not a mollusk. It is probably related to one of the early stages of the evolution of trochophore animals, when their extant phyla had not been yet formed (Ivantsov, 2009). Judging from isotope dating, *Kimberella* appeared within the time span of 558 to 555 Ma (Grazhdankin, 2003). If this animal did belong to the stem group of mollusks, the phylum Mollusca could not have occurred before that time.

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