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Vendia and Other Precambrian "Arthropods"

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Abstract—A new family, a new genus, and two new species of Metazoan (class Vendiamorpha, phylum Proarticulata) are described from the Upper Vendian of the Arkhangelsk Region. The body of the animal was composed of alternating mirror-symmetric elements and isomeres. Some animals possessed an unsegmented head area in front of the isomers. It is suggested that the animal had an intestine and branching alimentary glands in the head region. No appendages were found; however, the animal apparently had the ability to move.

INTRODUCTION

There is a group of animals among Vendian fossils which are preserved as transversely divided imprints. Some of them, which have structural elements located in a single plane, have some superficial similarity to segmented organisms or even to arthropods. However, several features (principally, the alternating elements) distinguish these organisms from Articulata and justify their position within the separate phylum Proarticulata (Fedonkin, 1985).

An extensive collection of Vendian Metazoa was recently made by the Laboratory of Precambrian Organisms of the Paleontological Institute, Russian Academy of Science (PIN). The material originates from the famous Zimnegorsk locality and some other sites along the winter and summer coasts of the White Sea. The collection is dominated by the remains of Proarticulata and also contains representatives of the class Vendiamorpha with an emphatic arthropod-like appearance. The results of the study of the latter are discussed in the present paper. It is noteworthy that finds of Vendiamorpha were formely extremely rare, and only about twenty specimens were known before our research.

The material studied is housed in the Paleontological Institute (PIN), Russian Academy of Sciences, in collections nos. 3993 and 4852.

LOCALITIES

Vendia janae sp. nov. originates from the local accumulations named "Kimberella Lens" and "Yorgia Bed," which occur on the winter coast of the White Sea within the Zimnegorsk locality of the Upper Vendian rocks. Several specimens of Archaeaspis fedonkini sp. nov. were also found in the Kimberella Lens. These accumulations of Metazoans are located in the lower part of the Yorga Beds correlated by A.F. Stankovsky with the Mezen' Formation (Stankovsky et al., 1985).

The locality is very rich in fossil Metazoans; every year field work reveals several new forms along with

numerous known taxa. Currently, only a small part of this extensive material has been studied and described (Fedonkin and Waggoner, 1997; Ivantsov, 1999).

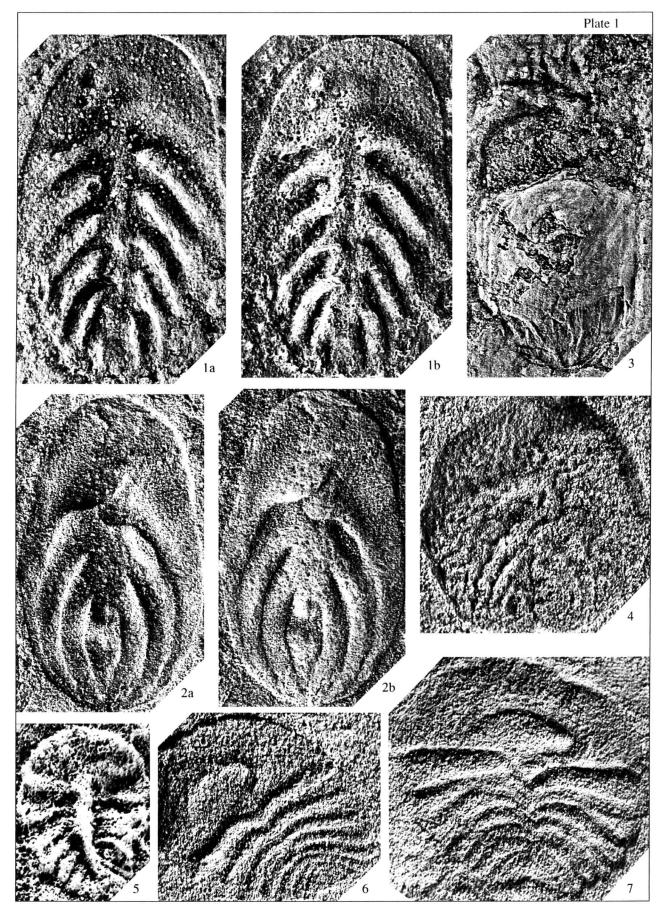
In spite of the surrounding rocks being apparently identical, the mass accumulations of imprints studied only occur on two bedding planes and within an area tens to hundreds of meters big. They have been given names for distinction, as they are found near each other and are stratigraphically similar, although they have different fossil assemblages. In addition, the accumulation Yorgia Bed shows perfectly preserved organic remains, which is extraordinary even for the winter coast of the White Sea.

The metazoan remains in the Kimberella Lens occur at the base of large (a few meters wide) massive sandstone lenses, faunal level no. 1 (Ivantsov, 1999). The lenses are composed of uniform fine-grained sandstone with a more finely grained, clayey–silty basal part. Usually the animals are preserved here as partially pyritized negative imprints. Positive relief is typical only in the cyclic forms. We found four imprints of *Vendia janae*, including a specimen with a combination of positive and negative relief, which was tentatively assigned to the species. Also, eight specimens of *Archaeaspis fedonkini* originate from this stratum.

The Yorgia Bed accumulation occurs at the base of more or less evenly laminated fine-grained sandstone that can be traced in the exposures for several hundred meters (faunal level no. 2 of Ivantsov, 1999), and contains negative and positive imprints. Imprints with a positive relief prevail but do not represent all of the forms. A single negative imprint of *Vendia janae* was found in this locality. This specimen was previously reported (Ivantsov, 1999) as *Vendia sokolovi*.

Two specimens of *Archaeaspis fedonkini* were also found on the summer coast of the White Sea (30 km west of Severodvinsk) in a small exposure on the left bank of a small forest stream of Karakhta. According to D.V. Grazhdankin (pers. com.) this locality could be correlated with the middle part of the Vendian strata exposed by the Solza River (between 7 and 10 m of the

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Explanation of Plate 1

Fig. 1. *Vendia sokolovi* Keller, 1969, holotype PIN, no. 3593/1, negative imprint, ×6: (a) positive photograph; (b) negative photograph; Arkhangelsk region, Yarensk borehole, 1552 m depth; Upper Vendian, Ust'-Pinega Formation.

Figs. 2 and 3. Vendia janae Ivantsov sp. nov.: (2) holotype PIN, no. 3993/5070, negative imprint, ×6: (a) positive photograph; (b) negative photograph; (3) specimen PIN, no. 3993/5071, positive-negative imprint, tentatively assigned to the species ×2.5; Arkhangelsk region, winter coast of the White Sea; Upper Vendian, Mezen' Formation, Kimberella Lens locality.

Fig. 4. Yorgia waggoneri Ivantsov, 1999, juvenile specimen, PIN, no. 3993/5135, negative imprint, ×8; Arkhangelsk region, winter coast of the White Sea; Upper Vendian, Mezen` Formation, Kimberella Lens locality.

Fig. 5. Vendomia menneri Keller, 1976, holotype Geological Institute, Russian Academy of Science (Moscow) no. 4464/57, latex cast from the negative imprint, ×10; Arkhangelsk region, summer coast of the White Sea; Upper Vendian, Ust'-Pinega Formation.

Figs. 6 and 7. Archaeaspis fedonkini sp. nov., negative imprints: (6) PIN, specimen no. 3993/5077, deformed specimen with induced opposite arrangement of the isomeres, ×8; (7) PIN, holotype no. 3993/5053, ×8; Arkhangelsk Region, winter coast of the White Sea; Upper Vendian, Mezen' Formation, Kimberella Lens locality.

stratigraphic section published by Grazhdankin and Bronnikov, 1997). The imprints occur at the base of three layers of fine-grained sandstone. Remains of two species of *Dickinsonia* and one species of a simple cyclic form dominate here. The new species *Archaeaspis fedonkini*, as well as *Kimberella quadrata* and several undescribed taxa, were found in small numbers.

The species *Vendia sokolovi* Keller was described and is currently known only from a single specimen. It was found in the Yarensk borehole in the Arkhangelsk region. The specimen originates from 1552 meters deep from the Upper Vendian strata of the Ust'-Pinega Formation (Keller, 1969; Fedonkin, 1985).

Another species, *Vendomia menneri* Keller, is also known from a single specimen, while any other specimens or imprints reported in the literature are absent in collections. The specimen originates from a classic Vendian locality situated on the bank of Syuz'ma River. It has a negative relief and occurs at the base of finegrained compacted sandstone. Remains of *Onega stepanovi* Fedonkin, *Albumares brunsae* Fedonkin, and imprints similar to *Dickinsonia* Sprigg were also found on the same rock surface (Keller and Fedonkin, 1976; Fedonkin, 1981; 1985).

PRESERVATION AND RECONSTRUCTION

The imprint of Vendia sokolovi (Pl. 1, fig. 1a) is small (14×8 mm), has a negative relief, and an elongated oval outline. It has several prominent structures: two rows of transverse ridges, an axial depression with a low median buttress, and a wide comparatively smooth zone that occurs at the end of one of the imprints and is up to one-quarter of the imprint's length. The transverse ridges are alternating, five ridges on one side and six on the opposite. Each ridge is bordered on one side by a sharp elongated depression. The first depression (adjoining the smooth zone) is longer than the others, and its inner edge reaches the longitudinal axis of the imprint and borders the axial depression from this side. In certain lights, the part of the depression located within the axial zone of the imprint appears to be separated by a weak construction from the rest of the depression, and appears as a rounded dimple.

The best preserved specimen of *Vendia janae* (Pl. 1, fig. 2a) bears two rows of three transverse ridges on both sides, which alternate with each other in respect to the longitudinal axis of the imprint. A wide axial depression and a relatively smooth zone up to one-quarter of the imprint's length are also prominent. Each of the ridges is delineated by a narrow and rather deep depression. The first of the depressions is longer than the rest and borders the axial depression from one side. It is noteworthy that the descriptions of both species of *Vendia* show a strong similarity between the two forms.

The negative imprint found at the base of the layer is a cast of the upper surface of an animal that had been buried and compressed by sediment pressure. This imprint shows not only the external topography of the organism, but also some internal anatomic structures. It is supposed that elevation or depression of the imprint originates from differences in the densities of the animal parts that have been squeezed (Wade, 1968; Ivantsov, 1999). This kind of imprint is reversed and, hence, it is difficult to use it in the study of the morphology. However, the original imprint could be replicated by making a latex cast from the imprint. I used such a method when studying the holotype of Vendomia menneri (Pl. 1, fig. 5). Unfortunately, it is difficult to make latex casts from the imprints of Vendia since they are formed by barely lithified clayey-silty rock. Instead of casts, I made negative copies from photographs. These negatives show the original, but mirrored, relief of the buried bodies (Pl. 1, figs. 1b and 2b).

The analysis of the original uninverted imprint revealed that the body of *Vendia* was composed of two rows of transverse elements (four elements per row in *Vendia janae* (Pl. 1, fig. 2b; fig. 1b) and six to seven elements per row in *Vendia sokolovi* (Pl. 1, fig. 1b; fig. 1a)). Each of the elements has a depression in the middle part. This indicates that the central part of the element was composed of a less dense substance during burial. Like all other Proarticulata, *Vendia* has similar transverse elements that differ from each other mainly in size. Such transverse elements are called isomeres in the present paper. Each isomere was probably a separate chamber, as in *Dickinsonia costata* and *Yorgia waggoneri* (Seilacher, 1989; Ivantsov, 1999). Paleontological material does not indicate what substance may

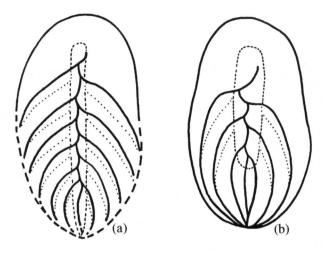


Fig. 1. Schematic reconstruction of the holotypes of the species of *Vendia*: (a) *Vendia sokolovi* Keller; (b) *V. janae* Ivantsov, sp. nov. (thin hatched lines show borders of the axial rod—suggested intestine); dotted line—the least dense transverse structures).

have filled these chambers. The "undivided field," which has been described for Vendia (Keller, 1969; Fedonkin, 1985) is formed by the expanded bases of the first pair of isomeres. No boundary was noted between the edge of the body and the first isomeres. It seems that the out-of-chamber zone is absent in this fossil genus. A rather dense linear structure, or axial rod, runs along the center of Vendia's body (along its longitudinal axis). The borders between isomeres may disappear within this zone. As the imprint of Vendia sokolovi has a median ridge along the axial furrow, we suppose that the axial rod may have been hollow. This hollow rod running from the posterior edge towards the first isomeres could have been a straight section of intestine, as is known in dickinsonians (Wade, 1972; Jenkins, 1992; Dzik and Ivantsov, 1999).

The posterior edge of the isomere appears to be more prominent than it would be if it were represented only by the interchamber membrane. At the same time, the anterior edge of the next isomere seems to be excessively concave. This structure looks like the articulation of the body segments of arthropod carapaces, which originate on the boundary between movable sclerites. Also the arthropod-like appearance could be caused by the tilelike overlying of the medial edges of the first and, probably, the last pairs of isomeres on the holotype of Vendia janae. This analogy may denote that the exterior tissues of Vendia's body were comparatively rigid, while isomeres could move slightly relative to each other. It follows that the body of Vendia sokolovi was able to bend in a dorsoventral direction, while the body of Vendia janae was able to expand and shrink (the first pair of isomeres straddled the remaining pairs and prevented the body from bending). Possibly, some linear structures similar to the "gonads" of Yorgia (Dzik and Ivantsov, 1999) could occur inside the animal's body along the chamber boundaries (shown by the dotted line on the schematic reconstruction in Fig. 1).

There is a single elongated specimen among the cyclic forms preserved as positive imprints in the Kimberella Lens that demonstrates a transition of the positive relief into a negative one on its edge (Pl. 1, fig. 3). The pattern of this edge is very similar to the most complete imprint of Vendia janae and shows the convergent ends of the isomeres. This type of mixed positive-negative imprints is not common in the Kimberella Lens accumulation but is typical of the Yorgia Bed, where the closely related fossil Yorgia waggoneri exhibits this preservation. In this case, the positive part of the imprint is a cast of the bottom side of the animal at the moment of burial (Ivantsov, 1999). If this specimen is not an artifact (its affinity to Vendia is not undisputable), the exterior or bottom side of Vendia janae could be smooth.

Another species, Vendomia menneri, is represented by a single, very small (4 mm long) negative imprint. This species has been described as a trilobite-like animal (Keller and Fedonkin, 1976) with a segmented body and as a cephalon possessing peculiar structures resembling eyes (Fedonkin, 1985). However, the study of the imprint and especially of the latex casts shows that the ridge analogous to the structures bordering all the transverse elements in the segmented region of the imprint runs along the head region (Pl. 1, fig. 5; Fig. 2a; also see the clear photograph from the latex cast in Sokolov, 1997, pl. 23, fig. 2). Similar to the above structures, this ridge gently bends near the margin of the imprint. This bending ridge has probably been erroneously interpreted as an eye. In fact, Vendomia has no eyes and the anterior zone is formed by the slightly expanded bases of the first pair of isomeres. The isomeres of Vendomia alternate as in other Proarticulata, and a narrow buttress runs along the body axis. Generally, Vendomia has a strong similarity to Vendia (Figs. 2a and 2b), but differs from the latter by the form and arrangement of the isomeres, which are shorter, rounded laterally, and the first pair does not straddle the rest.

Like Vendomia, the body of Archaeaspis is composed of a few short and laterally rounded isomeres. It differs from Vendomia and Vendia in that it has an unsegmented anterior zone (Pl. 1, figs. 6 and 7; fig. 2c). An unusual structure resembling a lobe occurs in the center of this unsegmented zone. This structure is bordered by a furrow only from the anterior and left (right on the imprint) margins. This intriguing asymmetry could be explained by comparison with Yorgia. The right isomere of Yorgia extends far onto the opposite side (Ivantsov, 1999) where it expands slightly and is bordered by a distinct furrow (Pl. 1, fig. 4; Fig. 2d). It could be supposed that the lobe on the unsegmented zone of Archaeaspis is formed by the partly reduced first pair of isomeres, or by a detached medial part of the first isomere. The surface of the unsegmented zone of *Archaeaspis* is ornamented with fine pits of equivalent size to the matrix grains and, consequently, they are hardly visible. Following the analogy with *Yorgia*, these pits could be interpreted as remains of the system of alimentary glands (caeca).

The species Vendomia menneri and Archaeaspis fedonkini are rather small and could possibly represent juvenile stages of some other taxa that have probably already been described. Yorgia waggoneri, which is abundant in the Kimberella Lens, could be regarded as a major candidate for the mature stage of Archaeaspis. Small specimens of *Yorgia*, 7.8 mm in length, and so of comparable size to Archaeaspis, have been already found (Pl. 1, fig. 4; Fig. 2d). This disk-shaped negative imprint has only one-third of the body segmented, and its isomeres are slightly angled with respect to the longitudinal axis and are surrounded by an unsegmented field from all of the margins except the posterior one. The surface of the field is ornamented by pit-furrow depressions. Such depressions found on the larger specimens of Yorgia are more prominent and probably represent the remains of caeca (Ivantsov, 1999; Dzik and Ivantsov, 1999).

There is one extremely important observation that should be noted in the description of *Yorgia*. The Yorgia Bed contains numerous well-preserved negative imprints of *Yorgia* surrounded or followed by a chain of positive imprints similar in shape and size (Ivantsov, 1999, pl. 1, fig. 4; pl. 2; figs. 1 and 4; Figs. 2 and 3). In that the imprints occur in isolated groups, and all of the specimens within the group are of similar size, one could suppose an obvious connection between such imprints.

Two of several possible explanations for this phenomenon have been published. According to the first hypothesis (Ivantsov, 1999), each group of imprints is composed of different specimens that have been preserved differently for uncertain reasons (the group is probably a colony of the same age). According to the second hypothesis (Dzik and Ivantsov, 1999), each group of imprints is attributed to a single body, and the negative imprint is a cast from the body itself, while several positive imprints are casts from traces of the animals on the sediment surface. The traces were the result of repeated acts of body transportation by water movements. This hypothesis does not explain the preservation of positive imprints adjacent to and far away from the negative ones (each act of hydrodynamic disturbance should damage the previous imprints). New finds of long chains of trace imprints convinced me that the imprints originated due to the animal's independent and active movements. M.A. Fedonkin suggested that the imprints may be preserved due to profuse mucous discharge of the animal, which cemented the sediment particles. Each imprint was formed during a separate resting period of the animal on the sediment surface, while no imprints were made by movement itself. The positive imprints show the finest details of the animal's surface structure and no appendages for locomotion are

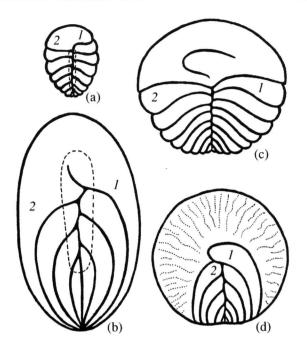


Fig. 2. Gross morphology of the genera of the class Vendiamorpha, dorsal views: (a) and (b) representatives of the family Vendomiidae Keller: *Vendomia* Keller, (b) *Vendia* Keller; (c) and (d) representatives of the family Yorgiidae Ivantsov fam. nov.: (c) *Archaeaspis* Ivantsov, gen. nov., (d) *Yorgia* Ivantsov (larval stage) (hatched lines show borders of the axial rod; dotted line—supposed caeca; *1* and 2—isomeres of the first pair).

present on them. The absence of any traces on the imprints (apart from the poor impression of the lateral flanks), which may have been caused by the animal pushing itself on the sediment during the initiation of movement, suggests that the movement was very smooth. Probably, the motion was caused by the undulation of the lateral flanks of the body or by ciliary epithelium, which were possibly present in this group of organisms.

Besides the capability of the Ediacarian organisms of motion, another important conclusion from this hypotheses is the determination of the anterior end of their body. This is the end which corresponds to the blunt margin of the negative imprint, which, in turn, finishes the train of positive imprints and fixes the death of the animal at the end of its trace. This blunt margin corresponds to the unsegmented zone of *Yorgia*.

Thus, the gross morphology of Vendiamorpha could be reconstructed as follows. The body is divided into equal transverse elements—isomeres (partly or completely in different groups). The isomeres alternate with each other. The first isomere lies on the right side of the body (left side of the imprint). The original morphology of each isomere was a chamber with a fairly rigid cover and a relatively less dense middle part, probably filled by the animal's internal organs. The supposed intestine occurred in the segmented part of the body. A rather broad, undivided anterior zone is located in

front of the segmented area in some of the forms. The remains of radial channels could be observed within this undivided zone. The channels may have been part of the digestive system.

TAXONOMIC AFFINITY

B.M. Keller (1969) in the description of the genus Vendia discussed three hypotheses on the nature of the organism: one of them was the arthropodian proposed by B.S. Sokolov (trilobitomorph), others were coelenteratian proposed by V.V. Menner (sea pens) and by A.Yu. Rozanov (jellyfish). Keller himself favored the coelenteratian affinity of Vendia. As many specialists have noted, the disk-shaped segmented bodies of Vendia, Vendomia and Precambridium are similar to the larval stage of primitive arthropods, trilobites, and merostomates (Menner, 1963; Glaessner and Wade, 1971; Keller and Fedonkin, 1976; Birket-Smith, 1981, etc.). The main distinguishing feature of the Vendian organisms is the alternating arrangement of half-segments along the longitudinal axis of the body. Such an arrangement is shown not to be an occasional defect as supposed by Glaessner and Wade (1971), but a common condition (Fedonkin, 1985; 1987). On the contrary, the opposed arrangement of the segments could appear as a result of imprint deformation (Pl. 2, fig. 6). The alternating arrangement of isomeres shows the presence of a septa running along the longitudinal axis of the body. This feature is absolutely untypical for the Articulata.

The Recent and extinct Phanerozoic solitary metazoans do not have this type of symmetry in the entire or the majority of the body; similar types of symmetry are extremely rare. For example, incomplete gliding reflection symmetry is present in the myomere arrangement of the lancelet, and the alternation of mirrored reversed metameres is present in the strobila of the cestode *Tatria mathevossianae* (Beklemishev, 1964).

However, the symmetry of gliding reflection commonly occurs among Vendian organisms and is observable in almost all of the longitudinally segmented forms. Only the Proarticulata show a symmetry that is uncomplicated by the additional axis of radial symmetry. The absence of lateral appendages have been ascertained for Proarticulata (see complete reconstruction of *Dickinsonia* and *Yorgia* by Jenkins, 1992; Ivantsov, 1999 and Fedonkin, 2000) along with the ability to crawl in some of their taxa. Therefore, the establishment of separate phylum of extinct metazoans (Fedonkin, 1985) seems very reasonable.

The extent of the study of different forms of the Proarticulata varies and is directly dependent on the number of finds. The species *Dickinsonia costata* and *Yorgia waggoneri* are the most fortunate in this sense (several hundred specimens are known from localities in Australia and Russia). Other species of Vendiamorpha are poorly studied since they are known from single, or a maximum of fifteen, often poorly preserved

specimens. Thus, we can compare these taxa only in general features.

The class Dipleurozoa Harrington et Moore includes forms lacking an unsegmented zone on the anterior part of the body (genera Dickinsonia Sprigg, Palaeoplatoda Fedonkin) with a radial arrangement of isomeres that is more distinct in juveniles and distorted in adults. The class Vendiamorpha Fedonkin unites the forms with posteriorly curved ends of the isomeres and sometimes with unsegmented anterior zones (Fig. 2). The latest feature is not present among all of the Vendiamorpha, since the new family Yorgiidae could be separated from the Vendomiidae Keller. Besides the type genus Yorgia Ivantsov, the new family will include the following forms: Archaeaspis gen. nov. (described below) and Andiva Fedonkin (description in press, but reconstruction and name already published by Fedonkin, 2000). Probably, the Australian genus *Praecambridium* Glaessner et Wade should also be assigned to the family. A published reconstruction of Praecambridium (Glaessner and Wade, 1971; Birket-Smith, 1981) maintains that the organism had true segments. However, the imprint morphology depends greatly on the size of the matrix grains, because the animal is so small (no known specimens exceed 5 mm); hence, other interpretations cannot be excluded. Probably, the segments of Praecambridium were not complete and had an alternating arrangement, i.e., they could be considered as isomeres, while the head lobe could be considered as an extension of the medial edge of the anterior isomere. This reconstruction brings Praecambridium together with juvenile specimens of Yorgia. It could possibly be considered as a larval stage of some Ediacarian organism (Birket-Smith, 1981). The genus Onega Fedonkin, which has been placed within the class Vendiamorpha (Fedonkin, 1985), has a wide, flat limb completely surrounding a small body. It differs significantly from other Vendiamorpha and probably has no affinity to Proarticulata.

The similar forms of *Valdainia* Fedonkin and *Podolimirus* Fedonkin from the Mogilev Formation of Podolia (Fedonkin, 1983; 1985) should also be included in the family Vendomiidae Keller in addition to the genera *Vendia* Keller and *Vendomia* Keller.

The species Archaeaspis fedonkini is similar to the soft-bodied trilobite from the Upper Vendian of Australia. The latter is known only from reconstructions and a single photograph of an incomplete specimen. The body of this animal is composed of two parts: the anterior unsegmented part with a large median lobe and posterior transversely segmented part. The wide median buttress runs along the axis of the body. R. Jenkins (1992, Figs. 10 and 15) reconstructed the animal with oppositely arranged transverse elements and the lobe of the anterior part that is completely bordered by the lateral furrows. However, the photograph by D. Geling (1991, Pl. 4, Fig. 4) shows that the furrow smooths out on the right edge of the lobe, while the wide depression runs along the axis of the body and

causes difficulty in resolving the exact interposition of the transverse elements; the elements probably alternate. If this assumption is true, *Archaeaspis fedonkini* differs from the Australian trilobite by its relatively larger head part, smaller number of isomeres, and the absence of the axial buttress on the imprint.

SYSTEMATIC PALEONTOLOGY

Phylum Proarticulata Fedonkin, 1985 Class Vendiamorpha, 1985

Family Vendomiidae Keller, 1976 Genus *Vendia* Keller, 1969

Trilobite-like organism: Menner, 1963.

Vendia: Keller, 1969, pp. 175-176; Fedonkin, 1985, p. 94.

Type species. Vendia sokolovi Keller, 1969.

Diagnosis. Body elongate oval, with one slightly sharpened edge. Body composed of two rows of isomeres, scalelike in shape and bent towards the sharpened edge. Angle of bending and width of isomeres decreases in the same direction. First two isomeres (counted from blunt edge) may have been several times wider than the rest. Each row consists of seven or fewer isomeres.

Composition. Two species: Vendia sokolovi Keller and Vendia janae sp. nov.

C o m p a r i s o n. The genus *Vendia* Keller is similar to *Yorgia* Ivantsov in the sharpened lateral edges of the isomeres and their unidirectional orientation, but differs from it by the elongated body and absence of the anterior unsegmented part.

Remarks. The new genus is similar to *Dickinsonia* Sprigg from the class Dipleurozoa Harrington et Moore in the elongated body and complete segmentation, but differs from it in the smaller number of isomeres, sharpened edges of the isomeres, and their unidirectional orientation. *Vendia* is very similar to *Podolimirus* Fedonkin and *Valdainia* Fedonkin from the Upper Vendian of Podolia, which is assigned to the Pteridiniids (Fedonkin, 1983; 1985). Although these taxa are only known from incomplete and deformed imprints, the absence of a typical pteridiniid feature, the third segmented lobe, is clearly visible. Possibly, the Podolian specimens could be assigned to the genus *Vendia*.

Occurrence. Northwestern part of the East European Platform, Arkhangelsk Region; Upper Vendian, Ust'-Pinega Formation and Mezen Formation.

Vendia janae Ivantsov, sp. nov.

Plate 1, figs. 2 and 3

Etymology. In honor of Jana E. Malakhovskaya. Holotype. PIN, no. 3993/5070; Arkhangelsk Region, winter coast of the White Sea, Upper Vendian, Mezen Formation, Kimberella Lens locality. Description. Four isomeres per row (Figs. 1b and 2d), the maximal inclination of the isomeres with respect to the longitudinal axis is about 30 degrees. The larger isomeres embrace the smaller ones from the outer side. The edges of the isomeres converge on the sharpened margin of the body.

Measurements, mm:

Specimen no.	Length	Width
3993/5070 (holotype)	13.5	8.0
3993/5071	36	18
3993/5072	13.5	7.0
3993/5126	19.5	10.5
3993/5079 (deformed)	15.0	7.0

Comparison. The species differs from *Vendia* sokolovi by the fewer isomeres that are less angled (Fig. 1).

Remarks. As can be noted from the least deformed specimens, the number of the isomeres does not alter when the size increases by 50%, but the width of the first isomere decreases (absolute width as well as relative): the maximum width of the first isomere in the holotype is 5.1 mm; in specimen no. 3993/5126, it is 4.2 mm; and the relative widths (to the length of the imprint) are 0.37 and 0.21, respectively. The lateral edge of the holotype of *Vendia sokolovi* is not preserved in two-thirds of the imprint. Thus, it is uncertain whether or not the edges of the isomeres reach the sharpened margin of the body, as in Vendia janae. Estimating by the large angle of their inclination towards the longitudinal axis, the isomeres probably could not reach the sharpened margin. Thus, it could be another feature that distinguishes the species.

Material. The holotype and four paratypes (nos. 3993/5071, 5072, 5079, and 5126) from the type locality.

Family Yorgiidae Ivantsov, fam. nov.

Type genus. Yorgia Ivantsov, 1999.

Diagnosis. Body composed of two zones: smaller unsegmented anterior zone and larger posterior zone, divided on transverse isomeres.

Composition. *Yorgia* Ivantsov, 1999, *Archaeaspis* gen. nov. and probably *Praecambridium* Glaessner et Wade, 1971.

Comparison. The family differs from other Vendiamorpha by the presence of an unsegmented zone on the anterior part of the body.

Genus Archaeaspis Ivantsov, gen. nov.

Et y mology. From Greek Archaeos (ancient, initial) and Aspis (shield).

Type species. Archaeaspis fedonkini sp. nov.

Diagnosis. Anterior unsegmented zone with unpaired lobe in middle section. Isomeres short, rounded on lateral edges.

Composition. Type species.

Comparison. The genus differs from *Yorgia* Ivantsov by the presence of an unpaired lobe on the anterior unsegmented part of the body, narrow isomeres with rounded lateral edges, and fewer isomeres.

Archaeaspis fedonkini Ivantsov, sp. nov.

Plate 1, figs. 6 and 7

Etymology. In honor of M.A. Fedonkin.

Holotype. PIN, no. 3993/5131; Arkhangelsk Region, winter coast of the White Sea, Upper Vendian, Mezen' Formation.

Description. The body is rounded or slightly truncated (Fig. 2c), composed of two parts: an unsegmented anterior part and a posterior part, divided into isomeres. The anterior part comprises about one-half of the whole length of the animal. An unpaired lobe with a sharp right edge (left on the imprint) lies in the middle of the anterior zone. The opposite edge is usually absolutely indistinct or sometimes scarcely visible. The isomeres have rounded lateral edges, the anterior pair of the isomere is perpendicular to the longitudinal axis of the body, the remaining pairs are bent posteriorly. The number of pairs of isomeres clearly visible on the imprint varies from four in small specimens to ten or more in larger specimens. The surface of the unsegmented zone is ornamented by barely prominent spots.

The age variability shows a slight decrease in the length of the anterior unsegmented zone (from 0.55 to 0.41 mm in the specimens 4.0 and 9.5 mm long, respectively), expansion of the segmented zone, which is wider than the unsegmented zone in larger specimens, and an increase in the number of visible isomeres.

Measurements, mm:

Specimen no.	Length	Width
3993/5053 (holotype)	7.4	8.3
3993/5074	19.5	23.5
3993/5077	7.0	5.9
3993/5131	6.6	6.0
3993/5132	9.5	11.0
3993/5134	10.0	11.0
4852/1	6.4	6.0
4852/3	4.0	4.2

Occurrence. Upper Vendian, Ust'-Pinega Formation and Mezen' Formation; Arkhangelsk region.

Material. Holotype and several paratypes; PIN, no. 3993/5074, winter coast of the White Sea, Upper Vendian, Mezen Formation, from debris on the slope (specimen collected by D.V. Grazhdankin); PIN, nos. 3993/5077 and 5131–5134 from the same area, the

Kimberella Lens locality; PIN, nos. 4852/1; summer coast of the White Sea, Karakhta Stream, Upper Vendian, Ust'-Pinega Formation.

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