CONULARIID-LIKE FOSSIL FROM THE VENDIAN OF RUSSIA: A METAZOAN CLADE ACROSS THE PROTEROZOIC/PALAEOZOIC BOUNDARY

by ANDREI YU. IVANTSOV *and* MIKHAIL A. FEDONKIN

ABSTRACT. A conulariid-like fossil is described for the first time from Upper Vendian (late Neoproterozoic) deposits. *Vendoconularia triradiata* gen. et sp. nov. is found with other fossils in poorly cemented, siliciclastic deposits of the lower part of the Ust'-Pinega Formation, exposed in the middle reaches of the Onega River, north of the Russian Platform. This fossil assemblage, stratigraphically lowermost in the region, includes *Swartpuntia* Narbonne, endemic *Ventogyrus* Ivantsov and Grazhdankin, *Calyptrina*-like tubular forms, and other new, as yet undescribed, species. *Vendoconularia* is described here using morphological terms developed for conulariids owing to their striking similarity. However, the six faces of the conical test and three-fold symmetry may reflect some phylogenetic connection with the larger clade of Trilobozoa, a cnidarian class that radiated during the Late Vendian–Early Cambrian and then became extinct.

KEY WORDS: conulariid, Vendian, Russia.

UPPER VENDIAN (late Neoproterozoic) deposits are exposed near the village of Yarnema, between the Somba and Teksa tributaries of the Onega River (Text-fig. 1A). Horizontal bedding of the soft, poorly cemented sandstones, siltstones and clays is complicated by landslides 30–50 m long. The Vendian sequence is represented here by fine interbedding of siltstones and clays that enclose small sandstone bodies. The exposed section is correlated with the lower portion of the Ust'-Pinega Formation, which is equivalent to the Redkino Regional Stage of the Vendian System (Stankovski 1997), but the exact stratigraphic position of the fossiliferous rocks within the Vendian succession, which is over 800 m thick in the region, has yet to be established. This locality is characterised by the abundant endemic form *Ventogyrus*, described in detail by Ivantsov and Grazhdankin (1997) as a petalonamean boat-like organism, and reinterpreted recently by Ivantsov and Fedonkin (in press) as a complex egg-shaped pneumatophore composed of three identical modules. Faunal remains are preserved in sandstone lenses in the upper part of the section. The Vendian deposits are overlain by Carboniferous conglomerate and limestone, which comprise the major part of the outcrops.

Vendoconularia triradiata gen. et sp. nov. was collected by one of us (MAF) in 1997 from a fine-grained reddish-brown sandstone exposed on the left bank of the Onega River about 1 km downstream from the mouth of Somba Creek. The large number of flat clay pebbles, which are especially abundant at the base of the sandstone lens, the channel-like and slightly asymmetric cross section of the fossil-bearing sandstone unit with a planar top surface (Text-fig. 1B), and the low angle cross bedding and gradual change in thickness indicate rather rapid sedimentation in a small linear erosional structure (gutter cast) at the bottom of the Vendian sea. In addition to the new fossil described herein, a few specimens of *Ventogyrus* Ivantsov and Grazhdankin exhibiting extraordinary preservation, and rare forms tentatively assigned to *Podolimirus* Fedonkin and *Swartpuntia* Narbonne, numerous tubular forms of *Calyptrina* Sokolov, and enigmatic sack-like fossils and other new species yet to be studied have been found. *Podolimirus* was originally described from the base of the Vendian sequence in the Dniester River, Ukraine (Fedonkin 1983), and *Swartpuntia* was first discovered in the topmost part of the Neoproterozoic section in Namibia (Narbonne *et al.* 1997).
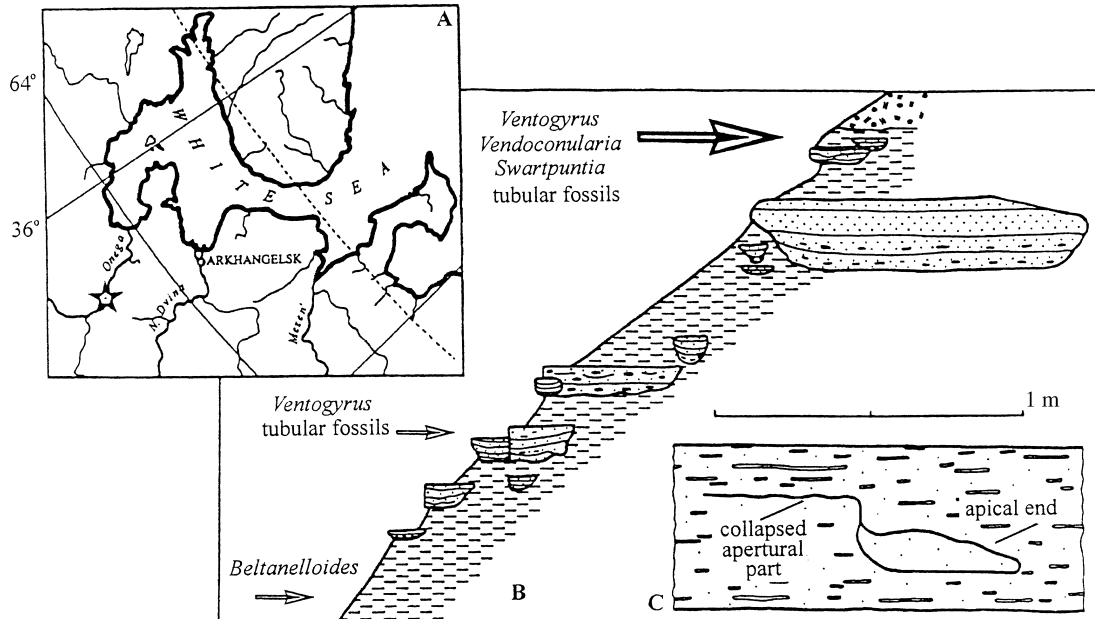
TEXT-FIG. 1. A, geographic position of the fossil locality indicated by star. B, geological setting of the sand lens with *Vendoconularia* in the natural outcrop on the left bank of the Onega River. Sandstone lenses are shown in cross section. C, position of *Vendoconularia* in longitudinal section within the sandy matrix with numerous flattened aleuropelitic pebbles.

PRESERVATION

Vendoconularia is preserved as an elongated complex cast. It is exposed along two bedding planes at different levels within the host rock (Text-fig. 1C). The upper part is preserved as an imprint of the surface with no definite outline. The lower part is preserved as a conical cast with a complete, perfectly preserved surface. Preparation of the specimen provided a mould, counterpart and a core of a fragment preserved in three dimensions (Pl. 1). Thus, one part of the fossil represents an impression of the flattened, collapsed body, and another part is a three-dimensional infill of the apical end of the cone-like test. The fossil exhibits six identical faces covered by fine, regularly spaced transverse lines (Text-fig. 2A–C).

In addition to the fine morphological details, the colours of the fossil played an important role in the study. The upper, flattened fragment has a rough, wavy relief and an earthy-brown colour that does not emphasise any morphological details. The surface of the lower, bag-like, conical fragment has very weak transverse undulations and a bright grey colour that serves as a contrasting background for peculiar forms altered by dark brown mineralisation. The nature of this colour may be related to the presence of hydrated iron oxides formed as a result of oxidation of pyrite. Pyrite is likely to have been precipitated diagenetically in the course of the decomposition of the organic matter as a surface coating of the decaying body, or infilling of the hollow spaces following deformation and collapse of soft parts (Briggs *et al.* 1991; Bartels *et al.* 1998). In the semi-closed geochemical system of the fine-grained sediment the volume of pyrite precipitated must have been in direct proportion to the volume of the organic matter. Variation in colour saturation of staining seems to reflect gradients in pyrite precipitation. We assume that those parts of the surface of the fossil that are darkest brown correspond to the thickest parts of the primary organic matter, which in turn corresponds to structures and/or folds of the body layers. Regular repetition of the deeply coloured parts indicates the high probability of this colour-structure relationship. Those parts of the fossil with no folds are almost the same colour as the host rock.
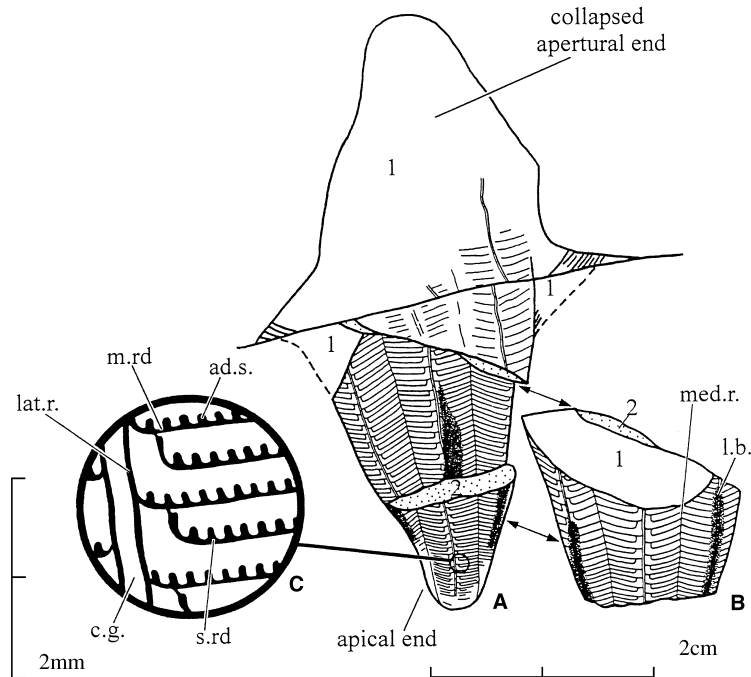
TEXT-FIG. 2. *Vendoconularia triradiata* gen. et sp. nov., schematic drawing of the fossil from photographs. A, imprint and the cast (without its middle part) lying over the former; 1, part of the fossil with no striated coloured pattern preserved; 2, surface of the crack across the cast. B, middle part of the inner core, removed from A; med.r., medial ridge of the face; l.b., longitudinal band. C, magnified fragment of the coloured pattern on the surface of the cast; ad.s., adapertural spine; c.g., corner groove; lat.r., lateral ridge of the face; m.rd., major rod; s.rd., secondary rod.

The major pattern exhibited by colours in *Vendoconularia* is the rows of parallel lines that correspond to the primary fine folds or linear thickenings in the wall (Text-fig. 2A–B). This pattern is more pronounced and more precise on the external mould than on the inner cast, which leads us to conclude that these linear structures were external. Present along with the major pattern of the regularly spaced transverse lines are wide longitudinal bands (seen on every second corner groove) of the fragment preserved. Their symmetrical position in places and their lack of correspondence to the external relief of the fossil as well as their darker colour on the core compared to the external mould, allow us to suggest that these dark longitudinal bands correspond to anatomical structures situated somewhere inside the body.

One of the reviewers of this paper attracted our attention to the fact that pyritisation as a form of replacement is known for soft tissues that have already been largely replaced by calcium phosphate (Wilby *et al.* 1996). The conulariid exoskeleton is composed of a multilayered, flexible integument bearing numerous calcium phosphate rods. It is possible that the dark brown staining of the transverse, regularly spaced lines in *Vendoconularia* is related to calcium phosphate rods. Three dark, longitudinal bands may correspond to some dense (and probably phosphatised) structures on the inner side of the cone wall that may be reminiscent of perradial teeth, a characteristic feature of the internal surface of the coronate exoskeleton (Jarms 1991). Otherwise, these structures can be compared with septa radiating inward from the wall like those reported by Wiman (1894) for *Conularia loculata*. The latter, however, have been reinterpreted as taphonomic features by Babcock and Feldmann (1986*b*). Interestingly, these dark, longitudinal bands are not expressed in the wider collapsed part of the fossil, which seems to show only external features of the apertural parts. Three-dimensional infill of the apical end seems to demonstrate both internal and external features that became superimposed and overprinted.

The occurrence of the fossil in a sandy gutter cast suggests allochtonous preservation. Like all the other gutter casts at the locality, the sand lens with *Vendoconularia* represents a rather narrow erosional structure with the cross bedding of its infilling dipping southward. Its striking preservation on different bedding planes within the finely laminated sandstone suggests the following burial scenario: a storm event induced an offshore bottom current that wiped away the benthic population and drowned it in the deeper zones of the shelf. The conical test of *Vendoconularia,* partially infilled with sediment, seems to have been dragged along in a sand-saturated flow before burial in the linear erosional structure. When the density current ceased and the conical test settled on the substrate, the water flow then eroded crescent-like scours along the upstream side of the test, thus causing the heavier apical part of the cone to sink deeper into the sediment. Downstream the collapsed part of the test remained at the same level as it landed. At least two conclusions can be drawn from this taphonomic reconstruction: (1) the wall of the conical test was rather elastic, otherwise the wider part of the cone would have retained its shape and been infilled with sand; and (2) the fine transverse structures interpreted here as rods were unaffected by the abrasive action of mechanical erosion, which may indicate their relative stiffness (probably owing to minor mineralisation).

RECONSTRUCTION

Relief and shape of the imprint that normally serves as a basis for judgement on the morphology of Vendian organisms provides little information in the case of *Vendoconularia*. The imprint shows that this organism had the shape of an empty cone open at the wider end. The presence of the traces related to elastic deformation only indicates that this cone was made of flexible, non-mineralised organic matter. Colour patterns produced by the iron oxide stains seem to reveal more anatomical information than the relief and shape of the imprint. The fossil consists of six identical linear elements (faces), each of which bears two rows of transverse bands having regular tooth-like elements on their sides facing the wide end of the cone (Text-fig. 2C). The overall shape and external relief of *Vendoconularia* exhibit a strong similarity to the Conulariida, which allow us to use the descriptive terms developed for typical conulariids (Moore and Harrington 1956; Babcock and Feldmann 1986*a, b*). The sack-like, not pyramidal, shape of the fossil may be explained by deformation during the course of burial in the sediments. Originally the organism could have had a strictly conical form with six faces. Along the boundaries between the faces on the mould and cast a light, uncoloured zone limited laterally by thin brown lines can be seen. We consider this to be an analogue of the corner groove of the conulariid test, although it does not show any prominent relief as a furrow and lappets do not make the corners (probably a taphonomic effect).

Internal structures are situated under every second corner groove which pass exactly along the axis of these structures with exception of the apical end of one of them (Pl. 1, fig. 3). Thus, although the test has a six-fold symmetry, the three internal structures reduce the whole organism to a three-fold symmetry (Text-fig. 3A).

DISCUSSION

Discoveries of shell-bearing invertebrates such as *Kimberella* (Fedonkin and Waggoner 1997) and *Vendoconularia* reveal the enormous potential of Vendian, and even older, metazoan fossil records. Varying palaeoecological and taphonomic conditions continually yield new taxa and anatomical information. On the other hand, rare finds or unique specimens of some Vendian species indicate the probability of an enormous hiatus in metazoan history as a result of taphonomic effects. Strengthening of the skeletons in many metazoan groups, partially because of biomineralisation, has increased their preservation potential and, thus, the expansion of the fossil record through the Vendian–Cambrian interval. As to the conulariids, exoskeletal strengthening is common among middle and late Palaeozoic forms (effectively, from about the Middle Devonian onwards). This might have been related to the selective pressure of predators (Babcock *et al.* 1987). Cleft and embayed injuries, found only on post-Silurian fossils, indicate the rise of several types of durophagous predators in the middle Palaeozoic. Perhaps in response to increased predation some conulariid species secreted thicker, harder skeletons.

The early evolution of this group might not have faced the pressure of durophagous predators, so that the

exoskeleton remained thin, weakly mineralised or basically organic. Indeed, some Ordovician conulariids have an extremely thin (0·2 mm and less) multilayered, black exoskeleton with virtually no signs of heavy mineralisation. This puts early conulariids into the category of organisms with a low preservation potential.

The Conulariida is a metazoan group of high taxonomic rank. Known mostly through remains of elongate, steeply pyramidal, generally four-sided tests of calcium phosphatic composition, these marine invertebrates are documented from the Ordovician through the Triassic (Babcock and Feldmann 1986a). This time range, however, may be expanded further back owing to the interpretation of Lower Cambrian small shelly fossils such as carinachitiids, arthrochitids, hexaconulariids (Conway Morris and Chen 1992) and, more tentatively, the anabaritids (Conway Morris and Chen 1989; Bengtson *et al.* 1990) as early representatives of the conulariids (Conway Morris 1994). The oldest Palaeozoic conulariids, collectively referred to as protoconulariids, demonstrate substantial morphological diversity and types of symmetry; carinachitids and gexagulaconulariids have four and six faces respectively. There is, however, a remarkable example of three-fold symmetry in the Early Cambrian *Emeiconularia*. This has been placed in the Family Carinachitidae because of its strong similarity in gross morphology and micro-structure (Qian Yi *et al.* 1997).

The numbers of protoconulariid taxa published so far are four families, 19 genera and 31 species, although after revision these become four, six and 12 respectively (Qian Yi *et al.* 1997). Species diversity of the protoconulariids would be increased if anabaritid species are added to the list, but even without them, the degree of differentiation of the Early Cambrian protoconulariids indicates Precambrian roots of the group.

The only Precambrian taxon that has been directly assigned to the cnidarian class Conulata is *Conomedusites*, a rare member of the Ediacara faunal assemblage (Glaessner 1971) known also from the Vendian of the Russian Platform (Fedonkin 1983). *Conomedusites* was considered to be an ancestral form of the conulariids and conchopeltids (Glaessner 1984). Later it was attributed to the hydrozoan family Conchopeltidae (Jenkins 1992). Although no skeletal material has been preserved the cast relief suggests that this sedentary organism might have had a theca with a short apical stem and an extensive medusiform body with marginal tentacles.

The taxonomic status of the Conulariida has been debated since the formal description of the genus *Conularia* Miller (Sowerby 1921). They have been associated with Mollusca, Cnidaria, Hemichordata, Conodonta, and 'Vermes' (Feldmann and Babcock 1986; Babcock and Feldmann 1986a and references therein). More recently the range of the discussion has been reduced to two major views. Some specialists retain the traditionally widespread view that conulariids were part of the cnidarian class Scyphozoa, either finding additional morphological, ecological and ultrastructural evidence in favour of this interpretation (Van Iten 1986 and references therein), or placing this group close to conchopeltids (Anderson 1993). Other authors see strong morphological reasons to consider conulariids as an independent phylum while conchopeltids remain cnidarians (Babcock and Feldmann 1986a, b).

R. Feldmann (pers. comm. 1999) has considered the construction and chemical composition of the rods to be characters of fundamental taxonomic weight. The architectural style of the conulariid skeleton, a thin integument supported by umbrella-like rods, is unknown within Cnidaria. Biochemical separation of the conulariids looks to be even more important. No Cnidaria produce skeletal material composed of calcium phosphate. There is, however, some evidence of phosphatic biomineralisation. The nematocyst batteries of the siphonophore *Nanomia cara* have bands of calcium phosphate spicules (Mackie and Marx 1988; Watabe 1990). Amorphous Mg-Ca phosphate is documented in the statoconia of the hydrozoan medusa *Aglantha, Lovenella, Obelia*, and *Phyalidium* (Chapman 1985). Interestingly, the statoconia of the Scyphozoa and Cubozoa are composed of calcium sulphate (Lowenstam and Weiner 1989). Thus, there is no physiological restriction in Cnidaria (at least in the Hydrozoa) for phosphatic biomineralisation.

Though biomineralisation-type is a fundamental part of the phenotype, it may not have the highest priority in taxonomic considerations for the following reasons: (1) many organisms deposit different minerals in their body simultaneously; (2) some groups may switch from one kind of biomineralisation to another, to lose or gain the ability to deposit biominerals in the course of their evolution; and (3) biomineralisation-type may be influenced by diet or the geochemical parameters of environment and temperature (Lowenstam and Weiner 1989).

Although a few examples of structural abnormalities attributable to genetic or life history events have been documented in Palaeozoic conulariids (Babcock *et al.* 1987), these examples can be considered to be indicators of an entire morphological space in the clade. In a sense, teratology and pathology mark the margins of the clade. A few specimens of Palaeozoic conulariids are of special interest when compared to *Vendoconularia*. *Paraconularia missouriensis* (Swallow) from the Mississippian of Ohio possesses six faces. *Conularia triangulata* (Raymond) from the Ordovician of New York and Quebec, was interpreted to be a six-sided (Raymond 1905) or a three-sided conulariid (Sinclair 1942). A number of other conulariid specimens showing three-fold symmetry have also been reported. Although *C. triangulata* has been removed from the phylum Conulariida and considered as *incertae sedis* (Babcock *et al.* 1987), we draw attention to this species. Specimens we re-examined revealed just two characters that were considered to be critical in removing this species from the phylum: (1) it has three-fold symmetry; and (2) there is no indication of a rod supporting the integument, which is so typical for the four-fold conulariids. For this reason *C. triangulata* was excluded from the Conulariida by Babcock and Feldmann (1986*b*). However, the taxonomic weight given to the two characters seems to be exaggerated.

Few authors have debated the primarily radial symmetry of the conulariids. Although conulariids demonstrate a weak bilateral symmetry, they may have functioned as radially symmetrical animals (Babcock and Feldmann 1986*a, b*). In living invertebrates, both primarily radial symmetry (as in jellyfish) and secondary radial symmetry (as in echinoderms) show a large number of variations from the dominant symmetry considered as the norm. That is why the taxonomic weight of the radial symmetry should not be overvalued (Gershwin 1999). The presence of a rigid, articulated, calcium phosphate rod in the wall of the test is a matter of the degree of the biomineralisation, which is not uniform even in a single test. Thus, exceedingly rare preservation of the pointed apices (in over 1200 specimens only two had complete, closed blunt points, as reported by Babcock and Feldmann 1986*a*, p. 141) indicate weak mineralisation (if any) of this part of the test. The evolutionary trend towards strengthening of the test in the late history of the conulariids allows us to consider this trend retrospectively and suppose that the earliest conulariids had a very thin test that was purely organic with no mineralised rods.

An essential contribution to understanding the nature of conulariids was made by Van Iten (1991, 1992*a, b*, 1996) and Van Iten and Cox (1992) following a detailed morphological and ultrastructural study of the conulariid test. The corners and midlines of the test were demonstrated to be similar to anatomical structures located, respectively, at the scyphozoan perradii and interradii (Van Iten 1992*a*). Analysis of the microstructure and patterns of malformations of healed injuries and growth abnormalities in conulariids indicated that conulariid tests and the theca of recent coronatid scyphozoans have so much in common that one can interpret the conulariid test and coronatid theca as homologous (Van Iten 1992*b*). Evidence of clonal budding in a radial cluster of at least some species (Van Iten and Cox 1992) may be an additional argument in favour of the cnidarian affinity of the conulariids. Scyphozoan affinities in conulariids and anabaritids have been discussed recently in the connection with cnidarian-like phosphatised embryos of late developmental stages from the Lower Cambrian in northern Siberia (Kouchinsky *et al.* 1999; Yue and Bengtson 1999).

Being found in exclusively marine sediments, conulariids are common in rocks that reflect very slow deposition (such as North American midcontinental black shales) or very rapid sedimentation (such as turbidites or tempestites). Very short transportation distance seems to be typical because the delicate conulariid test could not have survived prolonged transport. Conulariids are most common in low-diversity faunas. The allochtonous occurrence and palaeoecology of the only specimen of *Vendoconularia* seems to be consistent with the points mentioned above. *Ventogyrus* and tubular fossils referable to *Calyptrina* dominate the associated fauna of the gutter cast; other species are rare.


EXPLANATION OF PLATE 1

Figs 1–4. *Vendoconularia triradiata* gen. et sp. nov., PIN 4564/1025, left bank of the Onega River, 1 km downstream from the mouth of Somba Creek, Arkhangelsk District, NW Russia; Upper Vendian, Ust'-Pinega Formation. 1, counterpart; ×2. 2, imprint with the inner core (cast) lying over the former; ×2. 3, fragment of the middle part of the imprint; ×4·5. 4, narrowing apical end of the cast; ×4·5.

PLATE 1
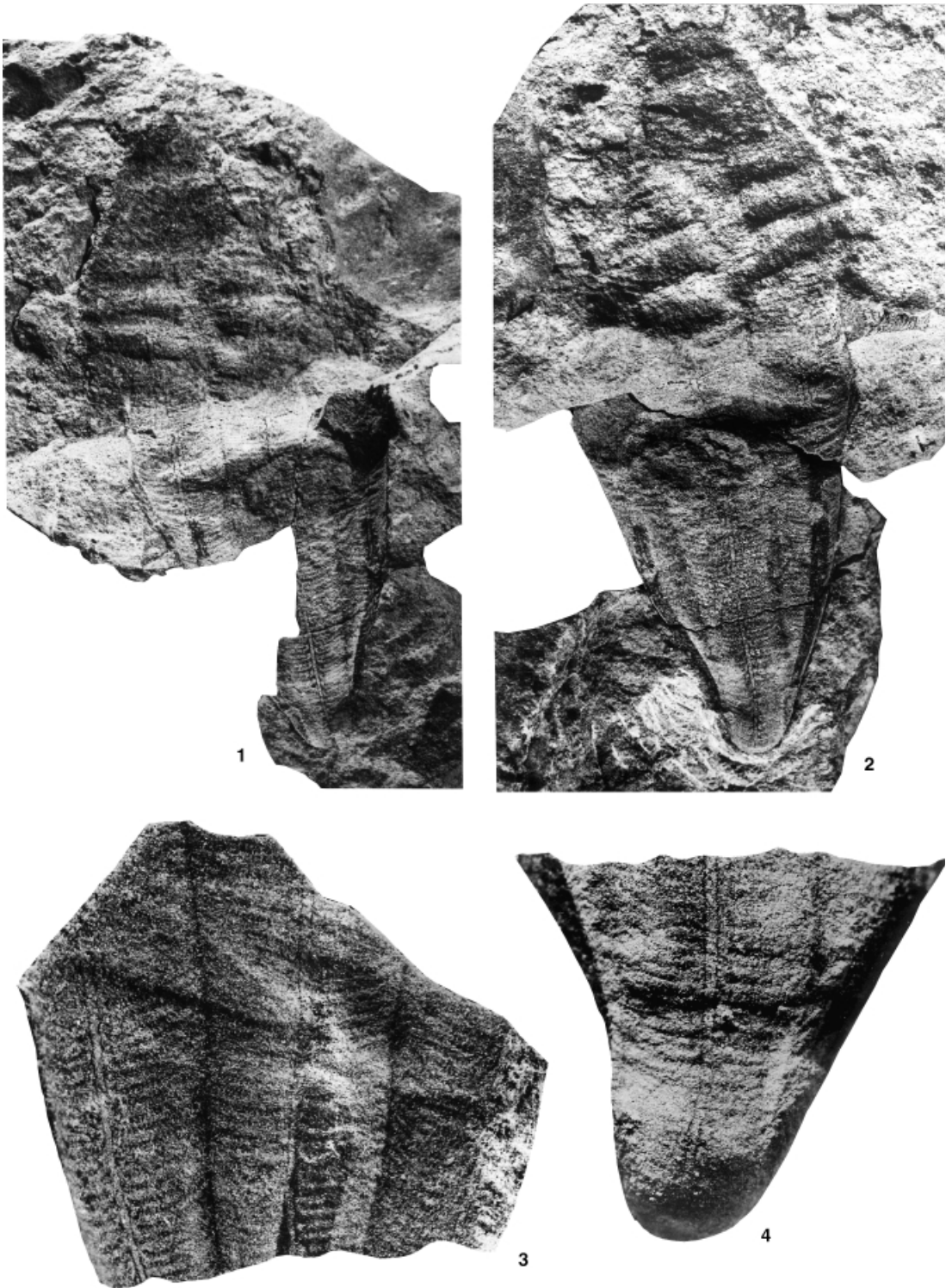
IVANTSOV and FEDONKIN, *Vendoconularia*
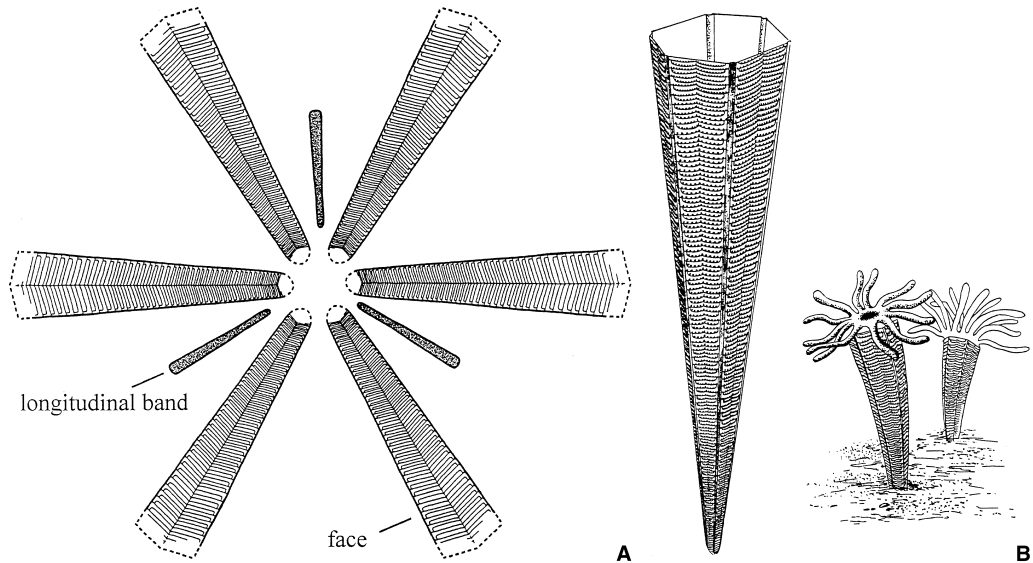
TEXT-FIG. 3. *Vendoconularia triradiata* gen. et sp. nov. A, schematic drawing shows the fossil unfolded in a plane and demonstrates a combination of a six- and three-fold symmetry. B, reconstruction of the test (on left) and life position (on right).

The three-fold symmetry of *Vendoconularia*, unusual and rare in typical conulariids, is a rather widespread phenomenon in the Vendian fauna. One class, Trilobozoa, may be considered as the basal group for a broader clade that unites the Vendian disk-like fossils *Albumares*, *Anfesta*, *Hallidaya*, *Tribrachidium* and, probably, *Rugoconites*, as well as the Early Cambrian angustiochreids (Anabaritida) and related taxa. In a wider context, Trilobozoa is a separate class that evolved slightly earlier and, to a great extent, in parallel with the class Scyphozoa within the phylum Coelenterata (Fedonkin 1990). Having just one specimen, it is premature to discuss the probable relationship of *Vendoconularia* and trilobozoans. Its three-fold symmetry seems to have less taxonomic weight compared to the other, typically conulariid characters. It is possible to suggest, however, a triradiate coelenterate polyp as a common ancestor of the Trilobozoa and Conulata.

Vendoconularia represents a life form that can be considered a full analogue of a conulariid within early metazoan history. Taking into account the very low stratigraphic position of the fossil and a number of conulariid-like forms with the three-fold symmetry in the Lower Cambrian one can suppose that the early evolution of the conulariid clade might have begun from three-fold forms like *Vendoconularia*.

As to the trilobozoans, this clade demonstrates quite a prolonged evolutionary history through the Vendian–Early Cambrian. Documented by the fossil record, their radiation passed the following stages: (1) *Albumares* and *Tribrachidum*, which demonstrate a wide range of disparity and specialisation within the clade; (2) *Anfesta* and *Rugoconites*; (3) *Hallydaya*; (4) Anabaritida; (5) Carinachitiida and Hexangulaconularida. This line of evolution seems to have been earlier than, and in part parallel to, that of the true conulariids. The precise place for *Vendoconularia* in this story has yet to be established.

SYSTEMATIC PALEONTOLOGY

Phylum CNIDARIA Hatschek, 1888
Class CONULATA Moore and Harrington, 1956
Order and family uncertain

Vendoconularia triradiata Ivantsov and Fedonkin gen. et sp. nov.

Plate 1, figures 1-4; Text-figures 2–3

Derivation of names. Genus, Vendian conularia; species, three radiating folds.

Holotype. PIN 4564/1025, left bank of the Onega River, 1 km downstream from the mouth of the Somba Creek, Arkhangelsk District, NW Russia; Upper Vendian, Ust'-Pinega Formation.

Diagnosis. Conical test with six faces and very characteristic pattern of rod arrangement demonstrating two series of major and secondary rods, both having short spines directed towards the aperture.

Description. Conical, elongated exoskeleton with a thin, flexible, non-mineralised wall comprising six identical faces. External surface of a face bears two rows of fine, transverse ridges (rods?) situated in an alternating position, and lateral longitudinal ridges extending along corner groove. There are two kinds of regularly alternating rods in every row of the face: major rods connect the midline and lateral ridges of the face; secondary rods do not reach the lateral ridge and their distal ends are turned towards the aperture meeting the next major rod. Rods of the opposite row on the same face are situated in an alternating position (symmetry of gliding reflection). Apertural side of the rods bears miniature spines (adapertural spines). Internal anatomy is represented by three linear structures extending along every other corner groove closer to the narrow apical part of the test. Apertural lappets are not preserved or absent.

Measurements (mm). Length of the imprint, 54; maximum width, 33; length of the cast preserved in three dimensions, 28; maximum width, *c*. 20; width of internal core, 16; height, 7; maximum width of one face, 6. At a distance of 1 cm from the narrow end of the internal core, the space between the two major rods, 0·8; length of the adapertural spine, 0·08–0·12; width of the latter, 0·07; space between the spines, 0·08; width of the zone separating the faces, 0·3; distance between the distal end of the secondary rod from the lateral edge of the face, 0·25; thickness of the rods, 0·03; thickness of the longitudinal ridge, 0·05. Maximum length of one of three internal structures (right on the inner core on Pl. 1, fig. 2), 16·3; minimum width, 1·1; maximum width of the structure (centre of the imprint, Pl. 1, fig. 3), 1·8.

Remarks. The new taxon is similar to Conulariida on account of its conical test made of identical, radially arranged bilateral elements (faces) bearing two rows of transverse ridges with spines. It differs from conulariids in lacking phosphatic mineralisation, the exoskeleton exhibiting six-fold symmetry, the general three-fold symmetry, and in the form of the external sculpture of the test (two kinds of rods and a lateral ridge).

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ANDREI YU. IVANTSOV

MIKHAIL A. FEDONKIN

Paleontological Institute
Russian Academy of Sciences
Profsoyuznaya ul. 123
Moscow 117997, Russia
e-mail mfedon@paleo.ru.