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REINTERPRETATION OF A CONULARIID-LIKE FOSSIL FROM THE VENDIAN OF RUSSIA

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Abstract: *Vendoconularia triradiata* Ivantsov and Fedonkin, recently described from Vendian (latest Proterozoic) strata of Russia, has been interpreted as a six-sided conulariid cnidarian. However, comparison of published illustrations of *V. triradiata* with Palaeozoic conulariids suggests that certain key features of the anatomy of *V. triradiata* should be reinterpreted. Specifically, features previously homologized with the corners of conulariid thecae may actually be homologous to the conulariid midlines. Under this new interpretation, the corners of the *Vendoconularia* theca were sulcate, and the midline of each face was non-sulcate and flanked by a pair of low internal carinae. This alternative set of hypotheses of homology makes the argument for a conulariid affinity for *Vendoconularia* stronger.

Key words: *Vendoconularia*, conulariids, scyphozoans, cnidarians, Vendian, homology.

In a recent article in this journal, Ivantsov and Fedonkin (2002) described a partial specimen of a conulariid-like, problematical fossil metazoan from Upper Vendian (latest Proterozoic) siliciclastic sediments in north-westernmost Russia. The specimen, about 5·4 cm long and 3·3 cm wide (maximum), is preserved in part as a sandstone cast and mould (the 'lower' part of the specimen; Ivantsov and Fedonkin 2002, p. 1220) that exhibits fine transverse surface relief, and transverse and longitudinal colour banding. The 'upper' part of the specimen consists of a uniformly dark-coloured imprint of the (external) surface, and exhibits a relatively coarse, undulatory ('wavy') relief consisting of broadly rounded transverse ridges. The wide end of the cast is broken, but the narrow end appears to be more or less smoothly rounded. According to Ivantsov and Fedonkin, the lower part of the specimen also exhibits six gently tapered, mutually similar sides ('faces'), and probably had the form of a six-sided cone in life. The authors argued further that the living animal was housed in an elastic test or theca composed of non-mineralized organic matter and exhibiting a fine surface ornament consisting of transverse and longitudinal ridges ('rods' and 'spines').

Ivantsov and Fedonkin named this fossil *Vendoconularia triradiata*, hypothesizing homology of its (putatively) non-mineralized theca with the apatitic theca of conulariids, and classifying it as a conulariid cnidarian. If these interpretations are correct, then *Vendoconularia* is the oldest conulariid or (alternatively) a close fossil relative of conulariids, and provides additional evidence of the presence of diploblastic metazoans in the latest Precambrian.

The purpose of this article is to present alternative interpretations of certain key aspects of the anatomy of *Vendoconularia*. These alternative hypotheses of homology make the case for a conulariid affinity for this Precambrian fossil firmer.

HYPOTHESES OF HOMOLOGY

Original hypotheses

According to Ivantsov and Fedonkin (2002), the narrow boundary between any two mutually adjacent faces of *Vendoconularia* is marked by a pair of slender brown lines that each measure about 0·1 mm wide and are spaced about 0·4 mm apart. In addition, every other pair of lines is associated with a relatively wide (roughly 1·5 mm) brown band that appears to overlap part of the paired brown lines. Both the paired brown lines and the brown bands are clearly distinguishable in Ivantsov and Fedonkin's

(2002, pl. 1) photographic illustrations. Judging from these photographs, the two members of a pair of fine brown lines diverge toward the wide ('apertural') end of the specimen, at an extremely low angle. Ivantsov and Fedonkin (2002, p. 1220) attributed the brown colour of the slender paired lines and broad bands to the presence of hydrated iron oxides, and proposed further that those parts of the fossil marked by brown lines or bands correspond to the 'thickest parts of the primary organic matter [i.e. theca]'. They also stated that the thecal structures corresponding to the broad colour bands were 'probably phosphatized' (Ivantsov and Fedonkin 2002, p. 1221). This statement is contradicted in several other places, including the final paragraph of the systematic palaeontology section, in which Ivantsov and Fedonkin (2002, p. 1227) conclude that *Vendoconularia* 'differs from conulariids in lacking phosphatic mineralization'.

Ivantsov and Fedonkin homologized the region bounded by a pair of thin brown lines with the (generally) sulcate *corners* of conulariid thecae, and thus also homologized the six gently tapered surfaces bounded by pairs of thin brown lines with the conulariid faces. Although conulariids generally have four faces, rare specimens exhibiting three, five or six faces have been documented (Babcock *et al.* 1987; Van Iten 1992*a*; Leme *et al.* 2004). In their line drawing of the *Vendoconularia* specimen, Ivantsov and Fedonkin (2002, text-fig. 2) labelled the narrow band bounded by a pair of fine brown lines as a 'corner groove'; however, and as they noted, there is no clear evidence of a groove or sulcus at this site (see Ivantsov and Fedonkin 2002, pl. 1). Moreover, we see no evidence in the photographs that the cast bends at this site, but this may simply be an artefact of compaction. The photographs provide strong evidence of a shallow sulcus at sites interpreted as facial midlines (see discussion below).

According to Ivantsov and Fedonkin (2002, p. 1221), the midline (the longitudinal centreline) of each face of *Vendoconularia* is marked by the junction of two sets or rows of fine transverse lines that correspond to 'primary fine folds or linear thickenings in the [original thecal] wall'. These transverse lines are putatively homologous to the transverse ribs of conulariids. Following Babcock and Feldmann (1986*a*), Ivantsov and Fedonkin (2002) referred to the transverse ribs as 'rods', and interpreted the transverse ribs as sites of a discrete, solid rod embedded within a finely lamellar 'integument'. As demonstrated by Van Iten (1992*b*) and Jerre (1994), however, the thickening of conulariid thecae at the transverse ribs is due to thickening of the lamellae, rather than to the presence of a discrete internal rod. Ivantsov and Fedonkin claimed further that *Vendoconularia* exhibits two kinds of transverse ribs, those that extend from the putative midlines to the edges of the putative corners ('major rods') and those that terminate just short of the edges of the putative corners ('secondary rods') and alternate with the 'major' ribs. In addition, the ends of the 'major' ribs of two mutually adjacent faces alternate where they intersect the putative shared corner sulcus. Ivantsov and Fedonkin (2002, p. 1227) also stated that each transverse rib is connected to a series of short, closely spaced longitudinal lines that extend toward the wide ('apertural') end of the specimen, and may be homologized with the 'adapertural spines' of conulariids. In conulariids, the 'adapertural spines' are more properly referred to as 'interspace ridges' (Van Iten *et al.* 1996), and represent corrugation of the region (interspace) between adjacent transverse ribs.

Although Ivantsov and Fedonkin's (2002, pl. 1) photographs show clearly the presence of transverse features resembling conulariid transverse ribs, we see no evidence of 'apertural spines'. Likewise, we see no evidence supporting a differentiation of 'major' from 'secondary' transverse ribs.

Alternative interpretations

Corners and midlines. A stronger case for homology with conulariids can be made by comparing the pairs of slender brown lines of *Vendoconularia* with paired longitudinal structures associated with the conulariid midlines. In *Metaconularia* Foerste and *Conularina narrawayi* Sinclair, the four midlines, which may be sulcate (*C. narrawayi* and some *Metaconularia*) or unfurrowed, are flanked by a pair of low, closely spaced internal ridges or carinae that diverge from each other at extremely low angles (Van Iten 1992*a*). These paired longitudinal structures are similar in spacing (relative to the width of the faces) and angle of divergence to the paired thin brown lines of *Vendoconularia* (compare, e.g. pl. 1, fig. 4 in Ivantsov and Fedonkin 2002 with pl. 1, figs 4–5 in Holm 1893 and pl. 2, figs 2–3 in Van Iten 1992*a*). Paired midline carinae also occur in certain specimens of *Paraconularia chesterensis* (Worthen) (Van Iten 1992*a*) and *Conularia splendida* Billings (Van Iten *et al.* 1996). In these conulariids too, the paired midline carinae are similar in spacing and angle of divergence to the paired brown lines of *Vendoconularia*. In *Climacoconus sinclairi* Van Iten, Fitzke and Cox (1996), the midlines are flanked by a pair of seriated carinae, and the thecal wall between the members of a pair is thickened.

These observations suggest an alternative interpretation of the paired thin brown lines of *Vendoconularia*, namely that they mark the positions of former paired carinae or thickenings flanking the midlines, not the corners. Similarly, the wide longitudinal bands may correspond to midline thecal material that was more broadly thickened (as in *C. sinclairi*). These alternative hypotheses of homology are consistent with Ivantsov and Fedonkin's

interpretations of the preservation and diagenesis of *Vendoconularia*. More specifically, and in accordance with the geochemical scenario of Ivantsov and Fedonkin, the thin brown lines and wide longitudinal bands may be composed of hydrated iron oxides that formed as the result of oxidation, respectively, of pyritized internal ridges and more broadly thickened thecal material.

Under the alternative interpretation of the paired thin brown lines and wide longitudinal bands proposed here, the corners of the *Vendoconularia* theca coincide with linear features homologized by Ivantsov and Fedonkin with the conulariid midlines. Again, inspection of Ivantsov and Fedonkin's (2002, pl. 1) photographs indicates that their 'midlines' are marked by a shallow furrow. This furrow is similar in relative size and topology to the conulariid corner sulcus, which has been interpreted as homologous in body position to the perradii of coronatid and stauromedusan scyphozoans (see Van Iten 1992*a* and references cited therein).

Other features. Reinterpreting the corners and midlines of *Vendoconularia* in the manner suggested above may require the reinterpretation of other aspects of its anatomy. For example, in their text-figure 2, Ivantsov and Fedonkin show the putative transverse ribs of a given 'face' approaching the 'midline' at an angle, thus forming a chevron pattern similar to that of the faces of many Palaeozoic conulariids (see, e.g. Van Iten *et al.* 1996, pl. 1, fig. 2; pl. 3, fig. 1). However, if our interpretations are correct, then the transverse ribs of *Vendoconularia* are perpendicular to the midlines, and in this respect are most similar to the transverse ribs of *Conulariella* Bouček (see, e.g. Bouček 1928, pl. 3, figs 14–15). One apparent difference between these two genera is that whereas the transverse ribs of *Conulariella* cross the midlines without disruption, those of *Vendoconularia* are apparently offset along the midlines, a condition also exhibited by many species of *Conularia* Miller and *Paraconularia* Sinclair (see, e.g. Babcock and Feldmann 1986*b*, fig. 25.3). As suggested by inspection of Ivantsov and Fedonkin's plate, the apparent arching of the transverse ribs of *Vendoconularia* may be due, in part at least, to inward curvature of the theca in the vicinity of the corners, which as proposed above, are sites of a shallow sulcus. In the corner sulcus of many Palaeozoic conulariids, the transverse ribs or transverse node rows arch or bend toward the aperture (see, e.g. Van Iten *et al.* 1996, pl. 1, fig. 4; pl. 3, fig. 2). As far as we are aware, no currently known Palaeozoic conulariid exhibits alternating long and short transverse ribs or node rows, and thus the putative presence of alternating 'major' and 'secondary' transverse ribs in *Vendoconularia* may be an autapomorphy of this taxon.

The wavy transverse relief of the upper part of the *Vendoconularia* specimen, mentioned above, is similar to the wavy relief exhibited by Palaeozoic conulariid specimens that appear to have been compressed parallel to the long axis of the body (Simões *et al.* 2000; Rodrigues 2002). Therefore, the wavy relief of the *Vendoconularia* specimen may be an artefact of taphonomy.

Finally, the rounded apical end of *Vendoconularia* can be interpreted as the internal mould of a transverse wall homologous to the conulariid schott (Van Iten 1991).

CONCLUDING REMARKS

Comparisons of the single known *Vendoconularia* with Palaeozoic conulariids suggest the existence of detailed and uniquely shared anatomical similarities. In agreement with Ivantsov and Fedonkin (2002), we think it reasonable to hypothesize that *Vendoconularia* was sheathed in a steeply pyramidal, ectodermal theca homologous to that of conulariids and coronatid scyphozoans. We propose further that the corners of the *Vendoconularia* theca were sulcate, and that the midline of each face was non-sulcate and flanked by a pair of extremely low internal carinae or thickenings. Two key predictions of this hypothesis are (1) that undistorted specimens should exhibit more or less distinct, furrowed corners bounding planar faces bisected by paired brown lines, and (2) that the paired brown lines and brown bands penetrate the cast. We also hypothesize that at least some of the putative homologies presented here are synapomorphous, i.e. that *Vendoconularia* and Palaeozoic conulariids were modified descendants of a thecate cnidarian ancestor uniquely shared by *Vendoconularia* and conulariids.

The discovery of a possible Vendian conulariid having a non-mineralized theca raises some interesting questions about conulariids whose preservation is similar to that of *Vendoconularia*. For example, the genus *Anaconularia* Sinclair, currently known from the Ordovician of the Czech Republic and Morocco (Van Iten and Vyhlasova 2004), is represented exclusively by sandstone steinkerns. Previous discussions of the anatomy of this genus (e.g. Van Iten 1992*a*) have tacitly assumed that the original theca was mineralized and apatitic. However, it is also possible that *Anaconularia*, like *Vendoconularia*, was non-mineralized or weakly mineralized. As suggested by the work of Ivantsov and Fedonkin (2002) on the preservation and taphonomy of *Vendoconularia*, this possibility should be evaluated by detailed analysis of the patterns of deformation of *Anaconularia* and by comparisons of this fossil with associated shell-bearing fossils whose original mineralogy is known.

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