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The aperture and its closure in an Ordovician conulariid

CONSUELO SENDINO, KAMIL ZÁGORŠEK, and ZDEŇKA VYHLASOVÁ

The conulariids, an enigmatic fossil group believed to be of cnidarian (scyphozoan) affinity, have four-sided, acutely pyramidal exoskeletons terminated in apertural closures. To date, three main closure types have been recognised in conulariids (plicated, triangular lappets, and lobate lappets) but the first type is poorly illustrated in the literature. Here we present the first photographic illustration of an unequivocal plicated closure in *Metaconularia? anomala*, based on study of the rich (1700+ specimens) material from the Upper Ordovician of the Prague Basin. This closure is formed by inwardly folded, triangular lappets centred on each of the four faces, with kite-shaped elements centred on the four corners forming a webbing between the lappets. Plicated closures were evidently rare in conulariids and restricted to a few Ordovician species.

Introduction

Conulariids are extinct marine organisms with a worldwide distribution and a fossil record ranging from the Ediacaran (Ivantsov and Fedonkin 2002; Van Iten et al. 2005) to the Triassic (Waterhouse 1979). Although some authors have reported Lower Jurassic conulariids (Argéliez 1856; Dana 1863; Kayser 1924; Zittel 1924, 1927), these however, remain disputable. At least 52 genera and 357 species have been described. Conulariids generally have a four-sided, acute pyramidal exoskeleton. The aperture, which is located at the widest part of the exoskeleton, can be partly or totally closed by infolding of the apertural ends or lappets.

Fossil conulariids may be preserved in the original calcium phosphate or as external moulds. A common alternative style of preservation is as an internal mould (steinkern). Exoskeletons range from a few millimetres to over 50 centimetres long (Kiderlen 1937; Bouček 1939; Lamont 1946). The shape of conulariids led some early palaeontologists to suppose that they were molluscs (Sowerby 1821; Archiac and Verneuil 1842; Sandberger 1847; Rouault 1851; McCoy 1855; Barrande 1867; Tromelin and Lebesconte 1876; Hall 1879; Lindström 1884; Barrois 1891; Holm 1893; Miller and Gurley 1896; Delgado 1897, 1908), but recent phylogenetic studies have indicated that they are scyphozoan cnidarians (Van Iten 1991; Van Iten et al. 1996, 2006).

The purpose of this note is to describe the unusual apertural closure of *Metaconularia? anomala* (Barrande, 1867) and compare it with other conulariids. This species has been recorded from the Drabov quartzites, Libeň and Letná formations (Sandbian) of the Barrandian area, Czech Republic (Barrande 1867; Bouček 1928; Havlíček and Vaněk 1966), and also from the Ordovician of

Galicia, Asturias and Guadalajara, Spain (Hernández-Sampelayo 1915, 1942: 614; see also Kindelán 1918). *M.? anomala* is unusual among conulariids because many individuals underwent torsion during their growth, some even losing one of the four faces and one of the corners to become three-sided in transverse section (as in *Paraconularia africana* [Sharpe, 1856] from Bolivia [Kiderlen 1937]).

Institutional abbreviations.—FSL, Faculté des Sciences de la Terre, Université Claude Bernard Lyon 1; NHM-L, Natural History Museum, London; NHM-V, Naturhistorisches Museum, Vienna; NMP, Narodni Museum, Prague.

Material

There are more than 1700 specimens of *Metaconularia? anomala* in the NMP. All specimens are from the Drabov quartzites, a shallow water facies of the Letná and Libeň formations (Upper Ordovician). Most come from the type locality of Drabov in the Prague Basin. The quartzite at Drabov was designated, along with the May Sandstone of Normandy, as the facies of “medusa conulariids” by Kiderlen (1937).

All studied specimens of *Metaconularia? anomala* in the NMP, FSL, NHM-L and NHM-V collections are steinkerns or moulds of steinkerns, probably representing individuals that were buried rapidly to preserve their morphology in three dimensions. It is difficult in steinkerns to see some of the main characters that define genera of conulariids, but accessory lines can be observed in a few specimens. These faint, very narrow vertical lines occur one third of the distance between midlines and corners. They have been interpreted as tentacular muscle tracks (Kiderlen 1937). None of about 40 specimens of *M.? anomala* housed in the NHM-L display these lines, but we report their presence here for the first time in specimens from the NMP (Fig. 1, arrowed).

Results

Only one specimen of *M.? anomala* (NM-PM2-L25097) was found to preserve a clear apertural closure (Fig. 1). According to the attached label, this specimen is the original figured by Bouček (1928: pl. 3: 13, 1939: fig. 4c), although Bouček's drawing (Fig. 2 herein) appears to be of a different specimen. The figure caption states that the drawing depicts a flattened specimen from Drabov, and seems to show two individuals side-by-side, whereas specimen NM-PM2-L25097 is solitary, not flattened and partly embedded in the matrix.



Fig. 1. Topotype of the conulariid scyphozoan *Metaconularia? anomala* (Barrande, 1867) from the Drabov quartzites of Bohemia, NM-PM2-L25097. The specimen is a steinkern with a plicated apertural closure. Arrows point to accessory lines which may be muscle tracks.

The preserved length of this incomplete specimen is about 58.3 mm, but its estimated full length would have been at least 90 mm. The apex is missing. Width at the aperture is approximately 22.5 mm. Therefore, the length/width ratio is about 3. The cross section is quadrangular (i.e., not 3-sided), and the apical angle about 15°, although this is difficult to determine accurately due to preservation. The corners are not as sharp as they are in some other specimens of *M.? anomala*, and the faces are slightly concave. It is possible to observe the midline marked by a groove with accessory lines forming very faint grooves about 4 mm on either side of the midline. No ornament (e.g., transverse ribs or tubercles) is visible but very gentle transverse corrugations can be perceived. The triangular apertural ends have a length of 11.3 mm, about 12% of total exoskeletal length.

As in other conulariids, the closure is formed by inwardly folded apertural ends or lappets of a triangular shape. In the case of *M.? anomala* (NM-PM2-L25097), however, the lappets comprise not only triangles centred on each of the four faces, but also kite-shaped elements, centred on the four corners, that form a webbing between the triangular lappets. Midlines of the kite-shaped elements are folded inwardly.

Therefore, the closure contrasts with those in most conulariids in which kite-shaped elements are apparently lacking (e.g., Van Iten et al. 2008: fig. 1.5). The closure in *M.? anomala* corresponds to the plicated type.

Discussion

Conulariid apertures were extensively discussed by numerous authors leading to recognition of three closure types (Fig. 3) that differ in shape and mechanics. According to Kiderlen (1937), Bouček (1939), Moore and Harrington (1956), and Bischoff (1978), the three closure types are plicated, triangular lappets, and lobate lappets. A plicated closure is described above for *M.? anomala*. Kowalski (1935: fig. 1) published a drawing of what appears to be a plicated closure in *Conularia plicosa* Barrande, 1867, but this type of closure has never been clearly illustrated photographically.

In conulariids with triangular lappets (Fig. 4), the lappets become juxtaposed when the aperture closes. This type of closure, which seals the aperture completely (Bischoff 1978), is the commonest type observed among conulariids in the NHM-L collections (Sendino 2007). A comparison can be made with the closure present in the rugose coral *Goniophyllum* which has four triangular opercula (see Gudo 2002). However, it should be noted that some conulariids with apparently triangular closures and completely occluded apertures may in fact have plicated closures in which the kite-shaped elements are totally hidden.

Lobate lappets occur in conulariids with semicircular apertural ends that do not become juxtaposed with the adjacent or opposite ends when the aperture closes. Therefore, the aperture could not be sealed completely. Transverse ribs usually parallel the apertural margin. Bischoff (1978) believed this to be the most common type of closure, and it is found, for example, in *Paraconularia tenuis* (Slater, 1907).

Growth of conulariid skeletons involved extension along the apertural margin together with centripetal accretion of mineralised lamellae. Apertural closures like the one described here for *M.? anomala* could have functioned only if the conulariid exoskeleton was flexible at the apertural margin. According to Kiderlen (1937), closure of the aperture may have been brought about by contraction of carinal muscles, located on the inner

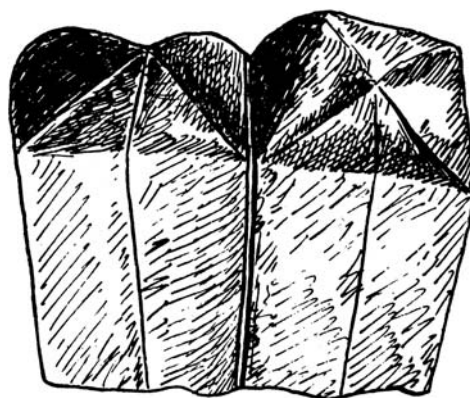


Fig. 2. Apertural ends in *Metaconularia? anomala* with a plicated type of closure as figured by Bouček (1939: fig. 4c).

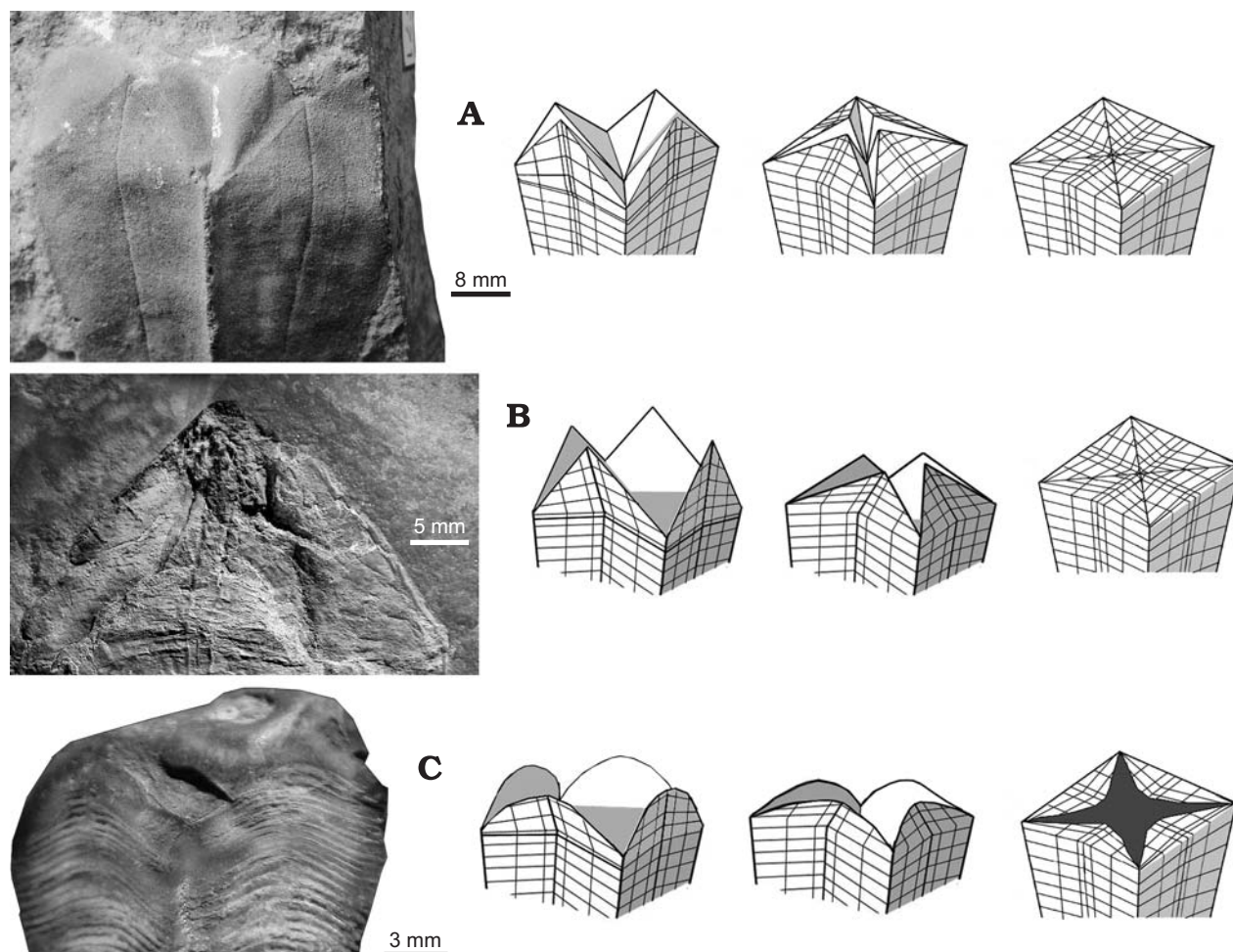


Fig. 3. Types of closures in conulariid scyphozoans. **A.** Plicated type closure in *Metaconularia? anomala* (Barrande, 1867) from the Drabov quartzites of Bohemia, NM-PM2-L25097. **B.** Triangular lappet type of closure in *Metaconularia aspersa* (Lindström, 1884) from the Lower Ludlow of Church Hill, Herefordshire, England, NHM-L-G5373. **C.** Lobate lappet type of closure in *Paraconularia quadrisulcata* (Sowerby, 1821) from the Carboniferous of Carlisle, Lanarkshire, Scotland, NHM-L 46784. All are accompanied by sketches (based on Moore and Harrington 1956) showing different stages in the closure.

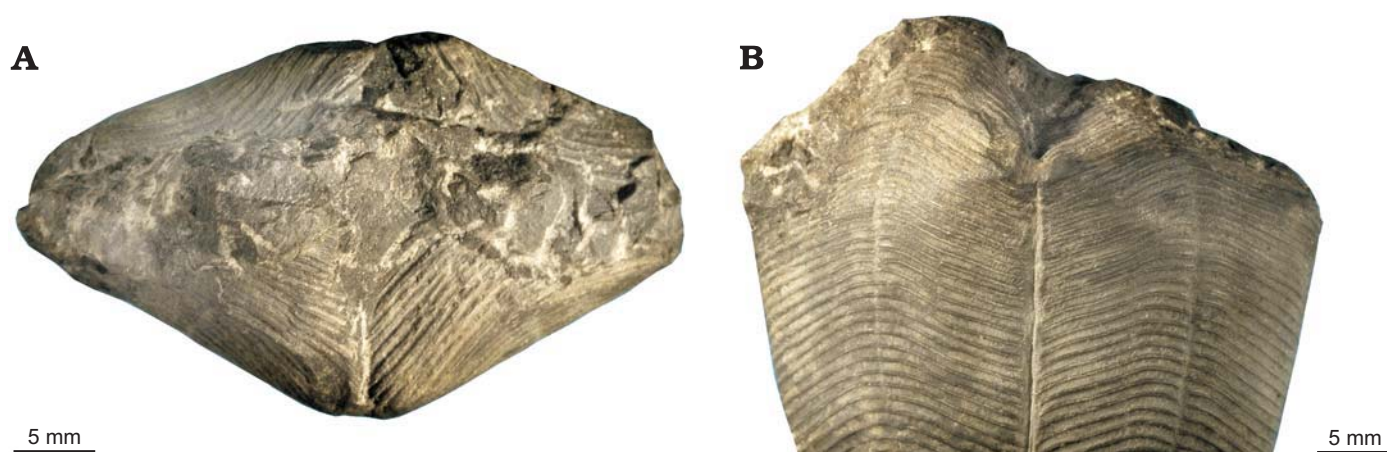


Fig. 4. Closure with triangular terminal ends in a toptype of *Conularia brongniarti* Archiac and Verneuil, 1842 from the Devonian of Néhou (Manche, France), FSL 15605, in apertural (**A**) and lateral (**B**) views.

sides of the reinforced corners, that pulled the exoskeleton towards the interior. Bischoff (1978), however, supposed that taxa without any reinforcement of the corners could not have pos-

sessed muscles attached to the corners of the shell. He also assumed that in plicate closures the corners were folded inwards first, followed by the four faces.

Table 1. Studied taxa with apertural margins at the similar levels.

Taxa	Specimens	Stratigraphy	Site
<i>Paraconularia quadrisulcata</i> (Sowerby, 1821)	FSL no number	Coal Measures, Carboniferous Limestone	Shropshire (UK), Carluke, Lanarkshire (UK), Redesdale, Northumberland (UK), Thorneybank, Scotland (UK)
	NHM-L no number		
	NHM-L G61		
	NHM-L G19135		
	NHM-L C3448		
	NHM-L G4014		
	NHM-L PG4480		
	NHM-L G41207		
	NHM-L 48818		
	NHM-L G4454		
	NHM-L 46784		
<i>Paraconularia africana</i> (Sharpe, 1856)	NHM-L PG4284	Bokkeveld Beds	Cedarberg and Hex River (South Africa)
	NHM-L 733		
<i>Paraconularia subtilis</i> (Salter, 1855)	NHM-L G4602	Ludlow	Usk, Monmouthshire (UK)
	NHM-L 43843	“Transition-Lime-stone”	Keswick, Cumbria (UK)
<i>Conularia subcarbonaria</i> Meek and Worthen, 1865	NHM-L G38	Mississippian	Floyd County, Indiana (US)
<i>Conularia trentonensis</i> Hall, 1847	NHM-L G19919	Trenton Limestone	Belleville, Ontario (Canada)
<i>Conularia plicata</i> Slater, 1907	NHM-L G46764	Starfish Beds	Thraive Glen, Ayrshire, Scotland (UK)
<i>Notoconularia inornata</i> (Dana, 1849)	NHM-L PG4265	Permo-Carboniferous	Ravenswood, New South Wales (Australia)

Moore and Harrington (1956) believed the apertural margin to be a flexion line along which the exoskeleton could be folded to close the aperture. However, Babcock and Feldmann (1986) questioned the occurrence of a distinct flexion line, being unable to find it in more than 70 specimens with closed or half-closed apertures, although they did not observe any specimens showing plicated closures like the one described herein. They also maintained that any flexion line would not be straight but rather would have to conform to the shape of the transverse ribs. This is not the case in the studied specimen of *M. ? anomala* which has straight flexion line.

In closures formed by triangular and lobate lappets, closing the aperture using muscles pulling from the corners would produce lines of flexion (accessory and secondary lines and the midline) in each face (Kiderlen 1937: 131). As this mechanism is complex, especially when the apertural margin is oblique to the transverse ribs, it is possible that closure happened only rarely, for example during periods of dormancy.

In all specimens that we observed, the lappets are continuations of the exoskeletal faces and show the same ornamentation. These could be bent to close the aperture (totally or partially). Although Babcock and Feldmann (1986) wrote that the line of flexure is not isolatitudinal across the four faces, individuals of the following species preserved in three dimensions and with complete apertures have been observed to have apertural margins at the same approximate levels (see Table 1).

Conclusion

It is unclear why plicate closures are seen in so few species of conulariids; according to Bouček (1939) they are present only in *Metaconularia ? anomala* and *M. exquisita*. However, it is possi-

ble that some plicated closures could have been misidentified as triangular lappet-type closures due to inadequate preservation. A closure identified by Van Iten et al. (2008) in *Conularia cf. subcarbonaria* Meek and Worthen, 1865 as plicated differs considerably from the plicated closure of *M. ? anomala* described here as it lacks the kite-shaped elements between the apertural flaps. This paper presents the first photographic illustration of an unequivocal plicated closure. It is evident that the drawing of Bouček (1928) is geometrically flawed, failing to show the kite-shaped elements that link the triangular apertural lappets at the corners of the apertural edge. The functional and phylogenetic significance of conulariid closure has yet to be fully explored.

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