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First record of true conulariids from the Upper Devonian of Poland

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ABSTRACT

Phosphatized remains indisputably belonging to conulariids have been found in the lower Famennian (Upper Devonian) deposits at the Kowala quarry in the Holy Cross Mountains, Poland for the first time. The ornamentation patterns and characteristics of the exoskeleton indicate that the conulariids, represented by at least two incomplete specimens, belong to a single species within the genus? *Paraconularia*. Some Polish Ordovician fossils previously described as conulariids either do not possess morphological characters seen in conulariids, or are too fragmentary to be confidently assigned to conulariids. Therefore, the fossils reported here not only represent the first documented record of conulariids in the Devonian of Poland, but the first *true* conulariids ever reported and illustrated from Poland. The exoskeleton of one specimen possesses at least three sublethal injuries. As the host deposit of marly shale originated in deep water, it is possible that the injuries did not result from purely physical factors, but rather from attempted predation. This interpretation is consistent with the fact that the lower Famennian deposits at Kowala preserve other predation-related structures such as fish coprolites, fragmented arthropod cuticle and regurgitated remains.

1. Introduction

Conulariids are extinct marine organisms with a global distribution and a fossil record ranging from the Ediacaran (Van Iten et al., 2016; Cunningham et al., 2016) to the Late Triassic (e.g., Ivantsov and Fedonkin, 2002; Sendino et al., 2012; Lucas, 2012; Van Iten et al., 2013a). They can be found isolated or in clusters. These fossils are not very common, but sometimes they are found in thousands, as in the Bohemian Basin (with a concentration of about 2000 specimens in only one site of about 100 m^2, mostly Ordovician), Central Andes, Bolivia (very abundant in the Lower Devonian, Conularienschichten) and Silurian of Gotland (Sweden). Characteristic features of most genera are exoskeletons (thecae) that are elongate pyramidal, four-sided, phosphatic (carbonate-rich apatite, see Bouček and Ulrich, 1929; Moore and Harrington, 1956; Ford, 2011; Vinn and Kirsimäe 2015; Ford et al., 2016) and bear distinct transverse ribs and sometimes longitudinal files of small tubercles. The aperture was terminated by a closure formed by inwardly folded lappets centered on each of the four faces (Van Iten et al., 2008; Sendino et al., 2011; Ford et al., 2016). Once considered as a problematical fossil taxon having no known relationships to any extant taxa, conulariids have even been placed within a separate phylum (e.g. Babcock and Feldmann, 1986a; Babcock, 1991). But phylogenetic analyses indicated that conulariids are scyphozoan cnidarians (Leme et al., 2008; Van Iten et al., 2016). The cnidarian affinity may also be supported by the preservation of tentacle-like structures extending from the aperture in some Ediacaran specimens from China (Van Iten et al., 2013a). The mode of life of conulariids have long been debated. Although it has been proposed that they may have been planktonic or pseudoplanktonic (see Feldmann and Babcock, 1986; Babcock and Feldmann, 1986b), the general consensus is that they were sessile, benthic organisms (e.g., Rodrigues et al., 2003; Simões et al., 2003; Van Iten et al., 2013b).

In the present paper we report on conulariids found in the Upper Devonian deposits of the Holy Cross Mountains, central Poland. Supposed 'conulariids' were previously reported and described from the Ordovician of Poland by Kozłowski (1968) and subsequently cited and figured by Dzik and Pisera (1994). However, the conulariid-like fossils studied by Kozłowski (1968) have morphological elements not seen in true conulariids, such as adapical hollow spines that are connected with the interior of the test, and an apical collar. Babcock (1991) undertook a cluster analysis of the skeletal characters of putative conulariids and found that Kozłowski's (1968) specimens from Poland were not true conulariids. They lack paired transverse ribs, segmental lines and

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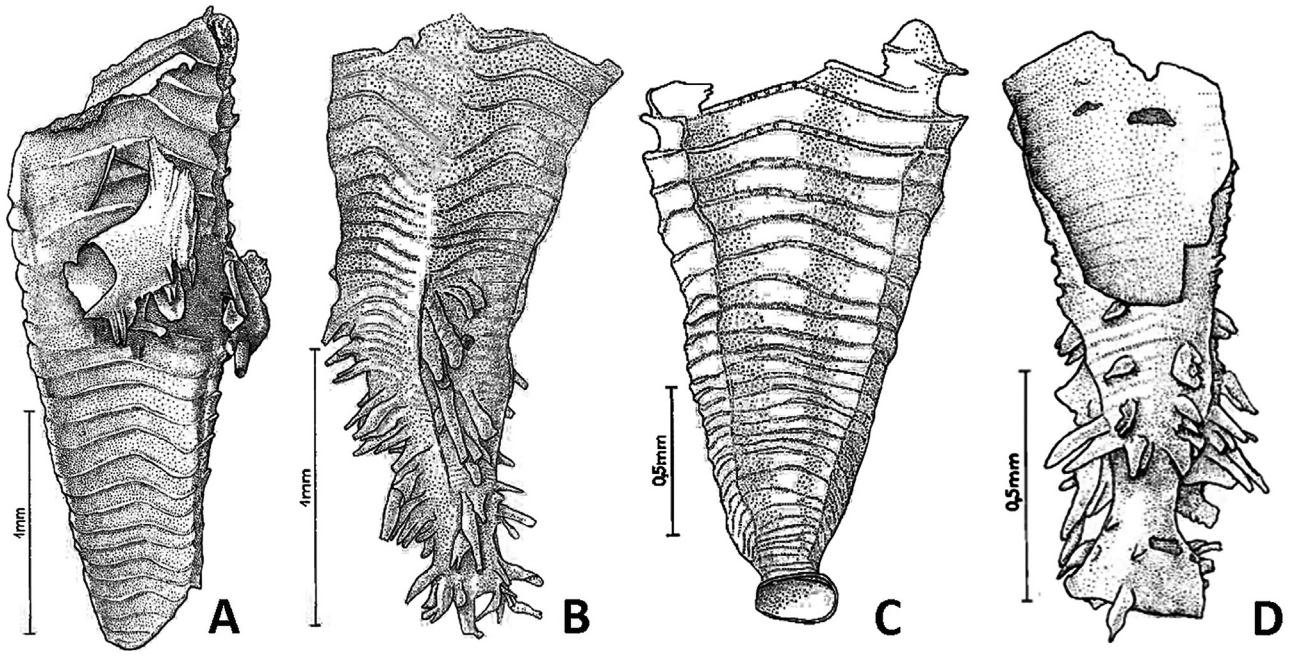

Fig. 1. Specimens published by Roman Kozłowski as 'conulariids' (taken from Kozłowski, 1968). (A) Specimen with two individuals attached by their apical parts with spines. (B and D) Adapical hollow spines. (C) Open apical collar.

have a skeleton that was secreted from the outside, i.e. an endoskeleton unlike the exoskeleton found in true conulariids (Fig. 1). In addition, some of these specimens did have circular cross section unlike conulariids. The absence of adapical hollow spines in conventional conulariids, as those described by Kozłowski in Ordovician specimens, cannot be a taphonomic effect as these have only been described in the Kozłowski's (1968) 'conulariids'.

Dzik and Pisera (1994) figured a supposed fragment as a conulariid but this is hard to identify as a conulariid rib comparable to those figured by Jerre (1993, 1994). Recently, Kozłowski (2012: 55) mentioned the occurrence of conulariids in Middle Devonian (Eifelian) dolomites from the Bardo Syncline in the Holy Cross Mountains. However, these specimens have neither been described nor illustrated and their status is unclear. Therefore, the specimens reported in this paper are the first true conulariids to be described and illustrated from Poland.

2. Geological background, material and methods

The specimens have been found in lower Famennian deposits outcropping in one of the trenches located in the northern part of the active Kowala Quarry in the Holy Cross Mountains, central Poland (for details see Zatoń et al., 2014). The Kowala Quarry is situated in the southern limb of the Gałęzice-Bolechowice Syncline in the southwestern part of the southern Kielce Region. The Upper Devonian deposits exposed in the quarry originated in the Chęciny-Zbrza basin which stretched along the southern shelf of the Laurussian continent during the Late Devonian (e.g. Szulczewski, 1971; Narkiewicz, 1988; Racki, 1993, 1997; Racki et al., 2002; Bond et al., 2004; Racka et al., 2010). The lower Famennian deposits investigated belong to the lithological set H-4 *sensu* Racki and Szulczewski (1996) and are composed of marls and marly shales, rhythmically intercalated with thin-bedded limestones. The depositional environment is interpreted as deep-water, below storm wave-base, but at least occasionally within the limits of the photic zone (Racki et al., 2002; Bond et al., 2004; Filipiak, 2009; Marynowski et al., 2011). The conulariids were found preserved in marly shale dated to the *Palmatolepis crepida* standard conodont Zone (e.g., Racki and Szulczewski, 1996; Marynowski et al., 2011; Zatoń et al., 2014).

The material consists of a single marly shale slab containing phosphatic, fragmentary specimens of conulariids situated parallel to the bedding. The specimens have been examined in an uncoated state using a LEO 1455VP low vacuum scanning electron microscope housed at the Natural History Museum, London, UK, and a Philips XL30 environmental scanning electron microscope (ESEM) housed at the Faculty of Earth Sciences, Sosnowiec, Poland. Images were generated using backscattered electrons (BSE detector).

The specimen is housed at the Faculty of Earth Sciences in Sosnowiec, abbreviated GIUS 4-3671.

3. Systematic palaeontology

Phylum Cnidaria Hatschek, 1888Class Scyphozoa Götte, 1887Subclass Conulata Moore and Harrington, 1956Order Conulariida Miller and Gurley, 1896Family Conulariidae Walcott, 1886Genus *Paraconularia* Sinclair, 1940*1940 *Conularia* (*Paraconularia*) Sinclair: 73–74.1956 *Paraconularia* Sinclair; Moore and Harrington: F65.1985 *Paraconularia* Sinclair; Hergarten [cop. Sinclair, 1940]: 277.1986a *Paraconularia* Sinclair; Babcock and Feldmann: 412.1987 *Paraconularia* Sinclair; Babcock et al. [cop. Babcock and Feldmann, 1986a]: 220.*Type species: Conularia inaequicostata* De Koninck, 1883 (De Koninck, 1883: p. 223). *Stratigraphical distribution*: Ediacaran (Van Iten et al., 2016) to Late Triassic.*Palaeoeographical distribution*: Avalonia, Baltica, South China, Gondwana, Kazakhstan, Laurentia and Siberia.? *Paraconularia* sp.Figs. 2–4

We have assigned these specimens to the genus *Paraconularia* Sinclair, 1940 with some doubt. They have distinct transverse ribs, with interspaces that are at least 6 times bigger than the ribs, which under transmitted light microscopy seem to be finely nodose and under SEM are seriated. The midline is marked by transverse ribs bent adaperturally that can meet there or be offset. Unfortunately, it is not possible to see the corner sulcus, but there is a fragment with the internal view of the theca where the ribs

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