



Conulariid soft parts replicated in silica from the Scotch Grove Formation (lower Middle Silurian) of east-central Iowa

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Abstract.—Two specimens of *Metaconularia manni* (Roy, 1935) from the lower Middle Silurian Scotch Grove Formation (eastern Iowa) exhibit well-defined, relict soft parts replicated in silica. One of these specimens bears phosphatic periderm, whereas the other specimen is a mold. Present within the erect, undistorted apical region of the specimen preserving periderm, on opposite sides of the peridermal cavity, are two small, elongate masses of silica located near the midlines of two of the four faces. Present in the central portion of the other specimen, at a somewhat greater distance from the apex, are five pairs of hollow, elongate, keeled pouch-like bodies (hereafter pouches), the long axes of which converge on the center of the fossil. Each pair of pouches is associated with a short, narrow, gently curved or broadly U-shaped tube, also composed of silica. Additionally, two of the pouch/tube combinations are associated with a pair of rectilinear furrows that correspond to the paired internal carinae that straddled the conulariid's facial midlines. We interpret the paired pouches and short tubes in the moldic specimen as relict conulariid soft parts homologous, respectively, to the interradial gonads and retractor muscles of extant, stauromedusan and polypoid scyphozoan cnidarians. Unlike most conulariids, which exhibit four faces, this individual had five faces, an aberrant morphology known in one other conulariid. The two small masses in the other specimen are more difficult to interpret, but they, too, could be relict gonads or longitudinal muscles. These interpretations suggest that, as in certain extant scyphozoans, at least one conulariid lost the free-living, sexual medusoid life phase.

Introduction

Previous interpretations of the soft-part anatomy of conulariids, an extinct clade of medusozoan cnidarians that ranges from the terminal Ediacaran to the Late Triassic (Lucas, 2012; Van Iten et al., 2016a; Leme et al., 2022), rely to a great extent on comparisons of the soft tissues of extant groups with the steeply pyramidal, generally four-sided conulariid periderm (e.g., Kiderlen, 1937; Van Iten, 1991b, 1992a; Jerre, 1994). Based on such comparisons, the facial midline of conulariids has been interpreted as the former site of a prominent, inwardly projecting gastric septum homologous to the four gastric septae of cubozoans, stauromedusozoans, and scyphozoans (Jerre, 1994, fig. 3). This hypothesis, together with detailed similarities between conulariids and the periderm of coronate scyphozoans, is a key component of the phylogenetic hypothesis that conulariids were medusozoans (e.g., Kiderlen, 1937; Werner, 1966, 1967; Van Iten, 1991a, b, 1992a, b; Jerre, 1994; Van Iten et al., 1996, 2006; Hughes et al., 2000; Marques and Collins, 2004).

Present in a small number of documented conulariids are features that have been interpreted as relict conulariid soft parts. Babcock and Feldmann (1986a, fig. 2.1; 1986b, fig. 30.2–30.6) interpreted elongate or tubular concentrations of iron oxides in specimens of *Paraconularia subulata* (Hall, 1858) as relics of an 'alimentary canal' and an associated 'globular body.' Van Iten (1991b, figs. 5, 6) hypothesized that lime-mud matrix exposed at the apical end of the holotype of *Eoconularia amoena* Sinclair, 1944 exhibits a transverse cross section through a conulariid ephyra (incipient medusa), an interpretation which has since been questioned (Mergl et al., 2016). Van Iten and Südkamp (2010) documented localized concentrations of microcrystalline pyrite within the apertural region of clustered specimens of *Conularia* sp. from the Lower Devonian Hunsrück Slate of Germany. These authors argued that the pyrite formed during anaerobic decay of the soft parts of conulariids that had been smothered, but they were unable to discern clearly delineated, specific anatomical structures, e.g., circumoral tentacles or a gastric cavity. Most recently, Van Iten et al. (2022) documented concentrations of microcrystalline iron oxides near the apical end of smothered *Archaeoconularia* cf. *A. imperialis* (Barrande, 1867) from the Upper Ordovician of Morocco,

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arguing that the precursor iron sulfide minerals formed through the decay of conulariid soft parts. Again, however, specific soft-part structures were not recognized. Other conulariids have been found in formations hosting Konservat Lagerstätte, including the Lower Silurian Brandon Bridge Formation (Wisconsin, USA; Mikulic et al., 1985; Miller et al., 2022), the Middle Silurian Eramosa Formation (Ontario, Canada; von Bitter et al., 2007), and the Lower Ordovician Fezouata Shale (Morocco; Van Roy et al., 2015; Van Iten et al., 2016b), which together have yielded invertebrate and vertebrate fossils preserving well-defined soft parts. So far, however, relic soft parts have not been detected in the associated conulariids, even though they occur in the same beds as arthropods preserving nonmineralized cuticle, conodont fossils preserving eyes and other tissues, or medusoid cnidarians preserving tentacles (*Conchopeltis* sp. from pyritic lime mudstones in the Trenton Group of eastern New York State; Oliver, 1984; Babcock, 2011).

The present article documents the occurrence of discrete, well-defined relic soft parts, replicated in silica, in two specimens of *Metaconularia manni* (Roy, 1935) from the siliceous dolomitic Welton Member of the lower Middle Silurian (Sheinwoodian) Scotch Grove Formation in east-central Iowa. The conulariids were collected in the Shaffton Quarry (41° 45' 1.43"N, 90° 20' 23.34"W), located ~3.5 km southwest of the village of Camanche, Clinton County, on the southern side of State Highway 67. Stratigraphic logs of the Welton Member at the quarry show that a 40-cm-thick interval of finely laminated, organic-rich shale has yielded a diverse assemblage of vertebrate and invertebrate fossils, in which soft tissues are preserved (John et al., 2010; Moore et al., 2011). *Metaconularia manni*, the narrowly pyramidal periderm of which was very thin and delicate, is the only conulariid currently known from this shale interval. Several specimens, including the two discussed in this paper, are preserved in an unusual aspect: the middle and apertural regions of the sides or faces of the periderm are outwardly splayed and lie parallel to bedding, whereas the three-dimensional (3-D) apical region is erect and largely undistorted, thus indicating preservation in situ by burial in muddy sediment deposited directly from above (John et al., 2010). The sediment was funneled downward into the apical region, protecting the apex, which likely also projected into the substratum during life, from complete flattening. The relic soft parts documented in this report occur within the upright, downwardly tapering apical region. Based on the locations and patterns of arrangement of these features, as well as on comparisons with soft-part structures of extant taxa, we argue that they are relic conulariid soft parts homologous with the gonads and longitudinal muscles of polypoid medusozoan cnidarians.

Materials and methods

The two fossil specimens examined in this study were collected from float and consist of the part only, but their original stratigraphical occurrence within the shale described above is well established by lithologic and geochemical characteristics. Unfortunately, the small bench and bedding plane exposure from which *Metaconularia manni* and associated fauna could be collected relatively easily has been destroyed by quarrying.

Nevertheless, the shale itself likely extends beyond the quarry, and there is at least the potential for future removal of rock overlying it.

The conulariids were photographed under reflected light using a Nikon D300 camera with a 105-mm macrolens and extension tube. The 3-D geometry of silicified relic soft parts preserved within the specimens and partially obscured by dolomitic rock matrix was determined using ultrahigh resolution, 3-D scanning tomography (Ketcham and Carlson, 2001) at the University of Texas High-Resolution X-ray CT Facility (Department of Geological Sciences, Jackson School of Geosciences, The University of Texas at Austin). The computerized tomography (CT) analysis gathered 625 slices, with a slice thickness and interslice spacing of 0.0554 mm and a field of reconstruction of 26 mm, yielding an interpixel spacing of 0.05078 mm. The resultant 3-D model (Fig. 5) was generated using VGStudioMax. The elemental composition of the relic soft parts and adjacent rock matrix in specimen UWGM 6834 was analyzed using a JSM-5910-LV scanning electron microscope (SEM) and the EDAX Genesis software package with a UTW detector at Florida International University (Miami), and a LEO 982 Fe-SEM and Bruker Quantax EDX system at Pomona College (Claremont, California). Additional compositional analysis of UWGM 6834 was conducted at the Musée National d'Histoire Naturelle (Paris) using synchrotron X-ray fluorescence. Synchrotron XRF spectral raster scanning was performed using the DIFFABS beamline of the SOLEIL synchrotron source (Saint-Aubin, France). The X-ray beam was collimated by two bendable mirrors, monochromatized ($\Delta E/E \sim 10^{-4}$) using a Si(111) double-crystal monochromator and focused using a Kirkpatrick-Baez mirror down to a diameter of $10 \times 6 \mu\text{m}^2$.

Repository and institutional abbreviation.—Both fossil specimens are housed at the University of Wisconsin (Madison) Geology Museum (UWGM), under catalogue numbers UWGM 6834 and 6835.

Results

Preservation of the periderm.—The periderm of *Metaconularia manni* from the Welton Member at Shaffton Quarry is well preserved in some specimens (John et al., 2010, figs. 7, 8, 24.3), but in others, it has undergone demineralization during diagenesis. Using dilute HCl etching and critical point drying, Ford et al. (2016) demonstrated that the periderm of *Conularia* Miller in Sowerby, 1821 and *Paraconularia* Sinclair, 1940 consists of extremely thin (~1–3 μm), mutually parallel or concordant microlamellae that are alternately organic-rich and organic-poor, with the organic-poor microlamellae consisting predominantly of fluorapatite. Similarities between SEM images of sectioned specimens of these conulariids and SEM images of sectioned *Metaconularia* sp. (Van Iten, 1992b, text-fig. 1b; John et al., 2010, fig. 8.2) suggest that the periderm of this genus likewise was a bicomposite laminate consisting of apatitic microlamellae alternating with microlamellae composed of organic material. Additionally, though, many *M. manni* from Shaffton Quarry show localized thinning and demineralization, particularly in the adoral (middle and apertural) portions of

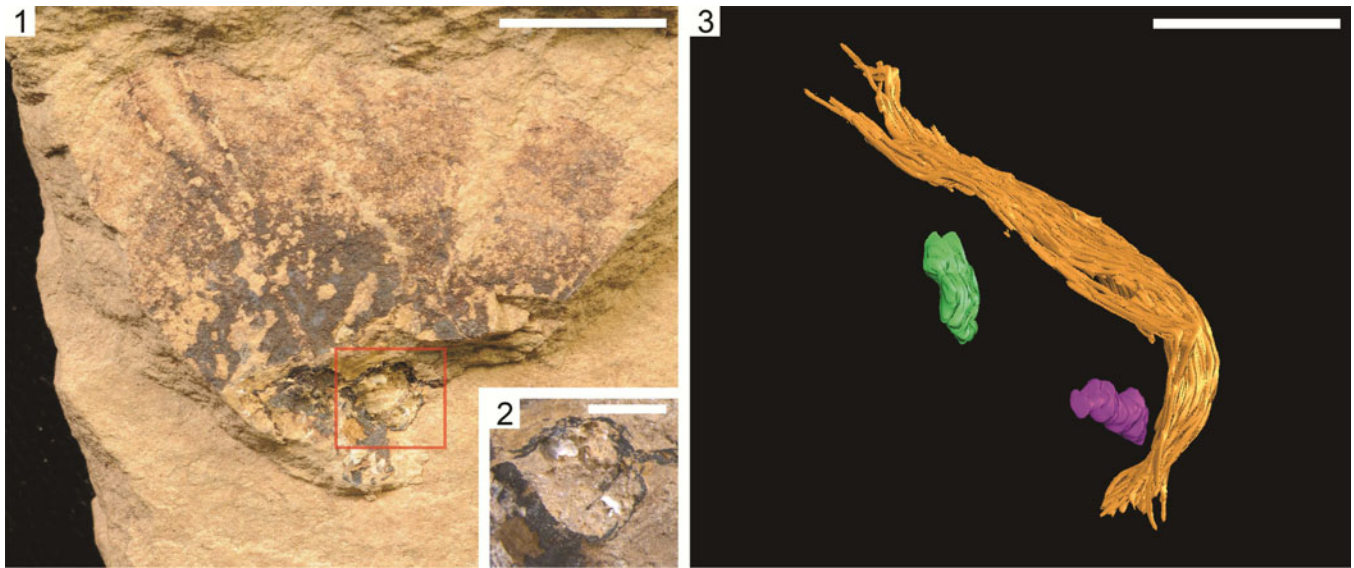


Figure 1. UWGM 6835, *Metaconularia manni* (Roy, 1935) from the Welton Member of the Scotch Grove Formation (lower Middle Silurian, Sheinwoodian) from Shaffton Quarry, Clinton County, east-central Iowa: (1, 2) light photographs: (1) view of the entire specimen, which consists of the flattened (on a bedding plane) apertural region with two exposed faces and the splayed corner between them, and the undistorted apical region (red box, see 2), which protrudes down into the layers of dolomitic siltstone beneath and is oriented perpendicular to bedding; (2) detail of the apical region (box in 1), highlighting the two small but clearly discernible, white silicic bodies in the peridermal cavity next to a pair of opposing facial midlines; (3) rendered 3-D model of a portion of the apical periderm (orange) and the oval silicic bodies (green and purple), with that in green being the one shown in the upper position in (1) and (2). Scale bars = 10 mm (1), 3 mm (2), ~2 mm (3).

the faces away from the paired midline carinae (John et al., 2010, figs. 24.1, 25.1, 25.3, 26.2). In these areas, peridermal material can be entirely absent or represented only by black carbonaceous matter presumably belonging to the organic microlamellae. Indeed, syngenetic remobilization of the phosphatic component of the periderm of *M. manni* could have triggered the phosphatization of the soft tissues of arthropods in the same beds (Moore et al., 2011); such soft tissues are preserved in combined phosphatic, organic, and aluminosilicate phases (Moore et al., 2011, fig. 1).

UWGM 6835.—Remnants of the very thin, dark brown to black, mostly flattened periderm of this specimen preserve anatomical features, including fine, regularly arrayed nodes and portions of the paired midline carinae (Fig. 1.1), which firmly establish it as *Metaconularia manni*. The minimum original length of the periderm was ~25 mm. Results of elemental analysis confirmed that the brown portions of the periderm contain abundant calcium phosphate, likely fluorapatite (John et al., 2010), although they can also contain some remnant of the organic carbon content of the periderm. The black areas lack phosphorous, suggesting that they are organic. Above the apical region, the faces are splayed outward on a single bedding plane, having separated from each other along the corners. The original specimen would have had four faces, midlines, and corners, but only two faces are preserved within the roughly 90° of periderm-covered arc occupying the bedding plane; nevertheless, one of the faces clearly displays the paired internal carinae flanking the midline. By contrast, the steeply pyramidal apical region, which measures ~5 mm long, is essentially undistorted, being oriented with its long axis perpendicular to bedding; thus, this part of the specimen penetrates the finely laminated host rock (Fig. 1.1, 1.2). Although the outwardly splayed portion of the specimen is incomplete (owing, in part at least, to splitting of

the laminated host slab along a different level), it was originally part of an individual preserved in the ‘Maltese-cross’ configuration, as is common among *M. manni* from Shaffton Quarry (John et al., 2010, figs. 5, 6.1, 6.5). Such splaying is characteristic of Maltese-cross preservation and represents ripping of the adoral periderm along the corners. This presumably happened when the in-situ specimen was buried by sediment falling from above and then compressed; it would not be expected in a specimen in which opposite sides of the periderm had collapsed on top of each other, such as might have happened if buried by a bottom-flowing current exerting shear stress.

UWGM 6834.—This specimen (Figs. 2–5) represents the extreme case in which original, organophosphatic peridermal material is almost completely absent (as indicated both by visual inspection and by results of X-ray elemental mapping, which yielded no peaks for phosphorous) and is now represented by an external mold. Identification of this fossil as *Metaconularia manni* was established in part by its similarity in overall geometry to relatively well-preserved specimens displaying a Maltese-cross configuration, in which, again, the adoral portions of the faces are splayed outward and lie parallel to bedding, whereas the undeformed apical region is oriented with its long axis perpendicular to bedding. In UWGM 6834, the adoral portion of the faces is represented on the probable upper surface of the slab by a roughly circular area of relatively smooth shale that parallels bedding and extends at least 30 mm beyond the central region. Additionally, this part of the specimen is crossed by two paired furrows that project radially from the center of the specimen and are separated from each other by an angular distance of ~150°. These furrows, the longest of which extends at least 28 mm from the central point, are similar in geometry and spatial disposition to the paired linear furrows associated with or corresponding to the internal midline carinae of specimens of

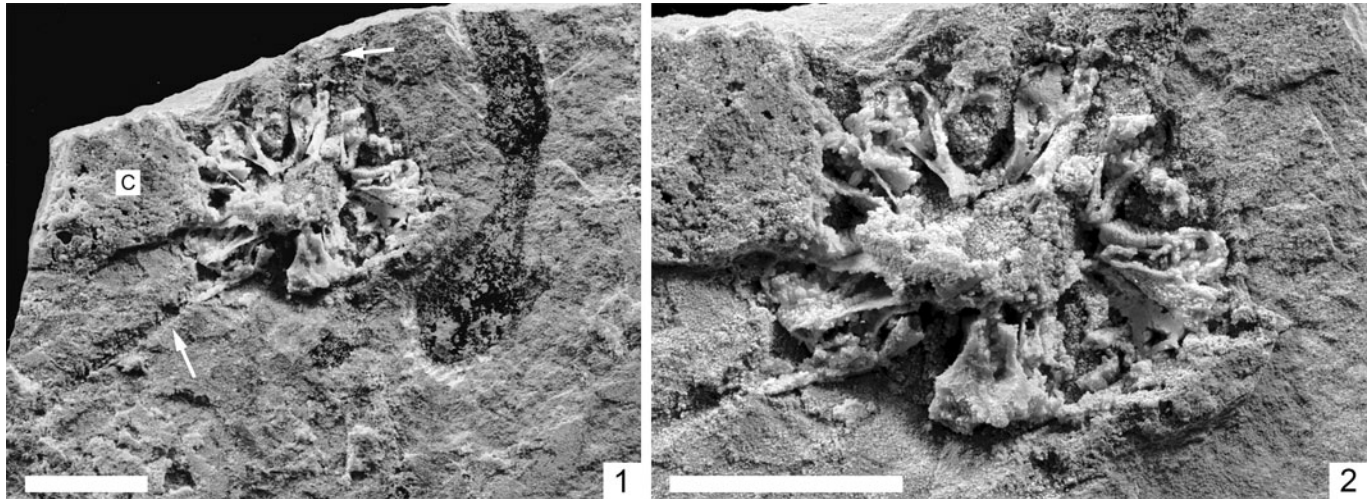


Figure 2. UWGM 6834, light photographs, *Metaconularia manni* (Roy, 1935) from the same locality and bed as UWGM 6835: (1) contextual view of the silicified rosette structure, which consists of five paired pouches and associated tubular structures arranged around a central point, from which two facial midlines (white arrows) extend across the bedding plane (C = position of moldic crinoidal material; see also Fig. 3); (2) detail of the rosette structure. Scale bars = 10 mm.

M. manni preserving portions of the periderm (John et al., 2010, fig. 26.1). Near the center of UWGM 6834, the mold curves smoothly and continuously downward into the narrow, 3-D apical region, the sides of which are steeply inclined to bedding (Fig. 4) and thus similar in geometry and orientation to the erect apical region of UWGM 6835 and other specimens preserving peridermal material. Owing to the absence of clearly defined corner grooves, it is difficult to establish the number of faces (four or otherwise) present in the apical region. Nevertheless, small, thin, isolated patches of black carbonaceous matter, possibly remnants of the organic part of the periderm, are present both in the splayed portion and in the erect apical region (Fig. 2.1).

Even though original peridermal material is almost entirely absent in UWGM 6834, we infer that the mutually confluent, bedding-parallel and steeply inclined surfaces described above correspond to the (now) missing periderm of *Metaconularia manni*, based on the observation that these features conform closely in their geometry to that of well-preserved specimens

of *M. manni* displaying a Maltese-cross configuration and present in the same deposit. Furthermore, this similarity in overall geometry enables us to establish that the surface over which the adoral portion of the conulariid has been splayed is the upper surface of the host rock slab. CT-scan images (e.g., Fig. 4) show the fine lamellae in the host rock adjacent to the apical region deflected downward beneath its axial/central portion, with corresponding upward deflection of the same lamellae along the sides of the region.

Our interpretation of UWGM 6834 as *Metaconularia manni* implies that the original, organophosphatic periderm has been lost, possibly during early diagenesis. This conclusion is further suggested by the selective thinning of the periderm observed in other specimens of this conulariid from Shaffton Quarry. Additional consideration of this problem in the preservation of *M. manni* is presented below.

Structures composed of silica within the conulariids.—UWGM 6835.—The apex and up to ~30% of the axial length of this specimen was apparently infilled by carbonate sediment prior to final burial, thus preserving its original 3-D shape and life orientation (Fig. 1.1). Present in the sediment infilling are two small, whitish, elongate masses located opposite the midlines of two opposing faces (Fig. 1.2, 1.3). The larger of the two

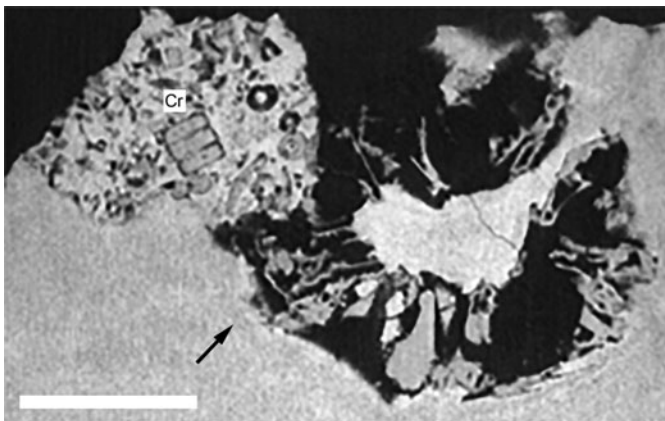


Figure 3. UWGM 6834, X-ray tomograph showing one horizontal (parallel to bedding) 'slice' section through the rosette and central pillar (arrow), as well as a patch of moldic crinoidal skeletal debris including articulated columnals (Cr). Scale bar = 5 mm.

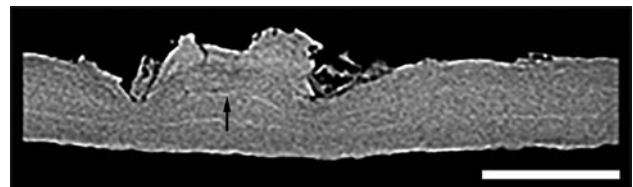


Figure 4. UWGM 6834, X-ray tomograph showing a vertical (orthogonal to bedding) 'slice' through soft-part structures replicated in silica and the deflection of sedimentary laminae beneath the impacted soft parts (assuming that the specimen is correctly oriented with the soft parts located on the upper surface). Note how the laminae deflect upward in the central pillar (arrow), suggesting that material has been forced upward into the central cavity. No skeletal material or echinoderm ossicles are evident within the matrix. Scale bar = 5 mm.

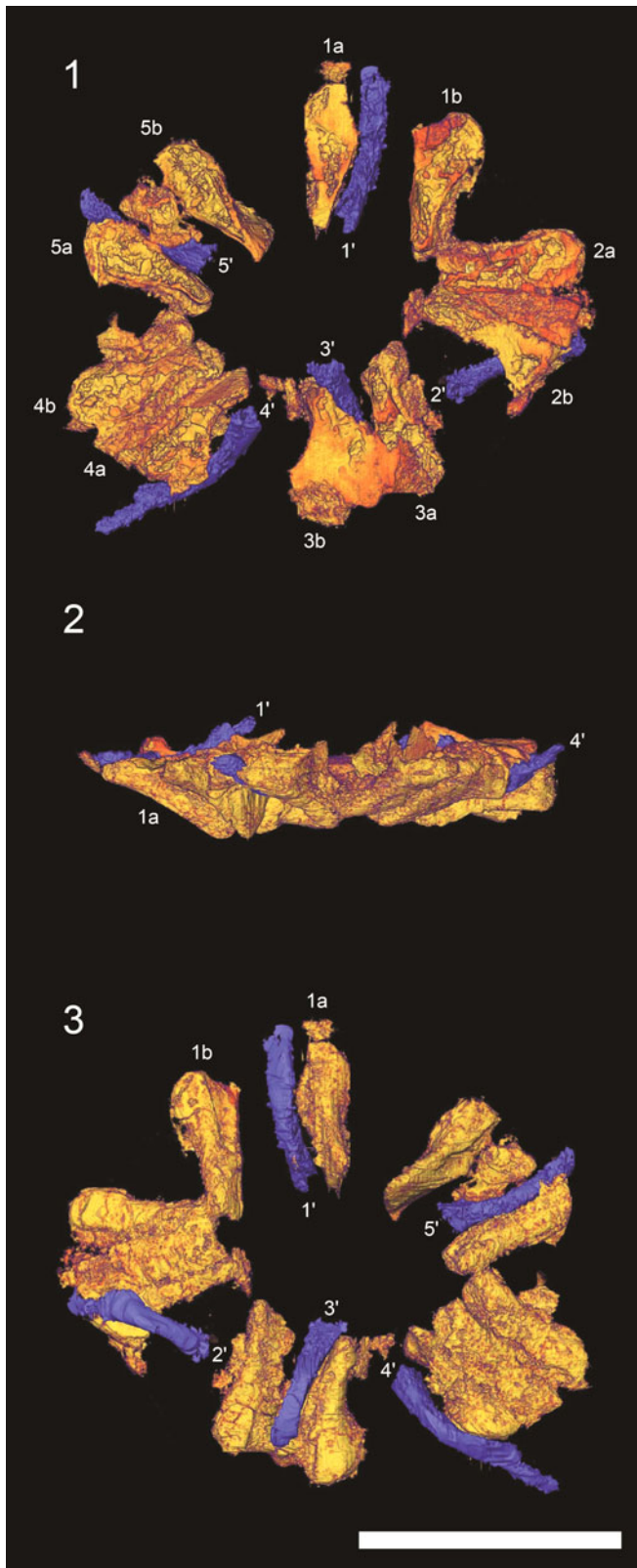


Figure 5. UWGM 6834, apical and lateral views of an X-ray tomographic model in which the silicic material, some of it replacing original soft tissues, has been isolated: (1) apical view of the presumed original upper surface of the rosette; (2) lateral view of the rosette, showing the strongly keeled structure of the pouches; (3) apical view of the presumed lower surface of the rosette. Pouches (e.g., 1a, 1b) and associated tubes (e.g., 1') are numbered 1–5. Blue = tubes; orange = pouches. Scale bar = 10 mm.

masses measures ~ 1.0 mm long and 0.5 mm wide (as viewed from above) and extends ~ 0.5 mm along a direction parallel to the long axis of the periderm. The smaller mass, similar in shape to its companion, measures ~ 0.8 mm long and 0.5 mm wide, extending ~ 0.5 mm in the vertical dimension. Results of EDAX analysis show that both masses are composed of SiO_2 . The CT scan of the apical part of the specimen (Fig. 1.3) was used to examine the form of the masses and to determine if additional structures composed of silica remained unexposed beneath. Results confirm that the two visible masses are the only such structures present, and that they do not extend significantly downward toward the apex of the conulariid.

UWGM 6834.—The single most conspicuous feature of this specimen, in which the periderm has been almost entirely lost, is a slightly oblong set of five pairs of whitish, hollow, keeled pouch-like structures (hereafter pouches) arranged in a pattern displaying pentaradial symmetry and situated within the specimen's upright, 3-D apical region (Figs. 2–5; see also 3-D rotating model in Supplementary File). Henceforth, we refer to the five pairs of radially arrayed pouches and associated features as the rosette. The rosette measures ~ 21 mm across its major axis and 15 mm across its minor axis. The pouches differ in shape from the two smaller bodies in UWGM 6835, in which the features are also situated closer to the apex. For the sake of convenience in describing the pouches in UWGM 6834, the five pairs are numbered from 1a-b to 5a-b (Fig. 5), with pair 1a-b being situated next to the short (~ 3 mm long) paired furrows interpreted above as partial molds of a pair of internal midline carinae (upper arrow in Fig. 2.1). Situated immediately adjacent to pouches 5a and 5b on a low mesa-like elevation is a cluster of well-defined molds of pelmatozoan echinoderm ossicles (Fig. 3). Present between pouches 2a and 2b is a shallow, narrowly triangular (transv.) void that is partially filled by small, euhedral crystals of silica and that tapers toward the center of the specimen. Similar crystals are present in a narrow, less clearly delineated void between pouches 4a and 4b. When viewed from above (Fig. 5), the pouches are mutually similar in shape and size, measuring ~ 4 –6 mm long, with a maximum width at the abaxial end of 1–2 mm and extending vertically (perpendicular to the bedding) from ~ 1.5 –2 mm. The thin solid walls of the pouches measure ~ 0.2 mm thick. The pouches exhibit an approximately tear-shaped transverse profile, with each pouch tapering toward the center of the specimen. X-ray tomographic imaging (Fig. 5) revealed that the overall 3-D shape of the pouches resembles that of the hull of a schooner, with a keeled bottom that expands and deepens from the narrow ('bow') end, located near the center of the rosette, to the wide ('stern') end near the faces of the former periderm. Especially in the case of pair 1a-b, the pouches appear to have undergone minor lateral displacement relative to each other. The rake of the pouches is not as steep as the sides of the specimen, and thus the rosette does not extend to the apex. Because the angle of adoral expansion of the periderm of *Metaconularia manni* ranges from 35 – 40° (John et al., 2010), the base of the rosette was likely originally situated at least 30 mm above the apex. Finally, the space within each pouch is partially filled by prismatic and/or botryoidal crystals that are similar in color to the walls of the pouches.

All five pairs of pouches are associated with a single, hollow, gently curved or broadly U-shaped, whitish tube that is subtriangular in transverse cross section, with the apex of the triangle pointing upward (Fig. 5.1). The two apparently broken ends of the tube also open upward, away from the apex. The tubes range from ~5–8 mm in length, with a constant outside diameter of ~1 mm and an inside diameter of ~0.9 mm. Two of the tubes (Fig. 5.1, 5.3, 1' and 3') are situated between two pouches. In pair 4 (Fig. 5.1, 5.3), the tube is located on the outer side of one of the pouches. The remaining two tubes (Fig. 5.3, 2' and 5') underlie one (pair 5) or both (pair 2) of the pouches. Finally, the basal side of one of the tubes (Fig. 5.3, 1') exhibits a narrow, shallow furrow running along the midline of the side.

Elemental analysis of UWGM 6834 showed that the whitish material composing the tubes and pouches, as well as space-filling crystals within the pouches, is silica. Results of EDAX analysis of the surrounding matrix were consistent with a dolomitic composition along with minor amounts of aluminosilicates, outside of the dumbbell-shaped dark area shown in Fig. 2.1, which is rich in carbon. This patch of carbonaceous matter could represent an isolated remnant of demineralized periderm. No concentrations of phosphorous were detected in the replaced soft tissues or in the area surrounding the soft tissues using either EDAX or synchrotron X-ray fluorescence. This includes the area with the radial structures that we infer to be facial midlines.

The pouches and tubes forming the rosette were evidently sufficiently robust to cause soft-sediment deformation beneath them (Fig. 4) during compaction, although deformation diminishes progressively farther away from the structures. The form of this deformation was downward warping of laminae below the pouches, matched by upward warping of laminae beneath the central axial region adaxially of the pouches. We hypothesize further that the curvature of the narrow tubes resulted from upward flexure in their central portion. If so, the tubes were evidently flexible at the time of deformation. This differential pattern could reflect differences in rigidity prior to silicification. Alternatively, the rosette might have been completely silicified at the time of compaction; if so, the curvature of the narrow tubes is more likely original. If the latter, then the presence of the central tube portion at the top of the central mound coincided exactly with the original axial height of the tube, which appears to us to be an unlikely coincidence.

Interpretations of the silicified structures

The unique assemblage of discrete, hollow, radially arrayed, geometrically regular bodies forming the rosette structure described above cannot plausibly be interpreted as inorganic in origin, nor is it similar to any known trace or skeletal body fossils. Therefore, the most probable interpretation of this assemblage is that it consists of biological soft parts replicated in silica. The smaller, much simpler but compositionally identical masses in UWGM 6835 could also be silicified soft parts. The silicified features described here are interpreted as soft parts of *Metaconularia manni*. In the fossil record, replication of nonmineralized, metazoan soft tissues in silica has been documented in fossil specimens as old as Ediacaran in age (Clites et al., 2012; Ren et al., 2018). Replication in silica of vertebrate soft tissues ranging in size from single cells to

entire organs has also been achieved under controlled laboratory conditions and involves precipitation of microcrystalline silica on organic templates (cell walls) from silicic acid solutions of very low pH (Townson et al., 2014; Ren et al., 2018). In the Scotch Grove Formation at Shaffton Quarry, possible silicification of a bacterial glycocalyx has been reported and documented by Moore et al. (2011, p. 87, fig. 1.7). The same authors also reported (and documented) replacement of synxiphosurine cuticle and muscle tissue by apatite (Moore et al., 2011, fig. 3.1–3.3). The preservation of *M. manni*, some specimens of which have lost much or all their original apatite, suggests that the source of at least some of the secondary apatite in the arthropod specimens might have been conulariids. Indeed, conulariids from the Lower Silurian (Telychian) Waukesha Lagerstätte (southeastern Wisconsin), including *M. manni*, have undergone partial to complete demineralization (Miller et al., 2022). Because apatite is most soluble in acidic waters (Guidry and MacKenzie, 2003), one possible scenario for the observed preservational characteristics of conulariids and associated arthropods at Shaffton Quarry is that silicification and dissolution of apatite occurred simultaneously, with reprecipitation of apatite occurring under different conditions of pH (and possibly other physical parameters) at some later time.

The additional fact that the silicified features described above occur within the apical region of two conulariids suggests that they must have originally belonged to these animals, especially because their position relative to specific peridermal features appears to be regular, with the paired structures straddling facial midlines. We are thus faced with an extraordinary opportunity, because if these structures are indeed relic conulariid soft parts, then (1) they have the potential to confirm or refute the hypothesis of a medusozoan affinity for these organisms decisively; and (2) they could be useful in testing alternative hypotheses of the phylogenetic position of conulariids within Medusozoa, namely whether they are the sister group of staurozoans (Marques and Collins, 2004) or the sister group of coronate scyphozoans (Van Iten et al., 2006, 2014, 2016a). Therefore, the relic soft parts in the two Shaffton Quarry conulariid specimens must be compared with soft parts of septate medusozoans and with soft parts of other plausible candidates. In our opinion, the only viable alternative hypothesis, developed below, is homology with certain soft parts of echinoderms.

Echinoderms.—The apparent five-fold radial symmetry of the siliceous rosette structure in UWGM 6834 invites comparisons with pentaradially symmetrical echinoderms, including stelleroids, ophiuroids, and echinoids. However, more detailed comparisons of the rosette structure with these and other echinoderms seem problematic. As noted above, well-defined molds of cylindrical pelmatozoan ossicles, which probably did not belong to the rosette-bearing organism itself, occur on a mesa-like mound immediately adjacent to the rosette (Figs. 2.1, 3). Yet no features interpretable as echinoderm ossicles occur within the depression housing the rosette structure (either in the sloping walls of the depression or in the central elevation) or within or near the two paired furrows extending radially away from the rosette structure, parallel to bedding. Given the presence of undeformed pelmatozoan ossicle molds right next to the rosette structure, it seems highly unlikely that if the host organism were an echinoderm, ossicles originally present

within its body would not be preserved (at least as molds; e.g., Hughes et al., 2014, fig. 6b). We think that this inference holds both for echinoderms containing numerous robust ossicles (e.g., the arms of ophiuroids) or enclosed within a rigid skeleton composed of close-fitting plates (e.g., echinoids), and for bodies containing isolated ossicles separated from each other by soft tissue (as in holothurians, the skeleton of which consists of isolated, microscopic, spicule-like ossicles and a circumpharyngeal ring of ~10 macroscopic plates; Brusca and Brusca, 2003).

Another problem with the echinoderm model involves the topography of the steep-walled depression containing the rosette structure and that of the bedding-parallel surface adjacent to the depression. Together, the depression and surrounding bedding plane with paired furrows extending radially from the depression show poor correspondence to the external surface topography of any echinoderm (e.g., the more or less flat or weakly convex underside of an echinoid or stelleroid). Rather, the topography of the fossil surfaces is most like that of (originally) associated *Metaconularia manni* preserving an undistorted, erect (long axis perpendicular to bedding) apical region passing adapertureward into flattened (i.e., aligned parallel to bedding), outwardly splayed faces, the midlines of which are marked (in some cases) by a ridge, furrow, or paired ridges and/or furrows (Fig. 2). Additional comparisons with particular groups of echinoderms are presented below.

Echinoids.—The rosette structure could perhaps be compared to Aristotle's lantern, the centrally located, calcified feeding structure of echinoids. However, there is strong disagreement in number, orientation, and shape/symmetry between the five, tooth-like biting/piercing plates in Aristotle's lantern and the pouches in the rosette structure, which are twice as numerous as echinoid teeth and are oriented with their long axis parallel to a radius of the rosette rather than perpendicular to it. Moreover, the frame-like part of Aristotle's lantern bears little resemblance to the rosette's five tube-like features. Similar problems arise when we make comparisons with echinoid soft parts. For example, unlike the paired pouches, the bursae and gonads of echinoids are unpaired. The ampullae are paired, but unlike the pouches, they do not extend deep into the body cavity. The tube-like features could perhaps be compared with echinoid radial and hemal canals, located next to the skeleton, but in view of the difficulties noted above, this comparison by itself does not make a strong case for homology.

Stelleroids and ophiuroids.—Unlike echinoids and other echinoderms, these two groups are characterized by elongate arms, normally five in number, which are connected to a disc-like central portion of the body. The paired furrows extending away from the rosette structure might be compared with parts of starfish or brittlestar arms. However, when fossilized, these structures tend to be sinuous rather than linear, and moreover they are associated with series of ossicles or their outlines (e.g., Hughes et al., 2014, fig. 6b). Stelleroid gonads, although paired, extend through the arms and thus are much longer in this direction (parallel to the substratum) than the paired pouches of the rosette structure. Finally, the rosette structure's tube-like features might be compared with the radial water canal or radial nerve of a stelleroid arm, but again this comparison by itself is hardly compelling.

Other groups.—Among the remaining groups of echinoderms, both extant (e.g., crinoids) and extinct (e.g., blastoids), the only one that exhibits any kind of soft-part structure comparable in number and arrangement to the five paired pouches of UWGM 6834 is the class Concentrocycloidea (concentrocycloids or sea daisies), members of which have five pairs of brood pouches (gonads) arranged in a pentaradial pattern (Pearse et al., 1987). However, these thin, discoidal animals compare poorly in overall shape with UWGM 6834, and they possess numerous calcareous plates and ossicles that ought to have left impressions of themselves if the fossil specimen were in fact a concentrocyloid.

Conulariids/medusozoans.—As noted above, conulariids are now generally classified as an extinct clade of medusozoan cnidarians. Normally, medusozoan polyps and medusae exhibit four-fold radial or biradial symmetry. However, in both conulariids and other medusozoans, instances of three-, six-, or five-fold symmetry have been documented; for example, some medusae bear five gonads and septa instead of four (Dong et al., 2013), and some conulariids have three, five, or six faces (e.g., Babcock et al., 1987; Leme et al., 2004). In particular, Leme et al. (2004, fig. 4.10) documented a single specimen of *Conularia quichua* Ulrich in Steinmann and Doderlein, 1890 having five fully-developed faces and corners. By itself, then, the apparent five-fold radial symmetry of the rosette structure here described is not phylogenetically informative. Among extant medusozoans, conulariids have been allied either with stauromedusans (class Staurozoa; e.g., Jerre, 1994; Marques and Collins, 2004) or with scyphozoans of the order Coronata (e.g., Werner, 1966, 1967; Van Iten et al., 2006, 2014). The latter hypothesis is based mainly on comparisons of conulariid hard parts with the chitinous coronate periderm (e.g., Van Iten et al., 1996, text-fig. 4), whereas the former hypothesis is based in large part on similarities between structures of the conulariid periderm and stauromedusan soft parts (e.g., Jerre, 1994, fig. 3).

Coronate scyphozoans.—Components of the rosette structure can be compared with soft-part structures of coronate polyps, which share certain basic similarities in their soft-part anatomy with other scyphozoans and also with cubozoans and stauromedusans (Hyman, 1940; Brusca and Brusca, 2003). These include possession of four (normally) interradial gastric septa, each housing a single longitudinal retractor muscle of ectodermal origin. Most coronate polyps are asexual and produce multiple, sexual medusae through serial transverse fission (polydisc strobilation) of the soft body. Normally during this process, the four gastric septa and associated longitudinal muscles are absorbed, being regenerated after the medusae have been released into the water column. In *Stephanoscyphus eumedusoides* Werner, 1974, however, the incipient medusae (ephyrae) remain connected to each other within the periderm of the strobilating polyp (strobila), and the four retractor muscles are not absorbed but remain intact, extending the full length of the periderm (Werner, 1974, figs. 9, 10; 1983a, fig. 1a, b). Each of the multiple ephyrae produces four subspherical gonads, and these are arranged in series along the retractor muscles. Following release of the planulae larvae, the septae are regenerated and the animal again assumes the anatomy of the asexual polyp. In

the strobila of another species, *S. racemosus* Komai, 1935, the longitudinal retractor muscles and seriated gonads are present while the developing ephyrae are still connected to each other within the periderm, with the strobila of the male polyp shedding sperm before the ephyrae detach from the strobilation chain (Werner, 1973a, figs. 3, 4).

The five tube-like features of the rosette structure, which in at least two cases line up with paired shallow furrows similar to a poorly preserved *Metaconularia manni* midline (interradius), are similar in position, arrangement, and diameter to the coronate retractor muscle. In coronates and all other scyphozoans (and stauromedusans), each of the (normally) four retractor muscles extends through the body of a gastric septum, from the apex of the polyp to a level close to or above its mouth. As argued above, the upward curvature of some of the tube-like features in the Shaffton Quarry specimen might have resulted from a combination of compaction and upward (i.e., abapical) injection/pushing of sediment through the apical region of a *M. manni* periderm. It is at least conceivable that such action displaced the muscles from their original course parallel to the peridermal faces and flattened the periderm above the apical region, thus truncating and perhaps squashing the muscles (and other soft tissues) above this portion of the periderm.

The pouches and the more-triangular feature present between some of them are more difficult to interpret under a coronate model, but one possibility is that some or all the pouches represent the apicalmost members of originally longitudinally seriated, paired gonads. Although, as discussed above, the gonads of strobilating coronate polyps are indeed seriated, they tend to be single (e.g., Werner, 1974, fig. 10).

Stauromedusans.—Members of this group, originally classified as scyphozoans but now thought to be an independent medusozoan clade closely related to them (e.g., Marques and Collins, 2004), are interpreted as sessile medusae oriented with their subumbrella and tentacles facing away from the attachment substratum. In addition to possessing the longitudinal retractor muscle present in the septa of scyphozoan polyps, the septa of stauromedusans are penetrated at their oral end by an elongate, ectoderm-lined invagination, called the peristomial/interradial pit or funnel, and during reproduction they also exhibit a pair of elongate gonads, one on either side of the septum (e.g., Hyman, 1940, fig. 165). The gonads, which in most species produce only eggs or only sperm, can be elongate with smooth sides or they can be looped and folded.

Retaining possible homology between the tube-like features in the rosette structure and the medusozoan retractor muscles, one can now also compare the paired pouches in the Shaffton Quarry fossil with the apical ends of the paired stauromedusan gonads. Additionally, the triangular to irregular body located between pouches 2a-b and 4a-b can be compared with the apical end of the stauromedusan interradian pit, which is located between the two elongate gonads. Under this model, though, the paired pouches, rather than corresponding to a single ‘whorl’ of gonads originally arranged in series along the longitudinal axis of the body, represent instead the adorally truncated, apical portions of originally elongate gonads that were not seriated. The agreement in shape, size (relative to the entire body), and arrangement/alignment between the paired pouches and the paired gonads of stauromedusans such as *Halicyclustus* James-Clark, 1863 and

Lucernaria Müller, 1776 is strong. Again, paired pouches 1a-b and 4a-b are in more or less close alignment with the two paired furrows, which probably correspond to the conulariid’s midlines, and these in turn are homologous to the interradii of extant scyphozoans and stauromedusans.

Cubozoans.—The only relevant point of comparison here is that like stauromedusans, the medusae of cubozoans exhibit paired gonads (two per septum; e.g., Werner, 1973b, 1983b).

Summary.—Whereas comparisons between Shaffton Quarry specimen UWGM 6834 and echinoderms are quite weak, there appear to be relatively strong grounds for hypotheses of homology between components of the rosette and specific soft-part structures of the gastric septa of coronate scyphozoans and stauromedusans. Hypotheses of homology between the rosette and soft parts of stauromedusans, namely the paired elongate (nonseriated) gonads and interradian pit, appear in turn to be stronger than those between the rosette and soft parts of coronate scyphozoans, in which the gonads of sexual polyps are not paired and an interradian pit or similar structure is absent. However, and as noted above, paired gonads also are present in the medusa of cubozoans. The apparent absence of four-fold radial symmetry is not a serious problem for these interpretations, because some conulariids and extant medusozoans show departures from normal tetradial symmetry.

Conclusions

The major results and interpretations of this study are: (1) the set of discrete bodies collectively referred to here as the rosette consists of animal soft parts replicated in silica; (2) the rosette occurs within the upright, 3-D apical region of a *Metaconularia manni*, the periderm of which has been demineralized and almost entirely lost; (3) the apparent pentaradial symmetry of the rosette invites comparisons with various echinoderms, however, the strongest hypotheses of homology are those between the rosette structure and the gonads and longitudinal retractor muscles of medusozoan cnidarians; (4) owing in part to incomplete preservation (probable loss of soft-part structures above the apical region), we are unable to address the problem of which group of septate medusozoans (cubozoans, scyphozoans, or staurozoans) was most closely related to conulariids; and (5) nevertheless, our interpretations suggest that in at least one species of conulariid, a free-living, sexual medusoid life phase could have been absent (i.e., production of eggs and sperm might have taken place within the body of the sessile polyp).

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Declaration of competing interests

The authors of this article declare none.

Data availability statement

A rotating tomographic 3-D model of the rosette is available on Zenodo at: <https://doi.org/10.5281/zenodo.7558933>

References

- Babcock, L.E., 2011, Exceptionally preserved *Conchopeltis* (Cnidaria) from the Ordovician of New York, USA: Taphonomic inferences: *Memoirs of the Association of the Australasian Palaeontologists*, v. 42, p. 9–14.
- Babcock, L.E., and Feldmann, R.M., 1986a, Devonian and Mississippian conulariids of North America, Part A: General description and *Conularia*: *Annals of Carnegie Museum*, v. 55, p. 349–410.
- Babcock, L.E., and Feldmann, R.M., 1986b, Devonian and Mississippian conulariids of North America, Part B: *Paraconularia*, *Reticulaconularia*, new genus, and organisms rejected from Conulariida: *Annals of Carnegie Museum*, v. 55, p. 411–479.
- Babcock, L.E., Feldmann, R.M., and Wilson, M.T., 1987, Teratology and pathology of some Paleozoic conulariids: *Lethaia*, v. 20, p. 93–105.
- Barrande, J., 1867, *Système Silurien du centre de la Bohême, Ière Partie, Recherches Paléontologiques*, Tome 3, Classe des Mollusques, Ordre des Pétropodes: Prague, Charles Bellmann, xv + 179 p.
- Brusca, R.C., and Brusca, G.J., 2003, *Invertebrate Zoology* (second edition): Sunderland, Massachusetts, Sinauer Associates, 936 p.
- Clites, E., Droser, M.L., and Gehling, J.G., 2012, The advent of hard-part structural support among the Ediacaran biota: Ediacaran harbinger of a Cambrian mode of body construction: *Geology*, v. 40, p. 307–310, <https://doi.org/10.1130/G32828.1>.
- Dong, X.-P., Cunningham, J.A., Bengtson, S., Thomas, C.-W., Liu, J., Stamparoni, M., and Donoghue, P.C.J., 2013, Embryos, polyps and medusae of the early Cambrian scyphozoan *Olivoides*: *Proceedings of the Royal Society B, Biological Sciences*, v. 280, p. 1–8, <https://doi.org/10.1098/rspb.2013.0071>.
- Ford, R.C., Van Iten, H., and Clarke, G.R. II, 2016, Microstructure and composition of the periderm of conulariids: *Journal of Paleontology*, v. 90, p. 389–399, <https://doi.org/10.1017/jpa.2016.63>.
- Guidry, M.W., and MacKenzie, F.T., 2003, Experimental study of igneous and sedimentary apatite dissolution: Control of pH, distance from equilibrium, and temperature on dissolution rates: *Geochimica et Cosmochimica Acta*, v. 67, p. 2949–2963, [https://doi.org/10.1016/S0016-7037\(03\)00265-5](https://doi.org/10.1016/S0016-7037(03)00265-5).
- Hall, J., 1858, Descriptions of new fossil species from the Carboniferous limestones of Indiana and Illinois: *Transactions of the Albany Institute*, v. 4, p. 1–36.
- Hughes, N.C., Gunderson, G.O., and Weedon, M.J., 2000, Late Cambrian conulariids from Wisconsin and Minnesota: *Journal of Paleontology*, v. 74, p. 828–838, [https://doi.org/10.1666/0022-3360\(2000\)074<0828:LCCFWA>2.0.CO;2](https://doi.org/10.1666/0022-3360(2000)074<0828:LCCFWA>2.0.CO;2).
- Hughes, N.C., Kříž, J., MacQuaker, J.H.S., and Huff, W.D., 2014, The depositional environment and taphonomy of the Homerician 'Aulacopleura shales' fossil assemblage near Loděnice, Czech Republic (Prague Basin, Perunican microcontinent): *Bulletin of Geosciences*, v. 82, p. 219–238, <https://doi.org/10.3140/bull.geosci.1414>.
- Hyman, L., 1940, *The Invertebrates: Protozoa through Ctenophora*, Volume 1: New York, McGraw Hill, 478 p.
- James-Clark, H., 1863, Prodrum of the history, structure, and physiology of the order Lucernariae: *Journal of the Boston Society of Natural History*, v. 7, p. 531–567.
- Jerre, F., 1994, Anatomy and phylogenetic significance of *Eoconularia loculata* (Wiman), a Silurian conulariid from Gotland: *Lethaia*, v. 2, p. 97–109.
- John, D.L., Hughes, N.C., Galaviz, M.I., Gunderson, G.O., and Meyer, R., 2010, Unusually preserved *Metaconularia manni* (Roy, 1935) from the Silurian of Iowa, and the systematics of the genus: *Journal of Paleontology*, v. 84, p. 1–31, <https://doi.org/10.1666/09-025.1>.
- Ketcham, R.A., and Carlson, W.D., 2001, Acquisition, optimization and interpretation of X-ray computed tomographic imagery: Applications to the geosciences: *Computers & Geosciences*, v. 27, p. 381–400, [https://doi.org/10.1016/S0098-3004\(00\)00116-3](https://doi.org/10.1016/S0098-3004(00)00116-3).
- Kiderlen, H., 1937, Die Conularien: Über Bau und Leben der ersten Scyphozoa: *Neues Jahrbuch für Geologie*, suppl., v. 77, p. 113–169.
- Komai, G., 1935, On *Stephanoscyphus* and *Nautilothoe*: *Memoirs of the College of Science of Kyoto University*, ser. B, v. 10, p. 289–317.
- Leme, J.M., Rodrigues, S.C., Simões, M.G., and Van Iten, H., 2004, Sistemática dos conulários (Cnidaria) da Formação Ponta Grossa (Devoniano), Estado do Paraná, Bacia do Paraná, Brasil: *Revista Brasileira de Paleontologia*, v. 7, p. 213–222, <https://doi.org/10.4072/rbp.2004.2.14>.
- Leme, J.M., Van Iten, H., and Simões, M.G., 2022, A new conulariid (Cnidaria, Scyphozoa) from the terminal Ediacaran of Brazil: *Frontiers in Earth Science*, v. 10, art. 777746, <https://doi.org/10.3389/feart.2022.777746>.
- Lucas, S.G., 2012, The extinction of the conulariids: *Geosciences*, v. 2, p. 1–10, <https://doi.org/10.3390/geosciences2010001>.
- Marques, A.C., and Collins, A., 2004, Cladistic analysis of Medusozoa and cnidarian evolution: *Invertebrate Biology*, v. 123, p. 23–42, <https://doi.org/10.1111/j.1744-7410.2004.tb00139.x>.
- Mergl, M., Frýda, J., and Ferrová, L., 2016, Armoured test of Early Devonian *Mesoconularia* (Conulariida) from the Prague Basin: Probable adaptation to increased predation pressure: *Bulletin of Geoscience*, v. 91, p. 561–581, <https://doi.org/10.3140/bull.geosci.1601>.
- Mikulic, D.G., Briggs, D.E.G., and Kluessendorf, J., 1985, A Silurian soft-bodied biota: *Science*, v. 228, p. 715–717.
- Miller, A.A., Jacquet, S.M., Anderson, E.P., and Schifffbauer, J.D., 2022, Conulariids from the Silurian (late Telychian) Waukesha Lagerstätte, Wisconsin: *Historical Biology*, v. 34, no. 12, p. 2374–2394, <https://doi.org/10.1080/08912963.2021.2017917>.
- Moore, R.A., Briggs, D.E.G., Braddy, S.J., and Schultz, J.W., 2011, Synziphosurines (Xiphosura: Chelicerata) from the Silurian of Iowa: *Journal of Paleontology*, v. 85, p. 83–91, <https://doi.org/10.1666/10-057.1>.
- Müller, O.F., 1776, *Zoologiae Daniae Prodrum, seu Animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium*: Copenhagen, Hallgeri, xxxii + 274 p.
- Oliver, W.A., Jr., 1984, *Conchopeltis*: Its affinities and significance: *Palaeontographica Americana*, no. 54, p. 141–147.
- Pearse, V., Pearse, J., Buchsbaum, M., and Buchsbaum, R., 1987, *Living Invertebrates*: Pacific Grove, California, Blackwell Scientific Publications and the Boxwood Press, 848 p.
- Ren, J.-J., Zhang, J., Bai, L., and Hua, H., 2018, Research of Precambrian silicified fossils' preservation mechanism: Fish egg silicified simulation experimental taphonomy: *Precambrian Research*, v. 312, p. 38–44, <https://doi.org/10.1016/j.precamres.2018.05.004>.
- Roy, S.K., 1935, A new Niagaran *Conularia*: *Field Museum of Natural History* (Chicago), *Geological Series*, v. 6, p. 147–154.
- Sinclair, G.W., 1940, The genotype of *Conularia*. *Canadian Field-Naturalist*, v. 54, p. 72–74.
- Sinclair, G.W., 1944, Notes on the genera *Archaeoconularia* and *Eoconularia*: *Transactions of the Royal Society of Canada*, Section 4, ser. 3, v. 38, p. 87–95.
- Sowerby, J., 1821, *The Mineral Conchology of Great Britain; or Coloured Figures and Descriptions of those Remains of Testaceous Animals or Shells, which have been Preserved at Various Times, and Depths in the Earth*, Volume 3, Part 46: London, W. Arding, 194 p.
- Steinmann, G., and Doderlein, L., 1890, *Elemente der Paläontologie*: Leipzig, Verlag von Wilhelm Engelmann, 848 p.
- Townson, J.L., Lin, Y.-S., Chou, S.-S., Awad, J.H., Coker, E.N., Brinker, C.J., and Kaehr, B., 2014, Synthetic fossilization of soft biological tissues and their shape preserving transformation into silica or electron-conductive replicas: *Nature Communication*, v. 5, art. 5665, <https://doi.org/10.1038/ncomms6665>.
- Van Iten, H., 1991a, Anatomy, patterns of occurrence, and nature of the conulariid schott: *Paleontology*, v. 34, p. 939–954.
- Van Iten, H., 1991b, Evolutionary affinities of conulariids, in Simonetta, A.M., and Morris, S.C., eds., *The Early Evolution of Metazoa and the Significance of Problematic Fossil Taxa*: Cambridge, UK, Cambridge University Press, p. 145–154.
- Van Iten, H., 1992a, Anatomy and phylogenetic significance of the corners and midlines of the conulariid test: *Paleontology*, v. 35, p. 335–358.
- Van Iten, H., 1992b, Microstructure and growth of the conulariid test: Implications for conulariid affinities: *Paleontology*, v. 35, p. 359–372.

- Van Iten, H., and Südkamp, W., 2010, Exceptionally preserved conulariids and an edrioasteroid from the Hunsrück Slate (Lower Devonian, SW Germany): *Palaeontology*, v. 53, p. 403–414, <https://doi.org/10.1111/j.1475-4983.2010.00942.x>.
- Van Iten, H., Fitzke, J. A., and Cox, R. S., 1996, Problematical fossil cnidarians from the Upper Ordovician of the north-central USA: *Palaeontology*, v. 39, p. 1037–1064.
- Van Iten, H., Leme, J.M., Simões, M.G., Marques, A.C., and Collins, A., 2006, Reassessment of the phylogenetic position of conulariids within the subphylum Medusozoa (phylum Cnidaria): *Journal of Systematic Palaeontology*, v. 4, p. 109–118, <https://doi.org/10.1017/s1477201905001793>.
- Van Iten, H., Marques, A.C., Leme, J.M., Pacheco, M.L.A.F., and Simões, M.G., 2014, Origin and early evolution of the phylum Cnidaria Verrill: Major developments in the analysis of the taxon's Proterozoic-Cambrian history: *Palaeontology*, v. 57, p. 677–690, <https://doi.org/10.1111/pala.12116>.
- Van Iten, H., Leme, J.M., Pacheco, M.L.A.F., Simões, M.G., Fairchild, T.R., Rodrigues, S., Galante, D., Boggiani, P.C., and Marques, A.C., 2016a, Origin and early diversification of phylum Cnidaria: Key macrofossils from the Ediacaran System of North and South America, in Goffredo, S., and Dubinsky, Z., eds., *The Cnidaria: Past, Present and Future*: Zurich, Springer, p. 31–40, https://doi.org/10.1007/978-3-319-31305-4_3.
- Van Iten, H., Muir, L., Simões, M.G., Leme, J.M., Marques, A.C., and Yoder, N., 2016b, Palaeobiogeography, palaeoecology and evolution of Lower Ordovician conulariids and *Sphenothallus* (Medusozoa, Cnidaria), with emphasis on the Fezouata Shale of southeastern Morocco: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 460, p. 170–178, <https://doi.org/10.1016/j.palaeo.2016.03.008>.
- Van Iten, H., Gutiérrez-Marco, J.C., Muir, L.A., Simões, M.G., and Leme, J.M., 2022, Ordovician conulariids (Scyphozoa), from the Upper Tiourine Formation (Katian), eastern Anti-Atlas Mountains, southern Morocco, in Hunter, A.W., Alvaro, J.J., Lefebvre, B., Van Roy, P., and Zamora, S., eds., *The Great Ordovician Biodiversification Event: Insights from the Tafalalt Biota, Morocco*: London, Geological Society Special Publications, v. 485, p. 177–199, <https://doi.org/10.1144/SP485.5>.
- Van Roy, P., Briggs, D.E.G., and Gaines, R.R., 2015, The Fezouata fossils of Morocco: An extraordinary record of marine life in the Early Ordovician: *Journal of the Geological Society of London*, v. 172, p. 541–549, <https://doi.org/10.1144/jgs2015-017>.
- Von Bitter, P.H., Purnell, M.A., Tetreault, D.K., and Stott, C.A., 2007, Eramosa Lagerstätte—Exceptionally preserved soft-bodied biotas with shallow marine and bioturbating organisms (Silurian, Ontario, Canada): *Geology*, v. 35, p. 879–882, <https://doi.org/10.1130/G23894A.1>.
- Werner, B., 1966, *Stephanoscyphus* (Scyphozoa, Coronatae) und seine direkte Abstammung von den fossilen Conulata: *Helgoländer Wissenschaftliche Meeresuntersuchungen*, v. 13, p. 317–347.
- Werner, B., 1967, *Stephanoscyphus* Allman (Scyphozoa, Coronatae), ein rezenter Vertreter der Conulata?: *Paläontologische Zeitschrift*, v. 41, p. 137–153.
- Werner, B., 1973a, New investigations on systematics and evolution of the class Scyphozoa and the phylum Cnidaria: *Publications of the Seto Marine Biology Laboratory*, v. 20, p. 35–61.
- Werner, B., 1973b, Spermatozeugmen und Paarungsverhalten bei *Tripedalia cystophora* (Cubomedusae): *Marine Biology*, v. 18, p. 212–217.
- Werner, B., 1974, *Stephanoscyphus eumedusoides* n. spec. (Scyphozoa, Coronatae), ein Höhlenpolyp mit einem neuen Entwicklungsmodus: *Helgoländer Wissenschaftliche Meeresuntersuchungen*, v. 26, p. 434–463.
- Werner, B., 1983a, Weitere Untersuchungen zur Morphologie, Verbreitung und Ökologie von *Stephanoscyphus planulophorus* (Scyphozoa, Coronatae): *Helgoländer Meeresuntersuchungen*, v. 36, p. 119–135.
- Werner, B., 1983b, Die Metamorphose des Polypen von *Tripedalia cystophora* (Cubozoa, Carybdeidae) in die Meduse: *Helgoländer Meeresuntersuchungen*, v. 36, p. 257–276.

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