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Underwater drunken forest: Changes in growth direction and ornamentation in *Conularia fragilis* Barrande, 1867 (Lower Devonian, Czech Republic)

Jana Bruthansová, Jiří Bruthans, Jana Schweigstillová, and Heyo Van Iten

ABSTRACT

A very high percentage of specimens of *Conularia fragilis* Barrande, 1867 from the Lower Devonian Prague Formation of Bohemia (Czech –Republic) show appreciable curvature or bending of the steeply pyramidal periderm, which in most other conulariids tends be straight. Curved or bent sections of the periderm in *C. fragilis* are invariably associated with substantial departure from normal patterns of the external ornamentation (transverse ribs) of the four faces. Based on these observations and on data on the microstructure and composition of the conulariids, we conclude that bending of the periderm occurred while the conulariids were alive. As in curved or bent rugose corals from the same formation, bending in the conulariids probably involved preferential addition of new peridermal material along that part of the oral growth margin on the outside of the curve and may have occurred in response to changes in ambient currents or shifting of a sandy (crinoidal) substrate distad or within crinoid-stromatoporoid bioherms.

Jana Bruthansová. Department of Paleontology, National Museum, Cirkusová 1740, 193 00, Prague 9, Czech Republic; Department of Geology and Palaeontology, Faculty of Science, Charles University, Albertov 6, 128 43 Prague 2, Czech Republic. jana.bruthansova@nm.cz (corresponding author)
Jiří Bruthans. Department of Hydrogeology, Engineering Geology and Applied Geophysics, Faculty of Science, Charles University, Albertov 6, 128 43 Prague 2, Czech Republic. bruthans@natur.cuni.cz
Jana Schweigstillová. Department of Applied Rock Mechanics, Institute of Rock Structure and Mechanics of The Czech Academy of Sciences, v. v. i., V Holešovičkách 94/41, 182 09 Praha 8, Czech Republic. jana@irsm.cas.cz
Heyo Van Iten. Department of Geology, Hanover College, Hanover, Indiana USA 47243 and Department of Invertebrate Paleontology, Cincinnati Museum Center, 1301 Western Avenue, Cincinnati, Ohio USA. vaniten@hanover.edu

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INTRODUCTION

Conulariids are an extinct order (Conulariida) of sessile benthic, polypoid medusozoan cnidarians (Van Iten et al., 2006a) ranging from the uppermost Ediacaran to the topmost Triassic (Van Iten et al., 2006a, 2014a, 2016; Lucas, 2012; Amorin et al., 2020; Leme et al., 2022). The group is most diverse in the Ordovician System, steadily decreasing in generic diversity following the End Ordovician Mass Extinction Event (Van Iten and Vyhlasová, 2004; Leme et al., 2010; Van Iten et al., 2014b, 2020). In the Czech Republic (Prague Basin), the diversity of conulariids mirrors the global trend, reaching a maximum in the Middle Ordovician (Brabcová, 2001; Van Iten and Vyhlasová, 2004) and then declining to a total of just nine species in the Devonian (Brabcová, 2001; Mergl et al., 2016).

Conulariids are characterized by an elongate, steep pyramidal periderm usually having four faces and sulcate corners. The microstructure and growth of the conulariid periderm have been treated in many publications (e.g., Bouček and Ulrich, 1939; Van Iten et al., 2006b, 2006c; John et al., 2010; Robson and Young, 2013; Ford et al., 2016; Mergl et al., 2016; Kröger et al., 2021; Miller et al., 2022; Vinn, 2022). Thanks mainly to scanning electron imaging of specimens etched in dilute HCl (Ford et al., 2016), is it now known that the conulariid periderm is composed of alternating apatitic and organic microlamellae measuring approximately 1 to 3 μm thick (Van Iten, 1992; Ford et al., 2016). The apertural end of the periderm may be open, or it may be partially or fully closed by inwardly folded, lobate, or triangular lappets. Where the opposite, or apical end of the periderm is preserved, it consists of a minute, subconical holdfast that is attached, in some cases, to hard biological substrates (Vinn et al., 2019). Bohemian specimens are truncated at varying distances above the apex (the closed aperture is preserved in some specimens), and many of them terminate in an outwardly convex apical wall, or schott, which may have been produced in response to mechanical severance of the originally sessile polyp (Van Iten, 1991; Van Iten et al., 2020; Bruthansová et al., 2022). None have yet been documented in a demonstrably original life orientation and relationship to their substrate.

The purpose of the present paper is to describe and interpret a large sample (89 specimens) of *Conularia fragilis* Barrande, 1867, from Lower Devonian (Pragian) limestones in the Prague Basin in Bohemia. *Conularia fragilis* is the most common of the nine species of conulariids collectively described and figured by Barrande (1867), Bouček (1928, 1939), and Mergl et al. (2016) from the Devonian of the Czech Republic. It is restricted to the Koněprusy Limestone of the Prague Formation, which consists in large part of biohermal and biodetrital limestones. Most of the specimens studied exhibit pronounced curvature or bending of the periderm together with abnormal patterns of external ornamentation. Such bending is well exemplified by a single, nearly complete specimen illustrated by Bouček (1928, plate V, fig. 8) and collected from a "yellowish crystalline limestone" from "Koněprusy". Detailed analysis of many such specimens may provide additional insights into the morphogenesis of the conulariid periderm and, potentially, the paleoecology of conulariids.

Geological and Paleontological Settings

The studied conulariid specimens are from limestone deposits in the Prague Basin (Figure 1), which extends about 110 km from just east of

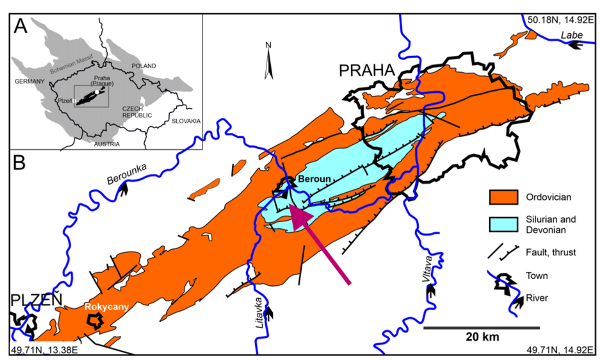

FIGURE 1. Geological map of the Prague Basin (Bohemia, Czech Republic), showing the approximate positions of the localities yielding *Conularia fragilis* (red arrow). A, location of the Prague Basin within the Czech Republic and the Bohemian Massif (shaded in grey). B, the Prague Basin. Figure modified from Zicha et al. (2020).

Prague to the city of Pilsen. The Prague Basin originated as a rift basin (Havlíček, 1981, 1998) in which subsidence and sediment accumulation took place from the Early Ordovician (Tremadocian) to the Middle Devonian (Givetian). The basin is now a folded and faulted denudation relic. The Devonian sequence in the Prague Basin consists of six formations collectively ranging from Lochkovian to Givetian in age (Figure 2) (Chlupáč, 1998). The six rock units consist predominantly of carbonates, with Middle Devonian paleomagnetic signatures recording the northward drift of the basin from high southern to subtropical southern (ca. 10–20°) paleolatitudes (Krs et al., 1988, 1997; Patočka et al., 2003). Gradual deepening of the Prague Basin is recorded in the Lower Devonian (Pragian) Prague Formation (Figure 2), which has been subdivided into five members ranging in origin from proximal marine near the base of the unit (Koněprusy, Slivenec, and Vinařice limestones) to distal or deep-water marine (Řeporyje and Dvorce-Prokop limestones; see Chlupáč, 1998, fig. 5) near the top (Chlupáč, 1998). The 89 study specimens were collected from the Koněprusy Limestone near the village of Koněprusy (Figure 3) in the north-western portion of the Prague Basin. Aspects of the stratigraphy and depositional environments of Devonian strata in the Koněprusy area have been discussed by Hladil and Slavík (1997), Hladil (1997, 1998), Janoušek et al. (2000, 2001), Chlupáč (2003), Slavík (2004), Slavík and Hladil (2007), Koptíková et al. (2010), Weinerová et al. (2017), Slavík and Hladil (2020), and Mergl (2022). The Koněprusy Limestone measures up to 150 m in thickness and consists of white to light grey, bioclastic crinoidal limestones and bioherms. The bioherms consist mainly of crinoids with massive stems and root systems (e.g., *Pernerocrinus* Bouška, 1946 and *Torrocrinus* Prokop and Petr, 1991), calcareous algae, and stromatoporoids (Chlupáč, 1998) along with minor tabulate and rugose corals. The bioherms also contain stromatolite-like, laminated stromatactis structures and localized accumulations of trilobite debris filling depressions and holes in the reef framework. The bioherms pass laterally into mostly unsorted, bioclastic material (size 1-20 cm, large, coarse) consisting of diverse crinoids, brachiopods, fenestellid bryozoans, rugose corals, algae, gastropods, and bivalves. Moving away from the reef cores, in the vicinity of Zlatý kůň, the amount of well-sorted crinoidal limestone increases (up to several cm large, fine), and stromatoporoids, algae, colonial anthozoans, and massive crinoid stems become absent (Plešivec Quarry area near Měňany) (Turek, personal commun., 2023). From Koněprusy towards the eastern and north-eastern portions of the basin, the proportion of coarse bioclastic material decreases with increasing water depth, and the proportion of fine-grained, silty carbonate material increases until it becomes the dominant sediment (Turek, personal commun., 2023).

MATERIAL AND METHODS

Material

Nearly all 89 specimens of *Conularia fragilis* were obtained from museum collections dating from the nineteenth or early twentieth centuries. All are now housed in the collections of the National Museum in Prague (collection number prefix NML or NMS). The specimens are incomplete, having been truncated well above the apex and below the aperture, and preserve peridermal material. None of the conulariids were collected in situ, and therefore, their original orientations in the outcrop and the specific localities from which they were collected are unknown. All are labelled with the name Koněprusy, which covers a large area including the village of Koněprusy and encompassing multiple quarries (Figure 3). Owing to the absence of host rock material and diagnostic facies indicators within the peridermal cavity of the conulariids, the facies provenance of the conulariids likewise cannot be established.

Methods

The studied conulariids were examined using optical microscopy (Olympus SZX12 binocular microscope) and photographed under low angle illumination using a Nikon EOS 6D digital camera. All conulariids greater than 30 mm in length (54 specimens) were photographed in orientations where the curvature or bending of the periderm was maximally apparent. From these photographs, the rate of expansion of the periderm along the longitudinal axis was estimated, as was whether the bending was gradual or abrupt. To establish the chemical composition of the conulariids and to obtain information bearing on their bending and malformed ornament, some of the conulariids were sectioned and analyzed using scanning electron microscopy (SEM) and energy dispersive X-ray spectroscopy (EDS) in the Institute of Rock Structure and Mechanics of the Academy of Sciences of the Czech Republic in Prague. Sectioned specimens were cut perpendicular or parallel to the longitudinal axis and following air drying were

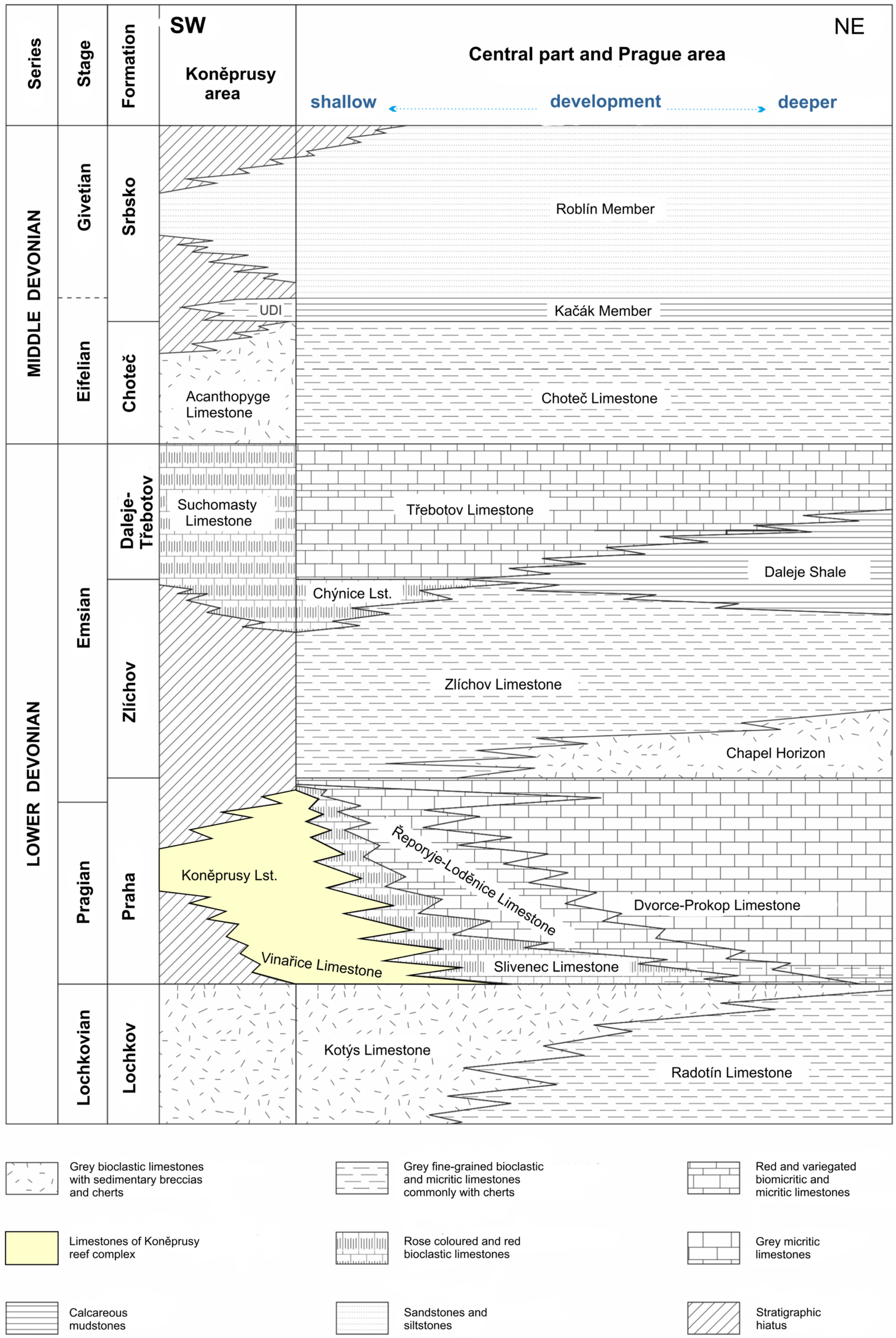

FIGURE 2. Stratigraphic chart of the Devonian of the Prague Basin, modified after Mergl and Kraft (2023). Koněprusy Limestones highlighted in yellow.

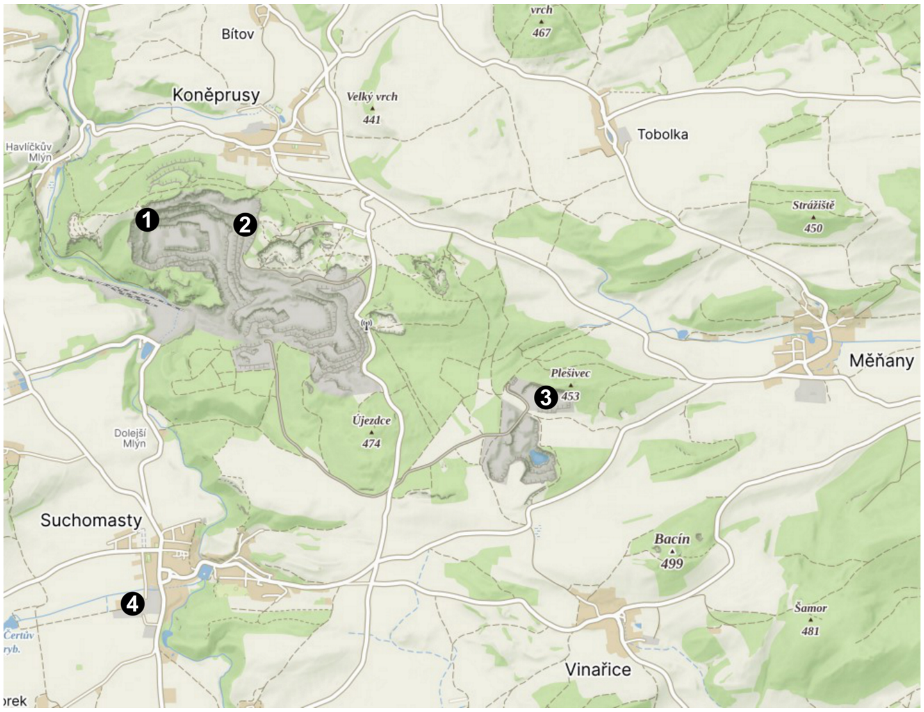

FIGURE 3. Selected localities yielding *Conularia fragilis* in the vicinity of Koněprusy village. 1, Zlatý Kůň; 2, the Čertovy Schody Quarry and the old Císař Quarry; 3, Plešivec; 4, Suchomasty.

impregnated with SpeciFix Resin epoxy resin before high–speed polishing with 0.5–micron aluminum oxide powder. After ultrasonic cleaning in deionized water the polished surfaces were coated with gold. The specimens were imaged and analyzed using a QUANTA 450 (FEI) scanning electron microscope equipped with a photomultiplier detector (Centaurus PMD) for backscattered electrons (BSE). This work was carried out under a high vacuum using BSE to detect differences in chemical composition. Powder X-ray diffraction (XRPD) data for small pieces of extracted peridermal material were collected using a PANalytical X´Pert Pro diffractometer operating at 40 kV and 30 mA, with a secondary monochromator producing CuKα1,2 radiation and a X´Celerator detector (X-ray diffraction Laboratory, Institute of Geochemistry, Mineralogy and Mineral Resources, Faculty of Science, Charles University, Prague). Identification of phases was achieved using the High-Score search-match algorithm with PDF-2 (ICDD) database.

To examine the peridermal cavity, micro-computed tomographic analysis was performed using the X-ray micro-tomography SkyScan 1172 (Bruker) instrument in the Natural Museum in Prague. This instrument produces multiple X-ray "shadow" transmission images at different angles while the object rotates. From these shadow images, cross-sections of the conulariids were constructed using N-Recon Version 2.0.0 software to create a three-dimensional visualization of both the exterior and interior surfaces of the periderm. Digital images were created using Avizo (Version: 2020.3) software, and information thus revealed was processed using the volume rendering and ortho-slice modes for surfaces, iso-surfaces, and cross-sections. The X-ray microfocus tube was operated at 100 μA and 100 kV with a 1 mm Cu filter. The rotation step was 0.3° (one frame per step) through 360°, and the average image pixel size was 27.08 μm

RESULTS

Preservation and Irregularities in Skeletal Growth

The studied conulariids exhibit four equally wide faces, with the two corners bordering any one face diverging at approximately 5 to 20° (Figure 4A-C and Supplementary Figure 1). In transverse cross sections the specimens are square or rhombic, and there are no terminal or internal schotts (apical walls) or longitudinal carinae (Figure 5). The largest specimen measures 127 mm in length, but it is truncated well above the apex and so its original length may have been about 200 mm. All specimens exhibit low, narrow, finely nodose trans-

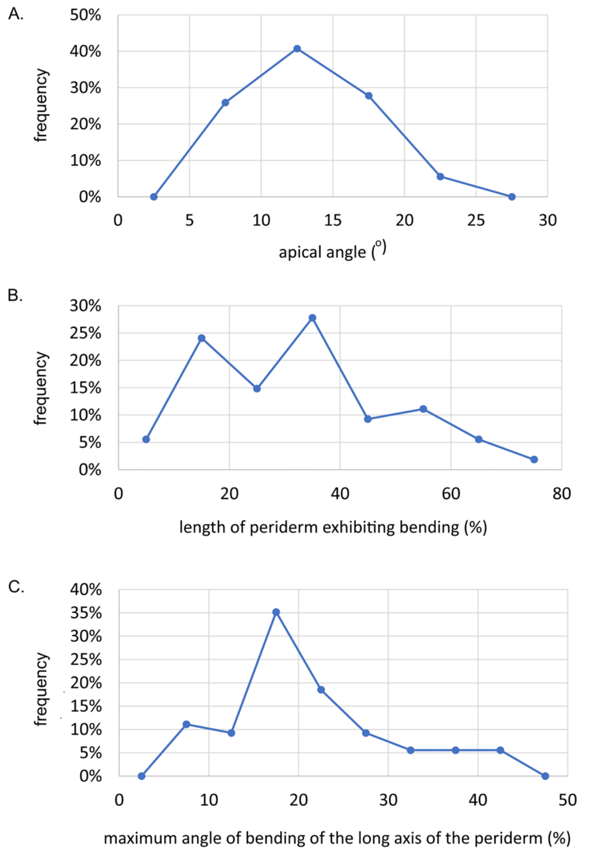

FIGURE 4. Measurements on the 54 specimens of *Conularia fragilis* measuring ≥ 30 mm in length. A, Apical angle of the periderm (º); B, Percentage of the total preserved length of the periderm exhibiting bending (%); C, Maximum angle of bending of the periderm (º). For explanation of parameters see Supplementary Figure 1.

verse ribs, spaced along the longitudinal axis from 8 to 15 per 5 mm, which arch towards the apertural end of the periderm and cross the facial midline without interruption.

All specimens measuring at least 30 mm in length exhibit one or (less frequently) two bends along the long axis (Figures 6-8). The bending ranges from gentle to pronounced (Figures 7-9), with the total angle of bending (measured on the straight portions of the conulariids below and above the zone of bending) ranging from 7 to 45°, though with most specimens (n = 25) bending at about 20° (Figure 4C). Both on the outside and the inside of a given bend, the transverse ribs are crowded, with approximately twice as many transverse ribs per 5 mm than below (adapically) or above (adaperturally) the bend. Additionally, the transverse ribs may be distorted, being irregularly undulatory and/or terminating well short of the nearest corner (Figure 10A-H). Segments that exhibit gradual bending constitute anywhere from 10 to 70% of the total preserved length of the conulariids (Figures 6-8). The square or rhombic transverse cross section of the periderm is preserved through the bend. Most of the specimens show a single bend, but 10 of them exhibit two bends (Figure 9F-G). In the latter specimens, the oral-most bend restores the original direction of extensional growth of the periderm. Because the conulariids are truncated above the apex and below the aperture, it is difficult to determine with certainty in which portion of the skeleton (apical, middle, or apertural) the observed bending is most frequent. Nevertheless, it appears from the size and shape

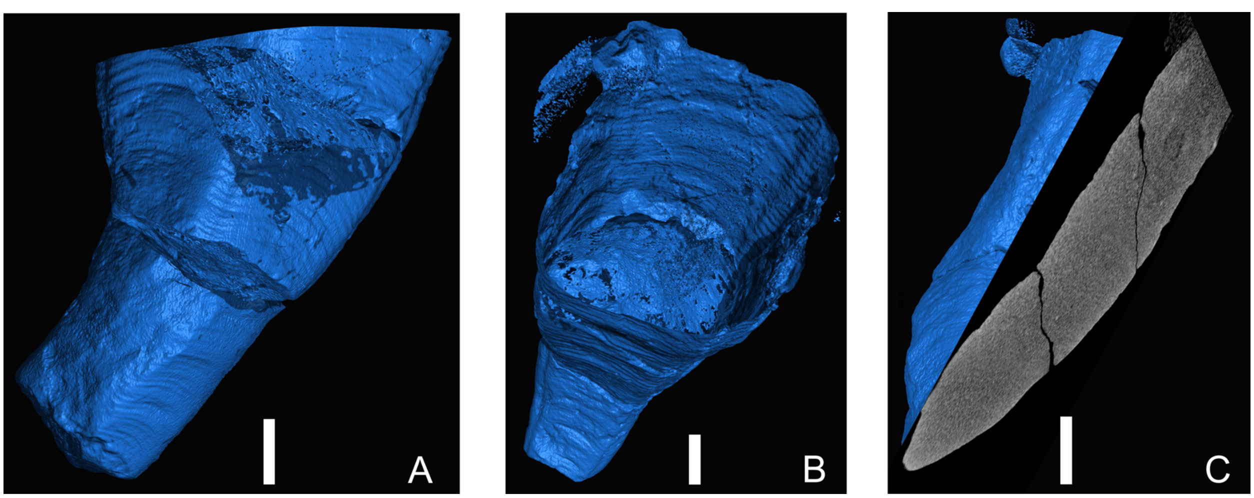

FIGURE 5. Micro-CT images of the peridermal cavity and inner surface of specimen NML 59518 (*Conularia fragilis*) from the Koněprusy locality. A-B, isosurface mode images showing both the back and front faces. C, visualization of the external surface and slice showing the interior of the periderm with two post-mortem fractures. Scale bar equals 5 mm.

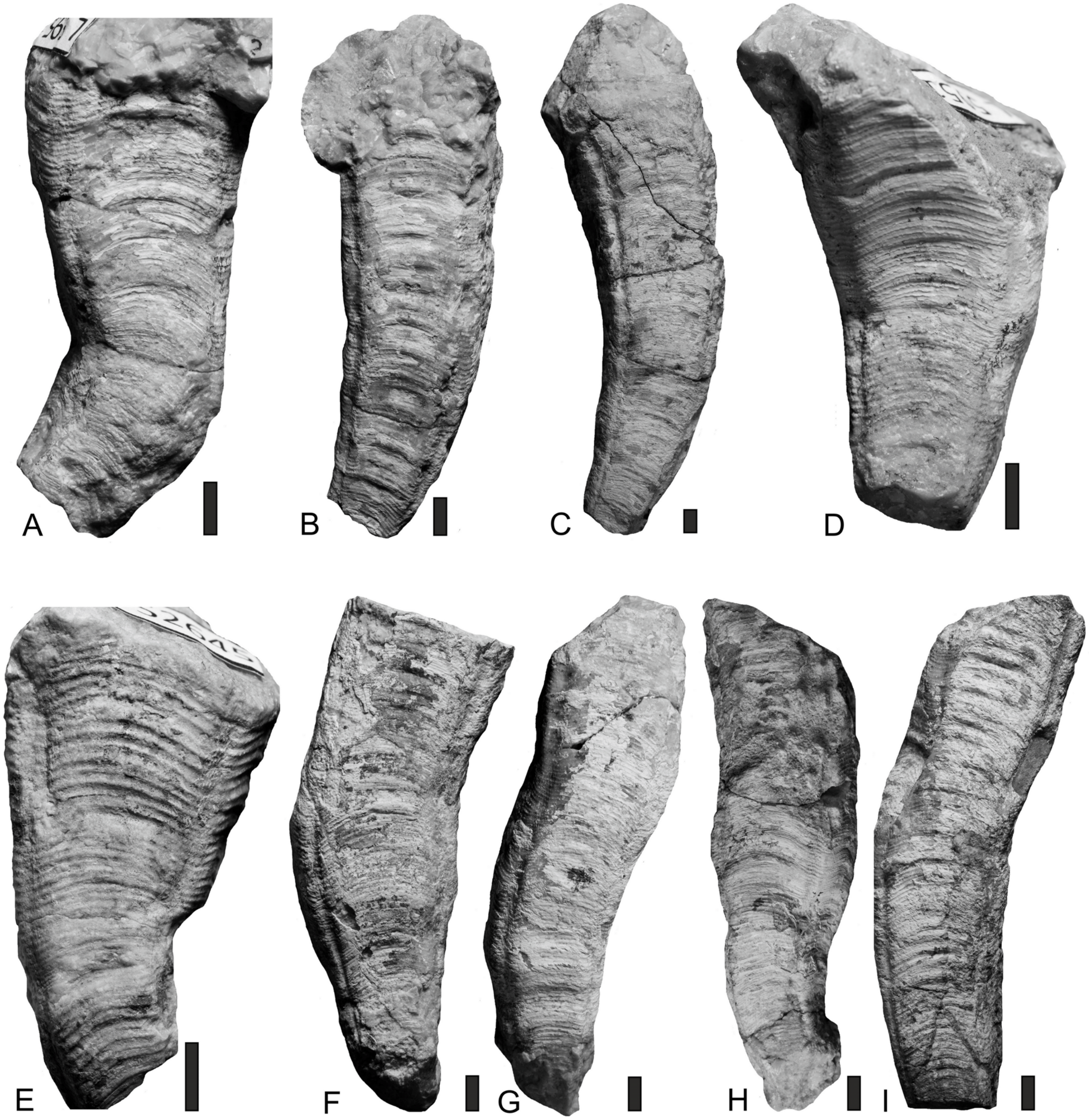

FIGURE 6. *Conularia fragilis* Barrande, 1867 from the Koněprusy Limestone of the Prague Formation (Lower Devonian, Pragian). A, NML 59518, Koněprusy locality; B, NML 52655, Koněprusy locality; C, NML 63463, Suchomasty locality; D, NML 59516, Koněprusy locality; E, NML 52645, Koněprusy locality; F-G, NML 59514, Koněprusy locality; H, NML 63487, Suchomasty locality; I, NML 63473, Suchomasty locality. Scale bar equals 5 mm.

of the specimens that bending occurs most frequently in the apical portion, with other specimens being bent in the middle or upper third.

Microstructure and Composition

The periderm of *Conularia fragilis* ranges from 200-400 µm in thickness and consists of numerous, microscopic lamellae (microlamellae; Ford et al., 2016) measuring approximately 1-3 µm thick. As seen in backscattered electron mode the microlamellae are alternately light and dark (Figure 11A-G). The lighter-colored laminae are fluorine-rich and contain more Ca and P than the darker ones, which appear to be rich in organic matter. The microlamellae generally parallel each other, gradually and smoothly widening within the transverse ribs and thus making the periderm thicker there than between the ribs. Importantly, the

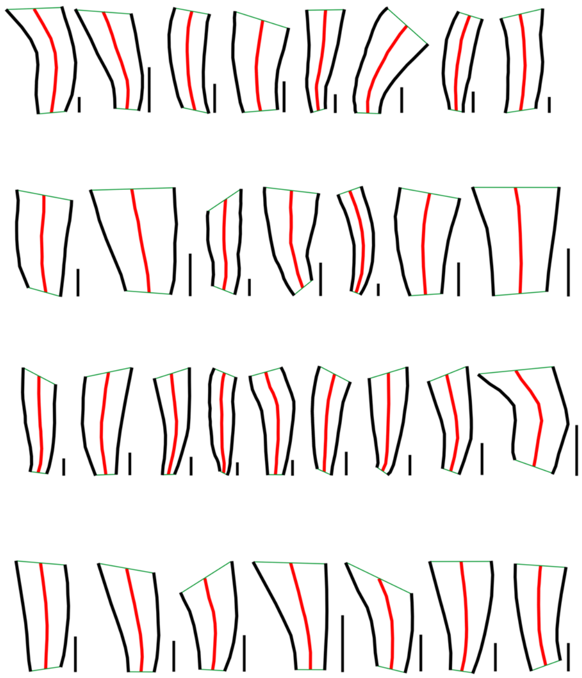

FIGURE 7. Schematic line drawings of peridermal bending in selected specimens of *Conularia fragilis*. Red lines indicate the facial midline, black lines the corners of the periderm, green lines the broken ends of the specimens. Scale bar equals 5 mm.

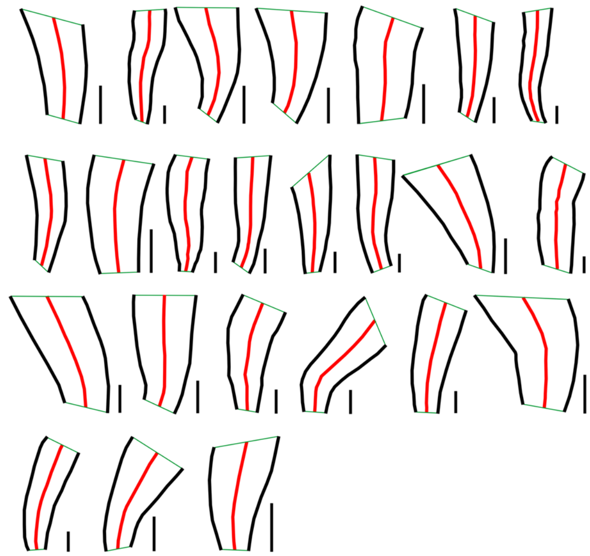

FIGURE 8. Schematic line drawings of peridermal bending in selected specimens of *Conularia fragilis*. Red lines indicate the facial midline, black lines the corners of the periderm, green lines the broken ends of the specimens. Scale bar equals 5 mm.

microlamellae continue without disruption through curved or bent portion(s) of the periderm, and thus there is no internal evidence of injury or interruption of the growth of the periderm. Small cracks cross-cutting the microlamellae and filled (in some cases) with diagenetic iron oxides or apatite clearly are post-morten in origin, indicating that the originally pliable periderm had become brittle.

DISCUSSION

Origin of the Peridermal Bending

Previous authors (e.g., Ford et al., 2016; Mergl et al., 2016) have agreed that the growth of the conulariid periderm involved accretion of new material along the apertural (oral) margin and thickening of the periderm by accretion of whole lamellae to its inner surface. Thus, the results of the present study suggest that bending of the periderm was brought about by preferential production of new peridermal material along that part of the apertural margin on the outside of a given bend. The bending clearly is neither tectonic nor diagenetic in origin (again, the microstructure of the periderm is unaffected by it), nor is there any evidence suggesting that it was associated with repair of damage caused by durophagous predation (see illustrations of healed conulariid injuries and growth abnormalities in Babcock et al., 1987; Mapes et al., 1989; Van Iten, 1992; Van Iten et al., 2022). Preferential addition of new periderm may have occurred at the oral edge of a single, outermost lamella or set of lamellae, followed later by accretion of additional lamellae to the inner surface of that or those lamellae involved in the formation of the bend. Associated with this process was disruption of normal patterns (spacing and geometry) of the transverse ribbing, which patterns were restored once the new growth direction was established. The cause of the observed bending of the periderm is unclear, but by analogy with solitary corals it may have taken place in response to changes in ambient currents or shifting of the conulariids' substrate, which may have consisted of crinoid debris (Figure 12). Thus, in present-day subaqueous environments, ambient currents and substrate movement affect the body shapes of diverse, sessile benthic organisms, including various algae, corals, sponges, and bryozoans. All these organisms can modify their growth direction in response to changes in the prevailing water currents, enabling them to feed more efficiently and/or to deal more effectively with drag (see e.g., Jebram, 1970; Koehl, 1999; Denny and Gaylord, 2002; Boller and Carrington, 2006; Martone and Denny, 2008; Infan-

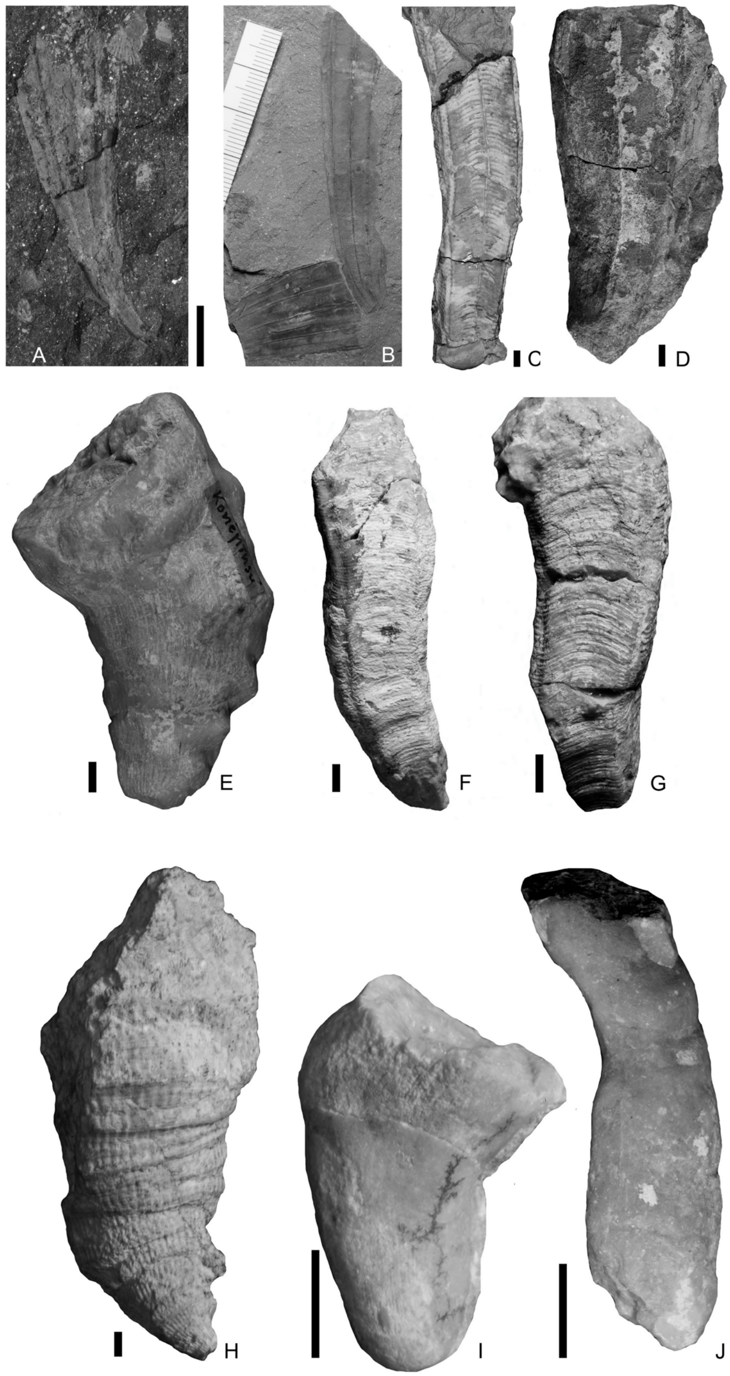

FIGURE 9. A-D, Other conulariids showing peridermal bending. A, *Archaeoconularia* sp., NML 65606 from the Vinice Formation (Sandbian, Upper Ordovician, Czech Republic), Knížkovice; B, Conulariid specimen NMS 6031 from the Sandbian (Upper Ordovician) of Morocco, N´Kob; C, *Paraconularia planicostata* (Dawson) NMS 4948 from the Upper Mississippian of western Newfoundland, Canada; D, *Archaeoconularia consobrina* (Barrande), NMS 6000 from the Upper Ordovician of Morocco, Erfoud; E, Rugose coral *Chonophyllum*, NML 66191 from the Koněprusy Limestone of the Prague Formation (Koněprusy locality). F-G, specimens of *Conularia fragilis* showing two peridermal bends. F, NML 63474, Suchomasty locality; G, NML 59518, Koněprusy locality; H, Rugose coral *Pselophyllum*, NML 67456 from the Koněprusy Limestone of the Prague Formation (Koněprusy locality); I, Rugose coral *Chonophyllum*, NML 67215 from the Koněprusy Limestone of the Prague Formation (Koněprusy locality); J, Rugose coral *Chonophyllum*, NML 67216 from the Koněprusy Limestone of the Prague Formation (Koněprusy locality). F-G F-G F-J Scale bar equals 5 mm.

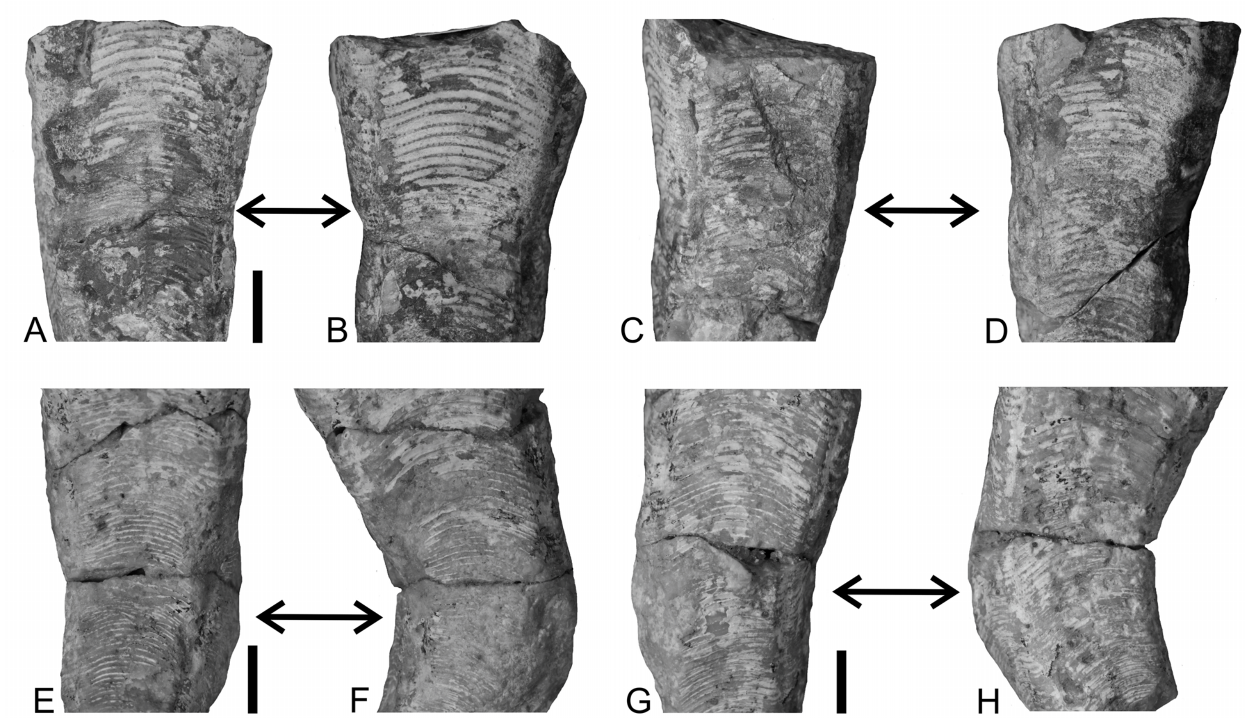

FIGURE 10. Details of malformed transverse ribs in bent portions of the periderm of *Conularia fragilis*. A-D, NML 61406, Plešivec locality; E-H, NML 59518, Koněprusy locality. Scale bar equals 5 mm.

tes et al., 2011; Luhar and Nepf, 2011; Rummel, 2014; Hays, 2017; Falcucci et al., 2021). In the Koněprusy Limestone, the animals most like the conulariids probably were the solitary rugose corals, many of which likewise are curved or bent (Figure 9E, H-J). These possibly semi-erect or recumbant, semi-infaunal polyps are thought to have changed the direction of extensional growth to maintain an optimal life position for feeding and reproduction (Neuman, 1988; Scrutton, 1998; Sorauf, 2001; Berkowski, 2012; Adomat et al., 2016). Hence, if analogy with horn corals is appropriate in the present case, it is tempting to suggest that like these animals, *Conularia fragilis* may have been semi-erect or even recumbent, changing its growth direction continuously (if, say, recumbent) or suddenly (if, say, semi-erect and subject to toppling) in order to maintain an optimal life posture relative to a mobile substrate.

Unfortunately, all the conulariid specimens examined in the present study came from old collections, and therefore we could not determine whether they occurred in their original life orientation (erect and with the apertural end up) in the outcrops or had undergone transport prior to final burial. Previously, Simões et al. (2000, 2003) and Rodrigues et al. (2003) investigated the taphonomy of Devonian conulariids from Brazil, some of which exhibit broad transverse folding (undulation or wrinkling) of the faces like that displayed by some of the conulariids examined in the present study (e.g., Figures 5B, 6B, 6I). In their material, Simões et al. (2003) observed the folding in erect specimens preserved in situ and interpreted it as a taphonomic artifact of vertical compaction of the host sediment following final burial of the conulariids. Because the Czech material lacks information on the original orientation of the conulariids in the outcrops, we could not evaluate the hypothesis that the observed folding in these specimens is a taphonomic artifact (as opposed to a primary anatomical feature).

Finally, we observed bending and irregular ornamentation in conulariids other than *Conularia fragilis*, namely *Paraconularia planicostata* (Dawson, 1868) from the Upper Mississippian of southwestern Newfoundland and Nova Scotia (see Van Iten et al., 2024, fig. 2), in *Archaeoconularia insignis* (Barrande, 1867) from the Upper Ordovician of Bohemia, and in *Archaeoconularia consobrina* (Barrande, 1855) from the Upper Ordovician of Morocco (Figure 9A-D). The possible causes of

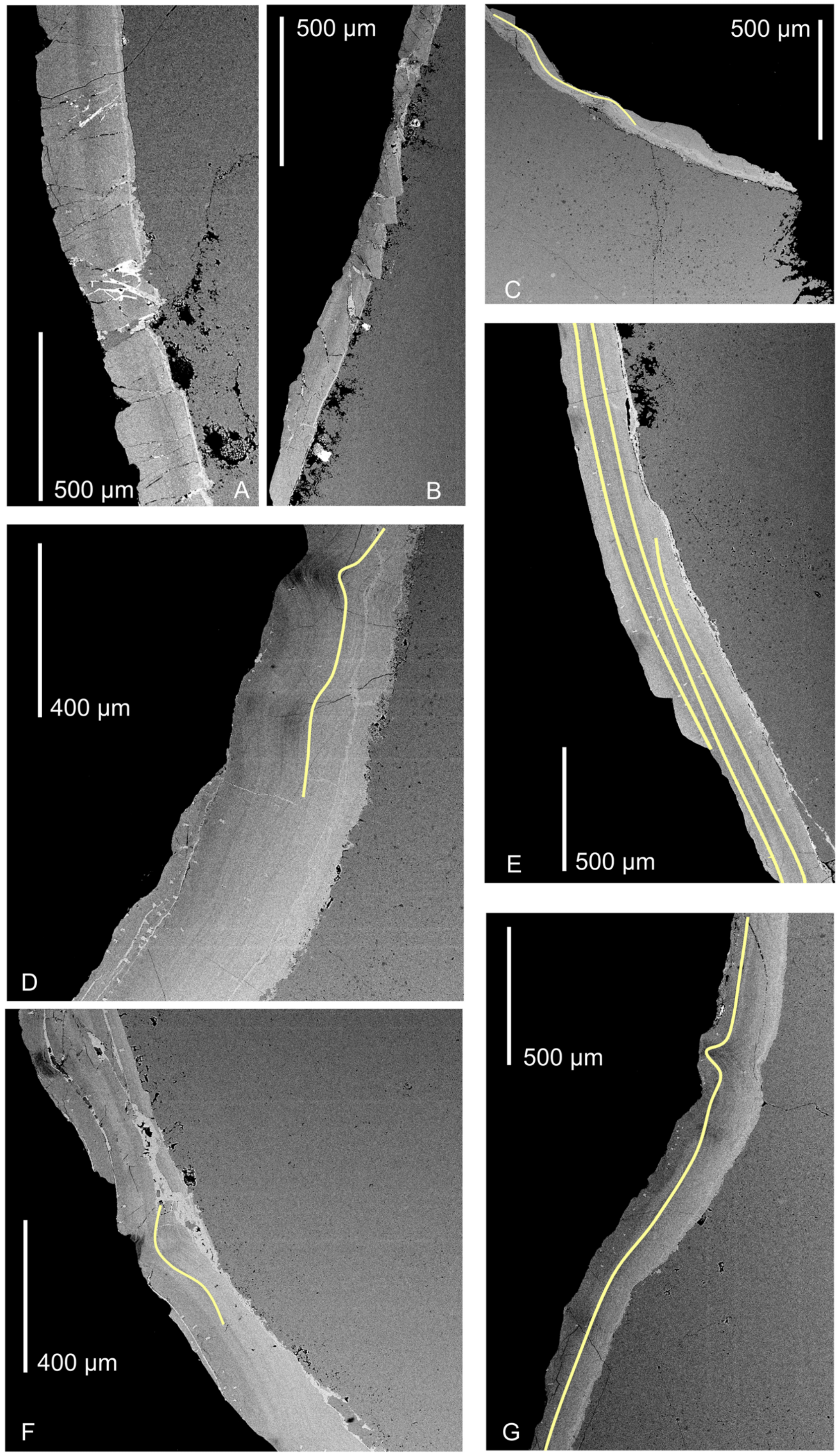

FIGURE 11. Backscattered electron (BSE) images of sectioned specimens of *Conularia fragilis*. A.-F, Specimen NML 59547, Koněprusy locality. A, Transverse section showing post-mortem fractures in the periderm filled with diagenetic Fe oxides; B, Transverse section showing pyrite crystals on the inner surface of the periderm; C, Transverse section showing the microlamellae; D, Transverse section showing light and dark microlamellae along with thickening of microlamellae within the transverse ribs; E. Transverse section showing microlamellae; F. Transverse section showing light and dark microlamellae along with thickening of microlamellae within the transverse ribs; G. Specimen NML 59514, Koněprusy locality. Transverse section showing light and dark microlamellae along with thickening of microlamellae within the transverse ribs.

FIGURE 12. Reconstruction of the Koněprusy fore-reef slope zone with *Conularia fragilis* and associated fauna. Drawing by Jiří Svoboda.

bending in these conulariids is a problem requiring further investigation, but it is important to note here that the phenomenon may be widespread taxonomically and thus indicative of fundamental growth processes common to the group.

Facies Provenance

As noted above in the introduction, we were not able to determine the facies provenance of the conulariids examined in the present study. Be that as it may, based on direct examination of multiple exposures of the Koněprusy Limestone and on discussions with colleagues having detailed knowledge of the unit, we think that the most plausible hypothesis is that *Conularia fragilis* inhabited relatively sheltered areas within the body of the reefs and/or on distal flanking sediments, in both cases among dense growths of calcareous green algae that may have acted to shelter the conulariids against current action (Figure 12). We have found fragmentary conulariid specimens at a few localities, for example the active quarries at Čertovy schody, Zlatý Kůň, and Cisař quarry, but the conulariid is a very rare faunal element, and no clear conclusions may be drawn from such a small sample.

Independent sedimentological evidence from these localities indicates high energy conditions on bioherm slopes, in waters up to 10 m deep (Bourillot et al., 2009; Denayer and Aretz, 2012; Duval-Arnould et al., 2024). However, such high energy environments are not generally suitable for larval attachment, and indeed larval supply is one of the principal factors determining the establishment, structure, and diversity of sessile benthic assemblages on reefs and bioherms (Bento et al., 2017). Thus, a more suitable environment for the attachment and further growth of conulariid larvae may have been sheltered, topographical heterogeneities within the bodies of the reefs, which in modern settings provide cryptic spaces that can act as refugia for coral and other larvae (e.g., Gallagher and Doropoulos, 2017; Martínez-Quintana et al., 2023). Sheltered algal meadows analogous to modern concentrations of seaweed and green alga may also have been favorable for conulariids (see e.g., Van Tussenbroek, 2011; Di Martino and Taylor, 2014; Wang et al., 2014; McNeil et al., 2021; East et al., 2023). Lastly, and again by analogy with solitary rugose corals, as well as by analogy with *Conularia* aff. *desiderata* Hall, 1847, from the Middle Devonian of New York State (USA) (Van Iten et al., 2013), we hypothesize that *C. fragilis* was semi-infaunal and oriented in life with the oral end facing directly or obliquely upward. The conulariid larvae probably attached to hard, biological substrates such as echinoderm ossicles, though, again, in relatively low energy settings where sudden shifting of the substrate was relatively infrequent, and where subsequent extensional growth of the conulariids was sufficiently rapid to prevent smothering by shifting or aggrading sediment.

CONCLUSIONS

Gross morphological and microstructural analyses of curved or bent, abnormally ornamented specimens of *Conularia fragilis* (Barrande, 1867), all from the Middle Devonian Koněprusy Limestone of the Prague Formation in Bohemia (Prague Basin), indicate that the bending occurred during the lifetimes of the conulariids, possibly in response to changes in ambient current action and/or to shifting of a (presumably) mobile sandy substrate. Similar bending is exhibited by solitary rugose corals from the same limestone unit, and in both cases was achieved through preferential addition of new skeletal material along one side of the oral (growth) margin. During the period of adjustment in growth direction, the spacing and relief of the transverse ribs along the bent or curved section of the conulariids changed markedly from the previous (pre-bending) stage, becoming "normal" again after establishment of the new and final growth direction. Owing in part to the lack of host rock matrix, the facies provenance of the bent conulariids is not known precisely, but it may have been sheltered portions of vuggy, shallow-water bioherm cores and/or deeper-water flank sediments farther from the paleoshoreline. Lastly, our results reinforce previously known similarities in anatomy and growth between conulariids and other, polypoid cnidarians.

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SUPPLEMENTARY FIGURE

SUPPLEMENTARY FIGURE 1. Parameters measured on the conulariid specimens. A, apical angle of the periderm; B, percentage of the total length of the periderm exhibiting bending; C, maximum angle of bending of the long axis of the periderm. Scale bar equals 5 mm.