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Late Ordovician cornulitids from Anticosti Island, eastern Canada, and their evolutionary implications

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Articles

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Abstract

Two Late Ordovician cornulitid species, *Cornulites richmondensis* (Miller, 1874) and *Cornulites hemistriatus* new species, from the Ellis Bay and Vaureal formations of Anticosti Island, eastern Canada, are each shown in this study to have a thick, punctate, cross-bladed lamellar, calcitic conch wall, a crested fold, a septate juvenile part, and endoconic chamber deposit. These Late Ordovician, free-living (i.e., nonencrusting) forms of *Cornulites* Schlotheim, 1820 have characters intermediate between *Cornulites* and the late Silurian-Devonian forms of *Tentaculites* Schlotheim, 1820, particularly by having incipient inner layers and poorly fused annuli, but lacking cornulitid-type vesicular microstructures. The described cornulitids are similar to brachiopods in their cross-bladed lamellae and pseudopunctae, but their lamellar layers are considerably finer and much less distinct than those of brachiopod shells.

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Non-technical Summary

Cornulitids and tentaculitids are two groups of very common yet enigmatic fossils lumped into 'Problematica' of the Paleozoic Era, characterized by relatively small, conically tubular conchs. These fossils have been interpreted to be related to various animal groups, including mollusks, annelid worms, arthropods, or brachiopods, but today are more commonly considered to be affiliated with polychaete tubeworms. In this study, new data on the general conch morphologies and microstructures of Late Ordovician cornulitid fossils from Anticosti Island of eastern Canada show a suite of intermediate morphological features between cornulitids and tentaculitids, thus shedding lights on the phylogenetic relationship between cornulitids and tentaculitids, especially relevant to the origin of tentaculitids during the early Silurian.

Introduction

The taxonomically enigmatic *Cornulites* Schlotheim, 1820 is widespread in Ordovician–Devonian rocks worldwide. In North America, many nonencrusting cornulitid species have commonly been assigned to *Tentaculites* Schlotheim, 1820, reported from Richmondian (upper Katian) rocks of Ohio, Kentucky, and Illinois (Davis, 1985; Bergström, 1996), including *T. tenuistriatus* Meek and Worthen, 1865, *T. oswegoensis* Meek and Worthen, 1865, *T. sterlingensis* Meek and Worthen, 1865, and *T. richmondensis* Miller, 1874, although most of these were treated subsequently as *Cornulites* (e.g., Hall, 1888; Fisher, 1962).

The free-living *Cornulites* and thick-walled tentaculitids likely shared a similar benthic mode of life, but their larval settlement behavior was different. All cornulitid larvae always settled on hard substrata, contrasting to early tentaculitid larvae that appear to have developed the ability to settle on soft substrata (Vinn and Mutvei, 2009; Vinn, 2010; Vinn and Zatoń, 2012; Tsujita and Baird, 2024). The confusion between *Tentaculites* and the so-called 'free-living' (i.e., nonencrusting) *Cornulites* partly stems from our generally poor knowledge of the conch microstructure of cornulitids. Hall's (1888) early drawings indicate that typical cornulitids tend to have flexuous, vesicular-walled conchs, either as independent, encrusting individuals or as gregarious clusters. His longitudinal sections of '*Tentaculites*' *richmondensis* (assigned to *Cornulites* in this study) can have straight to gently curved conchs, with or without vesicular wall structures. In their detailed examinations using scanning electron microscopy (SEM) and optical petrography, Vinn and Mutvei (2005) demonstrated convincingly that the conch walls of *Cornulites* are either completely vesicular or partially vesicular with parallel (foliated) lamellae. From the paleoecological point of view, however, there has been little detailed comparative study on encrusting versus free-living *Cornulites*, especially with regard to their conch microstructures. The microstructures of cornulitids as a group (family or order) have been reported inconsistently. Lardeux (1969)

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and Lardeux et al. (2003) indicated that *Conchicolites* Nicholson, 1872, considered a close relative of *Cornulites*, can have a microlamellar wall similar to that of *Tentaculites*, but these authors did not provide any illustrations. In their recent study of some Gotland forms considered to belong to *Conchicolites*, however, Vinn and Mutvei (2005) showed a prismatic microstructure, with calcite blades arranged perpendicular to the conch surface, although prismatic microstructure could have resulted from diagenetic recrystallization of an originally lamellar microstructure.

In conch shape, the flexuous curvature by itself is not a 'foolproof' diagnostic character for *Cornulites.* For example, the late Silurian *Corniculina* Klichevich, 1967, considered a form of the usually straight-conched dacryoconarid tentaculitids, has a flexuous to coiled conch like most encrusting forms of *Cornulites.* Inversely, some nonflexuous conchs of *Cornulites* can be superficially homeomorphic to the usually straight or weakly arched tentaculitids, particularly in the development of annular rings (annuli) and longitudinal lirae (= microcostules of Lardeux, 1969). The large, free-living forms of *Cornulites* from the upper Katian Vaureal Formation and the Hirnantian Ellis Bay Formation of Anticosti Island (Twenhofel, 1928; Bolton, 1972; Vinn and Mutvei, 2005, fig. 5.3 only; see also Schwarz et al., 2025 for a recent update on the age of the Ellis Bay Formation) have well-preserved microstructures, which are the main objectives of this study to document their morphological details and to explore their phylogenetic relationships with true tentaculitids because of their transitional morphological traits.

Materials and methods

Cornulitids and tentaculitids occur intermittently throughout the Upper Ordovician–lower Silurian carbonate-dominated succession of Anticosti Island, eastern Canada. This study deals only with the cornulitid material from the Upper Ordovician Vaureal and Ellis Bay formations (upper Katian–Hirnantian), in which both large, free-living forms and the usually smaller-sized encrusting forms of *Cornulites* often occur together in individual beds. The geological, chemostratigraphical, chronostratigraphical, and paleogeographical settings of the Upper Ordovician succession of Anticosti Island, together with general faunal characteristics, have been discussed in great details in many previous works (e.g. Jin and Zhan, 2008; Copper et al., 2013; Copper and Jin, 2014, 2017; Zimmt et al., 2024, 2025; Jin and Harper, 2025; Schwarz et al., 2025), and will not be repeated here.

All specimens examined during this study are embedded in relatively well-cemented brachiopod shelly packstones. It is difficult to isolate and extract the conchs because weathering has softened only a thin veneer of the micritic matrix and the slender, segmented cones tend to break easily. Thin sections were prepared, therefore, by cutting the slabs either parallel or perpendicular to the bedding surface. The generally abundant conchs in the rocks yielded numerous longitudinal, transverse, and oblique views in thin sections. Photomicrographs of the thin sections were taken with a Nikon DXM1200 microscope digital camera mounted on a Zeiss petrographic microscope. SEM micrographs were taken at Surface Science Western (University of Western Ontario, London), using natural specimens cleaned ultrasonically in water or transverse sections broken artificially by snapping a conch apart. Acid etching was not used for any photographed specimens. Whole specimens were coated with sublimated ammonium chloride and photographed digitally, either on a copy stand or with a Nikon SMZ15000 stereomicroscope.

Phylogenetic (cladistic) analysis was done using PAST 1.80 (Hammer et al., 2001) with an heuristic (NNI) algorithm, Fitch optimization, and 100 bootstrap replicates. For details of characters and character states used in the coding spreadsheet, see Appendix 1.

Repositories and institutional abbreviations. Types and figured specimens used in this study are deposited in the Geological Survey of Canada (GSC, Ottawa) and the Illinois State Museum (ISM), Springfield, Illinois. Topotype material is stored in the author's collection at the Department of Earth Science, University of Western Ontario (W, London). Locality numbers prefixed with the letter A denote Paul Copper's collections (with contributions from the author) from Anticosti Island; detailed locality information is available from the author.

General morphology of *Cornulites*

Conch shape. The conch of cornulitids is usually described as conical, tubicolous, or almost cylindrical (Vinn and Mutvei, 2005; Herringshaw et al., 2007). Similarly to the tentaculitids, the conch of cornulitids can be divided into four parts (Fisher, 1962; Lyashenko, 1958; Larsson, 1979): the embryonic chamber (initial chamber), the septate juvenile segment, the adult segment usually with large annuli ('annular rings'), and the apertural segment with closely spaced annuli (Fig. 1). In the well-preserved specimens of *Cornulites* of Anticosti Island, however, it is noted that the septate part of the shells usually can be discerned from the outside because of its whitish or translucent appearance (especially when the conch is immersed in water or alcohol), which results from the clean calcite cement in the chambers sealed by the septa. This contrasts to the long, aseptate, living chamber, which is usually filled by micritic mud and appears darker gray. In some specimens, the juvenile part of the conch can have a notably reduced diameter (Fig. 1.1).

Annulation of the conch. In the longitudinal sections of *Cornulites* of Anticosti Island, the adjacent annuli appear discontinuous in their lamellar layer, separated by an annular suture, which are artifacts resulting from deformation of specimens during sediment compaction. These sutures can be occupied by a thin veneer of primary layer (Fig. 1.1, 3). The suture gap can also be filled by a dark brown to black substance (probably a pyrite) between the outer surface of the thin, distal portion of an annulus and the inner surface of the thick, proximal portion of the subsequent annulus. The outer primary layer can also be seen to bifurcate at the junction of adjacent annuli, with one limb extending into the sutural gap and the other onto the outer surface of the subsequent annulus (Fig. 3.1). Along the axial surface (sensu Larsson, 1979, p. 41) of each annulus, a similarly thin line, termed a crest fold in this study, is present but developed at a nearly perpendicular angle to the conch surface (Figs. 1, 3), mostly likely as a result of the tightly bent lamellae around the annular crest. In well-preserved specimens, this perpendicular dark line does not appear to cut through the thin outer and inner layers (Fig. 3.1–3.4). Similar crest folds are prominent in some Devonian *Tentaculites* (e.g., Lardeux, 1969, pl. 14, figs. 2, 3, pl. 16, fig. 1) but seem poorly developed in most Silurian forms illustrated by Larsson (1979). A separate note of interest is that all Ordovician tentaculitid-like, free-living forms of *Cornulites* have only primary rings (i.e., annuli) and lack finer annulets that are typical of Late Silurian–Devonian tentaculitid species. In the early Silurian (mid-Telychian) forms of *Tentaculites* from the middle Jupiter Formation of Anticosti Island, the annulets are already well developed, although the species remains to be described.

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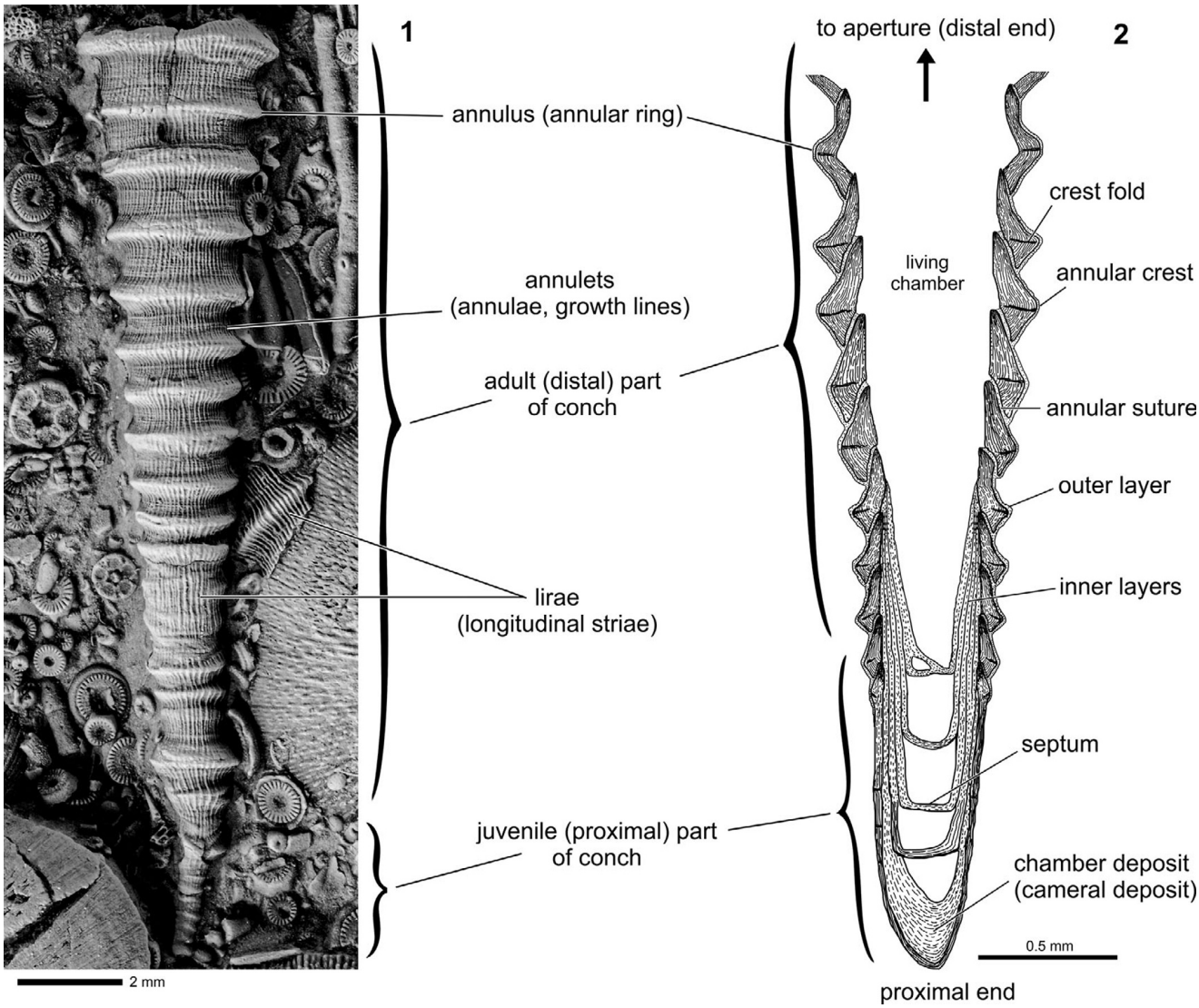


Figure 1. General morphology of free-living cornulitids. (**1**) External morphological features and terms used in this study, adapted from Larsson (1979), for a specimen of *Cornulites richmondensis* (Miller, 1874), GSC 153887, from locality A1339, Fraise Member (lower Hirnantian), Ellis Bay Formation. (**2**) Schematic drawing of internal structures (distal half of conch not shown), based on *Cornulites hemistriatus* n. sp. from the Vaureal Formation (upper Katian), locality A17, Anticosti Island.

Septa. In randomly cut longitudinal or oblique sections of the Anticosti Island material, some conchs of *Cornulites* are shown to have up to seven transverse septa, which can be flat but more commonly show a slight arch toward the proximal end (Fig. 4.1, 4.5). Similar septa have been described in Silurian cornulitids from Estonia, Sweden (Vinn and Mutvei, 2005), and Great Britain (Herringshaw et al., 2007). In the Anticosti Island material, endoconic deposits have been observed only in some transverse cross sections, with either a radial or concentric fabric of calcite (Fig. 4.7, 4.8). It is not clear at present whether the concentric thickening represents similar endoconic septa. The septa are typically very thin and susceptible to damage, and their presence can sometimes be determined by alternating sparry cement and 'dirty' matrix with sharp boundaries (Fig. 4.6). The color contrast is useful for estimating the length of the septate conch.

In specimens of *Cornulites* from Anticosti Island, the septa geniculate against the inner surface and extend for only a short distance in the direction of the aperture (Figs. 1, 4.1). The lack of septal lining in the Anticosti specimens make the middle and distal annuli largely discrete despite the overlap of adjacent annuli. In this respect, the Ordovician specimens are similar to the semivesicular-walled *Cornulites* illustrated by Vinn and Mutvei (2005) and Herringshaw et al. (2007, fig. 4).

Conch microstructures

To better understand the architecture of cornulitid lamellae, one should compare it to other calcareous skeletons with lamellar microstructure, because shell microstructures have been used in some previous studies as evidences of various taxonomic affinities for cornulitids and tentaculitids, including their relationships to polychaetes, mollusks, bryozoans, brachiopods, and arthropods (e.g., Towe, 1978; Dzik, 1991; Vinn and Mutvai, 2009; Vinn and Zatoń, 2012).

Lamellar wall. Late Ordovician forms of *Cornulites* have a relatively simple conch wall, which mainly consists of three layers. The bulk part of the conch wall is composed of thin, cross-bladed lamellae of

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calcite, with each lamella having a thickness of ~ 50 nm (Fig. 5.1–5.4). The bending lamellar layers around the annular crests and annular sutures in the Anticosti *Cornulites* are rather similar to those of Silurian tentaculitids from Gotland, Sweden (e.g., compare Fig. 5.1 and 5.2 with Larsson, 1979, p. 29, fig. 8), and cornulitids from Gotland of Sweden (Vinn and Mutvei 2005, p. 733, fig 4.8) and Much Wenlock Limestone, Great Britain (Herringshaw et al. 2007, p. 691, fig. 4). The outer conch surface is covered by a thin film of microgranular or structureless calcite. This thin outer layer (Figs. 1, 3.1–3.4) resembles the primary layer of a brachiopod shell. In the middle and distal portions of the conch, a similar primary layer can cover the inner surface but usually is poorly developed. The inner surface of the proximal portion can be lined by the geniculated lateral parts of the septa, or by various types of secondary deposits (thickening). In many Devonian tentaculitids, the juvenile portion of the conch can be filled by crowded to solidly stacked conical septa or deposit, leaving a small, off-centered, conical chamber (e.g., see Lindemann and Melycher, 1997). In the Late Ordovician cornulitids of Anticosti Island, a similar thickening deposit is found in some conchs; it can have a radial or concentric fabric in cross section or appear obliquely prismatic in longitudinal section (Fig. 3.4).

The longitudinal sections show that each annulus partly overlaps with its adjacent annulus, with approximately one-third of its length being free of any overlap. In cross sections, therefore, the conch can appear to be either single-ringed (annuli not overlapped) or double-ringed (adjacent annuli partly overlapped). The distal end of each annulus is considerably thinner than its proximal end, which coincides with the transverse crest of each annulus and overlaps with the previous annulus from outside. The outside annulus, therefore, always appears to be much thicker than the inner annulus in cross sections through the overlapped parts (Fig. 6.3). In transverse sections, the lamellar layers tend to be much denser and better defined in the thinner, distal portion than in the thicker, proximal portion of an annulus, although this might be due to the different orientation of the lamellae, which are subparallel to the long axis of the conch in the distal portion of each annulus but bend outward at the proximal end (thus subparallel to the cut surface in cross section).

The lamellae of the cornulitid conch are much less clearly defined compared to those of a brachiopod shell (Fig. 7.1). Some well-calcified trilobite carapaces can also have a clearly defined lamellar structure (Wilmot and Fallick, 1989; Clarkson, 1998), which is particularly clear when the carapace is partially pyritized (Fig. 7.2–7.5). The similarly layered skeletal construction in tentaculitids, brachiopods, and arthropods was also noted by Larsson (1979). In their fuzzy texture, the lamellar layer of the Late Ordovician *Cornulites* is more similar to the lamellar cuticle of trilobites than to a brachiopod shell.

In thin sections, cornulitid conchs and trilobites cuticles show a similar pseudopleochroism, characterized by a light reddish-brown color. In trilobite and ostracodes, the brownish color is considered the result of relatively high organic content incorporated into the calcitic skeleton during calcification from an organic base, although chitin has not been detected (Clarkson, 1998). In brachiopods and mollusks, the individual crystals (fibers or plates, calcite or aragonite) are commonly secreted separately and enveloped by an organic membrane, which accounts for the clean crystals and well-defined lamellar fabrics. In trilobites, the calcitic skeleton was secreted and thickened rapidly after molting by continuous and perhaps syntaxial biomineralization in a direction perpendicular to the cuticular surface, without organic membranes separating adjacent crystals or lamellae. This mode of calcification can be deduced from its characteristic sweeping, undulose extinction bands perpendicular to the shell surface, probably reflecting orientation of the calcite needles normal to the cuticular surface (Fig. 6.1). Interestingly, calcareous tubes of annelid worms (Fig. 6.4, 6.5) and cornulitid conchs (Figs. 6.3, 7.4, 7.5) have similar patterns of optical extinction, particularly in cross sections. In contrast, brachiopod and most molluscan shells have randomly oriented crystals in the lamellae and do not have perpendicular bands of extinction.

Conch perforations. Cornulitid shell is characterized by presence of pseudopunctae similar to those of some brachiopods (Vinn and Mutvei, 2005).

It should be noted that minute microperforations often can be misinterpreted in thin sections and SEM images. Brachiopod workers are familiar with the fact that fine punctae (especially those of dalmanelloid brachiopods; see Fig. 7.1) are difficult to photograph, using either petrographic microscopes or SEM. In thin sections of truly punctuate brachiopod shells, the entire diameter of a microscopic hollow tubule can be within the focal depth and a puncta, which can appear as a column of bent lamellae (e.g., Williams, 1997, p. 297). This was also clearly demonstrated by the coarse punctae of *Paucicrura fistulosa* Jin and Zhan, 2008 in the Anticosti Island material (Fig. 7.1)—the shell lamellae appear to go through the hollow punctae, a visual illusion as a result of the continuation of lamellae around the punctae. In this case, pyritization has created black outlines of the punctae, much like the 'lignes sombres' in tentaculitids of Lardeux (1969). Without pyritization, the hollow punctae in the brachiopod shells are difficult to observe in thin sections. The pseudopunctae of strophomenide brachiopods are reflected most commonly as bent lamellae. This could have led Larsson (1979) to compare *Tentaculites* conchs with pseudopunctate brachiopod shells, although some of his SEM images indicate that perforations of various orders in size are present in the Silurian tentaculitids (for example, see Larsson, 1979, figs. 7D, 66D, 67C). Similarly, the SEM images of pseudopunctae illustrated by Vinn and Mutvei (2005) for *Cornulites* closely resemble the fine, 'pustular' punctae of some orthide brachiopods when they are filled by calcite cement, such as those in the truly punctate shells of *Dicoelosia* King, 1850 from the lower Silurian of Anticosti Island (compare the SEM image of Vinn and Mutvei, 2005, fig. 4.2 with those of Jin and Copper, 1999, fig. 11.3–11.6). The chevron-bending of microlamellae, therefore, cannot be regarded as conclusive evidence for an imperforated shell microstructure. Both surface images and thin sections indicate that all of the Anticosti Island forms of *Cornulites* have well-developed perforations, which are clearly visible on slightly weathered outer surfaces or in thin sections of partially pyritized conchs (Figs. 2.5–2.6, 5.3, 5.4, 7.5). The perforations appear best developed near the crests of annuli. Most of the pores are susceptible to clogging by cement or matrix, which gives an apparently random distribution of exposed pores.

The microscopic canals or tubules observed in thin sections of trilobite cuticles (Wilmot, 1990; see also Whittington, 1997, p. 78–80) are remarkably similar to those of *Cornulites* from Anticosti Island. The similarity becomes even more conspicuous when both the lamellae and intersecting perforations are pyritized in the cornulitid and trilobite skeletons, which are often preserved together in the Anticosti Island material (Fig. 7.2–7.5).

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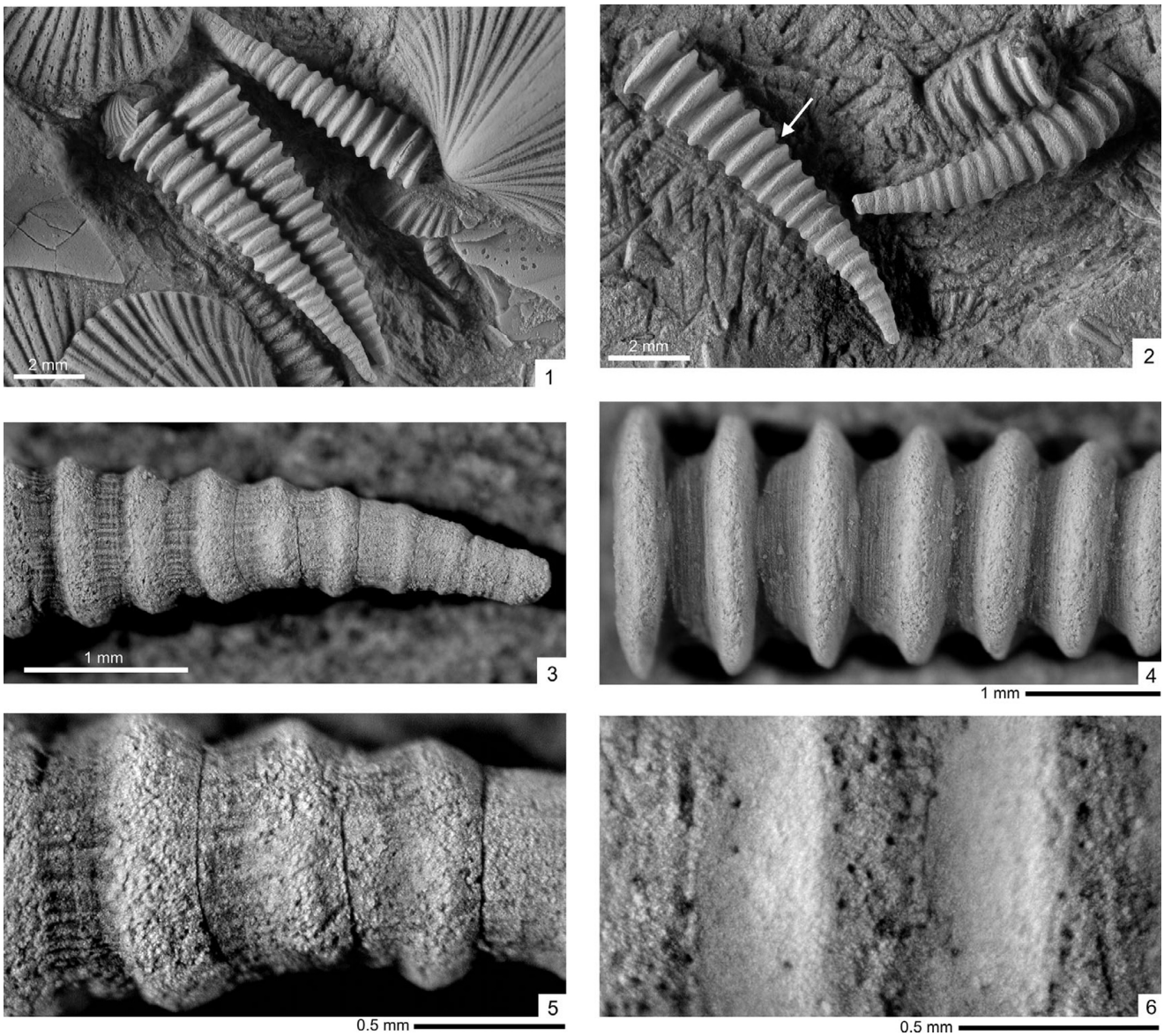


Figure 2. *Cornulites hemistriatus* n. sp., preserved in brachiopod (*Paucicrura* Cooper, 1956) shelly packstone, Vaureal Formation (upper Katian), locality A17, Anticosti Island: (**1**) three paratypes, GSC117815–117817; (**2–6**) holotype, GSC 117814 (arrow), together with two other partly buried conchs. Note holotype with weak lirae and annular sutures in proximal part (**3, 5**), fine transverse growth lines in distal part (**4**), and exposed or clogged perforations/pseudopunctae (**5, 6**).

Paleoecology of Late Ordovician cornulitids of Anticosti Island

Both encrusting and free-living cornulitids are common in the Vaureal (upper Katian) and Ellis Bay (Hirnantian) formations of Anticosti Island. The smooth, strongly biconvex, impunctate shells of *Hindella* Davidson, 1882 and concavoconvex pseudopunctate shells of *Leptaena* Dalman, 1828 have been found to be mostly commonly covered by encrusting cornulitids, especially in specimens from the reefal facies of the Laframboise Member (upper Hirnantian) of the Ellis Bay Formation. The encrusting cornulitids are usually found to have their apertures oriented toward the brachiopod shell commissure but they do not obstruct the commissure, suggesting an in-vivo symbiotic relationship.

Mode of life has been much more enigmatic for free-living cornulitids, which generally have larger and longer conchs than the encrusting forms. On Anticosti Island, they occur most commonly in brachiopod shell beds with dark gray, soft-weathering, micritic mud matrix (e.g., Figs. 2.1, 8.1–8.3, 9), like the host-rock lithology of free-living cornulitids from the Cincinnati Arch region (Fig. 9.1–9.6). Despite their co-occurrence, no attachment scars have been observed in either the free-living cornulitids or on brachiopod shells. It is likely that these free-living cornulitids were 'mud-stickers' on soft, muddy substrata, with their long, slender conchs buried (at least partly) in a vertical to subvertical life position, in a similar way as the Devonian tentaculitids preserved in situ in the soft, muddy facies of the Arkona Formation in southern Ontario (Tsujita and Baird, 2024). When living among the brachiopod shell beds, the vertical orientation would have been further supported by the relatively tight packing (often known as crowding) of brachiopod shells, favoring the filter-feeding activities of both brachiopods and cornulitids.

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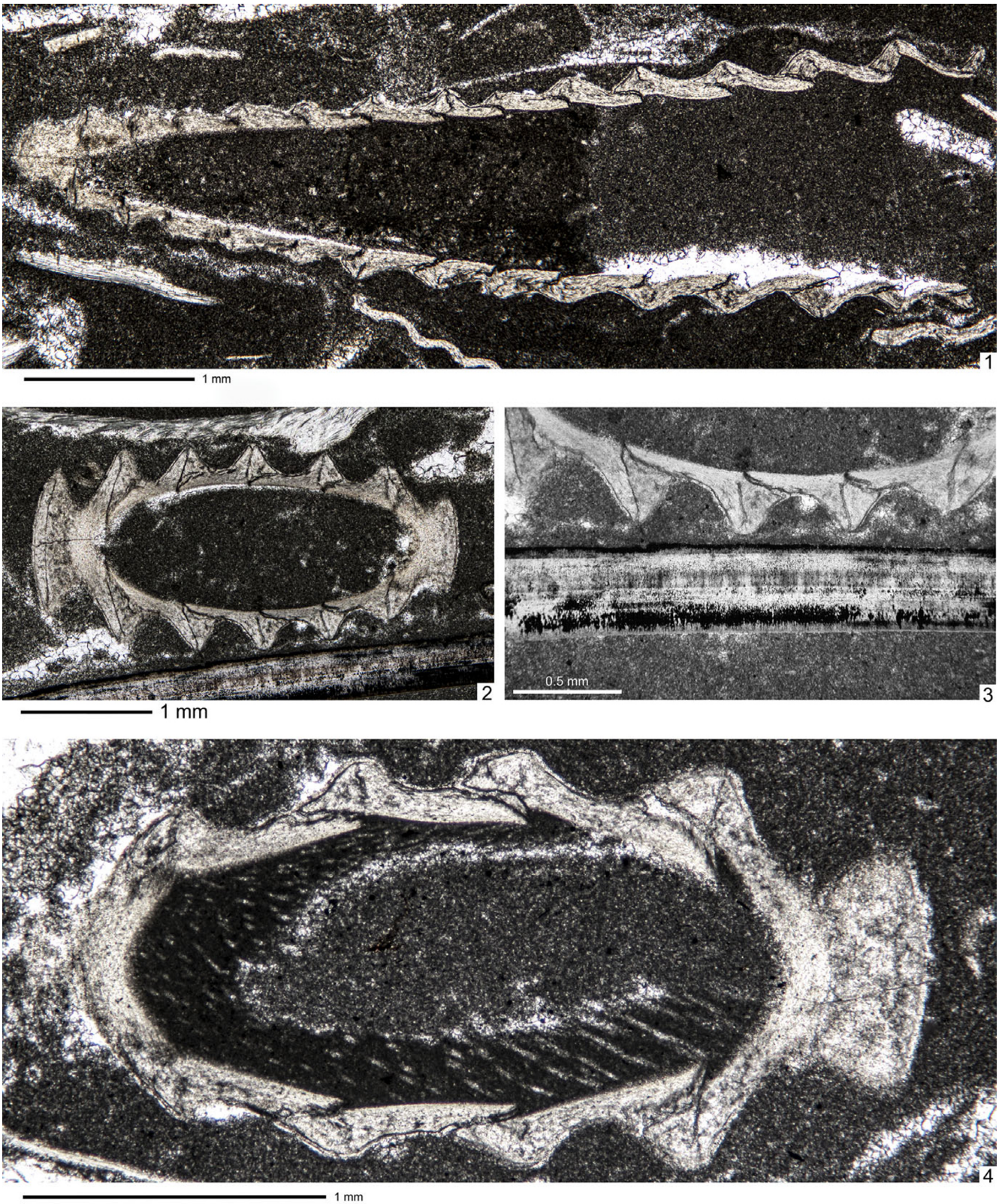


Figure 3. Thin-section slides cut from the same piece of shelly packstone, with numerous conchs of *Cornulites hemistriatus* n. sp. embedded in brachiopod-trilobite shelly packstone slab, paratype, GSC 117818, Vaureal Formation (upper Katian), locality A17, Anticosti Island: (**1**) proximal and middle portions of living chamber, showing ghost septa and chamber (marked by variable shades of dark matrix) in proximal portion, annular suture, and crest folds (refer to Fig. 1); (**2, 3**) oblique section through seven annuli (**2**) and detailed view (**3**) of annular sutures and crest folds, with flat trilobite cuticle below showing fine lamellae; (**4**) section through five annuli, showing obliquely oriented prismatic inner layer, which might have been primarily aragonitic and usually poorly preserved.

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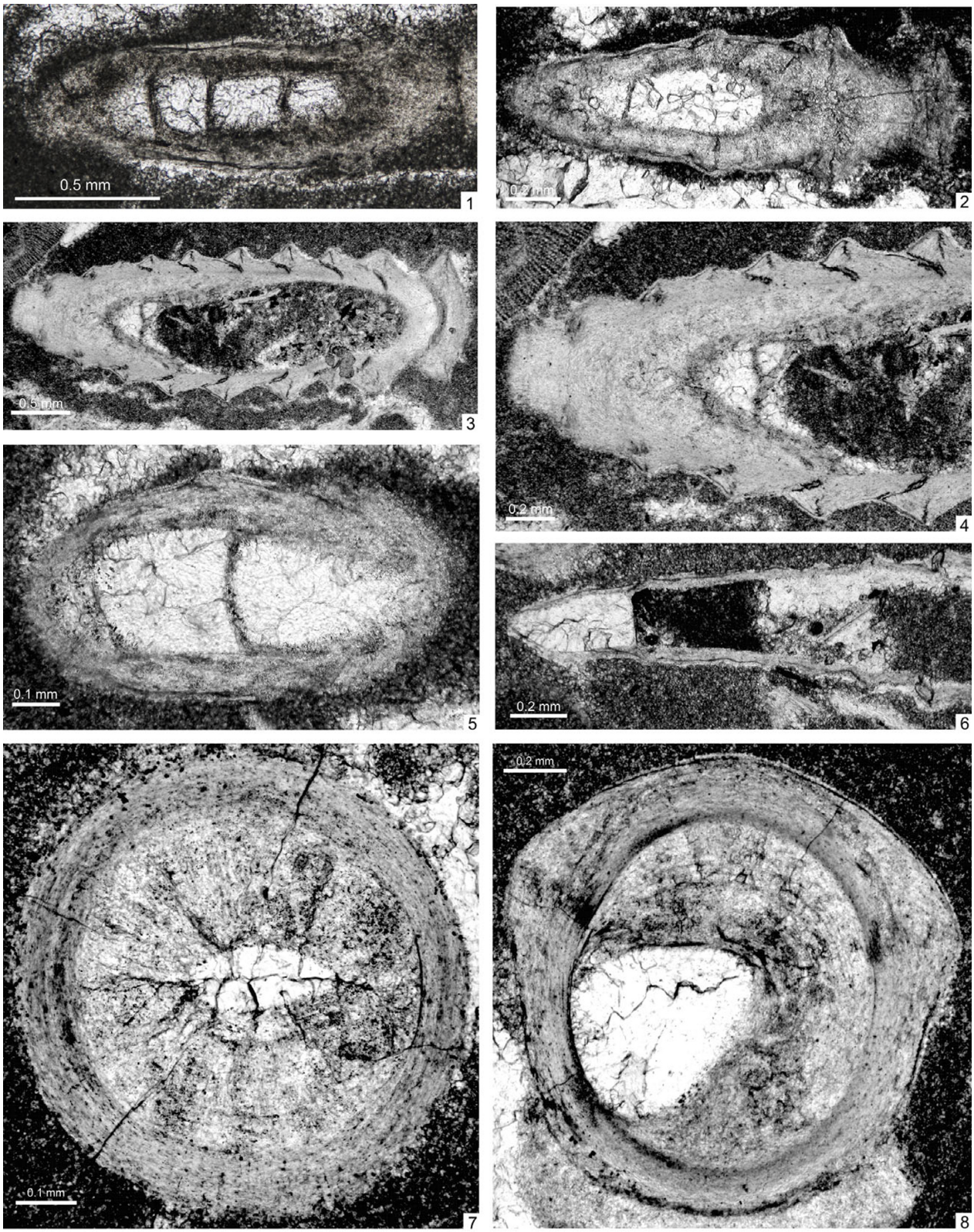


Figure 4. Thin-section slides cut from same piece of shelly packstone, with numerous conchs of *Cornulites hemistriatus* n. sp., embedded in brachiopod-trilobite shelly packstone slab, paratype, GSC 117818, Vaureal Formation (upper Katian), locality A17, Anticosti Island: (**1**) oblique longitudinal section of apical part with three septa; (**2**) oblique transverse section with one septum; (**3, 4**) oblique longitudinal section showing transition from septate conch to aseptate living chamber; note well-developed annular sutures, crest folds, and inner layers; (**5**) oblique transverse section with two septa; (**6**) longitudinal section of apical part, with nearly flat septa and cement-filled initial chamber; (**7, 8**) chamber deposit in apical portion, showing both radial (**7**) and concentric (**8**) calcite fabrics.

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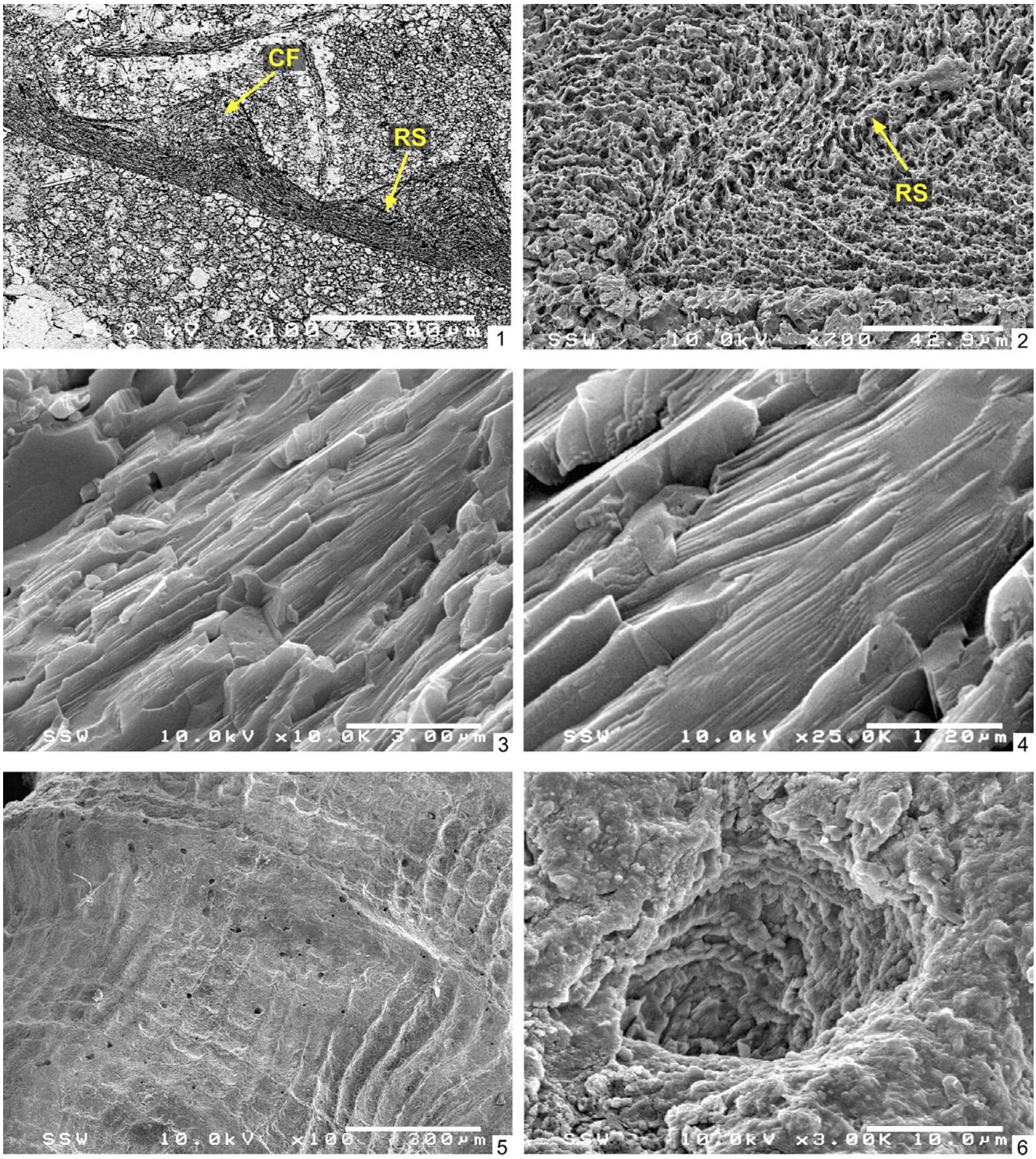


Figure 5. SEM micrographs of conch structures. (**1–4**) *Cornulites hemistriatus* n. sp., Vaureal Formation (upper Katian), locality A17, Anticosti Island: (**1, 2**) paratype, GSC 131885, slightly etched polished rock surface, showing microstructures of annular suture (RS) and crest fold (CF); (**3, 4**) paratype, GSC 117819, randomly broken cross sections showing fine calcite blades of lamellae structure. (**5, 6**) *Cornulites richmondensis* (Miller, 1874), hypotype, GSC 117823, Ellis Bay Formation, Fraise Member (basal Hirnantian), locality A1513, Anticosti Island; isolated conch showing coarse lirae, growth lines, randomly exposed perforations/pseudopunctae (**5**) and detail view of one perforation (**6**).

Phylogenetic implications

The discovery of *Tentaculites*-like, free-living *Cornulites* specimens from the Upper Ordovician of Anticosti Island presents important implications for our understanding of tentaculitoid evolution, particularly in the context of the relationship between cornulitids and tentaculitids. These specimens exhibit a suite of morphological and structural characteristics that appear intermediate between typical cornulitids and early benthic, thick-walled tentaculitids. This intermediate nature provides a potential evolutionary link between the two groups.

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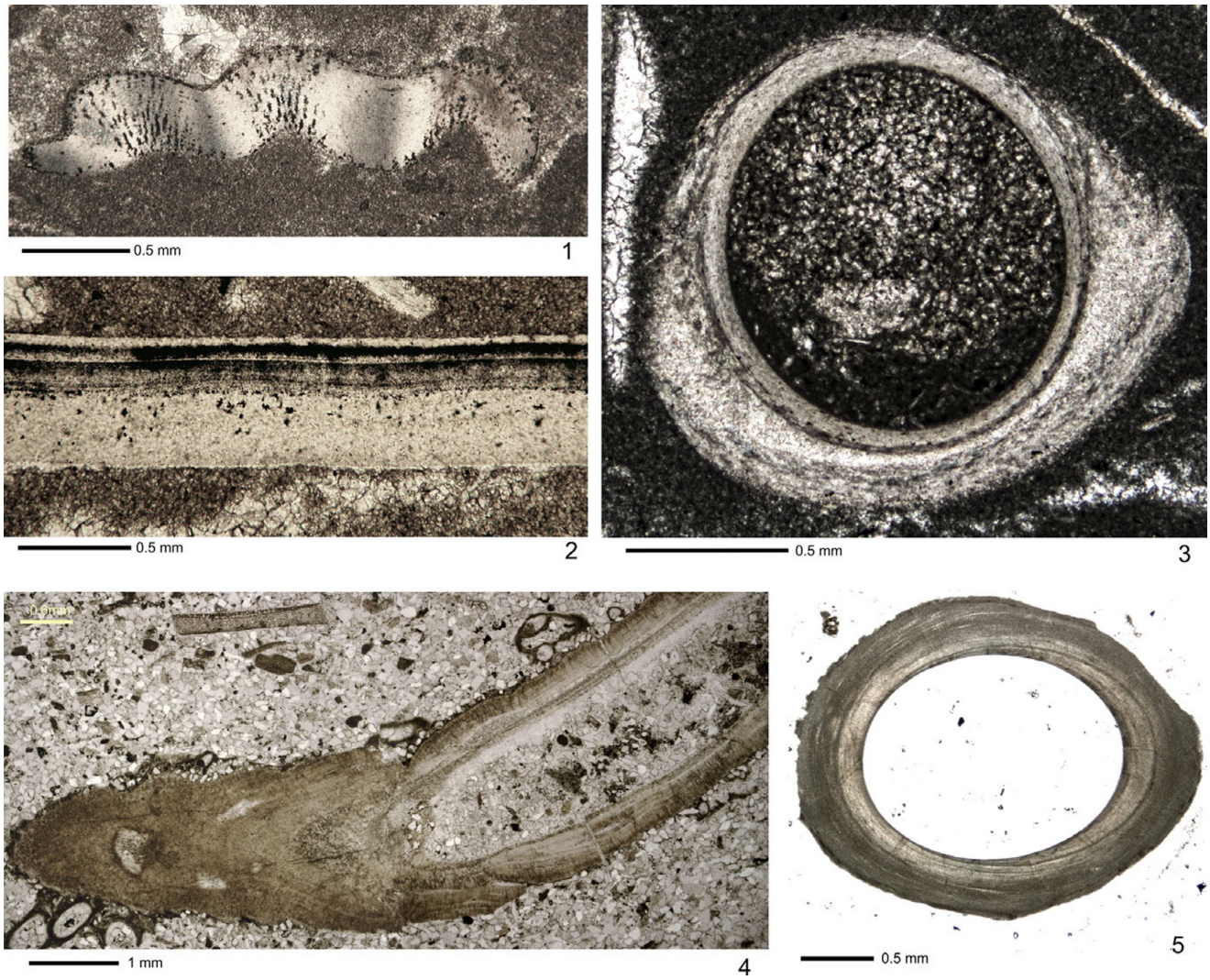


Figure 6. (**1–3**) Thin section slides cut from same piece of shelly packstone, with numerous conchs of *Cornulites hemistriatus* n. sp., embedded in brachiopod-trilobite shelly packstone slab, paratype, GSC 117818, Vaureal Formation (upper Katian), locality A17, Anticosti Island: (**1**) trilobite cuticle viewed in polarized light, showing perforations and perpendicular extinction bands; (**2**) isotelid trilobite fragment viewed in plain light; (**3**) distal end of annulus (inner) overlapped with proximal end (corresponding to crest) of succeeding annulus, with inner annulus showing extinction bands similar to those of trilobite cuticle (polarized light). (**4, 5**) Cross section of annelid worm tube, showing major banding (**4**) and its further enlarged view of densely foliated lamellae (**5**), Ben Nevis Formation, Cretaceous (Albian), Jeanne d'Arc Basin, Newfoundland (Guy Plint collection, University of Western Ontario).

The cladistic analysis of selected taxa provides us with some insight into the evolution of tentaculitoids (Fig. 10). However, the cladistic framework presented here should be regarded as preliminary, primarily because the presence or absence of several diagnostically important characters (e.g., vesicular microstructure and pseudopunctae) remain unknown for a substantial number of cornulitid taxa. This lack of comprehensive morphological data currently limits the feasibility of conducting a comprehensive cladistic analysis. Nevertheless, the preliminary result derived from the cladistic analysis here corroborates the hypothesis based on qualitative morphological data that free-living cornulitids characterized by regular annulation might have given rise to the tentaculitids. Such a relationship would suggest that certain structural and ecological adaptations observed in early cornulitids could have been precursors to the more specialized morphologies of tentaculitids, reflecting a potential evolutionary continuum between the two groups.

One of the most notable features of these *Cornulites* shells is the absence of a vesicular wall structure, a characteristic trait typically observed in the genus. Instead, the walls are composed of compact calcareous laminae, a condition more aligned with the tentaculitids. Furthermore, the external ornamentation of these organisms, characterized by extremely regular annuli, is unusual for cornulitids, suggesting a potential shift toward the tentaculitid morphological pattern.

The shell curvature of free-living *Cornulites* is another significant point of comparison. Rather than displaying the highly curved or sinuous morphology seen in many cornulitids (Vinn and Mutvei, 2005, 2009), these shells are straight to very gently curved—an overall geometry that closely resembles that of tentaculitids. Such a transition in shell morphology might reflect adaptation to a different mode of life or environmental conditions, possibly soft-substratum habitats, which is more consistent with those occupied by early tentaculitids. On a microstructural level, the similarity between free-living *Cornulites* and tentaculitids becomes even more apparent, which might have contributed to the close affinity between the two groups in the cladogram (Fig. 10). The shell microstructure of the former is notably akin to that of thick-walled

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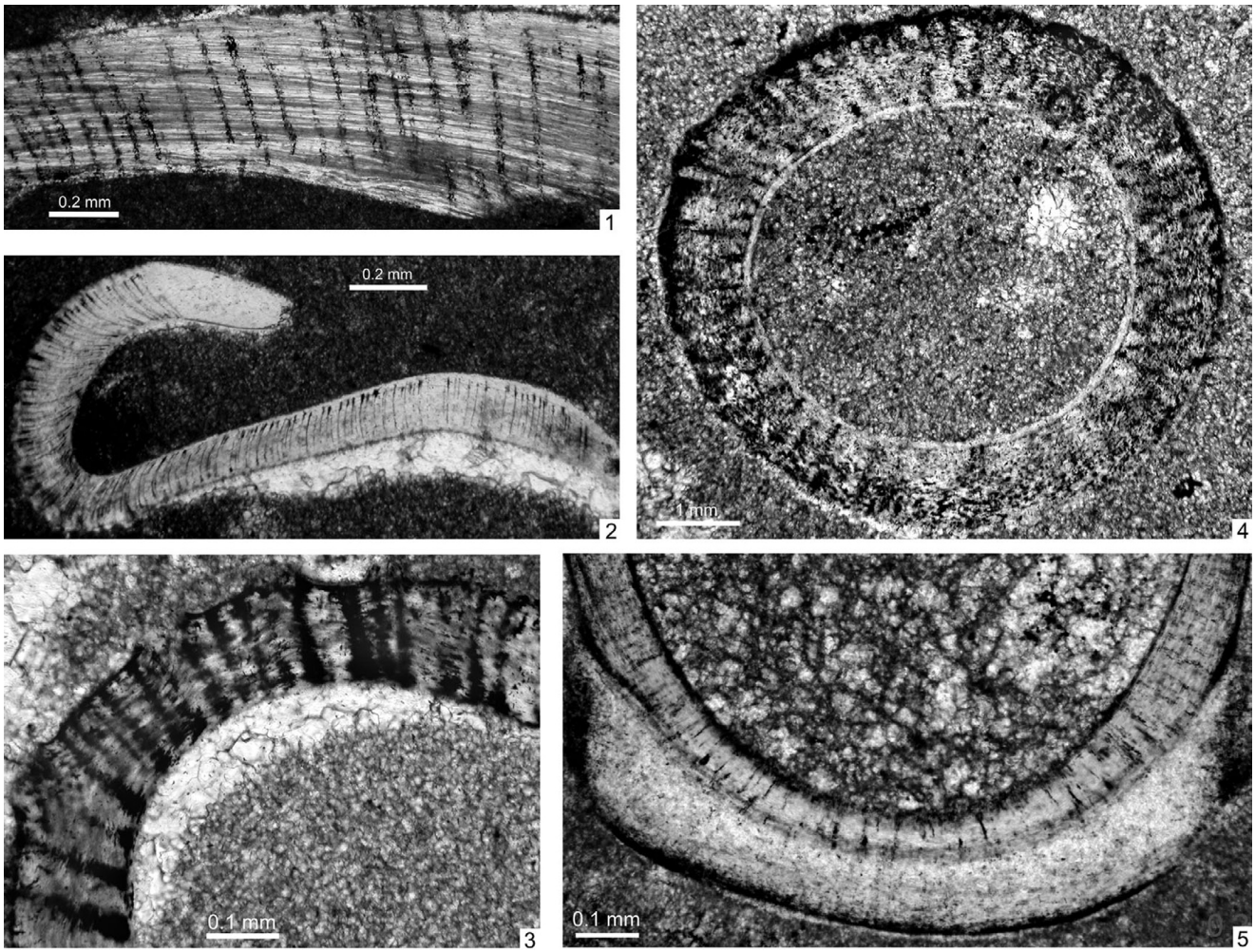


Figure 7. Thin-section slides cut from same piece of shelly packstone, with numerous conchs of *Cornulites hemistriatus* n. sp., embedded in brachiopod-trilobite shelly packstone slab, paratype, GSC 117818, Vaureal Formation (upper Katian), locality A17, Anticosti Island: (**1**) *Paucicrura fistulosa* Jin and Zhan, 2008, pyritized punctae in fibrous lamellar layer; (**2**) pyritized perforations in trilobite cuticle; note surface layer not penetrated; (**3**) pyritized perforations and laminae of strongly curved trilobite cuticle. (**4, 5**) *Cornulites hemistriatus* n. sp., partly pyritized annulus through nonoverlapping (**4**) and overlapping (**5**) parts, showing perpendicular perforations.

tentaculitids, with evidence suggesting a shift from a foliated structure (Vinn and Mutvei, 2005) common in cornulitids, to a cross-bladed lamellar organization (Larsson, 1979). This transformation in microstructure could have conferred increased mechanical strength or other functional advantages necessary for life in soft-bottom environments.

Evolutionarily, it is hypothesized that free-living *Cornulites* could represent a transitional form that eventually gave rise to the thick-walled tentaculitids, which is corroborated by the preliminary cladistic analysis (Fig. 10). This evolutionary trajectory would have involved the loss of the vesicular conch layer, modification of the shell microstructure, and the development of more complex layering within the inner shell wall. These changes appear to have occurred without substantial shifts in ecological strategy, because both the free-living *Cornulites* and thick-walled tentaculitids likely shared similar benthic lifestyles, possibly as infaunal or epifaunal suspension feeders. An important ecological distinction, however, lies in larval settlement behavior. Although cornulitid larvae, including those of free-living forms, always settled on hard substrata (Vinn and Mutvei, 2009; Vinn, 2010; Vinn and Zatoń, 2012), early tentaculitid larvae appear to have developed the ability to settle on soft substrata. This change would have marked a significant ecological transition, allowing tentaculitids to exploit new habitats and potentially avoid competition for limited hard substrata. Such a shift could have played a crucial role in the success and diversification of tentaculitids during the Paleozoic.

In conclusion, the Upper Ordovician *Cornulites* from Anticosti Island provide a compelling case of evolutionary transition between two major groups of enigmatic Paleozoic tube-dwelling organisms. Their morphology, shell microstructure, and inferred life habits support the hypothesis of a gradual, predominantly morphological evolutionary pathway from cornulitids to tentaculitids, driven by ecological innovation and microstructural modification rather than dramatic lifestyle change.

Systematic paleontology

Class Tentaculita Bouček, 1964
Order **Cornulitida** Bouček, 1964
Family **Cornulitidae** Fisher, 1962
Genus ***Cornulites*** Schlotheim, 1820

Type species. *Cornulites serpularius* Schlotheim, 1820. Silurian, Gotland, Sweden.

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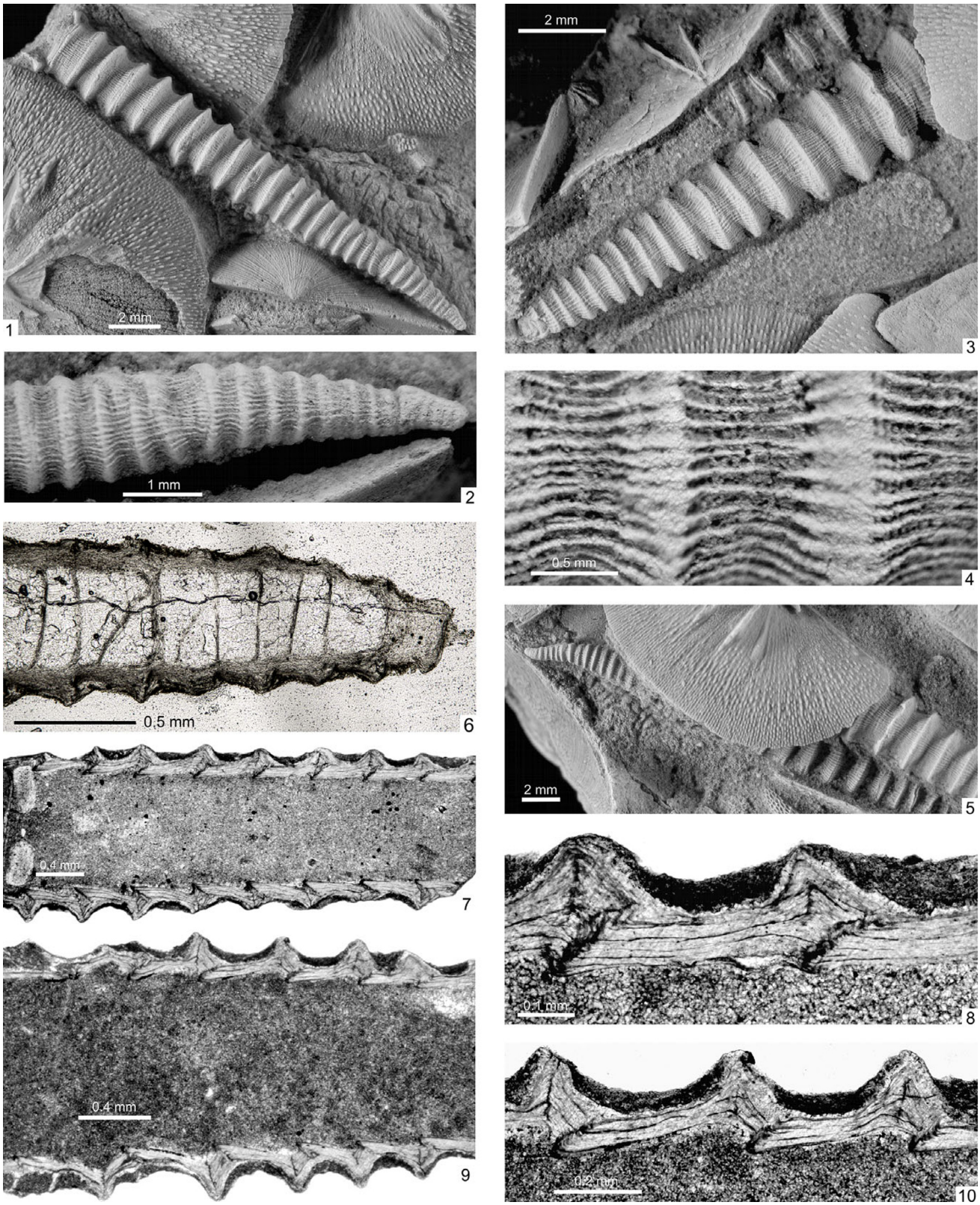


Figure 8. *Cornulites richmondensis* (Miller, 1874): (**1–5**) three hypotypes preserved on sowerbyellid shelly packstone, Ellis Bay Formation, Fraise Member (basal Hirnantian), locality A1513, Anticosti Island: (**1, 2**) GSC 117820, nearly complete specimen, with further enlarged view of proximal part (**2**); (**3, 4**) GSC 117821, partly buried specimen, showing proximal half of conch (**3**), lirae, and perforations/pseudopunctae (**4**); (**5**) GSC 117822, another conch buried side by side with GSC 117821, showing gently curved proximal part; (**6**) GSC 153884, thin-section slide, one of three broken, loose pieces of conchs embedded in epoxy, longitudinally cut, showing septa and chambers, Juncliff Member (middle), locality A1334a, Anticosti Island; (**7–10**) GSC 153886, thin-section slide, two of nine broken, loose pieces of conchs embedded in epoxy, longitudinally cut, showing annular sutures and crest folds.

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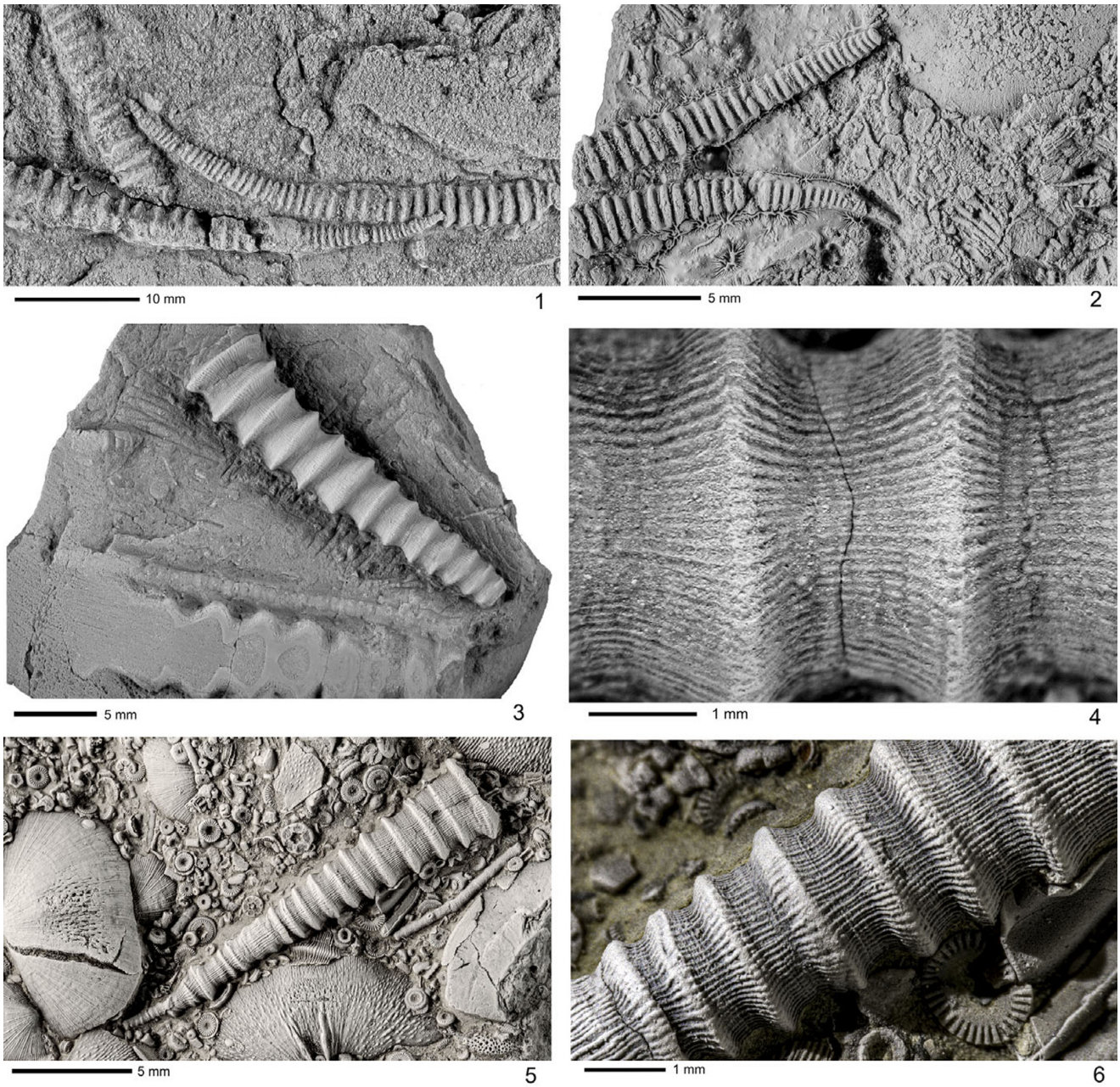


Figure 9. Various species of 'free-living' *Cornulites* spp.: (**1–4**) syntypes of three species of *Cornulites* from the 'Cincinnatian Group' (original labels), Katian, Illinois, USA, originally described in *Tentaculites*: (**1**) *Cornulites oswegoensis* (Meek and Worthen, 1865), five syntypes embedded in same block of shelly wackestone, ISM-12005, Oswego, Kendal County, Illinois; (**2**) *Cornulites sterlingensis* (Meek and Worthen, 1865), two syntypes preserved in sowerbyellid packstone, ISM-12013, Sterling, Illinois; (**3, 4**) *Cornulites tenuistriatus* (Meek and Worthen, 1865), two syntypes (one being longitudinally cut), ISM-12014, Alexander County, Illinois; note relatively larger conch diameter and sharply developed lirae (longitudinal striae); (**5, 6**) *Cornulites richmondensis* (Miller, 1874), GSC 153887, one of several conchs embedded in a piece of coquina; note well-preserved juvenile part of the conch (**5**) and sharp lirae (**6**; see also Fig. 1.1), from Fraise Member, Ellis Bay Formation, locality A1339, Cailloux Road, Anticosti Island.

Remarks. The genus *Cornulites* is characterized by vesicular wall structure, presence of longitudinal costae or striae, and well-developed internal annulation. The Anticosti cornulitids described here, however, lack any vesicular microstructures that are diagnostic of ordinary *Cornulites* (Vinn and Mutvei, 2005).

Cornulites hemistriatus new species
Figures 1–7

Type specimens. Holotype, GSC 117814, one of several conchs embedded in small block of coquina; 3 paratypes, GSC 117815–117817, conchs embedded in small block of coquina; paratype GSC 117818, a set of five thin sections from the same block of the coquina; and paratype GSC 131884, one small, slightly etched tablet of coquina for SEM. All the types are from the Vaureal Formation, 'Lavache Member' (informal), Richmondian (upper Katian), road-cut outcrop along Main Road by old gate to old Macdonald Lodge (locality A17), UTM 17, 489600E, 5510820N, Anticosti Island.

Materials. Numerous specimens embedded in brachiopod coquina from localities A17 and A130, 'Lavache Member' (informal), Vaureal Formation.

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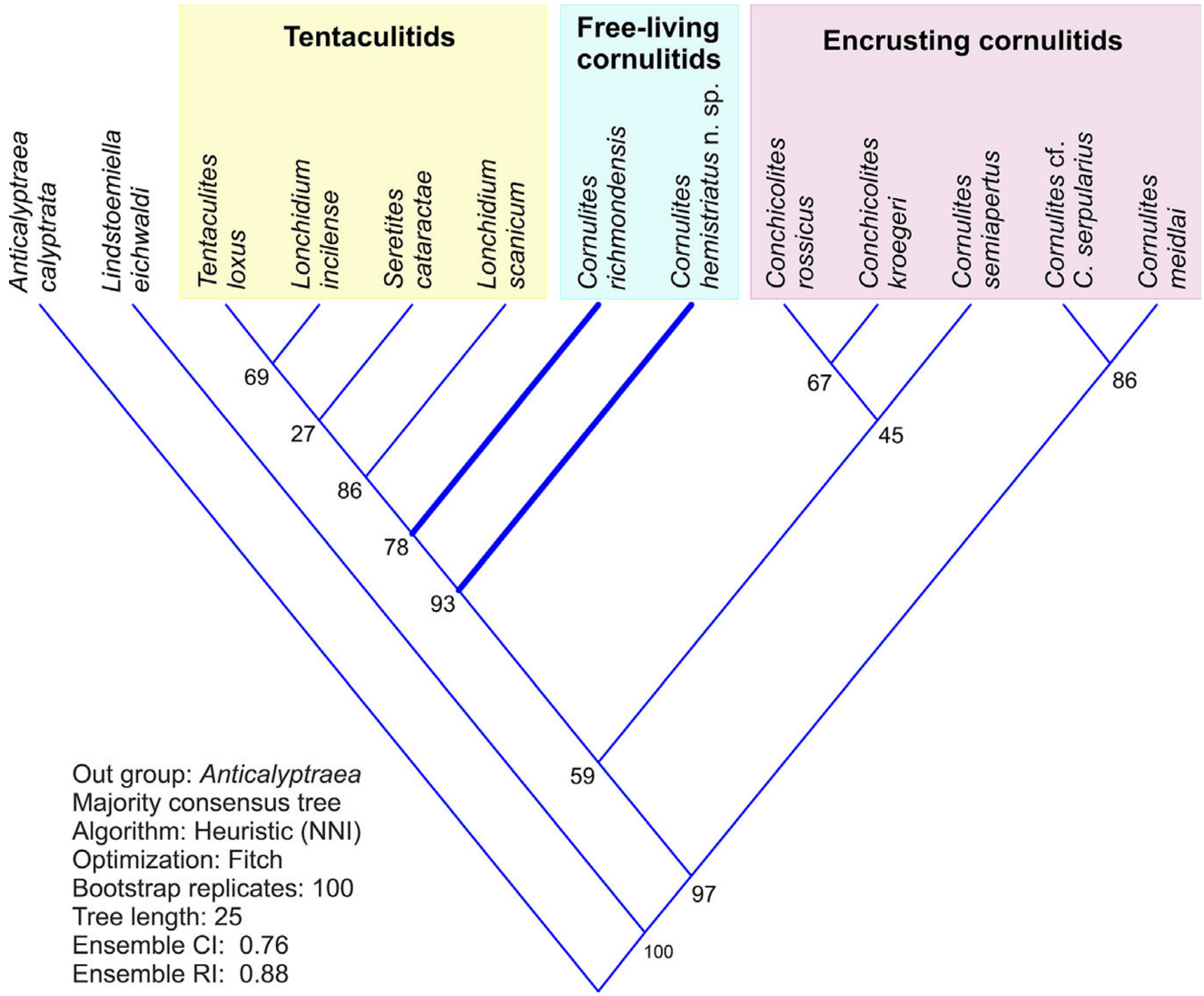


Figure 10. Cladistic analysis of representative species of free-living *Cornulites* spp., encrusting cornulitids, and tentaculitids of Late Ordovician–Silurian age. Number at each branching node in the cladogram denotes the percentage of bootstrap replicates that support that node. Software package: PAST ver. 1.80 (Hammer et al., 2001). See Appendix 1 for coding of characters and character states.

Diagnosis. Conch relatively small, up to 12 mm in length and 2 mm in apertural diameter, with slightly curved proximal portion; low, rounded lirae present in proximal half but absent in distal half; annular sutures conspicuous; inner layers poorly developed in living chamber.

Description. Conch small, up to 12 mm in length and 2 mm in diameter; proximal portion slightly arcuous, with apical angles of 8–12°; distal portion largely straight. Aperture and annuli perpendicular to long axis, with crest of some annuli slightly warped. The annuli are superficially symmetrical on the outer surface, but strongly asymmetrical when viewed in longitudinal section, with crest located at proximal end of each annulus, bending tightly to produce gentle distal limb and steep proximal limb (Figs. 1, 3). Subsequent annulus added from distal outer surface of previous annulus. Spacing between adjacent annular crests varying from 0.4 mm to 0.8 mm, somewhat closer in proximal portion of conch. Annulets absent. Fine growth lines well developed. Low, rounded lirae present in proximal one-third to one-half of conch, gradually disappearing distally (Fig. 2).

Embryonic chamber poorly differentiated. Up to three septa observed in juvenile part of conch, slightly convex toward apex, rarely flat, with geniculated edge of septa extending in distal direction, forming layers of smooth inner lining in juvenile conch (Figs. 1, 4). Endoconic deposit relatively thin, confined to apical area (Figs. 1, 4.7, 4.8). Inner surface of mid- and distal annuli not lined by additional layers, with terrace formed by outward bending of proximal end of each annulus. Oblique prismatic deposits observed on inner surface of middle part of conch in only one specimen (Fig. 3.4). Perforations present, aligned crudely along circular growth lines, commonly clogged by matrix or cement.

Etymology. The masculine adjective, *hemistriatus*, refers to the longitudinal lirae confined to the proximal half of the conch.

Remarks. The available collection indicates that *Cornulites hemistriatus* n. sp. is confined to the Vaureal Formation, whereas *Cornulites richmondensis* (Miller, 1874) to the Ellis Bay Formation. The assignment of the new species to *Cornulites* is based on its well-developed internal annulation and external longitudinal striae and

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slightly less regular annuli (i.e., annular rings) than in *Tentaculites*. The relatively wide apical angle is also more consistent with *Cornulites* than *Tentaculites*. Fisher (1962) noted that coarse lirae are usually well developed in *Cornulites*, covering either the entire conch surface or a portion (especially the distal portion) of it. In this respect, the new species resembles typical *Cornulites* except that its ornament is confined to the proximal portion. Both *Tentaculites* and *Cornulites* have well-developed septa and endoconic deposit in the proximal portion of the conch, but the obliquely oriented prismatic layer, seen in the proximal part of the living chamber of one specimen (Fig. 3.4), has not been reported previously in either *Tentaculites* or *Cornulites*.

Cornulites richmondensis (Miller, 1874)
Figures 1.1, 8, 9.5, 9.6

1874 *Tentaculites richmondensis* Miller, p. 235, fig. 28.
1888 *Tentaculites richmondensis*; Hall, p. 8–18, pl. 115, figs. 28–30, 33–39.
1910 *Cornulites richmondensis*; Schuchert and Twenhofel, p. 703.
1928 *Cornulites richmondensis*; Twenhofel, p. 142.
1985 *Tentaculites richmondensis*; Davis, 1985, p. 51, pl. 6, fig. 14.
1996 *Tentaculites richmondensis*; Bergström, p. 284, fig. 20-1.2–20-1.4.

Type specimens. Not traced. Miller's (1874) original illustrations and photographs of topotypes from the Waynesville and Whitewater formations (Richmondian, upper Katian) of Richmond area, Indiana, were figured by Bergström (1996).

Occurrence. Ellis Bay Formation, Fraise Member, localities A4, A1339, A1513. Juncliff Member (middle), A1334a (small, curved conchs of *Cornulites* sp. indet. also common). Lousy Cove Member, locality A94.

Description (Anticosti Island material). Conch medium-sized, largely straight, attaining maximum length of 20 mm and diameter of 3 mm. Apical (proximal) part straight or slightly curvy, with notably reduced diameter in some specimens (Figs. 1.1, 8.1, 8.2, 8.5, 9.5, 9.6), with apical angle of 10–14°; middle and distal parts nearly cylindrical, with expansion angle of < 5°. Annuli superficially symmetrical, or with sporadic portions of either proximal or distal limb becoming steeper; crest actually located toward proximal end of each annulus when viewed in longitudinal section (Fig. 8.7–8.10). Each subsequent annulus starting from distal-outer surface of previous annulus, expanding outward first, then bending smoothly inward-distally, thinning gradually toward distal end. Spacing between adjacent annular crests varying from 0.5 mm in proximal portion to 1 mm in distal portion, rarely reaching 1.5 mm (Fig. 8.3). Annulets absent. Lirae sharp, strong, covering entire conch surface; fine, circular growth lines present, somewhat more closely spaced than, and interrupted by, coarse lirae (Fig. 8.4).

Embryonic chamber conical, proximally tapering. Juvenile portion with up to seven septa (Fig. 8.6). Annular sutures and crest folds similar to those of *Cornulites hemistriatus* n. sp. (compare Fig. 8.7–8.10 with Fig. 3.1–3.4). Conch microstructures characterized by cross-bladed lamellae, regularly distributed perforations, and lack of vesicular layers (Fig. 8.6–8.10).

Remarks. Miller's (1874) species, originally described as *Tentaculites richmondensis* from the Cincinnati Arch area, was regarded as *Cornulites* by Twenhofel (1928), who also included material from the basal Ellis Bay Formation of Anticosti Island, an affinity recognized by Vinn and Mutvei (2005), although some fairly recent studies have retained the species in *Tentaculites* (e.g., Davis, 1985; Bergström, 1996). In this study, the species is assigned to *Cornulites* mainly because of its relatively large conch with strong, sharp lirae. This identification is in general agreement to Fisher's (1962) diagnosis of *Cornulites*. Hall's (1888) longitudinal sections of topotype material suggest that *Cornulites richmondensis* lacks the vesicular microstructure, except for one section. In the Upper Ordovician rocks of the Cincinnati area and Anticosti Island, *Cornulites richmondensis* commonly occurs together with generally smaller, flexuous conchs of typical *Cornulites*. The material used by Hall (1888), therefore, might have been a mixture of *Cornulites richmondensis* and *Cornulites flexuosa* (Hall, 1847), because he regarded all the Cincinnatian species of *Cornulites* as parts of a series at "various stages of development of what appears to be a single species of the genus *Cornulites*" (Hall, 1888, p. 17). Thin sections of the Anticosti Island specimens, however, indicate that *Cornulites richmondensis* lacks any vesicular microstructure in the conch wall, which is unusual for *Cornulites* (Vinn and Mutvei, 2005; Herringshaw et al., 2007). Apart from its larger size and more prominent lirae, *Cornulites richmondensis* from the Ellis Bay Formation can be distinguished *Cornulites hemistriatus* n. sp. from the underlying Vaureal Formation of Anticosti Island by having more sharply defined lamellae and a thicker outer layer (Fig. 8.7–8.10). There are three other Ordovician species of *Cornulites* known from the Upper Ordovician rocks of Illinois, also originally described in *Tentaculites* and adopted subsequently in various formal or informal literature of the Cincinnati arch area, although they have been poorly studied. These include *Cornulites tenuistriatus* (Meek and Worthen, 1865), *Cornulites oswegoensis* (Meek and Worthen, 1865), and *Cornulites sterlingensis* (Meek and Worthen, 1865) (see Fig. 9.1–9.4). Fisher (1962) regarded *T. sterlingensis* as a *Cornulites*, but Bergström (1996, p. 283) treated the species, together with *T. richmondensis*, as "Ordovician *Tentaculites*," although he did not provide any information on their conch microstructures. *Cornulites sterlingensis* is similar to *Cornulites richmondensis* in having well-developed coarse lirae but differs in its smaller conch, usually < 15 mm in length and 2 mm in diameter, with closely spaced annuli at 17–25 per 10 mm (Bergström, 1996). The other two species described by Meek and Worthen (1865, 1868) have notably larger conchs of > 30 mm in length and 4–5 mm in diameter, with prominent, sharp striae and lirae (e.g., *Cornulites tenuistriatus*; Fig. 9.4). The taxonomic identity of these forms needs further study, especially to determine the presence or absence of vesicular microstructure.

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Competing interests. The authors declare none.

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Appendix 1. Coding of tentaculitoid characters and character states

A. Embryonic conch	**H. Regularity of annulation**
1. Cemented to substratum	0. Absent
2. Free	1. Irregularly spaced
	2. Regularly spaced
B. Embryonic chamber size	**I. Annulation development**
1. Small	0. Absent
2. Large	1. Weak
	2. Strong
C. Conch (tube) attachment	**J. Annulets**
0. Absent	0. Absent
1. Secondarily free	1. Present
2. Attached	
D. Conch (tube)-sediment relationship	**K. Internal annulation**
1. Soft-sediment sticker	0. Absent
2. Solitary encruster	1. Present
3. Gregarious	
E. Conch (tube) expansion	**L. Conch (tube) vesicular structure**
1. Narrow	0. Absent
2. Broad	1. Present
F. Conch (tube) curvature	**M. Punctae (pseudopunctae)**
1. Non-coiled	0. Absent
2. Spiral	1. Present
G. Lirae	**N. Development of septa**
1. Absent	1. Sparse
2. Weak	2. Numerous
3. Strong	

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Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Anticalyptraea calyptrata (Eichwald, 1860)	1	2	2	2	1	2	0	0	0	0	0	2	1	1
Lindstoemiella eichwaldi Zatón et al., 2022	1	2	2	2	1	2	0	1	1	0	0	2	1	1
Cornulites cf. *C. serpularius* Schlotheim, 1820	1	2	2	3	2	1	2	1	1	0	1	2	1	1
Cornulites semiapertus (Öpik, 1930)	1	2	2	2	2	1	0	1	2	0	1	1	0	1
Cornulites meidlai Vinn et al., 2023	1	2	2	2	2	1	2	1	1	0	1	2	1	1
Cornulites hemistriatus n. sp.	1	2	1	1	1	1	1	2	2	0	1	1	0	1
Cornulites richmondensis (Miller, 1874)	1	2	1	1	1	1	2	2	2	0	1	1	1	2
Conchicolites rossicus Vinn and Madison, 2017	1	1	2	2	1	1	0	1	2	0	0	1	0	1
Conchicolites kroegeri Vinn et al., 2023	1	1	2	2	2	1	0	1	2	0	0	1	0	1
Lonchidium scanicum Larsson, 1979	2	2	0	1	1	1	1	2	2	1	1	1	0	2
Lonchidium incilense Larsson, 1979	2	2	0	1	1	1	1	2	2	1	1	1	1	2
Tentaculites loxus Larsson, 1979	2	2	0	1	1	1	1	2	2	1	1	1	1	2
Seretites cataractae Larsson, 1979	2	2	0	1	1	1	1	2	2	1	1	1	0	2

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