


Thecate stem medusozoan polyp from the Upper Ordovician of Québec

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Articles

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Abstract

The fossil record of medusozoan cnidarians is relatively sparse and, in some cases, contentious. Here, we describe a new genus and species of a well-preserved, soft-bodied, tubicolous polyp, *Paleocanna tentaculum* n. gen. n. sp., from the Upper Ordovician (Katian) Neuville Formation in Québec. These fossils, preserved as carbonaceous compressions, were found in association with typical shelly assemblages. Fifteen slabs of shaly limestone containing ~ 135 specimens of *Paleocanna tentaculum* n. gen. n. sp. were examined. Individual polyps occupied upright tubes, which occur either solitarily or in clusters. Some tubes exhibit a striated periderm near their base. The polyp is elongated, with a rounded aboral end and a consistent ring of tentacles protruding distally from the tube. A phylogenetic analysis of 69 taxa and 236 discrete morphological characters indicated that the species is more closely related to the extant crown group than it is to the other stem-group medusozoans, e.g., conulariids and carinachitids. The uniform orientation of specimens on single slabs suggests rapid burial. *Paleocanna tentaculum* n. gen. n. sp. represents an exceptionally preserved member of an Ordovician deposit exhibiting Burgess Shale-type soft-tissue preservation.

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Non-technical Summary

Jellyfish and their polyp relatives belong to an ancient group of animals called cnidarians. Because their bodies are soft, they almost never fossilize, leaving gaps in our understanding of their origins. We describe a new fossil species, *Paleocanna tentaculum*, from rocks approximately 450 million years old (Upper Ordovician) in Québec, Canada. These remains are preserved as thin, carbon-rich impressions in limestone, alongside other typical shelly marine species. This cnidarian species lived inside upright tubes, alone or in clusters. Some tubes show faint striations near their bases. The polyp itself was long and narrow, with a ring of tentacles that extended above the rim of the tube. By comparing *Paleocanna* with other living and fossil genera, we found that it is more closely related to modern jellyfish groups such as box jellies, true jellyfish, and stalked jellyfish than it is to other extinct tube-dwelling relatives. This places our species nearer to the modern branch of the family tree than most other known fossil polyps. The exceptional preservation of these fossils makes this discovery one of the rare cases in which delicate soft-bodied organisms are found in Ordovician rocks.

Introduction

The Neoproterozoic era marks the origin of the cnidarian crown group, possibly in the Ediacaran or Cryogenian period (Van Iten et al., 2014). Polypoid cnidarians are predominantly known from their mineralized representatives, e.g., rugose and tabulate corals, which exhibit well-documented skeletal morphologies. In contrast, tubicolous cnidarians with soft-bodied preservation remain relatively rare despite their potential to shed light on the early evolution within the phylum.

Among the earliest representatives are *Paraconularia ediacara* Leme, Van Iten, and Simões, 2022 from the Ediacaran Tamengo Formation of Brazil, considered the oldest documented conulariid and an example of early cnidarian skeletonization. Other carinachitids and hexangulaconulariids, e.g., *Hexaconularia* He and Yang, 1986 and *Carinachites* Qian, 1977 from South China, represent some of the earliest early Cambrian polypoid tubicolous cnidarians, interpreted as members of the stem group Medusozoa (Van Iten et al., 2010; Song et al., 2024). *Auroralumina attenboroughii* Dunn et al., 2022 from the Charnwood Forest, UK, is interpreted as a putative tubicolous stem-group medusozoan, with a bifurcating tubular structure and predatory behavior. *Haootia quadriformis* Liu et al., 2014 from the Ediacaran Fermeuse Formation of Newfoundland was assigned as a total-group cnidarian and a crown-group staurozoan (McIlroy et al., 2024).

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These fossils from late Ediacaran strata support the idea that cnidarians diversified before the Cambrian.

Fossil records of cnidarians are rare and controversial for the Cambrian Period, most of which come from the Chengjiang biota (Liu *et al.*, 2014; Van Iten *et al.*, 2014; Walde *et al.*, 2019; Dunn *et al.*, 2022; Zhang *et al.*, 2022). Among these taxa, *Archisaccophyllia kunmingensis* Hou *et al.*, 2005 might instead have a closer affinity to phoronids, whereas *Xianguangia sinica* Chen and Erdtmann, 1991 could be a cnidarian or a stem-group ctenophore, implying a sea anemone-like ancestor for ctenophores (Ou *et al.*, 2022; Zhao *et al.*, 2019). *Conicula striata* Luo *et al.*, 1999 has variously been classified as a lophophorate (Luo *et al.*, 1999; Zeng *et al.*, 2022), an anthozoan (Hu, 2005), and most recently as a stem-group medusozoan (Zhao *et al.*, 2023). The anthozoan hypothesis is based on a morphology that includes a polyp with an actinopharynx, characteristic of anthozoans, and enclosed within a conical, annulated periderm, suggesting that these traits were present in medusozoans and anthozoans. The Chengjiang hyolithid *Burithes* Missarzhevskii, 1969 is now reclassified as a stem-group medusozoan, *Palaeconotuba* Qu, Li, and Ou, 2023. This reinterpretation was based on the presence of a conical theca and a funnel-like gastrovascular cavity. These two species in *Palaeconotuba* and *Conicula* represent tubicolous forms, a morphological adaptation that appears to have been common in the Cambrian.

Other early Cambrian fossils provide evidence of cnidarian soft-bodied polyps and thecate species. *Nailiana elegans* Ou *et al.*, 2022, from the Chengjiang biota, is an early anthozoan. *Olivoooides* Jian *et al.*, 2016, from the early Cambrian of China, represents a possible stem-group cubomedusa because it exhibits a conical peridermal theca and features characteristics of polyp and medusa stages. *Gangtoucunia aspera* Zhang *et al.*, 2022, from the Wulongqing Formation, represents a total-group medusozoan like a modern scyphozoan polyp. This benthic polyp has a long, tubular, annulated theca that is a mineralized tube, reinforcing the idea that cnidarian biomineralization evolved early in the group's history.

In the context of previously described stem-group medusozoans, this study presents the first detailed description of an Ordovician, soft-bodied, tubicolous-polyp medusozoan. This discovery is particularly significant given the scarcity of nonbiomineralized organisms in the Ordovician and underscores the crucial role of exceptional soft-tissue preservation in reconstructing early cnidarian evolution.

Locality and geological setting

The fossil materials, preserved along the upper surfaces of shaly limestone beds, were collected from a small quarry located at Saint-Joachim, ~ 43 km northeast of Québec City, Québec, Canada, considered herein within the Upper (Grondines Member) Neuville Formation of the Trenton Group (Harper and Pickerill, 1996). The Trenton Group of Québec represents a transgressive continental (Laurentian), platform margin succession of Katian age, deposited on a carbonate ramp that primarily developed in warm-water tropical and later in temperate conditions (Lavoie, 1995; Desrochers *et al.*, 2023). The Upper Neuville Formation type locality near the town of Neuville, ~ 80 km southwest of Saint-Joachim, underlies the Utica Shale and consists of 98 m of beds of dark gray limestones up to 25 cm thick, separated by shale interbeds up to 15 cm thick (Clark and Globensky, 1973).

The associated biota includes rugose corals, conulariids, bryozoans, brachiopods, gastropods, cephalopods, trilobites, crinoids, carpoids, cystoids, and trace fossils.

Materials and methods

All material observed is curated in the Musée de Paléontologie et de l'Évolution in Montréal, Québec. Approximately 135 specimens preserved on 15 slabs were studied. Thirty-nine specimens were sufficiently complete and visible to be measured and photographed. Photos were taken using (1) soft-white halogen lightbulbs; (2) cross-polarized light with an optical filter enhancing contrast to reveal digestive features; and (3) submerged in water or ethanol to expose details not discernible through other methods. The specimens, being flat in relief, required no preparation before photography.

Elemental mapping (EDS) was conducted on *Paleocanna tentaculum* n. gen. n. sp., specimen MPEP713.3 using an Environmental Scanning Electron Microscope (ESEM) with a Field Emission Gun (FEG) Quanta 200 model at the University of Windsor Great Lakes Institute for Environmental Research, Ontario, Canada. The EDS mapping and point-elemental analyses were conducted in a low vacuum pressure chamber of 70 Pa. The EDS detector employed was an energy dispersive X-ray spectroscopic (EDAX) Octane Plus SDD detector, operated using TEAM software (<https://www.coherent.com.au/content/media/Edax/TEAM%20EDS%20For%20TEM.pdf>).

A phylogenetic analysis was performed using 69 taxa, including ctenophore species, and 236 discrete morphological traits. The morphological character traits used were modified from Zhao *et al.* (2023), especially those concerning the external periderm (see Data Availability Statement). Analysis was run using PAUP 4.0b10 (Swofford, 2002) under the assumptions of parsimony using the heuristic and branch-and-bound search algorithm by bootstrapping using 1,000 replicates. Characters were treated as unordered and with equal weight, unknown states were scored as '?'. Changes of individual characters along branches were tracked using Mesquite 3.51 (Maddison and Maddison, 2023).

Repository and institutional abbreviation. All specimens are deposited in the Musée de Paléontologie et de l'Évolution (MPEP) collections.

Systematic paleontology

Phylum **Cnidaria** Verrill, 1865
Subphylum **Anthozoa** Ehrenberg, 1834
Genus ***Paleocanna*** new genus

Type species. *Paleocanna tentaculum* n. gen. n. sp., by monotypy.

Diagnosis. As for the type species.

Etymology. *Paleocanna*: *palaio*, meaning old or ancient, plus *canna*, meaning flute or pipe.

Remarks. As for the type species.

Paleocanna tentaculum new species

Figures 1–4

Type specimens. Holotype: MPEP713.4. Paratypes: MPEP713.1–713.3, 713.5–713.15. Approximately 135 individuals are distributed on these 15 rock slabs.

Diagnosis. Cylindrical tubicolous periderm with fine, parallel, transverse annulations; polyp with anterior tentacle crown extending from aperture.

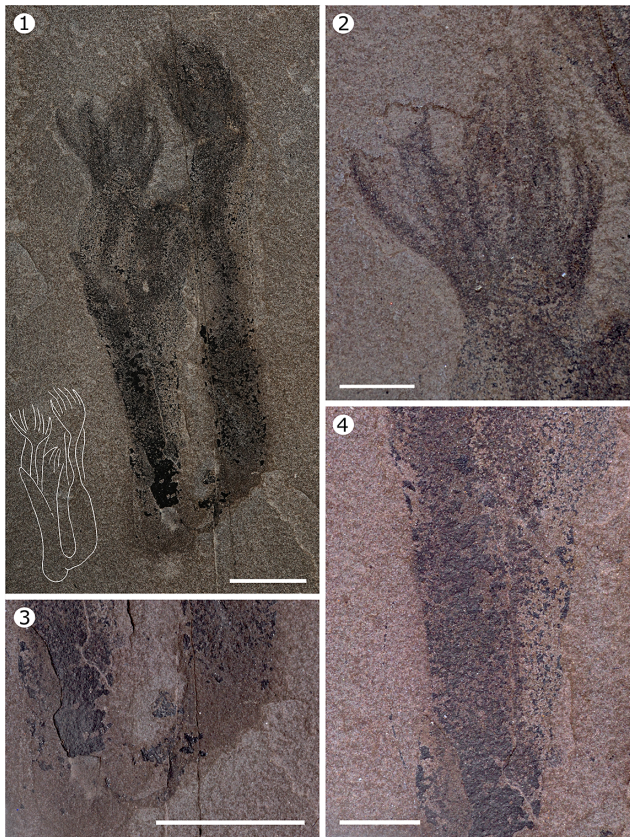


Figure 1. *Paleocanna tentaculum* n. gen. n. sp., holotype, MPEP713.4. (1) General view of the organism taken under cross-polarized light; accompanying line drawing illustrates the outline of the tube and tentacles. (2) Detail of the left set of tentacles. (3) Detail of the basal part of the tube. (4) Detail of the tube. Scale bars = 1 cm (1, 3), 0.5 cm (2, 4).

Occurrence. Upper Neuville Formation of the Saint Lawrence Lowlands of Québec, Canada (Clark, 1959).

Description. *Paleocanna tentaculum* n. gen. n. sp. is a long, uniform, tubicolous organism. Individuals have a mean length of 36.9 mm (ranging from 24.9–51.0 mm) and a mean width of 6.0 mm ($N = 39$). Some tubes are attached in groups at shared bases, whereas others grew as isolated individuals (Fig. 3). The outer surfaces of the tubes have no sand, broken shells, or other debris. The basal ends are dark black, and some specimens show some regular transverse striations at the base and along the organism (Fig. 4). These annulations appear to be continuous and arranged in parallel. No longitudinal grooves or midlines were observed. The base of the tubes is usually rounded, rarely sharp, and there is no clear evidence of a holdfast. The apical aperture of the tube, from which the animal emerged, ends horizontally and rarely in a sharp angle.

The soft body of the animal is elongated with a rounded aboral end. In all 135 fossils, the body extends from the aperture of the tube. Body septa were not found. Some individuals show a distinct gastrovascular cavity or coelenteron in the center of the tube that terminates blindly (Fig. 2.1, 2.3, 2.7). The midgut is ~ 1.388 mm (+ 4 mm) wide, and the posterior gut is 2.309 mm (+ 3 mm) wide. The tentacles are numerous, ~ 12 in the best-preserved specimens (Fig. 2), without clear evidence of their distribution in a single or multiple coronae. Three specimens show subtle details of the tentacles, which appear as finger-like to

feathery structures and represent ~ 20–25% of the total body length (Fig. 2.2, 2.5, 2.6). No individual circling of tentacles was found in the open, relaxed, feeding position. Instead, the circling of tentacles is tightly packed, intertwined, and extending anteriorly from the body. No mouth was observed but it was presumed to be situated at the center of the circling of tentacles. An interpretive drawing of *Paleocanna tentaculum* n. gen. n. sp. as a living animal is provided (Fig. 5).

Etymology. Species *tentaculum*, for tentacle.

Taphonomy. When multiple individuals are present, they are consistently oriented in the same direction, suggesting limited transport and rapid burial (Fig. 3.1, 3.3). Fossils were confined to the upper portions of the beds and did not appear in underlying or overlying strata, supporting rapid deposition events and minimal postburial disturbance. Although some specimens are well preserved (Figs. 1, 2.1, 2.3), most show only faint outlines. This faint preservation of certain structures, e.g., tentacles, could indicate limited decay prior to burial; however, the lack of disarticulation or fragmentation suggests minimal bioturbation or transport after death. This interpretation is supported by the associated taxa, notably echinoderms, which are often preserved as fully articulated specimens. Preservation likely occurred under anoxic to dysoxic conditions, inhibiting decay or scavenging.

Elemental analysis revealed that the darkest areas of the fossils are preserved primarily as carbon films, suggesting retention of original organic material. Other parts are slightly enriched in calcium (6%) and magnesium (5%), which could indicate localized mineralization, possibly reflecting differences in tissue composition or diagenetic overprinting. The surrounding matrix was composed primarily of aluminosilicates with dominant elements including silicon (26%) and aluminum (13%), consistent with a fine-grained siliciclastic sedimentary environment (Fig. 6). No sections of the fossil beds were made, but in situ observations were used to assess fossil occurrence and stratigraphic context.

Remarks. *Paleocanna tentaculum* n. gen. n. sp. is the first soft-bodied cnidarian polyp to be formally described from the Ordovician of North America, distinct from conulariids, anthozoan corals, and *Sphenothallus* Hall, 1847.

Phylogenetic results

The most recent phylogenies of cnidarians place the Anthozoa (Hexacorallia and Octocorallia) as sister group to Medusozoa (Staurozoa, Scyphozoa, Cubozoa, and Hydrozoa) (Van Iten et al., 2014; Forero-Mejia, 2020). *Paleocanna* n. gen. placed among other cnidarian taxa, within the medusozoan lineage (Fig. 7). Most fossil cnidarian polyps occupy positions as sister groups to either the total-group Medusozoa stem or the anthozoan clade (Dunn et al., 2022; Ou et al., 2022; Zhang et al., 2022; Qu et al., 2023; Zhao et al., 2023), whereas *Paleocanna* n. gen. nested nearer to the crown-group Medusozoa, which includes extant cubozoans, scyphozoans, and staurozoans.

Paleocanna tentaculum n. gen. n. sp. was placed in the phylogeny based on external morphological characters, including a tubular, organic periderm that extended along the entire polyp, and bore widespread striae-like annulations. Ecologically, it is inferred to have been solitary to colonial, with a microphagous feeding strategy. Characters associated with the preservation of soft tissues, e.g., tentacles, set *Paleocanna* n. gen. apart from

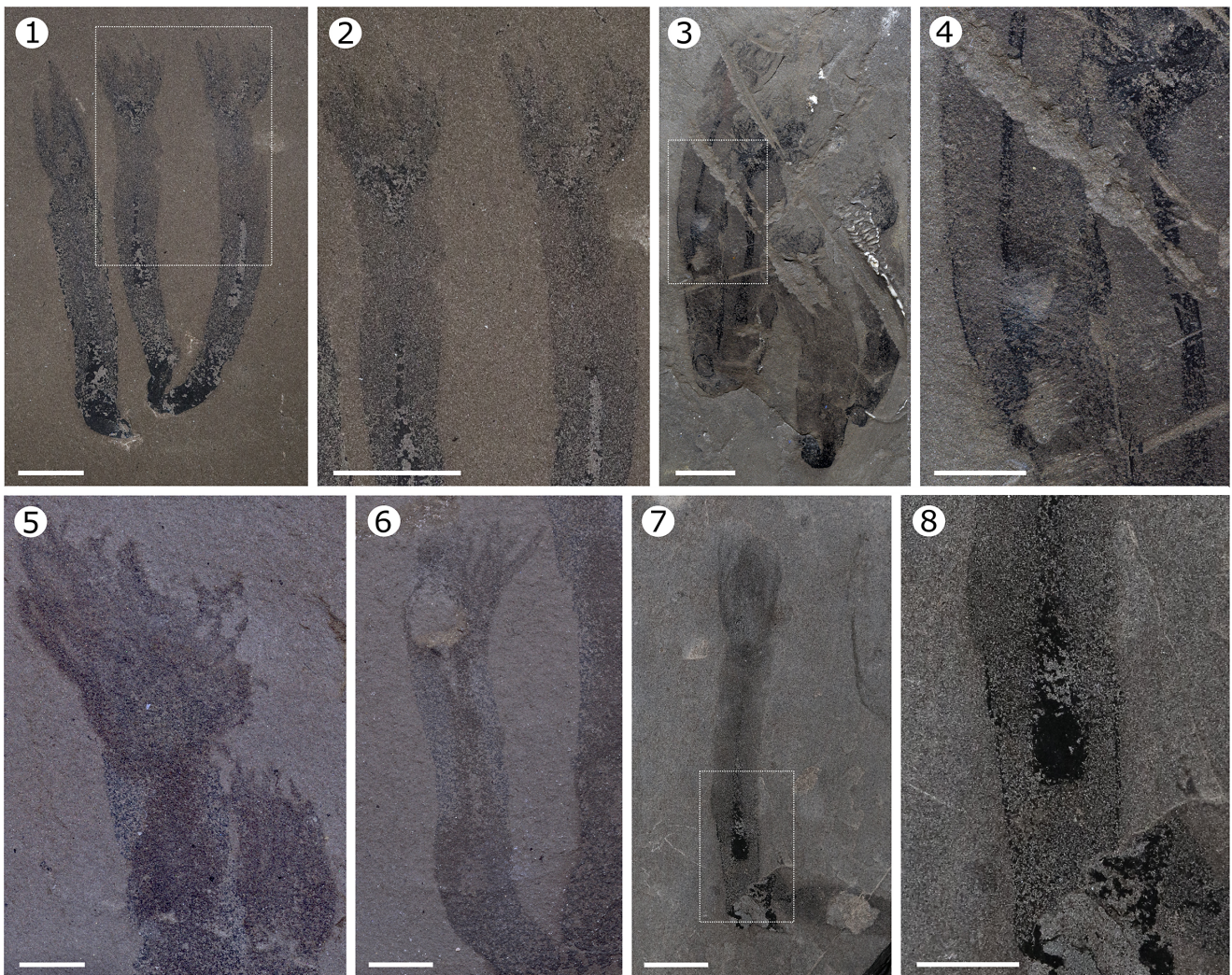


Figure 2. Internal and external anatomy of *Paleocanna tentaculum* n. gen. n. sp. (1) MPEP713.6 observed under polarized light showing details of the tentacles and gastrovascular cavity. (2) Detail of the squared region in (1), showing the continuity of the tentacles with the coelenteron. (3) MPEP1524.1 observed immersed in ethanol resembling the morphology of a hydrozoan, illustrating the tentacles, the digestive tract, and the rounded terminus of the periderm. (4) Detail of the squared region in (3), showing the gut and the periderm in greater detail. (5) MPEP713.11 observed under ethanol exhibiting an array of several tentacles. (6) MPEP713.11 showing detail of the tentacles and gut; the tentacles appear finger-like, whereas in other samples, they present a more feather-like form. (7) MPEP713.1 observed under polarized light displaying a sharper tube base, a rarely noted feature that likely helped anchor the organism to the substratum or bury it in sediment. (8) Detail of the squared region in (7), highlighting a central gut, indicating that, as in the other specimens, the gastrovascular cavity does not extend to the distal portion of the tube; a fragment of periderm is preserved at the base. Scale bars = 1 cm (1–4), 0.5 cm (5–8).

comparable extinct polypoid taxa that are typically known only from their mineralized periderm structures.

Symmetry is a key morphological character in early medusozoan evolution. In *Paleocanna* n. gen., the preserved structures suggest some sort of radial symmetry, consistent with a polypoid cnidarian body plan. However, the lack of clear longitudinal ridges or lamellae differentiates it from taxa like *Conularia* Sowerby, 1821 and the hexangulaconulariids, which typically exhibit well-defined tetraradial or hexaradial symmetry with fan-shaped geometries (Song et al., 2024). Similarly, taxa like *Carinachites* and *Olivoooides* show more derived symmetry with pronounced apical structures and often exhibit quadriradial to pentaradial symmetry (Jian et al., 2016; Song et al., 2024).

Paleocanna n. gen. nested outside the clade that contains other extinct taxa; this suggests that the genus is part of a lineage of medusozoans, possibly related to conulariids or similar extinct forms. The stem-group medusozoan reflects both morphological

and taphonomic diversity within the group. The presence of other extinct medusozoans in this clade implies that *Paleocanna* n. gen. represents a lineage that was relatively diverse in the past.

Discussion

Paleocanna tentaculum n. gen. n. sp. is an Upper Ordovician tubicolous polyp medusozoan from the Saint-Joachim Quarry, Neuville Formation, Québec. The tubes are interpreted as epibenthic, likely oriented perpendicular to the seafloor, sometimes found attached to one another, and possibly buried in or attached to the substratum (Fig. 3). The tubular periderm that extends along the polyp exhibits widespread, continuous, fine annulations. The occurrence of attached individuals suggests a facultative semicolonial mode of life with clusters of up to 15 specimens (Fig. 3.2). Based on its morphology, a polypoid phase is inferred, with the polyp possessing a stalk or peduncle.

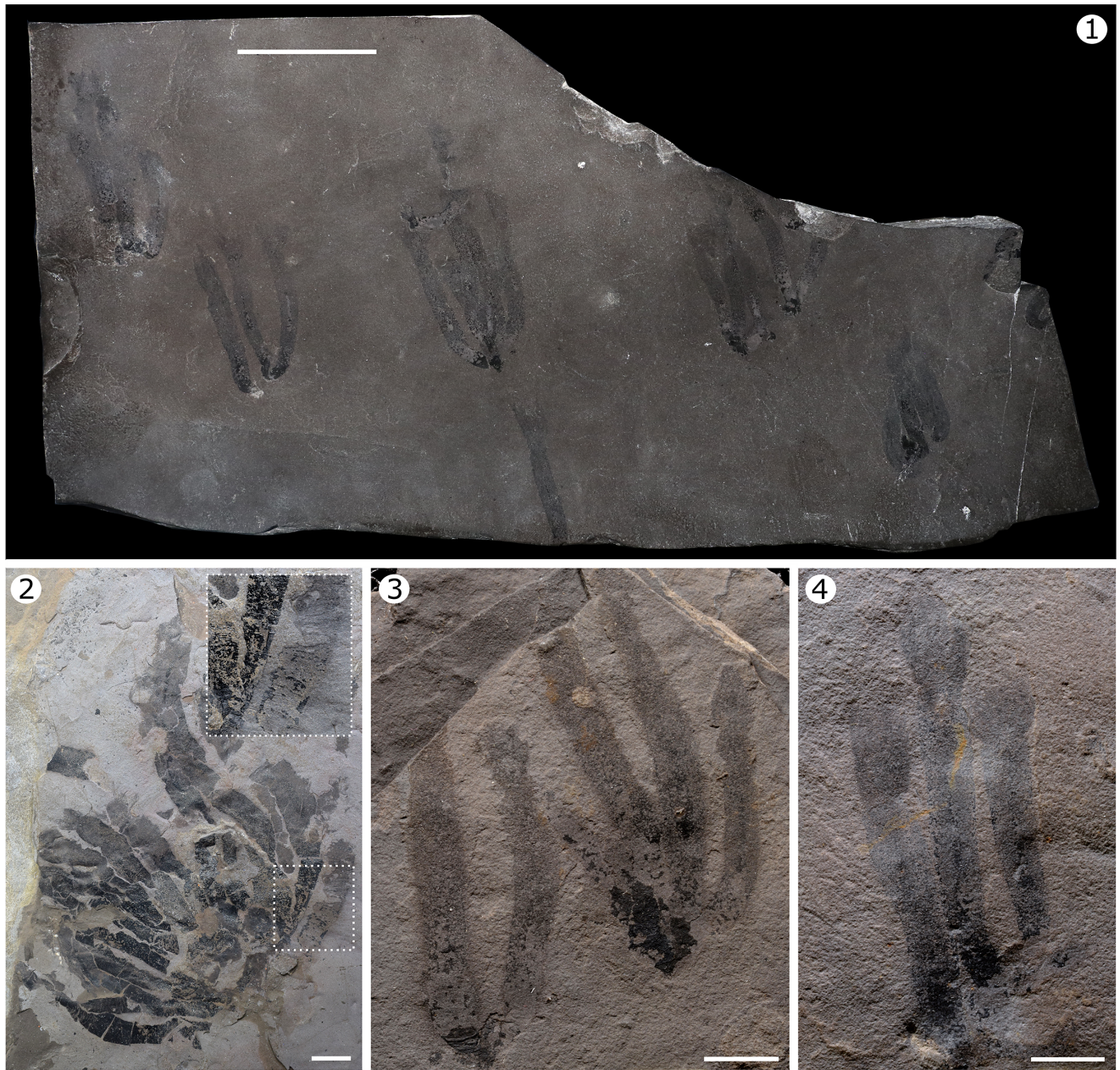


Figure 3. *Paleocanna tentaculum* n. gen. n. sp., living in clusters or individually. (1) MPEP713.6, containing clustered and individual specimens oriented in the same direction, suggesting rapid burial; attached individuals indicate a facultative semicolonial existence. (2) MPEP1525.1 showing a cluster of > 15 individuals; the boxed region (enlarged at upper right) highlighting part of the tubes that exhibit striations. (3) MPEP713.7 showing two clusters of two and four individuals; the former showing some wrinkle-like striations at the base. (4) MPEP713.8 showing one and two individuals, preserved oriented in the same direction. Scale bars = 5 cm (1), 1 cm (2–4).

Although the tentacles cannot be observed in detail, they differ from those of previously reported cnidarian species in being fine and numerous. These contrast with tentacles of *Gangtouncunia* Luo et al., 1999 and *Paleoconotuba*, which are short and thick (Qu et al., 2023; Zhang et al., 2022), and those of *Nailiana* Ou et al., 2022 and *Conicula* Luo et al., 1999 that are smooth, finger-like, and longer compared to those of other fossil species (Ou et al., 2022; Zhao et al., 2023). The number of tentacles also varies among genera from at least five in *Gangtouncunia*, at least six in *Conicula*, from three to five in *Palaeoconotuba*, and eight in *Nailiana*. Although the phylogenetic position of *Xianguangia sinica* is uncertain, its fine tentacles suggest that it was a filter feeder (Ou et al., 2017). Following this same logic, the fine

tentacles of *Paleocanna tentaculum* n. gen. n. sp. could have been used to filter food, by capturing food by gravitational deposition or by tentacle motion.

Due to the nature of soft-bodied preservation and the lack of part-counterpart material, it is not possible to completely rule out the possibility that the apparent termination of the gut is an artifact of preservation. However, the digestive structure appears consistently truncated at its posterior end across multiple specimens, with no evidence of continuation, disruption, or displacement (Fig. 2.1, 2.7). The preservation of surrounding tissues also suggests that the truncation is not the result of damage or incomplete exposure. Based on its repeated expression and anatomical context, we interpret this morphology as a blind gut.

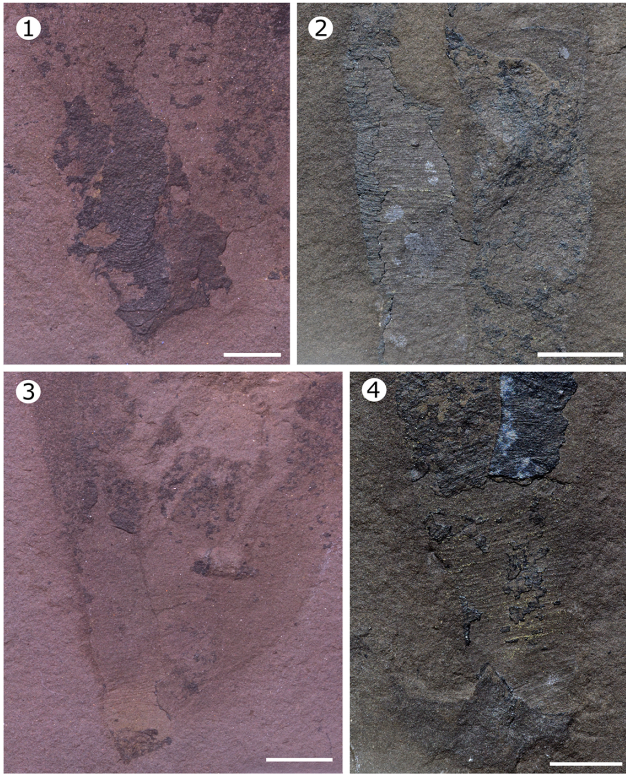


Figure 4. Periderm annulations of *Paleocanna tentaculum* n. gen. n. sp. Specimens MPEP713.7 (**1**, **3**) and MPEP713.15 (**2**, **4**) exhibiting different striations that occur parallel to each other in the most distal regions. These markings range from pronounced, wrinkle-like ridges to finer, straight lineations. Scale bars = 0.5 cm.

Tubicolous cnidarians have existed at least since the Ediacaran, with genera such as *Cloudina* Germs, 1972; *Corumbella* Hahn et al., 1982; *Haootia* Liu et al., 2014; and *Paraconularia* Sinclair, 1940 (Babcock et al., 2005; Vinn and Zatón, 2012; Liu et al., 2014; Leme et al., 2022). *Auroralumina attenboroughii*, also from the Ediacaran, appears to have been a transitional species, because it occupies a morphospace closer to Cambrian tubicolous genera, e.g., *Cambroctonus* Park et al., 2011, *Carinachites*, and *Olivoooides* (Dunn et al., 2022). These taxa exhibit characteristics of both anthozoans and medusozoans (Dunn et al., 2022). The early Cambrian *Gangtouwunia aspera* provides evidence for the origin of biomineralization in cnidarians (Zhang et al., 2022). Tubular fossils diversified into the Cambrian, suggesting adaptations to different ecological niches.

Paleocanna n. gen. differs from most of these species in having a tubular periderm rather than a conical one, as well as in having finely striated annulations instead of the sharper rib- or crest-like structures. This tubular body is preserved as a carbonaceous film, as confirmed by elemental analysis, and the annulations along its length suggest some degree of structural integrity. However, there is no indication of a rigid or biomineralized wall; the tube appears to have been originally organic. Some of these thecate species also exhibit longitudinal ridges and midlines characteristic of biomineralized conulariids, a trait not observed in *Paleocanna tentaculum* n. gen. n. sp. This distinction is remarkable given that most stem-group medusozoans are known from the Cambrian, whereas Ordovician assemblages are predominantly composed of conulariids, which were both diverse and widespread during this period. *Paleocanna* n. gen. more closely resembles Cambrian forms and appears to co-occur with conulariids, possibly representing a different phylogenetic branch. At least one species of conulariid is known

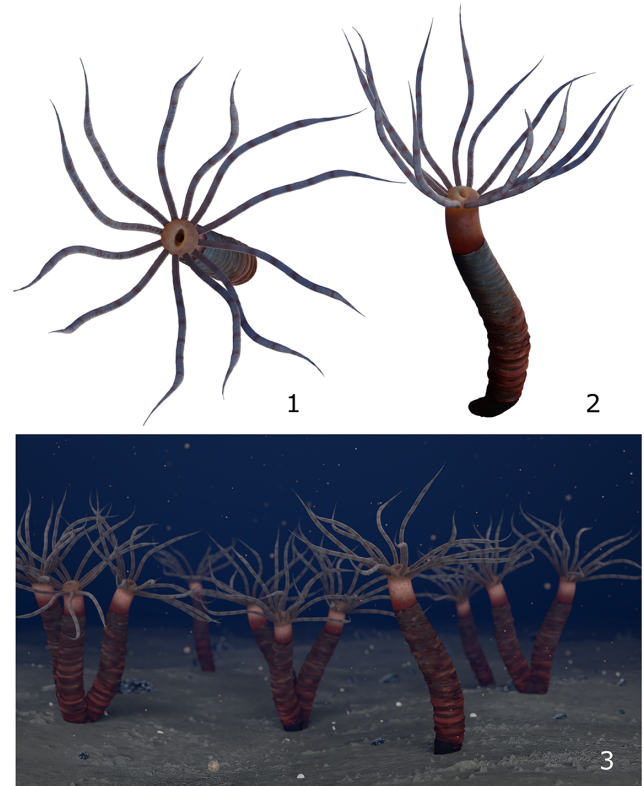


Figure 5. Interpretive drawings of *Paleocanna tentaculum* n. gen. n. sp. as living organisms. (**1**) Oral view showing a circle of tentacles. (**2**) Lateral perspective of the tube, highlighting the tube aperture and annular striations. (**3**) Depiction of individuals living in single tubes, as well as clusters of two or three tubes attached together.

from the locality, based on fragmentary but recognizable specimens. These conulariids do not exhibit evidence of soft-tissue preservation.

The annulations observed in the periderm of *Paleocanna* n. gen. bear some resemblance to those of *Sphenothallus*, which is also known to be preserved as carbonaceous compressions (Muscente and Xiao, 2015). However, several key differences suggest a distinct identity. *Sphenothallus* is typically preserved as a phosphatic structure with longitudinal thickenings and transverse walls (Muscente and Xiao, 2015; Van Iten et al., 2023), whereas *Paleocanna* n. gen. appears to be a full thin-walled tube and lacks any indication of phosphatization. Morphologically, *Paleocanna* n. gen. lacks the pronounced tapering and pointed apex usually seen in *Sphenothallus*. The latter is also most often found as isolated individuals, whereas *Paleocanna* n. gen. commonly occurs in clusters, potentially indicating a different life mode.

The growth of *Paleocanna tentaculum* n. gen. n. sp. was allometric, exhibiting minimal variation in width as the lengths increased, with a ± 36.9 mm length and ± 6.0 mm width ($N = 39$). Interpretation of this morphometric data requires caution due to the soft-bodied nature of cnidarians and the potential alterations in actual biological measurements caused by the fossilization process. Despite these challenges, allometric growth characterizes the development of most animals, and has been present since the Cambrian in trilobites, for example (Du et al., 2019; Holmes et al., 2021).

Paleocanna tentaculum n. gen. n. sp. was buried in a low-energy, anoxic, muddy bottom environment favorable to the preservation of solid organic matter and labile animal soft tissues. Elemental analysis of MPEP713.3 revealed pure carbon although a portion of

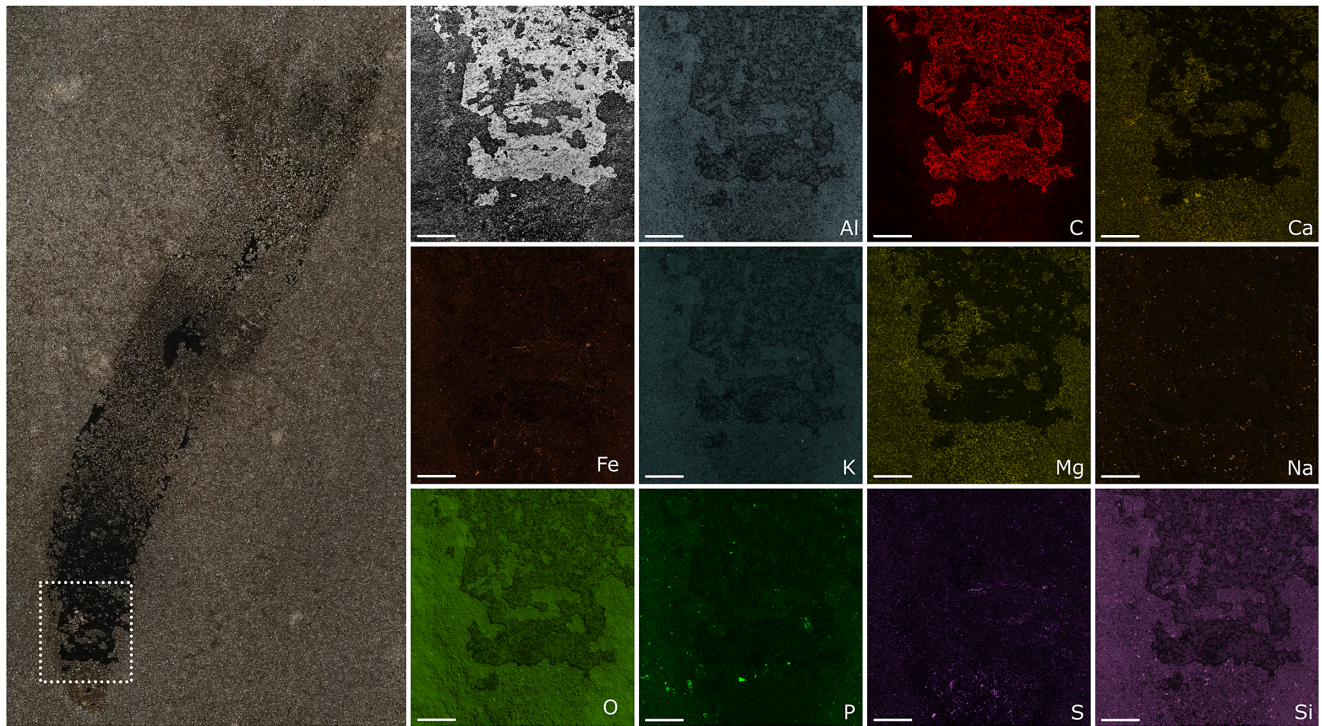


Figure 6. Elemental analysis of specimen MPEP 713.3 of *Paleocanna tentaculum* n. gen. n. sp. Entire specimen at left, with boxed region indicating the location of the mapped section. The figure includes a photograph of the mapped region and corresponding element maps. Elemental composition percentages are as follows: aluminum (13%), carbon (6%), calcium (6%), iron (1%), potassium (3%), magnesium (5%), sodium (2%), oxygen (32%), phosphorus (2%), sulfur (3%), and silicon (26%). These values indicate that organisms are mostly carbon, slightly enriched in calcium or magnesium, whereas the matrix is rich in aluminum and potassium. Scale bars = 1 mm.

the material appeared to be marginally enriched in calcium or magnesium, whereas the matrix itself exhibited higher concentrations of aluminum and potassium. None of these elements can be original, except for carbon. This mineral composition bears some resemblance to Burgess Shale-type (BST) fossilization. The siliclastic deposits that preserve BST fossils have high clay-to-organic ratios, which is one way to facilitate exceptional preservation by slowing the rate of decay (Anderson et al., 2018). The preservation of these cnidarian fossils is attributed to the transportation of the organisms within a moving sediment cloud and subsequent burial with all hollows and spaces filled with fine-grained clays (Gaines et al., 2012).

The Saint Joachim quarry fossils and shales exhibit the characteristics of a BST locality, including their occurrence in fine-grained sediment, the quality of preservation, high organic content, a low-energy depositional setting, and likely anoxic conditions. Comparable soft-bodied cnidarians have been described from the Burgess Shale, including a medusa with remarkable preservation of internal anatomy, e.g., gonads (Moon et al., 2023). Although the Saint Joachim fossils are more limited in anatomical detail, they nonetheless preserve key morphological features including annulated tubes and tentacle impressions.

Understanding the preservation of soft-bodied organisms like *Paleocanna tentaculum* n. gen. n. sp. provides a valuable contrast to most Ordovician deposits, which typically feature only mineralized organisms, especially given the rarity of soft-tissue preservation during this period (Moysiuk et al., 2022). This rare type of preservation is especially relevant in a group that represents some of the earliest metazoans to biomineralize, and in a locality where the associated biota includes typical hard-bodied species like

bryozoans, brachiopods, cephalopods, trilobites, and echinoderms (Clark and Globensky, 1973; Harland and Pickerill, 1982).

Conclusions

Paleocanna tentaculum n. gen. n. sp. represents a remarkable discovery from the Upper Ordovician Neuville Formation in Québec. As a tubicolous stem medusozoan that is more closely related to the crown group medusozoan than to the other stem group genera, this species shares several morphological and ecological similarities with both modern anthozoans and medusozoans, including an annulated periderm and a digestive tract, the structure of the tentacles, and an epibenthic lifestyle. The fossil evidence suggests semicolonial behavior with their tubes being attached to surfaces or buried in the sediment. This discovery provides a window onto the complex ecosystems of the Ordovician Period, offering an important comparison to both modern cnidarians and other fossilized medusozoans from earlier periods.

The preservation of soft tissues in *Paleocanna tentaculum* n. gen. n. sp. was facilitated by burial under environmental conditions of very low physical energy and sediment pore-water anoxia. This rare type of preservation is significant because it challenges the typical Ordovician fossil record, which predominantly features organisms with mineralized hard parts. Elemental analysis suggests that organic carbon was preserved, making this an important site for understanding the biology and fossilization of ancient soft-bodied organisms. The insights provided by *Paleocanna tentaculum* n. gen. n. sp. help fill gaps in our understanding of early anthozoan evolution, and how these ancient soft-bodied organisms adapted to and thrived in marine environments.

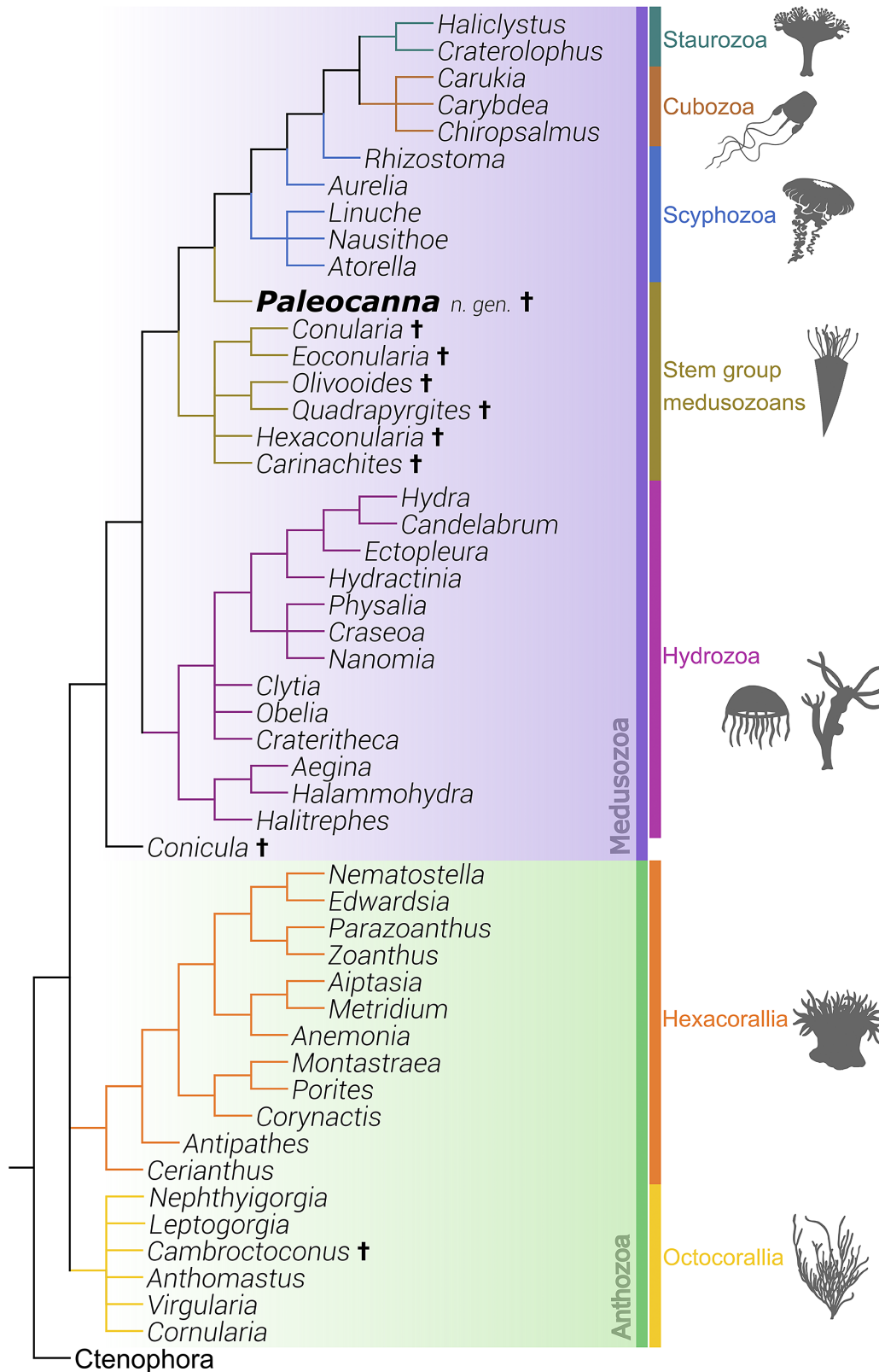


Figure 7. Phylogeny of Cnidaria, with *Paleocanna tentaculum* n. gen. n. sp., resolved as a stem-group medusozoan. Strict consensus tree generated using 69 ingroup taxa and 236 discrete hard and soft-part morphological characters, polarized using species of the phylum Ctenophora as the sole outgroup. *Paleocanna tentaculum* n. gen. n. sp. is resolved as a stem-group medusozoan that is more closely related to the crown group (Cubozoa, Scyphozoa, and Staurozoa) than it is to the other stem group medusozoans, e.g., conulariids. Animal silhouettes from PhyloPic (<http://phylopic.org/>). Taxa not otherwise mentioned in the text are *Aegina* Eschscholtz, 1829; *Aiptasia* Gosse, 1858; *Anemonia* Risso, 1827; *Anthomastus* Verrill, 1878; *Antipathes* Pallas, 1766; *Atorella* Vanhöffen, 1902; *Aurelia* Lamarck, 1816; *Candelabrum* de Blainville, 1830; *Carukia* Southcott, 1967; *Carybdea* Peron and Lesueur, 1810; *Cerianthus* Delle Chiaje, 1841; *Chiropsalmus* Agassiz, 1862; *Clytia* Lamouroux, 1812; *Corynactis* Allman, 1846; *Craseoa* Pugh and Harbison, 1987; *Crateritheca* Stechow, 1921; *Craterolophus* James-Clark, 1863; *Ectopleura* Agassiz, 1862; *Edwardsia* Quatrefages, 1842; *Eoconularia* Sinclair, 1943; *Halammohydra* Remane, 1927; *Haliclystus* James-Clark, 1863; *Halitrephes* Bigelow, 1909; *Hydra* Linnaeus, 1758; *Hydractinia* Van Beneden, 1844; *Leptogorgia* Milne Edwards, 1857; *Linuche* Eschscholtz, 1829; *Metridium* de Blainville, 1824; *Montastraea* de Blainville, 1830; *Nanomia* Agassiz, 1865; *Nausithoe* Kölliker, 1853; *Nematostella* Stephenson, 1935; *Nephthiyorgia* Kükenthal, 1910; *Obelia* Peron and Lesueur, 1810; *Parazoanthus* Haddon and Shackleton, 1891; *Physalia* Lamarck, 1801; *Porites* Link, 1807; *Quadrapyrgites* Li et al., 2007; *Rhizostoma* Cuvier, 1800; *Virgularia* Lamarck, 1816; and *Zoanthus* Lamarck, 1801.

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