

Articles

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Corresponding author:

Steffen Kiel;

Email: steffen.kiel@nrm.se

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Abstract

Three fossil tube fragments from middle Eocene to late Oligocene strata in western Washington State, USA, are here interpreted as those of ancient Ceriantharia (Hexacorallia, Cnidaria). The tube fragments are 3–6 mm in diameter, up to 60 mm long, and the surfaces show an overlapping, fibrous knitted pattern. This surface pattern resembles that of the extant ceriantharid *Cerianthus membranaceus*. One specimen has numerous benthic foraminiferans associated with, and apparently even embedded in, the tube wall, analogous to some extant Ceriantharia. These fossils likely represent the first fossil Ceriantharia and indicate that their present-day mode of tube construction using ptychocysts was established at latest by the middle Eocene.

Non-technical Summary

Ceriantharia are tube-dwelling Cnidaria related to corals and anemones, found today in marine waters worldwide. We document the first fossilized tubes of ceriantharids, from Eocene to Oligocene (about 40 to 23 million years old) sediments in Washington State, USA.

Introduction

The Ceriantharia Perrier, 1893, is an order of mostly sessile, tube-dwelling Cnidaria, commonly known as ‘tube anemones’. They have a worldwide distribution from the tropics to the Arctic and Antarctica, and from shallow-marine reefs to the deep sea (Stampar et al., 2020). Ceriantharid tubes are made of discharged, interwoven cnidae called ptychocysts, which are unique to Ceriantharia (Mariscal et al., 1977; Stampar et al., 2015). Because ptychocysts are sticky, the tubes often incorporate sediment particles (Stampar et al., 2015), and they are used as attachment substrates by a diversity of marine invertebrates (Ceriello et al., 2020).

The phylogenetic relationships of Ceriantharia to other Cnidaria have been a matter of debate. Current molecular phylogenetic studies place them in a basal position within the Hexacorallia, as sister taxon to all other hexacorals (McFadden et al., 2021; DeBiasse et al., 2022). This basal position suggests an ancient origin of the group and indeed, the split from other hexacorals has been placed well before the Cambrian explosion of life in a time-calibrated molecular phylogenetic tree (McFadden et al., 2021). However, although a number of Cambrian fossils have been interpreted as jellyfish (Cartwright et al., 2007; Han et al., 2016), anemones (Hou et al., 2005; Han et al., 2010), and anemone-like medusozoans (Zhao et al., 2023), to the best of our knowledge the Ceriantharia have no fossil record (Molodtsova et al., 2011). Similarities between the Ediacaran *Kuibisia glabra* Hahn and Pflug, 1985, and extant Ceriantharia were discussed but no direct relationship was implied (Hahn and Pflug, 1985). *Kuibisia glabra* was later subject to various re-interpretations (Grazhdankin and Seilacher, 2005; Ivantsov et al., 2016).

Material

Here we report three tubular fossils from late Eocene and Oligocene strata in western Washington State, USA, which, based on their surface structure and lack of tapering or segmentation, are interpreted as fossilized tubes of Ceriantharia. One specimen is from strata mapped as Makah Formation by Tabor and Cady (1978), found in a float concretion, from the beach approximately 1,700 m west of the mouth of Whiskey Creek, Clallam County, Washington (coordinates: 48.1555°N, 123.7979°W). Fossils are rare but include mollusks (Kiel et al., 2023), a deep-water crab (Feldman, 1989; Tucker, 1998), an isopod (Wieder and Feldmann, 1989, their loc. 8), a penguin-like bird (Goedert and Cornish, 2002; Mayr and Goedert, 2022), and a conifer (Crabtree and Miller, 1989). A small crinoid has also been found in these outcrops (Franzén-Bengtson and Oji, 2025). The age of this part of the Makah Formation is likely late Eocene (Kiel et al., 2023, p. 299). The specimen described herein is housed in the paleontological collections of the Swedish Museum of Natural History (NRM) in Stockholm, Sweden, as Cn 76105.

The second specimen is from the middle to late Eocene Hoko River Formation (as mapped by Snively et al., 1993) and is housed at the Burke Museum in Seattle, Washington, USA, as UWBMIP 106332 (UWBMIP loc. B6689) from a conglomerate lens exposed on the east side of logging road, NE

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¼, Sec. 36, T.32N., R.14W., Clallam County, Washington (coordinates 48.2338°N, 124.4389°W). The conglomerate contains a few reworked concretions, some of which contained fossil crabs, and a sandstone clast preserved a large fossil limpet and some barnacle plates. Similar conglomerates within the Hoko River Formation farther to the northwest have produced numerous fossils (e.g., Squires, 1988; Tucker, 1998). As noted by Garvie et al. (2020), the fossils from the Hoko River Formation conglomerate lenses are derived from diverse paleoenvironments and may differ significantly in age from the enclosing strata.

The third specimen (UWBMIP 117997) was found in a fine-grained, float concretion on a gravel bar along the Canyon River, south side of the Olympic Peninsula, adjacent to a small exposure of the upper part of the Lincoln Creek Formation (UWBMIP loc. B6749; coordinates 47.2615° N, 123.5306°W), Grays Harbor County, Washington. Wieder and Feldmann (1989) described deep-water isopods from this locality (their loc. 9), which Rau (1966) mistakenly mapped as Astoria Formation (Thompson, 1978; JLG, pers. observation, 2024), which resulted in the incorrect assumption that the isopods were early or middle Miocene in age instead of late Oligocene. The assemblage of foraminiferans indicates that deposition occurred at depths of approximately 200 to possibly as much as 760 m (Rau, 1966). The age of the upper part of the Lincoln Creek Formation on Canyon River is late Oligocene (Prothero and Armentrout, 1985).

A specimen of the extant ceriantharid *Cerianthus membranaceus* (Gmelin, 1791), collected at Napoli, Italy, from the Mediterranean

Sea, was used for comparison (NRM Zoology collection, No. 137355). The specimen is about 200 mm long, and about 37 mm wide just below the crown.

Repositories and institutional abbreviations. UWBMIP, University of Washington, Burke Museum of Natural History and Culture (Invertebrate Paleontology), Seattle, USA; NRM, Swedish Museum of Natural History, Stockholm, Sweden.

Description

Specimen NRM Cn 76105 consists of two parts, one is 19.3 mm long and 4 mm wide, the other is 26.5 mm long and 4 mm wide; both parts are fragmentary and neither part shows an obvious opening or closure at either end (Figs. 1.1, 2.2). The tube surface is blueish gray, with pyrite granules that are finely dispersed or concentrated in random areas on the surface. The tubes have an oval or elongate-oval cross section (Fig. 1.1), with the interior filled either with the same gray matrix as the embedding concretion, or a mixture of sparite and pyrite, with the pyrite sometimes forming a lining just underneath the surface, or being concentrated in the center of the tube, or just being randomly distributed. The tube surface shows a 'knitted pattern' composed of elongate wrinkles with elongate-pointed ends on both sides, arranged perpendicular to the tube axis (Fig. 1.3). The tubes are associated

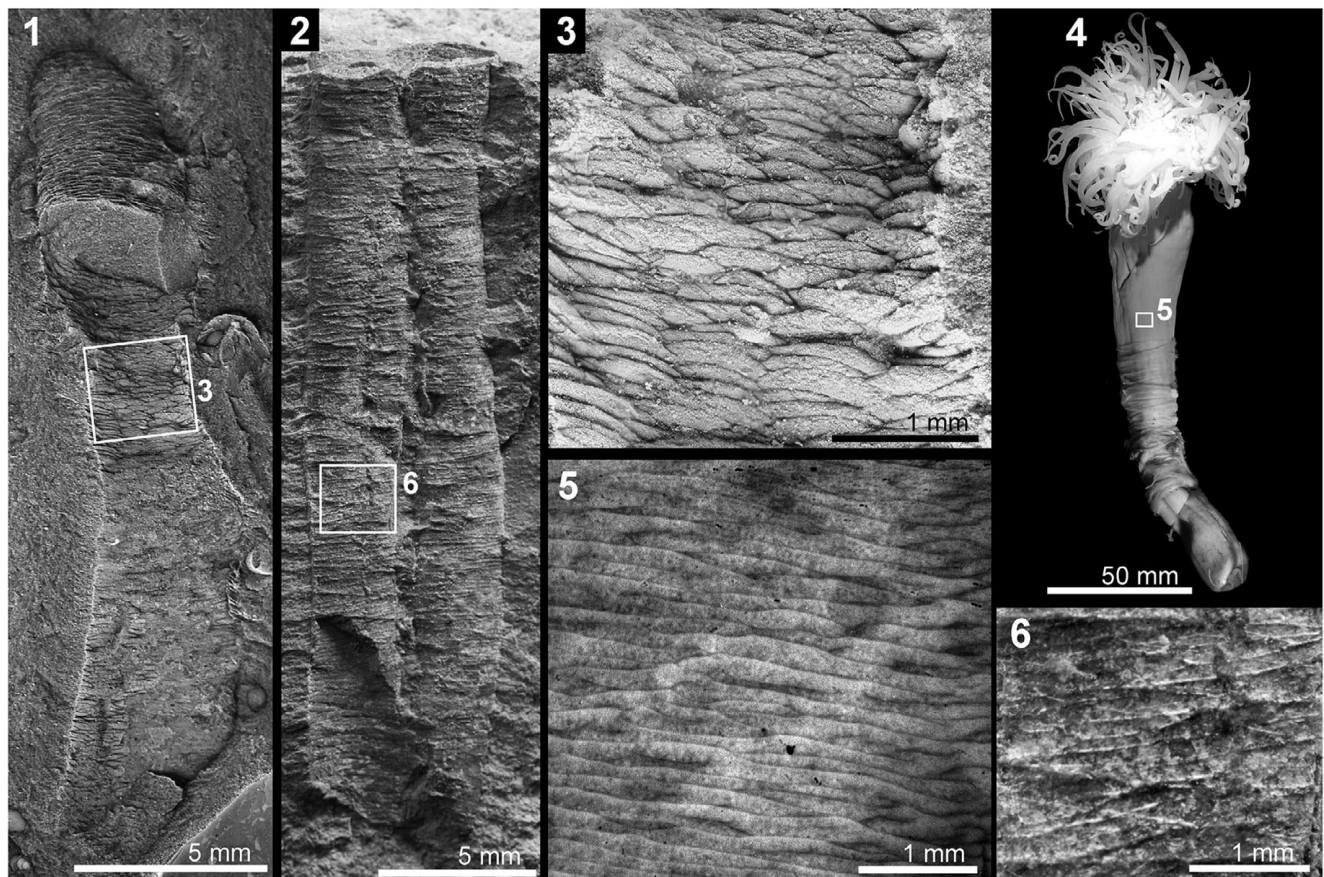


Figure 1. Eocene ceriantharid tubes from the Makah and Hoko River formations in Washington State, USA, and extant ceriantharid from the Mediterranean Sea near Napoli, Italy. (1) Overview of a ceriantharid tube fragment from the late Eocene Makah Formation (NRM Cn 76105). (2) Overview of the tube fragment from the middle to late Eocene Hoko River Formation (UWBMIP 106332). (3) Close-up on the surface structure showing the 'knitted pattern' (NRM Cn 76105). (4, 5) *Cerianthus membranaceus* (NRM Zool. coll. No. 137355); view of the whole specimen, photographed in alcohol (4), and close-up on its surface structure (5). (6) Close-up of the surface structure of the middle to late Eocene tube from the Hoko River Formation (UWBMIP 106332).

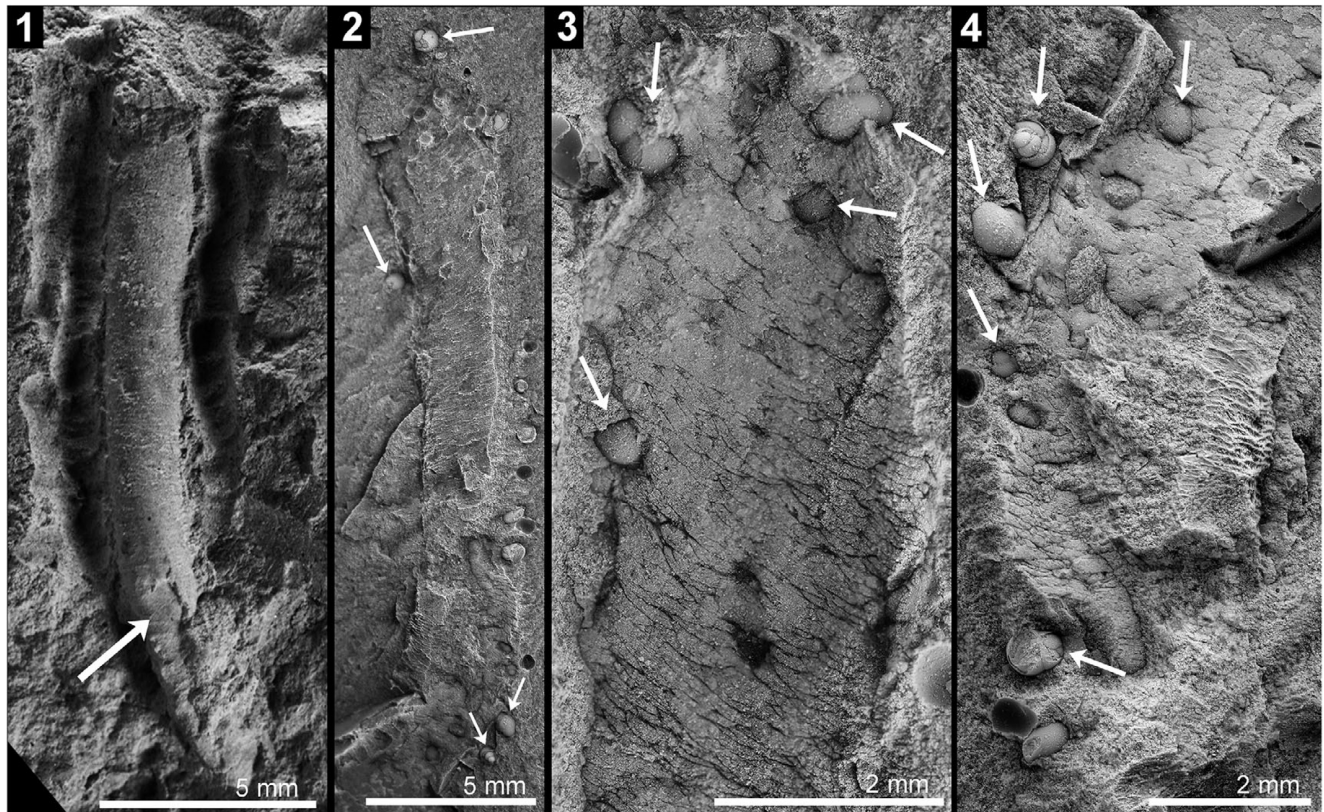


Figure 2. Eocene and Oligocene ceriantharian tubes from the Makah and Lincoln Creek formations in Washington State, USA. (1) Overview of part of the tube from the late Oligocene Lincoln Creek Formation (UWBMP 117997); arrow indicates partially folded and collapsed area. (2–4) Ceriantharid tube fragments from the late Eocene Makah Formation (NRM Cn 76105) with associated benthic foraminiferans (probably *Pullenia bulloides*; marked by arrows); overview of specimen with foraminiferans along the outside of the tube (2), and close-ups of areas of the fossil tubes with benthic foraminiferans embedded in the tube (3, 4).

with benthic foraminiferans along their length, some of which are embedded in the tube itself (Fig. 2.2–2.4). The foraminiferans are probably *Pullenia bulloides* (d'Orbigny, 1846), a species abundant in late Eocene to Oligocene deep-water deposits (Rau, 1964; Miller and Katz, 1987).

Specimen UWBMP 106332 is preserved in a small concretion, 25 mm long and 6 mm wide, and is open at both ends without any evidence of tapering (Fig. 1.2). Its surface shows an overlapping, fibrous knitted pattern (Fig. 1.6). The tube may have been slightly more rigid than the other tubes because it shows some axial folds from compaction of the sediment (Fig. 2.2).

Specimen UWBMP 117997 is more elongate, preserved mostly in three dimensions, and appears to be a single tube that was about 2.5 mm in diameter and more than 60 mm long originally (Fig. 2.1). The surface is not as well preserved as surfaces in the other two specimens but seems to have had a similar texture. The tube is partly folded and collapsed in one place, indicating that it was flexible. It is open at both ends and does not taper.

The wrinkled surface structure of the Eocene and Oligocene tubes resembles that of the extant *Cerianthus membranaceus* (Fig. 1.4, 1.5). The detail on the surface structure of the extant specimen was taken about 10 mm above the transparent–whitish tube and 40 mm below the crown. Furthermore, some extant ceriantharids incorporate particles including tests of foraminiferans in their tubes (e.g., Stampar et al., 2015, fig. 2B). The benthic foraminiferans embedded in the fossil tube are thus consistent with this feature of some extant ceriantharids.

Discussion and conclusion

Due to the similarity of the surface structure of the extant ceriantharid *Cerianthus membranaceus* with the surface structure of the fossil tubes from Washington (Fig. 1.3, 1.5, 1.6), we interpret them as the tubes of ancient ceriantharids. This makes them, to the best of our knowledge, the first fossils of Ceriantharia, although Frey (1970) had postulated that anemone burrows could possibly produce distinctive fossils. A putative fossil ceriantharid was reported from the Ordovician of Québec, Canada, in an unpublished master's thesis (Alghaled, 2019). These flattened carbonaceous fossils consist of a tubular 'body' and a 'tentacle crown', about 6 mm wide and 37 mm long, and do indeed resemble anemones. However, a full understanding of these fossils requires further work. Herringshaw et al. (2007) interpreted the Paleozoic cornulitids (small, solitary, and often encrusting calcitic tubes) as solitary, aseptate members of the stem-Zoantharia, and hence phylogenetically close to Ceriantharia.

The fossil tubes from Washington bear some resemblance to the Paleozoic trace fossil *Oikobesalon* Thomas and Smith, 1998, which was introduced for the older synonym *Trachyderma* Phillips, 1848 (Thomas and Smith, 1998). *Oikobesalon* represents tubular fossils with an organic, or at least originally organic, tube wall with a similar knitted surface pattern, (described as 'transverse fusiform bands' in the diagnosis by Thomas and Smith, 1998) as the fossils documented here. Those fusiform bands are notably broader in *Oikobesalon* (0.5–2 mm) compared to at most 0.1 mm in the fossils

from Washington and the extant *Cerianthus membranaceus*. The most distinct difference are the branched extensions of organic material that extend outward into the sediment from the *Oikobesalon* tubes, a feature not seen in the ceriantharid tubes documented here.

Because the tubes from Washington do not taper and lack segmentation, they differ greatly from tubes found in rocks of similar age in Oregon, that were attributed to pogonophorans (Adegoke, 1967). Pogonophorans are today considered part of the polychaete annelid family Siboglinidae (Rouse, 2001). The tubes of serpulids, certain cirratulids and sabellids, and the linings of tubes of the wood-boring bivalve *Teredo*, differ by being calcified (Grave, 1928; Vinn and Mutvei, 2009; Vinn, 2021). Some sabellids incorporate or even build their tubes of foraminiferan tests (Vinn et al., 2018). In an example from the Miocene Monterey Formation in California, the tests were agglutinated in a preferred orientation, resulting in a rhomboid pattern somewhat reminiscent of the knitted pattern documented here, but the individual rhombs were much larger than in the fossils from Washington (Finger et al., 2008, pl. 4, figs. 1–3). The organic tubes of chaetopterids typically show fine, longitudinal ridges or wrinkles (Kiel and Dando, 2009) rather than wrinkles perpendicular to the tube length, as in the fossils from Washington.

In a tabulation of the first appearances of orders of marine invertebrates since the Mesozoic, Jablonski and Bottjer (1991) showed that first appearances of clades with low fossilization potential have a rather random distribution throughout the geologic record. When added to this compilation, the ceriantharian tubes reported here would be the third youngest invertebrate order, which indeed seems unlikely given the basal position of Ceriantharia among the Hexacorallia (McFadden et al., 2021; DeBiasse et al., 2022). The tube-forming ptychocysts are a character unique to Ceriantharia (Mariscal et al., 1977; Reft and Daly, 2012). However, this does not necessarily imply that the present-day ceriantharian mode of tube construction originated immediately after the split of Ceriantharia from the remaining hexacorals. Anthozoan cnidarians are known to have repeatedly lost and re-established their modes of hard-part formation (Oliver, 1996; Stanley, 2003; Medina et al., 2006; Drake et al., 2020). The strong similarity between extant ceriantharids and the Paleogene tubes documented here suggests that the present-day mode of ceriantharid tube formation using ptychocysts was established at latest by the middle Eocene.

Stampar et al. (2015) reported that members of the extant ceriantharian family Ceriantharidae built relatively solid tubes, embedding rather little foreign material, when compared to the tubes of the other ceriantharian families Arachnactidae and Botrucnidiferidae. Thus, the Eocene tubes documented here could have been formed by members of the family Ceriantharidae, considering that only a few foraminiferans were incorporated in the tube walls, and that the tubes are preserved at all. However, using molecular data, Forero Mejia et al. (2020) found Cerianthidae and Botrucnidiferidae polyphyletic and only Arachnactidae monophyletic. Thus, it remains uncertain whether tube type is characteristic for individual clades within the order Ceriantharia.

The Eocene and Oligocene ceriantharid tubes reported here are rather inconspicuous fossils that may easily be overlooked, mistaken as trace fossils, or be ignored. We hope our findings encourage field paleontologists to carefully inspect older fine-grained sedimentary rocks for similar structures, as low-energy, deep-water conditions might be particularly conducive for the preservation of ceriantharid tubes. However, given that ceriantharids live in a wide range of habitats (Stampar et al., 2020), concretions from any marine environment might be worth investigating.

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Competing interests. The authors declare no competing interests.

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