

Subfossil cyclostome bryozoans from Daidokutsu submarine cave, Okinawa, Japan

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ABSTRACT

A sediment core (Core 19) taken in Daidokutsu cave on Ie Island, Okinawa, spans the last 7,000 years. The sampling of multiple taxa from this submarine cave has been aimed at understanding the Holocene history of biodiversity and ecological dynamics. The results have already been published for ostracods, molluscs, foraminifera and cheilostome bryozoans. The current study focuses on the cyclostome bryozoan fauna, establishing a taxonomic foundation that will contribute to an understanding of responses by the bryozoan community in this cave habitat to environmental and climate changes through the Holocene. Very little has been published on modern and Quaternary fossil cyclostomes from Japan, and nearly all publications predate the routine use of scanning electron microscopy in cyclostome taxonomy. Fifteen cyclostome species are described here from Daidokutsu. Eight of these are new species, the remaining seven were identified only to the genus level. The high proportion of new species may not only reflect the uniqueness of the Daidokutsu cyclostome fauna but also the scarcity of studies on Japanese cyclostomes and the inadequacy of descriptions and figures in older publications, which make it difficult or impossible to interpret the species they describe. Unlike cyclostome cave faunas from the Mediterranean, erect cyclostomes strongly outnumber species with encrusting colonies. In addition, the secondary homonymy of *Parasmittina ligulata*, used for both a new species from Daidokutsu Cave and a Western Atlantic species, is resolved by renaming the Japanese species *Parasmittina vieirai* nom. nov.

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Final citation: Taylor, Paul D., Di Martino, Emanuela, Rosso, Antonietta, Chiu, Ruby W.T., Fujita, Kazuhiko, Kitamura, Akihisa, and Yasuhara, Moriaki. 2025. Subfossil cyclostome bryozoans from Daidokutsu submarine cave, Okinawa, Japan. *Palaeontologia Electronica*, 28(2):a29.

<https://doi.org/10.26879/1546>

palaeo-electronica.org/content/2025/5573-holocene-cyclostomes-from-japan

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Keywords: Cyclostomatida; Holocene; new species; taxonomy

Submission: 5 March 2025. Acceptance: 7 July 2025.

INTRODUCTION

Biotic responses to climatic and environmental changes are being addressed through a multi-taxon study of subfossils sampled from cores spanning the last 7,000 years in Daidokutsu submarine cave on Ie Island, Okinawa, Japan. Results have already been published on ostracods (Chiu et al., 2016, 2017), molluscs (Kitamura et al., 2007a, b, 2013; Yamamoto et al., 2009, 2010; Chiu et al., 2017), foraminifera (Omori et al., 2010; Chiu et al., 2017) and cheilostome bryozoans (Di Martino et al., 2025). The current paper extends the study to cyclostomes, a lesser-known order of bryozoans.

According to Bock and Gordon (2013), cyclostomes are represented by an estimated 543 species in modern oceans. This is roughly one-tenth of the diversity of cheilostomes, which are the dominant order of bryozoans living today. Like cheilostomes, cyclostomes have calcareous skeletons and locally contribute significant quantities of biogenic carbonate sediment to the seafloor. The fossil record of cyclostomes extends back to the Ordovician (Taylor, 2020), and they have colonised submarine caves since at least the Late Jurassic (Taylor and Palmer, 1994). Cyclostome zooids have relatively simple skeletons which are typically tubular, in contrast to the more complex, generally box-shaped skeletons of cheilostome zooids. As a result, the range of skeletal morphological characters available for cyclostome taxonomy is more limited, a fact recognised by bryozoologists since the nineteenth century (e.g., Waters, 1884, 1887;

Gregory, 1896), and the first descriptions of species in the early bryozoan literature were considered to be inadequate even as far back as 1904 (Waters, 1904, p. 172). High levels of morphological plasticity also characterise cyclostome species (Harmelin, 1976a, b), while molecular phylogenetic studies have revealed major discordances between the existing classification of cyclostomes and phylogeny (Waeschenbach et al., 2009). These factors have contributed to cyclostomes being justifiably branded as a difficult group, which in part may account for the scarcity of modern taxonomic studies.

Knowledge of cyclostomes from Japan is particularly poor. While some studies of bryozoan faunas have included cyclostomes (Ortmann, 1890; Okada and Mawatari, 1936; Mawatari, 1952; Kataoka, 1960), very few papers have focused solely on cyclostomes. Okada (1917) reported and described 33 species of cyclostomes from the modern seas of Japan. Unfortunately, this paper, which introduces seven new species, lacks illustrations, making it particularly difficult to use for species identification. In a subsequent paper, Okada (1928) described 12 species of cyclostomes from Mutsu Bay, five new, this time accompanied by drawings and photographic illustrations. A checklist of Japanese cyclostomes (Mawatari, 1955), which included some fossils, listed 78 species from Japan. Mawatari and Mawatari (1973) described 10 species of crisiid cyclostomes around the coast of Hokkaido, two of which were new. From the

same region, they later described 21 species of non-crisiid cyclostomes, including a single new species (Mawatari and Mawatari, 1974). Finally, Taylor and Grischenko (2015) described two new cyclostome species unusual for forming heavily calcified colonies in the intertidal zone of Akkeshi Bay, Hokkaido. Turning to the Quaternary fossil record, Dick et al. (2008) compiled data from the literature on Japanese Pleistocene bryozoans. These authors recorded 22 cyclostome species, representing only 6.1% of the diversity of the total bryozoan fauna. However, a subsequently discovered Pleistocene locality in the Setana Formation at Kuromatsunai in Hokkaido alone was found to contain 24 species of cyclostomes (Taylor et al., 2013). This compares with 96 species of cheilostomes from the same locality, meaning that cyclostomes make up 20% of total bryozoan diversity at Kuromatsunai.

MATERIAL AND METHODS

Material used for this study was sorted from 62 samples (Di Martino et al., 2025, table 1), each corresponding to 1 cm sections of a sediment core (Core 19) obtained from a depth of 29 m inside the Daidokutsu submarine cave (26.72°N, 127.83°E; see Yamamoto et al., 2009; Chiu et al., 2017, figure 1A, B), which is located on the east coast of Ie Island, Okinawa, Japan. Core 19 was drilled 32.5 m from the entrance of the cave (see Chiu et al., 2017, figure 1C). Encompassing sediments deposited through approximately the last 7,000 years based on radiocarbon dating (Yamamoto et al., 2009; Kitamura et al., 2013), Core 19 is 5 cm in diameter and 233 cm long. Samples were wet-sieved using a 63 µm sieve, dried, and then dry-sieved using 150 µm, 250 µm, 500 µm and 1 mm sieves. Bryozoans were picked from the >500 µm size fractions.

Imaging of uncoated specimens employed low-vacuum scanning electron microscopes operating in back-scattered mode. These instruments were a LEO VP-1455 and a JEOL IT500 at the Natural History Museum, London, UK; a Tescan Vega 2 LMU at the Department of Biological, Geological and Environmental Sciences, University of Catania, Italy; and a Hitachi TM4000plus Tabletop at the Natural History Museum, University of Oslo, Norway.

Morphometric measurements were taken from SEM images using the image processing program ImageJ (available at <https://imagej.nih.gov/>). Each measurement is given as the mean value plus or minus the standard deviation, followed by the

observed range, with the number of specimens used and the total number of measurements both enclosed in parentheses. Please note that the measurements correspond to the illustrated specimens and occasionally to other specimens listed under each species.

Three of us (PDT, EDM and AR) were responsible for the systematic part of this paper and are to be considered the authors for all new species described.

All specimens are deposited in the collections of the Palaeontological Museum (PMC) of the Department of Biological, Geological, and Environmental Sciences, University of Catania (Italy).

SYSTEMATIC PALAEOONTOLOGY

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order CYCLOSTOMATIDA Busk, 1852
Suborder ARTICULATA Busk, 1859
Family CRISIIDAE Johnston, 1847
Genus *CRISIA* Lamouroux, 1812
Crisia ramalhoae sp. nov.
Taylor, Di Martino and Rosso
Figure 1

Zoobank

Type material. Holotype PMC. B74. 26.2.2025a, sample 19052 (Figure 1A–D, F); paratypes PMC. B74. 26.2.2025b1, sample 19056 (Figure 1E); PMC. B74. 26.2.2025b2 sample 19085 (Figure 1G–H); PMC. B74. 26.2.2025b3, sample 19085. Daidokutsu cave, Core 19, Holocene, Okinawa, Japan.

Etymology. Named for Lais Ramalho in recognition of her studies on bryozoans from Brazil and the Mediterranean Sea.

Diagnosis. *Crisia* with narrow internodes, comprising more than 10 zooids; nodes located immediately proximal of an autozooidal aperture, one or two per internode; autozooids small, apertures circular, pseudopores slit-shaped; brood chamber intervening between two autozooids along one side of internode, inverted pear-shaped, bulbous, densely pseudoporous, pseudopores slit-shaped; oeciostome very short, located distally of brood chamber; oeciopore transversely elliptical, about as wide as an autozooidal aperture.

Description. Colony erect, articulated, internodes narrow, 110–168 µm wide, comprising 10–14 or more zooids, biserial, autozooids opening alternately on either side of branch, zooidal boundaries not apparent on wrinkled colony surface. Articulation bases located immediately proximal of an autozooidal aperture, one or two per internode,

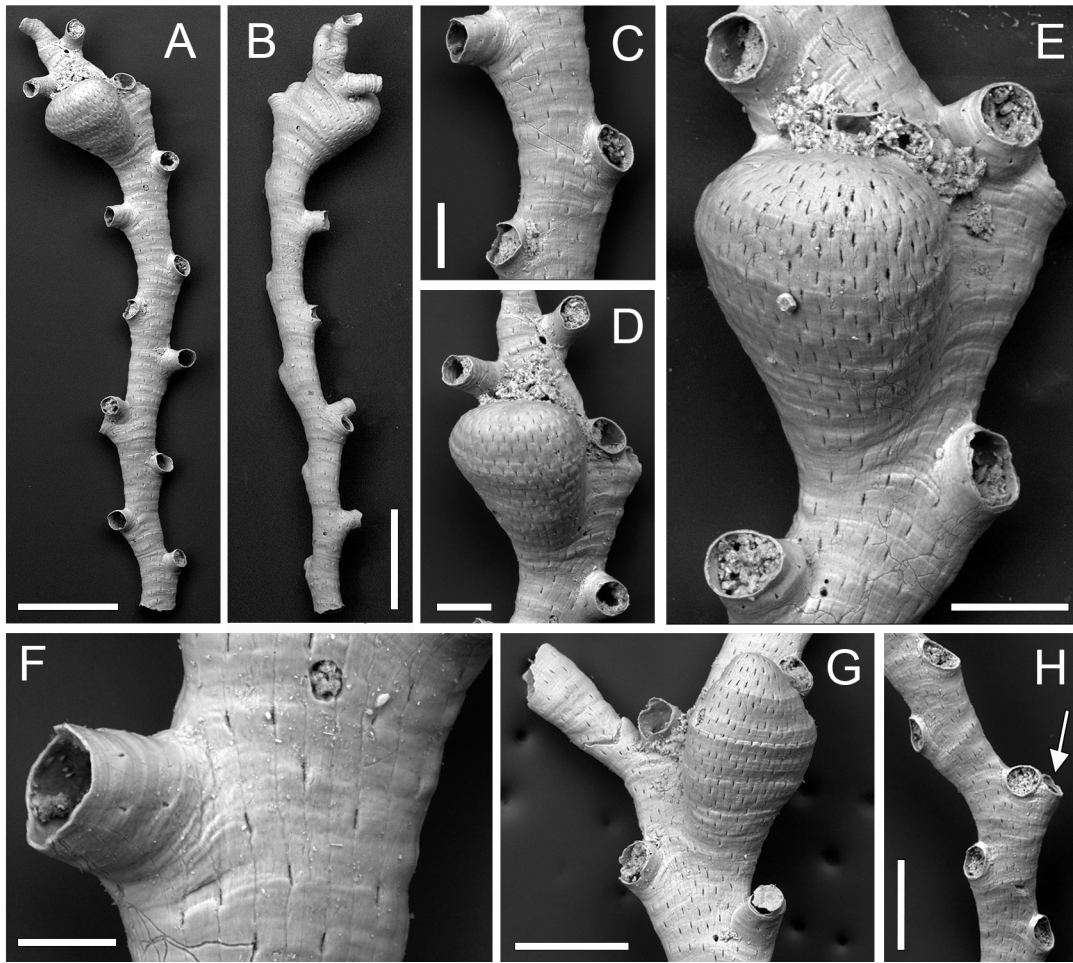


FIGURE 1. *Crisia ramalhiae* sp. nov. A–D, F, holotype PMc. B74. 26.2.2025a sample 19052. A, internode frontal (300 µm). B, internode abfrontal (300 µm). C, detail of frontal showing three apertures (100 µm). D, gonozooid (100 µm). F, peristome (left) and slit-like pseudopores on the frontal wall (50 µm). E, paratype PMc. B74. 26.2.2025b1, sample 19056, gonozooid (100 µm). G–H, paratype PMc. B74. 26.2.2025b3, sample 19085. G, gonozooid (200 µm). H, autozooids and node indicated by an arrow (200 µm).

about the same diameter or slightly larger than an autozooidal aperture, facing frontolaterally or outwardly. Ancestrula and colony base unknown. Autozooids small, slender, frontal wall covered by slit-shaped pseudopores located in shallow grooves between strips of calcification 14–20 µm wide, pseudopores 9–12 µm long by 1–2 µm wide, centre-to-centre spacing of pseudopores in same groove 45–105 µm; apertures small, circular, 52–83 µm in diameter, facing distolaterally; peristomes short with high angle of divergence and shorter pseudopores. Gonozooids inverted pear-shaped, bulbous, intervening between two autozooids along one side of internode; brood chamber densely covered by slit-shaped pseudopores located in grooves between narrow strips of calcification 7–13 µm wide, pseudopores 7–11 µm long by 1–2 µm wide, centre-to-centre spacing of pseu-

dopores in same groove 30–46 µm; oeciostome very short, terminal, located distally of brood chamber sometimes off-centred relative to brood chamber axis, slightly flared; oeciopore transversely elliptical, about as wide as an autozooidal aperture.

Measurements (µm). Zooid length 329 ± 32 , $307\text{--}397$ (2, 7); aperture diameter 63 ± 10 , $52\text{--}83$ (2, 10); brood chamber length 296 ± 40 , $255\text{--}350$ (4, 4); brood chamber width 246 ± 33 , $217\text{--}291$ (4, 4); oeciopore length 30 ± 6 , $24\text{--}36$ (3, 3); oeciopore width 76 ± 9 , $69\text{--}86$ (4, 4).

Remarks. *Crisia* is a speciose genus containing almost 80 extant species, very few of which have been illustrated or described comprehensively by modern standards. Ziko et al. (2012) identified six species of *Crisia* from the Red Sea, paying particular attention to the morphology of the pseudopores.

To judge from figure 6 of their paper, none of these species have pseudopores as elongate as those in *C. ramalhoae* sp. nov. where they are up to ten times longer than wide (Figure 1F). Slit-shaped pseudopores characterise *Crisia spissus* Chae, Kil, Zágorský and Seo, 2018, but this species from Korea has broader branches than *C. ramalhoae* sp. nov., and the oöciopore is circular rather than transversely elliptical. The Brazilian species *Crisia fragosa* Ramalho, Muricy and Taylor, 2009 also has slit-like pseudopores but the autozooids are much larger (length 863–1212 µm compared to 307–397 in *C. ramalhoae* sp. nov.) and the oöciostome is long rather than short. Another Brazilian species, *C. ficulnea* Buge, 1979, is distinctive among species of *Crisia* with slit-shaped pseudopores in lacking any trace of an oöciostome, while the Madeiran species *Crisia noronhai* sp. Souto, Ramalhosa and Canning-Clode in Souto et al., 2023 has an almost circular oöciopore contrasting with the transversely elliptical oöciopore of *C. ramalhoae* sp. nov. Finally, *C. guang* Liu, Liu and Zágorský, 2019, from the South Yellow Sea of China differs from the new species in having a very long and slender gonozooid.

Crisia prominens sp. nov.

Taylor, Di Martino and Rosso

Figure 2

Zoobank

Type material. Holotype PMC. B75. 26.2.2025a, sample 19056 (Figure 2A, C–D); paratype PMC. B75. 26.2.2025b1, sample 19036 (Figure 2B, E).

Daidokutsu cave, Core 19, Holocene, Okinawa, Japan.

Etymology. Named for the prominent brood chambers.

Diagnosis. *Crisia* with narrow internodes, zigzagging; nodes close to base of internode proximolaterally of an autozooidal aperture; autozooids very small, apertures circular, pseudopores longitudinally elongate, sparse; gonozooids small, bulbous, vicarious, replacing an autozooid in proximal part of internode, brood chamber protruding, bean-shaped, densely pseudoporous, pseudopores longitudinally elongate, oöciostome short, hooked, located on distal-facing top of brood chamber; oöciopore transversely elliptical.

Description. Colony erect, articulated; internodes narrow, 67–121 µm wide, zigzagging, comprising 9 or more zooids, biserial, autozooids opening alternately on either side of branch, zooidal boundaries not apparent on colony surface. Articulation bases located proximolaterally of an autozooidal aperture, close to base of internode, facing distolaterally. Ancestrula and colony base unknown. Autozooids small, slender, frontal wall covered by sparse, longitudinally elongated pseudopores located between ill-defined strips of calcification, pseudopores sparse, 5–8 µm long by 2–3 µm wide, nearest neighbour centre-to-centre spacing 23–29 µm; apertures small, circular, 45–58 µm in diameter, facing distolaterally; peristomes short. Gonozooids small, bulbous, vicarious, replacing an autozooid in proximal part of internode; brood

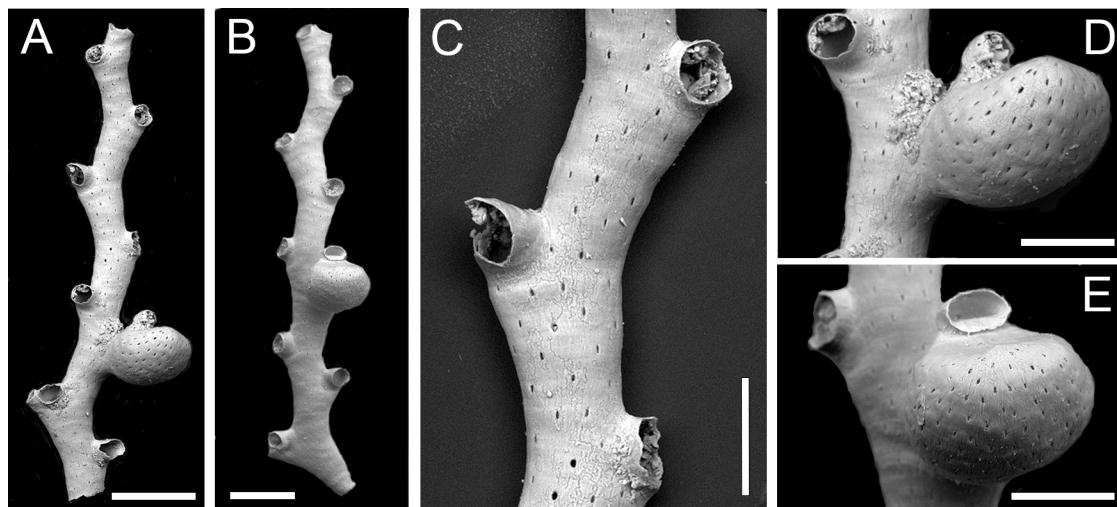


FIGURE 2. *Crisia prominens* sp. nov. A, C–D, holotype PMC. B75. 26.2.2025a, sample 19056. A, internode (200 µm). C, detail showing three apertures and longitudinally elongate pseudopores (100 µm). D, gonozooid with oöciostome (100 µm). B, E, paratype PMC. B75. 26.2.2025b1, sample 19036. B, internode (200 µm). E, gonozooid with oöciopore visible (100 µm).

chamber protruding from internode, bean-shaped, about 215 μm long by 190 μm wide, densely covered by longitudinally elongate pseudopores, 5–9 μm long by 2–3 μm wide, more closely spaced than on autozooidal frontal walls, nearest neighbour centre-to-centre spacing of pseudopores 11–20 μm ; oeciostome short, hooked, located on distal-facing top of brood chamber; oeciopore transversely elliptical, about as wide as an autozooidal aperture, 36 μm long by 58 μm wide in measured example, facing distolaterally.

Measurements (μm). Zooid length 299 ± 21 , 269–327 (2, 9); aperture diameter 49 ± 3.5 , 45–58 (2, 11).

Remarks. The most distinctive feature of *Crisia prominens* sp. nov. is the gonozooid with its bean-shaped, protruding brood chamber (Figure 2D, E). Brood chambers of similar morphology are found in *Crisia cuneata* Maplestone, 1905, as figured by Harmer (1915, pl. 8, figures 16–17) and Chae et al. (2020, figure 1E), *C. circinata* Waters, 1914, from Zanzibar, as well as *C. tenella longinodata* Rosso, 1998, from the Pleistocene of southern Italy (Rosso, 1998, plate 1, figures 9–10). However, the branches of *C. prominens* sp. nov. are more gracile than those of *C. cuneata*, with the autozooids appearing slenderer and aperture spacing about three times branch width compared to twice or less in *C. cuneata*. *Crisia circinata* has autozooids of

similar length (distance between autozooidal series about 0.27 mm according to Waters (1914) vs. 0.27–0.33 mm in *C. prominens* sp. nov.) and gonozooids positioned low in the internodes, apertural diameter is larger than in *C. bulbosa* sp. nov. (0.08 mm vs. 0.05–0.06 mm). Another East African species, *C. zanzibarensis* Brood, 1976, also has protruding brood chambers but the gonozooids in this species are larger and the internodes seemingly longer containing 15–30 zooids compared to fewer than 10 zooids seen in *C. prominens* sp. nov. *Crisia tenella longinodata* differs in having longer and more slender internodes as well as peristomes of smaller diameter.

The autozooids of *C. prominens* sp. nov. are slightly smaller than those of *Crisia ramalhoae* sp. nov. However, apart from the contrasting morphology of the gonozooids, the most obvious difference concerns the pseudopores. These are roughly three times longer than wide in *C. prominens* sp. nov. (Figure 2C), compared with about 5–10 times longer in *Crisia ramalhoae* sp. nov. (Figure 1F) where they are more clearly slit-shaped.

Genus *CRISIONA* Canu and Bassler, 1927

Crisiona sp.

Figure 3

Figured material. PMC EDM-Collection J. H. B.152a.1, sample 19031 (Figure 3A); PMC EDM-

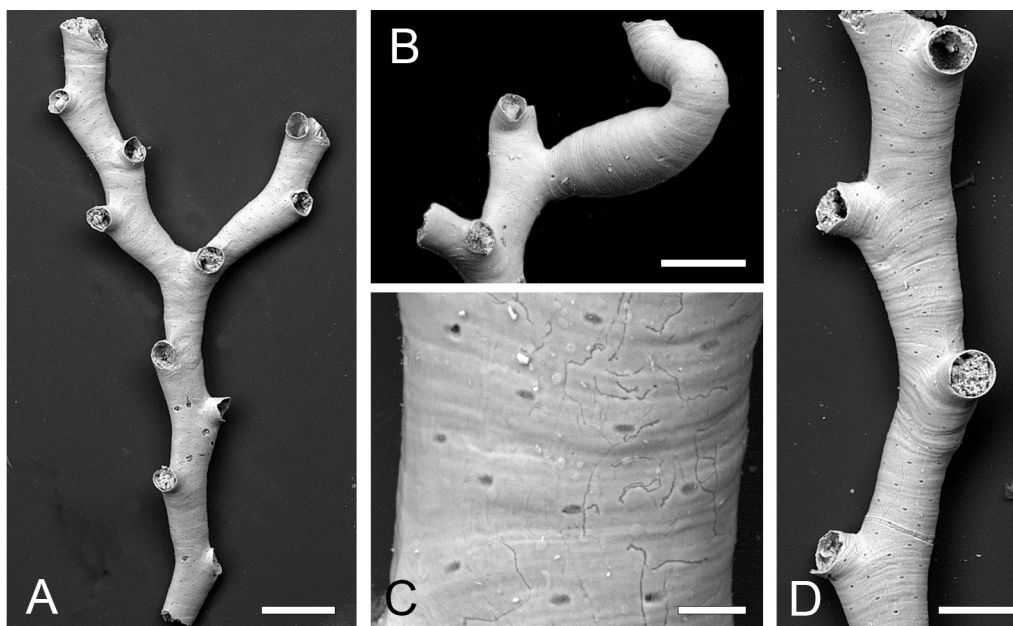


FIGURE 3. *Crisiona* sp. A, PMC EDM-Collection J. H. B.152a.1, sample 19031, bifurcating branch (200 μm). B, PMC EDM-Collection J. H. B.152a.3, sample 19058, peculiar bent branch (200 μm). C–D, PMC EDM-Collection J. H. B.152a.2, sample 19031. C, transversely elliptical pseudopores (20 μm). D, branch showing alternating arrangement of zooids (100 μm).

Collection J. H. B.152a.2, sample 19031 (Figure 3C–D); PMC EDM-Collection J. H. B.152a.3, sample 19058 (Figure 3B). Daidokutsu cave, Core 19, Holocene, Okinawa, Japan.

Description. Colony erect, seemingly not articulated; branches narrow, averaging 105 μm wide (range 72–143 μm), zigzagging mildly, biserial, autozooids opening alternately on either side of branch, zooidal boundaries not visible; bifurcations at an angle of about 80° , one of the daughter branches diverging immediately distally of an aperture. Ancestrula and colony base unknown. Autozooids slender, frontal wall relatively smooth; pseudopores small, about twice as wide as long, 2–3 μm long by 5–6 μm wide, nearest neighbour centre-to-centre spacing 17–29 μm , lacking spines or other constrictions; apertures very small, circular, facing somewhat laterally; peristomes short. Gonozooids unknown.

Measurements (μm). Zooid length 392 ± 57 , 285–461 (2, 10); aperture diameter 61 ± 6.7 , 48–73 (2, 10).

Remarks. This species is assigned tentatively to the little-known genus *Crisiona*, which was introduced by Canu and Bassler (1927) for crisiids with non-articulated colonies. The type species, *C. baculifera* Canu and Bassler, 1927, comes from Hawaii, and one other Recent species, two Cretaceous species and one Miocene species were referred by Canu and Bassler to their new genus. The type species has bifurcating branches with

long tubular prolongations (?kenozooids) on the sides of the branches. One specimen of the Daidokutsu species has two questionable bifurcations near the distal end of the fragment, one on the left is short and presumably broken, and a longer one on the right is strongly curved (Figure 3B). In the absence of a gonozooid, however, we hesitate to introduce a new species. The broad pseudopores (Figure 3C) enable distinction from the two species of *Crisia* described above in addition to the lack of articulation nodes.

Suborder TUBULIPORINA Milne-Edwards, 1838

Family ONCOUSOECIIDAE Canu, 1918

Genus FILISPARSA d'Orbigny, 1853

Filisparsa haywardi sp. nov.

Taylor, Di Martino and Rosso

Figure 4

Zoobank

Type material. Holotype PMC. B76. 26.2.2025a, sample 19085 (Figure 4D–E); paratypes PMC. B76. 26.2.2025b.1 (Figure 4C), PMC. B76. 26.2.2025b.2, PMC. B76. 26.2.2025b.3 (Figure 4F) sample 19085; PMC. B76. 26.2.2025b.4, sample 19029 (Figure 4A–B). Daidokutsu cave, Core 19, Holocene, Okinawa, Japan.

Etymology. Named for Peter J. Hayward in recognition of his numerous contributions to bryozoology, including a synopsis on British cyclostome bryozoans (Hayward and Ryland, 1985b).

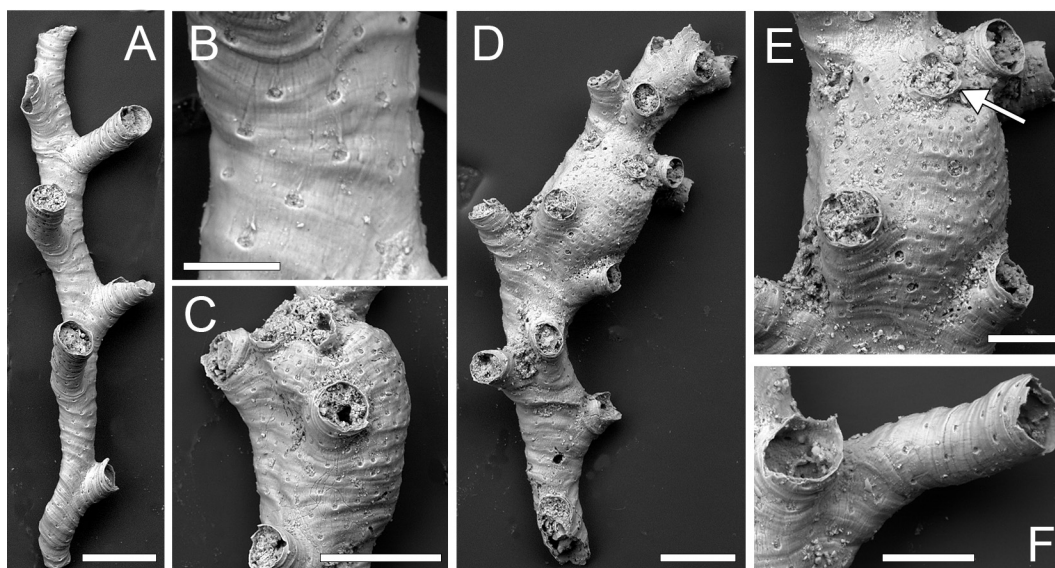


FIGURE 4. *Filisparsa haywardi* sp. nov. A–B, paratype PMC. B76. 26.2.2025b.4, sample 19029. A, infertile branch (200 μm). B, pseudopores (50 μm). C, paratype PMC. B76. 26.2.2025b.1, sample 19085, gonozooid (200 μm). D–E, holotype PMC. B76. 26.2.2025a, sample 19085. D, fertile branch (200 μm). E, gonozooid with oeciopore arrowed (100 μm). F, paratype PMC. B76. 26.2.2025b.3, sample 19085, long peristome (100 μm).

Diagnosis. *Filisparsa* with small autozooids, length averaging about 400 μm , frontal wall smooth with transversely elliptical pseudopores; gonozooids longitudinally ovoidal, margins indented by autozooidal peristomes, ooeciopore subcircular, small.

Description. Colony erect, seemingly not articulated, bifurcations not observed, branches narrow, averaging 166 μm wide (range 84–320 μm), biserial, becoming quadriserial where gonozooids occur, often slightly curved, autozooids opening alternately on either side of branch, zooidal boundaries obscure. Ancestrula and colony base unknown. Autozooids small, slender, frontal wall rugose with strong transverse folds; pseudopores transversely elliptical, 4–7 μm long by 6–10 μm wide, proximal edge somewhat raised, nearest neighbour centre-to-centre spacing 20–34 μm , with a sunken iris-like constriction restricting the opening; apertures small, circular, facing distolaterally; peristomes moderately long, up to 250 μm , pseudopores similar shape and density to frontal walls. Gonozooids small, moderately bulbous; brood chamber longitudinally ovoidal, 344–415 μm long by 220–257 μm wide, edges indented by adding autozooids, densely pseudoporous, the pseudopores subcircular, 5–8 μm in diameter, nearest neighbour centre-to-centre spacing 12–19 μm ; ooeciostome short, terminal; ooeciopore circular or variably elliptical, smaller than an autozooidal aperture 54–60 μm long by 42–66 μm wide.

Measurements (μm). Zooid length 402 ± 63 , 312–539 (3, 11); aperture diameter 80 ± 9.3 , 69–101 (3, 10).

Remarks. Although the type species of *Filisparsa* – *F. neocomiensis* d'Orbigny, 1853 – is of Early Cretaceous age, at least 15 Recent species have been assigned to the genus. Unfortunately, gonozooids have not been described in *F. neocomiensis* (Pitt and Taylor, 1990, p. 81) but in a second Early Cretaceous species, *F. gasteri* Pitt and Taylor, 1990, they are small and longitudinally ovate with an ooeciopore smaller than the autozooidal apertures, as in *F. haywardi* sp. nov. Among extant species, *F. haywardi* sp. nov. resembles *F. rugosa* Canu and Bassler, 1929 from the Philippines, which is described as having a transversely wrinkled surface. However, the Philippine species has much larger zooids, their length given as 1.12–1.84 mm (cf. 0.31–0.54 mm in the present species) and with peristomes measuring 0.28–0.30 mm in width, at least three times greater than in *F. haywardi* sp. nov. Canu and Bassler's material of *F. rugosa* was, unfortunately, infertile. The new species shares

with the East African species *F. gracilis* Brood, 1976 delicate colonies, but *F. gracilis* lacks surface wrinkles and has a larger ooeciopore with a hooked ooeciostome. The Mediterranean deep-water species '*Filisparsa*' *profunda* Harmelin and d'Hondt, 1982 has larger zooids than *F. haywardi* sp. nov., with peristomes 175–205 μm in diameter. A similar, unnamed species of *Filisparsa* described by Di Martino and Taylor (2014) from the Miocene of East Kalimantan differs from *F. haywardi* sp. nov. in having teardrop-shaped pseudopores; unfortunately, the gonozooid is unknown in this Indonesian fossil.

Family ANNECTOCYMIDAE
Hayward and Ryland, 1985a
Genus ANNECTOCYMA
Hayward and Ryland, 1985a
Annectocyma sp.

Figure 5

Figured material. PMC EDM-Collection J. H. B.153a.1, sample 19019 (Figure 5A–B); PMC EDM-Collection J. H. B.153a.2, sample 19112 (Figure 5C–D). Daidokutsu cave, Core 19, Holocene, Okinawa, Japan.

Description. Colony base encrusting, initially uniserial, rapidly giving rise to first erect branch, narrow, averaging 362 μm wide (range 289–555 μm), biserial, autozooids opening alternately on either side of branch, zooidal boundaries obscure. Ancestrula short, aperture 125 μm in diameter, protoecium 205 μm wide with pseudopores sparsely scattered over surface; three periancestrular zooids: a conventional distal bud and two adventitious lateral buds on either side of ancestrular aperture. Autozooids slender, frontal wall transversely wrinkled; pseudopores longitudinally elliptical or circular, tiny, 3–5 μm long by 2–4 μm wide, nearest neighbour centre-to-centre spacing 21–29 μm , lacking spines or other constrictions; apertures, circular, facing distolaterally; peristomes short. Gonozooids not observed.

Measurements (μm). Zooid length 963 ± 123 , 819–1124 (1, 10); aperture diameter 173 ± 29.1 , 149–215 (1, 4).

Remarks. Erect branches of this species resemble *Crisiona* sp. but the autozooids are considerably larger, have more rugose surfaces, and the pseudopores are pinprick-like (Figure 5B) and typically longitudinally rather than transversely elongate. Assignment to *Annectocyma* is based mainly on the presence of adventitious budding from the ancestrula, with zooids budded on either side of the ancestrular aperture in the Okinawan species

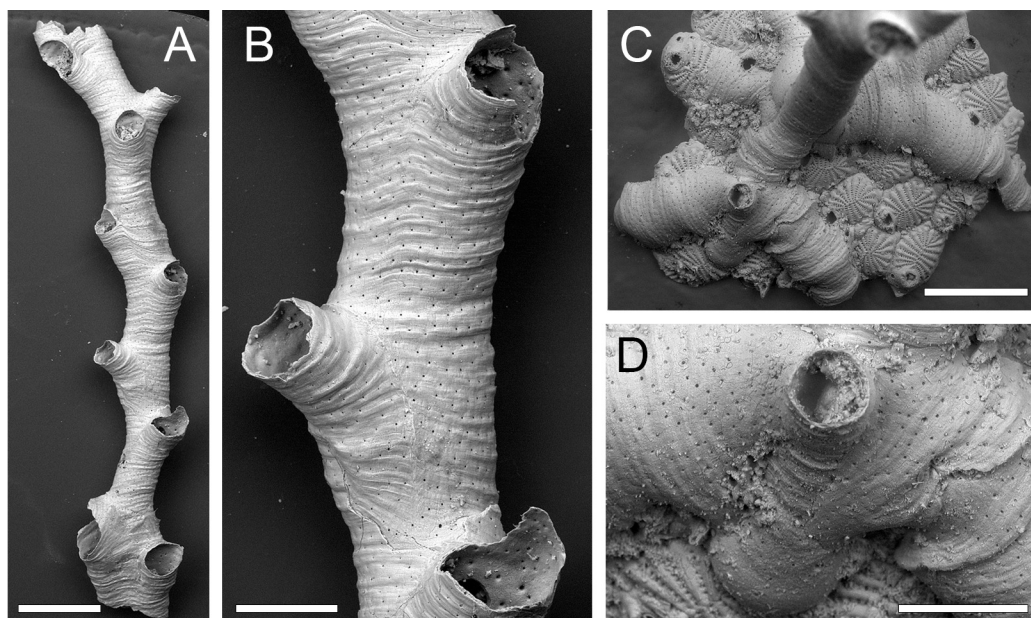


FIGURE 5. *Annectocyma* sp. A–B, PMC EDM-Collection J. H. B.153a.1, sample 19019. A, erect branch (500 µm). B, detail showing three zooids and pseudopores (200 µm). C–D, PMC EDM-Collection J. H. B.153a.2, sample 19112. C, base fouling a cheilostome with erect branch at the centre of the image (500 µm). D, ancestrula (200 µm).

(Figure 5D). While *Annectocyma* colonies are often entirely encrusting, erect branches sometimes occur and in the Daidokutsu species erect growth is initiated in very early astogeny. The discovery of gonozooids would help to test this generic placement, which for now must be somewhat tentative.

Family DIAPEROECIIDAE Canu, 1918

Genus *NEVIANIPORA* Borg, 1944

Nevianipora sp.

Figure 6

Figured material. PMC EDM-Collection J. H. B.154a.1, sample 19029 (Figure 6A–B); PMC EDM-Collection J. H. B.154a.2, sample 19056 (Figure 6C). Daidokutsu cave, Core 19, Holocene, Okinawa, Japan.

Description. Colony erect, branches narrow, about 300–700 µm wide, with a frontal and an abfrontal side, generally quadriserial with two rows of connate or closely spaced zooids on each side of branch opening alternately, zooidal boundaries very slightly grooved. Autozooids slender, frontal wall with faint transverse growth checks; pseudopores longitudinally elliptical, tiny, 4–6 µm long by 2–3 µm wide, nearest neighbour centre-to-centre spacing 16–29 µm, lacking spines or other constrictions; apertures, somewhat longitudinally elongate, facing distolaterally; peristomes short. Gonozooids narrow; brood chamber about three times longer than wide, 1268–1783 µm long by

478–552 µm wide (N = 2), modestly inflated, roof indented or penetrated by a few autozooids, densely pseudoporous, pseudopores larger than those on autozooidal frontal walls, longitudinally elongate, 4–7 µm long by 3–5 µm wide, nearest neighbour centre-to-centre spacing 14–23 µm; oeciostome located approximately mid-length, broken in both examples, off-centred in one; oeciopore transversely elongate, semielliptical, the distal edge almost straight, 73–97 µm long by 145–146 µm wide (N = 2).

Measurements (µm). Zooid length 1011±123, 822–1186 (1, 16); zooid width 227±22.5, 213–253 (1, 3); aperture length 193±43.3, 143–278 (1, 8); aperture width 172±8.4, 151–179 (1, 10).

Remarks. Two fertile branches of this species have been imaged using SEM, both showing an elongate gonozooid with an oeciostome situated at mid-length, corresponding to the non-terminal position typical of the genus. In *Nevianipora milneana* (d'Orbigny, 1842), the type species of the genus, the branches are flatter and wider, with three rows of autozooids on each side of the midline, compared with two rows in the Daidokutsu species. A couple of Chinese species of *Nevianipora* redescribed by Liu et al. (2019) also have broader branches with more rows of autozooids, as does *N. arcuata* Winston, Vieira and Woollacott, 2014 from Brazil. We defer from introducing a new species for the Okinawan species without a more

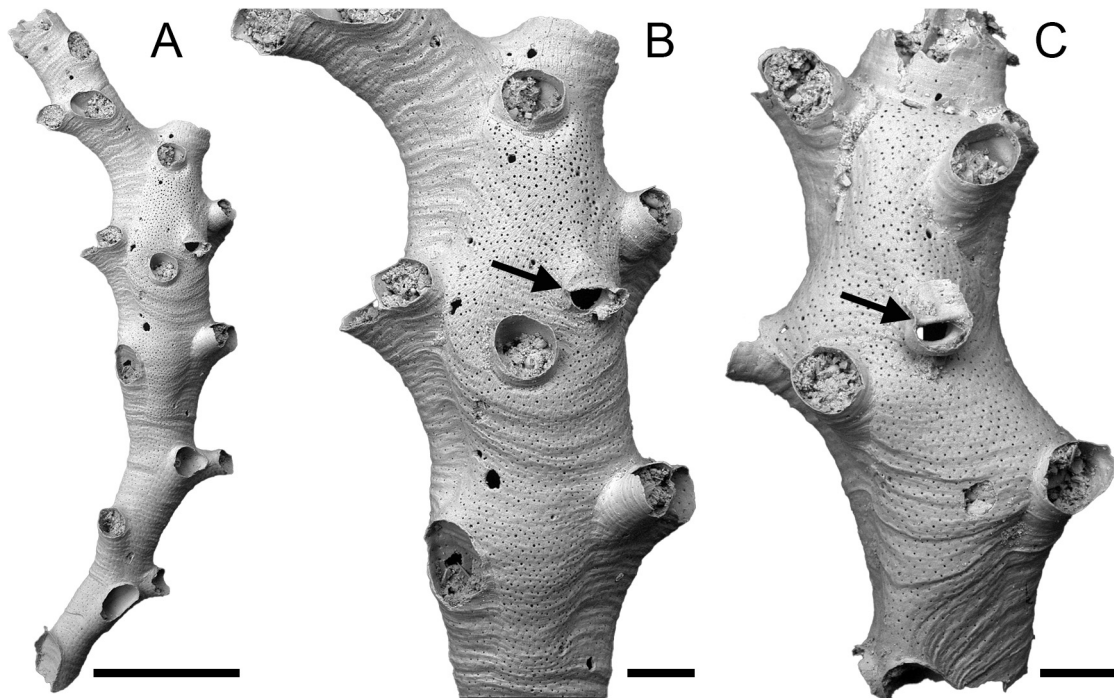


FIGURE 6. *Nevianipora* sp. A–B, PMC EDM-Collection J. H. B.154a.1, sample 19029. A, fertile branch (1000 µm). B, gonozooid with oöciopore arrowed (200 µm). C, PMC EDM-Collection J. H. B.154a.2, sample 19056, gonozooid with oöciopore arrowed (200 µm).

detailed study of its morphology, which is hindered by the small size of the fragments found.

Genus *PSILOSOLEN* Canu and Bassler, 1922

Psilosolen harmelini sp. nov.

Taylor, Di Martino and Rosso

Figure 7

Zoobank

Type material. Holotype PMC. B77. 26.2.2025a, sample 19013 (Figure 7A, E); paratypes PMC. B77. 26.2.2025b.1, sample 19031 (Figure 7B, D); PMC. B77. 26.2.2025b.2, sample 19058 (Figure 7C, F, H); PMC. B77. 26.2.2025b.3, sample 19018; PMC. B77. 26.2.2025b.4, sample 19035 (Figure 7G). Daidokutsu cave, Core 19, Holocene, Okinawa, Japan.

Etymology. Named for Jean-Georges Harmelin in recognition of his seminal research on cyclostome bryozoans.

Diagnosis. *Psilosolen* with narrow branches; about 8–15 autozooids opening all around branch circumference; autozooids small; pseudopores teardrop-shaped; gonozooids terminal with brood chambers circular to elliptical in outline penetrated or indented by about 5–8 autozooidal apertures; oöciostome adnate to a peristome, oriented subparallel to brood chamber roof; oöciopore transversely elongate.

Description. Colony erect, branches narrow vincularian, 300–1100 µm wide, broadening distally, autozooids opening around the entire circumference in about 8–15 longitudinal rows. Autozooids slender, zooidal boundaries marked by narrow fissures, frontal wall with transverse growth checks, convex; pseudopores teardrop-shaped, pointed distally, usually longer than wide, 13–17 µm long by 11–16 µm wide, nearest neighbour centre-to-centre spacing 28–48 µm, countersunk; apertures, longitudinally elliptical, some closed by terminal diaphragms lacking pseudopores; peristomes moderately long, preserved length up to 330 µm, oriented at a shallow angle to colony surface, sparsely pseudoporous. Gonozooids located at distal ends of branches; brood chamber circular or elliptical in outline, 565 by 308 µm and 788 by 629 µm in two measured examples, roof indented or penetrated by about 5–8 autozooidal apertures, sutured, densely pseudoporous, pseudopores teardrop-shaped, 10–13 µm long by 7–9 µm wide, nearest neighbour centre-to-centre spacing 14–23 µm, lumen occluded by about half a dozen stout spines; oöciostome adnate to a peristome, oriented subparallel to brood chamber roof; oöciopore transversely elongate, 50–65 µm long by 81–90 µm wide.

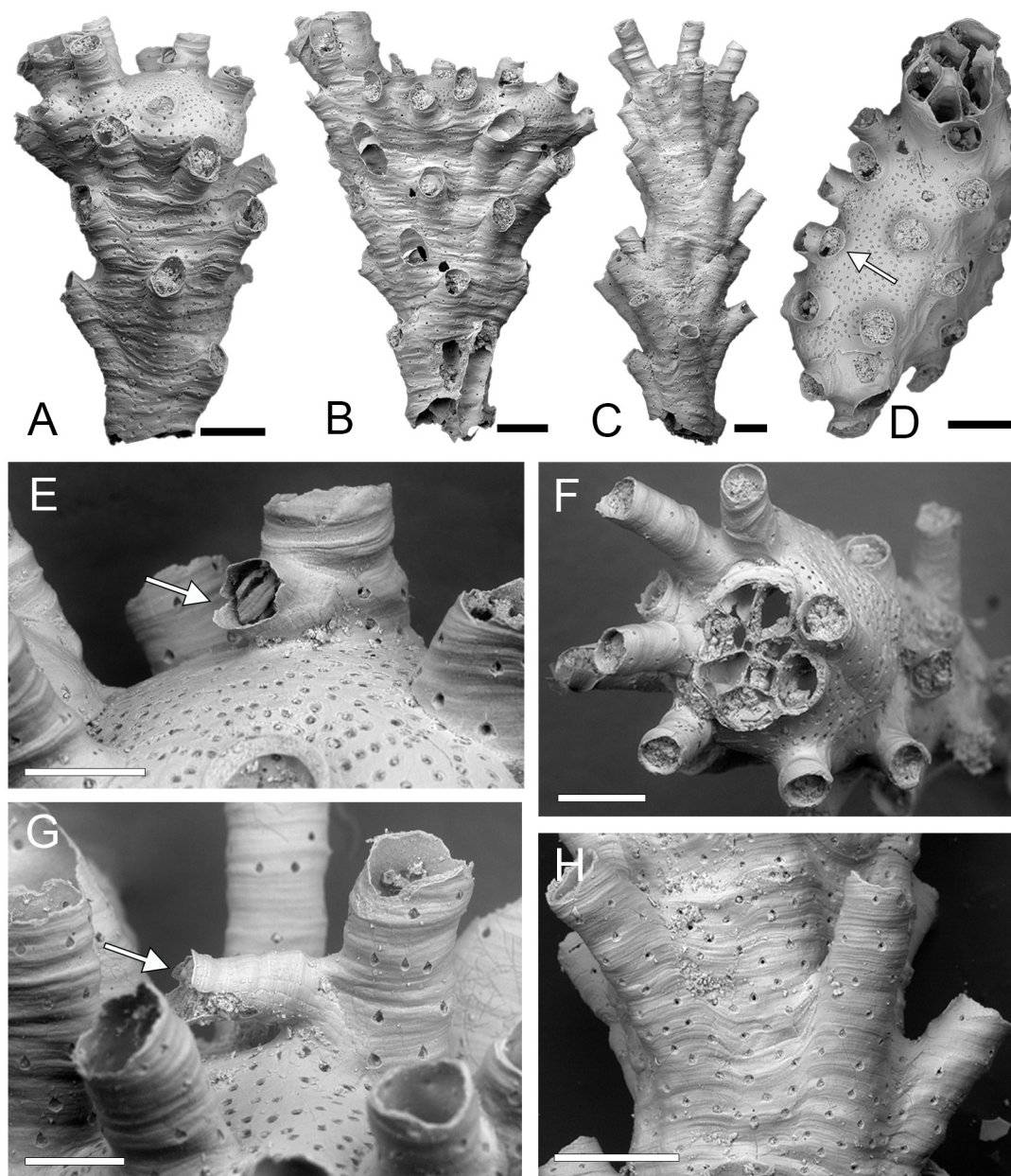


FIGURE 7. *Psilosolen harmelini* sp. nov. A, E, holotype PMC. B77. 26.2.2025a, sample 19013. A, fertile branch (200 µm). E, gonozooid with oeciostome (arrowed) adnate to an autozooidal peristome (100 µm). B, D, paratype PMC. B77. 26.2.2025b.1, sample 19031. B, fertile branch (200 µm). D, top view of the gonozooid and oeciopore (arrowed) (200 µm). C, F, H, paratype PMC. B77. 26.2.2025b.2, sample 19058. C, infertile branch (200 µm). F, broken distal end of branch (200 µm). H, branch surface showing pseudopores (200 µm). G, paratype PMC. B77. 26.2.2025b.4, sample 19035, oeciostome (arrowed) (100 µm).

Measurements (µm). Zooid length 443 ± 86.5 , 311–593 (2, 10); zooid width 134 ± 12.8 , 118–153 (2, 10); aperture length 102 ± 14.3 , 81–122 (2, 10); aperture width 90 ± 7.3 , 78–101 (2, 10).

Remarks. Several fragments of vincularian tubuliporines have terminal gonozooids capping the ends of branches. This trait characterises the little-known genus *Psilosolen* Canu and Bassler, 1922.

The type species of *Psilosolen*, *P. capitiferax* Canu and Bassler, 1922 from the Pleistocene of California, was more completely illustrated by Canu and Bassler (1923) whose figures (plate 44, figures 11–21) show the ‘*Entalophora*’-like branches, with fixed-walled autozooids opening all around the branch, and gonozooids with roofs penetrated by autozooidal peristomes at the terminal distal ends

of a couple of branches. Additional species seem not to have been assigned to this genus, but it has clear utility for vincularian tubuliporines with terminal gonozooids. The family placement of *Psilosolen* is unclear but previous assignments to Cerioporidae are inappropriate, as skeletal organization in the genus is tubuliporine, not cerioporine as in Cerioporidae. In view of the erect colony and perforated gonozooids, Diaperoeciidae is most apt.

Psilosolen harmelini sp. nov. is substantially more gracile than *P. capitiferax* in which the branches are up to 2 mm in diameter, twice the width of those in *P. harmelini* sp. nov. Transverse sections of *P. capitiferax* reveal 50 or more zooids (compared to about 10 in *P. harmelini* sp. nov., Figure 7F), and autozooidal length is 500–1350 μm (compared to 311–593 μm in *P. harmelini* sp. nov.).

Family TUBULIPORIDAE Johnston, 1837

Genus *EXIDMONEA*

David, Mongereau and Pouyet, 1972

Exidmonea lineata sp. nov.

Taylor, Di Martino and Rosso

Figure 8

Zoobank

Type material. Holotype PMC. B78. 26.2.2025a, sample 19058 (Figure 8A–B, E, H); paratypes PMC. B78. 26.2.2025b.1, sample 19049 (Figure 8C, I); PMC. B78. 26.2.2025b.2, sample 19059; PMC. B78. 26.2.2025b.3, sample 19055; PMC. B78. 26.2.2025b.4, sample 19069 (Figure 8D, J); PMC. B78. 26.2.2025b.5, sample 19019 (Figure 8F–G). Daidokutsu cave, Core 19, Holocene, Okinawa, Japan.

Diagnosis. *Exidmonea* with narrow branches generally having two series of initially connate autozooids either side of the midline; dorsal branch surface mildly convex, lineated with a series of longitudinal ridges; gonozooids simple, small, spanning two autozooidal series, with short, terminal oöciostome and transversely elliptical oöciopore typically larger than an autozooidal aperture.

Etymology. In reference to the lineations on the dorsal surface of the branches.

Description. Colony erect, branches narrow, 269–492 μm wide, widest at level of gonozooids, bifurcations not observed; autozooids opening on frontolateral surfaces, usually in series of two, occasionally apertures either side of midline; dorsal branch surface slightly convex, marked by longitudinal ridges 30–82 μm apart, with pseudoporous exterior wall between, the pseudopores simple, small, 4–5 μm in diameter, nearest neighbour centre-to-centre spacing 17–26 μm . Colony base

encrusting, the single observed example lacking the ancestrula and earliest autozooids, comprising six or seven autozooidal series along each side of a curved branch with a selvedge of kenozooids closed by pseudoporous calcification; some basal autozooids with emergent peristomes. Autozooids long, zooidal boundaries well defined, grooved; frontal wall with transverse growth checks, convex; pseudopores subcircular, small, 3–5 μm in diameter, nearest neighbour centre-to-centre spacing 20–33 μm , not constricted; apertures connate, rounded rectangular to subcircular, small, about 60–65 μm in diameter; peristomes long, preserved length up to 335 μm , oriented at about 60° to colony surface, with fewer pseudopores than frontal walls. Gonozooids small, located along branch midlines, sometimes closely spaced, spanning two or slightly more series of autozooids; brood chamber globular, almost circular in outline shape, 380–595 μm long by 439–506 μm wide ($N = 4$), densely pseudoporous, pseudopores subcircular, small, 3–5 μm in diameter, nearest neighbour centre-to-centre spacing 12–23 μm , lacking spines or other constrictions; oöciostome adnate to a proximal side of peristome of an autozooid close to branch midline, short, oriented subparallel to brood chamber roof; oöciopore transversely elongate, 47–71 μm long by 88–109 μm wide ($N = 4$).

Measurements (μm). Zooid length 551 ± 84.9 , 380–673 (3, 8); zooid width 111 ± 10.7 , 99–130 (3, 8).

Remarks. The main distinguishing feature of this new species is the presence of longitudinal ridges on the dorsal surface of the branches (Figure 8E). The ridges probably mark the basal interzooidal boundaries of the autozooids that open on the frontolateral surfaces of the branches, a hypothesis which would be testable using CT-scanning. Other species of *Exidmonea* generally lack such ridges, the dorsal surfaces often featuring arcuate growth lines instead. An exception is the Antarctic species *E. hula* (Borg, 1944), redescribed by Ostrovsky and Taylor (1996), but this species has longer gonozooids, which extend for 2–6 series compared to the single series of the globular gonozooid of *E. lineata*. *Exidmonea watersi* (Kluge, 1946) also has globular gonozooids but in this Arctic species the oöciostome opens to the side and not along the midline of the gonozooid. There are usually three apertures instead of one or two per series. Globular gonozooids are atypical of species assigned to *Exidmonea*. Indeed, Gordon and Taylor (2010) were led to refer an extant species with an *Exidmonea*-like colony-form to the Cretaceous genus *Fili-*

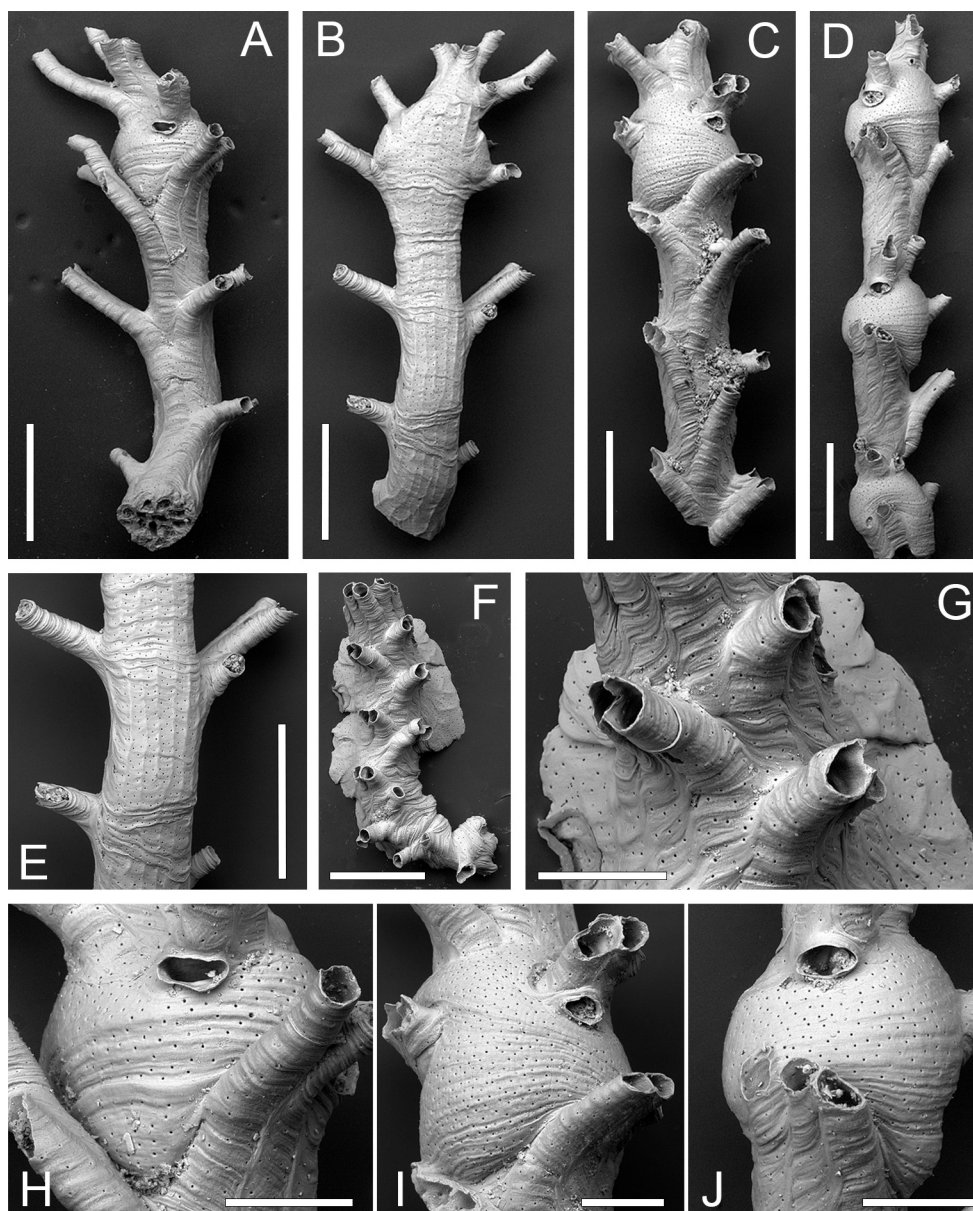


FIGURE 8. *Exidmonea lineata* sp. nov. A–B, E, H, holotype PMC. B78. 26.2.2025a, sample 19058. A, branch frontal (500 μ m). B, branch dorsal (500 μ m). E, detail of branch reverse showing longitudinal ridges (500 μ m). H, gonozooid (200 μ m). C, I, paratype PMC. B78. 26.2.2025b.1, sample 19049. C, branch frontal (500 μ m). I, gonozooid (200 μ m). D, J, paratype PMC. B78. 26.2.2025b.4, sample 19069. D, branch with three gonozooids (500 μ m). J, gonozooid (200 μ m). F–G, paratype PMC. B78. 26.2.2025b.5, sample 19019. F, encrusting colony base (500 μ m); detail showing autozooids and marginal kenozooids (200 μ m).

cisparsa (as *F. albobrunnea* Gordon and Taylor, 2010) on account of its simple gonozooids. The Daidokutsu species, however, lacks the pinnate colonies seen in the type species of *Filicisparsa* (see Girod and Martha, 2021, figure 12). An unnamed species of *Exidmonea* from the Miocene of East Kalimantan (Di Martino and Taylor, 2014) has similar shaped gonozooids to *E. lineata* but there are 3–4 connate autozooids in each series (cf. 2–3

in *E. lineata*) and no longitudinal striations on the dorsal surface.

Exidmonea unda sp. nov.
Taylor, Di Martino and Rosso
Figure 9

Zoobank

Type material. Holotype PMC. B79. 26.2.2025a, sample 19053 (Figure 9 A–B, D–F); paratype

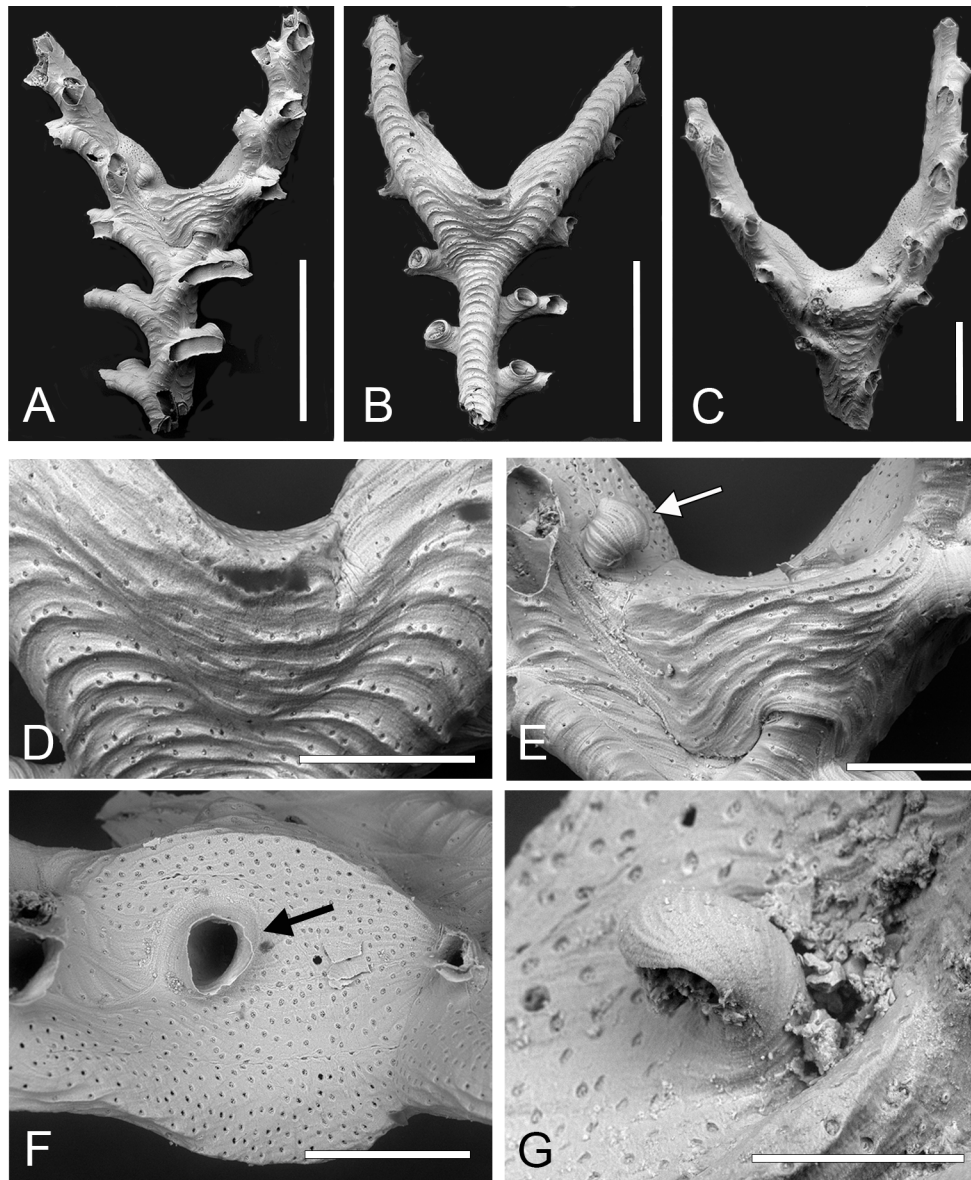


FIGURE 9. *Exidmonea unda* sp. nov. A–B, D–F, holotype PMC. B79. 26.2.2025a, sample 19053. A, branch frontal (500 µm). B, branch reverse (500 µm). D, bifurcation viewed from branch reverse showing rugose surface calcification that includes the buttressing of the gonozooid, which contains a broad hole believed to result from damage (200 µm). E, bifurcation viewed from branch frontal with ooeciostome arrowed (200 µm). F, gonozooid viewed obliquely from above with ooeciopore arrowed (200 µm) and smoothly calcified brood chamber roof. C, G, paratype PMC. B79. 26.2.2025b.1, sample 19044. C, branch frontal (500 µm). G, hook-shaped ooeciostome (100 µm).

PMC. B79. 26.2.2025b.1, sample 19044 (Figure 9C, G). Daidokutsu cave, Core 19, Holocene, Okinawa, Japan.

Etymology. From the Latin *unda* (used as a name in apposition) in reference to the ripple-like appearance of the ridges on the dorsal surface of the branches.

Diagnosis. *Exidmonea* with narrow branches having 1–2 series of initially connate autozooids either side of the midline; dorsal branch surface mildly

convex, coarsely rugose with arcuate pseudoporous ridges separated by concave hollows containing few or no pseudopores; gonozooids located in branch axils, buttressed by rugose calcification, brood chamber roof flat or concave, non-rugose, densely pseudoporous, ooeciostome off-centred, hooked, ooeciopore transversely elliptical, about the same size as an autozooidal aperture.

Description. Colony erect, branches bifurcating, narrow, 167–277 µm wide; autozooids opening on

frontolateral surfaces in 1–2 series either side of midline; dorsal branch surface slightly convex, coarsely rugose with arcuate, distally convex ridges 26–57 μm apart, pseudopores concentrated on ridges, sparse between ridges, small, subcircular, often teardrop-shaped, 7–9 μm long by 4–8 μm wide, nearest neighbour centre-to-centre spacing very variable, 9–35 μm . Autozooids long, zooidal boundaries grooved; frontal wall with transverse ridges, more irregular and less pronounced than on dorsal branch surfaces, convex; pseudopores teardrop-shaped, small, 4–5 μm in length by 4–7 μm in width, nearest neighbour centre-to-centre spacing 13–42 μm , partly occluded by septa-like spines; apertures connate, subcircular or rounded rectangular, diameter about 78–109 μm when peristomes are fully developed; peristomes long, up to 250 μm long, curved towards dorsal surface so that apertures face away from branch frontal, sparsely pseudoporous, bearing growth bands but not strongly ridged. Gonozooids located in axils at branch bifurcations, buttressed by a lunate expanse of ridged calcification stretching between the two daughter branches; brood chamber with flat or concave roof facing distally, lacking ridges, in the two measured examples 447 by 344 μm and 384 by 236 μm , densely pseudoporous, the pseudopores teardrop-shaped or subcircular, 5–9 μm long by 5–8 μm wide, nearest neighbour centre-to-centre spacing 11–19 μm , partly filled by spines; oeciostome positioned eccentrically closer to one of the daughter branches, about 95 μm long, hooked inwardly, the surface lacking pseudopores but with faint growth lines; oeciopore transversely elongate, 78 μm long by 90 μm wide in the single measured example.

Measurements (μm). Zooid length 377 ± 84.9 , 337–425 (2, 10); zooid width 100 ± 11.2 , 87–114 (1, 7).

Remarks. The buttressed, non-bulbous gonozooid located in branch axils is a distinctive feature of this new species, as are the prominent arcuate ridges on the surface of the branches on which the pseudopores are concentrated. Arcuate growth bands are known on the dorsal surfaces of branches of several species of *Exidmonea* and the related *Idmidronea*. These include *Idmidronea oblecta* Borg, 1944 and *I. fraudulenta* Ostrovsky and Taylor, 1996, both from the Antarctic, as well as *Exidmonea intercalata* Liu, Liu and Zágorský, 2019 from China and Korea (Chae et al., 2022), and *Exidmonea filiformis* (Canu and Bassler, 1929) from the Philippines. However, the bands in these species do not form pronounced ridges, unlike *E.*

unda sp. nov. (Figure 9B, D), and none of these species have gonozooids resembling those of *E. unda* sp. nov. Species erroneously identified by Canu and Bassler (1928, plate 34, figure 9) as *Idmonea atlantica* Forbes, 1847 [i.e., *Idmidronea atlantica* (Forbes in Johnston, 1847)] from the Pliocene of Panama, and also by Harmer (1915, plate 10, figure 4) from the Pacific as *Tubulipora atlantica* Forbes are notable in having arcuate lines of pseudopores on the dorsal surfaces of the branches. What was provisionally identified as the same species as that misidentified by Canu and Bassler (1928) was refigured by Taylor (2001), whose figure 4.11 shows the dorsal pseudopores to be large, longitudinally elongate and arranged in a single row spaced evenly along each ridge. This contrasts with the more disordered and smaller pseudopores found in *E. unda* sp. nov. There is some similarity between the gonozooids of this new species and those of an un-named species of *Exidmonea* from Singapore figured by Jain et al. (2022, figure 2A, B), particularly with respect to the location of the gonozooids at branch bifurcations and the off-centred and hooked oeciostome. However, the gonozooid in the Singaporean species is not buttressed, nor are the branch surfaces rugose.

Exidmonea sp.

Figure 10

Figured material. PMC EDM-Collection J. H. B.155a.1, sample 19140 (Figure 10C–D); PMC EDM-Collection J. H. B.155a.3, sample 19140 (Figure 10A, B). Daidokutsu cave, Core 19, Holocene, Okinawa, Japan.

Description. Colony erect, branches narrow, 220–350 μm wide; autozooids opening on frontolateral surfaces in three series either side of midline. Autozooids long, zooidal boundaries grooved; frontal walls flat; pseudopores inconspicuous, sparse, irregularly arranged, longitudinally elliptical or lens-shaped, 6–8 μm long by 4–6 μm wide, nearest neighbour centre-to-centre spacing 18–47 μm , lumen mostly occluded; apertures connate, rounded rectangular or subcircular, decreasing in size and becoming more circular in shape from inner to outermost series; preserved peristomes short, bearing growth bands. Gonozooid medial, brood chamber not bulbous, forming a zigzag axial ridge on branch frontal, elongate, in single incomplete example exceeding 1800 μm long by about 200 μm wide, extending for more than eight autozooidal series; pseudopores 7–11 μm long by 5–8 μm wide, slightly more abundant than on autozooi-

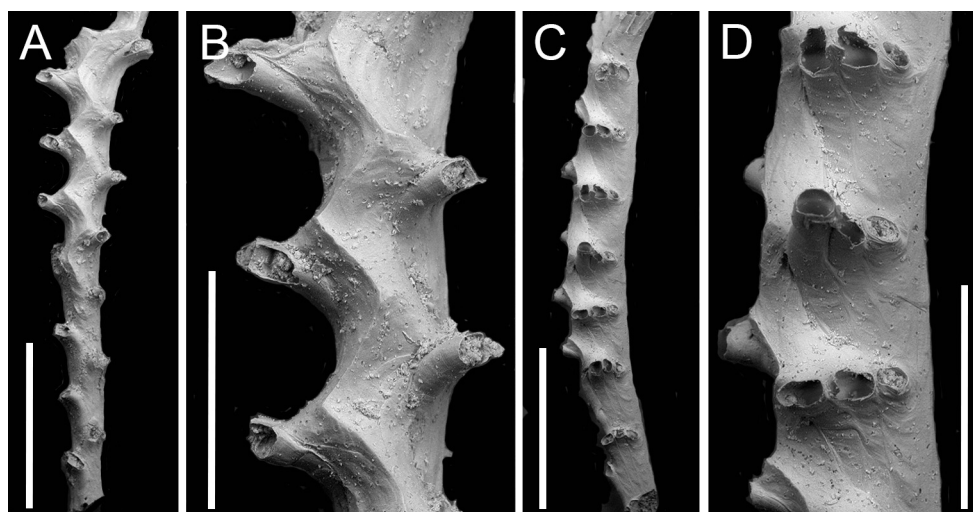


FIGURE 10. *Exidmonea* sp., sample 19140. A–B, PMC EDM-Collection J. H. B.155a.3. A, fertile branch frontal (1000 µm). B, gonozooid with zig-zag keel (500 µm). C–D, PMC EDM-Collection J. H. B.155a.1. C, fertile branch in lateral view (1000 µm). D, connate autozooids (500 µm).

dal frontal walls, nearest neighbour centre-to-centre spacing 11–30 µm; ooeciostome not observed.

Measurements (µm). Zooid length 391 ± 39.4 , 340–466 (2, 11); zooid width 79 ± 6.8 , 70–90 (1, 10).

Remarks. The gonozooid in this species is very different from those of the other two species of *Exidmonea* from the Daidokutsu cave being extremely long. The most obvious manifestation of the gonozooid is a zigzag ridge along the medial axis of branch frontal surfaces, dividing the left and right sides of the brood chamber (Figure 10B). Unfortunately, the ooeciostome cannot be identified in the single example available, compromising species identification. Although, we are unaware of any named species of *Exidmonea* (or *Idmidronea*) having a gonozooid with such a pronounced zigzag keel, Brood (1976, figure 15H–J) depicted a species he identified as *Crisina radians* (Lamarck, 1816) with a very similar gonozooid. Brood's material from East Africa is unlike material identified as *C. radians* by Harmer (1915) and Borg (1941), in which the large pores in the frontal walls of the autozooids and gonozooids point to a free-walled morphology that contrasts with the fixed-walled autozooids and gonozooids with pseudoporous frontal walls evident in Brood's material.

Family *PLAGIOECIIDAE* Canu, 1918

Genus *PLAGIOECIA* Canu, 1918

Plagioecia subcircularis sp. nov.

Taylor, Di Martino and Rosso

Figure 11

Zoobank

Type material. Holotype PMC. B80. 26.2.2025a, sample 19047 (Figure 11 A, C, E–F); paratypes PMC. B80. 26.2.2025b.1, sample 19058 (Figure 11B, G); PMC. B80. 26.2.2025b.2, sample 19058 (Figure 11D). Daidokutsu cave, Core 19, Holocene, Okinawa, Japan.

Etymology. Referring to the outline shape of the brood chambers.

Diagnosis. *Plagioecia* with lobate colonies; autozooids elongate, frontal wall with subcircular pseudopores containing about a dozen radial spines, apertures small, longitudinally elongate, sometimes closed by terminal diaphragms; secondary nanozooids developed in a few autozooids; gonozooids with bulbous, subcircular brood chambers partly covering proximal zooids, densely pseudoporous; ooeciostome terminal, pseudoporous; ooeciopore transversely elliptical, smaller than autozooidal apertures.

Description. Colony encrusting, multiserial, unilamellar, lobate, thin. Ancestrula and early astogeny unknown. Autozooids elongate, frontal walls convex, crossed by growth lines; pseudopores subcircular, occasionally rounded diamond-shaped, on average slightly longer than wide, length 9–11 µm, width 7–11 µm, nearest neighbour centre-to-centre spacing 18–35 µm, with about a dozen spines restricting the opening; apertures small, usually isolated and arranged quincuncially, sometimes aligned radially or clustered into small groups and connate, longitudinally elliptical and often somewhat pointed at distal end, or rounded polygonal when connate, short mural spines visible through

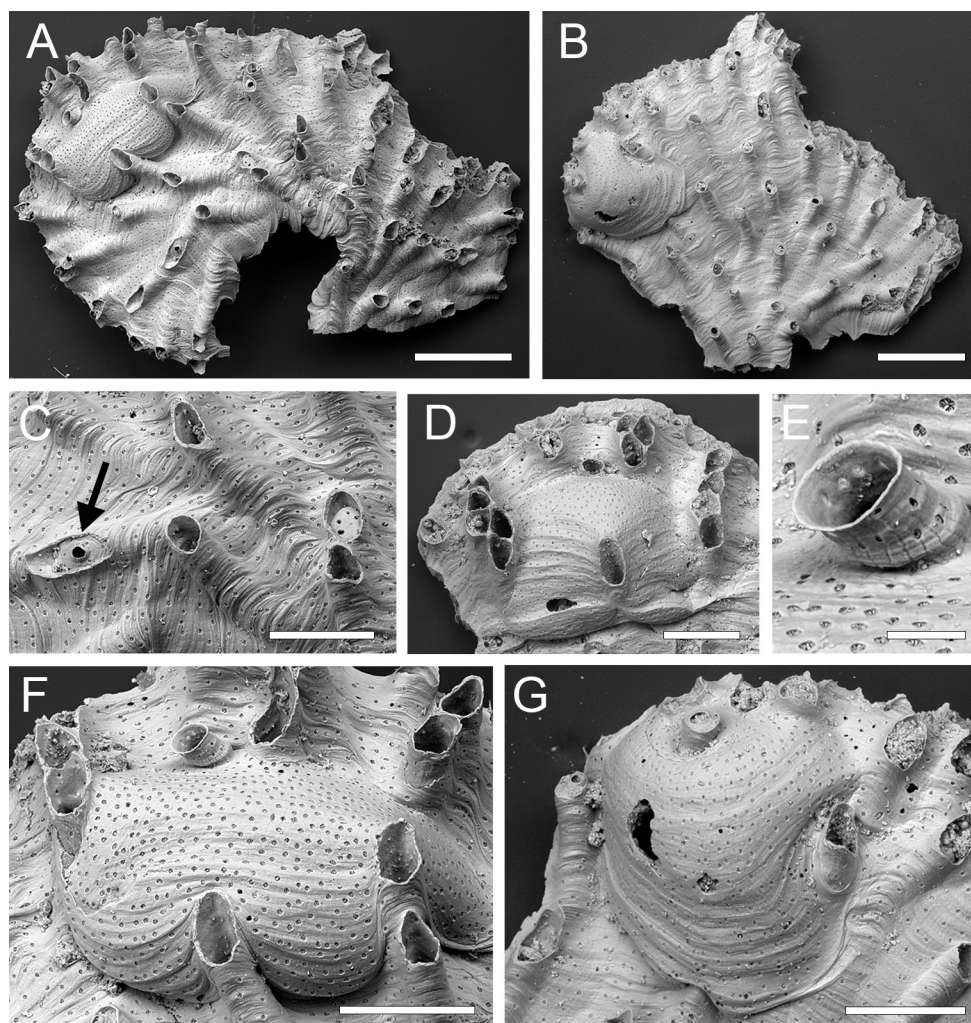


FIGURE 11. *Plagioecia subcircularis* sp. nov. A, C, E–F, holotype PMC. B80. 26.2.2025a, sample 19047. A, lobate colony (500 µm). C, autozooids and secondary nanozooid (arrowed) (250 µm). E, ooeciostome and ooeciopore (50 µm). F, gonozooid (250 µm). B, G, paratype PMC. B80. 26.2.2025b.1, sample 19058. B, colony (500 µm). G, gonozooid (250 µm). D, paratype PMC. B80. 26.2.2025b.2, sample 19058, gonozooid and radially aligned autozooidal apertures (250 µm).

apertures on interior walls; preserved peristomes short; terminal diaphragms with sparse pseudopores of variable size. Secondary nanozooids budded intramurally within some autozooids and possibly a gonozooid; a short, preserved peristome emerging from the centre of a pseudoporous terminal diaphragm, with an aperture about 25 µm in diameter. Gonozooids located close to distal growing edge; brood chamber bulbous, subcircular, in the three examples scanned measuring 545 µm long by 866 µm wide, 656 mm long by 548 µm wide, and 610 µm long by 547 µm wide, proximal edge extending proximally to overlap initial frontal wall and adjacent autozooids; autozooidal peristomes indenting edges of brood chamber, one peristome enveloped by brood chamber; pseudo-

pores similar to those of autozooids, 9–11 µm long by 8–12 µm wide, dense, nearest neighbour centre-to-centre spacing 11–25 µm, lumen occluded by radial spines; ooeciostome terminal, about 60 µm long, slightly flared, pseudoporous, the pseudopores smaller than those on the gonozooid/autozooid surface, and with longitudinal strips of calcification, not adnate to a peristome; ooeciopore transversely elliptical, 52–55 µm long by 67–68 µm wide (N = 3).

Measurements (µm). Zooid length 554 ± 88.3 , 459–750 (2, 10); zooid width 117 ± 10.1 , 97–130 (2, 10); longitudinal aperture diameter 84 ± 16.6 , 58–113 (3, 15); transverse aperture diameter 66 ± 7.5 , 56–78 (3, 15).

Remarks. The generic assignment of this new species deserves some explanation as the simple, subcircular gonozooids are unlike those of the type and most other species of *Plagioecia*, which have transverse brood chambers profusely penetrated by autozooidal peristomes. The occasional groups of connate peristomes seen in *P. subcircularis* sp. nov. (Figure 11F) are also not usually associated with *Plagioecia*. Two other genera were considered before opting for *Plagioecia*: *Tubulipora* and *Microeciella*. *Tubulipora* was discounted as terminal diaphragms and secondary nanozooids are absent in this genus and the brood chambers tend to have sinuous outlines. While *Microeciella* has gonozooids close in shape to those of *P. subcircularis* sp. nov., it too lacks terminal diaphragms and secondary nanozooids. In addition, the pseudopores of extant species of *Microeciella* do not have the radial spines seen in those of *P. subcircularis* sp. nov. (Taylor and Zatoń, 2008) nor have they been observed in fossil species of the genus (Zatoń and Taylor, 2009). In contrast, terminal diaphragms and secondary nanozooids (Figure 11C), both developed in *P. subcircularis* sp. nov., are typical of *Plagioecia* (Silén and Harmelin, 1974). It is, however, unusual in species of *Plagioecia* to have some zooids with terminal diaphragms but others with secondary nanozooids. There are some similarities with *Plagioecia ambigua* Osburn, 1953 from Alaska. This species also has simple gonozooids but there is no mention of secondary nanozooids, and the autozooids of *P. ambigua* are considerably larger with a width of 0.20 mm quoted by Osburn compared with less than 0.10–0.13 mm in *P. subcircularis* sp. nov. Compared with the new species, *Plagioecia parva* Gordon and Taylor, 2010 from New Zealand seamounts has small gonozooids but these are broader and have peristomes penetrating the brood chambers, and secondary nanozooids are not present.

Plagioecia sp.

Figure 12

Figured material. PMC EDM-Collection J. H. B.156a.1, sample 19019 (Figure 12 A–C). Daidokutsu cave, Core 19, Holocene, Okinawa, Japan.

Description. Colony encrusting, multiserial, unilamellar, discoidal. Ancestrula and early astogeny obscured by a fouling colony of *Annectocyma*. Autozooids very variable in length, frontal walls convex, rugose, crossed by strong growth lines; pseudopores subcircular, on average slightly longer than wide, length 4–6 μm , width 3–5 μm , sparse and unevenly spaced, nearest neighbour centre-to-centre spacing 19–42 μm , without spines or other constrictions; apertures small, non-connate, roughly aligned in radial rows, closely but unevenly spaced, generally circular; preserved peristomes short; terminal diaphragms common, irregularly pseudoporous, the pseudopores mostly marginal, some pseudopores seemingly enlarged by boring. Gonozooids not observed.

Measurements (μm). Zooid length 246 ± 76.3 , 132–355 (1, 10); zooid width 89 ± 7.3 , 73–98 (1, 10); longitudinal aperture diameter 65 ± 7.3 , 50–76 (1, 10); transverse aperture diameter 62 ± 6.5 , 50–72 (1, 10).

Remarks. Only one specimen of this species has been studied using SEM. A gonozooid is not present in this colony, and its assignment to *Plagioecia* is based on the overall similarity of the autozooids to those of the type species, *Plagioecia patina* Canu, 1918 (non *Tubulipora patina* Lamarck, 1816; see Håkansson et al., 2024, pp. 17–18). The close spacing of the apertures and tendency for them to be aligned radially seen in the Daidokutsu species are characteristic features of *P. patina* (e.g., Harmelin, 1976b, plate 18, figure 6; Hayward and Ryland, 1985b, figure 33B). In *P. patina*, however, the pseudopores contain spines (Hayward and McKinney, 2002, figure 53F), radial rows of aper-

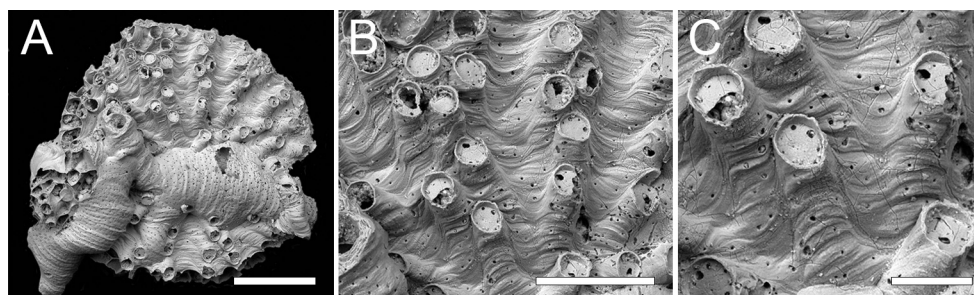


FIGURE 12. *Plagioecia* sp., PMC EDM-Collection J. H. B.156a.1, sample 19019. A, fouled colony (500 μm). B, irregularly arranged autozooids (250 μm). C, autozooids with terminal diaphragms (100 μm).

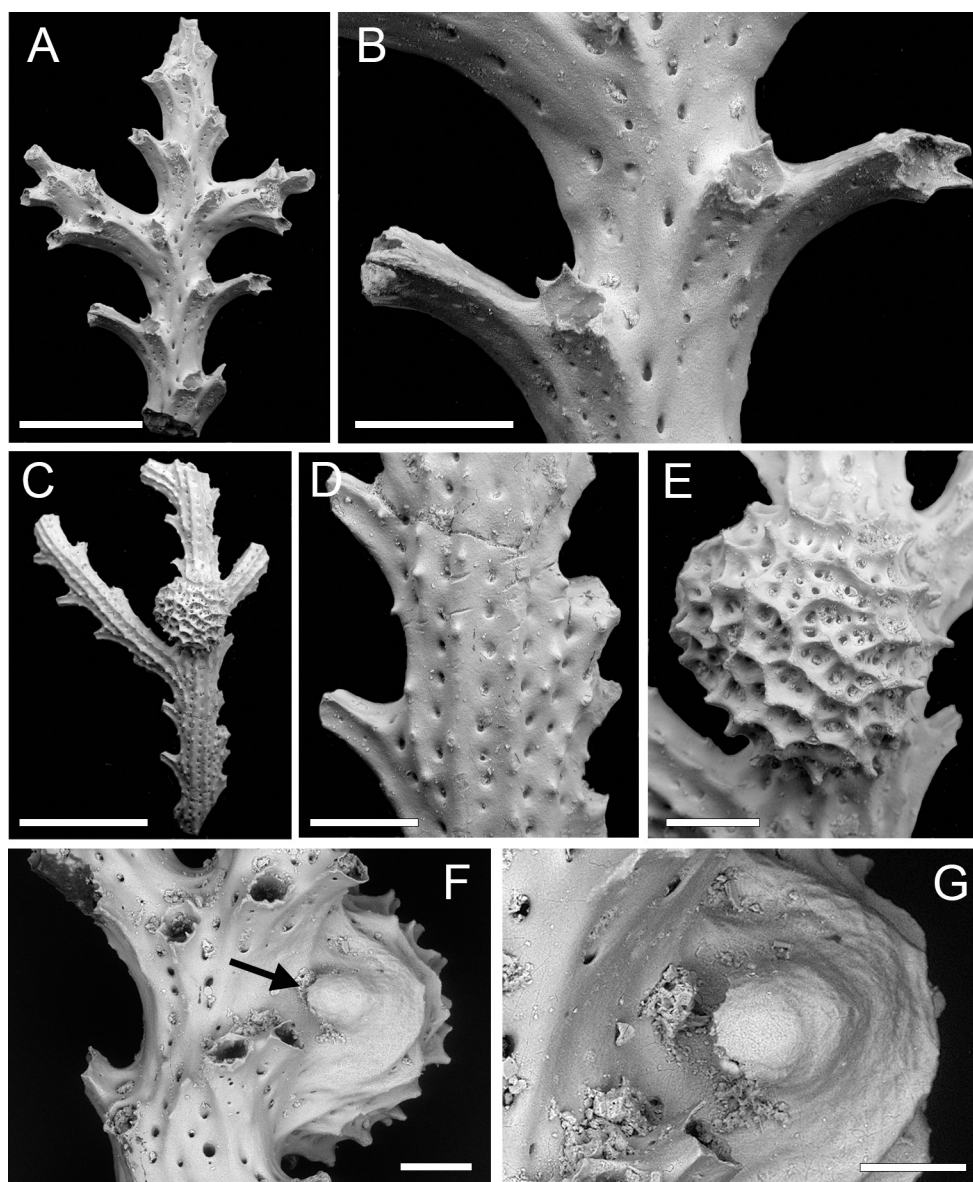


FIGURE 13. *Spinihornera parva* sp. nov. A–B, paratype PMC. B81. 26.2.2025b.1, sample 19132. A, pinnate colony in frontal view (500 µm). B, detail showing spines, peristomes and cancelli (200 µm). C–G, holotype PMC. B81. 26.2.2025a, sample 19125. C, branch reverse (1000 µm). D, dorsal surface showing lines of cancelli separated by nervi with low spines (200 µm). E, gonozooid (200 µm). F, oblique lateral view showing gonozooid and oeciostome (arrowed) (200 µm). G, oeciostome (100 µm).

tures are clearer, and the autozooids are larger than the Okinawan species; Hayward and McKinney gave a range for apertural width of 85–130 µm for *P. patina* compared with 50–76 µm for *Plagioecia* sp.

Suborder CANCELLATA Gregory, 1896
Family HORNERIDAE Smitt, 1867
Genus *SPINIHORNERA* Brood, 1979
Spinihornera parva sp. nov.

Taylor, Di Martino and Rosso
Figure 13

Zoobank

Type material. Holotype PMC. B81. 26.2.2025a, sample 19125 (Figure 13 C–G); paratype PMC. B81. 26.2.2025b.1, sample 19132 (Figure 13A–B). Daidokutsu cave, Core 19, Holocene, Okinawa, Japan.

Etymology. The name *parva* alludes to the small size of the zooids in this species.

Diagnosis. *Spiniornera* with small autozooids, aperture diameter averaging 64 μm , arranged in pairs on either side of branch, outermost autozooids with long peristome; gonozooids with brood chamber globular in shape, coarsely reticulate; ooeciostome located at side of branch, hook-like with ooeciopore directed downwards.

Description. Colony erect, pinnate, branches narrow, 230–375 μm wide, autozooids arranged in pairs alternating on either side of branch midline, the peristome of the outer zooid oriented at about 45–60° to the branch. Branch frontal smoothly calcified, median line of autozooids forming a ridge most pronounced distally on peristome; cancelli arranged in rows on each side of ridge, longitudinally elliptical, variable in size, 7–25 μm in diameter. Branch reverse with 3–4 nervi bearing a row of short spines; ridge-like nervi spaced approximately 70 μm apart, with a row of cancelli about 15 μm in diameter between nervi. Autozooids with tiny apertures, short mural spines visible on interior walls through apertures, spacing between apertures in successive series about 300–400 μm ; peristomes moderately long, terminating in about 6–8 apertural spines. Gonozooid known from a single example, small, located on branch reverse, off-centred; brood chamber bulbous, 597 μm long by 560 μm wide, cancellate, the surface a coarse reticulum of spine-bearing ridges surrounding groups of cancelli 9–30 μm in diameter; ooeciostome located at side of branch, short, strongly curved, hook-like with ooeciopore directed downwards towards branch surface.

Measurements (μm). Aperture diameter 64 ± 6.2 , 52–70 (1, 8); peristome length 125 ± 29.8 , 85–174 (1, 9).

Remarks. The type species, and hitherto only species attributed to *Spiniornera* is *Hornera spinigera* Kirkpatrick, 1888, originally described from Mauritius. Material of *S. spinigera* described by Brood (1979, p. 159) when he introduced the genus *Spiniornera* came from the Philippines, and the species has also been recorded from East Africa (Brood, 1976) and Lifou in New Caledonia (Harmer, 1915). Brood (1979, p. 159) diagnosed *Spiniornera* as a “Hornerid genus with pinnate branches, autozoecia arranged in lateral lines and with numerous apertural spines”. The gonozooid is mentioned by Brood as being located on the dorsal side of the branches, globular and with the ooeciostome turned towards the frontal side. These characters are all seen in *S. parva* sp. nov., but this new species differs from *S. spinigera* in having a more gracile colony. More similar in colony-form to

S. parva is *Hornera pinnata* Canu and Bassler, 1929, which should probably be transferred to *Spiniornera*. However, the small diameter of the zooidal apertures in *S. parva* distinguishes it from *S. pinnata* for which Canu and Bassler (1929) cited a peristome diameter of 0.10 mm. Canu and Bassler’s species also has shorter peristomes, although this may be related to the older age of the branches.

There are clear similarities between this new species and *Pseudidmonea johnsoni* Di Martino and Taylor, 2014 from the Miocene of East Kalimantan, Indonesia. However, the latter differs in having a well-developed median keel on the branch frontal surface, 3–4 rows of apertures on each side of this keel, and small, circular or polygonal cancelli on the branch dorsal surface.

Family Incertae sedis

Genus *MESONEA* Canu and Bassler, 1920

?*Mesonea* sp.

Figure 14

Figured material. PMC EDM-Collection J. H. B.157a.1, sample 19031 (Figure 14A–B); PMC EDM-Collection J. H. B.157a.2, sample 19029 (Figure 14C). Daidokutsu cave, Core 19, Holocene, Okinawa, Japan.

Description. Colony erect, branches bifurcating, narrow, 174–217 μm wide, autozooids arranged in pairs alternating on either side of branch midline, innermost apertures prominent, facing distolaterally, outermost apertures mostly hidden behind inner apertures in frontal view. Branch frontal smoothly calcified with a strong axial ridge and a few weaker lateral ridges; cancelli mostly arranged in a single longitudinal row along the axis of each zooid, longitudinally elliptical, 5–10 μm in diameter, spaced 26–50 μm apart, larger cancelli up to 70 μm long in bifurcation axil. Autozooids with small apertures, paired apertures connate; peristomes short, ragged. Gonozooid unknown.

Measurements (μm). Aperture diameter 98 ± 9.2 , 84–113 (2, 11); distance between apertural series 406 ± 61.9 , 352–535 (2, 8).

Remarks. The absence of gonozooids inhibits unequivocal generic identification of this species. The morphology of the colony and free-walled autozooids match species that are commonly referred to as the genus *Crisina* (e.g., Waters, 1914; Harmer, 1915; Borg, 1941). However, the type species of *Crisina*, *C. normaniana* d’Orbigny, 1853 from the Upper Cretaceous of Fécamp, Seine Maritime, France, has yet to be revised. Syntypes in the Muséum national d’Histoire naturelle

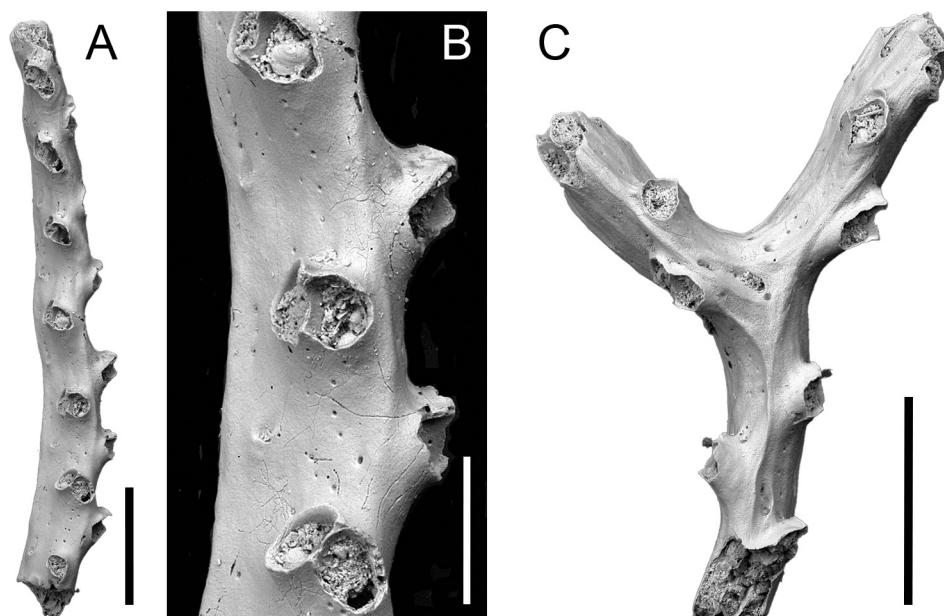


FIGURE 14. ?*Mesonea* sp. A–B, PMC EDM-Collection J. H. B.157a.1, sample 19031. A, lateral view of branch (500 µm). B, detail showing autozooidal apertures and sparse cancelli (200 µm). C, PMC EDM-Collection J. H. B.157a.2, sample 19029, frontal view of bifurcating branch (500 µm).

(MNHN), Paris, registered as d'Orbigny Collection 8332, examined by one of us (PDT) comprise a mixture of specimens with free- and fixed-walled morphologies, neither seeming likely to be cancel-late cyclostomes. *Mesonea*, with the extant type species *Retepora radians* Lamarck, 1816, has free-walled autozooids and seems a better fit for the Okinawan species. Although *Mesonea* is customarily placed in Crisinidae d'Orbigny, 1853, this assignment cannot be sustained in view of the ambiguous morphology of the type genus *Crisina*; hence the uncertain family placement of the Okinawan species.

Suborder RECTANGULATA Waters, 1887

Family LICHENOPORIDAE Smitt, 1867

Genus *DISPORELLA* Gray, 1848

Disporella sp.

Figure 15

Figured material. PMC EDM-Collection J. H. B.158a.1, sample 19038 (Figure 15B, E); PMC EDM-Collection J. H. B.158a.2, sample 19019 (Figure 15A, D); PMC EDM-Collection J. H. B.158a.3, sample 19029 (Figure 15C, F). Daidokutsu cave, Core 19, Holocene, Okinawa, Japan.

Description. Colony encrusting, discoidal, or semi-erect and formed by a vertical stack of 6 or 7 low cup-shaped subcolonies, autozooids arranged quincuncially near colony centre, becoming aligned into non-connate radial rows towards colony edge, separated by alveoli; surface calcification variably

pustulose, covered by tiny spines. Autozooids with small, longitudinally elliptical apertures, in one example occluded by pustulose calcification with a small central pore; peristomes up to about 100 µm long, with spines terminal processes visible in some. Alveoli not subdivided, polygonal, variable in size, iris-like with central elliptical lumen. Possible gonozooid present in one colony, chamber exposed by surface breakage, positioned close to colony centre; ooeciostome and ooeciopore not observed.

Measurements (µm). Longitudinal aperture diameter 84 ± 7.5 , 76–98 (3, 16); transverse aperture diameter 70 ± 5.2 , 62–77 (3, 16); alveolus maximum external diameter 110 ± 17.5 , 78–137 (3, 20); alveolus minimum lumen diameter 36 ± 14.8 , 21–66 (3, 20).

Remarks. As Håkansson et al. (2024, p. 19) remarked, rectangulate cyclostomes including *Dis-porella* present major taxonomic challenges. This is because the colony surface from which most morphological characters are recorded is dynamic, changing as the colony ages, develops gonozooids and subsumes these structures beneath further calcification. In some species, compound colonies may form by adding subcolonies, either at the outer margins of the colony or vertically stacked. The degree of variability within species has yet to be fully described, making it difficult to decide whether morphological differences in fossil samples repre-

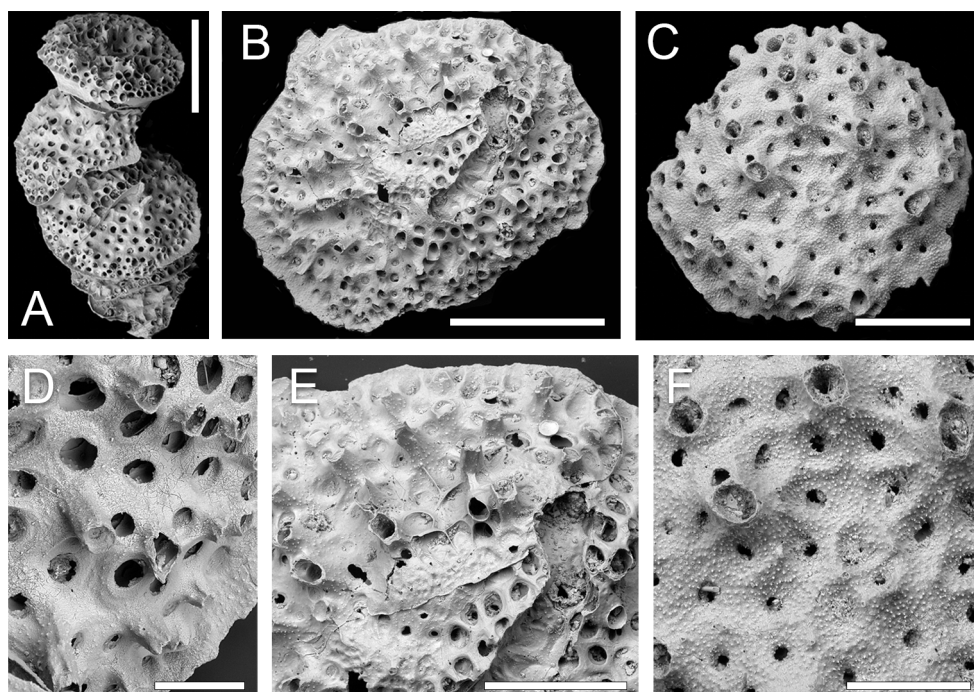


FIGURE 15. *Disporella* sp. A, D, PMC EDM-Collection J. H. B.158a.2, sample 19019. A, compound colony consisting of stacked subcolonies (1000 µm). D, detail showing raised autozooidal apertures and alveoli (200 µm). B, E, PMC EDM-Collection J. H. B.158a.1, sample 19038. B, colony (1000 µm). E, possible chamber of gonozooid in lower right (500 µm). C, F, PMC EDM-Collection J. H. B.158a.3, sample 19029. C, colony (500 µm). F, pustulose colony surface (250 µm).

sent intraspecific variations or signify different species. Of the three specimens imaged using SEM, one is compound and semi-erect (Figure 15A), and one of the two non-compound colonies differs in having a more densely pustulose surface (Figure 15F). However, the morphometrics, notably autozooidal aperture diameter, of the three colonies are close enough to suggest that they may represent ecophenotypic or astogenetic variants of a single species. Compared to *D. xianqiureni* Liu et al., 2019 from China, the alveoli are much more constricted in the Okinawan species, whereas several other species of *Disporella* from the Indo-Pacific have connate or very closely spaced apertures arranged in radial rows, e.g., *D. compta* Dick et al., 2006 from Hawaii, and *D. ovoidea* Osburn, 1953 from Galapagos and southern California.

Class GYMNOLAEMATA Allman, 1856
Order CHEILOSTOMATIDA Busk, 1852
Superfamily SMITTINOIDEA Levinsen, 1909
Family SMITTINIDAE Levinsen, 1909
Genus *PARASMITTINA* Osburn, 1952
Parasmittina vieirai nom. nov.

Zoobank

v. 2025 *Parasmittina ligulata* Di Martino, Rosso and Taylor in Di Martino et al., p. 56, fig. 32.

Remarks. After the publication of the study on the cheilostome bryozoans of Daidokutsu cave, Leandro Manzoni Vieira informed us that the name *Parasmittina ligulata*, proposed for a new species from the cave, was preoccupied. Farias et al. (2024) had established a new combination, *Parasmittina ligulata* (Ridley, 1881) for *Smittia trispinosa* var. *ligulata* Ridley, 1881. In recognition of Vieira's contributions to bryozoology and his courtesy in bringing this issue to our attention, we propose *Parasmittina vieirai* nom. nov. as a replacement name for the Japanese species.

DISCUSSION

Fifteen species of cyclostome bryozoans are recognised in Core 19 of the Daidokutsu submarine cave: *Crisia ramalhoae* sp. nov., *Crisia prominens* sp. nov., *Crisiona* sp., *Filisparsa haywardi* sp. nov., *Annectocyma* sp., *Nevianipora* sp., *Psilosolen harmelini* sp. nov., *Exidmonea lineata* sp. nov., *E. unda* sp. nov., *Exidmonea* sp., *Plagioecia subcircularis* sp. nov., *Plagioecia* sp., *Spinihornera parva* sp. nov., ?*Mesonea* sp. and *Disporella* sp.

Open nomenclature is employed for seven of the *Daidokutsu* species, either because critical characters, such as gonozooids, have not been observed, or species descriptions in the literature are inadequate to permit the *Daidokutsu* species to be confidently matched with them. Pseudopore morphology has been seldom described or illustrated, especially in pre-SEM studies, yet these minute perforations in the frontal exterior walls are of great utility in distinguishing between species among the character-poor cyclostomes (e.g., Zatoń and Taylor, 2009).

None of the *Daidokutsu* cyclostomes could be identified as an existing species. In contrast, 26 of the 63 cheilostome bryozoans in the same samples were identified either as existing species or designated as cf. an existing species (Di Martino et al., 2025). In addition to the increased challenges in cyclostome taxonomy already mentioned, this discrepancy may also reflect the scarcity of modern studies on cyclostome bryozoans in Japan and elsewhere as outlined in the Introduction. Aside from a paper by Taylor and Grischenko (2015) describing two intertidal species of cyclostomes from Akkeshi Bay in northern Japan, the most recent publications on living cyclostomes in Japan were published over 50 years ago and lack SEM imagery (Mawatari and Mawatari, 1973, 1974). Perhaps coincidentally in view of the greater uncertainties in cyclostome identification, the proportion of cyclostome species (53%) considered to be new is similar to the proportion of new cheilostome species (48%) in the *Daidokutsu* cave.

Three of the *Daidokutsu* cyclostomes are classified in the suborder *Articulata*, nine in *Tubuliporina*, two in *Cancellata*, and one in *Rectangulata*. Therefore, four of the five extant suborders of cyclostomes are represented at *Daidokutsu*, with only *Ceroporina* lacking. The dominance of *Tubuliporina* is unsurprising. Molecular phylogenetic studies (see Waeschenbach et al., 2009; Taylor et al., 2021 and references therein) have corroborated the non-monophyletic status of *Tubuliporina* previously suggested by morphological analysis (Taylor and Weedon, 2000). However, it should be noted that taxon sampling in cyclostomes is still too sparse to be certain that the other suborders are monophyletic.

In terms of colony-form, three of the *Daidokutsu* cyclostomes are multiseriate encrusters, whereas the remaining 12 species are narrow-branched erect forms, two with articulated colonies and 10 having rigid colonies. The high proportion of erect cyclostome species contrasts with some

Mediterranean submarine caves. Harmelin (1997, p. 149) noted a total absence of erect bryozoans (cyclostomes and cheilostomes) on the walls of the '3PP' cave near La Ciotat in France, although erect species did colonise settlement panels. In two Aegean submarine caves studied by Rosso et al. (2018), bryozoans with erect colonies were also less diverse than at *Daidokutsu*. Of the 14 cyclostome species listed by Rosso et al. (2018, table 1), slightly less than half (6) have characteristically erect colonies. A similar proportion is evident in Sicilian submarine caves (Rosso et al. 2013a, b).

The 15 cyclostome species recognised in the *Daidokutsu* submarine cave fauna can be added to the 63 cheilostome species described earlier by Di Martino et al. (2025), making a total of 78 bryozoan species. Proportionally, cyclostomes account for 19% of species diversity, which is typical for Holocene bryozoan faunas (Lidgard et al., 2021, figure 1a), including those from Mediterranean submarine caves (Harmelin, 1997; Rosso et al., 2018). A higher proportion of cyclostomes might have been predicted on the grounds that caves could provide a refuge for cyclostomes, which tend to lose competitive encounters for space with cheilostomes (McKinney, 1992) and seem on average to have lower energy intakes (McKinney, 1993), which may make them better suited to habitats with depleted food resources like caves. Regarding abundance, cyclostomes are also less common in the *Daidokutsu* cave where they are represented by 9912 fragments compared with 39239 cheilostome fragments. Therefore, cyclostomes comprise about 20% of total bryozoan abundance, a very similar proportion to the 19% of bryozoan species diversity in the cave.

ACKNOWLEDGEMENTS

We thank Sophie Crump and Tom Perkins for helping sorting bryozoans from the core samples during their year as volunteers at the Department of Earth Sciences of the Natural History Museum, London. EDM received support from the Leverhulme Trust Research Project 'Origin of high tropical diversity: a test using bryozoans' (2016–2018) (award no. RGP-2015-036 to PDT), the Young Research Talent Grant of the Research Council of Norway (2019–2025) (award no. 314499 to EDM), and the University of Catania through PIA_{no} di inCEntivi per la Ricerca di Ateneo 2020/2022 – Linea di Intervento 3 "Starting Grant" (2024). AR was funded by the University of Catania through PIA_{no} di inCEntivi per la Ricerca di Ateneo 2020/2022 – Linea di Intervento 2. Additional support to

EDM and AR was provided by PiaCeRi 2024/2026. MY was funded by Research Grants Council of the Hong Kong Special Administrative Region, China (project codes: RFS2223-7S02, C7013-19G to MY); the Seed Funding Programme for Basic Research of the University of Hong Kong (project codes: 202111159167, 2302101483 to MY); and

SKLMP Seed Collaborative Research Fund (project codes: SKLMP/SCRF/0073 to MY). We thank two anonymous reviewers for their constructive comments, which greatly contributed to improving the final version of this work. This is Catania Paleontological Research Group contribution no. 527.

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