

Descriptions of Three Cheilostomatid Bryozoan Species from the Continental Shelf off Boso Peninsula, Japan

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Three bryozoan species are described from the continental shelf east of the Boso Peninsula, Japan. One is a new species of *Tessaradoma* Norman, 1869, resembling Arctic and Atlantic species. Its colony form is, however, composed of zooids facing one side. The other two are species described from Sagami Bay as *Hippothoa connata* Ortmann, 1890 and *Diporula coronula* Ortmann, 1890. The former is assigned to the genus *Cribellopora* Gautier, 1957, having cribellate pseudopores on the frontal wall and oecium. The latter is provisionally placed in the genus *Hippomenella* Canu and Bassler, 1917. The biogeography of the genera and species groups including the three species in this study is discussed. The boreal origin of the Japanese *Tessaradoma* is inferred, and the two species established by Ortmann are related to the bryozoan fauna of Australia and New Zealand.

Key Words: Cheilostomatida, *Tessaradoma*, *Cribellopora*, *Hippomenella*, Japan.

Introduction

The Boso Peninsula lies in the Kanto region, central Honshu Island, on the Pacific coast of Japan. The warm Kuroshio Current changes direction from northeast to east near the eastern end of the Boso Peninsula, where the cold Oyashio Current slips under the Kuroshio Current in the region of the Kuroshio-Oyashio Confluence. These conditions and their temporal fluctuation are believed to have resulted in a high diversity of marine benthos in this area. For example, 2944 molluscan species were reported from the Boso Peninsula (including Tokyo Bay) between 1928 and 2001 (Shimizu 2001).

The southwest side of the Boso Peninsula faces the Sagami Sea (“Sagami-nada” in Japanese). The bryozoan fauna of the Sagami Sea and Sagami Bay is perhaps better known than that of any other part of Japan, with early collections made in the Meiji Era (see Spencer Jones et al. 2011), and more recent works by Grischenko and Mawatari (2006) and Hirose (2010, 2012). In particular, Hirose (2010) restudied four collections, including the material studied by Ortmann (1890), and provided descriptions for 261 cheilostomatid species, many of which, however, remain to be formally described.

In 1980, I collected many bryozoan specimens on cruise GH80-2 (Geological Survey of Japan) of R/V *Hakurei-Maru* along the continental shelf and slope east of the Boso Peninsula (Arakawa 1984). Although the taxonomic study of this material remains incomplete, previous reports have listed 143 species in Cheilostomatida (Arakawa 1999, 2020a), among which seven species have been formally described

in the genera *Micropora* Gray, 1848, *Microporina* Levinsen, 1909, *Metamicroporina* Arakawa, 2016, and *Monoporella* Hincks, 1881 (Arakawa 2016, 2020b).

In this study, I describe in detail three uncommonly encountered species collected on the above research cruise. One is new to science, and two are species erected by Ortmann (1890). I also discuss the biogeography of the Japanese bryozoan fauna related to these species.

Materials and Methods

The study material came from four stations on the continental shelf east of the Boso Peninsula, Japan, where sampling was undertaken on R/V *Hakurei-Maru* cruise GH80-2 (Geological Survey of Japan) in 1980 (Honza and Miyazaki 1984):

Station 1709, 35°14.02'N, 140°45.20'E, depth 144 m, medium to coarse sand interspersed with rocky bottom, 30 April 1980;

Station 1734, 35°03.13'N, 140°26.99'E, depth 155 m, medium sand bottom, 10 May 1980;

Station 1746, 35°09.01'N, 140°40.60'E, depth 154 m, medium to coarse sand interspersed with rocky bottom, 11 May 1980; and

Station 1748, 35°10.95'N, 140°32.20'E, depth 65 m, medium to coarse sand interspersed with rocky bottom, 11 May 1980.

Seafloor deposits were obtained with a Smith-McIntyre grab sampler, and bryozoan colonies and fragments were examined under a stereoscopic microscope. After cleaning, specimens were mounted on aluminum stubs with adhesive

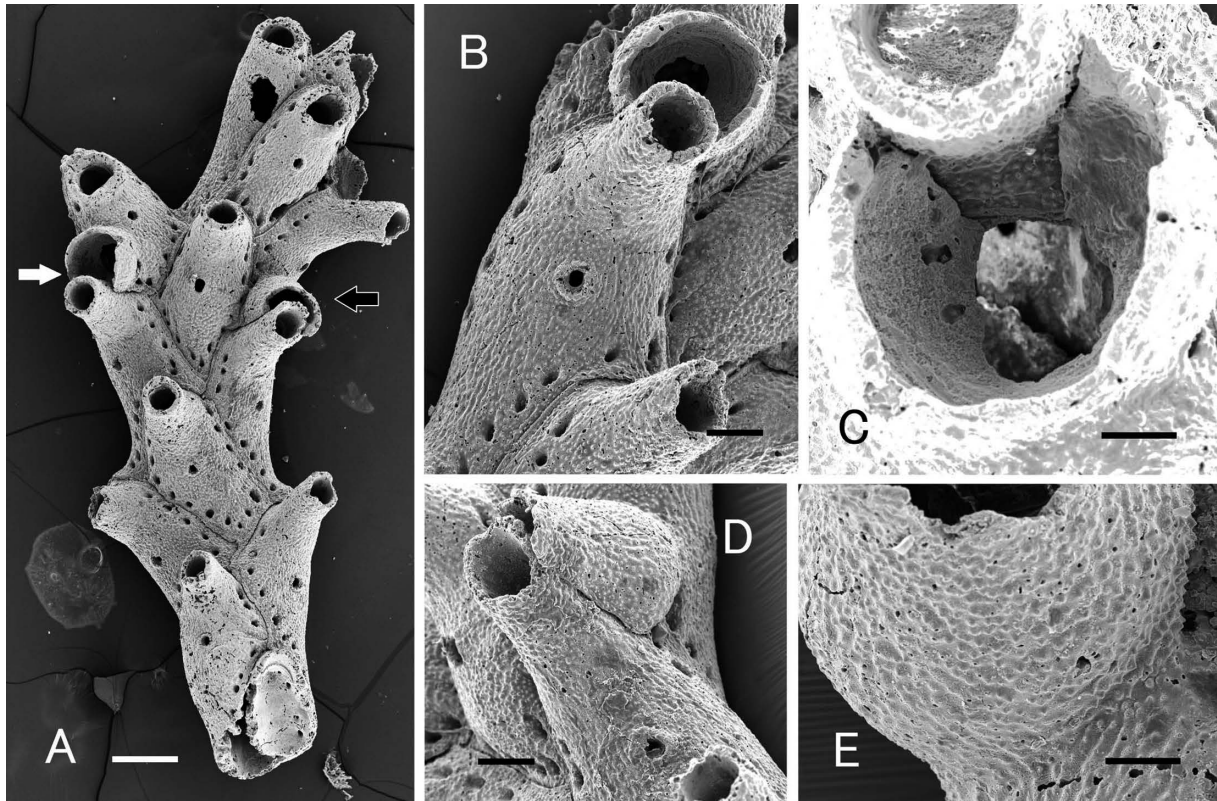


Fig. 1. *Tessaradoma japonicum* sp. nov., holotype, NMNS PA 20496. A, Complete view of specimen (white arrow, ovicell in B; black arrow, elongate ovicell in D); B, zooid with ovicell (indicated by white arrow in A); C, inner surface of ooecium in B; D, lateral view of elongate ovicell (indicated by black arrow in A); E, boundary between ovicell and the next zooid in D. Scale bars: A, 500 μ m; B, D, 200 μ m; C, E, 100 μ m.

tape, coated with Au in a SC-701 (Sanyu Denshi) ion coater, and observed with a JSM-5310 (JEOL) scanning electron microscope (SEM) at the National Museum of Nature and Science, Tsukuba.

Zooidal characters were measured from SEM images in millimeters, and presented as the range, followed by the arithmetic mean and standard deviation. Sample sizes (n) are given as the number of zooids from which a character was measured, followed by the number of colony fragments from which measurements were taken. Abbreviations used for characters measured are as follows: ZL, ZW, autozooid length and width; OrL, OrW, primary orifice length and width; SOrL, SOrW, secondary orifice length and width; AvL, AvW, avicularium length and width; OvL, OvW, ovicell length and width.

Type material and other specimens examined in this study are deposited in the National Museum of Nature and Science, Tsukuba (collection code NMNS PA).

Systematics

Order Cheilostomatida Busk, 1852

Family Tessaradomidae Jullien in Jullien and Calvet, 1903

Remarks. Jullien and Calvet (1903) placed *Tessaradoma* Norman, 1869 in their new family Lepralidae in the text, but also proposed the family Tessaradomidae in their plate 14,

comparing the position of the operculum with that in other families. In that article, new families were written as for example, "Famille Adeonidae J. Jullien 1903". According to this, the author of Tessaradomidae can be attributed to Jullien only (Hayward and Ryland 1979).

Genus *Tessaradoma* Norman, 1869

Diagnosis. Colony erect, unjointed, attached by encrusting base. Frontal shield striated, granular, or smooth, with an umbonuloid component and marginal pores. Tubiform spiramen present. Primary orifice semicircular, concealed by projecting peristome. Adventitious avicularia present or absent. Ovicell peristomial, imperforate.

Type species. *Pustulipora gracilis* Sars, 1851.

Remarks. The type species is now regarded as a synonym of *Tessaradoma boreale* (Busk, 1860) (originally *Onchopora borealis*) (e.g., Hayward and Ryland 1979, 1999; Winston 2005; Denisenko 2014), but I believe that *T. boreale* from the Atlantic and Arctic Oceans may include two or more species as discussed by Winston (2005) and Souto et al. (2016), although Sars (1863) also considered Busk's species as the synonym of *T. gracile*. Illustrations of the Arctic species (Smitt 1868; Kluge 1962) show smaller marginal pores and avicularia, and a more highly projecting peristome than the European species from Britain (Busk 1860; Alder 1864; Hincks 1880; Hayward and Ryland 1979, 1999), Denmark (Marcus 1940), southern Spain (Zabala and Malu-

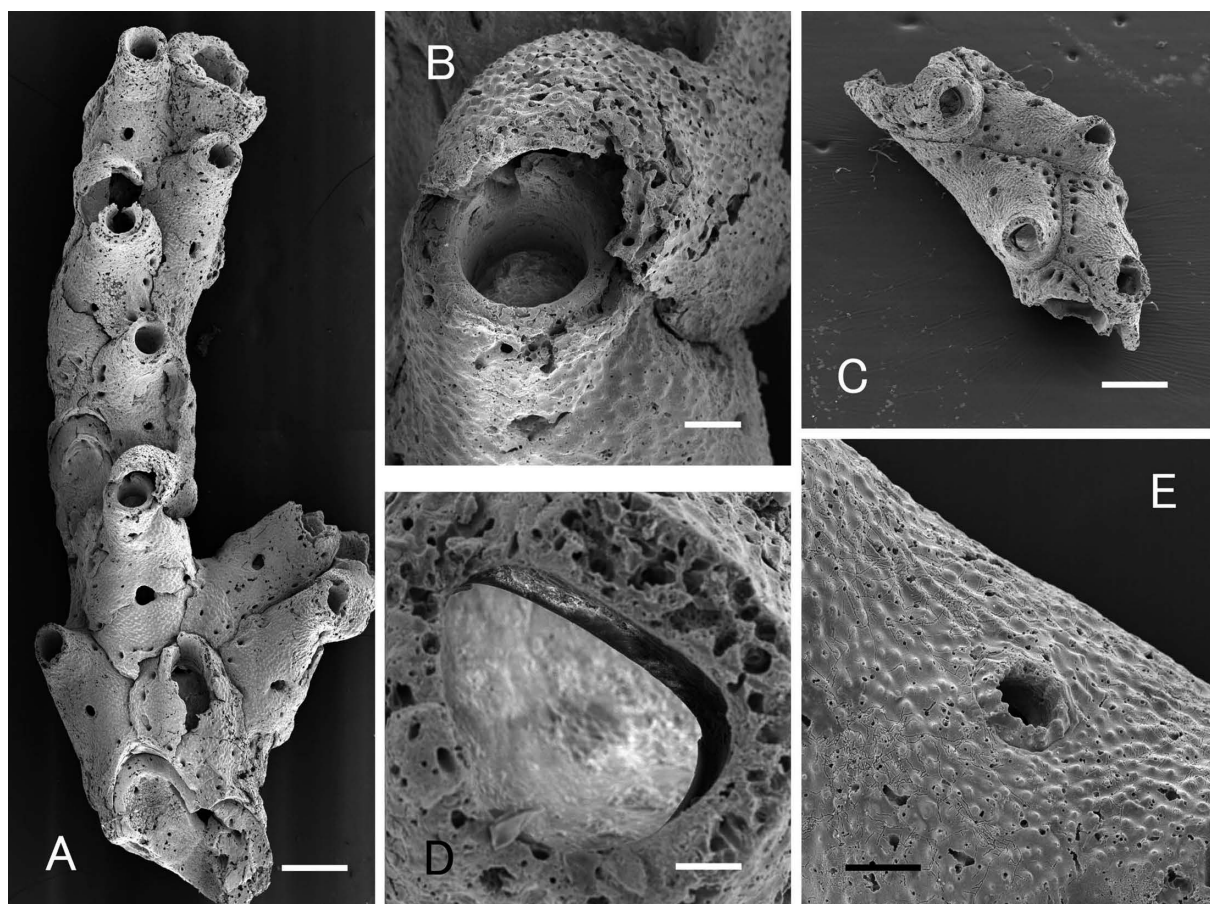


Fig. 2. *Tessaradoma japonicum* sp. nov., paratypes. A, Complete view of specimen NMNS PA 20497; B, ovicell and peristome in A; C, complete view of specimen NMNS PA 20498; D, primary orifice in C; E, spiramen in C. Scale bars: A, C, 500 μ m; B, E, 100 μ m; D, 50 μ m.

quer 1988) and the Azores (Jullien and Calvet 1903). However, as Souto et al. (2016) pointed out, ontogenetic changes in zooids have not been sufficiently compared, and thus no consensus on the synonymy has been reached.

Tessaradoma japonicum sp. nov.
(Figs 1, 2, 3A)

Tessaradoma (?) sp.: Arakawa 1999: 65, pl. 5, fig. D.
Semihawellia (?) sp.: Arakawa 2020b: 54.

Material examined. *Holotype*: NMNS PA 20496, Station 1709, R/V *Hakurei-Maru* cruise GH-80-2. *Paratypes*: NMNS PA 20497, Station 1734, R/V *Hakurei-Maru* cruise GH-80-2; NMNS PA 20498–20500, same station as holotype.

Diagnosis. Colony erect, composed of two or three series of zooids facing one side of the branches. Frontal shield granular, striated near lateral margin, with areolar pores. Semicircular orifice immersed at the bottom of a projecting peristome. Avicularia lacking. Ovicell peristomial; oecium imperforate.

Etymology. The specific name refers to the region of Japan.

Measurements (in mm). NMNS PA 20496–20499. Autozooids (23, 4): ZL, 1.25–1.96 (1.598 ± 0.175); ZW, 0.68–0.93 (0.806 ± 0.064); SO_rL, 0.15–0.26 (0.214 ± 0.033); SO_rW,

0.20–0.26 (0.230 ± 0.015). Ovicells (5, 2): OvL, 0.44–0.58 (0.513 ± 0.069); OvW, 0.48–0.54 (0.522 ± 0.033).

Description. Colony erect, bifurcate; branches about 1.0–1.4 mm in diameter. Zooids arranged in two or three longitudinal series, facing one side of the branches, hexagonal or pentagonal, separated by furrows (Figs 1A, 2A). Frontal shield inflated, granular, sometimes longitudinally striated near lateral margins, with a row of areolar pores; umbonuloid component relatively conspicuous on inner side (Fig. 3A). Spiramen situated in center of zooid, bordered by short, crown-like ring of calcification (Fig. 2E). Primary orifice (Fig. 2C, D) semicircular, with small lateral condyles, immersed at the bottom of a peristome. Peristome tall, raised, granular; secondary orifice circular, or horseshoe-shaped with straight proximal border. Avicularia lacking. Ovicell globular or bag-shaped, covering distal or distolateral side of peristome; oecium granular (Fig. 1B–D).

Distribution. East of Boso Peninsula, at depths of 144 and 155 m.

Remarks. This species resembles *Semihawellia umbrella* Gordon and Hondt, 1997 from New Caledonia in the colony form and in zooids having an elevated raised peristome and salient spiramen. However, my material cannot be placed in *Semihawellia* Canu and Bassler, 1917 because the frontal shield and oecium are imperforate. Although the frontal shield is striated mainly near the lateral margins,

my material appears to belong in *Tessaradoma*. *Tessaradoma boreale* shows conspicuous frontal striation, but younger zooids at the distal end of branches from Shetland are not striated (Gordon 1993), and ovicellate zooids in a Floridian specimen are also only granulated (Winston 2005).

Tessaradoma japonicum sp. nov. differs from other *Tessaradoma* species in colonies composed of zooids facing one side of the branches. In addition, the ovicell differs in structure from that in other species, except for *T. boreale* reported by Souto et al. (2016). The boundary between the ovicell and the next zooid is a deep furrow in British and Floridian examples of the genus (Hayward and Ryland 1979, 1999; Winston 2005), whereas the ooecium in *T. japonicum* sp. nov. (Fig. 1E) and *T. boreale* from the Galicia Bank is continuous with the frontal wall of the next zooid. In *T. japonicum* sp. nov., the ovicell extends upward along the peristome (Fig. 1C, D), and occasionally overhangs the distal edge of peristome due to the secondary calcification (? regeneration) of the next zooid (Fig. 2B).

The taxon referred as “*Margaretta* n. sp.” by Hirose (2010: 118, pl. 203) from northeast off Hachijo-jima may also be placed in *Tessaradoma*. Although its frontal granulation is not striated, Hirose’s species is very similar to *T. japonicum* sp. nov. in the imperforate frontal shield, the projecting peristome, and the position of the spiramen. The colony is, however, composed of 6–7 series of zooids facing all around the branches as in *T. boreale*.

Harmer (1957) inferred a colony fragment in the Mitsukuri Collection of the Cambridge Museum (now in the Natural History Museum, UK; see Spencer Jones et al. 2011) as his new species *Tessaradoma bipatens* Harmer, 1957 from west Waigeo Island, Indonesia. This species, however, is now placed in *Galeopsis* Jullien, 1888 (Bock 2016). The Mitsukuri’s Japanese collection also needs to be re-examined.

Family **Lacernidae** Jullien, 1888

Genus ***Cribellopora*** Gautier, 1957

Diagnosis. Colony encrusting. Frontal shield with cribellate or stellate pseudopores. Orifice semicircular, with proximal sinus. Oral spines present or absent. Avicularia lacking. Ovicell with cribellate or simple pseudopores, or imperforate with marginal pores.

Type species: *Cribellopora simplex* Gautier, 1957.

Remarks: The type species has been regarded as a synonym of *C. trichotoma* (Waters, 1918) (originally *Schizoporella trichotoma*) (e.g., Gautier 1962; Gordon 1984; Zabala and Maluquer 1988). However, Souto et al. (2010) re-examined original specimens of the two species, and concluded that they are clearly distinct. As discussed by Gordon (1989) and Winston (2005), this genus includes several species showing variation in such characters as the degree of development of the frontal pseudopores, the oral spines, and the surface texture of the ovicell.

Cribellopora connata (Ortmann, 1890)

(Figs 3B–F, 4A, B)

Hippothoa connata Ortmann, 1890: 52, pl. 4, fig. 7.

Cribellopora connata: Arakawa 1999: 78, pl. 9, fig. F; Arakawa 2020b: 55.

Rogicka connata: Hirose 2010: 113, pl. 193, figs A–F.

Material examined. NMNS PA 20501 (uncoated colony on molluscan shell), 20502 [colony on molluscan shell, with *Micropora plana* Arakawa, 2016 (NMNS PA 16836) and *Monoporella projecta* Arakawa, 2020 (NMNS PA 18452)], 20503 (single zooids A–C), Station 1734, R/V *Hakurei-Mar*u cruise GH-80-2. NMNS PA 20504 (a single ovicellate zooid), 20505 (single zooids A, B), Station 1746, R/V *Hakurei-Mar*u cruise GH-80-2.

Measurements (in mm). NMNS PA 20501, 20503–20505. Autozooids (12, 7): ZL, 1.03–1.18 (1.096 ± 0.051); ZW, 0.71–0.84 (0.791 ± 0.047); OrL, 0.13–0.18 (0.153 ± 0.016); OrW, 0.17–0.21 (0.182 ± 0.015).

Description. Colony encrusting, uniserial (Fig. 3B, C). Zooids oval, with communication pores at proximal and distal ends, and two or three on each side (Fig. 4B). Frontal shield much inflated, uniformly covered with small cribellate pseudopores; median imperforate area lacking. Orifice raised somewhat above frontal shield, semicircular, with rounded-v-shaped sinus and thick, grooved condyles (Fig. 3E, F); larger in ovicellate than non-ovicellate autozooids (Fig. 4A). Four stout oral spines present. Avicularia lacking. Ovicell globular, wider than long (0.403 mm long, 0.497 mm wide); ooecium completely covered with cribellate pseudopores (Fig. 4A). Ancestrula occluded with kenozooidal calcification (regenerated); a pair of daughter zooids budded (Fig. 3D).

Distribution. Sagami Bay, depth 370 m (Ortmann 1890); Fukuura, western Sagami Bay, depth 150 m (Hirose 2010); east of Boso Peninsula, depths 154 and 155 m (this study).

Remarks. The specimens from Sagami Bay (Ortmann 1890; Hirose 2010) have three oral spines, but this may represent intraspecific variation, because all other characters are as in my material. Although Hirose (2010) placed this species in *Rogicka* Uttley and Bullivant, 1972, based on the cribellate pseudopores and the presence of oral spines, these characters are also observed in *Cribellopora*. *Rogicka* differs from *Cribellopora* in having numerous close-set spines (Gordon 1984).

Among Recent species of *Cribellopora*, *C. siri* Gordon, 1989 from New Zealand and *C. constellata* Winston, 2005 from Florida resemble *C. connata* in the small frontal pseudopores. However, the former has an imperforate ovicell with small marginal pores, and the latter has stellate (not cribellate) pseudopores and an imperforate ovicell (Table 1). Ovicells evenly perforated by pseudopores as in *C. connata* have been illustrated for *C. trichotoma* by Cook (1985), “*Schizoporella trichotoma*” by Osburn (1952), and *Schizoporella pulchra* Neviani, 1895 (see Cook 1968).

Hirose (2010) reported another *Cribellopora* from Sagami

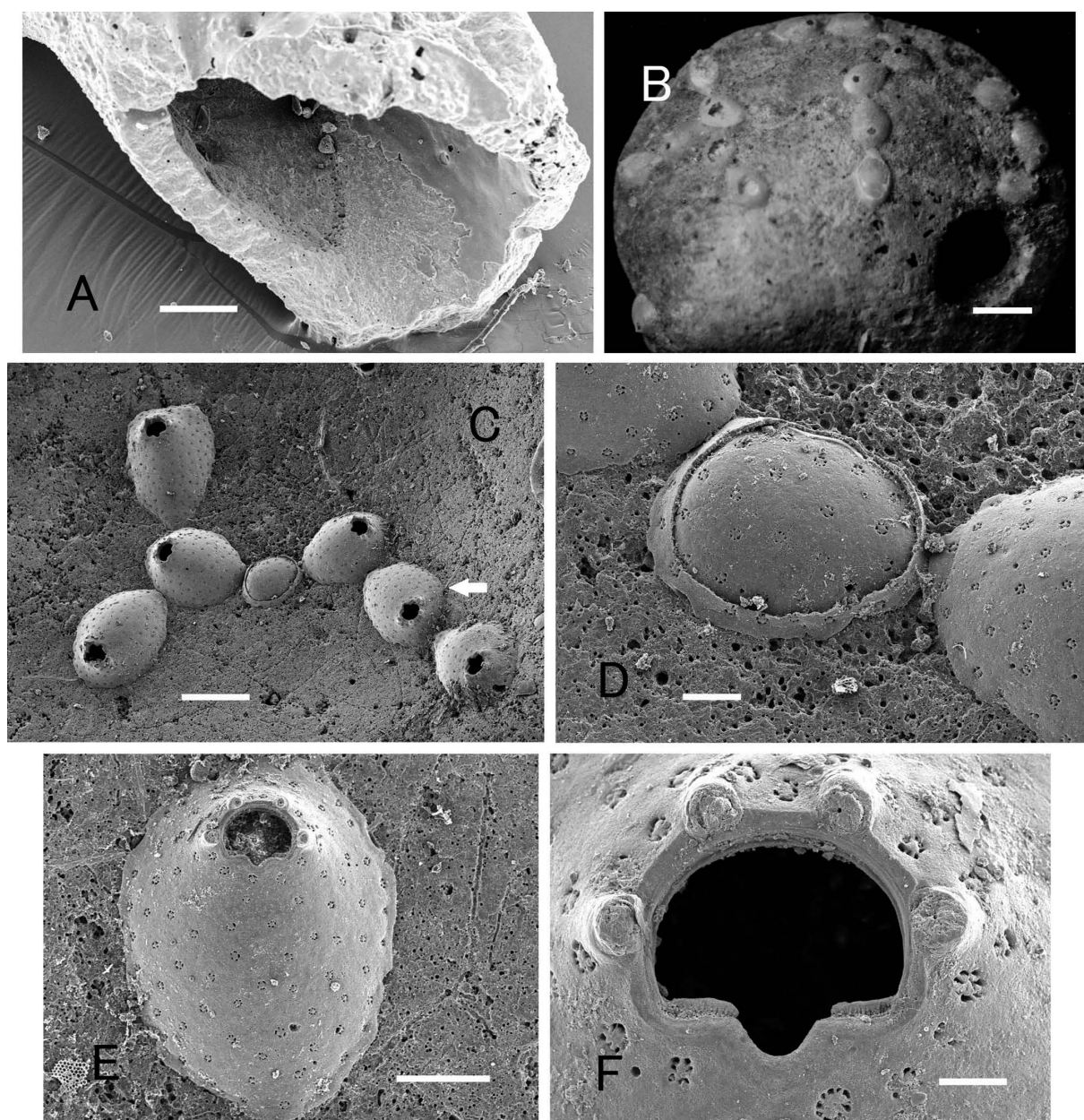


Fig. 3. *Tessaradoma japonicum* sp. nov. (A) and *Cribellopora connata* (Ortmann, 1890) (B–F). A, Inner surface of frontal wall, paratype, NMNS PA 20500; B, colony on molluscan shell, uncoated specimen, NMNS PA 20501; C, colony with ancestrula, NMNS PA 20502 (arrow, zoid enlarged in E); D, ancestrula in C; E, zoid indicated by arrow in C; F, orifice, NMNS PA 20503B. Scale bars: A, E, 200 μ m; B, 1 mm; C, 500 μ m; D, 100 μ m; F, 50 μ m.

Bay as *C. trichotoma*, based on the description of that species from New Zealand by Gordon (1984). Hirose's comparison is correct, but Gordon (1989) revised that species to *C. divisopora* (Waters, 1887), thus extending the known distribution of *C. divisopora* to Japan.

Family incertae sedis

Genus *Hippomenella* Canu and Bassler, 1917

Diagnosis. Colony encrusting. Frontal shield imperforate in suboral area, with umbonuloid component and two or more rows of areolar pores. Orifice horseshoe-shaped, rounded distally, with weakly concave proximal border and lateral condyles. Oral spines and adventitious avicularia present. Ov-

icell with partly pitted endooecium. (see Berning 2013).

Type species. *Lepralia mucronelliformis* Waters, 1899.

Remarks. The concept of this genus has been unclear since the type species does not coincide with the original generic diagnosis given by Canu and Bassler (1917). These authors considered *Hippomenella* to have laterally or proximally directed avicularia and "lateral crescentic areas" on the ovicell (Canu and Bassler 1929), but this feature of the ovicell was not based on the type species. The ovicell in the lectotype of *H. mucronelliformis* was not fenestrate but partly pitted (Brown 1949; Berning 2013).

As pointed out by Berning (2013), it must be discussed whether species with pseudopores on the ovicell, such as *H. vellicata* (Hutton, 1873), should be included in this genus.

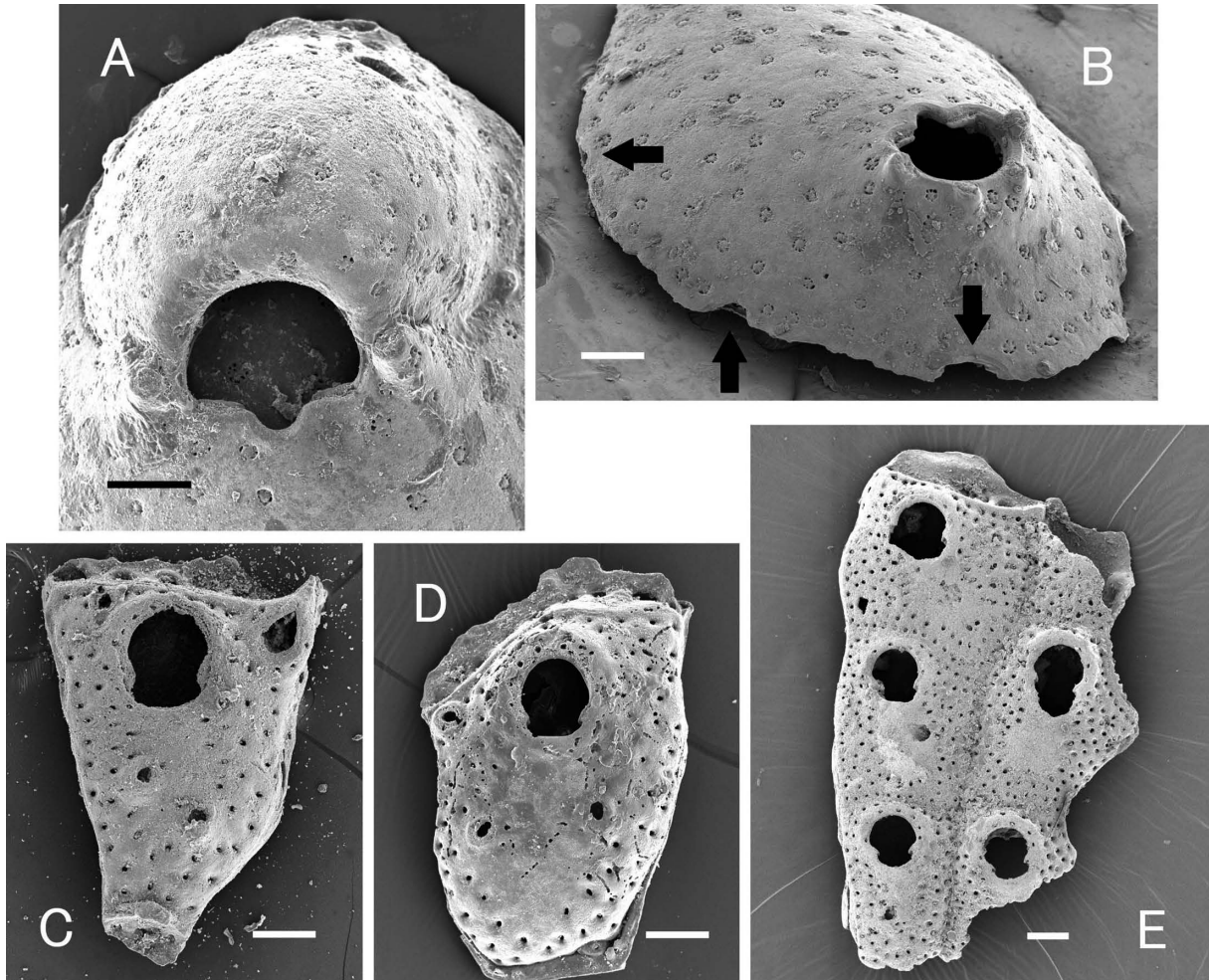


Fig. 4. *Cribellopora connata* (Ortmann, 1890) (A, B) and *Hippomenella* (?) *coronula* (Ortmann, 1890) (C–E). A, Ovicell and orifice, NMNS PA 20504; B, oblique view of zooid; arrows, three lateral communication pores, NMNS PA 20503B; C, single zooid with large avicularium, NMNS PA 20506B; D, single zooid, with relatively broad median imperforate area, NMNS PA 20506C; E, largest specimen, NMNS PA 20506A. Scale bars: A, B, 100 μ m; C–E, 200 μ m.

Based on a recent molecular analysis by Orr et al. (2022), *H. vellicata* is closely related to the genus *Escharoides* Milne Edwards, 1836, but *H. mucronelliformis* was not included in the material for their analysis. The relationship between a pitted oocidium and oocidal pseudopores also has not been elucidated.

Furthermore, the family affiliation of *Hippomenella* is presently unclear. Berning (2013) placed it in Romancheiniidae based on its resemblance to *Escharoides*, but no species in *Romancheina* Jullien, 1888 was included in molecular analysis by Orr et al. (2022).

Hippomenella* (?) *coronula (Ortmann, 1890)
(Fig. 4C–E)

Diporula coronula Ortmann, 1890: 39, pl. 3, fig. 7.

Hippomenella (?) *coronula*: Arakawa 1999: 79, pl. 9, fig. G.

Hippomenella coronula: Hirose 2010: 109, pl. 185, figs A–D;
Arakawa 2020b: 55.

Material examined. NMNS PA 20506 (fragment of colony A, and single zooids, B, C), Station 1748, R/V *Hakurei-*

Maru cruise GH-80-2.

Measurements (in mm). NMNS PA 20506. Autozooids (6, 3): ZL, 0.85–1.18 (1.048 ± 0.129); ZW, 0.57–0.95 (0.809 ± 0.139); OrL, 0.24–0.31 (0.262 ± 0.023); OrW, 0.22–0.25 (0.231 ± 0.015). Small frontal avicularia (8, 3): AvL, 0.11–0.13 (0.117 ± 0.008); AvW, 0.07–0.12 (0.086 ± 0.015)

Description. Colony encrusting. Zooids rectangular, or pentagonal to hexagonal, separated by furrows. Frontal shield imperforate in suboral area, with two to five rows of areolar pores. Orifice horseshoe-shaped, with broad poster separated from anter by proximomedially directed condyles. Oral spines five to seven. Small frontal avicularia generally two, sometimes absent (Fig. 4E); mandibular portion rounded or subtriangular, directed proximolaterally. One or two additional avicularia near distal corner of zooid, small, or large and elongate (Fig. 4C, D). Ovicell not found.

Distribution. Sagami Bay, depth 185 m (Ortmann 1890); eastern Sagami Sea, depth 65–77 m and 132–172 m (Hirose 2010); east of Boso Peninsula, depth 65 m (this study).

Remarks: My material comprises one colony fragment and two single zooids, but their zooidal characters corre-

spond to those of the lectotype for *H. coronula*, studied by Hirose (2010). Hirose considered Ortmann's species to be synonymous with *H. spatulata* Harmer, 1957 [= *Lepralia tuberculata* var. *avicularis* Livingstone, 1926; Hayward and Cook (1983) raised this taxon to species rank as *H. avicularis*]. However, *H. avicularis* has a large avicularium with a markedly expanded tip (Livingstone 1926; Harmer 1957; Powell 1967; Gordon and Hondt 1997); *H. coronula*, which shows gradual expansion of the avicularian tip, is a distinct species. For the same reason, the species from South Africa (Hayward and Cook 1983) and from Korea (Rho and Seo 1986) need to be restudied. I infer the Korean species as *H. coronula*, but the suboral imperforate area is narrower than in Japanese materials.

This species included in the species group of *H. vellicata* having proximally directed frontal avicularia and an oecium with radially arranged pseudopores. These features do not coincide with the diagnosis of *Hippomenella* amended by Berning (2013).

Discussion

Here I discuss the biogeography of the three species in this study.

***Tessaradoma*.** Among four Recent species in this genus listed in the web page of the International Bryozoology Association (Bock 2017a), *T. sinulabiata* David and Pouyet, 1986 from south of Madagascar may belong in some other genus, because the spiramen was not described. David and Pouyet (1986) also reported *T. boreale*, but it forms a dichotomously erect colony. O'Donoghue (1924) recorded *T. boreale* from South Africa, but this may also need to be restudied, because the peristome was not projecting. Except for these records, *Tessaradoma* is distributed in the following regions (though some records without description may possibly be doubtful):

1) The western Atlantic Ocean from the eastern end of Brazil to near the George Bank (Smitt 1873; Busk 1884; Canu and Bassler 1928; Osburn 1940; Maturo 1968; Cheetham 1972; Cheetham and Cook 1983; Hondt and Schopf 1984; Winston 2005);

2) The eastern Atlantic Ocean from the Great Meteor Bank to the south of Norway (Sars 1851, 1863; Busk 1860; Smitt 1868; Norman 1869, 1894, 1909; Hincks 1880; Jullien and Calvet 1903; Calvet 1907, 1931; Nordgaard 1907, 1918; Silén 1936; Marcus 1940; Ryland 1963; Hondt 1973, 1974, 1975, 1977; Hayward 1978, 1979; Hayward and Ryland 1979, 1999; Harmelin and Hondt 1992; Rouse et al. 2013; Berning et al. 2014; Souto et al. 2016);

3) Near the Mid-Atlantic Ridge between the Caribbean and the northwest coast of Africa (Busk 1884);

4) The Mediterranean (Gautier 1962; Lagaaij and Gautier 1965; Zabala and Maluquer 1988; Mastrototaro et al. 2010; Gerovasileiou and Rosso 2016; Rueda et al. 2019); and

5) The Arctic Ocean from Greenland to the Laptev Sea (Sars 1851, 1863; Busk 1860; Smitt 1868; Nordgaard 1900, 1905, 1918, 1927; Levinsen 1914; Kluge 1962; Akhmetchina

and Zakharov 2013).

Among these regions, *Tessaradoma* fossils have been found only from the Upper Miocene to Pleistocene in the Mediterranean region (Moissette 1988; Pouyet and Moissette 1992; El Hajaji 1992; Moissette and Spjeldnaes 1996; Rosso and Di Geronimo 1998; Rosso 2005; Moissette et al. 2021); all were described as *T. boreale*, but they seem to include two or more species. Cheetham (1972) erected a species of *Tessaradoma* from the Eocene of Tonga, but this is now placed in *Smithsonius* Gordon, 1988 (see Winston and Beaulieu 1999). Based on the fossil and Recent records, *Tessaradoma* probably appeared in the Miocene "proto-Mediterranean Sea" and extended its distribution mainly through the North Atlantic Subtropical Gyre.

***Cribellopora* and "*Hippomenella*".** In contrast to *Tessaradoma*, *C. connata* and *H. (?) coronula* show biogeographical affinities to the bryozoan faunas of Australia and New Zealand.

Cribellopora is widely distributed in the following four regions:

1) The Mediterranean and the west coast of Africa (Waters 1918; Gautier 1957; Cook 1968, 1985; Zabala 1986, 1993; Zabala and Maluquer 1988; Souto et al. 2010);

2) The North and South America (Smitt 1873; Hastings 1930; Osburn 1952; Soule 1961; Lagaaij 1963; Winston 2005);

3) Hawaii (Dick et al. 2006) [Souto et al. (2010) raised doubt on the generic status]; and

4) The West Pacific (Waters 1887; Ortmann 1890; Powell 1967; Wass and Yoo 1983; Gordon 1984, 1989; Hirose 2010).

As shown in Table 1, the frontal pseudopores in the American and Ghanaian species are stellate, with radial spokes in a circular depression, whereas those in the Euro-African region (except for *C. trichotoma* from Ghana) and the West Pacific are a radial set of small pores simply penetrating the frontal wall. The resemblance between *C. divisopora* from the Recent West Pacific Ocean and *C. latigastra* (David, 1949) from the Early Miocene to Pliocene of the Mediterranean and Eastern Europe (David 1949; David et al. 1970, 1972; David and Pouyet 1974; Moissette 1988; Pouyet and Moissette 1992; El Hajaji 1992; Pouyet 1997; Moissette et al. 2006; Zágorský 2010) is also remarkable. Although the origin of *Cribellopora* remains undetermined, two unnamed species from the Late Eocene of New Zealand (Lee et al. 1997) are currently the oldest records.

The species group, in which *H. (?) coronula* belongs, is mainly distributed in the Southern Hemisphere. Berning (2013) observed that species such as *H. vellicata* from New Zealand, *H. amaralae* Vieira, Gordon, Souza, and Haddad, 2010 from Brazil, *H. ramula* Hayward and Winston, 2011 from near Tierra del Fuego, and *Hippopleurifera belizae* (Winston, 1984) from Belize comprise a group with oecial pseudopores. These species have the radially arranged oecial pseudopores, and they are also characterized by a pair of small frontal avicularia directed proximally. *Hippomenella avicularis* from Australia, New Zealand, New Caledonia, South Africa and Korea, *H. bituberosa* Brown, 1952 from New Zealand, and Ortmann's *H. coronula* are also included

Table 1. Comparison of Recent and fossil species in the genus *Cribellopora*.

| Species | Distribution | Frontal pseudopores | Suboral imperforate area | Orificial sinus | Dimorphism of orifices | Oral spines | Ovicell |
|--|-------------------------------------|---------------------------|--------------------------|-----------------|------------------------|-------------|--|
| Recent | | | | | | | |
| <i>C. connata</i> (Ortmann, 1890) | Japan | small, cribellate | narrow | moderate | salient | 3–4 | small cribellate pores |
| <i>C. napi</i> Gordon, 1989 | New Zealand | large, cribellate | narrow | narrow | | 0 or 2 | small marginal pores, umbonate, distal rim |
| <i>C. siri</i> Gordon, 1989 | New Zealand | small, cribellate | moderate | narrow | salient | 0 | only marginal pores, distal rim |
| <i>C. divisopora</i> (Waters, 1887) | Australia, New Zealand | large, cribellate | narrow | broad | | 0–1 | cribellate marginal pores, umbonate, distal rim |
| <i>C. divisopora</i> sensu Bock (2016) | Australia | moderate size, cribellate | broad | narrow | salient | 1–3 | only marginal pores? |
| <i>C. souleorum</i> Dick, Tilbrook, and Mawatari, 2006 | Hawaii | large, stellate* | broad | narrow | | 6 | small pores, distal rim |
| “ <i>Schizoporella trichotoma</i> ” in Osburn (1952) | Gulf of California, Galapagos | moderate size, stellate | narrow | moderate | | 4** | stellate pores, proximal “peak” |
| <i>C. trichotoma</i> sensu Lagaaij (1963) | Gulf of Mexico (USA) | moderate size, stellate | broad | broad | | 0 | — |
| <i>C. constellata</i> Winston, 2005 | Florida | small, stellate | moderate | broad | | 0 | imperforate, distal rim |
| <i>C. trichotoma</i> sensu Cook (1985) | Ghana | moderate size, stellate | narrow | moderate | | 6 | small pores |
| <i>C. simplex</i> Gautier, 1957 | Mediterranean | large, cribellate | narrow | moderate | | 1–3 | cribellate marginal pores |
| <i>C. trichotoma</i> (Waters, 1918) | | large, cribellate | narrow | moderate | salient | 3–5 | cribellate marginal pores, proximal “peak”, distal rim |
| Fossil | | | | | | | |
| <i>C. latigastrea</i> (David, 1949) | Europe, North Africa (Mio–Pliocene) | large, cribellate | narrow | broad | salient | 0 | cribellate marginal pores |
| <i>C. hluchovensis</i> Žágoršek, 2010 | Czech Republic (Miocene) | small, cribellate? | narrow | moderate | | 0 | imperforate |
| <i>C. trasoni</i> Žágoršek, 2010 | Czech Republic (Miocene) | small, cribellate | narrow | narrow | | 0 | imperforate |
| <i>Schizoporella pulchra</i> Neviani, 1895*** | Italy (Pliocene) | large, stellate | narrow | narrow | | 1 or 3 | stellate pores |

* Only a row of marginal pores.

** Osburn (1952) did not illustrate any spines, but described “about 4 minute and evanescent spines”.

*** Homonym of *S. pulchra* MacGillivray, 1891. Cook (1968) thought Neviani’s species was a synonym of *C. trichotoma*.

in this species group, although the ovicell has never been observed in Japanese materials. Fossils of the former two were collected from the Middle Miocene to Pliocene of New Zealand (Brown 1952), and another species (*H. konnoi* Kataoka, 1961) was recorded from the Pleistocene of Japan (Kataoka 1961).

The three bryozoans in my study are isolated from other areas of the distribution of each species group. However, the ancestor of Japanese *Tessaradoma* probably migrated from the Arctic Ocean. The Laptev Sea where *T. gracile* was recorded (Kluge 1962) is not far from the Bering Strait, and the Bering Strait has been open intermittently since the latest Miocene or earliest Pliocene (e.g., Gladenkov and Gladenkov 2004).

In contrast, the two species reported by Ortmann (1890) are related to the history of the warm water fauna in Japan. The cheilostomatids from Sagami Bay, the Sagami Sea, and east of the Boso Peninsula (Arakawa 1999, 2020b; Hirose 2010) include several Indo-Pacific species such as *Calyptotheca wasinensis* (Waters, 1913), *Margaretta gracilior* (Ortmann, 1890), *Mucropetraliella thenardii* (Audouin, 1826) and *Robertsonidra argentea* (Hincks, 1881), and also some Western Pacific species such as *Iodictyum sanguineum* (Ortmann, 1890). Miocene fossils of *Iodictyum* Harmer, 1933 have been found from New Zealand (Brown 1952), India (Guha and Gopikrishna 2007) and Japan (Arakawa 2023), but most recent species in that genus are distributed only in the Western Pacific (Bock 2017b). Probably, such Western Pacific species appeared after the restriction of the Indonesian Throughflow (e.g., Auer et al. 2019) and the extinction of the Western Pacific Warm Pool (e.g., Sato et al. 2008) during the Pliocene.

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Shinji Arakawa: Conceptualization; Resources; Investigation; Visualization; Writing – original draft; Writing – review & editing.

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