New Species of Lower-Shelf to Upper-Slope Ctenostome Bryozoans From Pacific Japan, With a Family Range Extension

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Ctenostome bryozoans were collected from depths of 150–300 m in Suruga Bay, the Kumano Sea, and off Sendai Bay on the Pacific coast of Japan. Among these samples were five new species, three of which were epibiotic on other animals. *Alcyonidium clavum* n. sp., found encrusting cirri of the stalked crinoid *Metacrinus rotundus*, was previously reported in Japan as *Alcyonidium mamillatum*, but differs from the latter in lacking rings on the peristome. *Triticella parvacrista* n. sp. and *Triticella cunabula* n. sp. were epibiotic on the isopod *Bathynomus doederleini* and the pycnogonid *Ascorhynchus japonicum*, respectively. This is the first record of the genus *Triticella* from Japanese waters. These species differ from previously described species in autozooidal morphology, particularly the dimensions of the autozooidal dilatation, in the presence or absence of the frenaculum, and in the septate junction between the dilatation and pedicel. *Bockiella arcatumida* n. sp., found as erect colonies on pebbles and hydroids collected off Sendai Bay, differs from previously known species in the size and arrangement of the kenozoids in the branch. *Metalcyonidium morum* n. sp., collected southwest of the Izu Peninsula, occurred as small colonies having a peduncle of short kenozooids. This is the first record from the northwestern Pacific for both the genus *Metalcyonidium* and the family Clavoporidae. *Metalcyonidium morum* n. sp differs from *Metalcyonidium gautieri*, the only other species known in the genus, in having the capitulum divided into two parts, and in the length of the kenozooids comprising the peduncle.

Key words: *Alcyonidium*, *Bockiella*, Ctenostomatida, Kumano Sea, *Metalcyonidium*, Sendai Bay, Suruga Bay, *Triticella*

INTRODUCTION

Bryozoans are colonial sessile animals, widely distributed in freshwater and marine environments. More than 6000 living species have been reported worldwide, most of which are in the order Cheilostomatida (class Gymnolaemata) and form a hard skeleton of calcium carbonate (Bock and Gordon, 2013; Martha et al., 2020). In contrast, species in the order Ctenostomatida, a small paraphyletic group in the class Gymnolaemata, have a non-calcified body wall and are much less diverse than cheilostomes, with only about 300 species described worldwide (Taylor and Waeschenbach, 2015; Todd, 2000; Waeschenbach, 2012). Both cheilostomes and ctenostomes are primarily marine, although some occur in brackish habitats.

Relatively few ctenostome bryozoan species have been reported from Japan (Hirose, 2016). Among 53 species of bryozoans in 35 genera reported from Shimoda and around the Izu Peninsula, most were cheilostomes, with only 7 cyclostome species and no ctenostomes (Okada, 1934; Okada and Mawatari, 1935, 1936). Only 10 ctenostome spe-

cies in four genera have been reported from Sagami Bay, where the marine fauna has probably been best studied in Japan (Hirose, 2016). A possible reason for relatively few ctenostomes having been reported is that they often consist of small, transparent encrusting species attached to the surface of other organisms such as crustaceans or gastropods, or small colonies on sandy and muddy bottoms, making them difficult to detect during the sorting of benthic samples. This suggests that further surveys throughout Japan, including in Sagami Bay, will lead to the discovery of many new species.

Marine bryozoan diversity is greatest at depths of 0 to 100 m (Gordon, 1999), and remains relatively high at 200 m depth (Hirose, 2016), but decreases below that depth. Various studies have reported on Japanese bryozoans from slightly deeper waters such as lower-shelf to upper-slope over the past century and a half (Busk, 1884; Ortmann, 1890; Harmer, 1915, 1926, 1934, 1957; Okada, 1934; Okada and Mawatari, 1935, 1936; Silen, 1941, 1942). However, there have been only a few reports of deeper water ctenostomes from along the Pacific coast of Japan, including some species from around 100 m depth (Mawatari, 1953) and others from the deep sea (Silén, 1942).

Several recent surveys along the Pacific coast of Japan yielded specimens of five undescribed ctenostome species

from depths of around 200 m off Tohoku, Suruga Bay, and the Kumano Sea, representing four genera in three families. Three of the species were attached to other benthic organisms, while two were attached to sand grains or pebbles on sandy-mud bottoms. Here I describe and illustrate these five new species.

MATERIALS AND METHODS

Collecting was conducted from March 2013 to November 2015. Specimens were obtained (Fig. 1) from 200–300 m depth in the Kumano Sea, from a fishing boat; from 150–300 m depth in Suruga Bay, from a fishing boat; from 180–230 m depth southwest of the Izu Peninsula, by dredge from RV *Tsukuba II* (University of Tsukuba); and from 186–193 m depth off Sendai Bay by beam trawl from RV *Shinsei-maru*, during survey KS-14-1. Some specimens were photographed with a Nikon D7000 digital camera before fixation, either aboard the vessel or in the laboratory. Most specimens were fixed in 10% formalin in seawater, and the rest were placed directly in 70% or 99% ethanol.

Specimens were observed with Leica DM2500 LED and Olympus BX53 light microscopes and an Olympus SZX16 stereomicroscope. External morphology was photographed with a Leica MC170 HD digital camera attached to a Leica DM2500 LED light microscope or Nikon D7000 attached to an Olympus SZX16 stereomicroscope. Measurements were taken from digital photomicrographs by using ImageJ 1.37v software (Image Processing and Analysis in Java, Wayne Rasband, National Institutes of Health,

USA: http://rsb.info.nih.gov/ij/). Measurements in the text are presented in millimeters as the range, followed by the average ± standard deviation and then sample size in parentheses. For observation of internal morphology, parts of colonies of *Alcyonidium* and *Bockiella* were dehydrated in an ethanol series, cleared in *t*-butanol, embedded in paraffin, sectioned at a thickness of 6 μm, mounted on slides, and stained with hematoxylin-eosin (HE). All specimens have been deposited in the National Museum of Nature and Science, Tsukuba, Japan (NSMT).

RESULTS

Taxonomy

Order CTENOSTOMATIDA Busk, 1852
Superfamily ALCYONIDIOIDEA Johnston, 1838
Family ALCYONIDIIDAE Johnston, 1837
Genus *Alcyonidium* Lamouroux, 1813
***Alcyonidium clavum* n. sp.**
(Figs. 2, 3)

? *Alcyonidium mamillatum*: Silén, 1942, 18–19, figs. 12–14.
? *Alcyonidium mamillatum*: d'Hondt and Mawatari, 1986, 462, Pl. I, fig. 4.
Not *Alcyonidium mamillatum* Alder, 1857, 64, Pl. 5, figs. 3, 4.

Diagnosis. Colony encrusting, thin, unilaminar, coherent. Autozooids hexagonal or irregularly polygonal, smooth, transparent; with slightly raised distal end of zooid with long, tubular peristome lacking rings, up to 1/2–2/3 length of autozooid. Pseudo-operculum lacking. Polypide with 18 tentacles.

Material examined. *Holotype*: NSMT-Te1228, colony on cirrus of the stalked crinoid *Metacrinus rotundus*, collected by T. Moritaki on 7 March 2014, Suruga Bay, 150–300 m depth. *Paratypes*: NSMT-Te1229, colony on cirrus of the stalked crinoid *M. rotundus*, collection data as for holotype; NSMT-Te1230 single series of 6-μm sections stained with HE, collection data as for holotype.

Etymology. The specific name derives from the Latin *clavus* (nail), referring to the erect, cylindrical peristome.

Description. Colony encrusting, thin unilaminar, coherent (Figs. 2B–D, 3A). Autozooids hexagonal or irregularly polygonal in outline (Fig. 2D); length 0.59–0.81 (0.71 ± 0.06) mm, width 0.31–0.52 (0.42 ± 0.06) mm ($n = 27$). Frontal wall not strongly convex, surface smooth, lacking papillae, transparent, unpigmented; long tubular peristome at distal end, length up to 1/2–2/3 length of autozooid (Figs. 2C, 3A), length 0.09–0.37 (0.23 ± 0.10) mm ($n = 11$). Peristome lacking rings. Orifice lacking pseudo-operculum; length 0.09–0.16 (0.13 ± 0.02) mm, width 0.11–0.16 (0.13 ± 0.02) mm ($n = 12$). Most of polypide horizontal;
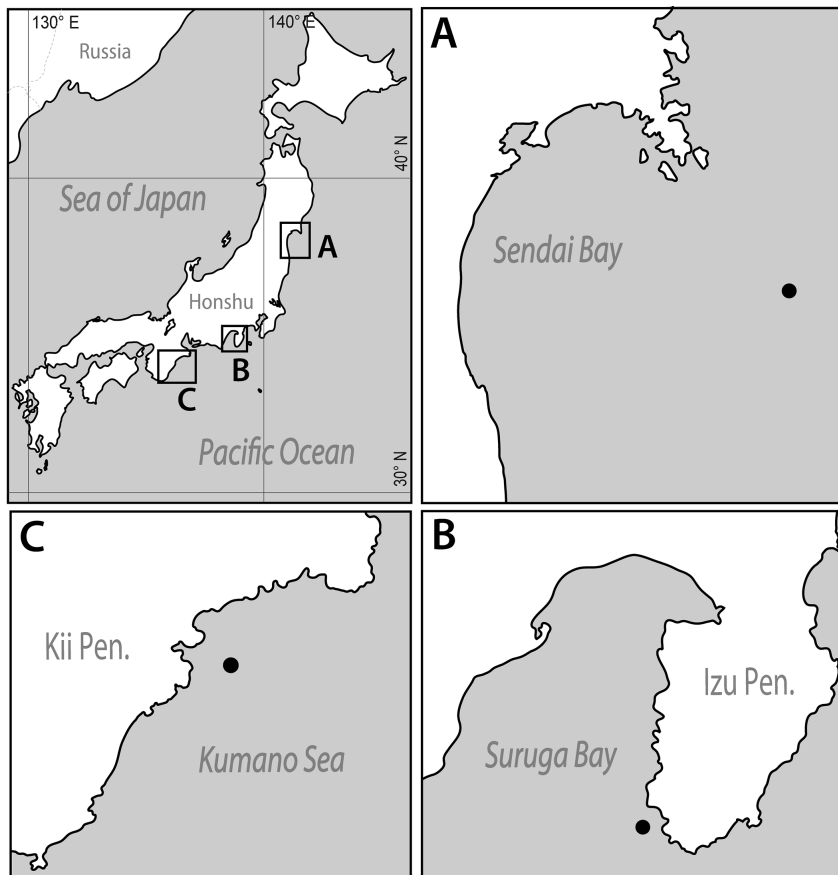

Fig. 1. Map showing localities where ctenostome bryozoans were collected for this study. **(A)** off Sendai Bay, showing the type locality of *Bockiella arcatumida* n. sp.; **(B)** Suruga Bay and the type locality of *Metalcyonidium morum* n. sp. southwest of the Izu Peninsula; **(C)** Kumano Sea and the type locality of *Triticella parvacrista* n. sp. off Owase.

Fig. 2. *Alcyonidium clavum* n. sp. from Suruga Bay. **(A)** Living colony on cirrus of stalked crinoid *Metacrinus rotundus* (NSMT-Te1228). **(B)** Living colony showing autozooids with extended lophophores (NSMT-Te1228). **(C)** Fixed colony, showing erect peristomes (NSMT-Te1229). **(D)** Fixed colony, showing polygonal autozooids with white polypides inside (NSMT-Te1229).
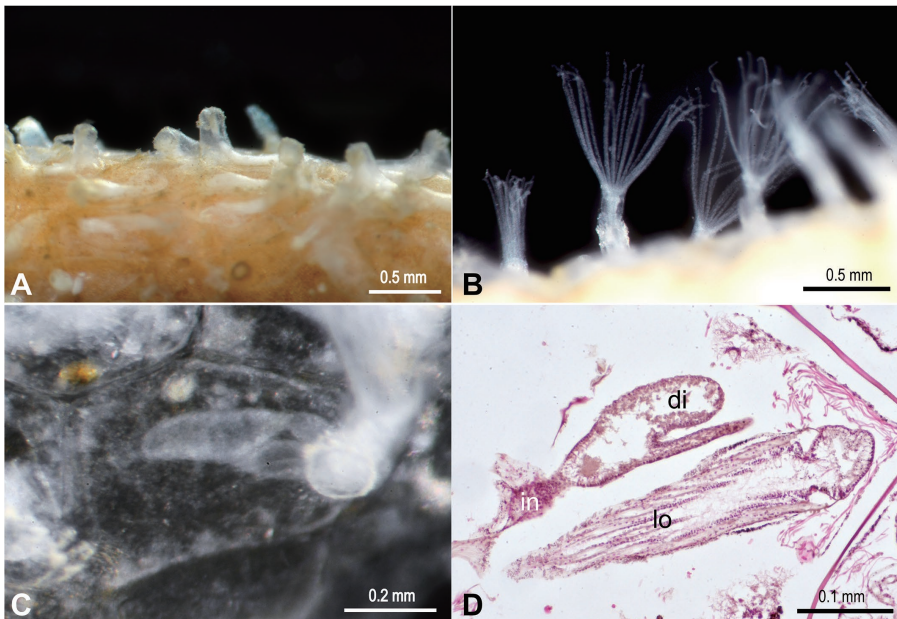

Fig. 3. *Alcyonidium clavum* n. sp. from Suruga Bay. **(A)** Fixed colony, showing autozooids with long peristomes (NSMT-Te1229). **(B)** Living colony, showing extended lophophores (NSMT-Te1228). **(C)** Autozooid, showing the polypide inside (NSMT-Te1229). **(D)** Longitudinal section showing polypide with highly developed digestive cecum (NSMT-Te1230). Abbreviations: di, digestive cecum; in, intestine; lo, lophophore.

larly polygonal in outline. Ancestrula and initial budding pattern not observed. Type of larva (lecithotrophic or planktotrophic) and reproductive mode (larviparous or oviparous) unknown.

Remarks. *Alcyonidium clavum* n. sp. resembles *A. mamillatum* Alder, 1857 in the irregularly polygonal autozooidal outline and the prominent orificial peristome near the distal end of the autozooid, with the peristome height up to 2/3 of autozooid length. *Alcyonidium clavum* n. sp. differs from *A. mamillatum* in having interzooidal kenozooids and fewer tentacles (20–21 in *A. mamillatum*; Hayward, 1985), and in lacking rings in the peristome (always distinctly ringed in *A. mamillatum*). *Alcyonidium mamillatum* was originally described from Europe and seems to be restricted to the Atlantic, with records of similar-looking species worldwide having subsequently been attributed to that species. *Alcyonidium clavum* n. sp. resembles the Brazilian species *Alcyonidium pulvinatum* Vieira, Migotto and Winston, 2014, also previously reported as *A. mamillatum* (Marcus, 1937), in the presence of kenozooids and an orificial peristome, autozooid size and shape, the mostly flat frontal autozooidal surface, and tentacle number, but *A. clavum* n. sp. has a smaller orifice (diameter 0.14–0.16 mm in *A. pulvinatum*) and smaller kenozooids, which also differ in placement in *A. pulvinatum*, occurring in anastomosing areas or in colony lobes.

Alcyonidium clavum n. sp. resembles *Alcyonidium albescens* Winston and Key, 1999, originally described from North Carolina in the western Atlantic, in having hexagonal autozooids with a flat frontal surface and in having interzooidal kenozooids, but *A. clavum* n. sp. has larger autozooids, more tentacles (14–17 in *A. albescens*), and a more conspicuous orificial peristome. *Alcyonidium clavum* n. sp. also resembles *Alcyonidium cellarioides* Calvet, 1900, originally described from Sete, Mediterranean, in having an encrusting colony with hexagonal autozooids bearing an orificial peristome, but *A. clavum* n. sp. has slightly larger autozooids, fewer tentacles (20 in *A. cellarioides*), a flat frontal autozooidal surface, and a thinner, completely unilaminar

rarely, slightly upright near peristome at distal end of zooid (Fig. 3C). Lophophore cup-shaped (Figs. 2B, 3B). Number of tentacles 18. Intertentacular organ not found in formalin-fixed specimens. Collar present; length 0.09–0.10 (0.09 ± 0.01) mm ($n = 3$). Digestive caecum large, conspicuous (Fig. 3D). Interzooidal kenozooids uncommonly present; irregu-

colony (the colony in *A. cellarioides* is up to 6 mm thick and multilaminar in developed colony; Hayward, 1985). *Alcyonidium clavum* n. sp. also resembles *Alcyonidium effusum* Norman, 1909, originally described from Madeira, in the shape and size of autozooids, the length of the orificial peristome, and the peristomial rings, which are indistinct in the latter species, but *A. clavum* n. sp. has a thinner autozooidal layer compared to the thick colony of *A. effusum* and completely lacks rings on the peristome.

Silén (1942) reported *A. mamillatum* from several localities around Japan (Sagami Bay, including Misaki, Okinose, Yokuska [Yokosuka], and Yodomi [off Misaki]; and Hirado, Nagasaki, west coast of Kyushu I.) and noted that it is difficult to distinguish Japanese specimens from North Atlantic specimens based on zooid morphology. Although specimens from the two regions are similar in most diagnostic features, the broad depth distribution of nominal *A. mamillatum* (infralittoral to bathyal; d'Hondt, 1983) suggests that previous descriptions of this species were possibly based on character states from several species. Although it is possible that Silén's (1942) *A. mamillatum* partly included *A. clavum*, I have listed his records as of uncertain synonymy with *A. clavum*, since I could not observe any of Silén's specimens.

I found *Alcyonidium clavum* n. sp. encrusting cirri of the stalked crinoid *Metacrinus rotundus*, while Silén (1942) similarly found his nominal *A. mamillatum* to be epibiotic on stalked crinoids, as well as on ray-fish egg cases and hydroid stalks.

Distribution. *Alcyonidium clavum* n. sp. is known from Suruga Bay, at 150–300 m depth.

Genus *Bockiella* Silén, 1942
Bockiella arcatumida n. sp.
(Figs. 4–6)

Bockiella sp. Schwaha, 2021, 633–649, figs. 1, 2, 9, 10, 14, 18.

Diagnosis. Colony erect, composed of a tangle of branches. Branches cylindrical, transparent, composed of 4–8 longitudinal columns of alternating autozooids and kenozooids. Autozooids small, thin, convex frontally. Orifice small, papilliform, with short peristome; pseudo-operculum lacking. Kenozooids same size as autozooids, covering most of proximal surface of next-distal autozooid. No spines. Polypide with 22–24 tentacles.

Material examined. *Holotype*: NSMT-Te1231, colony with many branches, collected by M. Hirose on 7 March 2013, off Sendai Bay (38°00.4072′N, 141°46.3060′E to 38°01.5301′N, 141°47.2456′E), 186–193

m depth, by beam trawl from RV *Shinsei-maru. Paratypes* (same collection data as for holotype): NSMT-Te1232, small colony attached to plastic sheeting; NSMT-Te1233 small colony attached to hydroid; NSMT-Te1234, small branches of colony; NSMT-Te1235–Te1239, five series of 6-μm sections stained with HE.

Etymology. The specific name derives from the Latin *arca* (box) and *tumida* (swollen), referring to the large kenozooids.

Description. Colony erect, composed of tangle of upright stalks and lateral branches, up to 3 cm in height (Fig. 4A); branches diverging from stalks in various directions, angled at approximately 75–80 degrees to stalk, some branches anastomosing distally, again becoming encrusting upon re-contacting substrate (Fig. 4B, C); branches cylindrical (Fig. 4C, D), circular in cross-section, usually uniform in diameter, but broader and slightly flattened at stalk bifurcations; diameter 0.79–1.70 (1.13 ± 0.25) mm (*n* = 12). Whole colony whitish brown or light yellow in living state, due to contracted white lophophores and brown bodies (Figs. 4, 5).
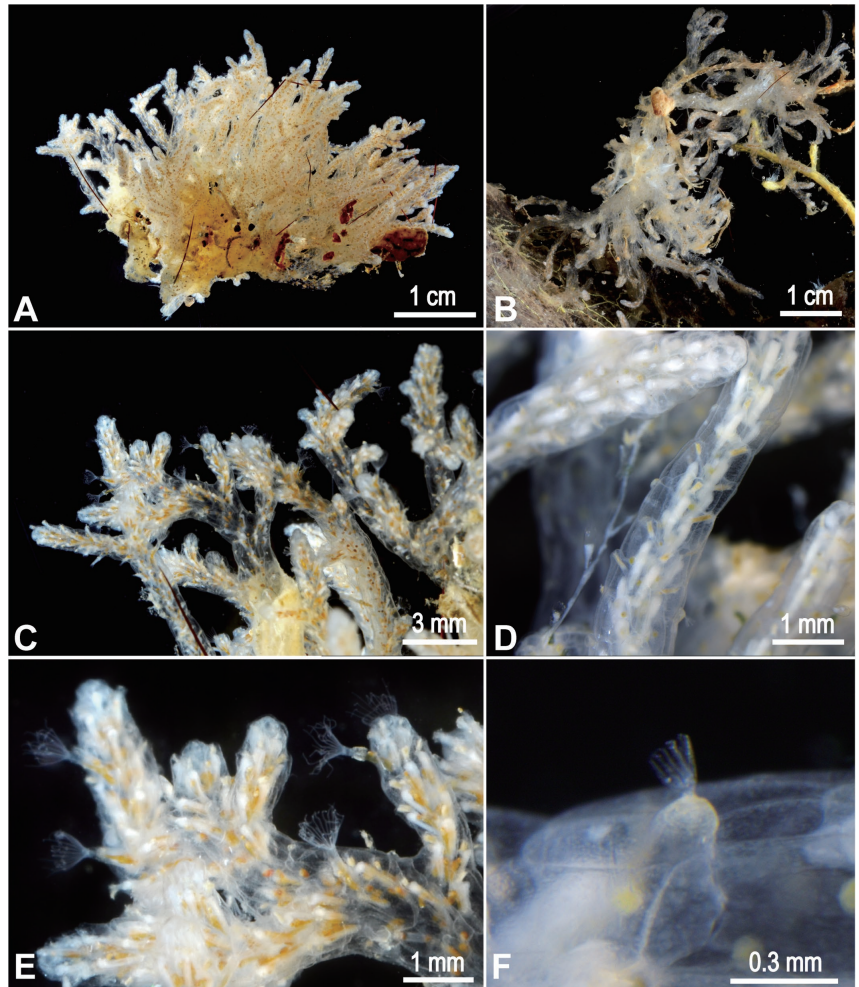

Fig. 4. *Bockiella arcatumida* n. sp. from off Sendai Bay. **(A)** Living colony, holotype (NSMT-Te1231). **(B)** Living colony, paratype, attached to plastic sheet (NSMT-Te1232). **(C)** Living colony showing branches of different widths and some extended lophophores (NSMT-Te1231). **(D)** Ends of branches, showing autozooidal columns (NSMT-Te1231). **(E)** Enlargement of **(C)** showing extended lophophores. **(F)** Autozooid with extruded collar.
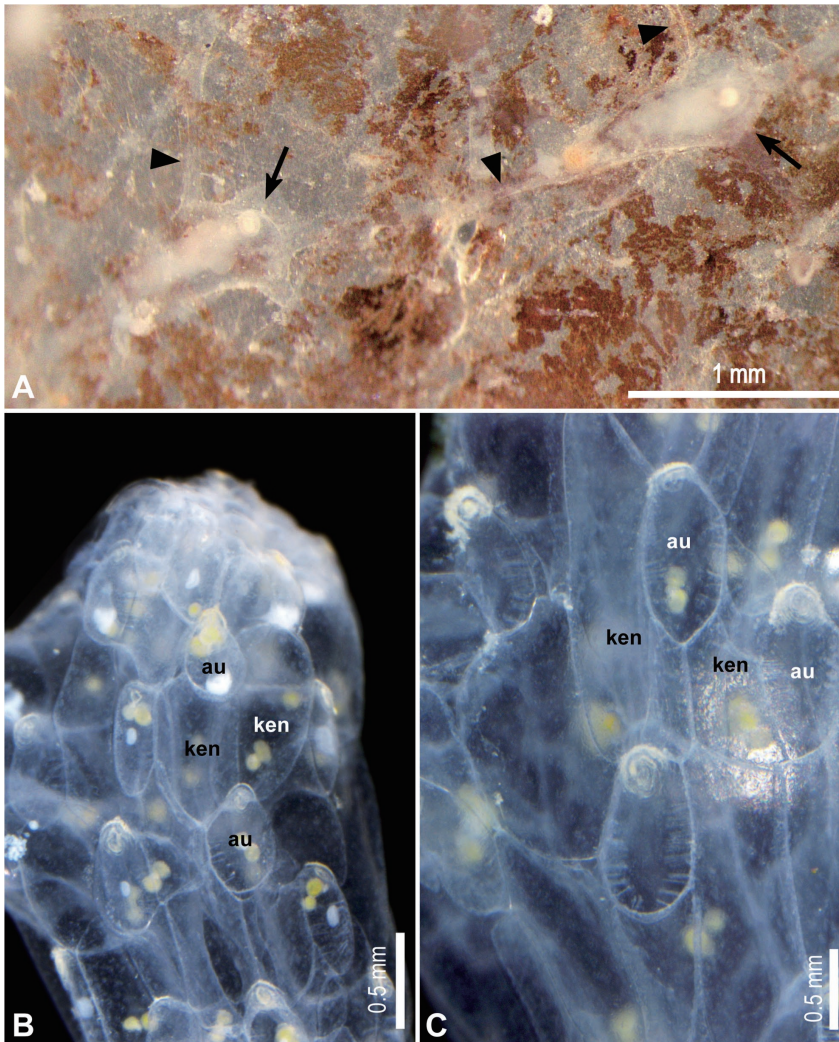
Fig. 5. *Bockiella arcatumida* n. sp. from off Sendai Bay. **(A)** Encrusting base of colony, showing narrow, triangular autozooids (arrows) and narrow stolons (arrowheads) (NSMT-Te1232). **(B)** End of branch, showing dense cluster of autozooids and kenozooids (NSMT-Te1231). **(C)** Enlargement of branch showing small, oval autozooids (frontal surface) surrounded by large, transparent kenozooids (NSMT-Te1231). Abbreviations: au, autozooid; ken, kenozooid.

nately in adjacent columns, separated by 1 to 1.5 autozooid widths, kenozooid column in between (Fig. 5C). Proximal end of each autozooid covered proximally and laterally by single or two kenozoids in each column, depending on the location in branch; kenozooids elongate-rectangular, transparent, smooth, slightly convex (Figs. 5C, 6A), nearly same width as autozooids when single but half their width when double. Frontal surface of kenozooids exposed on branch surface variable in size, length 0.72–1.04 (0.89 ± 0.13) mm, width 0.21–0.46 (0.36 ± 0.09) mm ($n = 7$). Distal end of the each autozooid abutting next-distal kenozoid. Type of larva and reproductive mode unknown.

Remarks. I found this species attached to small pebbles and hydroid colonies, and in one case a colony was attached to plastic sheeting by the distal ends of the erect branches. Species in *Bockiella* have erect colonies with cylindrical branches, and a kenozooidal budding pattern (Silén, 1942; Cook, 1964; Gordon, 1986). Silén (1942) described this genus as having twice as many kenozooids as autozooids, but Cook (1964) found this proportion to vary within colonies and removed this feature from the generic diagnosis. Branches in *Bockiella* are composed of both autozooids and kenozooids, but lack axial kenozooids (Cook, 1964). *Bockiella* resembles *Elzerina* Lamouroux, 1816, but differs from the latter in having kenozooids that lack spines and are smaller than autozooids (Cook, 1964; Schwaha, 2021). *Bockiella* also resembles *Lobiancopora* Pergens, 1889, *Neobockiella* d'Hondt, 1983 and *Flustrellidra* Bassler, 1953, but differs from *Lobiancopora* in having kenozooids, from *Neobockiella* in lacking a pseudo-operculum at the orifice, and from *Flustrellidra* in lacking kenozooidal spines (spinozooids) (d'Hondt, 1983; Hayward, 1985; Schwaha, 2021).

Until now, *Bockiella* included only two species, *B. angusta* Silén, 1942, reported from Japan (Goto Islands, Kyushu), and *B. minima* Cook, 1964, reported from the China Sea. *Bockiella arcatumida* n. sp. resembles *B. angusta* in having branches with columns of alternating autozooids and kenozooids, but differs from the latter in the size and arrangement of the kenozooids. Autozooids in *B. arcatumida* n. sp. have a frontal surface mostly covered by the proximal kenozooids, leaving a small, narrow surface exposed, whereas those in *B. angusta* have approximately half of the proximal part covered by the kenozooids, leaving a narrow, triangular exposed frontal surface proximally. Although the number of kenozooids varies depending on the part or the breadth of the branch, the above differences between *B. arcatumida* n. sp. and *B. angusta* may depend
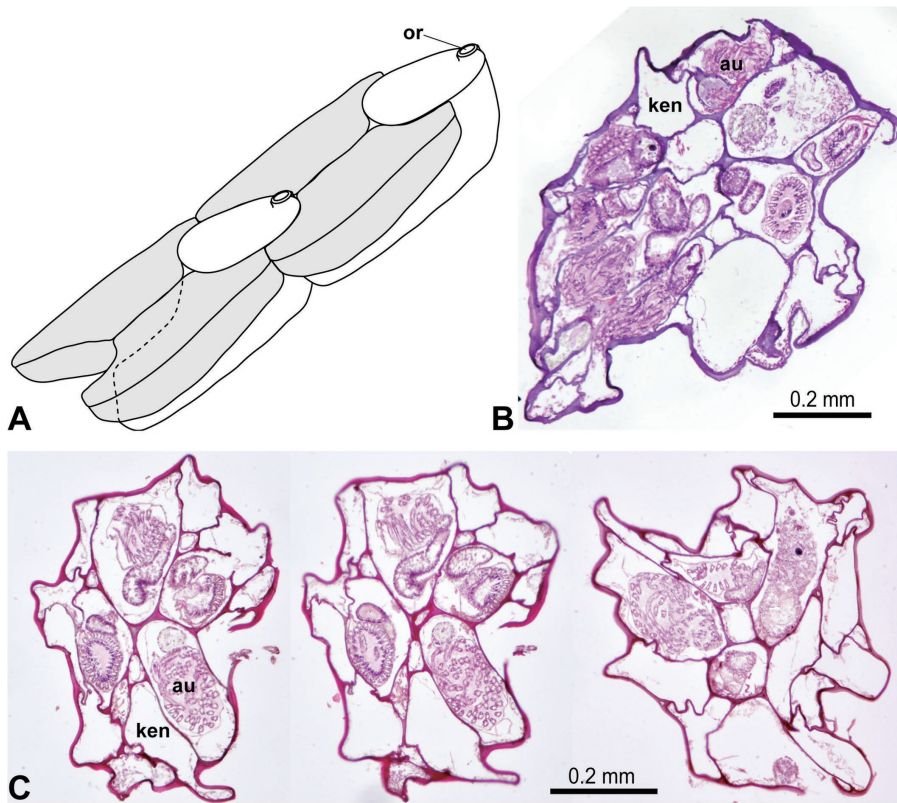
Base of colony and some branches where erect lobes reattach to substrate recumbent, encrusting, arachnidiform, with narrow, triangular autozooids and narrow stolon (Fig. 5A); orifice located at distal end of autozooid. Branches composed of both autozooids and kenozooids; axial kenozooids lacking (Fig. 5). Autozooids convex frontally, thin and transparent throughout colony; frontal surface of autozooids small and oval where exposed on branch surface (Fig. 5B, C), length 0.40–0.59 (0.50 ± 0.07) mm, width 0.26–0.34 (0.30 ± 0.03) mm ($n = 12$). Polypide easily seen through frontal wall; located middle to slightly distally in zooid. Orifice small, rounded, papilliform, with short peristome, pseudo-operculum lacking (Fig. 5C), length 0.10 – 0.13 (0.11 ± 0.01) mm, width 0.08–0.12 (0.10 ± 0.01) mm ($n = 5$). Tentacle number 22–24. Collar length 0.12–0.15 (0.13 ± 0.02) mm ($n = 3$). Alternating autozooids and kenozooids arranged in 4–8 longitudinal columns; kenozooid length equal to or slightly less than autozooid length (Figs. 5, 6). Autozooids arranged alter-

Fig. 6. *Bockiella arcatumida* n. sp. from off Sendai Bay. **(A)** Diagram of part of branch, showing general arrangement of autozooids (white) and kenozooids (gray). **(B, C)** Histological transverse sections of branches, stained with hematoxylin-eosin. **(B)** Branch showing eight autozooids and some kenozooids in transverse section (NSMT-Te1239). **(C)** Different parts of branch in transverse section, showing four autozooids and surrounding kenozooids, with small kenozooid at center (NSMT-Te1236). Abbreviations: au, autozooid; ken, kenozooid; or, orifice.

on the number of proximal kenozooids in each species, even in the broad, basal part of the colony; *B. arcatumida* n. sp. generally has a single kenozooid, whereas *B. angusta* has two. *Bockiella arcatumida* differs markedly from *B. minima*, in which the kenozooids not only fill the gaps between autozooids but also contribute to the structural strength of the colony by covering most of the frontal surface of the autozooids.

Distribution. *Bockiella arcatumida* n. sp. is known only from the type locality, off Sendai Bay, at 186–193 m depth. This is currently the northernmost record for this genus.

Family CLAVOPORIDAE Soule in Osburn & Soule, 1953
Genus *Metalcyonidium* d'Hondt, 1976
Metalcyonidium morum n. sp.
(Figs. 7–9)

Diagnosis. Colony small, consisting of autozooidal capitulum and peduncle of 40–50 short, cylindrical kenozooids. Capitulum comprising two parts, cylindrical upper capitulum with older autozooids, and conical lower capitulum with younger autozooids.

Material examined. *Holotype*: NSMT-Te1240, complete colony having upper and lower capitulum, with sand-grain substrate (the upper capitulum broke off from the lower

capitulum during transportation but was kept in the same bottle), collected by M. Hirose on 12 November 2015, southwest of Izu Peninsula (34°39.277′N, 138°43.913′E to 34°39.386′N, 138°43.562′E), 180–230 m depth, by dredge from RV *Tsukuba II*. Paratype: NSMT-Te1241, complete colony with lower capitulum only, with sand-grain substrate, collection data as for holotype.

Etymology. The specific name derives from the Latin *morum* (mulberry), referring to the oblong upper capitulum.

Description. Colony (Fig. 7) consisting of cylindrical or conical head (capitulum) and peduncle composed of short kenozooids. Colony small, height 13.6–17.9 (15.8 ± 3.0) mm (*n* = 2); attached to sand grain 1–2 mm in diameter. Capitulum elongate, length 3.9 mm (*n* = 1); consisting of upper and lower parts (Fig. 8). Upper capitulum (Fig. 8A) elongate, cylindrical, rounded at distal end, yellow or light-brownish orange; length 2.5 mm, width 1.6 mm (*n* = 1). Lower capitulum (Fig. 8B) shorter than upper capitulum, conical, flattened or slightly depressed in the center at distal end, white; length 1.3–2.0 (1.7 ± 0.5) mm (*n* = 2), diameter 1.2–1.7 (1.5 ± 0.4) mm (*n* = 2). Boundary between the upper and lower capitulum constricted, diameter at boundary 1.1 mm (*n* = 1). Autozooids densely clustered in capitulum, orifice terminal, facing outward. Autozooids in upper capitulum condensed and arranged perpendicular to the axis of capitulum, boundaries distinct, diameter 0.18–0.29 (0.24 ± 0.03) mm (*n* = 17); orifice small, papilliform. Autozooids in lower capitulum larger than in upper, diameter 0.29–0.41 (0.37 ± 0.05) mm (*n* = 5) boundaries and orifice indistinct. Peduncle (Fig. 9) long, white; length 9.7–15.9 (12.8 ± 4.4) mm (*n* = 2); consisting of 42–50 kenozooids (*n* = 2). Peduncular kenozooids mostly uniform in size, short, cylindrical; length 0.24–0.29 (0.27 ± 0.02) mm, diameter 0.28–0.32 (0.30 ± 0.01) mm (*n* = 13). Distal kenozooids at base of capitulum elongate in mature colony; length 0.46–0.92 (0.60 ± 0.18) mm (*n* = 5 distal kenozooids in single colony). Kenozooids near base of peduncle slightly shorter than others (Fig. 9B); length 0.14–0.15 (0.14 ± 0.01) mm, diameter 0.22–0.23 (0.23 ± 0.01) mm (*n* = 4). Basal kenozooids attaching to substrate broad; length 0.10 μm, diameter 0.30 mm (*n* = 1). Each kenozooid contains approximately four elongate, white myofibrils (Fig. 9A) equally long as the kenozooid; myofibril width 0.06–0.08 (0.07 ± 0.01) mm (*n* = 9). Type of larva and reproductive mode unknown.

Remarks. Clavoporidae contains five genera that are distinguished by the form and arrangement of kenozooids in the peduncle. *Ascorhiza*, *Clavopora*, and *Cephaloalcyonid-*

ium have multiple columns of kenozooids; *Pseudalcyonidium* has a single, long kenozooid occupying most of the peduncle; and *Metalcyonidium* has a uniserial column of uniform, cylindrical kenozooids. Until now, *Metalcyonidium* was monotypic, containing only *M. gautieri* d'Hondt, 1976, reported from the Bay of Biscay in the North Atlantic and western Mediterranean, at depths of 463–1250 m. *Metalcyonidium morum* n. sp. differs from *M. gautieri* in having a two-part capitulum, with the parts separated by a con-

striction, and much longer kenozooids contributing to the peduncle. In *M. morum* n. sp., the upper part of the capitulum is distinctly brownish, and the autozooids seem older than those in the lower part. The upper capitulum may contribute primarily to reproduction, whereas the lower part bears many newly budded autozooids and may contribute primarily to the growth of the colony. The upper capitulum easily breaks off at the constriction and detaches from the lower capitulum; the constriction seems to function to release the upper capitulum. Although the larval type is unknown for *Metalcyonidium*, the detachment and drifting away of the upper capitulum, with its mature reproductive zooids, may serve to increase the dispersibility of the species.

Distribution. *Metalcyonidium morum* n. sp. is currently known only from the type locality, southwest of the Izu Peninsula, at 180–230 m depth. This is the first record of this genus in the Pacific and the first record of this family in the NW Pacific.

Superfamily WALKERIOIDEA Hincks, 1880
Family TRITICELLIDAE Sars, 1873
Genus *Triticella* Dalyell, 1848
Triticella parvacrista n. sp.
(Figs. 10, 11)

Diagnosis. Colony consisting of network of creeping stolons that give rise to erect autozooids about 2 mm long, each having long kenozooidal pedicel and autozooidal dilatation. Stolon forms nodes where the autozooids are budded. Autozooidal dilatation spindle-shaped, transparent, smooth, glossy, length/width ratio about 4.0. Pedicel narrow, uniform in diameter. Paired frenacula traverse dorsal side of autozooidal dilatation, in proximal fourth of latter. Septate junction between dilatation and pedicel. Polypide with at least 16 tentacles.

Material examined. *Holotype*: NSMT-Te1242, colony on pereiopod of the isopod *Bathynomus doederleini*, collected 17 March 2013, off Owase, Kumano Sea, 200–300 m depth. *Paratype*: NSMT-Te1243, colony on pereon of the isopod *Bathynomus doederleini*, collection data as for holotype.

Etymology. The specific name derives from the Latin *parva* (tiny) and *crista* (plume), referring to the tiny, delicate colony on the body of the isopod.

Description. Colony tiny, compact, with scattered clusters of erect autozooids arising from nodal bases (Fig. 10); comprising at most 80 autozooids. Colony base consisting of network of creeping stolons (Fig. 11A), covering area on substrate 5–12 mm long (Fig. 10C). Stolon diameter uniform, approximately 0.01 mm ($n = 9$); slightly wider in nodal areas, approximately 0.02 mm ($n = 5$); stolons forming scattered knobby nodes, nodal knob width approximately 0.03 mm ($n = 5$) (Fig. 11A). Nodal base approximately 0.26 mm long, spaced at intervals of

Fig. 7. *Metalcyonidium morum* n. sp. from southwest of Izu Peninsula. **(A)** Living colony, holotype, with upper and lower capitulum (NSMT-Te1240). **(B)** Living colony, paratype, with only lower capitulum (NSMT-Te1241).
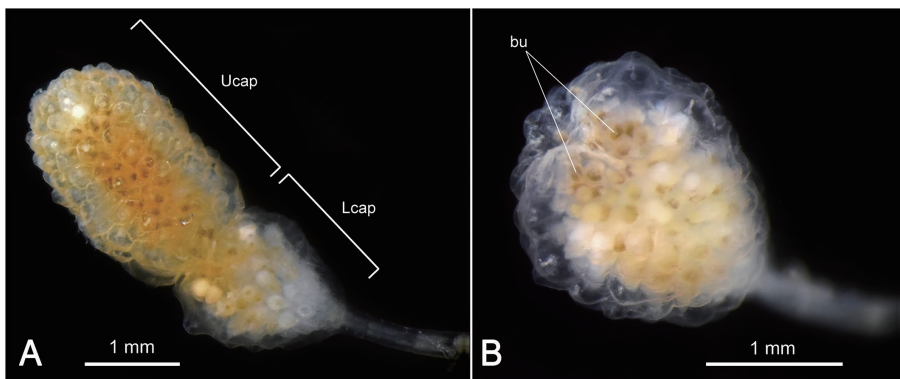

Fig. 8. *Metalcyonidium morum* n. sp. from southwest of Izu Peninsula. **(A)** Upper and lower capitulum, holotype colony (NSMT-Te1240). **(B)** Lower capitulum with small buds of autozooids inside, paratype colony (NSMT-Te1241). Abbreviations: bu, small bud; Lcap, lower capitulum; Ucap, upper capitulum.

0.80–1.50 (1.00 ± 0.20) mm (n = 9), each nodal base giving rise to 4–7 autozooids arising at interval of 0.03–0.06 (0.04 ± 0.01) mm (n = 4). Autozooids consisting of long, proximal tubular pedicel and autozooidal dilatation (Fig. 10A, B, D); length, including pedicel, 1.6–3.0 (2.1 ± 0.6) mm (n = 5). Autozooidal dilatation fusiform, slightly asymmetrical in lateral view, distally truncate (Fig. 11C, D); length 0.47–0.77

Fig. 9. *Metalcyonidium morum* n. sp. from southwest of Izu Peninsula. **(A)** Central part of peduncle, showing series of uniform kenozooids and white myofibrils (NSMT-Te1241). **(B)** Basal part of the peduncle in holotype (NSMT-Te1240). **(C)** Basal part of the peduncle in paratype (NSMT-Te1241). Abbreviation: myo, myofibril.

Fig. 10. *Triticella parvacrista* n. sp. from Kumano Sea. **(A)** Colony on pereon of isopod *Bathynomus doederleini,* showing four autozooids (NSMT-Te1243). **(B)** Colony on pereiopod of isopod *B. doederleini* (NSMT-Te1243). **(C)** Colony on pereiopod of isopod *B. doederleini* (NSMT-Te1242). **(D)** Autozooids, dense group erect from substrate (NSMT-Te1242).

(0.64 ± 0.08) mm, width 0.12–0.21 (0.17 ± 0.03) mm, length/width ratio 2.8–4.9 (3.9 ± 0.5) (n = 18). Pedicel narrow, length 0.86–2.23 (1.51 ± 0.47) mm (n = 20), diameter uniform, 0.02–0.04 (0.03 ± 0.01) mm (n = 9). Cystid transparent, smooth, glossy (Fig. 11C), wall constricted from pedicel by narrow neck (Fig. 11B) consisting of joint with septum. Paired frenacula (thickened chitinous ribs in wall of autozooidal dilatation) visible as bright lines under transmitted light (Fig. 11C, D), traversing dorsal side of autozooidal dilatation in proximal fourth of dilatation, extending obliquely distally on both sides, tapering before reaching ventral side. Polypide white, occupying entirety of dilatation (Fig. 11C, D); length 0.58–0.76 (0.67 ± 0.12) mm (n = 2). Stomach oblong; length 0.08–0.11 (0.09 ± 0.02) mm, width 0.03–0.07 (0.05 ± 0.03) mm (n = 2). Retracted lophophore approximately 0.40 mm long; tentacles at least 16 in number, diameter approximately 0.01 mm. No intertentacular organ or other reproductive organs observed.

Remarks. Twelve species are currently recognized in *Triticella*, reported from Europe, the northeastern and western Atlantic, New Zealand, and the North Pacific (d'Hondt, 1983; Hayward, 1985; Grischenko and Chernyshev, 2018). Previously known hosts for this genus include crustaceans, mollusks, hydroids, abyssal sipunculids, and bryozoans (d'Hondt, 1983; Grischenko and Chernyshev, 2018); *Triticella* is not strictly host specific, as some species have been reported from multiple host species. The short autozooids with a long pedicel in *Triticella parvacrista* n. sp. resemble those of *Triticella gracilis* d'Hondt and Hayward, 1981 from the northeastern Atlantic, but the autozooidal dilatation (length 0.47–0.77 mm) in *T. parvacrista* is markedly longer than that in *T. gracilis* (length 0.35–0.50 mm). The total autozooid length (dilatation + pedicel) in *T. parvacrista* n. sp. (1.33–2.99 mm) overlaps considerably with that in *T. maiorovae* Grischenko and Chernyshev, 2018 from the Sea of Okahotsk (2.02–3.18 mm), but the former differs in having the transparent cystid (brownish in *T. maiorovae*), and in having shorter dilatation length (0.47–0.77 mm; 0.69–1.12 mm in *T. maiorovae*). The host of *T. parvacrista* n. sp. is the deep-sea isopod *Bathynomus doederleini*, whereas *T. maiorovae* and *T. gracilis* occur on the deep-sea sipunculid worm *Golfingia muricaudata* (Southern) (Grischenko and Chernyshev, 2018) or other deep-sea sipunculids (d'Hondt and Hayward,
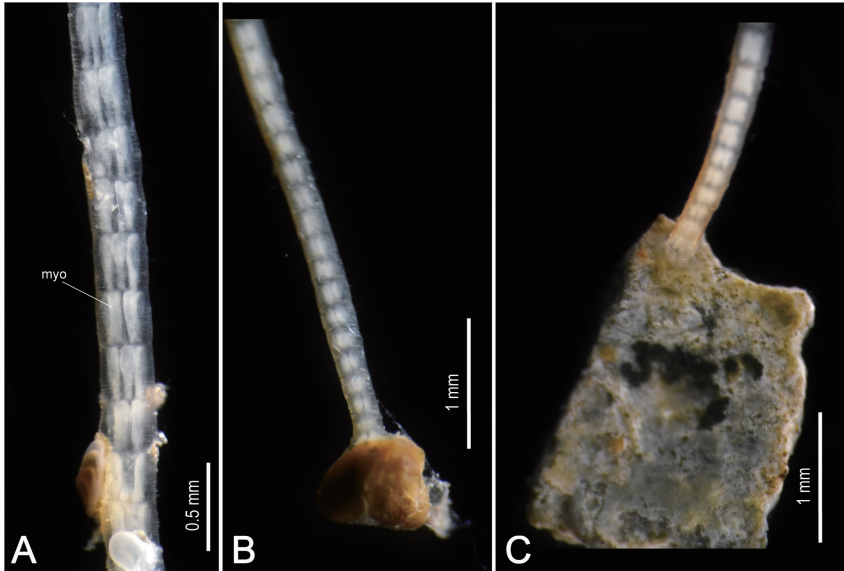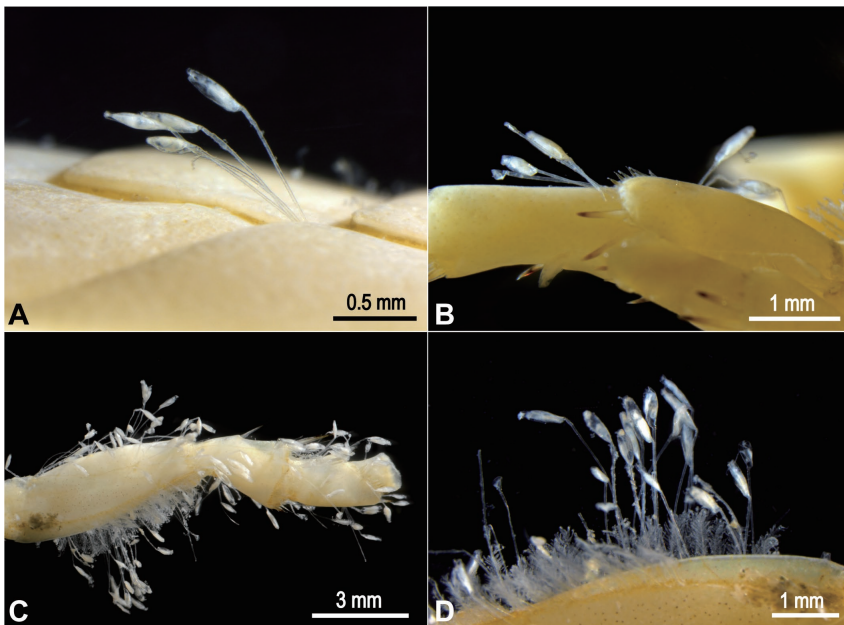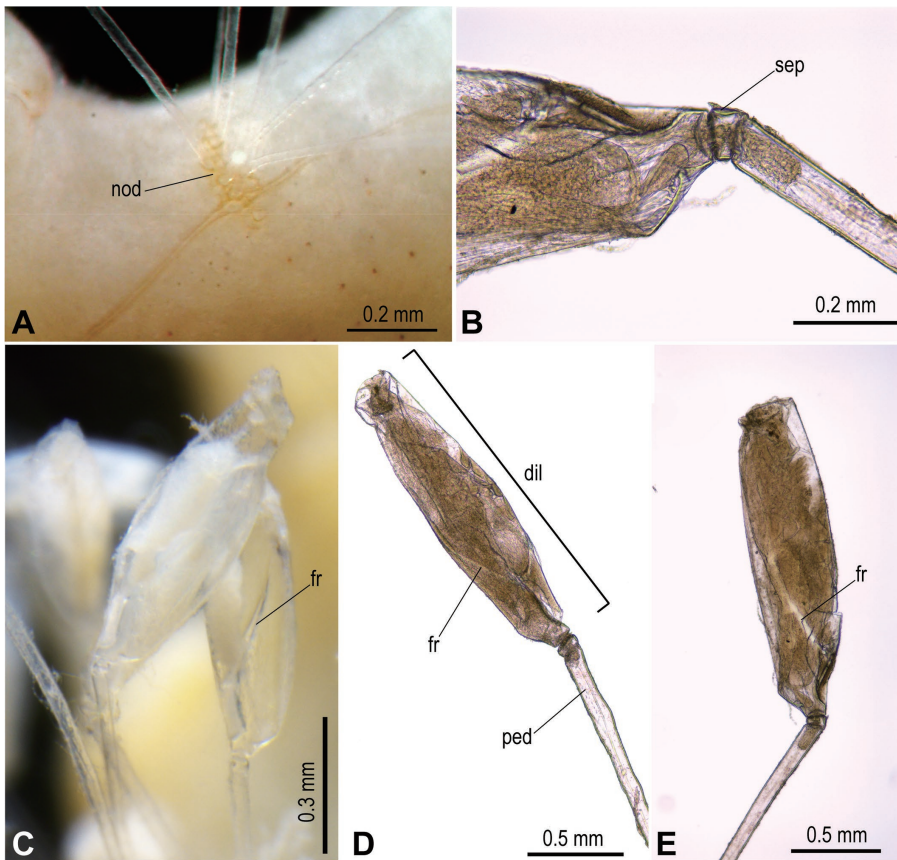
Fig. 11. *Triticella parvacrista* n. sp. from Kumano Sea. **(A)** Creeping stolon and nodal area (NSMT-Te1242). **(B)** Septate junction between dilatation and pedicel (NSMT-Te1243). **(C)** Frenaculum traversing dorsal side of autozooidal dilatation (NSMT-Te1242). **(D)** Dorsal (left) and **(E)** lateral (right) view of autozooidal dilatation showing white line of frenaculum (NSMT-Te1243). Abbreviations: dil, dilatation; fr, frenaculum; nod, nodal area; ped, pedicel; sep, septate junction.

1981). *Triticella parvacrista* n. sp. resembles *Triticella pedicellata* (Alder, 1857) from Europe in the proportions of the zooids, but differs from the latter in having a septate junction between the autozooidal dilatation and the pedicel.

Triticella parvacrista n. sp. resembles the European species *Triticella flava* Dalyell, 1848 in having autozooids up to 3 mm long, in having a frenaculum in the autozooidal dilatation and a septate junction between the dilatation and pedicel, and in having a crustacean host, but differs from the latter in having smaller autozooidal dilatation and slightly fewer tentacles (17–24 in *T. flava*).

Distribution. *Triticella parvacrista* n. sp. is currently known only from the type locality.

Triticella cunabula n. sp.
(Figs. 12, 13)

Diagnosis. Colony consisting of network of creeping stolons and dense cluster of erect autozooids about 3 mm long, with long kenozooidal pedicel and long autozooidal dilatation. Basal nodal areas indistinct. Autozooidal dilatation elongate, fusiform, transparent. Pedicel diameter slightly greater distally than proximally. No frenaculum or septate junction between dilatation and pedicel. Polypide with 16–23 tentacles.

Material examined. Holotype: NSMT-Te1244, colony on oviger of the pycnogonid *Ascorhynchus japonicum* Ives, collected by T. Moritaki, 28 February 2015, off Mikisaki, Owase, Kumano Sea, 200–300 m depth.

Etymology. The specific name derives from the Latin *cunabula* (cradle), referring to the fluffy colony on the pycnogonid oviger.

Description. Colony encrusting, consisting of a network of creeping stolons (Fig. 12D) covering area of substrate approximately 4.5 mm long and containing 80–100 autozooids. Stolon diameter uniform, 0.03–0.06 (0.04 ± 0.01) mm (*n* = 10); slightly broader in nodal areas, 0.06–0.10 (0.08 ± 0.02) mm (*n* = 5). Basal nodes indistinct, approximately 0.55 mm long (Fig. 12D). Autozooids arising in dense tufts (Fig. 12A, C) from nodal bases that are closely spaced at intervals of 0.55–0.82 (0.72 ± 0.10) mm (*n* = 5), each node with 4–10 autozooids. Within nodes, autozooids arising at interval of 0.08–0.19 (0.14 ± 0.04) mm (*n* = 8). Autozooids smooth, transparent, consisting of autozooidal dilatation and long, tubular pedicel; total length 2.33–4.28 (3.19 ± 0.68) mm (*n* = 11). Autozooidal dilatation elongate, fusiform, nearly symmetrical in lateral view, distally truncate (Fig. 13A, B); length 1.19–2.40 (1.82 ± 0.32) mm, width 0.17–0.30 (0.23 ± 0.03) mm, length/width ratio 5.8–11.8 (8.2 ± 1.6) (*n* = 24). Pedicel length 2.03–2.64 (2.29 ± 0.28) mm (*n* = 4), diameter approximately 0.05 mm (*n* = 13); pedicel slightly wider near junction with dilatation (Fig. 13C). Septum between the autozooidal dilatation and pedicel indistinct; dilatation bent at angle to pedicel; boundary between the dilatation and pedicel wrinkled on surface (Fig. 13D). Frenaculum absent. Polypide white, small relative to size of dilatation, occupying only distal part (Fig. 13B); length 0.62–0.83 (0.73 ± 0.15) mm (*n* = 2). Stomach short, oval, approximately 0.34 mm long by 0.14 mm wide. Lophophore length 0.57–0.85 (0.72 ± 0.10) mm (*n* = 10); tentacles 16–23 in number, approximately 0.01 mm in diameter (Fig. 12B). No intertentacular organ or other reproductive organs observed.

Remarks. A characteristic feature of *Triticella cunabula* n. sp. is the elongate autozooidal dilatation (average length/width ratio, 8.2), in which this species resembles *T. fusiformis* d'Hondt and Hayward, 1981 (average length/width ratio, 8.67) described from the north Atlantic. However, the pedicel in *T. cunabula* n. sp. (length 2.29 mm) is markedly longer than that in *T. fusiformis* (0.4 mm), and the length ratio of the autozooidal dilatation to the pedicel is thus markedly smaller (average of 0.8 in *T. cunabula* n. sp.; 3.0 in *T.*
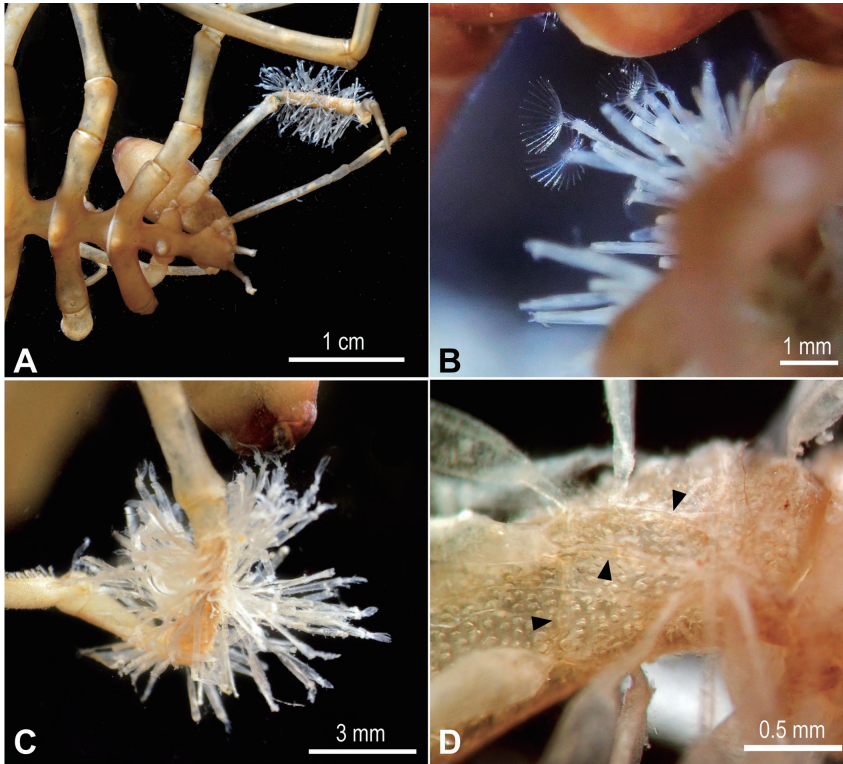
Fig. 12. *Triticella cunabula* n. sp. from Kumano Sea. **(A)** Colony on oviger of pycnogonid *Ascorhynchus japonicum* (NSMT-Te1244). **(B)** Living colony with extended lophophores (photograph by T. Moritaki) (NSMT-Te1244). **(C)** Colony on oviger of pycnogonid *A. japonicum*, showing dense tuft of autozooids (NSMT-Te1244). **(D)** Basal part of colony, showing creeping stolons (arrowheads) (NSMT-Te1244).
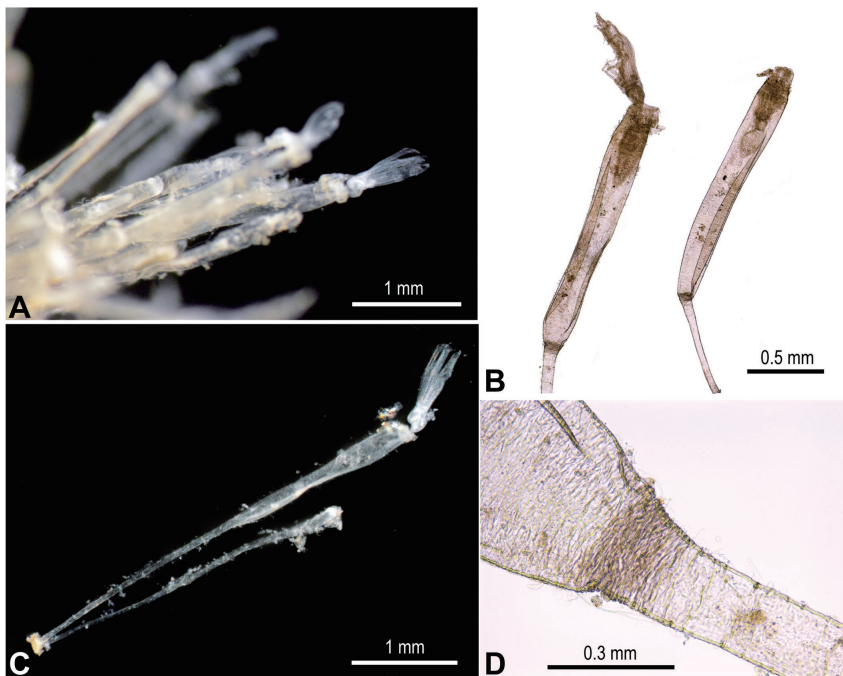

Fig. 13. *Triticella cunabula* n. sp. from Kumano Sea. **(A)** Fixed specimens showing autozooids, some with partly extended lophophore (NSMT-Te1244). **(B)** Autozooidal dilatations, showing polypide occupying only distal part (NSMT-Te1244). **(C)** Autozooids, showing long pedicel (NSMT-Te1244). **(D)** Zone between dilatation and pedicel, lacking septate junction; note wrinkled surface of zone (NSMT-Te1244).

fusiformis). The total length of the autozooids in *T. cunabula* n. sp. (dilatation + pedicel, 2.33–4.28 mm) resembles that in *T. maiorovae* (2.02–3.18 mm), but *T. cunabula* n. sp. differs from the latter in having a transparent cystid and longer autozooidal dilatation (1.19–2.40 mm; 0.69–1.12 mm in *T. maiorovae*). The host of *T. cunabula* n. sp. (the pycnogonid *Ascorhynchus japonicum*) is also different from that of *T. maiorovae* (the deep-seal sipunculid worm *Golfingia muricaudata*). *Triticella cunabula* n. sp. resembles *T. flava* in zooid length, but differs from the latter in lacking both a frenaculum and a septate junction between the dilatation and pedicel.

Distribution. *Triticella cunabula* n. sp. is currently known only from the type locality.

DISCUSSION

Three of the five species described in this study (*Alcyonidium clavum* n. sp., *Triticella parvacrista* n. sp., and *Triticella cunabula* n. sp.) were found attached to the surface of other benthic organisms, which are important substrates for sessile bryozoans on sandy-mud bottoms. Epibiotic species are difficult to find unless they are intentionally searched for on the surface of other organisms. It is possible that specimens of these epibiotic bryozoans exist on specimens of potential host organisms collected in past surveys and deposited in museums. One of the five species described in this study (*Metalcyonidium morum* n. sp.) forms small colonies that live erect on sandy-mud bottoms. This is one of the least-studied habitats in bryozoan research, and the diversity of such sediment-dwelling species, including cheilostomes, has been inadequately investigated.

The dispersibility of larvae should be taken into account when considering the local diversity of bryozoan species in Japanese waters. There are many cases in which nominal bryozoan species have widely disjunct distributions between geographically distant areas, often in different seas (Hayward, 1981). This is largely because bryozoan taxonomists previously tended to lump morphologically similar species, found in different seas, into a single species; even in regions distant from Europe, such as Japanese waters, species were often identified with the most similar species previously described from Europe (e.g.,

Alcyonidium mamillatum). Considering the dispersibility of bryozoan larvae, however, the ranges of bryozoan species may be narrower than previously expected, and many of the disjunct records possibly involve two or more different species.

Bryozoan larvae vary in dispersibility depending on the larval type. Two basic types of larvae occur in both Ctenostomatida and Cheilostomatida (Zimmer and Woollacott, 1977): planktotrophic larvae that actively feed and spend a relatively long time in the water column before metamorphosis, and coronate larvae, which are brooded, non-feeding, and spend a short time in the water column before metamorphosis. Hence, the larval type and its dispersibility may be related to the geographic speciation of bryozoan species. Both types of larvae have been reported in the genus *Alcyonidium* (Ryland and Porter, 2012), and thus the distribution and the diversity of species in this genus have been reconsidered taxonomically and phylogenetically in some studies (Thorpe et al., 1978; Porter et al., 2002). In the genus *Triticella*, coronate larvae have been reported from *Triticella flava* (reported as *T. koreni*) (Ström, 1969). If this larval type is common to other *Triticella* species, members of this genus may show low dispersibility, resulting in low gene flow between populations and an increased likelihood of geographical speciation. Thus, increased knowledge of larval types will be relevant to understanding diversity and distributional ranges in bryozoan species previously regarded as having a "cosmopolitan" distribution. Furthermore, molecular data are necessary to verify new ctenostome species erected based on morphology, especially for genera like *Alcyonidium* and *Triticella*, where the morphologies of the colony and zooids are superficially similar among many species.

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COMPETING INTERESTS

The author declares no competing interests.

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