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Freshwater Bryozoa of Okinawa, Japan, with descriptions of *Rumarcanella* gen. nov. (Phylactolaemata: Plumatellidae) and two new species

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Abstract

We identified nine species of phylactolaemate bryozoans collected from ponds and dams on Okinawa Island, Japan. This is the first report on freshwater bryozoans from Okinawa and includes the first record of *Plumatella javanica* from Japan. Phylactolaemate species were identified on the basis of colony and statoblast morphology and are illustrated by light microscopy and scanning electron microscopy (SEM). We detected two new plumatellid species that, like *Plumatella minuta* and *Plumatella vorstmani*, have a transparent, weakly chitinized colony and hypertubercles on the floatoblast fenestra. A previous molecular study showed these four species to form a clade separate from *Plumatella* and *Hyalinella*. We here establish the new genus *Rumarcanella* to accommodate these species and describe *Rumarcanella gusuku* **n. sp.** and *R. yanbaruensis* **n. sp.** We discuss the dispersal of bryozoans to and from Japan by birds carrying statoblasts and provide a key to the Phylactolaemata of Japan.

Key words: Freshwater Bryozoa, new species, Okinawa, Phylactolaemata, Plumatellidae, *Rumarcanella gusuku*, *Rumarcanella yanbaruensis*, *Rumarcanella minuta*, *Rumarcanella vorstmani*

Introduction

The bryozoan class Phylactolaemata comprises only species inhabiting fresh water. Plumatellidae, the largest phylactolaemate family, contains about 55 species worldwide. To date, 24 plumatellid species in six genera have been reported from southern and southeastern Asia, 10 species in two genera from Europe, 15 species in three genera from North America, and 11 species in three genera from Japan. The most speciose plumatellid genus is *Plumatella*, with about 40 species. Their colonies are reportedly well chitinized and partially adherent, show dichotomous antler-like branching or form a fused mass, and produce both sessoblasts and floatoblasts as dormant bodies. *Hyalinella*, a genus closely related to *Plumatella*, currently contains only two species (Wood *et al.* 2006). Their colonies are thick and transparent, with less profuse branching than in *Plumatella*; individual zooids are indistinct, usually arranged linearly, and lack interzooidal septa; and colonies produce only floatoblasts. Species of the East-Asian genus *Gelatinella* have characters intermediate between *Hyalinella* and *Plumatella*; colonies are thick and gelatinous rather than heavily chitinized and produce only sessoblasts.

In fact, characters distinguishing *Hyalinella* from *Plumatella* are not clear-cut, a problem referred to by various authors as the "*Hyalinella* problem" (Toriumi 1956b, 1972; Bushnell 1965b, c; Lacourt 1968, 1975; Wiebach 1973; Ricciardi & Wood 1992; Mukai 1999). This problem arises partly because the diagnosis of *Hyalinella* is based on the transparency and thickness of the colony wall (ectocyst), but the condition of the ectocyst depends to some extent on environmental factors; for example, it tends to be heavier in sheltered waters with a heavy suspension of sediment (Wood & Okamura 2005). Several species originally assigned to *Hyalinella* have been transferred to *Plumatella* (Lacourt 1968; Wiebach 1973; Ricciardi & Wood 1992; Wood *et al.* 2006). Discussions of the relationship between *Plumatella* and *Hyalinella* (Lacourt 1968; Wiebach 1973) have focused mainly on characters of the ectocyst, and the generic placement of some species has remained unstable.

In 2005–2007, the first author collected phylactolaemate bryozoans on Okinawa Island (hereafter referred to as 'Okinawa') in the Japanese subtropics. This island had been poorly studied; despite a long history of phylactolae-

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mate studies in Japan, only one phylactolaemate species had been reported (Iseto 2003). Our collections from Okinawa encompassed nine species, two of which proved to be of particular significance. Hirose *et al.* (2008) found in a molecular phylogenetic study that these two apparently undescribed plumatellid species from Okinawa grouped with *Plumatella minuta* and *Plumatella vorstmani* (both of which are among the "*Hyalinella* problem" species) in a sister clade to one containing *Hyalinella*, *Gelatinella*, and *Plumatella*, suggesting a clear-cut genus-level separation in Plumatellidae. The two main clades were highly supported with 100% and 87–99% bootstrap support in trees resulting from four methods of phylogenetic analysis (maximum parsimony, neighbor joining, maximum likelihood, and Bayesian analysis).

In this paper, we 1) report on the nine phylactolaemate species detected on Okinawa based on the collections made from 2005–2007, and 2) erect a new genus, *Rumarcanella*, for the clade that includes *Plumatella minuta*, *Plumatella vorstmani*, and the two new species (herein described as *Rumarcanella gusuku* and *R. yanbaruensis*) detected on Okinawa.

Material and methods

Study area. Okinawa Island, located in the center of the Ryukyu Archipelago, southwestern Japan, is 1207 km^2 in area and 108 km long, with a shore length of about 560 km (Nishida *et al*. 2003; Okinawa Meteorological Observatory 2005–2008). The southern part of the island is low and flat, whereas the northern part (called Yanbaru) is mountainous, with a maximum altitude of about 500 m. Okinawa is subtropical in climate, with an average annual temperature of 23º C (range 16–30º C); the warmest month is July or August and the coldest is January or February. The average annual rainfall is about 2300 mm. There are more than 200 rivers on Okinawa Island, but no large rivers in the mountainous Yanbaru region. Dams are the only means of water retention in the summer, when they are fed by hard typhoon rains. From late summer to early winter, water from the dams is used for irrigation and for cities, and water levels decrease during the autumn and winter.

Collection and treatment of specimens. Eleven localities on Okinawa Island (one lake, one river, one small stream, four ponds and five dam reservoirs) were surveyed; bryozoan colonies and/or statoblasts were found at seven localities (three ponds and four dams) (Table 1; Fig. 1). At Benoki Dam and Fukuji Dam, the patrol vessel of the dam control branch office was used for access to shore localities. Bryozoan colonies were collected with their substrata, including stones, aquatic plants, and sunken wood. Floatoblasts were collected by examining floating debris that had accumulated downwind or downstream at each collecting locality. Specimens were fixed in 80% ethanol or 10% formalin.

Some statoblasts were collected in ambient fresh water and were allowed to germinate by keeping them in the laboratory in light at 25º C for five days. Ancestrulae were removed to a slide glass or plastic plate for rearing in a freshwater tank containing goldfish to remove algae, as described by Wood (1996).

For scanning electron microscopy (SEM), statoblasts were dehydrated through an ethanol series and with HMDS (hexamethyldisilazane), attached to stubs with double-sided tape, coated with Pd-Pt in a Hitachi E-1030 sputter-coater, and observed with a Hitachi S-2380N SEM at 15 kV accelerating voltage.

Measurements of statoblasts were taken from SEM images with ImageJ 1.37v software (Image Processing and Analysis in Java, Wayne Rasband, National Institutes of Health, USA; http://rsb.info.nih.gov/ij/). In general, we made measurements on free statoblasts collected from the wild, and these likely originated from more than one colony; the exception was *Plumatella javanica*, for which we measured floatoblasts from a single colony. Hirose et al. (in press) demonstrated that measurements taken from dried statoblasts coated for SEM do not differ significantly from those taken from wet statoblasts using an ocular micrometer. Measurements in the text are presented in micrometers as the range, followed by the mean ± standard deviation (SD) and sample size in parentheses.

Systematic account

Class Phylactolaemata Allman, 1856

Order Plumatellida Allman, 1856

Family Plumatellidae Allman, 1856

Genus *Plumatella* Lamarck, 1816

Type species. *Tubipora repens* Linnaeus, 1758.

Diagnosis. Colony composed of branching tubules, well chitinized; ectocyst varies in thickness and form depending on the species, the age of the colony and the environment. Colonies produce both floatoblasts and sessoblasts; a type of floatoblast called a leptoblast that lacks the internal capsule has been reported only from *Plumatella casmiana*.

TABLE 1. Surveyed localities, main substrata, and the number of bryozoan species found.

Locality		Substratum	No. of bryozoan species
Dam			
1 Benoki Dam	26º47’ 16.80”N 128º15’ 39.50”E	wood and stone	4
2 Fukuji Dam	6º38’ 39.70”N 128º10’ 55.10”E	wood and stone	5
3 Kanna Dam	26º29’ 31.80”N 127º56’ 41.40”E	aquatic plants	2
4 Kurashiki Dam	26º23’ 29.60”N 127º48’ 03.60”E	statoblasts only	2
5 Haebaru Dam	26º12’ 54.80”N 127º44’ 30.30”E	-	not found
Lake			
6. Lake Man, Naha City	26º11’38.20”N 127º41’23.10”E	-	not found
Pond			
7. Ryutan-ike, Naha City	26º13’ 07.10”N 127º43’ 05.90”E	statoblasts only	2
8. Pond in Okinawa City	26º22’ 39.80”N 127º48’ 25.10”E	statoblasts only	1
9. Pond in Uruma City	26º25’ 21.60”N 127º47’ 51.60”E	statoblasts only	2
River or stream			
10. O-ura River, Nago City	26º33’ 54.70”N 127º02’ 22.40”E	-	not found
11 Small stream, Ginowan City	26º16’ 48.00”N 127º44’ 43.40”E	-	not found

Plumatella casmiana Oka, 1907
(Figures 2A, B)

Plumatella casmiana Oka, 1907b: 121, fig. 3; Rogick 1941: 211, pl. 1(1–4), pl. 2(5, 6); 1943: 265, pl. 1(1–8); Toriumi 1955b: 76, text-figs 1–3; Mukai 1999: 56, figs 3D, 4D, 4E, 6E; Wood & Okamura 2005: 46, 78, figs 16–18, 45–46; Wood *et al*. 2006: 12, figs 11–13.

Plumatella repens var. *annulata* Hozawa & Toriumi, 1940: 428, fig. 3; 1941: 236, fig. 3, pl. 14(2); Rogick & Brown 1942: 131, pl. 2(10, 14–16, 26), pl. 3(30).

Plumatella repens var. *casmiana*: Toriumi 1941a: 203, fig. 7, pl. 12(4–5), pl. 13(15); 1942: 209, figs 1–3.

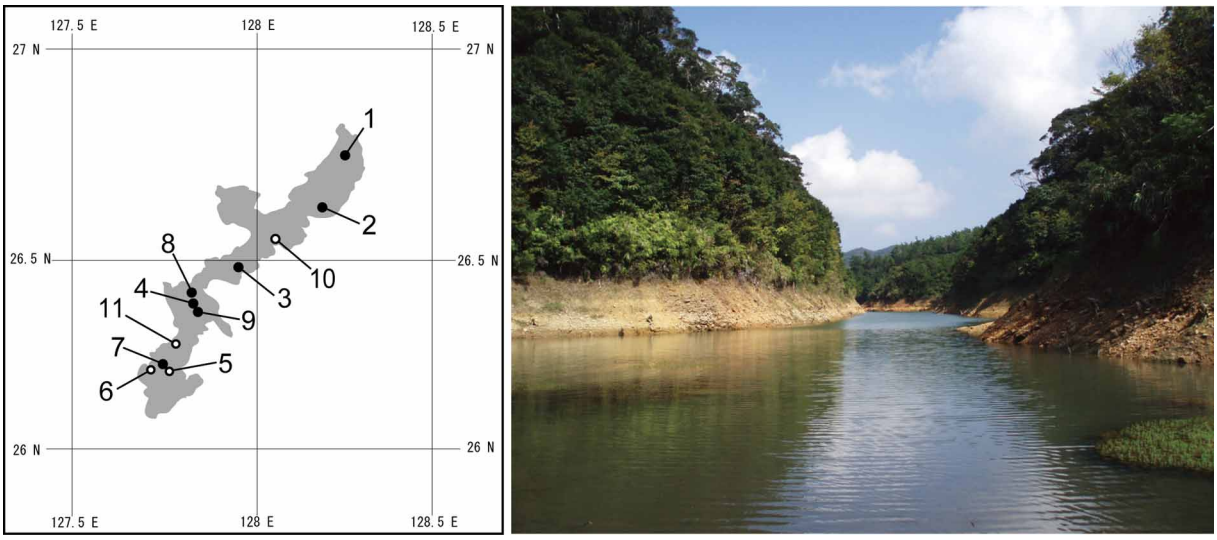

FIGURE 1. (Left) Map of Okinawa showing phylactolaemate collecting localities; (right) photograph of the collecting locality at Benoki Dam. The numbers denoting the localities pertain to Table 1. Filled circles indicate localities where bryozoans were found, open circles where they were not found.

Material examined. Several floatoblasts and leptoblasts from a pond in the city of Okinawa; small colonies with sessoblasts from Kanna Dam, village of Ginoza.

Description. Colony variable; tubular, light brown, almost entirely attached to substratum; compact colonies sometimes assuming a honeycomb-like shape; tentacle number about 21–25 (Hozawa & Toriumi 1940; Bushnell & Wood 1971). Two types of free floatoblasts, the normal plumatellid floatoblast (capsuled floatoblast) and another lacking the internal capsule (leptoblast). In sampled Okinawan population, the capsuled floatoblast is oval, 334–369 (348±11) μm long by 192–212 (203±7) μm wide (n=10), with length/width ratio of about 1.7, symmetrical in lateral view; surface of fenestra with weak tubercles or sometimes almost smooth (Fig. 2A). Leptoblast elliptical, longer than capsuled floatoblast, 369–390 (378±11) μm long by 164–197 (179±17) μm wide (n=3), with length/width ratio of about 2.1. Sessoblast 285–312 (296±11) μm long by 206–232 (224±12) μm wide (n=4), with length/width ratio of about 1.3; annulus wide and smooth, the surface of the capsule smooth (Fig. 2B).

Distribution. Distributed worldwide (Bushnell 1973; Wood *et al*. 2006); recently reported from Thailand (Wood *et al*. 2006); widely distributed in Japan, from Okinawa to northern Hokkaido.

Remarks. Rogick (1941, 1943) showed detailed drawings of the colony and statoblasts of *P. casmiana* from North America.

Plumatella emarginata Allman, 1844

(Figure 2C)

Plumatella emarginata Allman, 1844a: 330; Allman 1856: 104, pl. 7(5–10); Braem 1890: 9, pl. 1(9, 12, 14); Annandale 1911: 220, pl. 3(2), pl. 4(1, 1a); Toriumi 1954: 287, pl. 8(1–47); 1971: 127, pl. 12(3); Mukai 1999: 51, figs 2A, 3C, 5A, 7A (part); Wood & Okamura 2005: 51, 80, figs 21, 47, 48.

Plumatella repens var. *emarginata*: Rogick 1935a: 246, 255, pl. 41(6); 1940, 198, pls. 1(1–3), 3(11, 12). Hozawa & Toriumi 1940: 427, fig. 2, Pl. 1(7); 1941: 234, fig. 2, pl. 14(7). Toriumi 1941a: 198, fig. 3, pl. 12(6, 9); 1941b: 416, fig. 3; 1942: 208, figs. 3–6.

Material examined. Floatoblast from pond in city of Uruma; floatoblasts from Ryutan-ike pond next to the castle, city of Naha; floatoblasts and colony with floatoblasts and sessoblasts from Fukuji Dam, village of Higashi; floatoblasts and colony with floatoblasts and sessoblasts from Benoki Dam, village of Kunigami.

Description. Observed colonies tubular, branching, shiny dark brown or well encrusted. Tentacle number 20 to 50. Floatoblasts in Okinawan populations elliptical, elongate, 329–527 (427±67) μm long by 211–248 (226±11) μm wide (n=10), with length/width ratio of about 1.9 (Fig. 2C); fenestra of ventral valve almost circular, more than

four times diameter of fenestra of dorsal valve; both ventral and dorsal fenestrae covered with tubercles; annuli textured with coarse pavement; floatoblast valves asymmetrical in lateral view, the ventral valve convex, the dorsal almost flat. Sessoblasts with tuberculate surface and smooth annulus, 437–466 (451±12) μm long by 273–301 (282±13) μm wide (n=4).

Distribution. Broadly distributed worldwide; distributed in Japan from Okinawa to Hokkaido.

Remarks. Floatoblasts of *P. emarginata* from Okinawa are larger than in other regions (average length 427 μm; SD 67.0) and sometimes have strongly elevated tubercles. Colonies and floatoblasts appear to be variable in form, and the nominal species may include several synonymous species. Although we did not observe sessoblasts of this species from Okinawa, we identified our material as *P. emarginata* on the basis of the floatoblast and colony morphology.

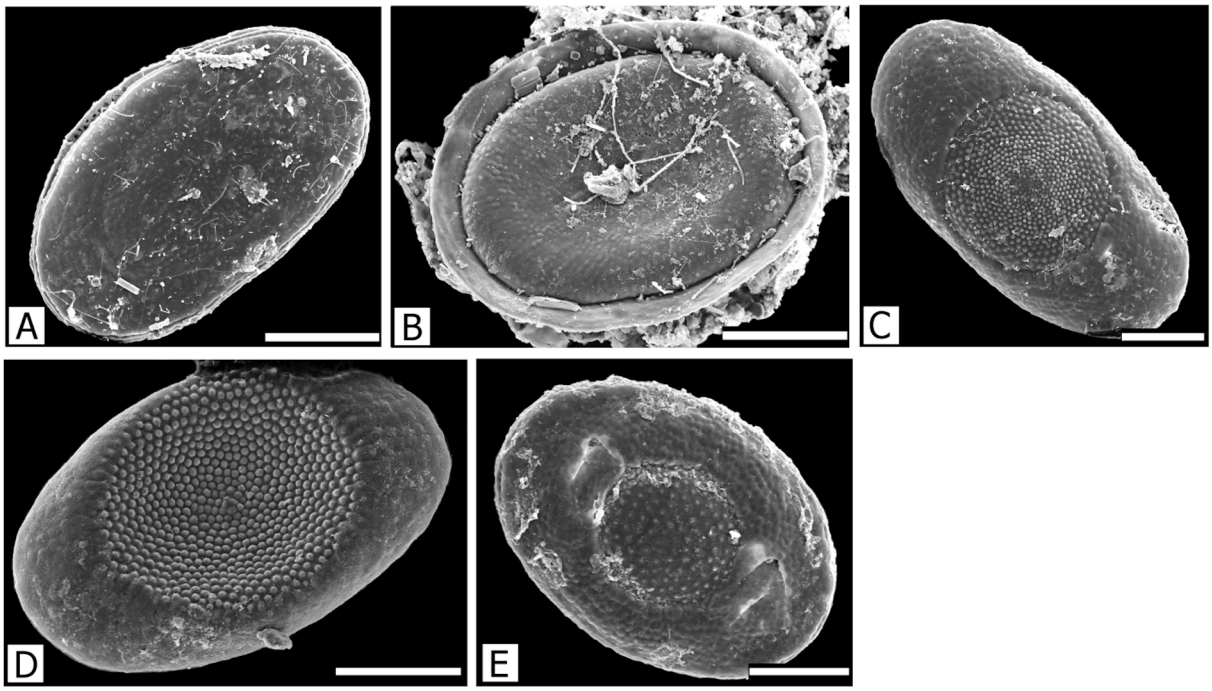

FIGURE 2. SEM micrographs of statoblasts from three phylactolaemate species from Okinawa. **A,** *Plumatella casmiana* Oka, 1907, floatoblast, dorsal view. **B,** *Plumatella casmiana*, sessoblast. **C,** *Plumatella emarginata* Allman, 1844, floatoblast, ventral view. **D,** *Plumatella mukaii* Wood, 2001, floatoblast, ventral view. **E,** *Plumatella repens* (Linnaeus, 1758), floatoblast, dorsal view. Scale bars: 100 μm.

Plumatella javanica Kraepelin, 1906

(Figure 3)

Plumatella javanica Kraepelin, 1906: 143, figs 1–3; Annandale 1910: 42, 50; 1911: 221; Toriumi 1952a: 267; Wiebach 1964: 12, figs 4–8, pl. 1(4,) pl. 2(5–7), pl. 3(8–12), pl. 4(13); 1967: 77, pls 1, 2(1–8); 1970, 356, pl. 1(4a, 4b, 5a, 5b); Lacourt 1968: 72, pl. 15(j); Rao 1973: 529; 1976, 339, fig. 4H; Rao *et al*. 1985: 261; Smith & Wood 1995: 362, fig. 1; Wood & Wood 2000, 423, fig. 1; Wood *et al*. 2006: 14, figs 20–21, 36.

Plumatella emarginata var. *javanica*: Loppens 1908: 162.

Material examined. Mature colony with floatoblasts from Fukuji Dam, village of Higashi.

Description. Observed colony light brown or reddish brown, its surface encrusted (Fig. 3A); almost entirely recumbent, with pronounced keel, ends of branches often rising from substratum (Fig. 3B). Tentacle number about 45. Floatoblast elliptical in our specimen, large, about 340–410 (366±38) μm long by 180–236 (215±31) μm wide (n=3) (Fig. 3C); length/width ratio about 1.8. Fenestrae of floatoblast large; in SEM view, surface entirely covered with minute, rounded tubercles that are rounded-hexagonal in outline, with 5–8 (average 6) small, irregular pores in the angles (Fig. 3D). Ventral fenestra 200–246 (225±23) μm long by 182–211 (194±15) μm wide; dorsal fenestra about 150–180 (174±10) μm long by 130–160 (139±16) μm wide (n=3). Floatoblast valves asymmetrical in lateral

and transverse views, the ventral valve strongly convex and dorsal valve almost flat. Suture line of both valves with a simple ridge. Sessoblast also with tuberculate surface (Wood *et al*. 2006).

Distribution. Distributed mainly in tropical regions (Bushnell 1973), including Southeast Asia (Lacourt 1968; Wood *et al*. 2006), central Africa (Wiebach 1964), and the Amazon River in South America (Wiebach 1967, 1970). This is the first record of *P. javanica* from Japan, where it occurs on Okinawa and the Pacific side of southern Honshu (Ibaraki, Tokyo, and Kochi Prefectures).

Remarks. Kraepelin (1906) originally described *P. javanica* from Indonesia. Previous authors have considered statoblast morphology, colony color and colony form as important diagnostic characters of this species. Annandale (1911) reported a transparent, glassy ectocyst and a strong raphe, and Smith & Wood (1995) also indicated these characters. However, as with other plumatellid species, these characters vary ecophenotypically; for example, Annandale (1911) specifically mentioned variation in the form of colonies attached to dead wood. Like *P. javanica*, *P. vorstmani* (see below) also has a transparent ectocyst, but the tentacle number in *P. javanica* is almost twice that in *P. vorstmani*, and statoblast size and morphology are different.

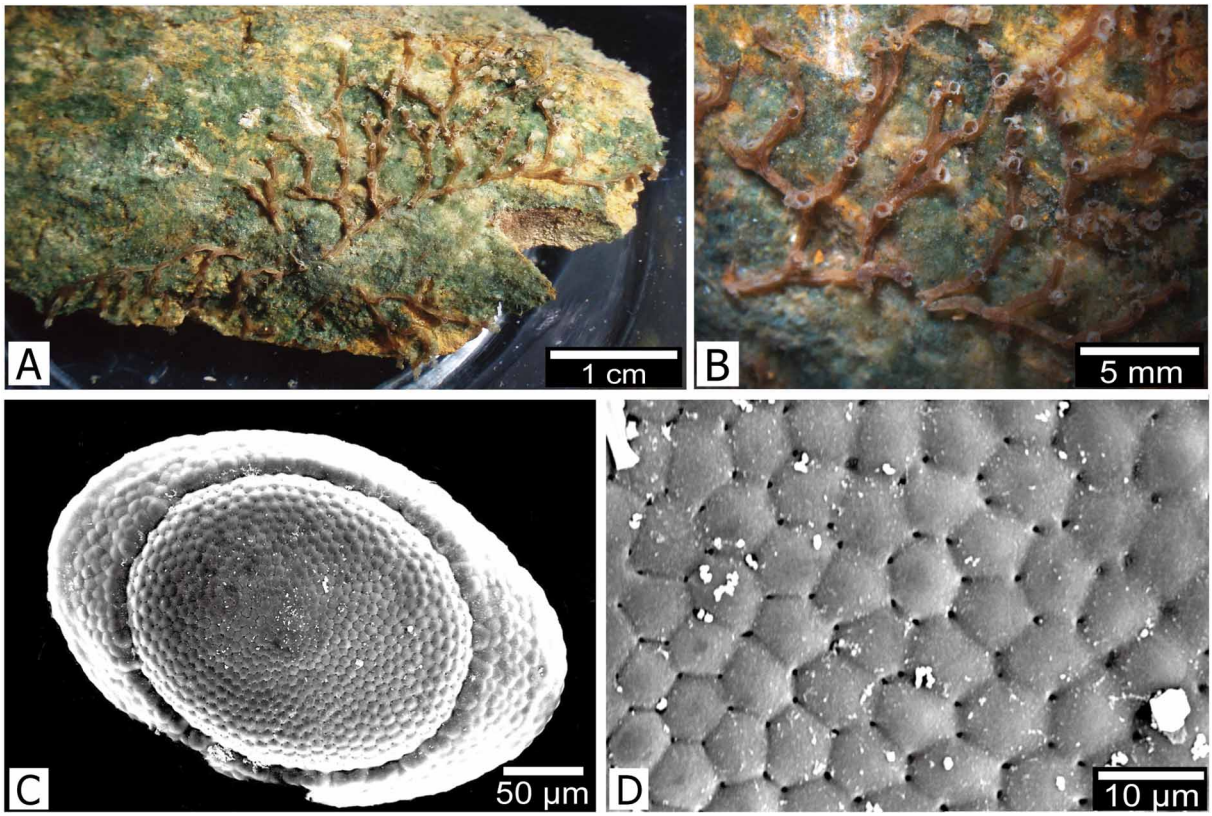

FIGURE 3. *Plumatella javanica* Kraepelin, 1906. **A, B,** colony on a stone at two magnifications. **C,** SEM micrograph of floatoblast, ventral view. **D,** enlarged view of the fenestra surface in C, showing the small, irregular pores.

Plumatella mukaii **Wood, 2001**
(Figure 2D)

Plumatella mukaii Wood, 2001: 51, figs 1, 3–6.
Plumatella princeps emarginata: Kraepelin 1887: 119, pl. 4(108), pl. 5(123).
Plumatella emarginata: Toriumi 1952b: 320 (part); Mukai 1999: 51, figs 2A, 3C, 5A, 7A (part); Mukai & Kobayashi 1988: 205 (part); Mukai *et al*. 1990: 51 (part).

Material examined. Several floatoblasts from Benoki Dam, village of Kunigami.

Description. Colony tubular, branched, well chitinized (Wood, 2001). Floatoblasts elliptical in our specimen, shorter than those of *P. emarginata*; 307–408 (360±32) µm long by 195–237 (214±13) µm wide (n=10), with length/width ratio of about 1.6. Ventral fenestra almost circular. Surface of both valves entirely covered with villi

(Fig. 2D). Dorsal fenestra small, less than half the length of the ventral fenestra. Annulus of floatoblast sculptured with very coarse pavement and covered with minute villi. Floatoblast valves asymmetrical in lateral view, the ventral valve markedly convex, the dorsal valve almost flat.

Distribution. Reported from eastern Asia and Thailand (Wood *et al.* 2006); collected from many localities in Japan; ranging from Okinawa to Aomori Prefecture, northern Honshu Island.

Remarks. *Plumatella mukaii* was originally reported as *P. emarginata* (Toriumi 1952b; Mukai 1999; Mukai & Kobayashi 1988; Mukai *et al*. 1990). Wood (2001) discovered that the floatoblast of Japanese *P. emarginata* is much shorter than that of *P. emarginata* from North America and Europe and has minute villi on the surface, and described the Japanese material as a new species, *P. mukaii*.

Plumatella repens (Linnaeus, 1758)

(Figure 2E)

Tubipora repens Linnaeus, 1758: 790; Allman 1844b: 74; 1851: 330; Jullien 1885: 100, figs 16–68; Braem 1890: 2, pl. 1(4, 5, 7), pl. 2(21); Toriumi 1955a: 51, pl. 1(1–42); Wood *et al*. 1998: 642, figs 7, 11; Mukai 1999: 56, figs 2B, 3E, 5B, 7B. Wood & Okamura 2005: 59, 89, figs 29b, 30, 31, 52.

Material examined. Floatoblasts from pond in city of Uruma; floatoblasts from Kurashiki Dam, city of Okinawa; colony with floatoblasts, Benoki Dam, village of Kunigami.

Description. Observed colony tubular, branching, light or yellowish brown; almost entirely recumbent, with ends of branches usually swollen; surface encrusted. Tentacle number 32–64. Floatoblasts in our material oval, 353–378 (366±6) μm long by 235–272 (256±11) μm wide (n=10), with length/width ratio of about 1.4. Fenestra of floatoblast almost circular; surface of fenestra covered with rounded tubercles; annulus smooth (Fig. 2E); valves almost symmetrical in lateral view. Sessoblast fenestra also covered with tubercles; annulus weakly reticulate (Wood & Okamura 2005).

Distribution. *Plumatella repens* is common, and broadly distributed worldwide; distributed from Okinawa to Hokkaido in Japan.

Remarks. The colony and statoblasts of *Plumatella repens* vary environmentally, and the floatoblast is the commonest gross morphological type among plumatellids. Accordingly, other species with similar gross floatoblast morphology (e.g. *P. fungosa* and *P. rugosa* may have been misidentified as *P. repens* before SEM was used for observations.

Genus *Rumarcanella* nov.

Type species. *Plumatella vorstmani* Toriumi, 1952.

Diagnosis. Colony entirely adherent, composed of narrow, branching tubes, weakly chitinized; ectocyst thin, transparent, with almost no encrustation. Colonies producing floatoblasts (sessoblast known only from *Rumarcanella vorstmani* and *R. yanbaruensis*), floatoblast with hypertubercles on fenestra.

Etymology. The genus name is from the Latin *ruma*, meaning "breast," in reference to the mammiform hypertubercles on the floatoblast fenestra, and *arcanus*, meaning "secret/hidden/esoteric," some species pertaining to the "*Hyalinella* problem" being included in the scope of the genus.

Remarks. We include four species in this genus — *Rumarcanella minuta*, *R. vorstmani*, *R. gusuku*, and *R. yanbaruensis*. Although *R. gusuku* and *R. yanbaruensis* are known only from subtropical Japan (Okinawa), *R. vorstmani a*nd *R. minuta* occur in Thailand (Wood *et al*. 2006) and boreal northern Japan (Tohoku and Hokkaido).

Rumarcanella gusuku n. sp.

(Figures 4, 5)

Plumatella sp. 2. Hirose *et al*. 2008: 65.

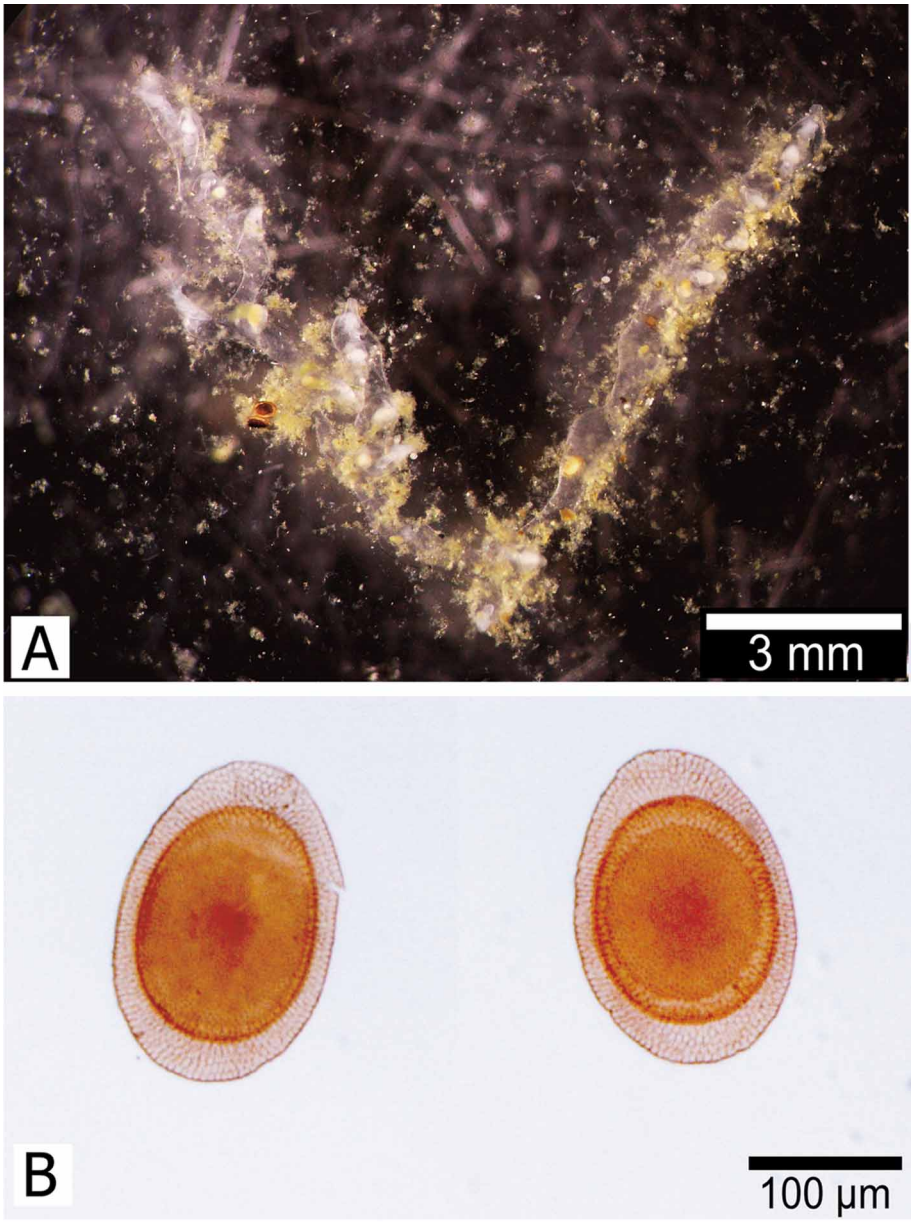

FIGURE 4. *Rumarcanella gusuku* **n. sp. A,** colony. **B,** floatoblast, ventral (left) and dorsal (right) valves.

Material examined. *Holotype*. Cultured colony originating from a floatoblast, collected 21 January 2008 by Tohru Iseto from Ryutan-ike pond next to the castle, city of Naha; specimen deposited in National Science Museum, Tokyo (NSMT-Te678). *Paratype*. Cultured colony originating from a floatoblast, collection data as for holotype; specimen deposited in National Science Museum, Tokyo (NSMT-Te679). *Other material*. Floatoblasts from Ryutan-ike pond next to the castle, city of Naha.

Etymology. The species name is from the Ryukyuan language *gusuku*, meaning "castle," in reference to the type locality.

Description. Laboratory-cultured colony composed of narrow tubes, branching, weakly chitinized, transparent (Fig. 4A). Floatoblasts oval, small, 315–346 (328±11) µm long (n=14) by 215–248 (228±10) µm wide; length/width ratio about 1.4 (Figs 4B, C). Ventral fenestra oval; 182–223 (203±12) µm long by 158–185 (175±7) µm wide. Dorsal fenestra almost circular, 176–202 (194±9) µm long by 143–162 (155±6) µm wide. In SEM images, surface of fenestrae entirely covered with rounded tubercles, each topped with a small hypertubercle (Fig. 5). Floatoblast valves asymmetrical in lateral and transverse views; ventral valve strongly convex, dorsal valve less convex, sometimes almost flat. Floatoblast suture with small irregular protuberances. Annuli sculptured with irregular pavement; ventral annulus narrow (~ 20 µm) along sides, wider (~ 50 µm) at both ends. Sessoblast unknown.

Distribution. Presently known only from southern and central Okinawa.

Remarks. Cultured colonies of *R. gusuku* resemble those of *R. minuta* and *R. vorstmani* in having a thin, transparent colony wall; unfortunately, we did not find any colonies in the wild, and these might differ in morphology from cultured colonies. Although the floatoblast of *R. gusuku* is very similar to that of *R. minuta;* the annulus is uniform in width in *R. minuta*, but narrower on both sides in *R. gusuku*; symmetrical in lateral view in *R. minuta*, but asymmetrical in *R. gusuku*, with a strongly convex ventral valve.

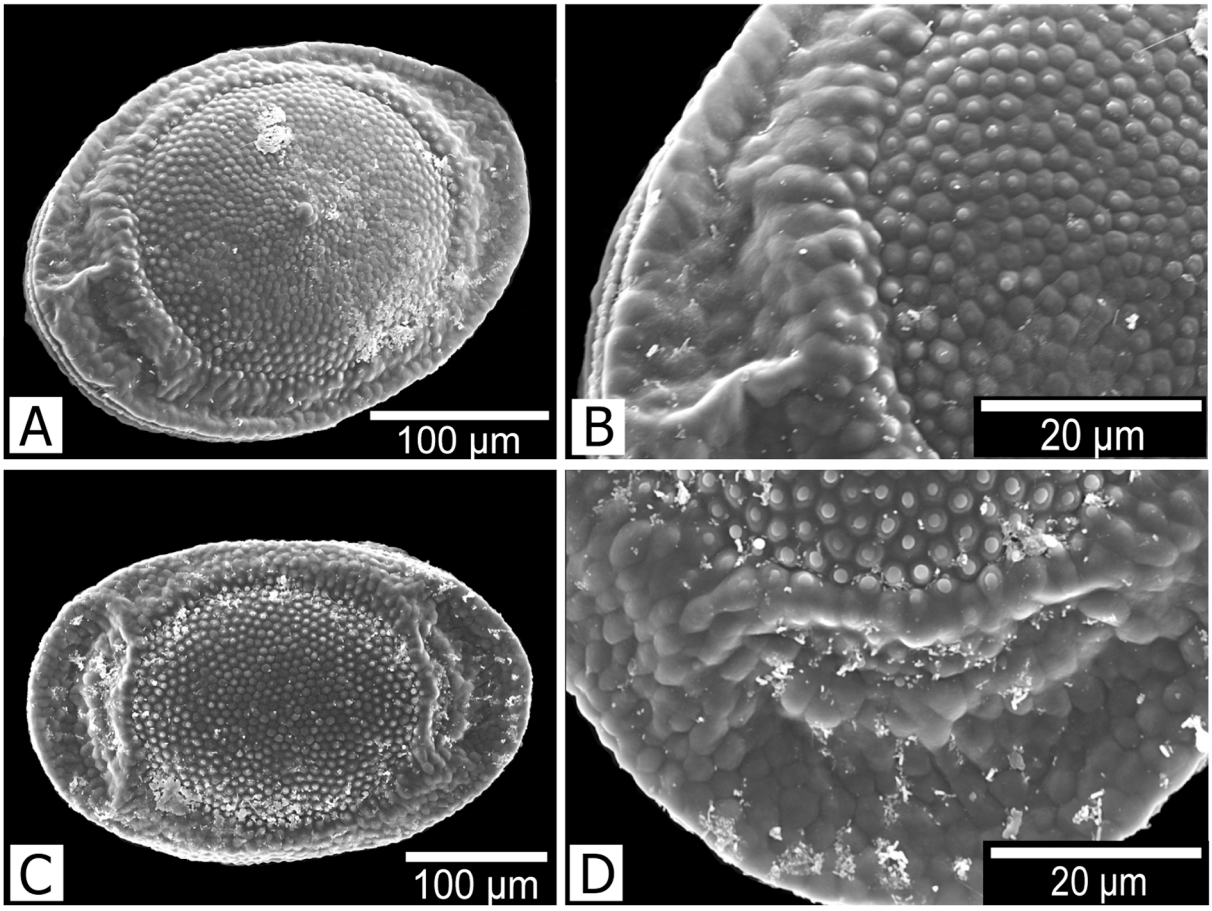

FIGURE 5. *Rumarcanella gusuku* **n. sp.** SEM micrographs of floatoblast. **A,** ventral valve. **B,** enlargement of A, showing hypertubercles on the fenestra. **C,** dorsal valve. **D,** enlargement of C, showing hypertubercles on the fenestra.

***Rumarcanella yanbaruensis* n. sp.**
(Figures 6, 7)

Plumatella sp. 1. Hirose *et al*. 2008: 65.

Material examined. *Holotype*. Colony with floatoblasts, collected 2 November 2007 from Benoki Dam, village of Kunigami; specimen deposited in National Science Museum, Tokyo (NSMT-Te680). *Paratype*. Colony with floatoblasts, same collection data as for holotype; specimen deposited in National Science Museum, Tokyo (NSMT-Te681). *Other material examined*. Floatoblasts, Fukuji Dam, village of Kunigami.

Etymology. The species name is from the Ryukyuan language *yanbaru*, in reference to the Yanbaru area, where the type locality is located.

Description. Colony tubular, branching, transparent; brownish transparent only in basal part (Figs 6A, B). Floatoblast (Fig. 6D) oblong-elliptical; large, 350–416 (387±21) µm long (n=16) by 205–262 (231±21) µm wide; length/width ratio about 1.8; sides almost parallel (Figs 6C, D); ventral fenestra oval, 203–249 (242±11) µm long by 168–196 (192±7) µm wide; dorsal fenestra 171–202 (192±9) µm long by 137–161 (153±6) µm wide. Surface of

floatoblast fenestrae entirely covered by low, rounded tubercles topped with hypertubercles (Figs 7A–D). Floatoblast valves nearly symmetrical in lateral and transverse views; both valves nearly flat; fenestra of ventral valve convex; floatoblast suture line finely denticulate (Figs 7B, D). Annulus wider at both ends; annulus of ventral valve 15–20 μm wide on sides, 70–80 μm wide at ends; annulus of dorsal valve about 20–25 μm wide on sides and 90–120 μm wide at ends; annulus sculpturing comprising a coarse pavement of circular elements. Sessoblast (Fig. 7E) rounded-elliptical, 258–310 (288±21) μm long by 205–237 (219±13) μm wide (n=5), length/width ratio about 1.3; fenestra covered with small cylindrical tubercles; annulus weakly reticulate; margin of annulus coarsely serrate (Fig. 7F).

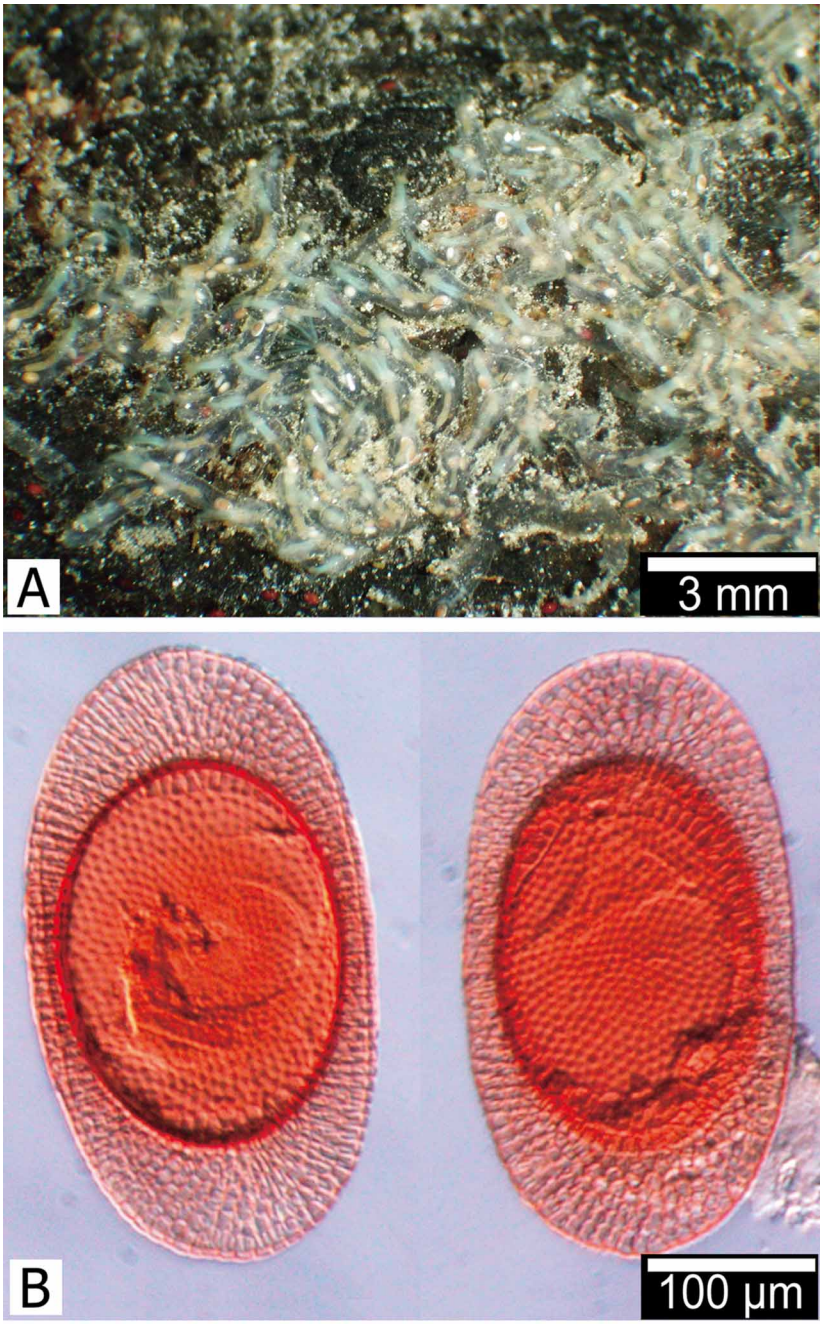

FIGURE 6. *Rumarcanella yanbaruensis* **n. sp. A,** colony. **B,** floatoblast, ventral (left) and dorsal (right) valves.

Distribution. Known only from the Yambaru area, northern Okinawa.

Remarks. Although colonies of *Rumarcanella yanbaruensis* resemble *Hyalinella* colonies, the tuberculate sessoblast and thin colony wall are very similar to those in *R. vorstmani*. The floatoblast of *R. yanbaruensis* resembles that of *Hyalinella lendenfeldi* in the wide annulus and flat form, but is smaller with larger fenestrae than in *H. lend-*

enfeldi. The fenestrae of *R. yanbaruensis* are similar in size to fenestrae in old illustrations of *Plumatella princeps* (e.g. Kraepelin 1887), but *R. yanbaruensis* clearly differs from *P. princeps*, *P. emarginata*, and related species in having a large dorsal fenestra, wide flat annulus and denticulate suture line. A molecular phylogeny (Hirose *et al*. 2008) showed *R. yanbaruensis* to be basal in a clade containing the four species of *Rumarcanella*.

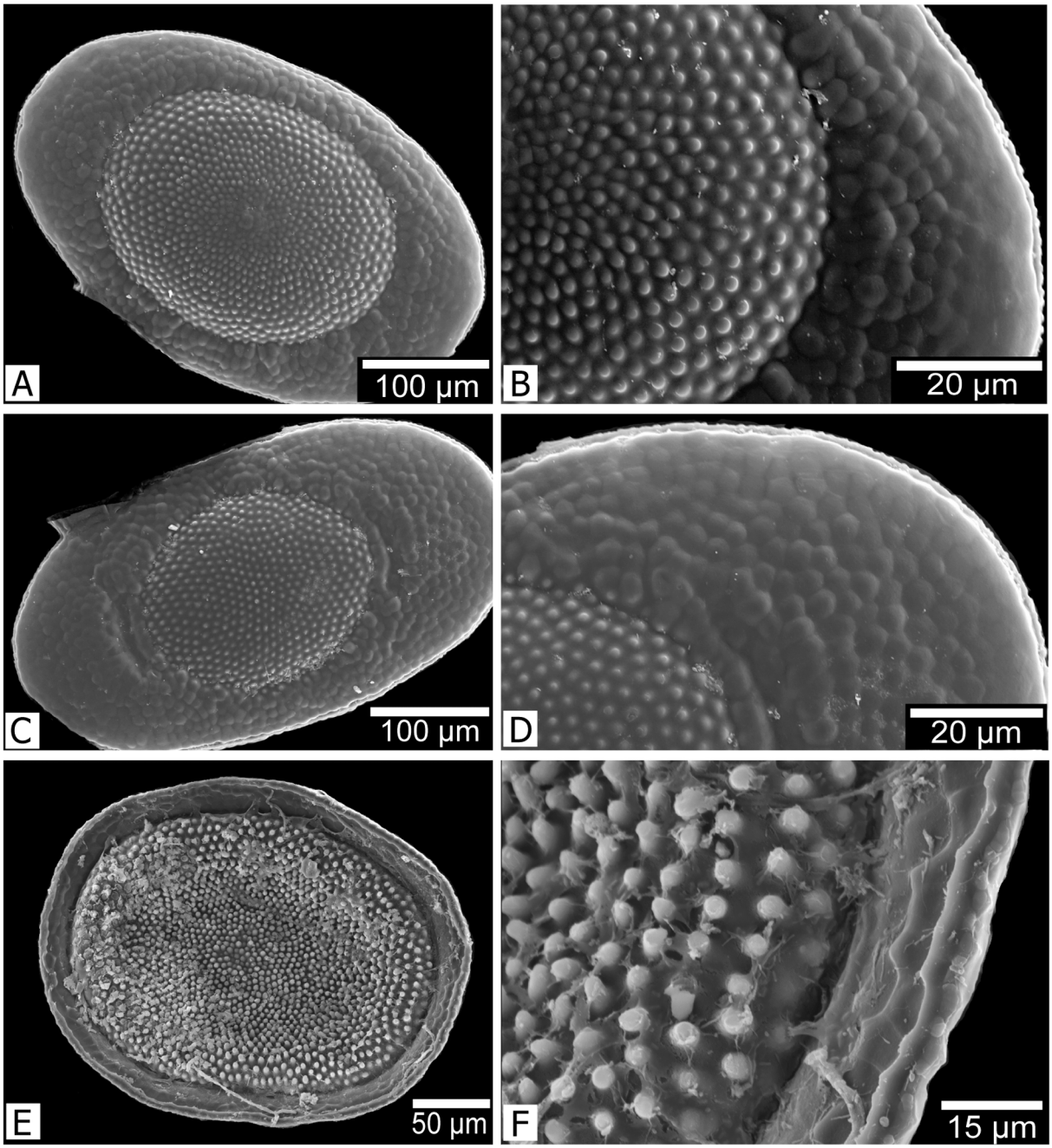

FIGURE 7. *Rumarcanella yanbaruensis* **n. sp.** SEM micrographs of statoblasts. **A,** floatoblast ventral valve. **B,** enlargement of A, showing hypertubercles on the fenestra. **C,** floatoblast dorsal valve. **D,** enlargement of C, showing hypertubercles on the fenestra. **E,** sessoblast. **F,** enlargement of E, showing cylindrical tubercles on the fenestra.

Rumarcanella vorstmani **(Toriumi, 1952)**

(Fig. 8)

Plumatella vorstmani Toriumi, 1952a: 268, figs 1–19; Mukai 1984: 51, fig. 2; 1999: 56, figs 3B, 4C, 6D; Wood *et al*. 2006: 18, figs 28–29, 39.
Plumatella javanica: Vorstman 1928a: 6, fig. 4, pl. 2(6–7); 1928b: 163.
Hyalinella vorstmani: Lacourt 1968: 86, pl. 12(g, i); Wiebach 1973: 546.

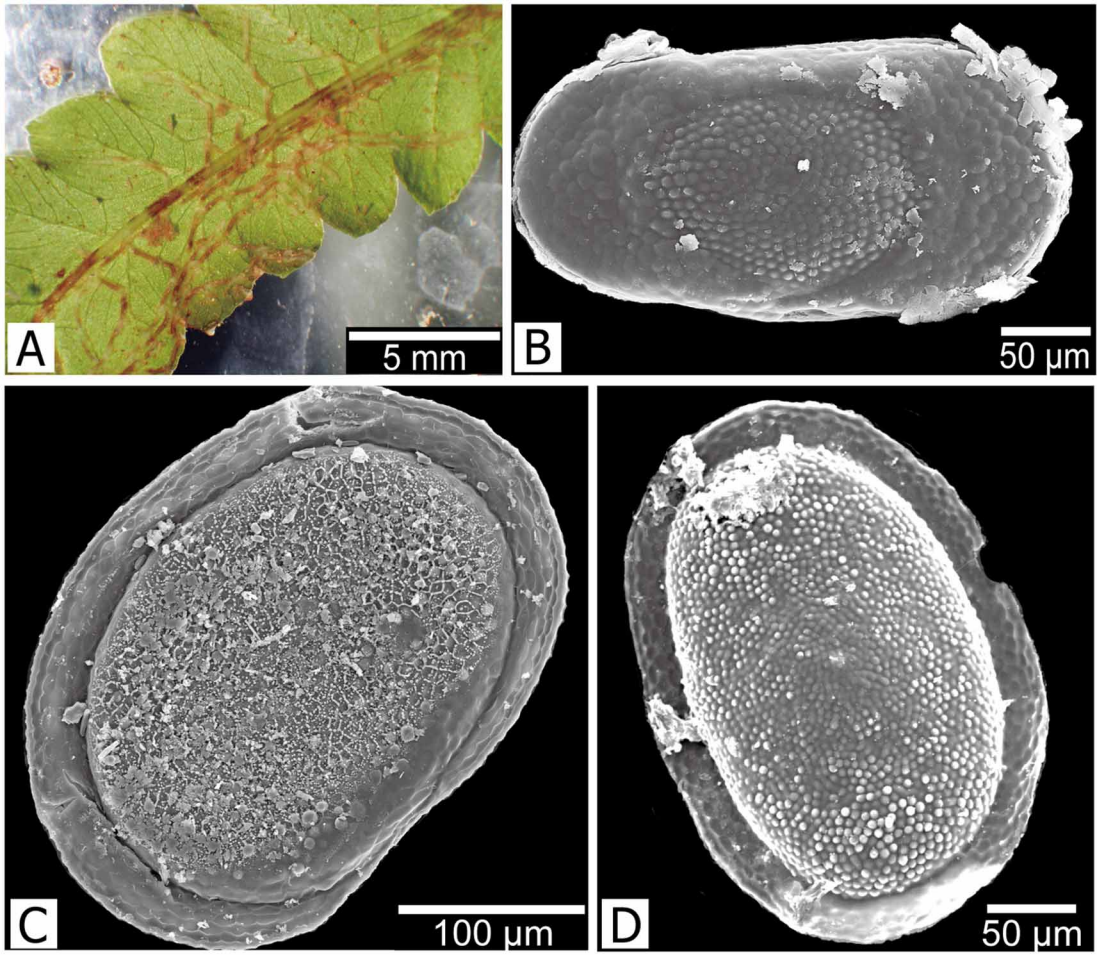

FIGURE 8. *Rumarcanella vorstmani* (Toriumi, 1952). **A,** colony on a leaf of an aquatic plant. **B,** floatoblast, ventral view (SEM). **C,** sessoblast (SEM) with villous reticulation over tubercles on the fenestra. **D,** Sessoblast with tubercles but no reticulation on the fenestra.

Material examined. Floatoblasts from Fukuji Dam, village of Higashi; several mature colonies with floatoblasts and sessoblasts, Kanna Dam, village of Ginoza.

Description. Colony with narrow branches, transparent, almost entirely recumbent (Fig. 8A). Tentacle number 20–27 (Wood *et al*. 2006). Floatoblast (Fig. 8B) oblong-elliptical, small, 295–322 (310±12) µm long by 155–182 (168±14) µm wide (n=4), with length/width ratio of about 1.8; symmetrical in lateral view; both ventral and dorsal fenestrae subcircular, both with tubercles bearing single hypertubercles. Sessoblast (Figs 8C, D) small, 288–358 (324±28) µm long by 215–248 (229±14) µm wide (n=5); fenestra with tubercles, annulus with weak reticulation.

Distribution. *Rumarcanella vorstmani* has been reported from mainland Asia (Bushnell 1973; Wood *et al.* 2006), India (Lacourt 1968), Java and Indonesia (Vorstman 1928a, b), and from Okinawa to Miyagi Prefecture in Japan (Toriumi 1952a; Mukai 1984).

Remarks. *Rumarcanella vorstmani* was originally described as *Plumatella javanica*, but Toriumi (1952a) recognized the former as a distinct species on the basis of tentacle number, floatoblast size, and the surface microsculpture of the sessoblast. The transparent, weakly chitinized colony wall of *R. vorstmani* has made generic placement difficult. Lacourt (1968) included this species in *Hyalinella* owing to the soft, transparent ectocyst, but because the species produces sessoblasts, Wiebach (1973) transferred it to *Plumatella*. In a similar case, *R. minuta* had long been reported to produce only floatoblasts and was placed in *Hyalinella*. Toriumi (1972) reported the occurrence of sessoblasts, and Wood *et al.* (2006) transferred the species to *Plumatella*.

Toriumi reported tubercles on the sessoblast of *R. vorstmani*. When Wood & Wood (2000) reexamined specimens that Mukai (1984) had identified as *P. vorstmani*, they found the surface of the capsule to be reticulate rather than tuberculate. However, Wood *et al*. (2006) reported *R. vorstmani* sessoblasts with a tuberculate fenestra from many sites in Thailand. In our collection, the reticulation (Fig. 8C) on the sessoblast fenestra is easily lost from the

surface, and the strong tubercles underneath become apparent (Fig. 8D). Thus, the reticulation may be associated with the membrane that covers the sessoblast surface.

Family Lophopodidae Rogick, 1935

Genus *Lophopodella* Rousselet, 1904

Type species. *Lophopodella thomasi* Rousselet, 1904.

Diagnosis. Colony lobed, soft and gelatinous; tubes dichotomously branching. Only floatoblasts are known; oval, with wide, flat annulus; some species have one to several spines with small hooks at both ends of the annulus.

Lophopodella carteri (Hyatt, 1866)
(Figure 9)

Pectinatella carteri Hyatt, 1866: 203.
Pectinatella davenporti Oka, 1907a: 716, fig. 3; 1907a: 117, figs 1, 2; Annandale 1911: 234.
Lophopodella carteri: Annandale 1910: 55; 1911: 232, fig. 46; 1919: 96; Annandale & Kemp 1912: 143; Kraepelin 1914: 64, pl. 1(2); Loppens 1908: 166, figs 14–15; Mukai & Oda 1980: 1, figs 1–2, 6A, 7A, B, 8–13, 29, 31, 34; Oka & Oda 1948: 39, figs 1–18; Oda 1954: 211; 1955: 1, figs 1, 2, 4; 1959: 93, figs 1, 6, 7; 1965: 3, figs 9–10, 13, pls 1, 2; 1980, 238, fig. 1; 1990: 50, figs 1, 15–18; Oda & Mukai 1985: 233, figs 1, 2, 3A, B, 7C, 8B; Oda & Nakamura 1973: 523; Rogick 1934: 416; 1936: 327, pl. 36(1, 2), pl. 37(3–16); 1957: 85; Rousselet 1904: 47, 53, pl. 3(6, 7); Toriumi 1941a: 209, figs 12–14, pl. 13(13); 1941b: 423, fig. 13; 1942: 212; 1956a: 35, figs 1–33; 1956b: 57. Vorstman 1928a: 10, fig. 8, pl. 3(11); Bushnell 1965a: 239, figs 2, 3; Bushnell & Rao 1979: 85, pl. 3(2, 3); Wood 1989: 46, fig. 27; Wood & Okamura 2005: 71, 97, figs 41, 42; Wood *et al*. 2006: 90, figs 4, 45–46.
Lophopodella carteri var. *davenporti*: Rogick 1934: 420.
Lophopodella carteri var. *himalayana*: Annandale 1911: 233; Rogick, 1934: 419.
Lophopodella carteri var. *typica* Rogick, 1934: 417, pl. 41(1–3), pl. 42(1); 1935a: 250; 1935b: 457, pl. 1(1–8), pl. 2(1–5); 1935c: 155, 157; 1937: 367, pl. 1(1–6), pl. 2(7–14), pl. 3(15–19), pl. 4(20–25), pl. 5(26, 27), pl. 6(28–33), pl. 7(34–41); 1938: 178, pl. 1(1–4), pl. 2(5–10), pl. 3(11–16).
Lophopus brisbanensis Colledge, 1917: 123, pl. 3(1–3); Hastings 1929: 305.
Lophopus carteri: Annandale 1908b: 171, fig. 3.
Lophopus himalayanus: Annandale 1908b: 171, fig. 4.
Lophopus lendenfeldi: Annandale, 1907b: 92, Pl. 2(1–4).
Lophopus lendenfeldi var. *himalayanus* Annandale, 1907a: 145, fig. 1; 1908a: 110.

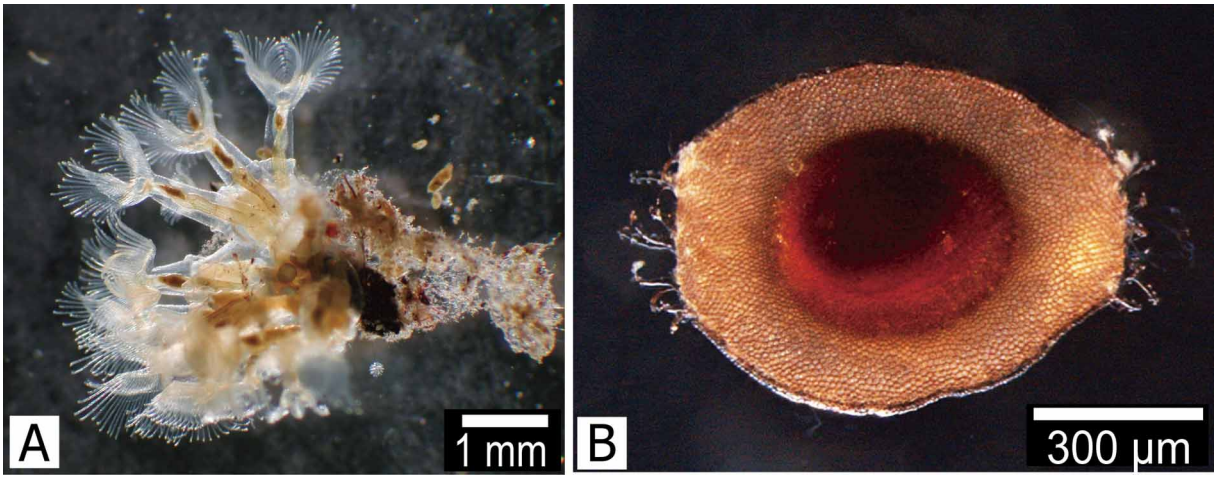

FIGURE 9. *Lophopodella carteri* (Hyatt, 1866). **A,** colony. **B,** floatoblast (spinoblast), dorsal view.

Material examined. Several mature colonies and floatoblasts from Fukuji Dam, village of Higashi.

Description. Okinawan colonies transparent, soft, gelatinous, sac-like or lobate in form; our specimens up to about 5 mm in diameter, attached to sunken wood. Ectocyst of colony hyaline, thick, soft, not encrusted (Fig. 9A);

ectocyst of polypides in the short, tubular colony soft. Tentacle number 68–82. Floatoblast (spinoblast) a flat, elliptical, disk, 797–821 (813±10) μm long by 614–631 (621±7) μm wide (n=5) (Fig. 9B). Annulus of floatoblast 153–192 (175±15) μm wide at sides, 212–274 (240±24) μm wide at ends (n=5); floatoblast with 6–10 spines at each end; spines 40–60 μm long, with small, hook-shaped lateral projections. Both fenestra and annulus with weak surface reticulation.

Distribution. Reported from Asia (India, Java, China, Korea, and Japan), North America, Europe, Africa, Australia, and New Zealand (Lacourt 1968; Wood & Okamura 2005); in Japan, widely distributed from Okinawa to Hokkaido, reported mainly from large lakes on Honshu (Lake Biwa, Kasumiga-ura, Hachiro-gata) and Hokkaido (Utonai Lake).

Remarks. Hyatt (1866) first reported *Lophopodella carteri* from southern Asia, and the species was subsequently reported globally. Variation in the statoblasts of *Lophopodella carteri* has been well studied (Rogick, 1936; Oda, 1955).

Discussion

In all, 23 phylactolaemate species have been reported from Japan to date; some areas such as Shikoku and Kyushu Islands have not been well studied, and the diversity may actually be somewhat higher. The known diversity in Japan is slightly greater than in North America or Europe, where about 20 and 17 species have been reported, respectively. Compared to these other regions, the number of plumatellid species is particularly high in Japan.

Most of the plumatellid species we identified from Okinawa have broader distributions; *Plumatella casmiana*, *P. emarginata*, and *P. javanica* have been reported from both paleotropical and neotropical regions. Some of the species identified on Okinawa are apparent endemics or limited in distribution — *Rumarcanella yanbaruensis* and *R. gusuku* are known only from Okinawa, whereas *Rumarcanella minuta*, *Rumarcanella vorstmani*, and *Plumatella mukaii* occur in both Japan and Southeast Asia.

Phylactolaemate bryozoans generally tend to be broadly distributed (Lacourt 1968; Bushnell 1973; Wood & Wood 2000; Wood 2002; Wood & Okamura 2005) because their floatoblasts provide an efficient mechanism for dispersal. Ducks, some amphibians, and some reptiles feeding on the water surface are known to ingest floatoblasts, which can remain viable and germinate after passing through the digestive tract (Brown 1933; Charalambidou *et al*. 2003; Figuerola *et al*. 2005; Green *et al*. 2008). In addition, floatoblasts can attach to the feathers of waterfowl (Okamura & Hatton-Ellis 1995; Freeland 2001; Wood 2002) or be ingested by waterfowl and can be especially broadly dispersed in this manner.

Connectivity and intersections among waterfowl migration routes may help explain the high phylactolaemate diversity in Japan. One of the main flyways of Japanese waterfowl is the great East Asian–Australian flyway extending from Australia through Southeast Asia and Japan to eastern Russia and Alaska (Fig. 10). The distributions of *Plumatella javanica*, *Plumatella minuta*, and *Plumatella vorstmani* in both Southeast Asia and Japan are consistent with dispersal along this flyway. In addition, many species of Japanese waterfowl, including European widgeon (*Anas penelope*), pintail (*Anas acuta*), mallard (*Anas platyrhynchos*), greater scaup (*Aythya marila*), tufted duck (*Aythya fuligula*) and European pochard (*Aythya ferina*), breed in Siberia in summer (Bianki & Dobrynina 1997), while the Black Sea–Mediterranean flyway crosses Europe and also reaches western Russia and Siberia. Thus, waterfowl from Europe and Japan meet in the same place in summer (Bianki and Dobrynina, 1997) and statoblasts carried by the birds could potentially be transferred from one bird to another. This may be why some phylactolaemate species occur in both Europe and Japan. Likewise, some North American geese migrate to Alaska, where they could potentially transfer statoblasts to pintail ducks (*Anas acuta*) that winter in Japan, thus accounting for phylactolaemate species occurring in both North America and Japan. The Central Asian Flyway may also facilitate phylactolaemate dispersal. Evidence for statoblast dispersal to and from Japan in this fashion will require metapopulation studies that include Japanese populations, similar to studies on *Cristatella mucedo* in Europe and North America (Freeland *et al*. 2001a, b). The species composition of the Japanese phylactolaemate fauna may have been affected by human-mediated dispersal as well, e.g. dispersal of colonies or statoblasts with freshwater-fish introductions to and from Japan.

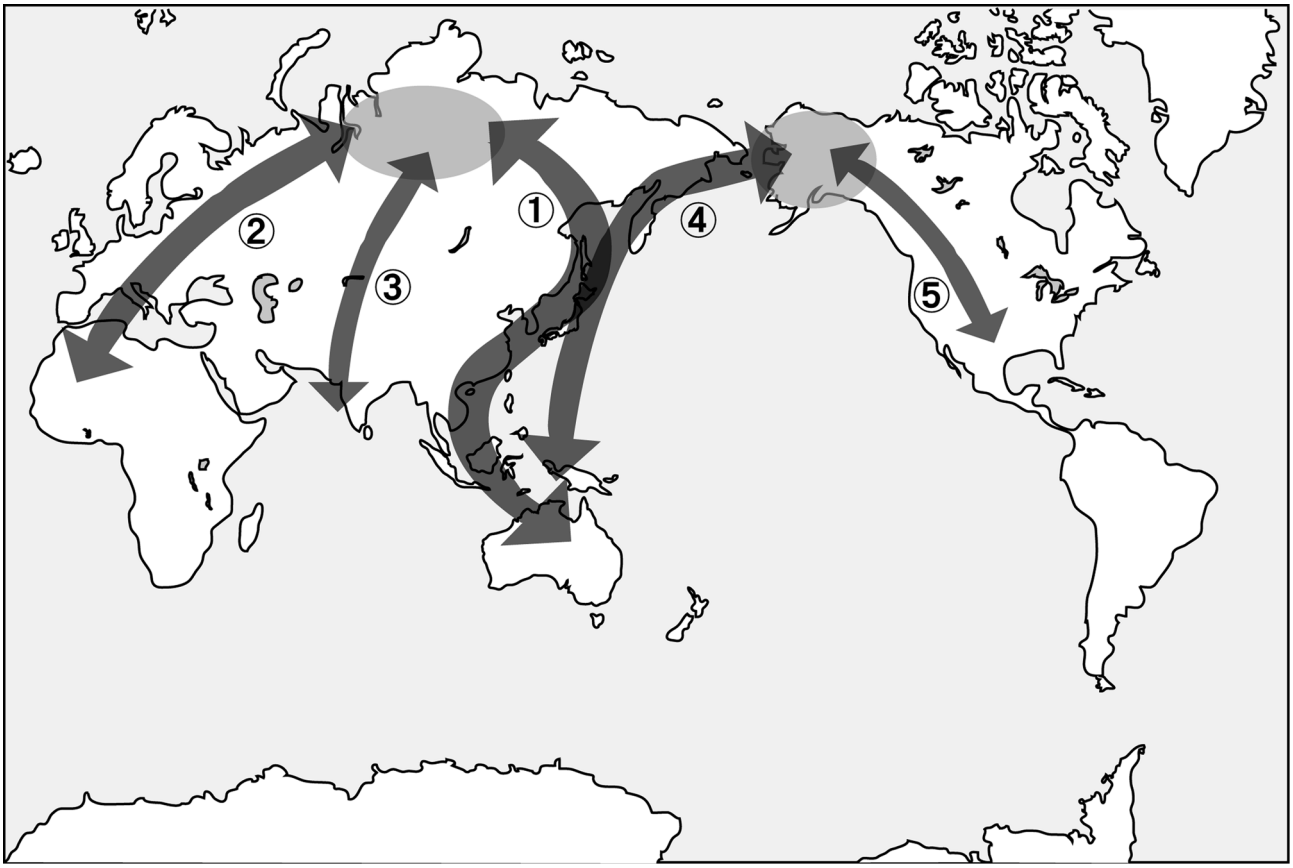

FIGURE 10. Waterfowl flyways implicated in statoblast dispersal to and from Japan. The far-northern areas shaded light gray indicate the main breeding grounds for some duck species that overwinter in Japan. (1) East Asian-Australian Flyway. (2) Black Sea-Mediterranean Flyway. (3) Central Asian Flyway. (4) West Pacific Flyway. (5) Mississippi and Central Flyway.

Identification key to phylactolaemate species in Japan

1. Colony globular or elongate and worm-like; colony wall not chitinized 2
- Colony tubular and branching; colony wall chitinized 5
2. Colony elongate, worm-like; statoblasts with spines from margin of fenestra . . . . . *Cristatella mucedo*
- Colony globular; statoblasts with spines on periphery of annulus 3
3. Colony globular; both ends of statoblasts bearing spines with minute hooks . . . . . *Lophopodella carteri*
- Colony often forming a compact mass; spines around entire statoblast periphery 4
4. Zooid mouth with red granules; white spots at each end of tentacles; statoblasts almost circular with about 16 hooked spines and large fenestra . . . . . *Pectinatella magnifica*
- Zooid mouth never colored; no white spots at tentacle ends; statoblasts somewhat square with many short hooked spines and small fenestra . . . . . *Asajirella gelatinosa*
5. Lophophore circular; no floatoblasts. . . . . Fredericellidae... 6
- Lophophore horseshoe-shaped 7
6. Piptoblast shiny when completely dried; capsule surface smooth . . . . . *Fredericella sultana*
- Piptoblast dull when dried; capsule surface with granular reticulation . . . . . *Fredericella indica*
7. Tubular colony embedded in gelatinous ectocyst mass 8
- Colony tubular and never make a gelatinous mass 9
8. Gelatinous ectocyst soft, transparent; floatoblasts almost circular with surface reticulation; sessoblasts with strong reticulation . . . . . *Stephanella hina*
- Gelatinous ectocyst hard; floatoblasts and sessoblasts both with conspicuous protuberances in center of ventral fenestra . . . . . *Gelatinella toanensis*
9. Colony wall thick, soft, hyaline, colorless; floatoblast length 400–500 μm; sessoblasts absent . . . . . *Hyalinella punctata*
- Colony wall chitinous, brownish or transparent, encrustation variable; floatoblast length varying; sessoblast often present . 10
10. Floatoblast length–width ratio > 1.5 11
- Floatoblast length–width ratio < 1.5 17
11. Floatoblast dorsal fenestra more than half floatoblast length; colonies also producing leptoblasts; floatoblasts and sessoblasts

	both with smooth surface	*Plumatella casmiana*
-	Floatoblast dorsal fenestra half or less than floatoblast length	12
12.	Floatoblast dorsal fenestra half or more than ventral fenestra length	13
-	Floatoblast dorsal fenestra less than half ventral fenestra length	14
13.	Floatoblast ventral valve strongly convex; tiny pores between fenestra tubercles	*Plumatella javanica*
-	Annulus wide, almost flat; small hypertubercles on fenestra; floatoblast margin rough	*Rumarcanella yanbaruensis*
14.	Floatoblast and sessoblast lengths more than twice their width	*Plumatella fruticosa*
-	Floatoblast width more than half of length	15
15.	Floatoblast valve symmetrical laterally; sessoblast capsule strongly reticulated	*Plumatella reticulata* [new to Japan]
-	Floatoblast valve asymmetrical laterally; sessoblast capsule tuberculated	16
16.	Statoblast lacking lamellar structures	*Plumatella emarginata*
-	Statoblast with lamellar structures on both fenestra and annulus	*Plumatella mukaii*
17.	Floatoblast lacking hypertubercles on fenestra	18
-	Floatoblast fenestra with small hypertubercle on each tubercle	20
18.	Floatoblast valve asymmetrical in lateral view, dorsal valve concave around fenestra; floatoblast fenestra and annulus weakly reticulate, with small tubercles; sessoblast annulus with tubercles	*Plumatella fungosa*
-	Floatoblast valve almost symmetrical in lateral view	19
19.	Floatoblast annulus completely smooth or with low tubercles; sessoblast annulus reticulate	*Plumatella repens*
-	Floatoblast fenestra and annulus both weakly reticulate; sessoblast annulus smooth	*Plumatella rugosa*
20.	Floatoblast dorsal and ventral fenestra differ in size	*Rumarcanella vorstmani*
-	Floatoblast dorsal and ventral fenestra almost the same size	21
21.	Floatoblast annulus uniformly narrow; floatoblast dorsal and ventral fenestra with similar convexity	*Rumarcanella minuta*
-	Floatoblast annulus wider than sides at both ends; floatoblast ventral fenestra strongly convex	*Rumarcanella gusuku*

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