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Authors: Grischenko, Andrei V., Gordon, Dennis P., Nojo, Ayumu, Kawamura, Makoto, Kaneko, Naotomo, et al.

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New cheilostome bryozoans from the Middle Miocene of Hokkaido, Japan, and the first fossil occurrences of *Kubaninella* and *Hayamiellina* gen. nov.

ANDREI V. GRISCHENKO[1], DENNIS P. GORDON[2], AYUMU NOJO[3], MAKOTO KAWAMURA[4], NAOTOMO KANEKO[5] AND SHUNSUKE F. MAWATARI[1]

[1] *Laboratory of Systematics and Evolution, Division of Biological Sciences, Graduate School of Science, Hokkaido University, Sapporo 060-0810, Japan (e-mail: gat@bio.sci.hokudai.ac.jp, shunfm@bio.sci.hokudai.ac.jp)*

[2] *National Centre for Aquatic Biodiversity & Biosecurity, National Institute for Water & Atmospheric Research (NIWA), PO Box 14901, Kilbirnie, Wellington, New Zealand (e-mail: d.gordon@niwa.co.nz)*

[3] *Department of Science Education, Iwamizawa College, Hokkaido University of Education, Iwamizawa 068-8642, Japan (e-mail: nojo@iwa.hokkyodai.ac.jp)*

[4] *Division of Earth and Planetary Sciences, Graduate School of Science, Hokkaido University, Sapporo 060-0810, Japan (e-mail: mkawa@ep.sci.hokudai.ac.jp)*

[5] *Geological Museum, Geological Survey of Japan, AIST, Tsukuba 305-8567, Japan (e-mail: n.kaneko@aist.go.jp)*

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Abstract. Three new species and one new genus of cheilostome Bryozoa are described from the Kaigarabashi Sandstone Beds (Kunnui Formation, late Middle Miocene) of southwestern Hokkaido. These are *Hayamiellina constans* (Cribrilinidae), *Integripelta sakagamii* (Eurystomellidae), and *Kubaninella miocenica* (Adeonidae). Monotypic *Hayamiellina* gen. nov. is also reported living at shelf depths off the Commander Islands, Bering Sea, and in the Gulf of Alaska. The finding of *K. miocenica* constitutes the first fossil record of the formerly monotypic genus *Kubaninella*. These new records, from a locality previously sampled for Bryozoa, underscore the inadequate level of sampling and taxonomic work on the evidently biodiverse and highly endemic bryozoan fauna of the Japanese Cenozoic.

Key words: Bryozoa, Cheilostomata, new taxa, Hokkaido, Middle Miocene, Kaigarabashi Sandstone Beds

Introduction

Bryozoans are common in the seas and younger Cenozoic deposits of the Japanese Islands but the full scope of their diversity has yet to be ascertained. Hayami (1975) reviewed all previous studies of the Bryozoa of the Japanese Neogene and Pleistocene, at the same time describing numerous new species herself. Chronologically, earlier work comprises the studies of Sakakura (1935, 1938) (Pleistocene: Boso Peninsula, Chiba Prefecture), Kataoka (1957) (Pliocene: Daishaka Formation, Aomori Prefecture), Kataoka (1960) (Pleistocene: "Ryukuyu Limestone", Kagoshima Prefecture), Hayami (1970) (Miocene: Kunnui Formation, southwestern Hokkaido), Hayami (1971) (Pliocene: Shimajiri Formation, Okinawa Prefecture) and Hayami (1974) (Mizunami Group, Gihu Prefecture). Hayami (1975, 1976, 1980, 1981) described further material from several additional localities: Miocene: Moniwa Formation, Miyagi Prefecture; Nanao Calcareous Sandstone, Ishikawa Prefecture; Tanosawa Formation, Akita Prefecture; Utsuno Formation, Miyagi Prefecture. Pliocene-Pleistocene: Ananai Formation, Kochi Prefecture; Daishaka and Hamada Formations, Aomori Prefecture; Hirose and Narusawa Formations, Aomori Prefecture; Onma Formation, Toyama Prefecture; Sasaoka and Shibakawa Formations, Akita Prefecture; Setana Formation, southwestern Hokkaido. Pleistocene: Hiradoko Formation, Aomori Prefecture; Kamayachi Formation, Akita Prefecture.

Hayami's (1975) review of northern Japanese (north of 36° N) fossil Bryozoa yielded a list of 123 species and 2 subspecies in 69 genera. This is a much lower level of diversity than would be expected of the sedimentary settings from which the bryozoans came, which are rich in molluscan shell gravel and contain other hard substrata like rock and gravel and echinoid spines. Certainly, more species have been reported from another temperate-region setting of equivalent area and latitudinal range, namely New Zealand (Brown 1952), which has more than 215 species of Bryozoa from the Miocene alone, more than half of which are undescribed (Gordon 2000). The Neogene and Pleistocene bryozoan fauna of Britain is also nominally more diverse than that of northern Japan (Busk 1859; Lagaaij 1952; Bishop & Hayward 1989). The New Zealand Neogene is rich in limestone deposits that contain 20–70% bryozoan fragments by volume (Nelson *et al.* 1988), which is not the case in Japan, but British Neogene deposits containing Bryozoa are far fewer than in Japan, suggesting that reasons other than intrinsically low natural diversity must be sought to explain the smaller Japanese faunal list. In the first instance, Hayami's (1975) annotated checklist did not include species of the bryozoan orders Ctenostomata (represented by borings in mollusc shells) or Cyclostomata. But species in these groups would be expected to increase nominal diversity only by less than 20%.

Sakagami *et al.* (1980) published a checklist of all known Japanese Cenozoic Bryozoa, including faunas from the Ryukyu Islands. This list tallied 454 species, not all named, comprising 407 species of Cheilostomata, 25 species of Cyclostomata, and 2 shell-boring ctenostomes. The cyclostome data were taken from the papers of Sakakura (1935, 1938) and the ctenostomes (*Immergentia* sp., *Penetrantia* sp.) from the papers of Fukuda (1976, 1978). Again, this level of diversity is much lower than would be anticipated for the entire Japanese archipelago, including, as it does, species from cool-temperate to tropical settings throughout the Cenozoic. Also, the tally of 27 species of Ctenostomata and Cyclostomata comprises only 5.9% of the total bryofauna, indicating that the diversity of species in these two orders could be at least doubled. Arakawa (1995) added 16 more Pleistocene species, including 3 new, to bring the total to 470 species.

We recently collected bryozoans from two localities where the Kaigarabashi Sandstone Beds (Sawada 1961) of Middle Miocene age are exposed in southwestern Hokkaido. One of these localities had previously been sampled by Hayami (1970) and the bryozoans found there studied by her. Our samples yielded plentiful material of one misidentified species, described here as a new species of the eurystomellid genus *Integripelta*. Additionally, we found two new species of cheilostomes not previously encountered in the Japanese Neogene. Both also represent the first fossil occurrences of otherwise Recent genera. One is *Kubaninella* Grischenko and Mawatari, 2002 (family Adeonidae). The other, remarkably, represents a new genus of Cribrilinidae, based not only on specimens from the Yakumo Formation but also from living conspecific material from the Commander Islands off the Kamchatka Peninsula.

The SEM micrographs of Kaneko (1993, 1997) and Arakawa (1995) show that preservation of Japanese Neogene bryozoan fossils is frequently excellent, with high resolution achievable. We have found this to be the case concerning the present samples. Here, we describe the new taxa and comment on their taxonomic, phylogenetic, and biogeographic significance. One of our aims is to stimulate renewed interest in the fossil bryozoan fauna of Japan.

Geologic setting

The fossil bryozoan specimens described below were collected from two localities (Figure 1) where

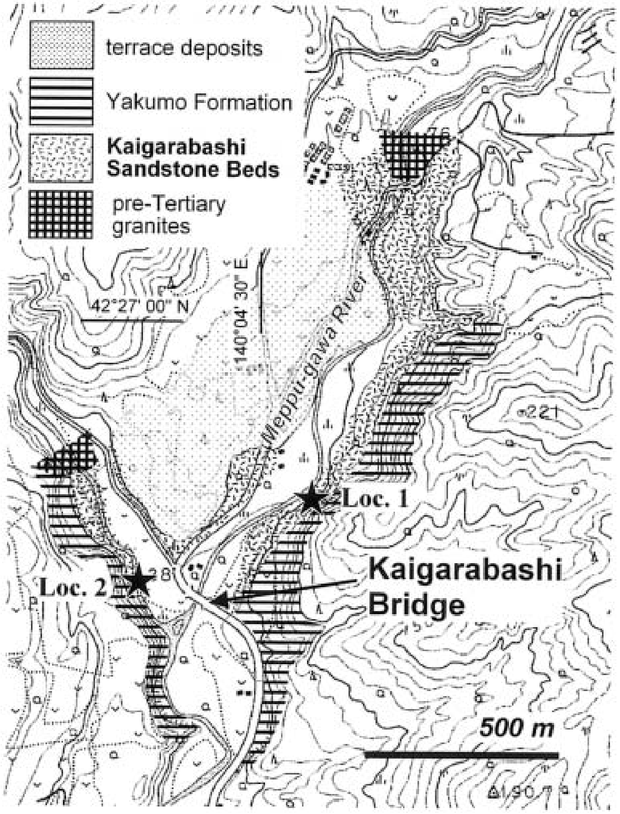

Figure 1. Index map of the fossil locality; geological distribution after Hasegawa (1988). The topographic map is a part of the 1:25,000 Map Sheet "Imakane" published by The Geographical Survey Institute of Japan.

the Kaigarabashi Sandstone Beds, Yakumo Formation, are exposed. One is the streamside cliff (42°26.48′4″ N, 140°04.34′9″ E) of the Meppu-gawa River, north of Tanekawa [Tane-gawa in Hayami 1970] immediately northeast of the Kaigarabashi Bridge, in the Imakane area of southwestern Hokkaido. It has been described by Sawada (1962) and Hayami (1970). The second locality (42°26.41′5″ N, 140°04.15′2″ E), nearby, is west of Kaigarabashi Bridge, also at a streamside section. The Kaigarabashi Sandstone Beds appear at the top of the Kunnui Formation in both Sawada (1962) and Hayami (1970) but may be classed as the basalmost member of the succeeding Yakumo Formation. While both formations are Middle Miocene in age, the Kaigarabashi Sandstone Beds are dated as 15–12 Ma from foraminifers (Hasegawa 1998; Uchida *et al.* 2001).

At both localities the sandstone is richly fossiliferous, mostly comprising valves of pectinids, in particular *Nanaochlamys notoensis* (Yokoyama, 1929) and associated species. These provide an excellent substratum for encrusting bryozoans but the non-indurated sandstone sediment contains many broken fragments of fixed-erect colonies belonging to the genus *Myriapora* and internodes of erect, articulated forms attributed by Hayami (1970) to *Cellaria diffusa* Robertson, 1905 and *Microporina articulata* (Fabricius, 1821). Internodes of *Crisia* sp. (Cyclostomata) are also common but she referred neither to these nor to the presence of *Myriapora*. She interpreted the assemblage as occurring in a nearshore, shallow coastal setting, free from muddy sediment, that was likely to have been temperate to warm (inferred in part from the presence of the bryozoan *Monoporella*) (Hayami 1975).

Materials and methods

Bryozoan-encrusted shells and bulk samples of associated unconsolidated sediment were collected and the sediment washed, sieved, and dried. Sieved samples were microscopically examined. *Inter alia*, these yielded broken fragments of two of the species described here that were better preserved than colonies still attached to shells and also revealed details of the interiors of zooids.

Some Recent specimens were also examined. These were collected from the shelf and slope of the Commander Islands, Bering Sea, by the Institute of Marine Biology (IMB), Vladivostok, in 1973, by the Pacific Institute of Bio-Organic Chemistry (PIBOC), Vladivostok, in 1991, and by the Kamchatka Institute of Ecology and Nature Management (KIENM), Petropavlovsk-Kamchatskyi in 1992. Other samples were collected near Kodiak Island, Gulf of Alaska, by PIBOC in 1991.

Cleaned colonies were coated with Pd–Pt by a Hitachi E-1039 ion sputter coater and photographed using a Hitachi S–2380N scanning electron microscope at 15 kv accelerating voltage. Measurements of zooidal characters were made using an eyepiece graticule in a Nikon SNZ–10 binocular microscope and compared to the scale bars in the electron micrographs. Measurements of autozooids are given as ranges, with means and standard deviations in parentheses for 30 zooids.

The specimens described here are deposited in the Zoological Institute, Faculty of Science, Hokkaido University (ZIHU), Sapporo, Japan, and the Zoological Institute of the Russian Academy of Science (ZIRAS), St. Petersburg, Russia. A.V. Grischenko and D.P. Gordon are to be considered authors of the new taxa.

Systematic description

Class Gymnolaemata Allman, 1856
Order Cheilostomata Busk, 1852
Suborder Neocheilostomina d'Hondt, 1985
Infraorder Ascophora Levinsen, 1909
Superfamily Cribrilinoidea Hincks, 1879
Family Cribrilinidae Hincks, 1879
Genus ***Hayamiellina*** Grischenko and Gordon gen. nov.

Type species.—*Hayamiellina constans* Grischenko and Gordon sp. nov.

Etymology.—The name honors the late Tomoko Hayami, who contributed greatly to knowledge of Japanese Cenozoic Bryozoa before her untimely death in 1988.

Diagnosis.—Colony encrusting, multiserial. Zooids with a frontal shield of broad flat costae with usually a pair of lumen pores (pelmata); costae simple, non-pinnate, occupying the entire frontal surface, with no gymnocyst visible. Suboral costae may be ridged or bossed. Orifice wider than long, condylar processes well developed; a pair of spinelike tubercles associated with the orifice, no articulated oral spines. Ovicells recumbent, noncostate, with several perforations that resemble costal lumen pores. Basal pore-chambers present. Ancestrula not seen.

Remarks.—Taxonomically, *Hayamiellina* appears closest to *Reginella* Jullien, 1886. The type species, *R. furcata* (Hincks, 1882), and congeners have a similar perforated ovicell and costal lumen pores, lateral-oral tubercles, and no avicularia or frontal exposure of gymnocyst (Osburn 1950; Soule *et al.* 1995). There are also no pore chambers. *Hayamiellina* differs in having well developed pore-chambers and simple nonpinnate costae with no intercostal lacunae.

Hayamiellina constans Grischenko and Gordon sp. nov.

Figures 2–3

Material.—Holotype: ZIRAS 1/50131. One colony encrusting a stone, KIENM Collection, 10 August 1992, Stn 152, Beringian coastal water off Mednyy Island, Cape Gladkiy (54°44.8′N, 167°45.3′E, 46 m depth, by scuba from rock face, (0.25 m^2), collector V.V. Oshurkov. Paratype: ZIHU–2319, two colonies encrusting pectinid bivalves, Yakumo Fm, Imagane area of SW Hokkaido, late Middle Miocene. Other material: 58 specimens from 18 stations in the area of the Commander Islands, collected by IMB (1973), PIBOC (1991), and KIENM (1992); and 2 colonies from 2 samples near Kodiak Island, Gulf of Alaska (58°22.4′N, 150°56.8′W, and 57°42.8′N, 151°00.9′W), collected by PIBOC (1991).

Type locality.—Cape Gladkiy (54°44.8′N, 167°45.3′E), Mednyy Island, Commander Islands, Bering Sea, 46 m depth.

Distribution.—Recent, Commander Islands, Bering Sea, 15–350 m depth, and near Kodiak Island, Alaska, 61–70 m depth; and in the Kaigarabashi Sandstone Beds, Imakane area of southwestern Hokkaido, Middle Miocene.

Etymology.—From Latin *constans*, constant, alluding to the persistence of this species in time from the Miocene to the present day.

Description.—Living colonies bright red to orange-coloured and sporadically light green, drying to light orange, encrusting, multiserial, unilamellar, of irregular form, attaining c. 4 cm in any one direction. Zooids (Figure 2.1–2.2) more or less quincuncially arranged, 0.50–0.75 mm long (0.63 ± 0.06 mm), 0.32–0.50 mm wide (0.42 ± 0.04 mm). Frontal shield of 8–12 broad flat costae (Figure 2.1, 2.3), each with usually a pair of lumen pores (pelmata), but small costae may have a single pore and 3 may occur in others; pores closest to midline of zooid occasionally closed; costae simple, nonpinnate, occupying the entire frontal surface, with no gymnocyst visible laterally or proximally; a short, low median carina may develop in some zooids. An internal view of the frontal shield (Figure 2.5–2.6) shows costae to have broad openings into their hollow interiors. Suboral costae may be ridged or bossed, especially in zooids far from the growing edge or in ovicelled zooids. Orifice wider than long, 0.11–0.17 mm long (0.15 ± 0.02 mm), 0.14–0.20 mm wide (0.18 ± 0.02 mm), with well developed condylar processes (Figure 2.3), these being inward extensions of the proximal corners of the anter; orifice widest at poster, the proximal rim straight or slightly sinuous; a pair of spinelike tubercles associated with the orifice, no articulated oral spines. Ovicells recumbent (Figure 2.2, 2.4), noncostate, with 5–9 frontal perforations that resemble costal lumen pores. Basal pore-chambers well developed, comprising a distolateral pair and a large semicircular chamber distally. Ancestrula not seen.

Fossil material morphologically identical except for transverse crests on suboral costae of all zooids (Figure 3.3–3.4). Zooids (Figure 3.1) 0.45–0.80 mm long (0.54 ± 0.09 mm), 0.31–0.50 mm wide (0.41 ± 0.05 mm); orifice (Figure 3.2) 0.10–0.15 mm long (0.12 ± 0.01 mm), 0.13–0.22 mm wide (0.16 ± 0.03 mm). Ovicells not seen in fossil specimens.

Remarks.—The species is comparatively abundant in the area of the Commander Islands where it was collected from depths ranging from 15–350 m. It encrusts boulders, stones, and occasionally shell fragments of *Pododesmus macrochisma* (Deshayes, 1839) in the upper shelf zone of the archipelago. On the continental slope of the islands where the seabed comprises soft sediment, some colonies were found on the erect bryozoans *Microporina articulata* (Fabricius, 1821) and *Tricellaria ternata* (Ellis and Solander, 1786). Near Kodiak Island, Alaska, *Hayamiellina constans* encrusts erect colonies of other bryozoans, viz. *Bugulopsis beringia* Kluge, 1952 and *Semibugula birulai* Kluge, 1929. Fossil specimens were found on shells of pectinids, typically on the concave interior surfaces.

It is unusual to discover an extant new monotypic genus concurrently with fossil specimens of the same species 10 million years older from the Neogene. The air-dried living material and the fossil specimens are morphologically identical. The only apparent difference is the occurrence in the fossils of transverse crests on all suboral costae, even in zooids near the growing margin, but this level of difference is well within the normal range of variation in frontal calcification in cheilostomes and can be interpreted as environmentally induced.

What is significant about this dual find is that the ecological requirements of populations from the late Middle Miocene may be assumed to have been similar, at least, to those of living populations. Hayami (1974) inferred a temperate to warm setting when the Kaigarabashi Sandstone Beds were laid down, in contrast to the much cooler temperatures that *Hayamiellina constans* experiences today. Mean zooid

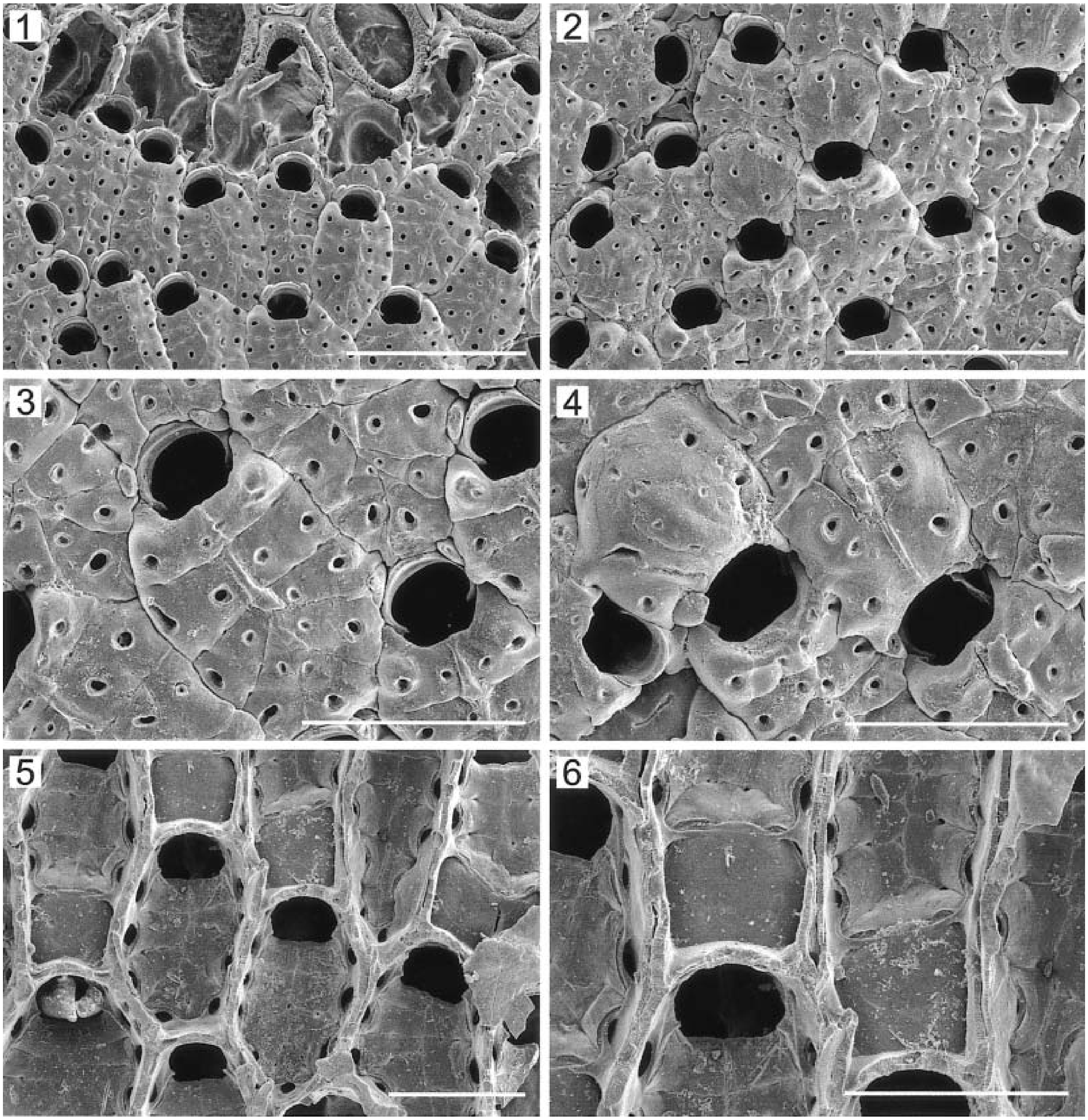

Figure 2. *Hayamiellina constans* sp. nov. ZIRAS 1/50131, Recent, Cape Gladkiy, Mednyy Island, Commander Islands, Bering Sea, depth 46 m, colony encrusting gravel. **1**. Neanic zooids at a colony margin in the act of overgrowing a species of *Caulorhamphus* (Calloporidae). **2**. Ephebic zooids, showing two complete ovicells and parts of two others. Note the crests on the suboral costae of ovicelled zooids. **3**. Close-up of autozooids and orifices, with details of the costal shield. **4**. Close-up of two ovicells. **5**. Underside of autozooids and ovicelled zooids. **6**. Close-up of same. **1–2**, scale bar = 1 mm. **4–6**, scale bar = 500 μm.

length is greater in living *H. constans* (0.63 mm) than in the fossil material (0.54 mm), which conforms with expectations since zooid size tends to be inversely correlated with cooler temperatures (Okamura and Bishop 1988).

Superfamily Catenicelloidea Busk, 1852
Family Eurystomellidae Levinsen, 1909
Genus ***Integripelta*** Gordon, Mawatari and Kajihara, 2002

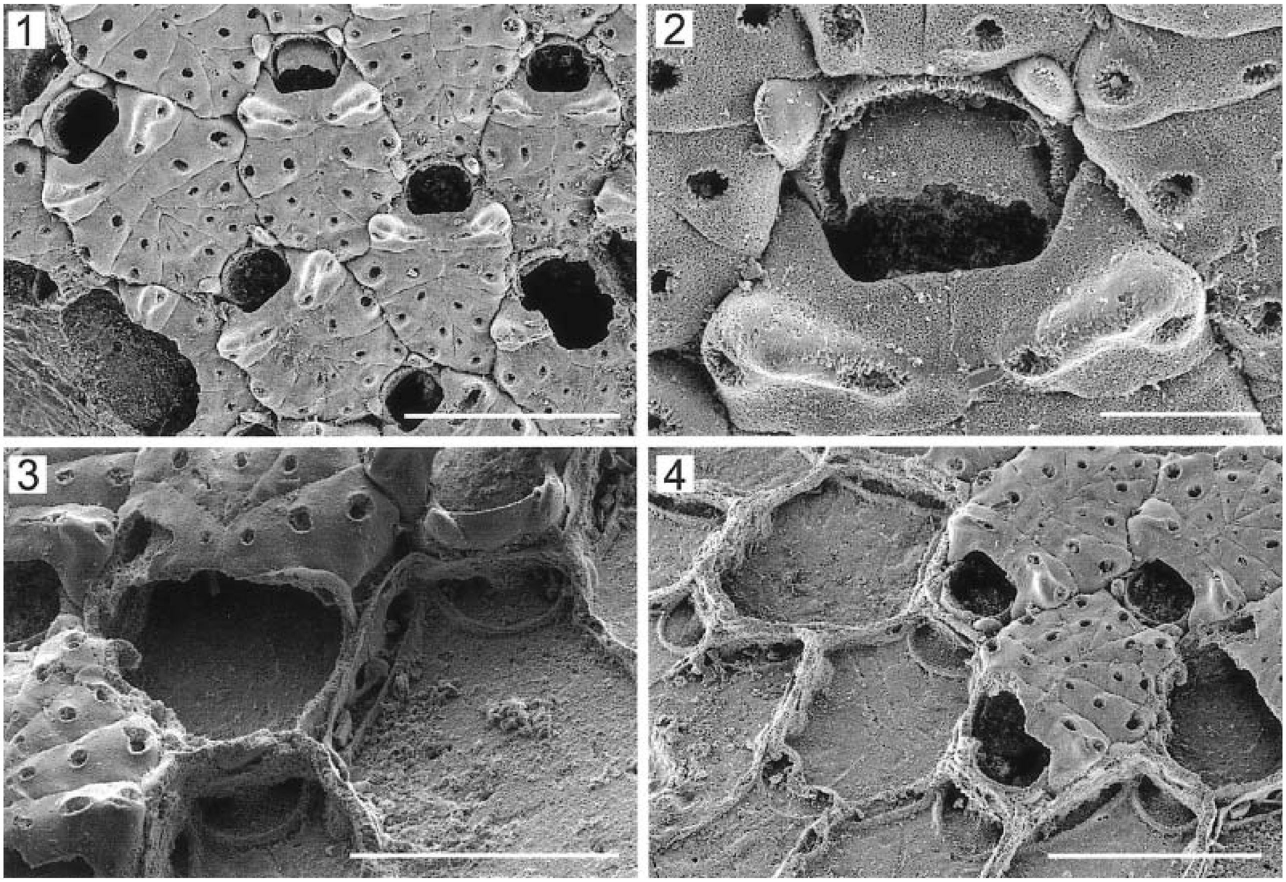

Figure 3. *Hayamiellina constans* sp. nov. ZIHU–2319, late Middle Miocene, southwestern Hokkaido, Japan. **1**. Ephebic autozooids. Note the conspicuous crests on the suboral costae. **2**. Close-up of orifice. Note the distolateral tubercles. Debris occupies the orifice. **3**. Colony margin showing distal and lateral pore-chambers. **4**. Same, another part of colony. **1**, **4**, scale bar = 500 μm. **2**, scale bar = 100 μm. **3**, scale bar = 400 μm.

Diagnosis.—Colony encrusting, multiserial. Autozooids with gymnocystal frontal shield lacking foramina. Zooidal orifices with proximolateral indentations, and shallow excavations in the adjacent gymnocyst; oral rim lacking median suboral suture. No spines or avicularia. Maternal orifice usually slightly larger than autozooidal orifice, or obviously so, brooding internal. Distal kenozooid with a central perforation. Ancestrula with a membranous frontal wall only, no peripheral spines. Basal pore-chambers lacking, interzooidal communications via uniporous mural septula. (After Gordon *et al.* 2002.)

Type species.—*Lepralia bilabiata* Hincks, 1884, by original designation. Recent, western North America from Alaska to Mexico, and Pleistocene of southern California.

Remarks.—Gordon *et al.* (2002) showed in their cladistic analysis of living and fossil eurystomellids that encrusting species lacking large frontal foramina and basal pore-chambers could be segregated at the genus level. Accordingly, they proposed the genus *Integripelta* to accommodate such species. This left *Eurystomella sensu stricto* as comprising three Recent species endemic to New Zealand. *Integripelta*, on the other hand, comprises two Recent species in New Zealand, three in Japan, and one along the Pacific coast of North America.

Integripelta sakagamii Grischenko and Gordon sp. nov.

Figure 4

Eurystomella bilabiata Hincks: Sakakura 1935, p. 25, fig. 7; Hayami 1970, p. 330, pl. 36, fig. 3; 1974, p. 224, pl. 69, figs 2a,b; 1975, p. 88; 1976, p. 44; 1980, p. 40; 1981, p. 111.

Material examined.—Holotype: ZIHU–2315. One colony encrusting shell of pectinid bivalve. Paratype:

ZIHU–2316. Two colony fragments. Same data as for holotype.

Etymology.—The species is named in honour of Professor Sumio Sakagami, Tokyo, in recognition of his contributions to Japanese geology and paleontology.

Type locality.—Kaigarabashi Sandstone Beds, at the streamside cliff of the Meppu-gawa River, north of Tanekawa, immediately northeast of the Kaigarabashi Bridge, in the Imakane area of southwestern Hokkaido.

Distribution.—Miocene: Mizunami Group, Gihu Prefecture (Hayami 1974); Yakumo Formation, Imagane area of southwest Hokkaido. Pliocene-Pleistocene: Hamada Formation, Aomori Prefecture; Shibakawa Formation, Akita Prefecture (Hayami 1975).

Description.—Colony encrusting, multiserial, unilamellar. Autozooids (Figure 4.1) contiguous, quincuncially arranged, 0.45–0.77 mm long (0.57 ± 0.08 mm), 0.33–0.48 mm wide (0.39 ± 0.03 mm). Gymnocystal frontal shield somewhat flat proximally, the anterior half frequently rising toward the orifice, the interior surface (Figure 4.2) with a corresponding change in slope, smooth-surfaced, hyaline or glassy. Autozooidal orifice wider than long, somewhat helmet-shaped owing to small proximolateral indentations in the corners (Figure 4.3), the anter with its proximal corners bluntly condyle-like, the proximal rim of the poster typically gently convex, rarely almost straight; a slight excavation of the gymnocyst occurs adjacent to each proximolateral indentation, with a very short proximal curvature. Maternal zooids (Figure 4.4) encompassed in the size range of autozooids but the orifice larger overall and higher-arched than in autozooids, 0.11–0.20 mm long (0.16 ± 0.03 mm), 0.15–0.27 mm wide (0.22 ± 0.03 mm). Distal kenozooidal chamber of moderate size (Figure 4.4–4.5), extending to basal wall, frontally variable, either somewhat squared in outline with the moderate-sized transversely oval foramen facing more distally than frontally, or produced forward and the foramen facing more frontally than distally. Basal wall of zooid calcified only around the margins (Figure 4.6), leaving a large window in the center. Interzooidal communications via uniporous septula. Ancestrula not seen.

Remarks.—*Integripelta sakagamii* most closely resembles *I. japonica* Gordon, Mawatari and Kajihara, 2002, especially in the form of the frontal shield and the very small gymnocystal excavations at the proximolateral corners of the orifice. Indeed, infertile specimens of both specimens are nearly identical. Fortunately, maternal zooids are common in most colonies and these clearly distinguish the two species. Maternal zooids in *I. sakagamii* have orifices larger than autozooidal orifices, the distal kenozooid descends to the basal wall, and its frontal foramen is conspicuous and transversely oval, in contrast to *I. japonica* in which the orifices are not dimorphic, the kenozooid does not descend to the basal wall, and the foramen is tiny.

Sakakura (1935) reported putative *I. bilabiata* from the Pleistocene Dizodo Beds, Bozo Peninsula, noting that the "furrows behind the corners of the aperture" are very long, up to twice the height of the orifice. His accompanying illustration of a Recent specimen said to resemble his fossils shows that, in both cases (i.e., the Recent and Pleistocene specimens) they belong neither to *I. bilabiata* nor *I. sakagamii* but to *I. shirayamai* Gordon, Mawatari and Kajihara, 2002.

Specimens of *I. sakagamii* were found on shells of pectinids, mostly on the concave interior surfaces. These evidently provided a favorable microhabitat as *I. sakagamii* is a common species in the Kaigarabashi Sandstone Beds.

Integripelta sakagamii is the first encrusting eurystomellid known solely as a fossil. It is also the earliest known encrusting eurystomellid (in contradistinction to *Selenariopsis* Maplestone, 1913, which is lensoidal and rooted). Gordon *et al.* (2002) commented that frontal shields with a suboral suture, indicative of vestigial costal spines, should be more primitive than entire frontal shields lacking sutures and frontal foramina, but the earliest known species of foraminate *Eurystomella* is from the New Zealand Pliocene (Brown 1952).

Superfamily Adeonoidea Busk, 1884
Family Adeonidae Busk, 1884
Genus ***Kubaninella*** Grischenko and Mawatari, 2002

Diagnosis.—Colony encrusting, multiserial. Zooids with umbonuloid frontal shields, centrally perforated by a spiramen that may remain single or become compound with several pores. Numerous marginal areolar pores around the zooidal margin. Avicularium suboral, on distolateral slope of well developed suboral umbo. Orifice suboval. Vicarious avicularia, oral spines, and kenozooids absent. Ovicells or enlarged brooding zooids unknown. Numerous small basal pore-chambers present, the septula uniporous. Ancestrula tatiform, budding proximally. (Modified after Grischenko and Mawatari 2002.)

Type species.—*Kubaninella relicta* Grischenko and Mawatari, 2002, by original designation. Recent, Sea of Okhotsk.

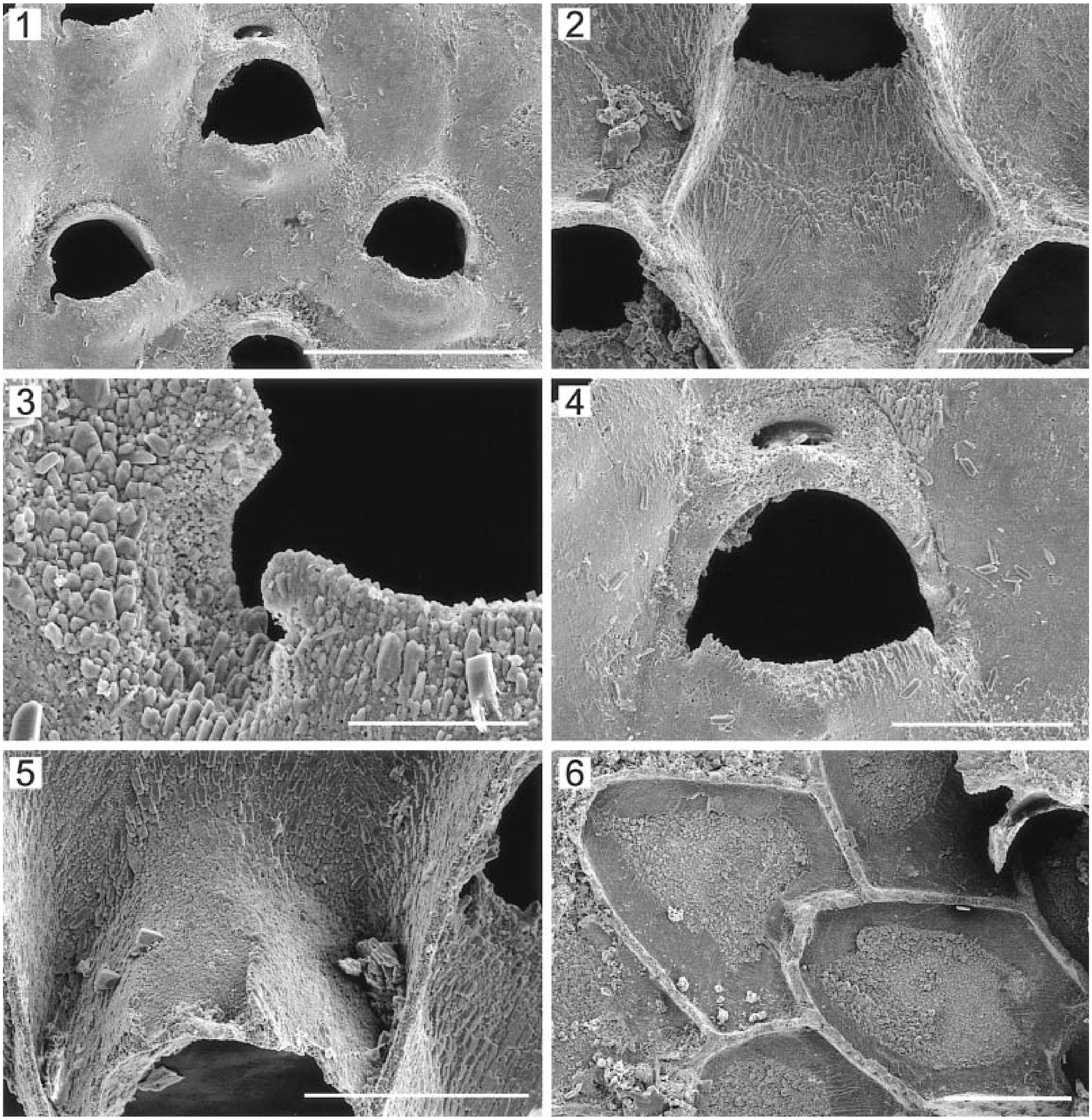

Figure 4. *Integripelta sakagamii* sp. nov. ZIHU–2315, late Middle Miocene, southwestern Hokkaido, Japan. **1**. Frontal view of autozooids and a maternal zooid. **2**. Underside of a zooid showing the curved change of slope in the frontal shield. **3**. Proximolateral corner of an orifice showing the short, curved excavation in the gymnocyst. **4**. Maternal orifice with ovicell-like kenozooid with apical foramen. **5**. Interior view of outer distal wall of kenozooidal chamber. **6**. Zooidal outlines at colony margin showing a large window in the basal calcification of each zooid and the absence of basal pore-chambers. **1**, scale bar = 500 μm. **2**, **4–6**, scale bar = 200 μm. **3**, scale bar = 50 μm.

Kubaninella miocenica Grischenko and Gordon sp. nov.

Figure 5

Material examined.—Holotype: ZIHU–2317. One colony encrusting a pectinid bivalve. Paratype: ZIHU–2318. Five colony fragments encrusting pectinid shells. Same data as for holotype.

Etymology.—The species name reflects the age of the geological formation in which it was found.

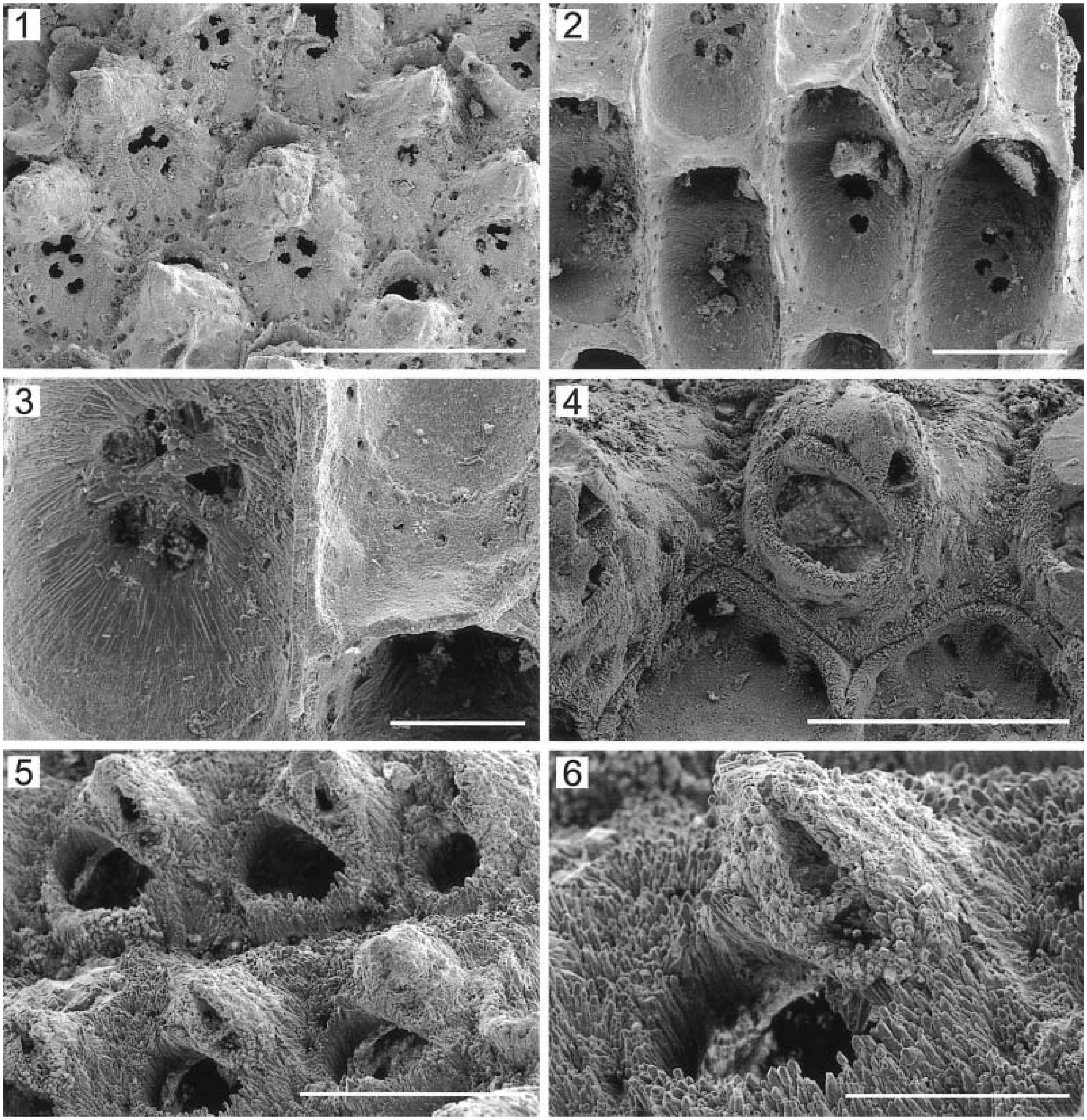

Figure 5. *Kubaninella miocenica* sp. nov. ZIHU–2317, late Middle Miocene, southwestern Hokkaido, Japan. **1**. Frontal view of autozooids showing robust suboral umbones and compound spiramina. **2**. Zooidal interiors showing spiramina. **3**. Close-up of zooidal interiors, showing compound spiramen in zooid at left (note umbonuloid microstructure) and a curved row of interior openings of areolar pore canals in zooid at right. **4**. Zooids at colony margin, showing orifices, adventitious avicularia in suboral umbones, and small basal pore-chambers. **5**. Colony with some diagenetic recrystallization, showing orifices and asymmetrical aviculiferous umbones. **6**. Same, close-up. **1**, scale bar = 1 mm. **2**, **4**, **5**, scale bar = 500 μm. **3**, **6**, scale bar = 200 μm.

Type locality.—Kaigarabashi Sandstone Beds, at the streamside cliff of the Meppu-gawa River, north of Tanekawa, immediately northeast of the Kaigarabashi Bridge, in the Imakane area of southwestern Hokkaido.

Distribution.—Kaigarabashi Sandstone Beds, Imakane area of southwestern Hokkaido, Middle Miocene.

Description.—Colony encrusting, multiserial. Zooids (Figure 5.1–5.2) with umbonuloid frontal shields, 0.57–0.85 mm long (0.69 ± 0.07 mm), 0.45–0.70 mm wide (0.57 ± 0.07 mm), centrally perforated by a compound spiramen (Figure 5.1, 5.3) with 2–5 pores. Numerous (usually >20) marginal areolar pore openings around the zooidal margin (Figure 5.1, 5.2). Orifice (Figure 5.4) suboval, 0.11–0.15 mm long (0.13 ± 0.01 mm), 0.17–0.25 mm wide (0.22 ± 0.02 mm). Avicularium suboral, on distolateral slope of a robust suboral umbo (Figure 5.4–5.6) that is coarsely sculptured, the rostrum triangular, the cross-bar complete. Vicarious avicularia, oral spines, and kenozooids absent. Ovicells or enlarged brooding zooids unknown. Numerous small basal pore-chambers present, the septula uniporous. Ancestrula not seen.

Remarks.—*Kubaninella miocenica* is clearly congeneric with *K. relicta*, the type species of the genus. Both share the same encrusting habit (the majority of adeonids are erect) and asymmetrical suboral aviculiferous umbo. The fossil species has a larger, more perforated, spiraminal pore complex and a more robust umbo. It is likely that other species of *Kubaninella* existed in the northwestern Pacific Ocean or in the back-arc basinal seas of the region. At present, with only two species known, it may be possible to suggest that a trend in the genus from the Neogene to the present day is to simplify the compound spiramen.

Specimens of *K. miocenica* were found on shells of pectinids, on the concave interior surfaces. The species is rare in the Kaigarabashi Sandstone Beds. Extant *Kubaninella relicta* also occurs on pectinids, including *Chlamys* (species not determined). It is apparently restricted to the Sea of Okhotsk off western Kamchatka, where it is known from a single locality at 57°36′N, 156°09′E at a depth of 78–81 m, where a late summer bottom temperature of 0.9°C has been reported (Leonov 1960).

Discussion

Hayami (1970) reported that the bryozoans from the Kaigarabashi Sandstone Beds generally exhibit good preservation and show two modes of occurrence – either attached to the valves of molluscs or free as fragments of erect broken stems or encrusting forms. We can confirm these observations but we have also noted some small colonies attached to echinoid spines and large sand particles. Our samples included most of the species that Hayami (1970) encountered, allowing us to comment on two aspects of the reported bryozoan diversity.

First, Hayami (1970) attributed to many of the species the names of taxa that were first described from the present day at geographical localities remote from the Middle Miocene of Hokkaido, e.g. *Corbulella* (as *Pyrulella*) *corbula* (Hincks, 1880) (Recent, southeastern Australia), *Micropora coriacea* (Johnston, 1847) (Recent, Britain), *Integripelta* (as *Eurystomella*) *bilabiata* (Hincks, 1884) (Recent, California), *Watersipora* (as *Dakaria*) *subtorquata* (d'Orbigny, 1852) (Recent, tropical Atlantic), *Microporella lunifera* (Haswell, 1880) (Recent, Queensland, Australia). Taxonomic work on all of these genera since 1970 (e.g. Ryland and Hayward 1977; Hayward and Ryland 1979; Gordon 1986, 1989; Dick & Ross 1988; Soule *et al.* 1995; Mawatari and Suwa 1998; Suwa and Mawatari 1998; Suwa *et al.* 1998; Gordon *et al.* 2002) gives evidence that none of these species (and several others) described by Hayami (1970) occurs in the Middle Miocene of Hokkaido. For example, Gordon *et al.* (2002) showed that Recent Japanese specimens of eurystomellid cheilostomes previously attributed to *Eurystomella bilabiata* represented three new species of *Integripelta* endemic to Japan. Hayami (1970) reported *E. bilabiata* from the Yakumo Formation in southwestern Hokkaido, but as shown above, our scanning electron micrographs of newly collected specimens demonstrated yet another new species of *Integripelta*. In short, the level of endemicity of bryozoans in the Japanese Neogene will be higher than that reported.

Our finding of two new species not encountered by Hayami (1970) at a locality sampled and analysed by her strongly indicates that the Japanese Neogene has been inadequately sampled for Bryozoa. It is clear from these discoveries that more intensive collecting at all known Japanese fossil localities, coupled with detailed taxonomic revision and study using scanning electron microscopy (SEM), will certainly increase Neogene bryozoan diversity. Such has begun with the work of Arakawa (1995). Better taxonomic knowledge will permit phylogenetic analyses of improved resolution. Hayami (1975) categorically stated that knowledge of the Tertiary bryozoans of Japan is ''inadequate'', suggesting that apparent low species diversity is more the consequence of limited taxonomic work, rather than because of intrinsically low natural diversity. We agree with her assessment.

The Middle Miocene at 16–14 Ma was a warm period known as the Mid-Neogene Climatic Optimum, and a subtropical front lay across southwestern Hokkaido where the marine environment was generally shallow (Suzuki *et al.* 1994). The Kaigarabashi Sandstone Beds (15–12 Ma based on planktonic foraminifera) were deposited during a transitional period, beginning at 12 Ma, when temperatures were cooling gradually, owing to the diminishing effect of a warm current. Molluscan fossils in the Kaigarabashi Sandstone Beds include warm-current species (Masuda and Ogasawara 1982) and temperate to warm-water benthic foraminiferans also occurred (Uchida *et al.* 2001). Paleodepth is estimated as deeper than the middle to outer sublittoral zone (90–100 m) (Hasegawa 1998; Uchida *et al.* 2001).

Hayami (1970) had also interpreted the assemblage in the Kaigarabashi Sandstone Beds as occurring in a nearshore coastal setting that was likely to have been temperate to warm (inferred in part from the presence of *Monoporella*). On the other hand, the presence of *Hayamiellina constans* sp. nov. indicates cool temperatures, judging from the present-day temperature regime at the Commander Islands and Gulf of Alaska where the species lives. Hayami (1970) identified her specimens of *Monoporella* as *M. fimbriata* Canu and Bassler, 1927, which is common in the Recent tropics (e.g. Indonesia, Philippines). It is clear, however, from our examination of *Monoporella* in the Kaigarabashi Sandstone Beds that it is not conspecific. *Inter alia*, there is no trace of oral spines, and the zooids are smaller and proportionally narrower.

Molluscan fossils and benthic foraminiferans from the Kaigarabashi Sandstone Beds indicate a warm climate, but the peak of Miocene warm water had passed by the time of the deposition of the beds. Because the sea area around Hokkaido at that time, as at the present day, belonged to a cool-water regime except during the Mid-Neogene Climatic Optimum event, the sporadic occurrence of warm-current species in the beds is considered as indicating that event. Uchida *et al.* (2001) described some depositional cycles inferred to be formed by a cool–warm climatic change such as a glacial sea-level change, based on their detailed observation of an eastern outcrop. Coexistence of warm- and cool-water species in one outcrop is therefore likely to occur.

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