Two new species of heavily calcified cyclostome bryozoans from the intertidal of Akkeshi Bay, Hokkaido, Japan

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Cyclostome bryozoans are relatively uncommon in intertidal habitats, where they are subordinate to cheilostomes and ctenostomes. Those that do occur tend to have small colonies that are relatively weakly calcified. Here we describe two new species of intertidal cyclostomes from Akkeshi Bay in northern Japan that are unusual in having large, heavily calcified colonies. One of these – \textit{Favosipora ainui} sp. nov. – is the first species of this genus recorded from Japan. The second species – \textit{Disporella ezoensis} sp. nov. – although belonging to a genus well known from Japan and elsewhere globally, is unusual for \textit{Disporella} in possessing colonies that are vivid red in colour.

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Introduction

Of the two orders of living bryozoans with calcareous skeletons, species belonging to the Cyclostomata are considerably less abundant and diverse than are those of the Cheilostomata: Bock and Gordon (2013) estimated that the modern biota contains 543 species of cyclostomes compared with 4921 cheilostome species. This pattern of cheilostome dominance, which extends across all major marine habitats and biogeographical regions, is particularly evident intertidally: apart from some small encrusting epiphytic species of \textit{Tubulipora} and jointed erect species of crisids, cyclostomes are seldom found in intertidal habitats. For example, Ryland’s (1986) key to intertidal bryozoans from British waters listed only five species of cyclostomes compared to 40 cheilostomes and 13 ctenostomes. Large, heavily calcified cyclostomes are notably seldom recorded from intertidal settings.

Information about the intertidal cyclostomes from Far Eastern Seas and indeed the entire North Pacific Region is sparse: the majority of regional and local studies (Kubanin 1976; Dick and Ross 1988; Grischenko 1994, 2004; Dick et al. 2005, 2006; Grischenko et al. 2007) have focused on the orders Cheilostomata and Ctenostomata. Kubanin’s (1997) comprehensive checklist of intertidal bryozoans of the Far Eastern Seas listed only seven cyclostome species (5.5\%) among 128 intertidal bryozoans for the enormous shoreline of the region. He recorded \textit{Entalophoroecia capitata}...
(Robertson, 1900), *Crisis* sp. and *Lichenopora verrucaria* (Fabricius, 1780) from the Commander Islands; *Crisis eburnea* (Linnaeus, 1758) from the Commander Islands and Middle Kuril Islands; *Lichenopora radiata* (Audouin, 1826) and *Tubulipora* sp. from the Southern Kuril Islands; and *Fилиcria* sp. from the Peter the Great Gulf in the Sea of Japan.

Akkeshi Bay on the Pacific side of Hokkaido in northern Japan contains a diverse intertidal fauna of cheilostome bryozoans that was described by Grischenko et al. (2007). These authors reported the presence of 39 cheilostome species and also estimated the presence of five species of cyclostomes, all unidentified (Grischenko et al. 2007, footnote to table VI). The objective of the current paper is to describe two of the five Akkeshi Bay intertidal cyclostomes, which are noteworthy in having large, heavily calcified colonies atypical of such environmental settings globally.

**Intertidal cyclostomes in Japan**

Busk (1884) published the first records of bryozoans from Japan. Since then, most studies have dealt primarily with subtidal species, and only incidental records of intertidal occurrences are to be found scattered through the large literature. Many early reports fail to provide adequate bathymetric data, or provide only oblique indications of intertidal occurrences.

The works of the eminent Japanese bryozoologist Yaichirō Okada and his colleagues indicated that a number of species occurred intertidally. In a report on the cyclostomatous Bryozoa of Japan, Okada (1917) noted that *Crisis aburneo-denticulata* Smitt, 1865 was abundant between tidemarks near Misaki, Sagami Bay, attached to stones and shells. In the same report, data for five additional species (*Crisulipora occidentalis* Robertson, 1910, *Tubulipora pacifica*, Robertson, 1910, *T. pulchra* MacGillivray, 1885, *T. misakiensis* Okada, 1917, and *Lichenopora novae-zelandiae* (Busk, 1875)) indicates that they also occurred intertidally in the same area, attached to seaweeds, stones and shells. Okada (1918) reported *Tubulipora misakiensis* on *Zostera* sp. from Mutsu Bay, and noted that this species occurred abundantly in shallow waters along the Misaki shore, attached to seaweeds and stones. Almost two decades later, Okada and Mawatari (1937) recorded *Tubulipora pulchra* MacGillivray, 1885 from the intertidal belt along Onagawa Bay (north-eastern Honshu Island). Unfortunately, the checklist of 78 known species of Japanese cyclostomes published by Mawatari (1955) is not accompanied by bathymetric or other environmental data.

Since the early 1970s faunal surveys have become more common in the coastal waters around Hokkaido Island, giving some indication of the importance of bryozoans in intertidal communities. Mawatari and Mawatari (1973) published descriptions of 10 species of crisisiid cyclostomes from Hokkaido (including three new species: *Crisis globosa*, *Bicrisia erecta* and *Crisiella oblique*), all of which occurred in Akkeshi Bay. In a subsequent paper on non-crisiid cyclostomes, Mawatari and Mawatari (1974) reported 14 of 24 species, including the new species *Fasciculipora yesoensis*, as occurring in Akkeshi Bay. Thus, 24 of 31 cyclostome bryozoan species recorded from Hokkaido are known Akkeshi Bay. Although none of these records are accompanied by bathymetric information, some do seem to have been collected intertidally. A recent intensive study of the intertidal bryozoan fauna of Akkeshi Bay focusing on cheilostomes (Grischenko et al. 2007) has found at least five cyclostome species occurring intertidally.
This first summary of existing information on the intertidal cyclostome bryozoans from Japan demonstrates that almost all previous records have been incidental; no efforts have been made in Japan to study specifically an intertidal cyclostome assemblage or to investigate diversity, biogeographical composition and ecology. Nonetheless, a moderately rich intertidal cyclostome bryozoan fauna evidently exists in the region.

Study area and methods
The study area was described in detail by Grischenko et al. (2007) and only the most important points will be repeated here. Akkeshi Bay (Figure 1) on the north-eastern coast of Hokkaido Island is about 13 km long by 9 km across and about 30 m deep at its mouth, gradually shallowing towards the inner part. It opens to the Pacific Ocean in the south and south-east and is influenced by the cold Oyashio Current and to a lesser extent by an offshoot of the warm Tsushima Current. Recorded temperatures in the bay range from −1.4°C to 21.1°C, with salinity relatively constant at approximately 30 psu.

Figure 1. Map of Akkeshi Bay showing sampling stations (filled squares). Inset shows the location of Akkeshi Bay on Hokkaido Island, northern Japan. From Grischenko et al. (2007).
The cyclostomes described here were collected from two sites at Aikappu Cape, and one site at Aininkappu Cape and Mabiro Cape, all located on the eastern coast of the bay. Abbreviations and details of these localities (based on Grischenko et al. 2007) are as follows.

Aikappu Cape, west side, 43°00.46'N, 144°50.15'E; 2 June 2004; 0.02 m mean lower low water (MLLW) at 08:39 h; rocky, creviced reef flat with boulders and cobbles, and pebbles and shell fragments under the boulders and wedged in cracks; zone of Laminaria spp.; specimens obtained from rocks and broken shells. Disporella ezoensis sp. nov. (1 specimen), Favosipora ainui sp. nov. (1 specimen).

Aikappu Cape, tip, 43°00.42'N, 144°50.12'E; 3 June 2004; 20.06 m MLLW at 09:16 h; prominent rocky reef flat with crevices and pools, overlain by shingle, cobbles and boulders, with broken shells and gravel under the boulders and wedged into crevices; zone of Laminaria spp.; specimens collected from rocks and shell fragments. Disporella ezoensis sp. nov. (16 specimens), Favosipora ainui sp. nov. (8 specimens).

Aininkappu Cape, 42°59.56'N, 144°51.30'E; 5 June 2004; 20.10 m MLLW at 10:31 h; prominent rocky reef flat with crevices, pools, caves and layered boulders and cobbles, with many smaller rocks under the boulders; Fucus sp. and Laminaria spp. zones; specimens obtained from various rocky surfaces. Disporella ezoensis sp. nov. (19 specimens), Favosipora ainui sp. nov. (14 specimens).

Mabiro Cape, 42°58.57'N, 144°53.21'E; 4 July 2004; 20.04 m MLLW at 10:20 h; prominent rocky reef flat with layered boulders and cobbles, with numerous smaller rocks under the boulders; zone of Laminaria spp.; specimens collected from rock substrates. Disporella ezoensis sp. nov. (4 specimens constituting additional material not registered into the Natural History Museum, London, UK (NHMUK) collections).

Specimens collected were initially preserved by drying. After soaking for a few hours in 10% commercial bleach, specimens were rinsed and dried prior to scanning electron microscopy. A low vacuum Leo 1455-VP instrument was employed to image uncoated specimens using back-scattered electrons.

Taxonomy

Order CYCLOSTOMATA Busk, 1852
Suborder RECTANGULATA Waters, 1887
Family LICHENOPORIDAE Smitt, 1867
Genus Disporella Gray, 1848
Disporella ezoensis sp. nov.
(Figures 2A and 3)

Bimulticavea variabilis: Mawatari and Mawatari, 1974, p. 356, plate 29, figures 3–5 (non Bimulticavea variabilis d’Orbigny, 1853, p. 983, plate 779, figures 9–13).

Material examined
Holotype: NHMUK 2014.11.18.1 (Figures 2A, 3A–E), Aininkappu. Paratypes: NHMUK 2014.11.18.2, Aininkappu; 2014.11.18.11–12 (Figure 3F), Aikappu; 2014.11.18.8–10, Aikappu; 2014.11.18.4–7, Aininkappu; 2014.11.18.3, Aininkappu.
Derivation of name
From Ezo, an old Japanese name for Hokkaido and smaller islands in the north of the country.

Description
Colony encrusting, multiserial, unlilamellar or multilamellar, roughly circular, oval to irregular, with undulating margins, attaining about 4 cm in maximal dimension; red in colour, amaranth or crimson when alive; surface irregularly mounded, with monticules of varying shape and size, some subcircular, others elongate. Individual layers about 1.4 mm thick. Distal fringe of basal lamina narrow (<500 µm). Skeletal organization free-walled throughout. Mural spines simple, dense at growing edge. Early astogeny unknown.

Autozooids with circular to elliptical apertures, 130–170 µm long by 100–140 µm wide, one or two stout, distally tapering, unbranched oral spines, variable in length, some > 100 µm long. Apertures often connate, sometimes in rows, occasionally separated by kenozooids. Convex, thin diaphragms, some with a median pore, developed locally.

Kenozooids (alveoli) moderately abundant, slightly outnumbering autozooids, apertures subcircular, smaller and more variable in size than those of autozooids, 60–110 µm long by 60–80 µm wide. Walls thick with a sharp median ridge. Apertures locally occluded by thin, convex diaphragms.

Gonozooid with strongly digitate to dendritic outline, indented and penetrated by single or groups of autozooids. Roof of porous interior wall, the pores large and partly occluded by fine radial spines. Brood chamber about 350 µm high, becoming overgrown by autozooids and kenozooids. Short mural spines closely spaced on vertical walls lining brood chamber close to roof. Ooeciopore not observed.
Figure 3. *Disporella ezoensis* sp. nov. (A–E) holotype, NHMUK 2014.11.18.1: (A) surface of fertile colony; (B) large autozooidal apertures with smaller kenozooids overgrowing the roof of a dendritic gonozooid; (C) oblique view showing apertural spines; (D) thin diaphragms closing autozooidal and kenozooidal apertures; (E) partly formed gonozooid with aperture of probable fertile zooid indicated by an arrow; (F) paratype, 2014.11.18.12, vertical fracture through a gonozooid showing cylindrical autozooids passing through the brood chamber. Scale bars: A = 1 mm; B, E, F = 100 µm; C = 200 µm; D = 100 µm.
Opening of fertile zooid in floor of gonozooid elliptical and about half the diameter of an autozooidal aperture.

**Remarks**

Notwithstanding the work of Alvarez (1995 and references therein), *Disporella* is a speciose genus in need of a thorough revision, beginning with the type species *D. hispida* (Fleming, 1828) which has not only been variously interpreted but also lacks valid type material (see Gordon and Taylor 2001, p. 259). There can be considerable changes in skeletal morphology as colonies grow, develop additional cormidial units and become fertile with gonozooids that may subsequently be overgrown. As these changes have been documented for very few of the nominal species of *Disporella*, species identification is difficult.

The vivid red colour of unbleached colonies of the new species is unusual for *Disporella*, although a pink coloration was noted for *D. wanganuiensis* (Waters, 1887) by Gordon and Taylor (2001) but this New Zealand species has autozooids arranged in well-defined radial rows 1–3 zooids wide that form distinct ridge-like fascicles, and apertural spines are wanting. The European species *Disporella mamillata* (Lagaaij 1952), considered by Hayward and Ryland (1985, p. 130) to be a form of *D. hispida*, has compound colonies reminiscent of *D. ezoensis* sp. nov. but lacks the intense red coloration seen in the Japanese species.

The checklist of Japanese cyclostome bryozoans published by Mawatari (1955) listed 11 species of lichenoporids, all assigned to the genus *Lichenopora* Defrance, 1823 (now *Patinella* Gray, 1848; see Gordon and Taylor 1997). Mawatari and Mawatari (1974) subsequently described six lichenoporid species from Hokkaido, five assigned to *Lichenopora* and one to *Bimulticavea*. The latter – *B. variabilis* d’Orbigny, 1853 – was collected from Akkeshi and described as forming thick crusts of two or three layers encrusting stones. From the description and illustrations, it is likely that this species is *D. ezoensis* sp. nov. It is not conspecific with *B. variabilis*, which is a Late Cretaceous fossil from France (see [http://www.nhm.ac.uk/research-curation/research/projects/dorbigny/dOrbgenus/Bimulticavea/Bimulticavea.html](http://www.nhm.ac.uk/research-curation/research/projects/dorbigny/dOrbgenus/Bimulticavea/Bimulticavea.html)), characterized by stellate clusters of autozooidal apertures surrounding broad maculae.

**Occurrence**

Colonies of *D. ezoensis* sp. nov. were recorded at four localities along the eastern coast of the Akkeshi Bay, showing local abundance near the tip of Aikappu Cape and at Aininkappu Cape. All colonies encrusted rock surfaces (smaller rocks and pebbles) lying beneath large stones, layered boulders, cobbles and clods. Close proximity of adjacent colonies resulted in their mutual overgrown and the formation of a continuous wrinkled cover on the substrata, attaining 12 × 4 cm in dimensions, and possessing a typically vivid red colour.

**Family DENSIPORIDAE** Borg, 1944

**Genus Favosipora** MacGillivray, 1885

*Favosipora ainui* sp. nov.

(Figures 2B and 4)
Figure 4. *Favosipora ainui* sp. nov., holotype, 2014.11.18.13: (A) colony surface showing autozooidal and kenozooidal apertures as well as the larger opening (left) of a symbiont tube; (B) two bicuspat autozooids surrounded by smaller kenozooids; (C) partly developed gonozooid with roof calcification growing centrifugally from the autozooids passing the brood chamber; (D) ooeciopore (centre), with flared ooecistome, pseudoporous gonozooid roof and autozooidal apertures closed by pseudoporous terminal diaphragms; (E) two complete gonozooids, that on the left with some of the penetrant autozooids arranged connately. Scale bars: A, C, E = 500 µm; B, D = 200 µm.
Material examined
Holotype: NHMUK 2014.11.18.13 (Figure 4), Aikappu. Paratypes: NHMUK 2014.11.18.14–16, Aikappu; 2014.11.18.23 (Figure 2B), Aininkappu; 2014.11.18.17–22, Aikappu.

Derivation of name
In reference to the native people of Hokkaido, the Ainu.

Description
Colony encrusting, multiserial, unilamellar or multilamellar, irregularly circular to oval, attaining about 3 cm across; corn or lemon when alive; surface irregularly mounded, with occasional monticules, some elongated parallel to local growth direction, and chimney-like prominences formed around tubes of symbionts. Distal fringe of basal lamina variable in width, locally extending about 1 mm beyond budding zone. Skeletal organization free-walled with the exception of fixed-walled gonozooids. Mural spines short and sparse. Early astogeny unknown.

Autozooids with elliptical apertures and bicuspid apertural rims standing slightly above the surrounding kenozooids with prolongations at opposite ends of the long axis of the aperture, diameter typically 125–138 µm by 110 µm. Apertures typically separated by kenozooids, occasionally connate.

Kenozooids abundant, outnumbering autozooids, apertures subcircular, smaller and more variable in size than those of autozooids, about 50–110 µm in diameter. Walls between kenozooids thick, with a slight median ridge.

Gonozooids frequent, subcircular in overall outline shape, about 1.50–1.65 mm in diameter, a salient wall forming the slightly digitate outer border. Roof of pseudoporous exterior wall penetrated and supported by about 30 circular autozooidal apertures having short, sharp-edged peristomes, often closed completely or partly by a terminal diaphragm and either isolated or connate and arranged in radial rows of up to five apertures. Polygonal pattern of sutures in roofs of complete gonozooids, as well as morphology of partly formed gonozooids, show calcification developing outwards from peristomes of penetrative autozooids. Ooeciopore located at centre of gonozooid, strongly elliptical in shape, the maximum width similar to that of apertures of the penetrative autozooids, 50 µm by 95 µm in diameter, a short, funnel-like, ooeciostome with a subcircular opening about 145 µm by 155 µm in diameter.

Remarks
Twelve species of *Favosipora* have been recognized, comprising 11 recent species from the Pacific and Indian oceans and one fossil species from the Miocene of Italy (Gordon and Taylor 2001, 2010; Dick et al. 2006; Toscano and Taylor 2008). *Favosipora ainui* sp. nov. is the first species recorded from Japan. Gonozooids in species of *Favosipora* fall into two main morphological groups: in the majority of species, the gonozooid has a sinuous outline and the roof is not penetrated by autozooids, but in a second group, including the new species, autozooids pass
through the roof and support it. Among species in this second group, *Favosipora ainui* sp. nov. most closely resembles *F. otagoensis* (Taylor et al. 1989), an obligate, tube-building symbiont of hermit crabs from New Zealand. However, the new species has a greater number of autozooids penetrating the roof of the gonozooid (c. 30 vs. c. 20) and their apertures are not bicuspidate, unlike apertures elsewhere in colony. Furthermore, the ooeciostome is shorter and the ooeciopore appreciably smaller in *F. otagoensis* than in *F. ainui* sp. nov. Another species from New Zealand, *F. marmorosa* Gordon and Taylor, 2001, also has gonozooids penetrated by autozooids but the gonozooids in *F. marmorosa* contrast with those of the new species in having a markedly digitate outline. In addition, colonies of *F. marmorosa* are strongly monticulate, with pale monticules surrounded by more heavily pigmented intermonticular areas, whereas colonies of *F. ainui* are corn or lemon in colour.

**Occurrence**

Specimens of *F. ainui* were detected at three localities on the eastern coast of Akkeshi Bay, being locally abundant at Ainkinkappu Cape. The great majority of colonies (22 of 23) formed roughly circular encrustations, up to 3 cm across, on various smaller rocks and pebbles lying beneath boulders, or occasionally on the undersides of boulders. A single colony was found encrusting a fragment of an unidentified bivalve shell. Some colonies were densely penetrated by tubes occupied by sedentary polychaetes (Figures 2B, 4A).

**Discussion**

Large, heavily calcified cyclostomes such as the two new species described here are not usually associated with the intertidal zone. Such habitats are dominated by cheilostomes and ctenostomes, the few cyclostomes that are present tending to be ‘weedy’ species of *Crisia* and *Tubulipora*, although the robust ramose cyclostome *Heteropora* can be found at extreme low tide in Oregon and Washington State (Ross 1973). Whether Akkeshi Bay in northern Japan is globally unique in supporting two species of robust encrusting cyclostomes intertidally, or occurrences are more widespread in Japan and elsewhere, requires investigation. The geological record too provides almost no examples of stenolaemate bryozoans related to *D. ezoensis* sp. nov. and *F. ainui* sp. nov. inhabiting intertidal environments except perhaps for a single record of small mounds constructed by bryozoans in an Ordovician sequence of dominantly intertidal sediments in south-western Virginia (McKinney et al. 2001). In addition, *Disporella ezoensis* sp. nov. and *Favosipora ainui* sp. nov. merit further investigation to ascertain whether they have exhibit any particular physiological or anatomical adaptations, not evident in the skeletons, that enable them to survive and develop large colonies in typically stressed intertidal settings.

The skeletons of both of the new species from Akkeshi contain protuberant tubular structures. The apertures of these tubes are more than twice the diameter of the autozooidal apertures. By analogy with similar structures found in other bryozoans (see Taylor 1991; Ernst et al. 2014), the tubes were secreted by the bryozoans around a symbiont, most likely a spionid polychaete. d’Hondt and Mascarell (2004, figure 2.2) figured a similar symbiont tube in a lichenoporid cyclostome from French
Polynesia, erroneously interpreting it as an ooeciostome and using it to justify the creation of their new species *Disporella julesi*.

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