Overview of Pleistocene Bryozoans in Japan

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ABSTRACT

We compiled a list of bryozoan taxa reported between 1935 and 1995 from Pleistocene deposits in Japan. Our list adds many Pleistocene records to the 1980 checklist of Sakagami *et al*.: although only a handful of additional Pleistocene records of bryozoans have been published since 1980, many deposits previously considered to be of Pliocene age have now been more accurately dated as Pleistocene. These include the Setana, Hamada, Hirose, Daishaka, Shibikawa, Sawane, Haizume, and Omma Formations. Our list contains 358 taxa, including 97 new to science described from Pleistocene Japan. Previous studies have been concentrated in four regions of Japan: 1) Boso Peninsula, central Honshu, Pacific side; 2) SW Hokkaido and N Honshu in the vicinity of Tsugaru Strait; 3) Noto Peninsula and Niigata, central Honshu, Sea of Japan; and 4) Kikai-jima Island in the Nansei Archipelago south of Kyushu. We present the number of total taxa and new taxa reported per region and formation, and compare the similarities among regions. We report newly discovered Pleistocene deposits from two regions: the Setana Fm. near Kuromatsunai, Hokkaido, and the Oe and "Kita Arima" Fms. on the Shimabara Peninsula, Kyushu. Pleistocene bryozoans are relatively well known in Japan, and with increased taxonomic resolution can provide a 'model system' for investigating the effects of climate change on assemblages of sessile benthic marine animals.

Keywords: Benthic, Biodiversity, Bryozoa, Climate change, Ectoprocta, Fossil, Japan, Paleoclimate, Pleistocene, Polyzoa, Taxonomy

INTRODUCTION

During the Pleistocene Epoch (1.8–0.01 Ma), cyclical oscillations occurred between cool and warm periods, with corresponding episodes of glaciation alternating with interglacial periods and marine transgressions. The response of organisms, both terrestrial and marine, to these climatic oscillations and the role of climatic changes in speciation and extinction are fundamental questions for evolutionary biologists [1] and are also relevant to predicting the effects of anthropogenically induced rapid climate change today. In contrast to fossil marine molluscs, which have been relatiely well studied from the

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viewpoints both of reconstructing Pleistocene environments and examining the effects of climate change on benthic assemblages [e.g., 2], members of the largely marine phylum Bryozoa have scarcely been utilized to address these questions. Bryozoans are moderately diverse in modern oceans, with at least 10,000 species, and have left a substantial fossil record due to the calcified outer skeleton in most marine groups. The most diverse group among living bryozoans is the Order Cheilostomata, which originated in the Jurassic Period and has undergone an explosive radiation since the Late Cretaceous.

It is important to study macrobenthic groups other than molluscs, for different groups may have characteristics that cause them to respond differently to climatic changes. For example, compared to marine molluscs, bryozoans are relatively uniform in life history. Molluscs can be epibenthic or infaunal, sessile or mobile; show a large variety of feeding strategies, including predation and filter-feeding; and show a large variety of reproductive strategies ranging from planktotrophic development to direct development in egg cases. In contrast, the vast majority of marine bryozoans are sessile; virtually all are epibenthic or are epizoic on epibenthic organisms; all are filter feeders; and most reproduce by a poorly dispersing, brooded larva.

In this report, we review the status of studies of Pleistocene bryozoans in Japan. Pleistocene marine deposits are common and widespread on both the Pacific and Sea of Japan coasts of the main islands of Japan, as well as in the Nansei archipelago to the southwest. Bryozoans are abundant in most of these deposits, attached to a variety of hard substrates such as mollusc shells, corals, barnacles, and pebbles, and have been relatively well documented. Furthermore, the Pleistocene geology of Japan has been extensively studied. For these reasons, we conclude that Pleistocene bryozoans in Japan comprise a potential resource for studying the effects of climatic oscillations on benthic marine organisms.

METHODOLOGY

A 1980 checklist of Japanese Cenozoic fossil Bryozoa by Sakagami, Arakawa, and Hayami [3] provided the starting point for our review. This checklist, which summarizes the literature on Cenozoic bryozoans in Japan through 1978, is organized as an annotated alphabetical species list, with each entry reflecting updated taxonomy in some cases, citations of previous reports with page and illustration numbers, and stratigraphic formations and ages from which each species had been reported. We constructed an Excel database of the Pleistocene bryozoans tabulated in the checklist, listing for each species sources in the primary literature; whether or not illustrations were provided in the primary sources; grade of bryozoan (cyclostome, ctenostome, anascan, cribrimorph, or ascophoran); and stratigraphic formations from which the species was reported. This last entry allowed us to compare the known species diversity and composition of Pleistocene bryozoans among formations and among sub-regions of Japan, data that were difficult to access from the checklist.

Although the 1980 checklist was extraordinarily comprehensive at the time of its publication, it is now out of date with regard to Pleistocene bryozoans, for two reasons. First, a few taxa have been added to the known Japanese Pleistocene bryozoan fauna since 1978. Second, and more importantly, several formations considered to be of Pliocene age at the time of the checklist have now been more accurately dated as Pleistocene, thus adding many records to the known Pleistocene fauna. These include the Setana Fm. [4] of southwestern Hokkaido; the Hamada [5], Hirose [6], and Daishaka [4] Fms. of Aomori Prefecture and the Shibikawa [7] Fm. of Akita Prefecture, northernmost Honshu; and the Sawane [8], Haizume [9], and Omma [9] Fms. in the vicinity of the Noto Peninsula and Niigata, western central Japan, Sea of Japan coast. Ages and durations of Pleistocene formations known to contain bryozoans are shown in Fig. 1, which also correlates current names with those used in ref. 3. The age and nomenclature of formations considered both in ref. 3 and currently to be Pleistocene are treated in the following references: Kayamachi Fm. [10], Hiradoko Fm. [11], Narita Fm. [12], Jizodo Fm. [12], Semata Fm. (= Yabu Fm., Shimosa Group) [13], and the Ryukyu Group [14].

For purposes of tabulation and comparisons of known diversity among strata and regions, we use the term "taxon" to refer to formally described nominal species, subspecies, and varieties; unidentified specimens listed only as "*Genus* sp." or "*Genus* Indet."; and collective taxa listed as "*Genus* spp." Finally, we also include taxa that appeared only in lists, without illustration or description.

RESULTS

Distribution of studies on Pleistocene bryozoans in Japan

Pleistocene bryozoans have been extensively studied in four parts of Japan (Fig. 2), which we list be-

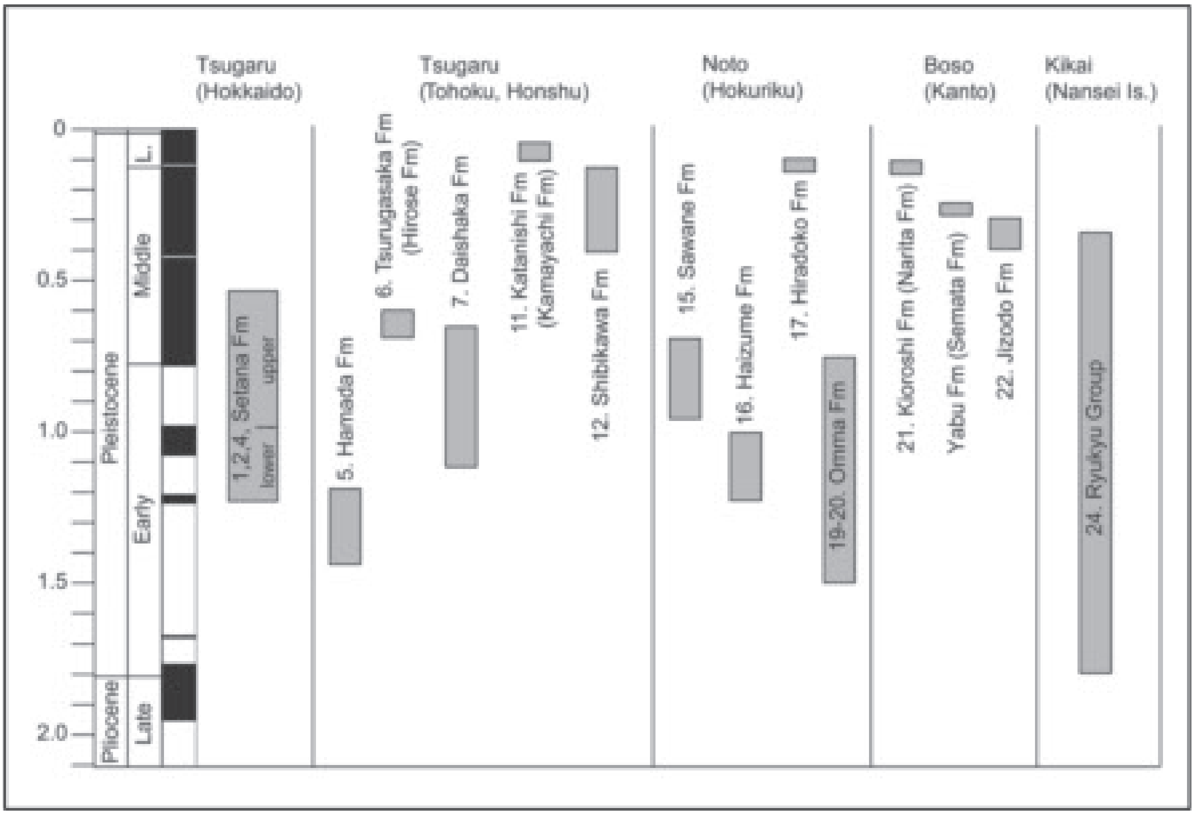

Fig. 1 Age and stratigraphic range of Pleistocene formations in Japan known to contain bryozoans. Numbers preceding current formation names correspond to numbers in Fig. 1 of ref. 3, with older names in parentheses if usage has changed. Formations are grouped according to the regions shown in Fig. 2, except that the Hokkaido and Honshu areas adjacent to Tsugaru Strait are separated here.

low in order of historical effort. Numbers of total taxa and new taxa are listed in Table 1 by region and formation.

Boso: central Honshu on the Pacific side (Boso Peninsula, Chiba Prefecture; ~35.5°N). This was the first region studied and remains the best studied. Between them, Sakakura [15, 16], Arakawa [17], and Fukuda [18] documented 145 taxa from this region, primarily from the Jizodo Fm., but also from the Narita Fm. and Semata Fm.

Tsugaru: southwestern Hokkaido and northern Honshu (~39.7–42.7°N). Oshima Peninsula in southwestern Hokkaido (Setana Fm.); Aomori Prefecture (Hamada, Hirose, and Daishaka Fms.) and Oga Peninsula, Akita Prefecture (Kamayachi and Shibikawa Fms.) in northern Honshu. Due to the proximity to Tsugaru Strait connecting the Sea of Japan with the Pacific Ocean, the faunal composition of deposits in this region was potentially influenced by both oceans; this consideration applies more to the formations of the Oshima Peninsula and Aomori Prefecture than to those of the Oga Peninsula. Between them, Kataoka [19] and Hayami [20–22] documented 129 taxa from this region.

Noto: west central Honshu, Sea of Japan Coast (~37°N). This region includes the Noto Peninsula of Toyama and Ishikawa Prefectures (Hiradoko and Omma Fms.) and the mainland in the vicinity of Niigata (Haizume Fm.); the fauna was well isolated from influences from the Pacific side of Japan. This region was exclusively studied by Hayami [22], who documented 26 taxa there.

Kikai: Kikai-jima Island, Nansei Archipelago of southwestern Japan (28.3°N). This island lies in the Pacific Ocean, with the archipelago to which it belongs forming the boundary between the North Pacific proper and the East China Sea. Kataoka [23] reported 122 species from this locality ["Ryukyu Limestone," Ryukyu Group], although our tally from refs. [3, 23] is 133 taxa.

The Japanese Pleistocene bryozoan fauna

Our list of Japanese Pleistocene bryozoans includes 358 taxa, including 99 (27.7%) anascans, 221

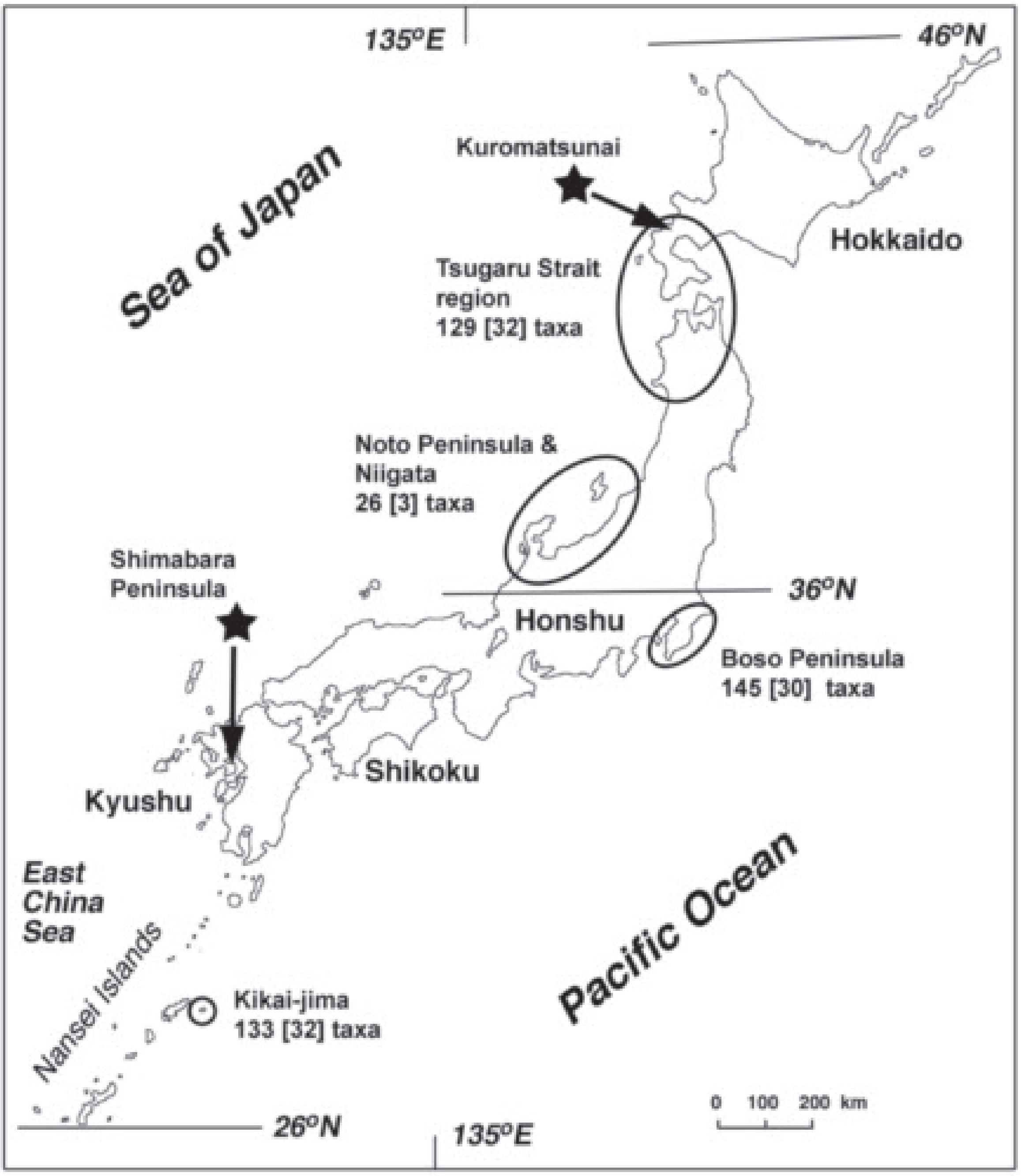

Fig. 2 Map of Japan showing the main areas of Japan (circled) where Pleistocene bryozoans have been studied. Following each region name are the number of bryozoan taxa reported from the region and [in square brackets] the number of taxa new to science originally described from Pleistocene material from the region. Stars with locations indicated by arrows indicate promising new localities that we have examined.

(61.7%) ascophorans, 14 (3.9%) cribrimorphs, two (0.6%) ctenostomes, and 22 (6.1%) cyclostomes. The only ctenostomes reported were unidentified species of *Penetrantia* and *Immergentia* [18b], recognized from their bore holes in shells. The cyclostomes have not been well studied. Only Sakakura [15, 16] attempted to identify all the cyclstomes in his material, although other workers reported a few [18e, 19].

Of the 358 taxa recorded, 37 (10.3%) were identified to genus only, and 30 (8.3%) were indicated as questionable identifications by the inclusion of

Table 1 Number of total taxa and new bryozoan taxa reported from the Pleistocene of Japan, by region and formations within regions. Region names refer to the circled areas in Fig. 1. Formation names appearing in refs. 3, 22 are used here; see Fig. 1 for corresponding names currently in use.

	total taxa	new taxa		total taxa	new taxa
Boso	145	30	**Tsugaru**	129	32
Jizodo Fm	124	26	Hamada Fm	32	3
Narita Fm	32	4	Hirose Fm	9	-
Semata Fm	2	-	Daishaka Fm	77	11
			Kamayachi Fm	13	2
Noto	26	3	Shibikawa Fm	40	12
Haizume Fm	1	-	Setana Fm	13	4
Hiradoko Fm	19	3			
Omma Fm	8	-	**Kikai**		
			Ryukyu Gr.	133	32

"?", "aff.", or "cf." between the genus and species name. This leaves 291 taxa (81% of total) solidly identified with a nominal taxon. Of the 291 fully identified nominal taxa, 97 (33%; 27% of total taxa) were originally described as new taxa from the Pleistocene fauna of Japan, including 85 new species, 6 new subspecies, and 6 new varieties (see Fig. 2 and Table 1 for a breakdown of new taxa by region and formation).

A relatively high number (258 of 358 taxa, or 72%) of Japanese Pleistocene bryozoan taxa were illustrated by one or more authors. Only Arakawa [17] included illustrations made by scanning electron microscopy (SEM); previous workers relied primarily on light micrographs, but also included some line drawings. The quality of the light micrographs varies considerably; in some cases it is difficult to discern key characters, but in many cases the illustrations are adequate for identification.

Affinities among regions

A high proportion of the Pleistocene taxa, 300 (84%) of 358, were reported from only a single one of the four (Tsugaru, Noto, Boso, Kikai) regions of Japan defined here; 42 taxa (12%) were reported from two of the regions, 15 taxa (4%) from three of the regions, and only one nominal species, *Microporella ciliata* (Pallas), from all four regions. This taxon has been ascribed virtually a global distribution, though it is probably actually limited to the temperate North Atlantic, with records from other regions erroneous. The records from Pleistocene Japan thus need to be reexamined.

The proportion of taxa in common between regions is shown in Table 2. This can be interpreted as a rough index of similarity between regions. Most similar were the Tsugaru and Noto regions

Table 2 Percent similarity among Pleistocene bryozoan faunas reported from four regions of Japan. Percentages are the number of taxa in common between two regions divided by the combined total taxa occurring in either of the two regions. Region names refer to the circled areas in Fig. 1.

	Boso	Tsugaru	Noto
Kikai	10% (25 / 253)	5% (12 / 250)	4% (6 / 153)
Boso		8% (21 / 253)	6% (10 / 161)
Tsugaru			14% (19 / 136)

(See Fig. 2), which are either on or partly bounded by the Sea of Japan, with 14% taxa in common. Next most similar were the Kikai and Boso regions, both on the Pacific side, with 10% taxa in common. All other comparisons among regions showed only 4–8% taxa in common.

Newly discovered bryozoan-bearing Pleistocene deposits in Japan

Despite the considerable previous research, there remains a wealth of relatively unexplored deposits in Japan that contain abundant Pleistocene bryozoans. Here we mention two areas from which we have already made collections.

Setana Formation, southwestern Hokkaido [24]. Several fossiliferous sections of this formation are well exposed in the vicinity of Kuromatsunai at the base of the Oshima Peninsula, including deposits at Soebetsu River (Upper Setana, 1.0–0.6 Ma), and Utasai, Nakasato, and Neppu Quarry (all three, Lower Setana, 1.2–1.0 Ma). In 2005, an international expedition (R. Takashima, S.F. Mawatari, M. Dick, A. Ostrovsky, A. Grischenko, M. Hirose, and L. Taranto) to this region found bryozoans to be abundant in these four deposits and made a collection at each. The Utasai deposit, a quarry currently

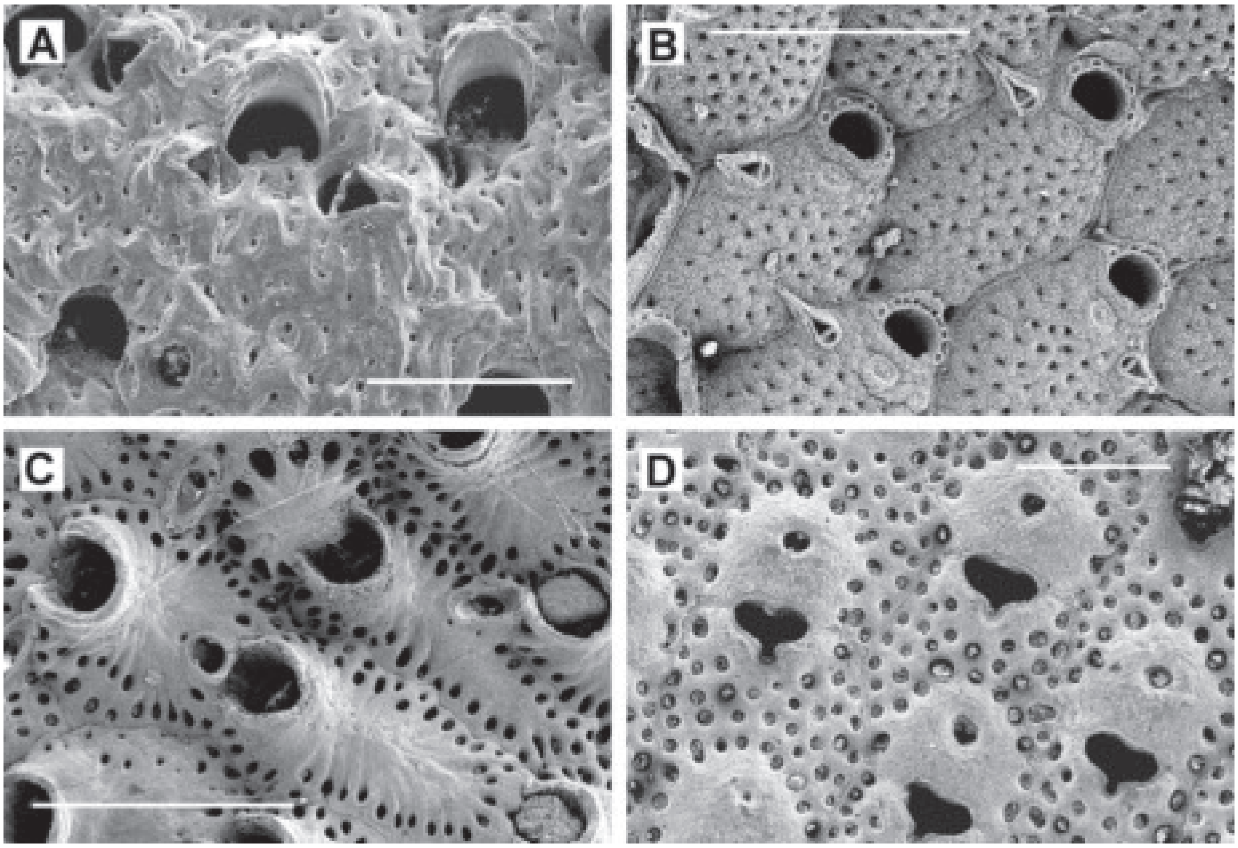

Fig. 3 Representative species from "Kokemushi Paradise," Utasai section, Lower Setana Formation (~1.2–1.0 Ma), Kuromatsunai; images by scanning electron microscopy (SEM). Scale bars = 500 μm. (A) *Parasmittina bidentata* (Androsova, 1958). (B) *Microporella* sp. (C) *Escharoides hataii* Hayami, 1975. (D) *Stomachetosella perforata* (Canu and Bassler, 1929) [= *S. magniporata* (Nordgaard, 1906)?].

being mined for stylasterine hydrocoral fragments that are ground up to be used as fertilizer, is so rich in bryozoans, which encrust virtually every pebble and mollusk shell, that it came to be referred to as "Kokemushi Paradise" (*kokemushi* = 'Bryozoa' in Japanese), a name that has stuck. The quality of preservation of the bryozoans at these sites is very good (Fig. 3). We visited most of these deposits again in 2006 and 2007 for additional collecting, stratigraphic sampling [25], and rockmagnetic measurements [26]. In 2006 and 2007, Dr. Paul Taylor collected at several of the deposits for the Natural History Museum, London. Prior to their "discovery" as productive sites for Pleistocene bryozoans, some of these sections of the Setana Formation were already known, and indeed several studies on the molluscan fauna had been conducted in this region [e. g., 2, 27, 28]. However, the mollusk specialists did not report on the bryozoans they might have encountered. To date, only 13 bryozoan taxa have been reported from the Setana Fm. in the literature: *Porella concinna hanaishiensis* Hayami, 1975; *Smittina ordinata hanaishiensis* Hayami, 1975; *Cleidochasma tuberculata* Osburn, 1952; *Coleopora*? *tsugaruensis* Kataoka, 1957; *Diatosula marionense* (Busk, 1884) [= *Myriozoella plana* (Dawson, 1859)?]; *Petraliella*? *pirikaensis* Hayami, 1975; *Microporella ciliata* (Pallas, 1766); *Microporella pirikaensis* Hayami, 1975; *Microporina articulata* (Fabricius, 1821) [29]; *Myriapora subgracilis* (d'Orbigny, 1852); *Stomachetosella producta* (Packard, 1863); *Porella acutirostris* Smitt, 1868; and "*Stephanosella biaperta* (Michelin, 1845)". However, we estimate there are at least 80 bryozoan taxa (including cyclostomes) in our collections from various deposits of this formation.

Oe and" Kita Arima" Formations, near Hara Castle and Kita Arima, respectively, Shimabara Peninsula, Kyushu. The deposit of the Oe Formation comprises a Late Pleistocene (~0.1 Ma) site with abundant, well-preserved gastropod and bivalve fossils that are often heavily encrusted with well-preserved bryozoans. The stratigraphy and molluscan fauna of this deposit have been studied [30]. The Kita Arima deposit, which is older (mid-Pleistocene), has not been studied in detail. Bryozoans occur predominantly on pebbles, though some are found on bivalve shell fragments. Preservation is variable, with degradation of some of the bryozoans due to abrasion and also to an apparently acidic taphonomic environment in parts of the deposit. Nonetheless, in a couple of hours of collecting we obtained many identifiable bryozoan specimens at this site, some of them in very good condition.

DISCUSSION

It is interesting to compare the effort devoted to Pleistocene bryozoans in California, along the west coast of North America, with that in Japan. Whereas Sakakura's 1935 [15] paper was the first in Japan to deal with Pleistocene bryozoans, effort in California had started much earlier, in 1862, with the publication of 17 taxa including 15 new to science from Quaternary deposits at Santa Barbara [31]. Canu and Bassler's [32] large monograph of 1923 included numerous Pleistocene bryozoan records: four taxa from Los Angeles, 44 from Santa Barbara, 45 from Santa Monica, and 19 from Dead Man's Island off San Pedro. Most taxa were illustrated with light photomicrographs, much as appeared in the Japanese literature on Pleistocene bryozoans prior to 1995. In 1957, Soule and Duff [33] published an annotated list of 56 species from the Pleistocene of Southern California. This list contains neither illustrations of the taxa nor information on the geology (exact localities, formations, deposits, ages, or depositional environments) of collecting sites; it describes no species new to science, nor any Pleistocene taxa that are not also Recent taxa. Nothing appears to have been published since. In summary, although studies of Pleistocene bryozoans began in California over 70 years before those in Japan, by 1940 (largely through the efforts of Sakakura), studies in Japan had reached approximate parity with those in California. The year 1957, which saw the last study of Pleistocene bryozoans in California, coincidentally saw the publication of Kataoka's paper on the bryozoa of the Daishaka Formation, which presaged the huge amount of work by Kataoka and Hayami that would follow within two decades. As a result, both Pleistocene bryozoans and their geology are now better documented in Japan than along the western coast of the United States.

One of the main questions of interest in Pleistocene studies is the degree to which Pleistocene climatic oscillations caused species extinctions. Taken at face value, the current list of Pleistocene bryozoans seems to suggest that a great deal of extinction occurred in Japan from the Pleistocene to the Recent. Among the 358 taxa on our list, 97 (27%) were originally described from Pleistocene material. Considering only the 291 taxa firmly identified with a nominal taxon, 33% were original descriptions from Pleistocene material. Few of these have subsequently been reported in modern faunas. For example, only three species originally described from Pleistocene Japan [*Ellisina canui* (Sakakura, 1935), *Labioporella elegans* Sakakura, 1935, and *Membraniporella subpetasus* Sakakura, 1935] appeared among taxa included in checklists of Recent Japanese bryozoans [34, 35]. This apparent high level of discontinuity between Pleistocene and Recent faunas may well be an artifact due to insufficient taxonomic sampling in both time intervals, especially given that surveys of Recent Pacific cheilostome faunas in the past two decades have reported similarly high proportions (23–40%) of new species [36, p. 1153]. In addition, we suspect that taxonomic specialists on Recent bryzoans have often ignored the literature on late Neogene and Quaternary bryozoans.

In number of species in common, the highest similarity among the four regions of Japan for which we compared Pleistocene bryozoans was 14%. This overall low similarity among regions is not surprising considering that variables among the regions include latitude, ocean, geological age of the predominant fossiliferous strata, and depositional environment (facies, habitat) of these strata. For example, the majority of taxa detected in the Boso region (Pacific side, ~35.5°N) came from the Jizodo Fm. (later Middle Pleistocene), whereas the majority of taxa detectged in the Tsugaru Strait region (~39.7–42.7°N) came from the Daishaka Fm. (late Early to early Middle Pleistocene) (Fig. 1).

In investigating the effects of climatic fluctuations on bryozoan assemblages, several sorts of comparisons need to be made. One involves comparisons among contemporaneous assemblages to determine the effects of ocean, latitude, or facies on the species composition of paleoassemblages. Several sets of contemporaneous assemblages are evident (Fig. 1) among known bryozoan-fossiliferous deposits in Japan: for example, the Hamada Fm., lower Omma Fm., and part of the Ryuku Group represent Early Pleistocene deposits in three regions; the Setana Fm., Daishaka Fm., Upper Omma Fm, Sawane Fm., and part of the Ryukyu Group represent upper Early to lower Middle Pleistocene deposits in four regions; the Hiradoko Fm., Narita Fm., and newly discovered Oe Fm. deposit represent Late Pleistocene deposits in three regions. Another sort of comparison involves time series of assemblages within regions (and ideally within a single habitat). For example, the Hamada., Daishaka, Hirose, Shibikawa, and Kamayachi Fms. represent a series in northern Honshu from the mid-Early to the Late Pleistocene. These comparisons through time in a single region should allow assessment of the effects of climatic changes on the composition of species assemblages.

Perhaps the most important next step in further developing the study of Japanese Pleistocene bryozoans is a reliable, up-to-date taxonomic treatment with SEM illustrations. In compiling the list of Japanese Pleistocene bryozoans, we encountered a number of inconsistencies and amibiguities. The generic names of taxa need a thorough check in light of the current classification, and species identifications need to be checked for accuracy and for consistency of usage both among previous workers on Quaternary bryozoans in Japan and with the Recent literature of the past three decades, especially that of the Pacific. As the number of sampling sites, intensity of sampling, and reliability of taxonomy increase, Japanese Pleistocene bryozoan faunas should provide an increasingly powerful model system to investigate the effects of climate change on assemblages of shelf-dwelling sessile animals.

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