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A new Miocene whale-fall community dominated by the bathymodiolin mussel *Adipicola* from the Hobetsu area, Hokkaido, Japan

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Abstract. **We report the fourth record of a fossil whale-fall community in Japan. The new material consists of a single whale bone in association mainly with small bathymodiolin mussels, *Adipicola* sp., found in the Karumai Formation (late middle Miocene–early late Miocene) in the Hobetsu area of Hokkaido, Japan. This association of whale bone and *Adipicola* sp. and its mode of occurrence resembles the description of some other ancient whale-fall communities dominated by small mussels from the Olympic Peninsula in Washington State (early Oligocene), Shosanbetsu in Hokkaido (early middle Miocene) and Carpineti in northern Italy (middle Miocene) and constitutes an example of a chemosynthesis-based community sustained by whale-fall decay in the Miocene deep sea. The new example extends the Miocene distribution of bathymodiolin-dominated whale-fall communities to the northwestern Pacific Ocean.**

Key words: bivalve, chemosynthesis-based ecosystem, deep sea, Miocene, Pacific Ocean, whale-fall community

Introduction

Sunken whale carcasses on the deep-sea floor sustain chemosynthetic life fueled by the decaying organic matter of the carcasses (Smith and Baco, 2003). The communities that develop in this way are cognate to hydrothermal vent and hydrocarbon seep ecosystems. Smith and Baco (2003) proposed four stages in the ecological succession of ecosystems supported by decaying carcasses, i.e., (i) a mobile-scavenger stage, (ii) an enrichment opportunist stage, (iii) a sulphophilic stage and (iv) a reef stage. The sulphophilic stage is characterized by the ubiquity of animals exploiting the chemosynthetic processes mediated by chemoautotrophic microbes. These animals include vesicomyid and bathymodiolin bivalves harboring symbiotic sulfur-oxidizing bacteria in their gills and flourishing thanks to hydrogen sulfide seeping out of the decaying carcasses. Smith and Baco (2003) also argued that the whale carcasses may have acted as both dispersal and evolutionary stepping stones for hydrocarbon seep and hydrothermal vent taxa. Distel *et al.* (2000) presented a phylogenetic tree of deep-sea mytilids based on molecular data indicating that the seep- and vent-restricted mytilids (e.g. *Bathymodiolus*) had adapted to seep and vent environments through whale- and wood-falls. This hypothesis has been supported by further molecular studies (e.g. Lorion *et al*., 2009, 2010, 2013; Miyazaki *et al.*, 2010) but still needs to be confirmed by fossil record of such communities. However, the fossil counterparts of whale-fall and wood-fall communities are extremely rare with the possible exception of the Eocene to Oligocene of Oregon and Washington states in the USA (Kiel and Goedert, 2006a, b). In spite of an intensive investigation of deep-water sequences, only three fossil whale-fall communities from Japan have been so far described (Hachiya, 1992; Amano and Little, 2005; Amano *et al.*, 2007; Amano and Little, 2014). Here we report an additional Miocene whale-fall association from Mukawa Town, Hokkaido, Japan, that constitutes the fourth example of an ancient whale-fall community in Japan.

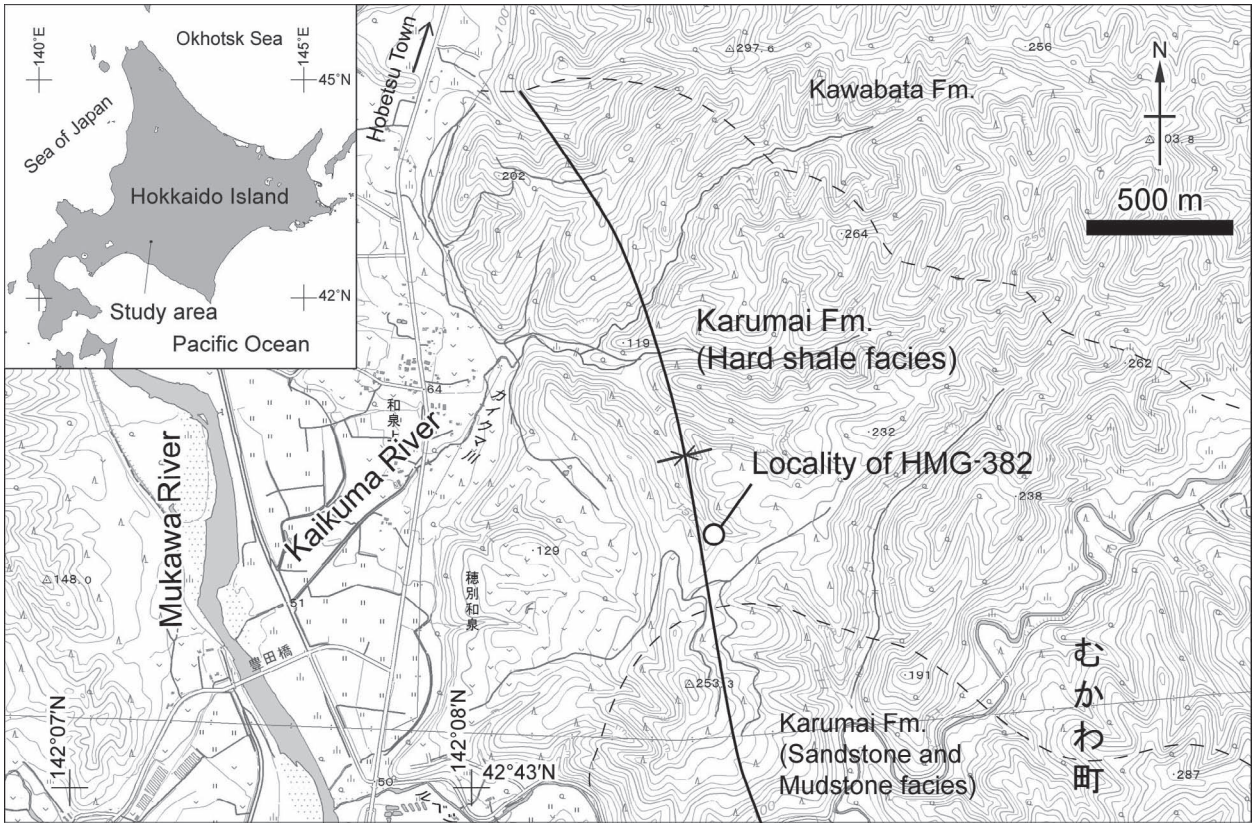

Figure 1. Locality map of the single whale-bone (HMG-382, stored in Hobetsu Museum Geological Collections). The map is based on the topographic map published by the Geographical Survey Institute of Japan.

Material and method

A single fossil whale bone (HMG-382) was collected in 1981 by Yoshitaka Otsuka and members of the Education Board of Hobetsu Town from the eastern slope of Kaikuma River valley south of Hobetsu, Mukawa Town, Hokkaido, Japan (Figure 1). This material was mentioned and illustrated in a popular paper by Kaim (2009) but no description was provided. The fossil was collected as a float in an area where only the Karumai Formation is outcropping. The Karumai Formation is composed mainly of hard shale frequently intercalated by turbiditic mudstone and sandstone beds (Takahashi and Wada, 1987) and has been interpreted as an abyssal fan deposit that formed at more than 1000 m depth (Kawakami *et al.*, 1999; Motoyama and Kawamura, 2009). The age of the Karumai Formation is assigned to the late middle Miocene to the early late Miocene (12.5–9.7 Ma; Motoyama and Kawamura, 2009). The described material is stored in the geological collection of the Hobetsu Museum (HMG) in Mukawa Town.

The specimen HMG-382 is probably part of a limb bone of an unidentified species of baleen whale (Mysticeti gen. et sp. indet.). The bone was mechanically cleaned up by the collector prior to our investigations. We refrained from cutting the bone because it is the one and only specimen. Instead we used X-ray computed tomography using a 16-channel multidetector CT scanner, SOMATOM Emotion (Siemens Healthcare), at the School of Health Science, College of Medical, Pharmaceutical and Health Sciences, Kanazawa University, to check the bone for macro-boring traces. The DICOM images thereby obtained were reconstructed and observed using 3D image viewer Molcer Plus (White Rabbit Corp.).

Results

Although the host rock had been almost entirely removed prior to our observations, a small portion of gray muddy matrix remained attached to the bone. The specimen is composed of cancellous bone only and there are no traces of cortical bone that should have existed as an outermost layer of the bone. The bone has been lithified by carbonate cements.

In total we found 15 mytilid and one probable thyasirid bivalves (HMG-1797–1812) attached to or very close

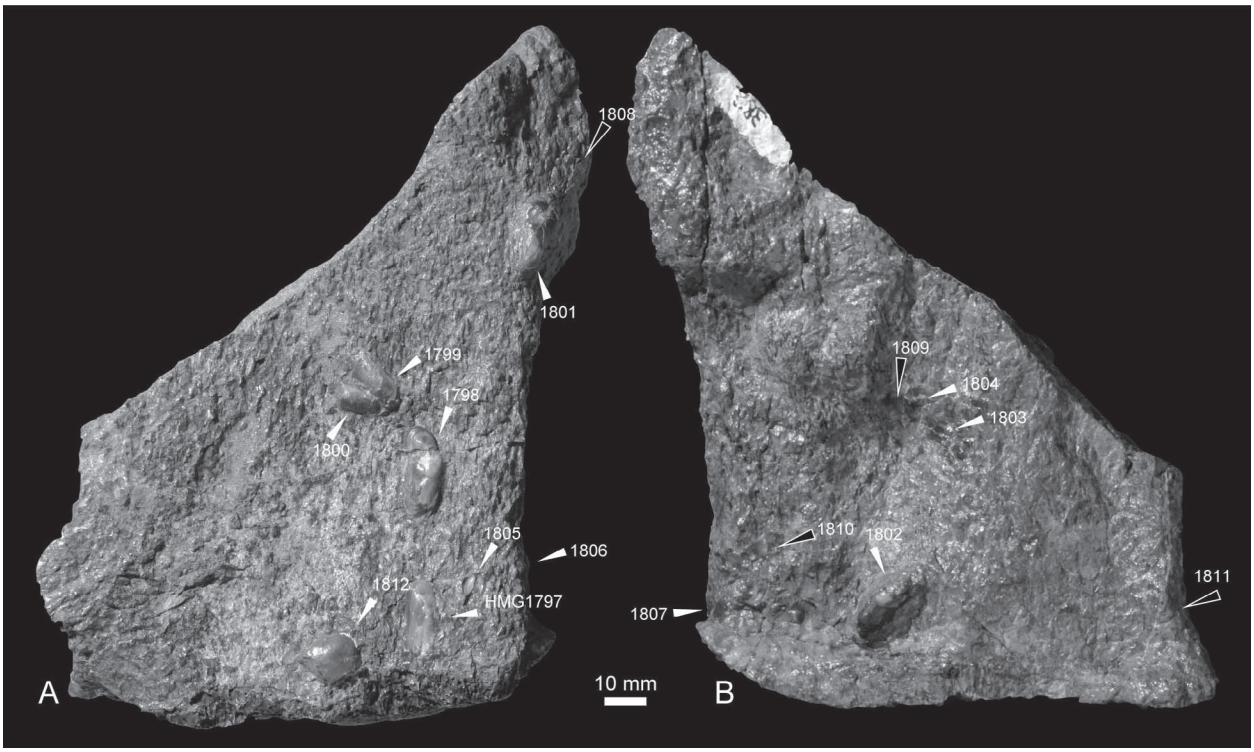

Figure 2. Photograph of the Miocene whale bone (HMG-382) and its attached bivalves (HMG-1792 to 1812) from the Karumai Formation, Hobetsu area, Hokkaido, Japan. **A,** one side of the whale-bone (HMG-382); **B,** its opposite side. Arrows indicate bathymodiolin mussels *Adipicola* sp. (HMG-1792 to 1811) and probable thyasirid bivalve (HMG-1812). White and black arrows indicate shells and molds, respectively. HMG, Hobetsu Museum Geological collection.

(within a few millimeters) to the bone surface. Among the mytilid specimens, 5 specimens are almost complete (HMG-1797–1799, 1800, 1801 in Figures 2, 3) and the other 10 specimens are partially preserved, some of which are partial external molds (Figure 2). We have identified the mytilid specimens as *Adipicola* sp.

We carefully observed reconstructed 3D images of the bone with different topographic layers. Although structures of cancellous bone and some Haversian canals can be seen in the CT reconstructed images (white arrows in Figure 4), there are no macro-boring traces, which might be attributed to bone-eating siboglinid polychaetes *Osedax* (Higgs *et al.*, 2011). There are some particles of high density, probably pyrite, in marrow spaces between the trabeculae and in the Haversian canals (black arrow in Figure 4).

Systematic description

Superfamily Mytiloidea Rafinesque, 1815
Family Mytilidae Rafinesque, 1815
Genus ***Adipicola*** Dautzenberg, 1927

Type species.—*Myrina denhami* H. and A. Adams, 1854 = *Adipicola pelagica* (Woodward, 1854), Recent, South Atlantic).

Remarks.—The systematic position and diagnostic characteristics of the genus are still controversial (see e.g. Danise *et al.*, 2016). Monophyly of *Adipicola* is ambiguous, because some molecular analyses carried out on Recent bathymodiolins show that some *Adipicola* species belong to different clades within the bathymodiolins (Miyazaki *et al.*, 2010; Lorion *et al.*, 2010, 2013). There are still many undescribed species (Lorion *et al.*, 2010, 2013), and the species, *A. pelagica* (Woodward, 1854) has never been examined from the viewpoint of molecular phylogeny. Therefore, some malacologists have pointed out the necessity of thorough reexamination of the generic position of *Adipicola* species (e.g. Okutani, 2008; Huber, 2010). Although further taxonomic work is needed in the future, in this paper, we follow Dell's (1987) redefinition of the genus.

Adipicola sp.

Figure 3A, B

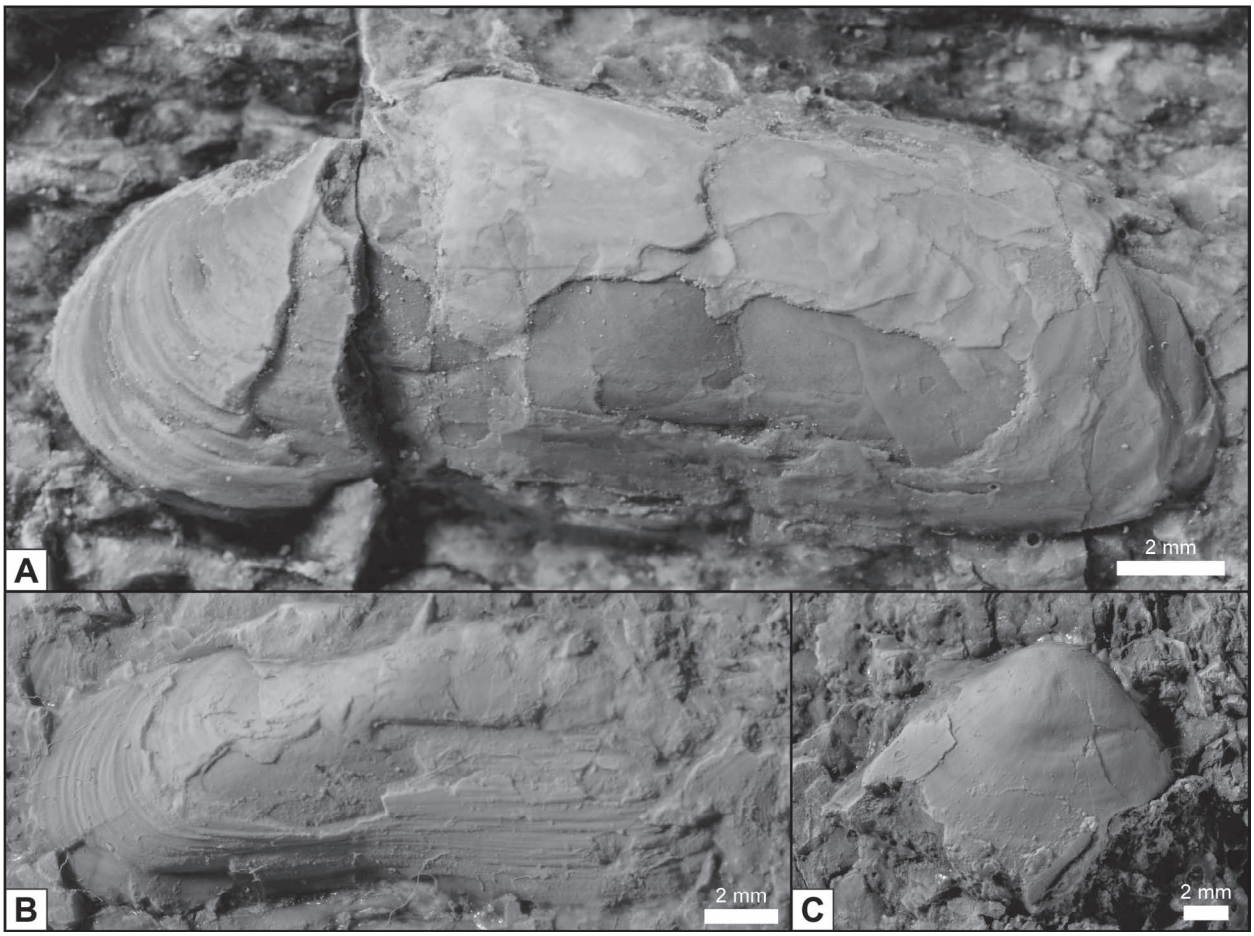

Figure 3. Fossil bivalves attached to the Miocene whale bone (HMG-382) from the Karumai Formation, Hobetsu area, Hokkaido, Japan. **A,** *Adipicola* sp. (HMG-1798 in Figure 2); **B,** *Adipicola* sp. (HMG-1797 in Figure 2); **C,** unidentified bivalve, probably thyasirid (HMG-1812 in Figure 2). HMG, Hobetsu Museum Geological Collection.

Material examined.—Fifteen specimens, HMG-1797–1811, attached to a single fossil whale bone (HMG-382) which was collected from the eastern slope of the Kaikuma River valley south of Hobetsu, Mukawa Town, Hokkaido, Japan.

Description.—Shell rather small, 23.6 mm long for an almost complete specimen (HMG-1798 in Figures 2, 3A), thin, transversely cylindrical (height/length ratio = 0.4), moderately inflated, inequilateral. Antero-dorsal margin short, broadly arcuated; anterior margin semicircular; ventral margin slightly concave; postero-dorsal margin nearly straight and gently sloping; postero-dorsal corner angulated and continuing gently to form curved posterior margin. Blunt ridge running from beak to postero-ventral corner. Umbo prominent and located at anterior one-third of shell length. Outer surface smooth except for distinct growth lines. Inner shell layer nacreous. Internal features invisible.

Remarks.—Although the hinge characters of this species cannot be observed, another small mussel, *Idas* Jeffreys, 1876, has a higher shell and generally expanded posterior part. Judging from the outline of the shells, the Hobetsu species belongs to the genus *Adipicola.* However, we refrained from assigning it to any known *Adipicola* species or establishing a new one because all our specimens are imperfectly preserved.

The Hobetsu species is similar to *Adipicola chikubetsuensis* (Amano, 1984) from the lower middle Miocene Chikubetsu Formation in northern Hokkaido, but differs from *A. chikubetsuensis* in having a longer anterior part and much more weakly concave ventral margin. The Hobetsu species is also similar to *Adipicola* sp. from the middle Miocene Nupinai Formation illustrated by Amano *et al.* (2007), but the longer anterior part and slightly concave ventral margin of the Hobetsu species enable us to separate it from the Nupinai species.

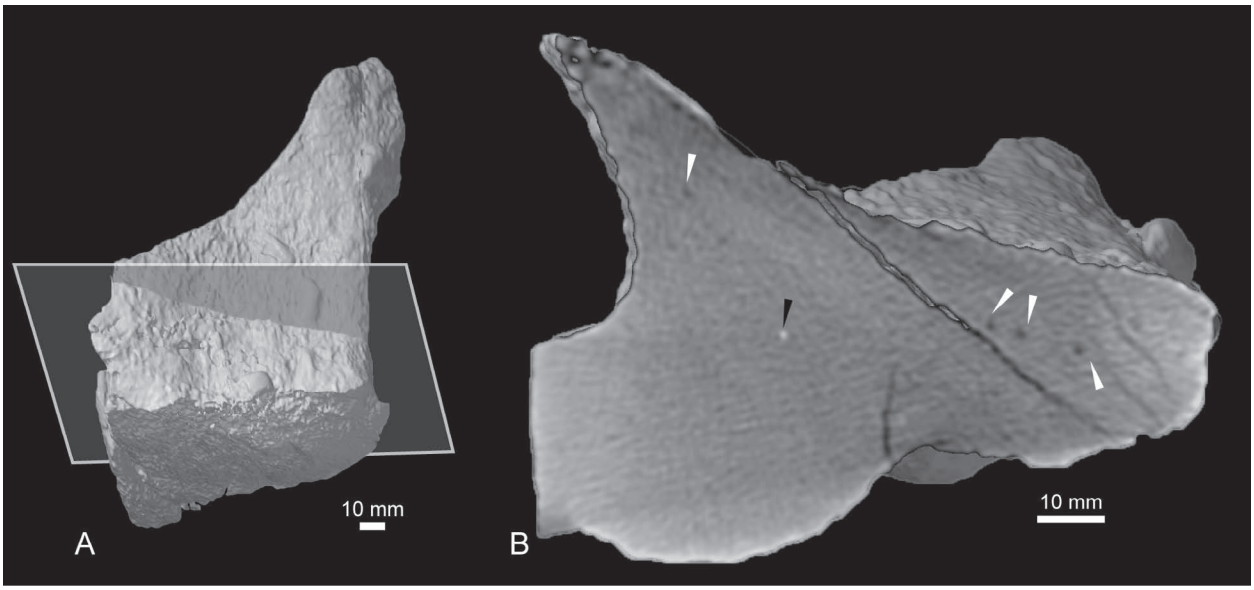

Figure 4. CT scanned image of the whale bone (HMG-382) from the Karumai Formation, Hobetsu, Hokkaido, Japan. **A,** 3D image of the bone. Square indicates location of cross section B. **B,** reconstructed image of the bone section. Structure of cancellous bone is visible. White arrows indicate existence of Haversian canals. Black arrow indicates dense part, probably pyrite mineralized within the bone.

Locality.—Float from the eastern bank of the Kaikuma River in Hobetsu, Mukawa Town, Hokkaido, Japan.

Occurrence.—Karumai Formation. Upper middle Miocene to lower upper Miocene.

Discussion

A nearly monospecific composition dominated by *Adipicola* sp. in our whale-fall specimen might be at least partially caused by imperfect preservation of the whale bone and lack of the rock matrix surrounding it, but may also reflect the original community attached to the whale carcasses, because the modern whale-fall communities are commonly densely packed with bathymodiolins, *Adipicola* and *Idas* in particular (Fujiwara *et al.*, 2007), both of which have been confirmed as possessing symbiotic sulfur-oxidizing bacteria in their gills (Fujiwara *et al.*, 2010). The Miocene fossil community dominated by *Adipicola* reported in this paper relied on decaying whale fall in the sulphophilic stage, like its modern analogues. Probable pyrite aggregations recognized by the CT reconstructed images within the bone also support this interpretation, as pyrite formation usually follows sulfate reduction (Berner, 1984; Vietti *et al.*, 2015). We named our specimen the Hobetsu whale-fall community.

The Hobetsu whale-fall community lacks vesicomyids, provannids, and other molluscan fossils commonly known as members of chemosynthetic communities, apart from a single specimen of a probable thyasirid. This may have resulted from the extraction of the bone from its host sedimentary rocks prior to our observations. Thus, it is difficult to compare the whole faunal assemblage with other whale-fall communities. Nevertheless, the ubiquity of bathymodiolin mussels is a distinct character of our community, and there is a possible opening for a discussion on the spatiotemporal distribution pattern of bathymodiolin mussels in whale-fall communities worldwide.

There have only been three examples of fossil whale-fall communities from Japan so far. Among them, the early middle Miocene Shosanbetsu whale-fall community from northern Hokkaido is the only example showing dominance of *Adipicola* mussels, like the Hobetsu whale-fall community. In contrast, the other two whale-fall communities from Japan, i.e., the middle Miocene Rekifune whale-fall from eastern Hokkaido (Amano *et al.*, 2007) and the early Miocene Morozaki whale-fall from central Japan (Hachiya, 1992), do not display dense occurrences of bathymodiolin mussels. Paleogeographically, the location of the Hobetsu community faced the Pacific Ocean (Kawakami *et al.*, 1999) while that of the Shosanbetsu whale-fall community faced the Sea of Japan. It might therefore be inferred that bathymodiolin dominant whale-fall communities developed in both basins by the early late Miocene.

Among the ancient whale-fall communities reported from other regions, aggregations of bathymodiolins have been found in the communities from the Olympic Peninsula, Washington State, USA (early Oligocene,

eastern Pacific; Kiel and Goedert, 2006b), and Carpineti, Northern Italy (middle Miocene, proto-Mediterranean-Atlantic Ocean; Danise *et al*., 2016). All these data show that Miocene whale-fall communities dominated by bathymodiolin mussels had a wide distribution at least in the northern hemisphere (Danise *et al.*, 2016).

Conclusions

We report a new Miocene molluscan fossil association attached to a whale bone, which is dominated by bathymodiolin mussels *Adipicola* sp., from the Karumai Formation, deep-sea fan deposits facing the northwestern Pacific Ocean. The taxonomic composition and the mode of fossil occurrence indicate that the fossil association is interpreted as a chemosynthetic community fueled by a decaying whale carcass. It constitutes the fourth example of an ancient whale-fall community in Japan. The new example extends the distribution of bathymodiolin-dominated whale-fall communities to the northwestern Pacific Ocean in the Miocene.

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Author contributions

R.G.J initiated the study and was primarily responsible for the observations on the fossil association and taxonomic aspects of the bivalves. A. K. and K. A. examined the whole specimen and responsible for taxonomic aspects of the bivalves as well as R.G.J. K. S. studied on the geological background and the taxonomy of the whale. K. M. carried out analysis of the CT. All authors contributed to the writing of the paper.