“Papers in Press” includes peer-reviewed, accepted manuscripts of research articles, reviews, and short notes to be published in Paleontological Research. They have not yet been copy edited and/or formatted in the publication style of 

*Paleontological Research*. As soon as they are printed, they will be removed from this website. Please note they can be cited using the year of online publication and the DOI, as follows:

doi:10.2517/2017PR006

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

ROBERT G. JENKINS¹, ANDRZEJ KAIM², KAZUTAKA AMANO³, KAZUHIKO SAKURAI⁴ and KOSUKE MATSUBARA⁵

¹College of Science and Engineering, Kanazawa University, Kakuma, Kanazawa, Ishikawa 920–1192, Japan (e-mail: robertgj@staff.kanazawa-u.ac.jp)

²Institute of Paleobiology, Polish Academy of Sciences, ul. Twarda 51 / 55, 00-818 Warszawa, Poland

³Department of Geoscience, Joetsu University of Education, 1 Yamashina, Joetsu, Niigata 943–8512, Japan

⁴Hobetsu Museum, 80-6 Hobetsu, Mukawa, Hokkaido 054-0211 Japan

⁵College of Medical, Pharmaceutical and Health Sciences, Kanazawa University, 5-11-80 Kodatsuno, Kanazawa, Ishikawa 920-0942, Japan
Abstract. We report the fourth record of a fossil whale-fall community in Japan. The new material consists of a single whale bone associated mainly by 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 seafloor 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
phylogenetic tree of deep sea mussels based on molecular data indicating that the seep and vent
restricted mussels (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 records of such
communities. However, fossil record of whale-fall and wood-fall communities is 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 investigations 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, constitutes the fourth example of an ancient whale-fall community in 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 located more than 1000 m in 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 multi detector 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 (within 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 mold (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 pyrites, 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. & 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 bathymolins (Miyazaki et al., 2010; Lorion et al., 2010; Lorion et al., 2013). There are still many undescribed species (Lorion et al., 2010; Lorion et al., 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 the *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

*Material examined.* —15 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 the curved posterior margin. Blunt ridge running from beak to postero-ventral corner. Umbo prominent and located at the anterior one-third of the 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.

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

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

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 (Bernar, 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 a chemosynthetic community, 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 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.

Acknowledgements

We would like to thank two anonymous reviewers for their constructive comments and editors for helpful comments. This study was partly supported by JSPS KAKENHI Grant Number 16H05740, 15H04412, 26287131 and 26400500, and Grant for Program to Disseminate Tenure Tracking System (JST) to RGJ. Andrzej Kaim’s research has been supported by the National Science Centre (Poland) research grant no. 2012/07/B/ST10/04189.
References


Danise, S., Bertolaso, L., and Dominici, S., 2016: Bathymodioline mussel dominated Miocene whale fall from Italy. *Bollettino Della Societa Paleontologica Italiana*, vol. 55, p. 47–53.

Dautzenberg P., 1927: Mollusques provenant des campagnes scientifiques du Prince Albert Ier de Monaco dans l’Océan Atlantique et dans le Golfe de Gascogne. *Résultats des campagnes*


Hatano. (in Japanese)


Palerme, Barravecchia.


Figure captions

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.
Figure 2. Photograph of the Miocene whale bone (HMG-382) and its attached bivalves (HMG-1792 to 1812) from Karumai Formation, Hobetsu area, Hokkaido, Japan. A, one side of the whale-bone (HMG-382); B, its opposite side. Arrows indicate bathymodiolin mussel 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.

Figure 3. Fossil bivalves attached to the Miocene whale bone (HMG-382) from 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.

Figure 4. CT scanned image of the whale bone (HMG-382) from Karumai Formation, Hobetsu, Hokkaido, Japan. A, 3D image of the bone. The 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. A black arrow indicates dense part, probably pyrite mineralized within the bone.
Kawabata Fm.

Karumai Fm. (Hard shale facies)

Locality of HMG 382

Karumai Fm (Sandstone and Mudstone facies)

Mukawa River

Kakuma River

Hokkaido Island

Okhotsk Sea

Study area

Pacific Ocean

500 m