

Drill Holes in Bathymodiolin Mussels from a Miocene Whale-fall Community in Hokkaido, Japan

KAZUTAKA AMANO

Department of Geoscience, Joetsu University of Education, 1 Yamayashiki, Joetsu, Niigata 943-8512, Japan
(e-mail: amano@juen.ac.jp)

STEFFEN KIEL

School of Earth and Environment, University of Leeds, Leeds LS2 9JT, United Kingdom
(e-mail: steffen.kiel@gmx.de)

Abstract. Three specimens of *Adipicola chikubetsuensis* (Amano) with drill holes ranging from 0.9 mm to 1.2 mm in width were found in a Miocene whale-fall community in northern Hokkaido, Japan. This is the first record of drilled chemosymbiotic mussels (bathymodiolins) and of drilling predation at whale-falls. With two percent of the recovered mussels being drilled, the drilling intensity at this whale-fall site is low compared to that among mytilids and other heterotrophic bivalves in shallow water environments. This low drilling intensity may be caused by the low tolerance of naticids for sulfide. We propose that the delayed onset of naticid predation at whale falls in the Miocene relates to the changing mechanism of sulfide production at whale-falls at the transition from the Oligocene to the Miocene.

INTRODUCTION

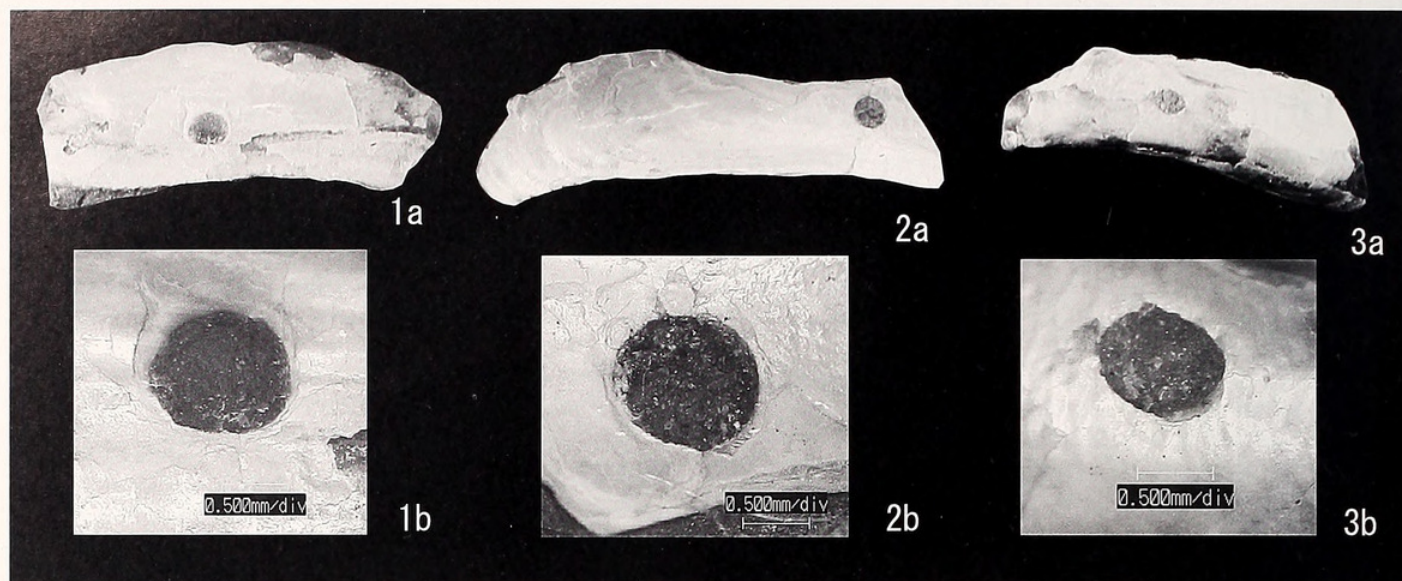
Chemosymbiotic macrofauna such as tube worms, clams, mussels, snails, and crustaceans has been found in deep-sea reducing microenvironments around hydrothermal vents, cold seeps, whale-falls, and sunken wood (e.g., Van Dover, 2000). Predation is known to structure the faunal composition of these communities (Micheli et al., 2002) and has also been suggested as a major factor in the confinement of these communities to water depth below 350 m (Sahling et al., 2003). Most higher taxa of the modern vent and seep macrofauna appeared in the late Mesozoic (Little & Vrijenhoek, 2003; Kiel & Little, 2006), concurrent with the Mesozoic Marine Revolution (Vermeij, 1977, 1987). Thus predation may also have played an important role in the evolution of invertebrate communities in these extreme environments.

Unfortunately, direct evidence for predation, such as drill holes in molluscan shells from fossil chemosynthetic environments, is still sparse. Most records are from Eocene to Miocene cold seeps in Japan, and a few additional examples are known from the Oligocene of Washington State, USA. Amano (2003a) described drill holes in the vesicomyid *Calyptogena pacifica* Dall and in the thyasirid *Conchocele bisecta* (Conrad) from the upper Miocene Morai Formation in Hokkaido that were presumably made by the co-occurring naticids *Euspira pallida* (Broderip & Sowerby) and *Cryptonatica* sp. *Calyptogena pacifica* with an unsuccessful drill hole

was described from the upper Miocene Nodani Formation in central Honshu by Amano & Kanno (2005). Amano & Jenkins (2007) noticed that a specimen of *Adulomya chitanii* Kanehara illustrated by Kamada (1962) from the lower Miocene Taira Formation in the Joban coal-field was drilled successfully, and the vesicomyid *Hubertschenkia ezoensis* (Yokoyama) and *Conchocele bisecta* with drill holes presumably made by *Euspira*? sp. were collected from the upper Eocene Poronai Formation in Hokkaido (Amano & Jenkins, 2007).

On the eastern side of the Pacific Ocean, from cold-seep carbonates in the Oligocene part of the Lincoln Creek Formation in Washington State, Kiel (2006) reported a drill hole in a specimen of the nuculanid bivalve *Nuculana*? cf. *grasslei* Allen, and one specimen of *Provanna antiqua* Squires with a healed injury probably caused by a crab. In addition, we recently found a drilled vesicomyid in cold-seep carbonates in the same sediments (Amano & Kiel, 2007). The oldest evidence for predatory animals at seeps are crustacean fragments and coprolites from Late Jurassic (Oxfordian) methane seep deposits near Beauvoisin in southern France (Senowbari-Daryan et al., 2007), but there are no traces of shell peeling or crushing in the mollusk shells from that site (SK, personal observation).

In this paper we present the first direct evidence for predation at a fossil whale-fall site. Newly collected material from the Miocene 'Shosanbetsu' whale-fall site



Figures 1–3. Drill holes in *Adipicola chikubetsuensis* (Amano) from the middle Miocene Chikubetsu Formation in Hokkaido, Japan. The upper figures show the complete specimens, the lower figures are close-ups on the drill holes. Fig. 1a, b, JUE no. 15821-1; Figs. 2a, b, JUE no. 15850; Figs. 3a, b, JUE no. 15821-2.

(cf. Amano & Little, 2005) yielded three specimens of the bathymodiolin *Adipicola chikubetsuensis* (Amano) with drill holes. These specimens are described and their significance is discussed.

OCCURRENCE

The Shosanbetsu whale-fall community occurs in concretions within siltstones of the uppermost part of the lower middle Miocene Chikubetsu Formation, at a road-cut on the northern side of the Setakinai River; about 5.5 km upstream from Shosanbetsu Village in northwestern Hokkaido (see Figure 1 of Amano & Little, 2005). *Adipicola chikubetsuensis* and the gastropod *Provanna* sp. dominate the community, minor elements are *Adulomya hokkaidoensis* Amano & Kiel, *Solemya* sp., the buccinid *Trominina* sp., and a poorly preserved naticid. Based on foraminifers, this part of the Chikubetsu Formation was probably deposited in water deeper than the middle bathyal zone (Maiya et al., 1982). From a total of 121 specimens of *Adipicola chikubetsuensis*, the shells of three specimens had drill holes. Almost all of the specimens are articulated and occurred in dense clusters without any apparent orientation directly attached or a few millimeters away from the whale bones. All of the studied drilled shells are housed at the Joetsu University of Education (JUE).

DRILL HOLE DETAILS

Among 121 specimens of *Adipicola chikubetsuensis* only three specimens (2%, which equals a drilling intensity of 0.02) have drill holes. The most common mode of preservation of these shells is that the outermost

(calcitic?) layer is detached from the nacreous inner layer, and both sides adhere to their respective side of the concretion. In two cases the drill holes are preserved on the outer side of the inner layer of a right and a left valve (Figure 1a, b, 3a, b), in one case it is preserved on the inner side of the outer layer of a left valve (Figure 2a, b). The drill holes are small with a diameter ranging from 0.9 to 1.2 mm, have a circular or elliptical outline (Table 1), and, considering the protruding shape shown on Figure 1b, they are parabolic in cross section. All three holes occur at the central portion of the shell, where the ventral margin is most concave. We have not seen drill holes in any of the other species that occur at the Shosanbetsu whale-fall site.

DISCUSSION

Generally, parabolic drill holes are attributed to naticids, and cylindrical drill holes to muricids (e.g., Aitken and Risk, 1981). The holes in *Adipicola chikubetsuensis* at the Shosanbetsu whale-fall site are parabolic and are drilled in the central portion of the shells. This is a common position for naticid drill holes in Recent mytilids. For example, Griffiths (1981) reported that *Tectonatica tecta* (Anton) drilled the central part of the shell of the South African *Choromytilus meridionalis* (Krauss), and in the western Atlantic *Euspira heros* (Say) has been observed to drill *Mytilus edulis* Linnaeus at this position (G. Dietl, personal communication, 2007). Considering the shape and position of drill holes and that four small naticids were found at the Shosanbetsu whale fall site while muricids appear to be absent (Amano & Little, 2005;

Table 1
Measurements of the holes in *Adipicola chikubetsuensis* (Amano).

Specimens	Shell length (mm)	Diameter of hole (mm)
JUE no. 15821-1	12.2+	1.2
JUE no. 15821-2	11.9+	0.9
JUE no. 15850	16.9+	1.1

present study), it seems straightforward to assume that the drill holes reported here were made by naticids.

Reports of naticid predation of mussels in shallow water are rare (Edwards, 1975; Griffiths, 1981), whereas predation by muricids occurs quite frequently (Wright & Francis, 1984; Vermeij et al., 1989; Harper & Skelton, 1993; Gordillo, 2001). This is not very surprising considering that mussels are usually byssally attached to some sort of hard substrate, a habitat frequently visited by muricids but not by naticids, which are soft-bottom dwellers (Taylor et al., 1980). A clue to how and why naticids may be able to attack mytilids at whale falls was provided by Okutani et al. (2003, p. 62), who reported *Adipicola pacifica* specimens from experimentally submerged whale bones in 219 to 254 m depth offshore Cape Nomamisaki (Kyushu, Japan) that were actively moving around using their foot, and *A. crypta* specimens from the same bones that were living very close to the sediment-water interface. Such specimens are potentially available for sediment-dwelling naticids like *Tanea magnifluctulata* (Kuroda), which was reported from near that whale-fall community (Okutani et al., 2006). It is likely that also the Miocene *Adipicola chikubetsuensis* at the Shosanbetsu whale-fall site lived very close to the sediment and would thus be accessible for the co-occurring naticids.

However, Gordillo (1994, 1998) showed that also the trophonine muricid *Trophon geversianus* Pallas produces parabolic holes, and Recent trophonines are thought to drill *Calyptogena gallardoi* Sellanes & Krylova and *Thyasira methanophila* Oliver & Sellanes at methane seeps off Concepción in Chile (Houart & Sellanes, 2006). Thus, the possibility remains that undetected trophonines are responsible for the drill holes in *Adipicola chikubetsuensis* at the Shosanbetsu whale-fall site.

Interestingly, drill holes have neither been found in the Eocene and Oligocene whale-fall communities in Washington State, USA, nor in the wood-falls in the same sediments, although naticids and muricids were present (Goedert et al., 1995; Kiel & Goedert, 2006a, b, and unpublished data). This led Kiel & Goedert

(2006b) to suggest that in the case of the Eocene and Oligocene wood-falls the 'naticid'-like shells may in fact belong to the herbivore gastropod family Ampullinidae (= Ampullospiridae of some authors) which builds shells that are convergent in shape to those of naticids (Bandel, 1999; Kase & Ishikawa, 2003). Kiel & Goedert (2006a) proposed that whale-fall communities in the Eocene and Oligocene resembled wood-fall communities in that the sulfide used by chemosymbiotic bivalves was derived from a cover of organic material around the whale skeleton, analogous to the cover of shipworm fecal pellets around wood falls. At modern-type whale falls from the Miocene onwards sulfide is released from the bones as a result of anaerobic breakdown of bone lipids (Smith & Baco, 2003).

This ecologic difference between the Eocene and Oligocene whale falls on the one hand, and the Miocene to modern ones on the other, may also affect naticid predation. Naticids are very rare at seeps (Warén & Bouchet, 2001) and may have a low tolerance for sulfide. Thus they might have disliked the carpet of decaying organic material around the early whale falls (and wood falls, too), whereas at the Miocene to modern whale falls the sulfide is very localized at the bones and may not form a barrier for the naticids. However, this interpretation is based on very few data and needs to be tested when more information on modern and fossil whale-fall communities and their ecology becomes available. Although naticids are known from modern whale-falls (Okutani et al., 2006) there is no direct evidence yet for their drilling activities.

The drilling intensity among the bathymodiolins at the Shosanbetsu whale-fall is about 0.02. Except for two cases (0.20 in *Calyptogena pacifica* from the Morai Formation and 0.27 in the Recent *Thyasira methanophila*), drilling intensities in deep-sea chemosynthetic environments do not exceed 0.1 (Table 2). Shallow-water heterotrophic bivalves usually show higher intensities. For example, naticid predation on *Glycymeris* in the Neogene of Japan and the US east coast usually has intensities above 0.1 and occasionally reaches more than 0.6 (Thomas, 1976; Amano, 2003b, 2006). A similar range was recognized in North American bivalve assemblages from the Cretaceous through Recent (e.g., Kelley & Hansen, 2003). Based on the few data presently available, drilling intensities in chemosynthetic environments appear low compared to shallow marine environments. Although drilling activities at cold seeps start in the late Eocene, the drilling intensities show no increase or other tendencies through time. The most likely explanations for these low drilling intensities at chemosynthetic environments are the reducing conditions at these sites and symbiont-bearing species may be protected from predation by metabolites produced by the chemoautotrophic endo-

Table 2

Drilling intensities in fossil and Recent chemosynthetic communities. DI = Drilling intensity.

Age	Site	Species	DI	References
Recent	Cold Seep	<i>Thyasira methanophila</i>	0.27	Houart & Sellanes (2006)
		<i>Calyptogena gallardoi</i>	0.01	Houart & Sellanes (2006)
Late Miocene	Cold seep	<i>Conchocele bisecta</i>	0.09	Amano (2003)
		<i>Calyptogena pacifica</i>	0.20	Amano (2003)
Middle Miocene	Whale fall	<i>Adipicola chikubetsuensis</i>	0.02	Present study
Late Eocene	Cold seep	<i>Conchocele bisecta</i>	0.09	Amano & Jenkins (2007)
		<i>Hubertschekia ezoensis</i>	0.06	Amano & Jenkins (2007)

symbionts that deter predators from feeding on them (Kicklighter et al., 2004).

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