

# Antiquity of the substrate choice among acmaeid limpets from Late Cretaceous chemosynthesis-based communities

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Two Campanian methane seep sites in the Nakagawa area of Hokkaido (northern Japan) yield fossils of the limpet genera *Serradonta* and *Bathyacmaea* that appear to have had the same substrate preference as do their modern counterparts. *Serradonta* cf. *vestmentifericola* was a species having an elongated and strongly compressed shell adapted to living on vestimentiferan tubes, like its modern relatives. *Bathyacmaea* cf. *subnipponica* was an acmaeid with a relatively elongated shell but with a more rounded aperture than *Serradonta* and thus apparently attached to small hard objects other than worm tubes. One *Bathyacmaea* specimen was found attached *in situ* to an ataphrid gastropod shell. The restricted present-day distribution of *Serradonta* possibly reflects its spreading route exclusively through the hot vent and cold seep communities settled by vestimentiferans.

Key words: Gastropoda, paleoecology, chemosynthetic community, methane-seep, Cretaceous, Hokkaido, Japan.

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## Introduction

Since the surprising discovery of high biomass communities of novel animals at hydrothermal vents on the Galápagos Rift (Lonsdale 1977), studies of vent ecosystems have revealed new modes of life in the animal kingdom. The trophic structure of such communities is based on chemoautotrophic bacteria that gain energy through the oxidation of reduced compounds, such as hydrogen sulfide or methane (for reviews see Van Dover 2000; Campbell 2006). In the 30 years since those exciting discoveries similar chemosynthetic communities have been found at various other sites in the world's oceans where bottom water is enriched with reduced compounds, e.g., cold-seeps, sunken whale carcasses, sunken drift wood and even the rotting cargo of a sunken ship (Marshall 1988; Smith et al. 1989; Dando et al. 1992; Tunnicliffe 1992; Hasegawa 1997; Sibuet and Olu 1988; Van Dover 2000).

The fossil record of chemosynthesis-based communities goes back to the Silurian (Barbieri et al. 2004; Little 2002; Little and Vrijenhoek 2003; Campbell 2006). However, the faunal composition of these communities underwent profound modifications since then. In the Palaeozoic brachiopods were predominant, but in the Mesozoic these were largely replaced by molluscs (Campbell and Bottjer 1995; Little and Vrijenhoek 2003). Molecular analyses of the modern animals endemic to chemosynthetic communities also indicate a late Mesozoic or even Cenozoic origin (for molecu-

lar data see, e.g., Peek et al. 1997; Halanych et al. 1998; McArthur and Koop 1999 and for discussion Van Dover et al. 2002; Little and Vrijenhoek 2003; Kiel and Little 2006). In order to elucidate the Mesozoic change in chemosynthesis based faunas, it is important to trace autecology of specific taxa. Herein we provide such a case study for two acmaeid limpet gastropods, *Bathyacmaea* cf. *subnipponica* and *Serradonta* cf. *vestmentifericola*, found at two Late Cretaceous methane-seep sites from the Nakagawa area of Hokkaido in northern Japan. The Recent species of *Serradonta* and *Bathyacmaea* are restricted to methane-seeps and hydrothermal vents (Warén and Bouchet 2001) and herein we report that their attachment behavior was established as early as the Late Cretaceous.

*Institutional abbreviations.*—DEPUT, Department of Earth and Planetary Science, Faculty of Science, University of Tokyo, Japan; UMUT, University Museum, University of Tokyo, Tokyo, Japan.

## Material and methods

The gastropods were found in the Omagari and Yasukawa methane-seep sites (for the seep descriptions see Hikida et al. 2003 and Jenkins et al. 2007 respectively) located along the Abeshinai River, Nakagawa area, Hokkaido (Fig. 1). The localities are Campanian (Late Cretaceous) seep carbonates surrounded by siliciclastic sediments of the Omagari Forma-

tion in the Yezo Group (Takahashi et al. 2003; Jenkins et al. 2007).

The fossils were extracted by wet-sieving weakly consolidated muddy sediments (mesh size 0.5 mm). The samples were first examined using a Keyence digital microscope VHX-500 and detailed observations were carried out with a Hitachi S-2400S scanning electron microscope at the DEPUT. The latter required coating the specimens with platinum-palladium.

Carbonate isotopic signatures are expressed per mil relative to the PDB standard.

## Geological background

The Omagari methane-seep deposit consists of an approximately 10 m wide carbonate body having a very negative carbonate carbon isotopic composition (as low as  $-45\%$  versus PDB) (Hikida et al. 2003). The Yasukawa methane-seep deposits are composed of several carbonate bodies, none of which exceeds 2 m maximum diameter. These also have very negative carbon isotopic signatures ( $-43.5\%$  versus PDB) (Jenkins et al. 2007). They have brittle and ductile fabrics, probably caused by strong flow rates (Jenkins 2006). Fossils at the two methane-seep sites are present both within and near the carbonate bodies (see also Hikida et al. 2003; Amano et al. in press; Jenkins et al. 2007). Some of the fossils closely resemble modern vent and seep taxa (compare e.g., Tunnicliffe 1991; Sibuet and Olu 1988; Warén and Bouchet 2001). The most striking examples are probable vestimentiferan worm tubes (Fig. 2D), acmaeid limpets (*Serradonta* cf. *vestmentifericola* and *Bathyacmaea* cf. *subnipponica*; Fig. 2A and B), lucinid, thyasirid, solemyoid, and nuculid bivalves. However, the component ratios of the fossils differ significantly between the Yasukawa and Omagari sites. The epifaunal vestimentiferans and acmaeid limpets flourished at the Omagari methane-seep but are much less common at the Yasukawa site. In contrast, infaunal thyasirid and solemyoid bivalves were much more common at the Yasukawa methane-seep. Detailed taxonomic treatment of these faunas will be published elsewhere.

## Results

The fossil *Serradonta* cf. *vestmentifericola* specimens have an extremely tall and compressed shell (Fig. 2A) and strikingly resemble the Recent *S. vestimentifericola*. The shell surface has only growth lines which are curved towards the apex on the anterior and posterior sides of the shell (Fig. 2A<sub>3</sub>). The aperture of *Serradonta* found at the Omagari and Yasukawa sites neatly fits the worm tubes found at the same localities. The mean width of *Serradonta* shells from the Omagari site is 1.85 mm (45 specimens measured) while the

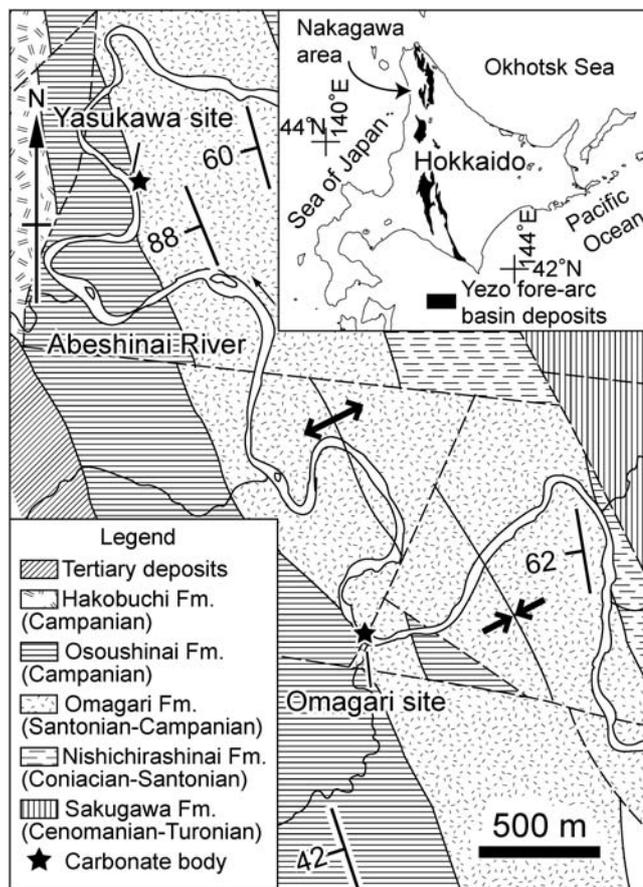


Fig. 1. Geological map of the Nakagawa area, Hokkaido, showing the location of the Yasukawa and Omagari sites. Modified from Takahashi et al. (2003).

mean diameter of the worm tubes is 1.42 (68 specimens measured) but both samples were from slightly different areas of the outcrop and it cannot be excluded that the tubes were slightly wider at the collection site of *Serradonta*. Indeed, Hikida et al. (2003) reported tube diameters at the Omagari site ranging from 1 to 4 mm.

*Bathyacmaea* cf. *subnipponica* also has an elongated shell in the early stages (Fig. 2B), but its aperture expands later in the ontogeny. The shell is ornamented by strong concentric growth lines with small knobs. The aperture is weakly concave dorsally and its outline becomes irregular. One specimen of *B. cf. subnipponica* was found attached to an ataphrid shell in a bulk sediment sample collected from the Yasukawa methane-seep (Fig. 2C). Its aperture line fits perfectly to the ataphrid gastropod shell surface and there is no sediment between the two shells (Fig. 2C).

## Discussion

A tall shell shape is rather unusual for limpets (Denny 2000) and is observed mostly among those species utilizing other organisms of limited surface area as a substrate. For example, some groups of Recent limpets have both tall and flat

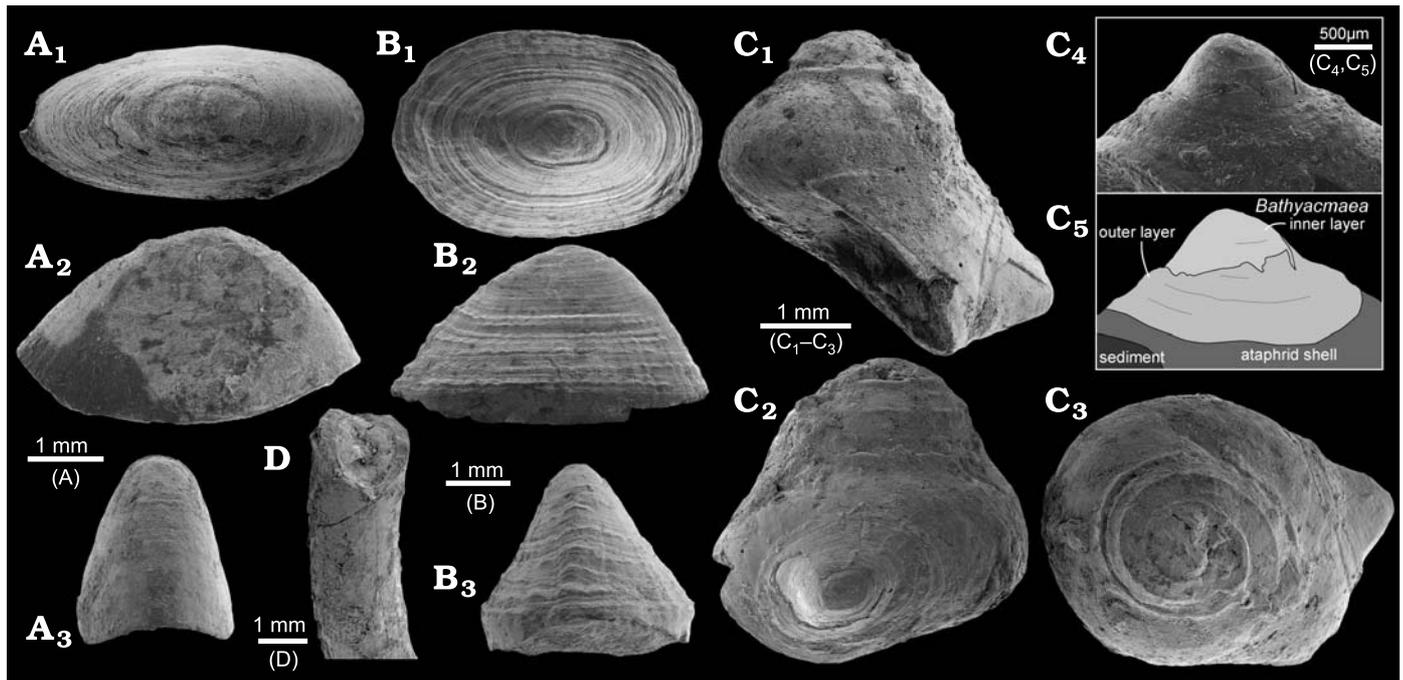


Fig. 2. Campanian (Late Cretaceous) molluscs and probable vestimentiferan fossils from the Yasukawa (A–C) and Omagari (D) sites (Hokkaido, Japan). A. *Serradonta* cf. *vestimentifericola* UMUT MM29351. Apical (A<sub>1</sub>), lateral (A<sub>2</sub>) and anterior (A<sub>3</sub>) views. B. *Bathyacmaea* cf. *subnipponica* UMUT MM29352. Apical (B<sub>1</sub>), lateral (B<sub>2</sub>) and anterior (B<sub>3</sub>) views. C. Acmaeid limpet *Bathyacmaea* cf. *subnipponica* attached to ataphrid gastropod (UMUT MM29353). Lateral (C<sub>1</sub>, C<sub>2</sub>) and apical (C<sub>3</sub>) views; close up of the limpet: photograph (C<sub>4</sub>) and explanatory drawing (C<sub>5</sub>). D. Tube of ?vestimentiferan worm (UMUT MW29354).

species in the same genus, the shape of which depends strictly on the substrate utilization. The *Patelloida heroldi* group is a striking case, where *P. conulus* on living *Batillaria* has a tall conical shell, but *P. heroldi* on rocks and *P. pygmaea* on oyster beds show more depressed profiles like other typical patellogastropod limpets (Sasaki and Okutani 1994, Nakano and Ozawa 2005; Nakai et al. 2006). In these species, the difference in habitat selection has resulted in reproductive separation as revealed by allozyme and mitochondrial gene analyses (Nakano and Ozawa 2005; Nakai et al. 2006).

The shape of the fossil *Serradonta* cf. *vestimentifericola* specimens, with their concave apertures and extremely tall shells (Fig. 2A), is just like that of the modern species, which attaches to vestimentiferan tubes (Okutani et al. 1992; Sasaki et al. 2003), and, indeed, fossil tubes, that are probably those of vestimentiferans occur abundantly in the Omagari methane-seep carbonate body. Both *Serradonta* and vestimentiferan tubes are relatively rare at the Yasukawa methane-seep site. These facts strongly suggest that *S.* cf. *vestimentifericola* used the tubes of the vestimentiferans as a preferred substrate (Fig. 3). Moreover, it seems that the relatively small diameter of the worm tubes in the Campanian methane seeps provided the selective pressure for these limpets to keep an elongate and strongly compressed shell shape.

There are also other Recent limpets known to live on the vestimentiferan tubes, e.g., several species of *Lepetodrilus*. The species *L. fucensis* living on the small sized tube worm

*Ridgeia piscesae* have elongated shells indeed (Desbruyères et al. 2006) but the other small-sized species (e.g., *L. elevatus*, *L. ovalis*, and *L. pustulosus*) have relatively flat shells because they live on the large sized tubes of *Riftia pachyptila*, a tube surface which would appear to be almost flat relative to the small-sized *Lepetodrilus* (compare Desbruyères et al. 2006: 89–90).

*Bathyacmaea* cf. *subnipponica* probably lived on substrates of small size judging from its elongated shell shape and supported by direct observation of the specimen still attached to the ataphrid shell (Fig. 2C). Living *Bathyacmaea* were observed attached to bivalve shells, pieces of rock and even crawling through the sandy sediment or browsing on bacterial mats (Okutani et al. 1992; Hashimoto et al. 1995; Sasaki et al. 2005). Shell elongation depending on the substrate type affects not only patellogastropods but also other limpet gastropods living in chemosynthesis-based communities, e.g., a moderately elongated cocculiniform limpet *Pyropelta corymba* lives attached to the gastropod *Provanna laevis* (Warén and Bouchet 2001) but it is not known from vestimentiferan tube worms (Desbruyères et al. 2006).

The Recent species of *Serradonta* are restricted exclusively to the marine waters of the Japanese Archipelago (e.g., Sasaki et al. 2005) and its fossil record is also restricted to Japan (Hikida et al. 2003; Jenkins et al. 2007; own unpublished data). This relatively weak dispersal over prolonged geological time may suggest that species of *Serradonta* could flourish only those chemosynthesis-based communities already

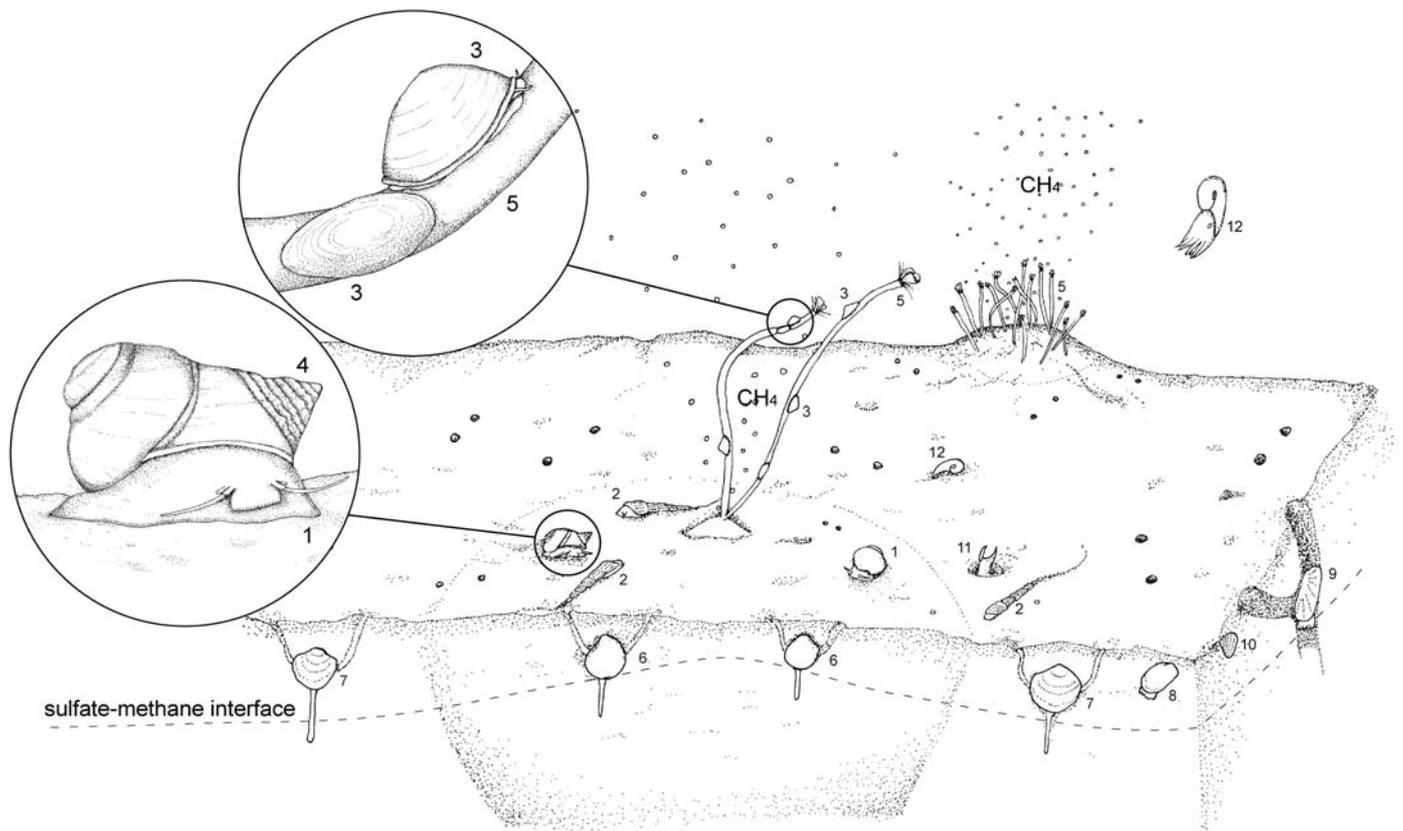


Fig. 3. Reconstruction of the Campanian (Late Cretaceous) Yasukawa methane-seep community. Abundant ataphrid and abysssochrysid gastropods and a few vestimentiferans inhabited the carbonate mound that formed due to anaerobic oxidation of methane and was covered by sandy/silty sediments. The bivalves *Nucinella* and *Acharax* lived in the peripheral zone of the seep. *Bathyacmaea* cf. *subnipponica* attached to an ataphrid shell and *Serradonta* cf. *vestimentifericola* grazed on the surface of vestimentiferan tubes. 1, Ataphrid gastropod; 2, abysssochrysid gastropod; 3, *Serradonta* cf. *vestimentifericola*; 4, *Bathyacmaea* cf. *subnipponica*; 5, ?vestimentiferan tube; 6, *Thyasira* sp.; 7, *Miltha* sp.; 8, *Nucinella* sp.; 9, *Acharax cretacea*; 10, *Leionucula formosa*; 11, unidentified decapod; 12, ammonoid. Soft part reconstructions based on Recent counterparts, ataphrid soft body reconstruction based on Recent turbinid gastropods.

settled by vestimentiferan tube worms. This contrasts to *Bathyacmaea* which could live on a variety of substrates and was able to disperse from Japan (the only fossil occurrence) to other chemosynthesis-based communities in the Western Pacific (Warén and Bouchet 2001; Sasaki et al. 2005 and references therein) including those not settled by vestimentiferans (e.g., Beck 1996). It is worth noting that acmaeid limpets were not found in the extensive fossil record of Cenozoic seeps in Japan (e.g., Majima et al. 2005). This might be related to the apparent absence of tubes worms at all but one (Kanie et al. 1992) of these sites. There is, however, little knowledge about larval dispersal ability and food preference of Recent *Serradonta* and *Bathyacmaea* and these factors may also influence the pattern of their distribution.

## Conclusions

The mode of acmaeid limpet occurrences in ancient methane-seeps of the Nakagawa area of Hokkaido suggests that by the Campanian these gastropods had a mode of life similar

to that of their Recent counterparts. *Serradonta* already preferred vestimentiferan tubes for attachment; *Bathyacmaea* could utilize a wider variety of small substrates including shells of other small gastropods, as do some other Recent tall limpets. The difference in substrate preference is probably responsible for the present-day distribution of these gastropods. *Serradonta* has a more restricted distribution than *Bathyacmaea* because it could spread only through those hot vents and cold seeps which were already settled by vestimentiferans.

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