

A New Gigantic *Nucinella* (Bivalvia: Solemyoidea) from the Cretaceous Cold-seep Deposit in Hokkaido, Northern Japan

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Abstract. *Nucinella gigantea*, sp. nov. is described from the Campanian cold-seep deposits in Hokkaido, northern Japan. This species is characterized by its gigantic size within the genus and by its radiating interior striation. Its morphological features, associated fauna, lithofacies and carbon isotope suggest that *N. gigantea* lived in the bathyal cold-seep site, and depended on chemosymbiosis. In addition, this new species is the oldest known *Nucinella* invader of deep cold-seep environments.

INTRODUCTION

Species of the genus *Nucinella* Wood, 1851 are rare bivalves ranging from shallow waters to lower bathyal depths (La Perna, 2005, Table 1; Okutani & Iwasaki, 2003). Based on the soft-part anatomy and shell structure, the genus was transferred from Arcoida of Pteriomorpha to Solemyoidea of Protobranchia (Allen & Sanders, 1969; Waller, 1978).

In Japan, seven species of Recent and fossil nucinellids have been described: *Nucinella kanekoi* Matsukuma, Okutani & Tsuchi, 1982, *N. viridis* Matsukuma, Okutani & Tsuchi, 1982, *N. surugana* Matsukuma, Okutani & Tsuchi, 1982, *Huxleya sulcata* A. Adams, 1860, *H. decussata* A. Adams, 1862, *H. ochiaiensis* (Chinzei, 1959) and *H. cavernicola* Hayami & Kase, 1993. *H. sulcata* and the extinct *H. ochiaiensis* have been recorded from the Plio-Pleistocene formations in the Northeast Honshu and Kanto district of central Honshu (Baba, 1990) whereas *N. kanekoi* is also known from the Pliocene Takanabe Formation of the Miyazaki Group in Miyazaki Prefecture, southern Kyushu (Matsukuma et al., 1982).

A new gigantic species of *Nucinella* was collected from the Cretaceous cold-seep site in Nakagawa Town in northern Hokkaido. This is the second record of *Nucinella* from cold seep sites, after the Recent species *N. viridis* (Okutani & Iwasaki, 2003; Sasaki et al.,

2005). Therefore, this is the oldest record of *Nucinella* in Japan and the first record from a fossil cold-seep site.

MATERIALS AND METHODS

Fossil specimens of the present new species were collected from the Campanian Omagari Formation of Upper Yezo Group (Takahashi et al., 2003) at about 400 m downstream of Abeshinai River from the junction with Tanno-sawa Creek (Figure 1). The name coined for the locality is Yasukawa site (Jenkins, 2006). Four carbonate bodies, each larger than 50 cm in diameter, here named A to D, were identified at the Yasukawa site. We examined the largest carbonate body and surrounding sandy siltstone (Carbonate body A, 1 m × 2 m) which yields some small bivalves, including the new species of *Nucinella* and gastropods (Jenkins, 2006). The new species of *Nucinella* was also collected from mudstone overlying the cemented sandstone, and mudstone located laterally 5 m away but on nearly the same horizon as Carbonate body A (the name coined for the locality is Yasukawa Peripheral Site; YPS). All fossil specimens are housed at the University Museum, the University of Tokyo (UMUT).

According to Jenkins et al. (2007), the carbonate body can be divided into upper and lower parts (40 cm and 60 cm thick, respectively). The lower part is composed mainly of fractured micritic limestone. The

Table 1

Associated species with a new species of *Nucinella*.

Species
<i>Serradonta</i> sp.
Ataphridae gen. et sp. indet.
Abyssochrysidae gen. et sp. indet.
<i>Acharax cretacea</i> Kanie and Nishida
<i>Leionucula formosa</i> (Nagao)
<i>Acila</i> (<i>Truncacila</i>) <i>hokkaidoensis</i> (Nagao)
<i>Nuculana</i> (<i>Ezonuculana</i>) <i>maetraeformis</i> Nagao
<i>Propeanussium yubarensis</i> (Yabe and Nagao)
<i>Myrtea ezoensis</i> (Nagao)
<i>M.</i> ? sp.
<i>Miltha</i> sp.
<i>Thyasira</i> sp.
<i>Fissidentalium</i> cf. <i>otatunnei</i> (Nagao)

upper part is mainly composed of cemented sandstone (i.e., grainstone) with cements of radiaxial bladed calcite and sparry calcite. Isotopic composition of early cemented phases, i.e., micrite and radiaxial bladed calcite, ranges from -43.5 to 37.7% for $\delta^{13}\text{C}$ (vs. PDB) and from -2.7 to -0.4% for $\delta^{18}\text{O}$ (vs. PDB). These oxygen isotope values closely resemble the values from Campanian shells of benthic animals examined from the outer shelf to upper slope settings in the north-western Pacific (Moriya et al., 2003). The negative $\delta^{13}\text{C}$ values of the early precipitated carbonates indicate that their carbon was derived from biogenic and/or thermogenic methane (Peckmann & Thiel, 2004). This

fact, as well as the variable sulphide sulphur isotopic compositions, high carbonate contents, and *in situ* fractures in the carbonates, strongly suggest that this locality was a methane-seep site (Jenkins, 2006).

On the measurement of shells, Matsukuma et al. (1982) proposed to measure "shell length" along the antero-posterior axis passing through the supposed locations of mouth and anus. However, most authors measured shell length as parallel to hinge axis. We use this traditional method to measure the shell length and height, as claimed by La Perna (2005) for comparing the new species with other ones. La Perna (2005) measured height as the beak-ventral distance and length as the antero-posterior one at right angle to height.

SYSTEMATICS

Family Manzanellidae Chronic, 1952

Remarks: This family includes *Manzanella* Girty, 1909 (Early Permian), *Nucinella* Wood, 1851 (Early Jurassic to Recent) and *Huxleya* A. Adams, 1860 (Pliocene to Recent). Assignment of these genera to a single family (Manzaniellidae) or two families (Manzaniellidae and Nucinelidae Vokes, 1956) is controversial. Habe (1977) and Pojeta (1988) separated Nucinelidae including some living species from the extinct Manzanellidae. Vokes (1956) considered *Manzanella* is included in the same family to *Nucinella* and *Huxleya* when he summarized supraspecific group of Nucinelidae and all species of *Nucinella*. Then, he regarded Nucinelidae as a junior synonym of Manzanellidae (Vokes, 1980). In his cladistic work on bivalves, Waller (1990, 1998) shows high-rank segregation of Nucinelidae and Manzanellidae from other solemyoids and consequently combined two families. Thus, we follow the conclusions of Vokes (1980) and Waller (1990, 1998).

Genus *Nucinella* Wood, 1851

Nucinella gigantea Amano, Jenkins and Hikida,
sp. nov.

(Figures 2–7)

Diagnosis: A gigantic *Nucinella* having nuculid shape and with many radiating interior striae and narrow flat area below dentition.

Holotype: Length—18.4 mm, height—18.8 mm, width—10.4 mm, both valves, UMUT MM29245; Carbonate body A.

Paratypes: Length—8.9 mm, height—9.8 mm, width—4.9 mm, both valves, UMUT MM29246; length—7.9 mm, height—7.9 mm, width—4.2 mm, both valves, UMUT MM29247; length—6.5 mm, height—6.9 mm,

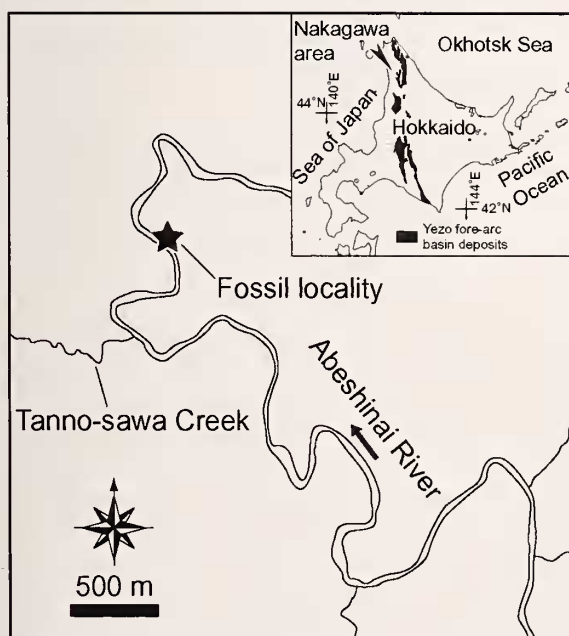
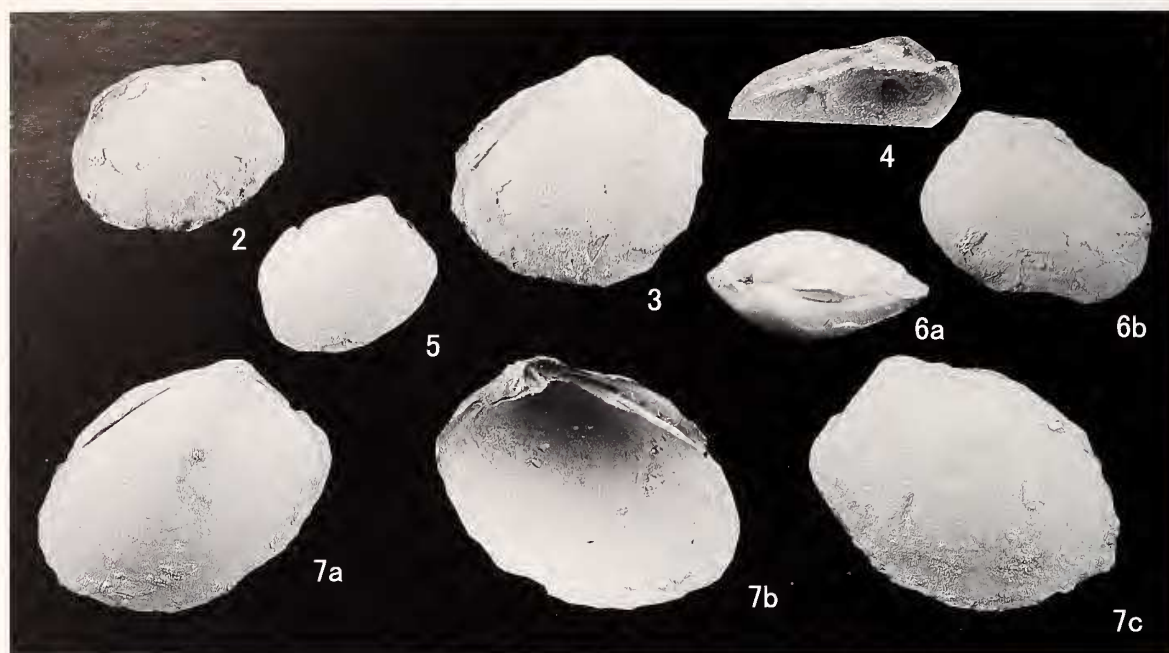


Figure 1. Locality of a new species of *Nucinella*.



Figures 2–7. *Nucinella gigantea* Amano, Jenkins & Hikida. Figure 2, Paratype, length = 7.9 mm, UMUT MM29247. Figure 3, Paratype, length = 13.2 mm, UMUT MM29250. Figure 4, Paratype, length = 12.1 mm, UMUT MM29249. Figure 5, Paratype, length = 6.5 mm, UMUT MM29248. Figures 6a–b, Paratype, length = 8.9 mm, UMUT MM29246. Figures 7a–c, Holotype, length = 18.4 mm, UMUT MM29245; Figure 7b, rubber cast of Holotype.

width—3.1 mm, both valves, UMUT MM29248; length—12.1 mm, height—5.4 mm (deformed), right valve, UMUT MM29249; YPS: Length—13.2 mm, height—11.2 mm, left valve, UMUT MM29250; Carbonate body A.

Type locality: 400 m downstream of Abeshinai River from the junction with Tanno-sawa Creek, Nakagawa Town, Hokkaido (44°40'27"N, 142°1'45"E); Omagari Formation.

Stratigraphic and geographic distribution: Late Cretaceous (Campanian), Omagari Formation; known only from the type locality.

Description: Shell gigantic in size, thin-walled, moderately inflated, nuculiform, equivalve, inequilateral. Umbo projecting above dorsal margin, opisthogyrate, posteriorly situated at about one-third of shell length. Antero-dorsal margin long, broadly arcuated, grading into rounded anterior margin; antero-ventral margin well rounded; postero-ventral margin nearly straight; postero-dorsal margin short, steeply sloping, making right angle with postero-ventral margin. Surface smooth, except for very weak growth lines. Hinge plate not so wide, consisting of subumbonal taxodont teeth and anterior lateral tooth. In right valve; two central teeth large, but thin; more than two anterior teeth small; two posterior teeth small, chevron shaped, parallel to hinge, just behind central teeth; anterior

lateral tooth long and elevated. In left valve; one central tooth strong; more than five posterior teeth small; three anterior teeth parallel to hinge; one anterior lateral tooth strong and long. Ligament pit wide and deep, immediately situated at posterior of beak, occupying postero-dorsal margin. Monomyarian condition advanced, anterior adductor muscle scar large and ovate. Inner surface with very fine radial striations. Pallial line entire.

Comparison: Most species of fossil and Recent *Nucinella* have very small adult shells (length = about 1 to 3 mm). Exceptionally, three Recent species attaining and even exceeding 1 cm in shell length are known from the deep sea: *Nucinella maxima* (Thiele & Jackel, 1931) from Zanzibar Channel, eastern Africa (463 m deep), *N. viridis* Matsukuma, Okutani & Tsuchi, 1982 from off Nojimazaki, central Honshu (2630–3581 m deep) and *N. boucheti* La Perna, 2005 from Bondoc Peninsula, Philippines (1580–1610 m deep). *N. gigantea* is a member of such a large shelled species group. Among them, *N. boucheti* closely resembles *N. gigantea* in its large shell size (length = 25 mm), nuculiform outline and fine radiating interior striation. However, *N. boucheti* differs from *N. gigantea* in having a wide triangular flat area below dentition and more numerous teeth (13 in the holotype). *N. maxima* is another species similar to *N. gigantea*, with two vertical central teeth, similar number of teeth (6 or 7) and interior

striation. Smaller size ($L = 12.5$ mm) and the obtusely rounded posterior corner of *N. maxima* enable us to separate this species from *N. gigantea*. *N. viridis* differs from *N. gigantea* by having a smaller shell ($L < 10.4$ mm), fewer teeth (5) and obtusely rounded posterior corner.

Two other species of *Nucinella* have been recorded from Cretaceous deposits: *N. glabrata* Stoliczka, 1871 from the Ootatoor Group in South India and *N. sohli* Pojeta, 1988 from the Blufftown Formation in Georgia, USA (Vokes, 1956; Pojeta, 1988). However, their small size (length = 3.1 mm in *N. glabrata* and length = 2 mm in *N. sohli*) easily distinguishes them from *N. gigantea*. Although the inner surface of *N. glabrata* is unknown in detail, *N. sohli* distinctly lacks the radiating interior striation.

Associated species and paleoenvironment: At the type locality, this new species was collected from the Carbonate body A, and its surrounding sandy siltstone and mudstone, and YPS together with many taxodont bivalves, lucinids and thyasirids (Table 1). Among them, *Acharax cretacea* Kanie & Nishida, 2000, *Myrtea ezoensis* (Nagao, 1938), *Miltha* sp. and *Thyasira* sp. might be chemosymbiotic bivalves. In contrast, *Leionucula formosa* (Nagao, 1930), *Acila (Truncacila) hokkaidoensis* Nagao, 1932, *Nuculana (Ezonuculana) mactraeformis* Nagao, 1932 might be deposit feeders. *Propeamussium yubarensis* (Yabe & Nagao, 1928) is thought to be a carnivore (Hickman, 1984). The high ratio (0.5) of protobranch bivalves to total bivalve species shows a habitat deeper than the lower sublittoral zone (Amano et al., 1987; Amano & Nonaka, 2001; Amano, 2003). On the other hand, the Recent records of small associated gastropod *Serradonta* Okutani, Tsuchida & Fujikura, 1992 is restricted to bathyal depth in the Pacific (Warén & Bouchet, 2001; Sasaki et al., 2005). Judging from these associated fauna and lithology, this new species lived at around the bathyal cold-seep site.

Etymology: This species named after its size.

DISCUSSION

La Perna (2005) suggested that the large body size of *N. boucheti*, together with deep sea colonization, may be an expression of the evolutionary diversification of *Nucinella*. In fact, other than *N. maxima* living in the upper bathyal zone, large species of *Nucinella* now live in the middle to lower bathyal depth while most small species live in the upper sublittoral to upper bathyal zones (La Perna, 2005). However, it is difficult to explain how low nutrient conditions of the deep sea could sustain such large species.

Taylor & Glover (2000) estimated chemosymbiosis of fossil Lucinidae, partly based on the study of

symbiosis-associated morphological features. Reid (1990) listed the genera possessing sulphide-oxidizing bacteria including *Solemya* Lamarck, 1818, *Acharax* Dall, 1908, *Calypptogena* Dall, 1891, *Bathymodiulus* Kenk & Wilson, 1985, *Lucinoma* Dall, 1901, *Parvilucina* Dall, 1901, *Anodontia* Link, 1807, *Codakia* Scopoli, 1777, *Linga* De Gregorio, 1884, *Myrtea* Turton, 1822, *Thyasira* Lamarck, 1818 and so on. Although the exact reason is unknown, most species of these genera have radiating interior striation. The large-sized *N. boucheti*, *N. maxima* and *N. gigantea* have such striation while small-sized *N. serrei* Lamy, 1912 and *N. adamsi* (Dall, 1889) lack this feature (Lyle Campbell, personal communication). Moreover, Reid (1990) inferred that the large species *N. maxima* may harbor sulphide-oxidizing bacteria based on its gutless condition pointed out by Kuznetsov & Schileyko (1984). In contrast, Allen & Sanders (1969) described a normal gut in the small species, *N. serrei*. In addition, as above noted, another large species, *N. viridis*, has been found at the cold seep sites (Okutani & Iwasaki, 2003; Sasaki et al., 2005). Furthermore, all solemyid species live in symbiosis with sulfur-oxidizing bacteria (Fisher, 1990). The solemyid bivalves first entered cold-seep conditions in the Carboniferous (Peckmann et al., 2001) and are widely distributed in post-Carboniferous hot-vent and cold-seep environments (Campbell, 2006). Molecular phylogeny of the endosymbiotic bacteria suggest that the solemyid bivalves harbored the bacteria in ancient times (Imhoff et al., 2003). Based on these criteria and on the ecology of related species, we believe that the large size of *Nucinella* may be attributed to chemosymbiosis. Conversely, small size of fossil and living species of *Nucinella* may indicate deposit feeding, as in other protobranchs and shallow water dwellers. Of course, to settle this hypothesis, it is necessary to make a direct examination of the symbiosis on the Recent large *Nucinella*. *N. gigantea* appears to be the earliest *Nucinella* to invade the cold seeps, presumably because of its chemosymbiosis.

When he discussed paleobiogeographic history of European nucinellids, La Perna (2004) pointed out that the fossil species, other than the Pleistocene *N. seguenzae* (Dall, 1898), lived in shelf environment and then later migrated to deeper water. The oldest record of *Nucinella* is from the early Jurassic of Europe (Vokes, 1956). Based on this record, La Perna (2004) also postulated that this genus originated in the western Tethys region. Our new data show that the migration from the western Tethys to the eastern part occurred in pre-Cretaceous time and the invasion to the deep sea dates back to the Campanian.

In the northeastern Pacific region, a small species, *N. oregona* (Vokes, 1956) has been recorded from the Nestucca Formation in Oregon whose age is late middle Eocene (Prothero, 2001). From the middle

Eocene Cook Mountain Formation, *N. allenii* Vokes, 1966 was found in the eastern coast of America. By our data, it is possible to infer two migration routes of the northeastern Pacific *Nucinella*. As the Central American Seaway was present at that time (e.g. Coates & Obando, 1996), it was possible for *Nucinella* to migrate from the Atlantic to the Pacific side as did the venerid genus *Securella* Parker, 1949 (Vermeij, 2001). Another possibility is the eastward trans-Pacific migration as shown in some cold-water mollusks (Amano, 2005). The current through the Central American Seaway in the Eocene (Iturralde-Vinent, 2003) supports the former alternative. For settling this problem, much more fossil data of *Nucinella* are needed especially from the North Pacific region.

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