

Middle Miocene Chemosynthetic Thraciid *Nipponothracia gigantea* (Shikama, 1968) from Central Japan is a Large Lucinid Bivalve (Lucinoidea: Mollusca)

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Abstract. *Nipponothracia* Kanie & Sakai, 1997, a recently proposed bivalve genus with the type species *Thracidora gigantea* Shikama, 1968 from the middle Miocene of central Japan, was previously regarded as amongst the largest in Thraciidae and only the member in this family which participates in fossil cold-seep assemblages. We found and examined a large specimen referable to *N. gigantea* in the collection of National Museum of Nature and Science, Tokyo, which reveals that *N. gigantea* belongs to Lucinidae. The genus *Nipponothracia* still remains as a distinct genus of Lucinidae due to its remarkable shell characters; nevertheless its familial position changed drastically from Thraciidae to Lucinidae. *Nipponothracia ponbetsensis* Kanie & Sakai, 1997 from the Albian of northern Japan and *Thracia yezoensis* Kanie & Kuramochi, 1996 from the Cenomanian of northern Japan are also large lucinids referable to *Nipponothracia*, but their positive assignment to that genus awaits better preserved specimens. *Nipponothracia* is a candidate for generic identification of poorly known, large and edentulous lucinid bivalves from Mesozoic and Cenozoic cold-seep assemblages.

INTRODUCTION

Three specimens of a large bivalve from the Miocene of Japan were originally described as *Thracidora gigantea* and placed in the anomalodesmatan family Thraciidae (Shikama, 1968). These specimens were collected from the upper part of the Morito Formation (now remapped as Oyama Formation by Eto et al., 1998) of the Hayama Group at a cliff (now destroyed) near the northern exit of a road tunnel in Higashihayami [sic] (= Higashihemi), Yokosuka City in Miura Peninsula, central Japan. Research Group for Giant Clam Communities of the Hayama Group (1995) mentioned an additional occurrence of this species from the Hayama Group at Ikegami about 300 m southeast of the type locality in the same city, where it was found associated with a cold-seep chemosynthetic molluscan assemblage (Kanie et al., 1995b; Kanno & Kanie, 1995; Naganuma et al., 1995). Later, Kanie & Sakai (1997) established the new genus *Nipponothracia* on the basis of *T. gigantea* as the type species, along with a description of a new species *Nipponothracia ponbetsensis* from the upper Albian (Cretaceous) of

Hokkaido, northern Japan. Kanie & Sakai (1997) regarded *N. ponbetsensis* as a member of an Albian chemosynthetic community. The two *Nipponothracia* species are the only examples of the family Thraciidae in chemosynthetic communities (see Majima et al., 2005; Kiel & Little, 2006).

However, interpretation of *Nipponothracia* as belonging to Thraciidae by these authors is open to question. Thraciids have a posteriorly directed (opisthogyrate) beak, an edentulous hinge, a posterior external ligament, a pallial sinus, granular shell surface, etc. The most difficult point to agree on is the position of the ligament within the shell. Shikama (1968:15) correctly described the ligament groove located behind the hinge plate (therefore posterior) but this structure is positioned along the antero-dorsal instead of the postero-dorsal margin, assuming that it belongs to Thraciidae. This ligament groove is clearly observable in one of the two illustrated syntypes (Shikama, 1968, pl. 2), which was later designated as the lectotype by Kanie & Sakai (1997). Kanie & Sakai (1997), in contrast, suggested that the ligament is small and positioned along the postero-dorsal margin (see Kanie

& Sakai, 1997 fig. 2). However, we could not find any structure in the posterior hinge plate indicative of the presence of ligament in the lectotype. They did not mention the groove that Shikama (1968) described as the ligament. These authors stated that the right valve is more convex and smaller than the left. However, the "left" valve is slightly crushed by sediment compaction, so that it is still uncertain whether or not the shell is inequivalve in *N. gigantea*. Goedert et al. (2003) already suggested that this species actually belongs to Lucinidae. However, the crucial evidence of this has never been provided. Therefore, documentation of additional reliable shell characters is indispensable to ascertain the systematic position of this interesting bivalve.

We here report additional shell characters of *N. gigantea* based on a specimen stored in the National Museum of Nature and Science, Tokyo and show that *N. gigantea* belongs to Lucinidae.

MATERIAL AND LOCALITY

The specimen described here is in the collection of the National Museum of Nature and Science, Tokyo with registration number NSM PM11610, which was identified as *Schizothaerus keenae* Kuroda and Habe (*Tresus* in current generic assignment), a mactrid bivalve common in modern shallow waters and younger Pleistocene shallow-marine beds in Japan. The label attached to this specimen indicates that the specimen was collected by late Dr. Hiroshi Ozaki (a previous director of the Department of Geology, National Science Museum, Tokyo) on September 15, 1952. The label also indicates that the specimen was obtained from 'Miocene Amatsu mudstone' and cites 'Tenjinyama junior high school, Nashizawa, Kimitsu County' as the collection site. The place name is now in the southern part of Futtu City in Boso Peninsula, Chiba Prefecture. 'Tenjinyama junior high school' seems to be the collection site of this specimen, and it seems that it was incorrectly recorded for a branch school of Tenjinyama elementary school once located in Nashizawa and closed in 1967 (Figure 1).

Younger Cenozoic forearc-basin sedimentary rocks in the Nashizawa area comprise the underlying Kinone Formation and overlying Amatsu Formation with either conformable or in fault contact each other; both belong to the Awa Group of Middle Miocene age (Nakajima and Watanabe, 2005). Both formations in this area consist mainly of massive mudstone deposited at lower to middle bathyal depths (Saito, 1992), so that it is difficult to confirm from which formation NSM PM11610 derived on the basis of its matrix alone. A nannofossil analysis of the matrix from NSM PM11610 with light microscopy, identified heavily over-calcified, poorly preserved nannofossils with derived forms from late Oligocene through early Miocene rocks. In the

matrix, *Sphenolithus heteromorphus*, which identifies the base of zone CN3 and the top of CN4, are abundant, and other nannofossils indicative of middle Miocene age are totally absent. Therefore, the age of NSM PM11610 can be estimated in the range between 18.1 and 13.6 Ma (Okada & Bukry, 1980; Backman et al., 1990). The Kinone and Amatsu formations on the Boso Peninsula have been dated as 16–13 Ma and 13–5 Ma, respectively, by micropaleontological, fission track and K-Ar isotope datings (Oda, 1977; Mita & Takahashi, 1998; Motoyama & Takahashi, 1997; Watanabe & Takahashi, 1997; Takahashi & Danhara, 1997; Kameo et al., 2002). Therefore, it is highly probable that NSM PM11610 was derived from the Kinone Formation. Our extensive survey in the Nashizawa area found neither additional specimens nor any chemosynthetic assemblages in the Kinone Formation. We are tempted to assume that NSM PM11610 is a solitary occurrence in the formation.

The collecting site of NSM PM11610 is located on the opposite side of Tokyo Bay and about 25 km east-southeast of the type locality of *N. gigantea*. The Hayama Group in the Miura Peninsula is an accretional complex in origin and is the western extension of the Hota Group on the Boso Peninsula, on which the Kinone Formation overlies unconformably. Microfossil analyses demonstrate that the Hayama Group exposed at Ikegami is early Middle Miocene (ca. 15 Ma) and deposited in the middle bathyal zone (Aita, 1995; Akimoto et al., 1995; Kanie & Asami, 1995; Okada, 1995; Taketani, 1995). It is highly probable that the Hayama Group at the type locality is also early Middle Miocene in age because both localities are in same stratigraphic unit and located only 300 m apart. Therefore, NSM PM11610 is almost equivalent to the lectotype in age despite both fossil-bearing beds being of different tectonic origin (see also Kanie et al., 1991).

SYSTEMATIC PALEONTOLOGY

Family LUCINIDAE Fleming, 1828

Genus *Nipponothracia* Kanie & Sakai, 1997

Type species: *Thracidora gigantea* Shikama, 1968: Middle Miocene, central Japan.

Diagnosis: Shells very large (up to ca. 220 mm long), sub-elliptical and longer than high, weakly inflated, moderately thin-shelled, anterior margin more broadly rounded than posterior one, with surface ornamented only by rugose growth lines. No escutcheon and lunule. Hinge plate edentulous, arched, with a shallow concavity below beak and a shallowly sunken dorsal ligament. Umbones not prominent, located well anterior to vertical midline, only slightly bent anteri-

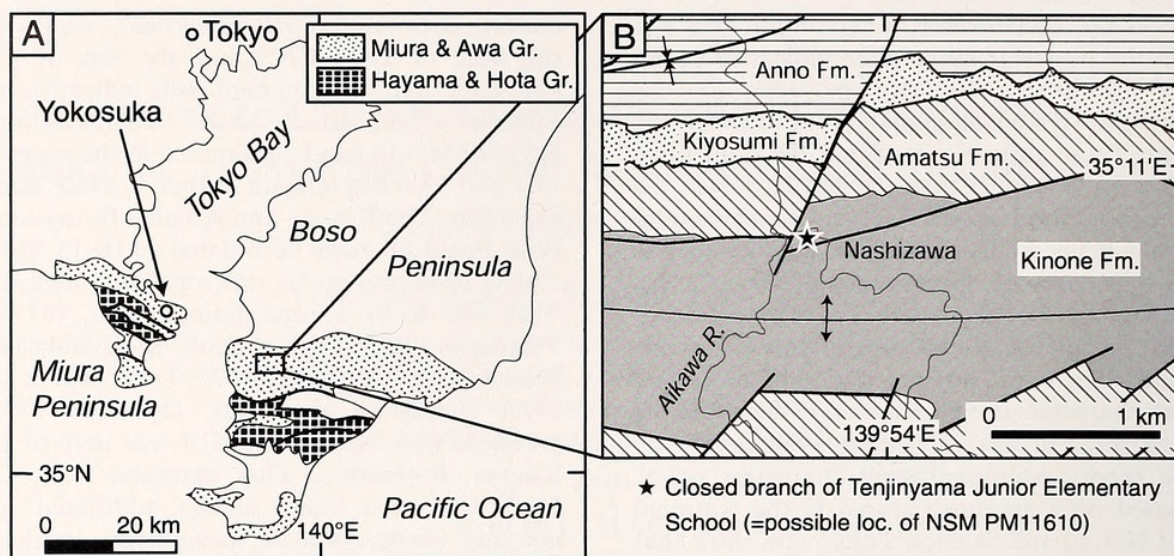


Figure 1. (A) Geologic sketch map of the Boso and Miura Peninsula. (B) Geologic map around the fossil locality of NSM PM11610 (modified after Nakajima & Watanabe, 2005).

only. Anterior adductor scar moderately short and thick, as long as posterior one, dorsally diverging from pallial line for half of its total length. Posterior adductor scar large and elliptical. Valve inner margin smooth.

Nipponothracia gigantea (Shikama, 1968)

(Figures 2–8)

Thracidora gigantea Shikama, 1968:14, pl. 2, figs. 1–3; text-fig. 1.

Thraciidae (gen. nov.) *gigantea* (Shikama). Kanie et al., 1995a:66, fig. 4.

?*Thracia kakumana* (Yokoyama). Kanie et al., 1995a:66, fig. 4.

Nipponothracia gigantea: Kanie & Sakai, 1997:210, fig. 5.

Type material: Lectotype, designated by Kanie & Sakai, 1997, YCM-GP. Ig01A, in Yokosuka City Museum, Yokosuka. Two paralectotypes, not found but seemingly in the collection of Yokohama National University.

Type locality: Higashiemi 4-chome, Yokosuka City, Miura Peninsula, central Japan (35°16'09"N, 139°38'50"E, see Kanie & Sakai, 1997:fig. 1).

Description: The description here is based on the lectotype (Figure 2) and NSM PM11610 (Figures 3–8). Both specimens exhibit a similar state of preservation in that the shells are fragmented into many pieces and some shell pieces subside into the matrix by compaction as to even the surfaces of shell and internal mold to the same level. This is particularly evident in the right valve of NSM PM11610. In addition to this,

the left valve is dislocated anteriorly more than 10 mm from the right valve, so that the anterior margin of the left valve is missing, although NSM PM11610 consists of conjoined valves.

The shell is unusually large and moderately thin for a lucinid. NSM PM11610 may attain ca. 220 mm long if the lost posterior shell margin is complete, and 150 mm high and ca. 80 mm thick (joined valve), which is about 1.5 times larger than the lectotype. Although Shikama (1968) and Kanie & Sakai (1997) described the lectotype as inequivalve (the right valve is more convex than the left in their interpretation), NSM PM11610 is evidently equivalve (Figure 3). This disagreement between the two specimens is likely to be due to sediment compaction for the lectotype. The outline, well seen in the lectotype, is elliptical, inequilateral, with a height/width ratio of 7.7. The umbones are situated well anterior to the vertical midline, bend weakly forward, and protrude only slightly beyond the dorsal margin. The anterior margin is much more narrowly rounded than the posterior one, the anterodorsal margin is almost straight, and the ventral margin is broadly and evenly rounded, without any angulation between the anterior and posterior margins. The shell exterior is ornamented entirely with rugose concentric growth lines, and, in NSM PM11610, with two, faint, axial ribs extending from the umbones to the anterior margin.

The hinge plate, seen only in the lectotype (Figure 2), is moderately narrow and arched with a narrow ligamental nymph behind the beak, thin and short in front of the beak, and is edentulous only with a shallow notch below the beak. The lunule and escutcheon are absent.

The features of the shell interior are seen only in NSM PM11610 (Figures 4–8). The anterior adductor

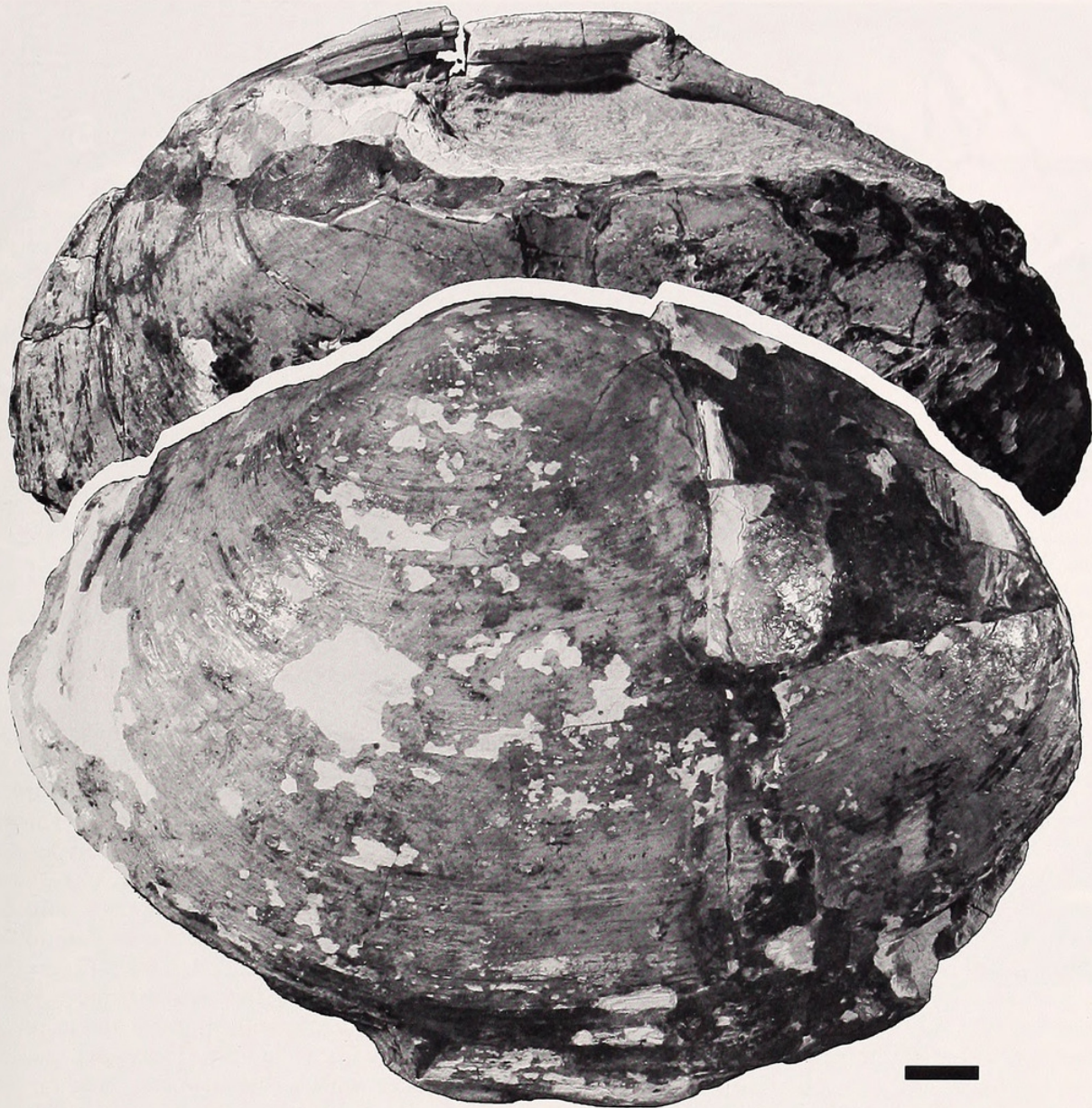
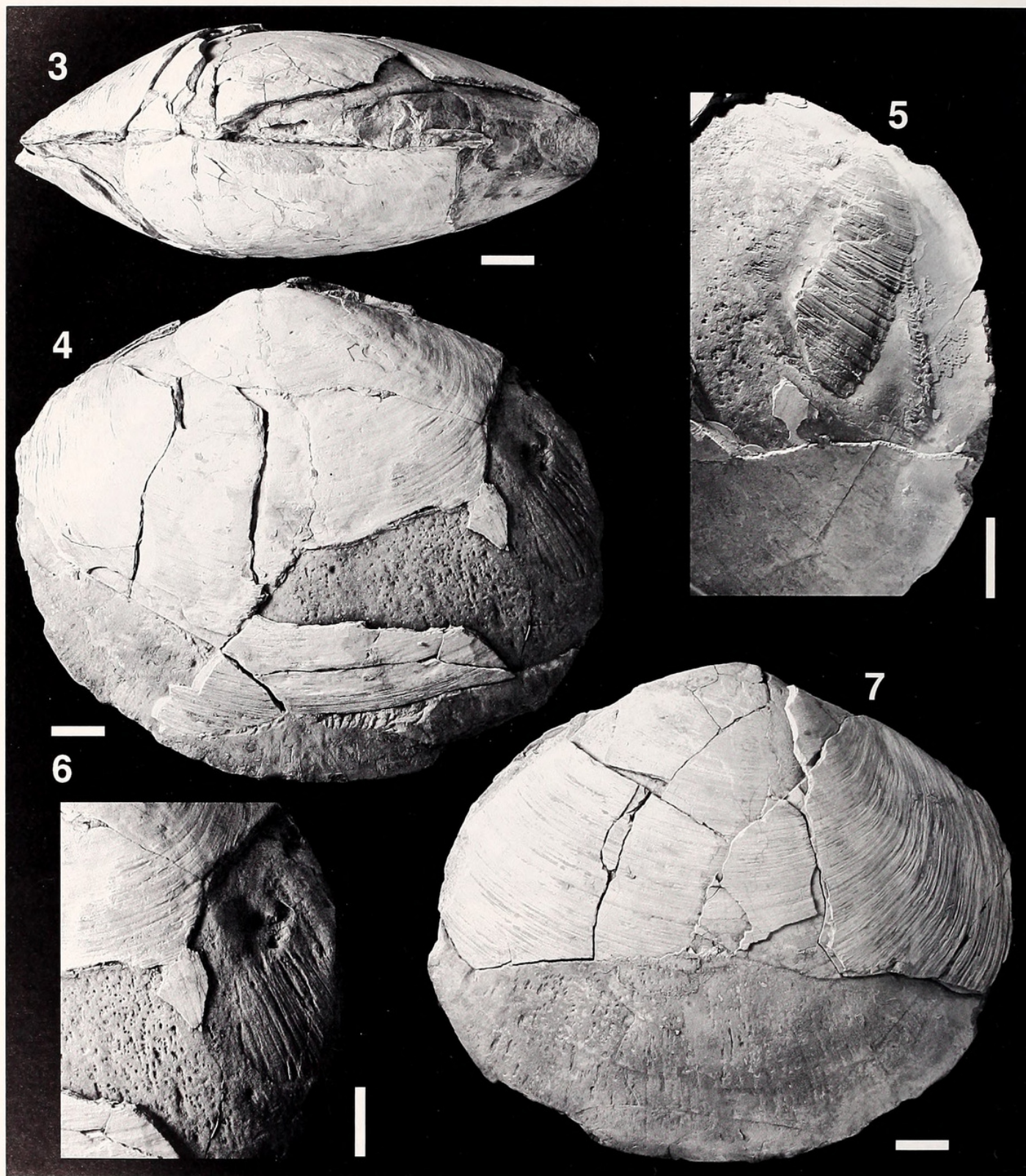


Figure 2. *Nipponothracia gigantea* (Shikama), lectotype, YMC-GP Ig01A, in the collection of Yokosuka City Museum, Yokosuka. Scale bar 10 mm.

scar, clearly visible on the inner mold of the right valve, is short, as long as the posterior adductor scar, broad, and truncated obliquely at the distal end, with irregular striae. The posterior adductor scar, visible on the inner mold of the left valve, is large and elliptical. The pallial line is obscure in most part due to abrasion of the inner mold, but is clearly seen near the anterior adductor scar that diverges dorsally from the pallial line for slightly more than the half of its total length. The inner shell surface has many radial striae near the ventral margin and its ventral edge is smooth. No trace of the pallial blood vessel can be seen on the internal mold.

DISCUSSION

Our detailed observation on NSM PM11610 demonstrates that *Nipponothracia gigantea* is unequivocally a member of Lucinidae because it has the adductor muscle scars and pallial line typical of Lucinidae: the anterior adductor scar is more enlarged than the posterior one and detached from the lines of pallial attachment scars for slightly more than half of its total length. Previous assignment of *N. gigantea* to Thraciidae is therefore due to the absence of the information on the shell interior in the type specimens as well as the



Figures 3–7. *Nipponothracia gigantea* (Shikama), NSM PM11610 in the collection of National Museum of Nature and Science, Tokyo, specimen coated with ammonium chloride. Figure 3. Umbonal view. Figure 4. Left valve. Figure 5. Inner mold of the anterior muscle adductor scar in the right valve, photographed after removal of shell. Figure 6. Inner mold of the posterior muscle adductor scar in the left valve. Figure 7. Right valve. Scale bars 20 mm.

incorrect interpretation of shell orientation and features.

Although the systematic position of *N. gigantea* has changed drastically from Thraciidae to Lucinidae, *Nipponothracia* is likely to survive as a genus even within the Lucinidae. Lucinidae have traditionally been classified into four subfamilies, Lucininae, Myrteinae, Milthinae and Divaricellinae (Chavan, 1969). Bretsky (1976) proposed a different scheme of classification, and recognized seven groups within the family based on North American Cenozoic forms without suprageneric categories. A recent molecular phylogenetic analysis using 18S and 28S rRNA genes has provided results that are incongruent with the previous classifications by shell morphology as well as exclusion of Thyasiridae and Ungulinidae from Lucinoidea (i.e., non-monophyly of Lucinoidea) and inclusion of *Fimbria* (only the modern member of Fimbriidae) within the Lucinidae (Williams et al., 2004). Taylor & Glover (2006) stated that it is at present premature to erect a new classification without developing rigorous studies of molecular and morphological analyses. Therefore, it would be unwise to discuss the subfamilial position of *Nipponothracia* at present.

The only species confidently assignable to *Nipponothracia* at present is *Lucina (Miltha) hetzeli* Martin, 1933 from the late Oligocene asphalt bed in Buton, Indonesia (see also Beets, 1943). The Buton asphalt bed was recently revised by Janssen (1999) as a late Miocene in age (Tortonian to Messinian). *L. (M.) hetzeli* has overall shell characteristics similar to *N. gigantea* except for its much smaller shell size. One of us (TK) recently found several specimens referable to *L. (M.) hetzeli* from an early Pliocene cold-seep assemblage in northwestern Leyte, Philippines. The largest and seemingly adult specimen attains 91 mm in length. There is a possibility that *N. gigantea* is a junior synonym of *L. (M.) hetzeli*, but the final decision requires additional material and studies.

Kanie & Sakai (1997) included a large bivalve (*N. ponbetsensis*) in a seep-related chemosynthetic association from the early Late Albian deposit in the Mikasa area of central Hokkaido, Japan to *Nipponothracia*. The shell characteristics of this species are, according to their description, represented by oval shell shape, concentric surface ornamentation, absence of a lunule and escutcheon, and edentulous hinge, which match well with *N. gigantea*. In addition to these characters, we observed the presence of a long ligamental nymph posterior to the beaks and the absence of the purported "posterior ligament" by those authors. Although the muscular nature is not known, this species appears to belong to Lucinidae. Kanie & Kuramochi (1996) described *Thracia yezoensis*, another large bivalve in a possibly seep-related association from the Cenomanian deposit of the Obira area, northwestern Hokkaido,

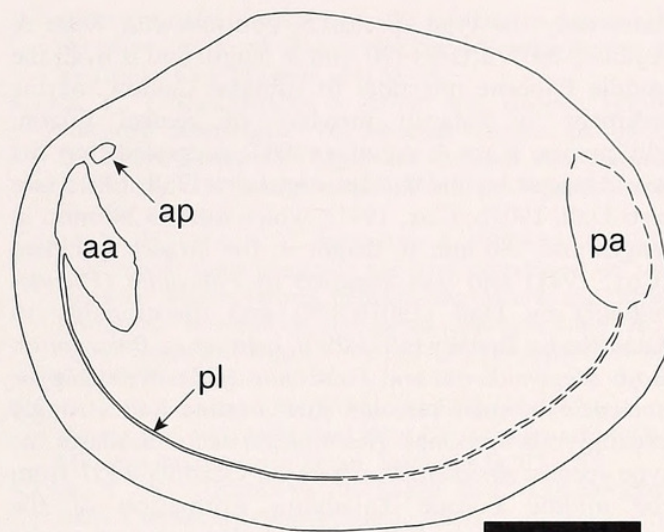


Figure 8. Semi-schematic drawing of the muscle scars and pallial line in *Nipponothracia gigantea* (Shikama) based on NSM PM11610. Right valve. Abbreviations: aa, anterior adductor muscle scar; ap, anterior pedal retractor muscle scar; pa, posterior adductor muscle scar; pl, pallial line. Scale bar 50 mm.

Japan (see also Kanie et al., 1996). This species has almost the same shell characteristics as *N. ponbetsensis*, being seemingly congeneric and even conspecific with *N. ponbetsensis*. We found an internal mold of this species, which was collected by Y. Shigeta of the National Museum of Nature and Science, Tokyo from the type locality of *T. yezoensis*. This specimen reveals the presence of an elongate anterior muscle adductor scar that is more elongate than the posterior one and seemingly detached from the pallial line, supporting an allocation to Lucinidae instead of Thraciidae. Hikida et al. (2003) recorded bivalves probably assignable to *N. ponbetsensis* within a Santonian or Campanian fossil cold-seep community in the Upper Yezo Group of Nakagawa area, northern Hokkaido, Japan. Allocation of these Cretaceous forms from Hokkaido to *Nipponothracia* requires further study to clarify the characteristics of the shell interior for generic determination as well as more specimens for species comparisons.

Several large (sometimes giant) lucinids with edentulous hinge plates have been reported from modern and fossil cold-seep and normal shallow marine assemblages. These are *Meganodontia* Bouchet & Cosel, 2004, *Cryptolucina* Saul et al., 1996, *Bulacanites* Kase & Aguilar, 2007, and *Hadrallucina* Woodring, 1982. *Meganodontia* was described as a monotypic genus, and its type species *M. acetabulum* Bouchet & Cosel, 2004 attains 150 mm in length and is from bathyal depths off Taiwan, most probably of cold-seep in origin. We found a fossil example of this species from an early Pliocene cold-seep assemblage in Leyte, Philippines (unpublished). *Bulacanites* also accommo-

dates only the type species *B. obtusiplicatus* Kase & Aguilar, 2007, attains 120 mm in length and is from the middle Pliocene intertidal to subtidal shallow marine sediment in Bulacan province of central Luzon, Philippines. Kase & Aguilar (2007) suggested that the world largest lucinid *Lucina megameris* Dall, 1901a (see also Dall, 1901b; Cox, 1941), which attains 290 mm in length and 280 mm in height in the largest specimen (Cox, 1941) and was assigned to *Phacoides* (*Pseudomiltha*?) by Dall (1901b:829) and questionably to *Eomiltha* by Bretsky (1976:290), belongs to *Bulacanites*. Both *Meganodontia* and *Bulacanites* differ from *Nipponothracia* in their circular shell outline and strongly prosogyrous umbones. *Hadrallucina* accommodates the type species *Anodontia? angustana* Gardner 1951 from the middle Eocene Tallahatta Formation of the southeastern United States and *Hadrallucina zenica* Woodring (1982) from the Miocene La Boca Formation in Panama. These species were suggested to be shallow marine dwellers (Saul et al., 1996:791). Although the muscular-scar patterns and detailed hinge structures are unknown, *H. angustana* has thin, almost equilateral valves and swollen umbones like *Anodontia*, and is therefore distinct from *Nipponothracia*.

The only lucinid genus with a large shell and edentulous hinge resembling *Nipponothracia* is *Cryptolucina*, which includes the type species *C. megadyseides* Saul et al., 1996 and *C. ellasodyseides* Saul et al., 1996, both from cold-seep assemblages in the middle to late Eocene Hamptulips Formation, western Washington, USA (Saul et al., 1996). Another species referable to *Cryptolucina*, as already suggested by Majima et al. (2005) and Kase & Aguilar (2007), is *Saxolucina* (*Megaximus*) *matsushitai* Matsumoto, 1971 from the lower Miocene Setogawa Group in central Japan. *S. (M.) matsushitai* has strongly prosogyrate and protruding umbones above the dorsal shell border and coarse concentric lamellar growth lines, which are quite similar to *C. megadyseides*. *Cryptolucina* clearly differs from *Nipponothracia* in having strongly prosogyrate umbones, concave antero-dorsal margin and coarse concentric lamellar growth lines. *C. ellasodyseides*, on the other hand, is not so typical of *Cryptolucina* as it has a more elongate shell outline and weakly prosogyrate and seemingly inconspicuous umbones. These shell characters are rather similar to *Nipponothracia*. However, *C. ellasodyseides* is unique as it has radial swellings both in the anterior and posterior parts with a slight median depression in the shell surface, which is not known in *C. megadyseides* and *N. gigantea*. A final decision on the generic position of *C. megadyseides* is deferred until rigorous revision of Mesozoic large lucinid-like bivalves is undertaken. Kelly et al. (2000) described another new species, *Cryptolucina kuhnpassetensis* from the late Barremian seep-related limestone mounds in Northeast Greenland. This species is very

similar to *N. gigantea* in shell form and in muscular and ligamental features. We suggest that *C. kuhnpassetensis* is similar to *Nipponothracia* rather than to *Cryptolucina*.

Saul et al. (1996) and Kelly et al. (2000) enumerated many examples of large and seemingly edentulous bivalves possibly referable or similar to *Cryptolucina* from the Mesozoic and Cenozoic formations, mostly of cold-seep in origin, of which '*Lucina*' *colusaensis* Stanton (1895:pl. 11, figs. 4, 5) from the Upper Jurassic and Upper Cretaceous Knoxville Beds, California is an additional species comparable to *Nipponothracia*. However, the hinge and muscle-scars are totally unknown for this species (Saul et al., 1996:791). In addition to this, a large bivalve reported by Gill et al. (2005:fig. 7C) as 'lucinid B' from the Miocene Freeman's Bay Limestone, Trinidad is similar to *N. gigantea* in having a laterally expanded oval shell. These cannot be assigned properly to *Nipponothracia* without detailed descriptions on the hinge and muscle-scars.

This study demonstrates that no Thraciidae have yet been found associated with cold-seep chemosynthetic assemblages. Although Lucinidae are not common in modern cold-seep chemosynthetic communities probably due to the difficulty of sampling with the submersible manipulator (e.g., Sibuet & Olu, 1998), they are a major group of bivalves found associated with cold-seep assemblages in the Cenozoic and Cretaceous in Japan (see Majima et al., 2005).

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