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Bivalves from Cretaceous cold-seep deposits on Hokkaido, Japan

STEFFEN KIEL, KAZUTAKA AMANO, and ROBERT G. JENKINS

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Cretaceous cold-seep deposits of the Yezo Group on Hokkaido, Japan, yield a rich and well-preserved mollusk fauna. The systematics of nine bivalve species previously reported from these deposits can now be reevaluated using newly collected fossils. The fossils include a Cenomanian specimen of *Nucinella gigantea* with a drill hole possibly made by a naticid, by far the oldest record of a drill hole from a cold seep site. In Japan, Cretaceous seep bivalve assemblages are characterized by (i) the unique occurrence of large specimens of *Nucinella* (Manzanellidae), (ii) the commonly present nuculid *Acila* (*Truncacila*), and (iii) a high diversity of lucinids, possibly as many as four distinct genera. Two new species described are the Albian *Acharax mikasaensis* (Solemyidae) and the Albian to Campanian *Thyasira tanabei* (Thyasiridae), of which the former had previously been misidentified as the oldest vesicomyid, the latter as the oldest *Conchocele*.

Key words: Solemyidae, Manzanellidae, Lucinidae, Thyasiridae, hydrocarbon seeps, chemosymbiosis, Cretaceous, Japan.

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Introduction

Bivalves with chemotrophic endosymbionts play a major role in the ecosystems around hydrothermal vents and hydrocarbon seeps today and have been the dominate part of the molluscan megafauna in these environments since the Late Cretaceous (Campbell and Bottjer 1995). The origin and evolutionary history of these highly endemic faunas is the subject of a long and ongoing debate (e.g., Newman 1985; Tunnicliffe 1992; McArthur and Tunnicliffe 1998; Baco et al. 1999; Distel et al. 2000; Little and Vrijenhoek 2003; Kiel and Little 2006; Samadi et al. 2007). The fossil record provides direct evidence for the evolutionary history of these faunas, but most fossil seep communities described to date are of Cenozoic age (Majima et al. 2005; Campbell 2006). The deep-water sediments of the Cretaceous Yezo Group on Hokkaido, northern Japan, yield a wealth of fossil-rich Cretaceous seep carbonates that is unrivalled world-wide (Kanie et al. 1993; Kanie et al. 2000; Hikida et al. 2003; Amano et al. 2007; Jenkins et al. 2007a, b; Kaim et al. in press). Many of the modern clades inhabiting vents and seeps apparently have their origin in the Cretaceous (Kiel and Little 2006). Because several earliest records of these clades are from seep deposits of the Yezo Group on Hokkaido, solid taxonomic work on this fauna is of special importance for deciphering the evolutionary history of these extraordinary ecosystems. The purpose of this study is to use recently collected fossil bivalves from the Yezo Group to clarify the identity of six previously described species, including the presumed oldest records of Vesicomyidae and the thyasirid *Conchocele*, and to describe two new species. Two species are described in open nomenclature.

Institutional abbreviations.—UMUT, University Museum, University of Tokyo, Tokyo, Japan; USNM, United States National Museum of Natural History, Washington, USA.

Material

The fossils used in this study were collected from four Cretaceous cold-seep deposits in the Yezo Group on Hokkaido, Japan (Fig. 1, Table 1). These localities have already been described in detail, hence they are only briefly characterized here and the appropriate references are given. All figured and supplementary specimens are catalogued in the University Museum of the University of Tokyo (UMUT MM 29523-29545).

Ponbetsu.—This site consists of two silty carbonate blocks that crop out on the right (north) bank of the Ponbetsu River in Mikasa City, and is of Albian age (Kanie et al. 1993; Kanie and Sakai 1997; Majima et al. 2005). Species from this site include: *Acharax mikasaensis* sp. nov., *Thyasira*

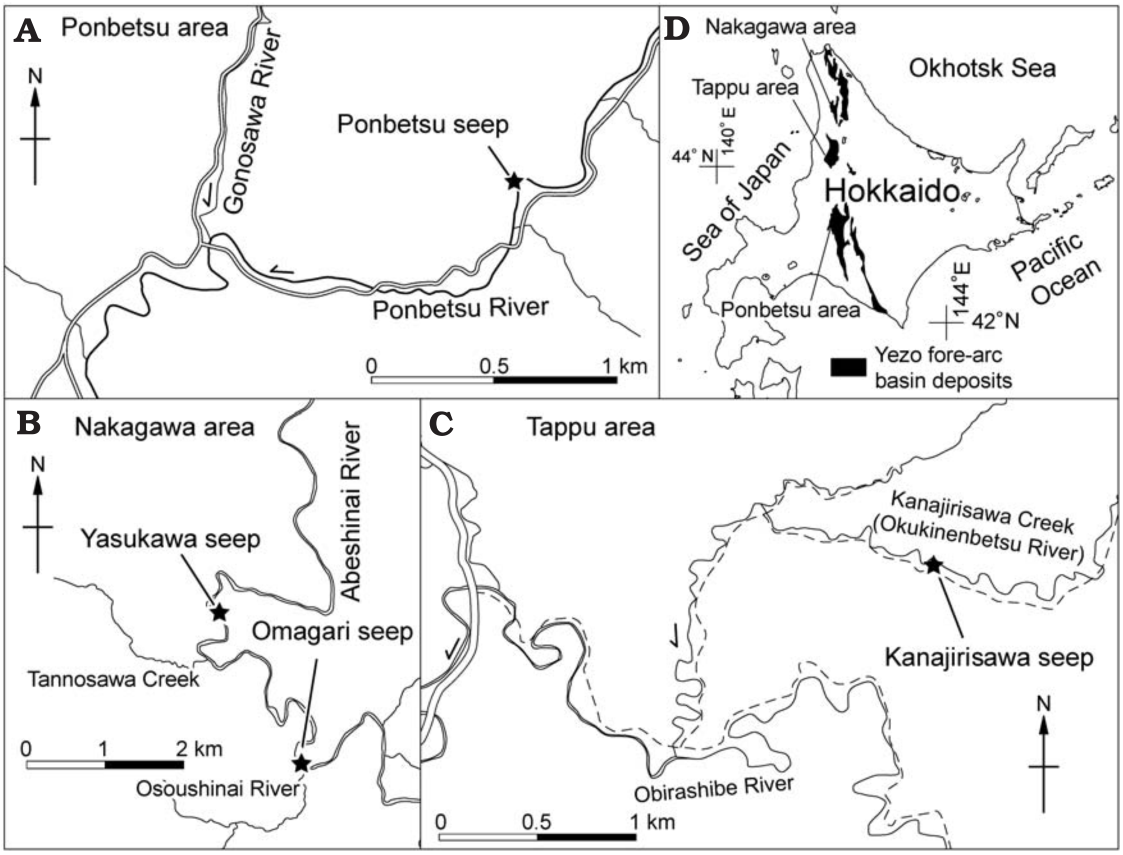

Fig. 1. Maps showing the fossiliferous seep deposits. **A**. The Albian Ponbetsu site. **B**. The Campanian Yasukawa and Omagari sites. **C**. The Cenomanian Kanajirisawa site. **D**. Overview.

tanabei sp. nov., and *Nipponothracia ponbetsensis* Kanie and Sakai, 1997.

Kanajirisawa.—This large seep carbonate deposit of Cenomanian age with numerous small, silicified gastropods crops out between a road and Kanajirisawa Creek (also called Okukinenbetsu River) in Obira Town (Kanie and Kuramochi 1996; Majima et al. 2005; Kaim et al. in press). The bivalves from this site include an unidentified solemyoidean, *Nucinella gigantea* Amano, Jenkins, and Hikida, 2007, *Acila* (*Truncacila*) *himenourensis* Tashiro, 1985, the inoceramid *Birostrina pennatulus* (Pergament, 1966), *Thyasira tanabei* sp. nov., *Thyasira* sp., and *Nipponothracia yezoensis* (Kanie and Kuramochi, 1996).

Omagari.—This approximately 10 m wide seep carbonate deposit with alleged vestimentiferan worm tubes, abundant small gastropods, and several large lucinid bivalves crops out in Nakagawa Town as an islet in the Abeshinai River near the mouth of its tributary Osoushinai River (Hikida et al. 2003; Jenkins et al. 2007a; Kaim et al. in press). The age of the deposit is considered to be Campanian (Takahashi et al. 2007). The bivalves from this site include an unidentified solemyid, *Acila* (*Truncacila*) *hokkaidoensis* (Nagao, 1932), *Nuculana* sp., *Nipponothracia* cf. *ponbetsensis*, *Thyasira* sp., and a poorly preserved lucinid that was previously identified as *Miltha* sp.

Yasukawa.—Several carbonate bodies that are less than 2 m wide are distributed on the bank of the Abeshinai River, about 3 km downstream from the Omagari site (Amano et al. 2007; Jenkins et al. 2007a, b; Kaim et al. in press). This site is early Campanian in age (Takahashi et al. 2007). Species from this site include: *Acharax cretacea* Kanie and Nishida, *Nucinella gigantea* Amano, Jenkins, and Hikida, 2007, *Leionucula formosa* (Nagao, 1930), *Acila* (*Truncacila*) *hokkaidoensis* (Nagao, 1932), *Nuculana* (*Ezonuculana*) *mactraeformis* Nagao, 1932, *Propeamussium yubarense* (Yabe and Nagao, 1928), *Thyasira tanabei* sp. nov., and several poorly preserved lucinids that have previously been identified as *Myrtea ezoensis* (Nagao, 1938), *Myrtea*? sp., and *Miltha* sp.

Systematic paleontology

Class Bivalvia Linnaeus, 1758

Subclass Protobranchia Pelseneer, 1889

Family Solemyidae Gray, 1840

Genus *Acharax* Dall, 1908

Type species: *Solemya johnsoni* Dall, 1891; Recent, NE Pacific.

Acharax mikasaensis sp. nov.

Fig. 2A, B.

Table 1. Occurrence and number of specimens of the taxa discussed herein.

Species / Locality	Ponbetsu	Kanajirisawa	Omagari	Yasukawa
Acharax mikasaensis sp. nov.	60			
Acharax cretacea Kanie and Nishida, 2000				10
Nucinella gigantea Amano, Jenkins, and Hikida, 2007		12		6
Acila (*Truncacila*) *hokkaidoensis* (Nagao, 1932)			1	27
Acila (*Truncacila*) *himenourensis* Tashiro, 1992		1		3
Thyasira tanabei sp. nov.	9	5		29
Thyasira sp.		1		
Nipponothracia yezoensis (Kanie and Kuramochi, 1996)		4		
Nipponothracia ponbetsensis Kanie and Sakai, 1997	22			
Lucinidae gen. et sp. indet.		3		

1993 *Solemya* (*Acharax*) sp.; Kanie et al. 1993: 34, fig. 2.
1993 *Calyptogena* sp.; Kanie et al. 1993: 34, fig. 2.
1997 *Solemya* sp.; Kanie and Sakai 1997: 218, fig. 8.3 (but listed as *Solemya* cf. *angusticaudata* Nagao, 1932 in their table 2).
1997 *Calyptogena* sp.; Kanie and Sakai 1997: 210, fig. 8.1.
2002 *Solemya* (*Solemya*) *angusticaudata* Nagao; Kanie and Kuramochi 2002: 51, fig. 2.1.

Etymology: For Mikasa City, place of the type locality.

Type material: Holotype: UMUT MM 29524; an internal mold showing internal features, 41 mm long, 19 mm high; paratype: UMUT MM 29523; a large specimen showing external features, 55 mm long, 21 mm high.

Type locality: Seep carbonate on the banks of the Ponbetsu River in Mikasa City, Hokkaido, Japan.

Type horizon: Albian (Lower Cretaceous) of the Yezo Group.

Material.—60 specimens and fragments from the type locality.

Diagnosis.—An elongate-oval *Acharax* with elongate and slightly concave posterior adductor scar, anterior adductor D-shaped with a close, almost vertically ascending band extending from its posteroventral corner.

Description.—Shell with elongate-oval outline, dorsal margin straight, anterior margin rounded, ventral margin slightly convex, posterior margin truncated and pointed. Sculpture of broad radial ribs, grooves between ribs ca. 1/3 of rib width, about 10 ribs on anterior part of shell, ribs weak to absent below umbo. Anterior lateral extension lacking; posterior adductor scar elongate, curved, tapering towards the umbo; posterior ligament external, distinct and strong. Anterior adductor scar broad D-shaped, from its posteroventral corner undulates an ascending band to the dorsal margin where it broadens out.

Discussion.—A very unusual feature of this species is the undulating band extending from the posteroventral corner of the anterior adductor scar: in most if not all solemyids this band ascends obliquely to the dorsal margin (Pojeta 1988; Taylor et al. in press; and observations by SK on Recent solemyids in the USNM zoology collection), whereas in *Acharax mikasaensis* sp. nov. it is almost perpendicular to it. In his description of *Solemya angusticaudata* from the Yezo Group of Hokkaido Nagao (1932) does not mention the ligament but describes the posterodorsal margin as “sloping backward and downward towards the posterior end”, and indeed, his figure shows a specimen in which the posterodorsal margin is slightly concave, which is in contrast to *Acharax mikasaensis* where the posterodorsal margin is clearly convex. *Acharax cretacea* Kanie and Nishida, 2000 is more elongate than *Acharax mikasaensis* and appears to have a more angular anterior margin. The posterior adductor scar of *Acharax mikasaensis* is more elongate than in the Recent type species *Acharax johnsoni* but resembles that of *Zesolemya parkinsoni* Smith, 1874 from New Zealand (Taylor et al. in press: fig. 1D). Clearly distinct is the lower Miocene *Solemya* (*Acharax*) *tokunagai* Yokoyama, 1925 as figured by Kamada and Hayasaka (1959) from the Joban coal-field, because it has a more elongate posterior end than *Acharax mikasaensis*.

Stratigraphic and geographic range.—Only known from the Albian type locality on Hokkaido, Japan.

Acharax cretacea Kanie and Nishida, 2000

Fig. 2C–E.

2000 *Acharax cretacea* sp. nov.; Kanie and Nishida 2000: 82, fig. 4.
2007 *Acharax cretacea* Kanie and Nishida; Jenkins et al. 2007b: fig. 5.8.

Material.—Kanie and Nishida’s (2000) type material was examined in the Yokosuka City Museum; ten newly collected specimens from the Yasukawa seep site.

Discussion.—Kanie and Nishida (2000: 83) suggested the presence of a long external ligament. A newly collected small specimen from the Yasukawa seep site shows that the ligament is external and rather short (Fig. $2D_1$). Another specimen from this site shows the prismatic shell microstructure (Fig. 2E), typical for solemyids.

Stratigraphic and geographic range.—Cenomanian sulfide-rich sediments (own observation) and Campanian seep carbonates of the Yezo Group on Hokkaido, Japan.

Family Manzanellidae Chronic, 1952

Genus *Nucinella* Wood, 1851

Type species: *Pleurodon ovalis* Wood, 1840; Recent.

Nucinella gigantea Amano, Jenkins, and Hikida, 2007

Fig. 3.

2007 *Nucinella gigantea* sp . nov.; Amano et al. 2007: 85, figs. 2–7.

Material.—Twelve specimens from the Kanajirisawa seep site in Obira Town.

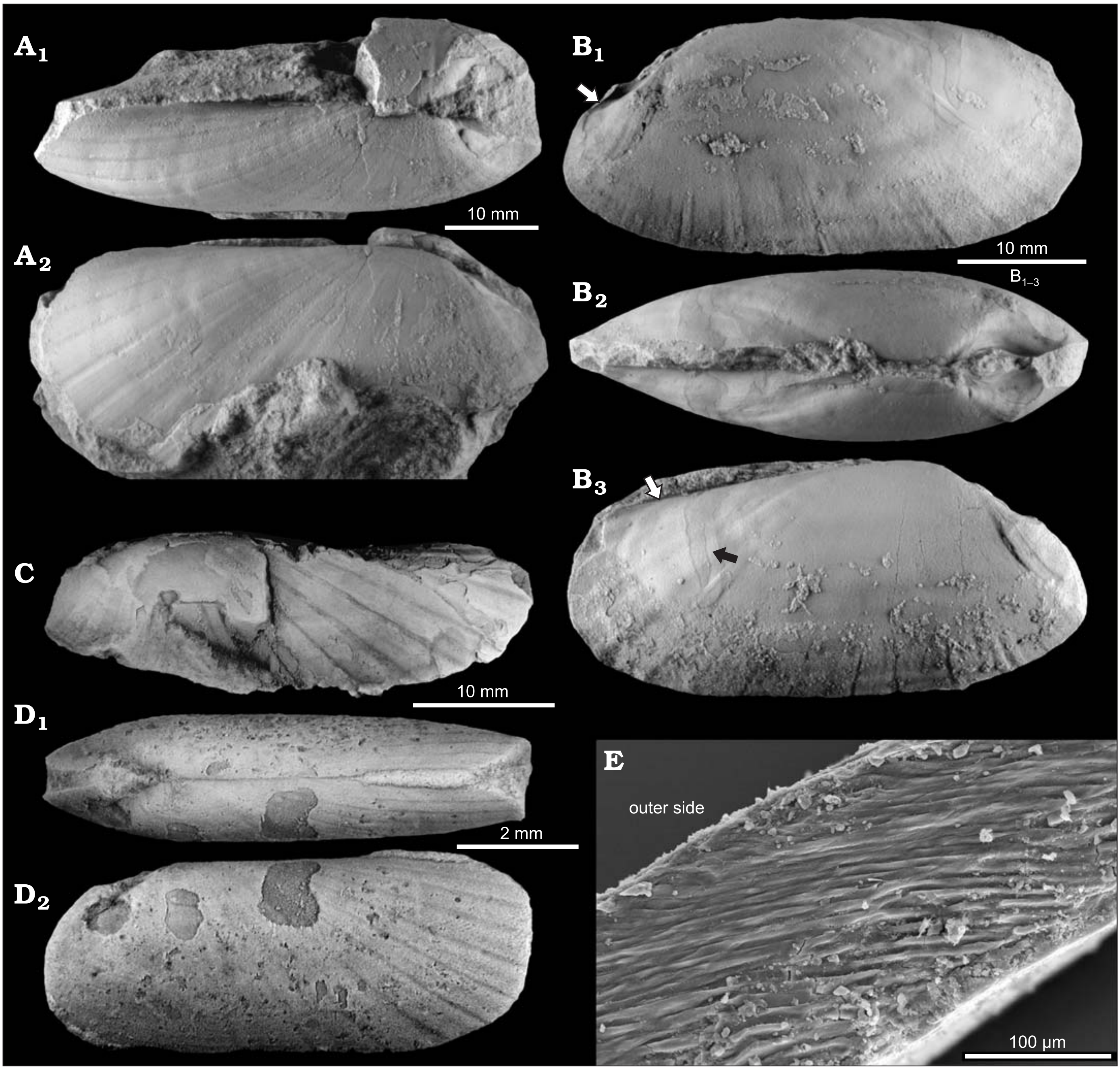

Fig. 2. Solemyid bivalves from Cretaceous cold seep deposits on Hokkaido, Japan. **A**, **B**. *Acharax mikasaensis* sp. nov., from the Albian Ponbetsu site in Mikasa City. **A**. Paratype (UMUT MM 29523) showing external sculpture, dorsal (A_1) and lateral (A_2) views. **B**. Holotype (UMUT MM 29524) showing features of the shell interior; arrow in B_1 indicates posterior adductor muscle scar, B_2 shows a dorsal view, white arrow in B_3 indicates the anterior adductor muscle scar, black arrow indicates the narrow band that ascends from its posteroventral margin. **C**–**E**. *Acharax cretacea* Kanie and Nishida, 2000, from the Campanian Yasukawa site. **C**. Right valve of a slightly deformed, medium-sized specimen (UMUT MM 29525), length 34 mm. **D**. Small specimen (UMUT MM 29526) (length 8 mm) showing the rounded posterior shell margin, dorsal (D_1) and lateral (D_2) views. **E**. Cross section of shell showing the prismatic microstructure.

Discussion.—The specimens from Kanajirisawa are similar in size (18 mm in length) and outline to the type material of *Nucinella gigantea*. In the right valve, a central tooth thin and oblique anteriorly, and three small teeth are recognized before the central tooth (Fig. 3C). One posterior tooth can be recognized behind the central tooth. In the left valve, three anterior teeth are present, among which the anterior-most tooth is shaped like a reverse "S" and is parallel to the hinge base (Fig. 3D). The two central teeth are large but thin, and connected to a small posterior tooth. A narrow flat area is also present below the dentition. The number of teeth in the specimens found at the Kanajirisawa site (five in the right valve and six in the left valve) is slightly lower than in the type specimens (six in the right valve and nine in the left

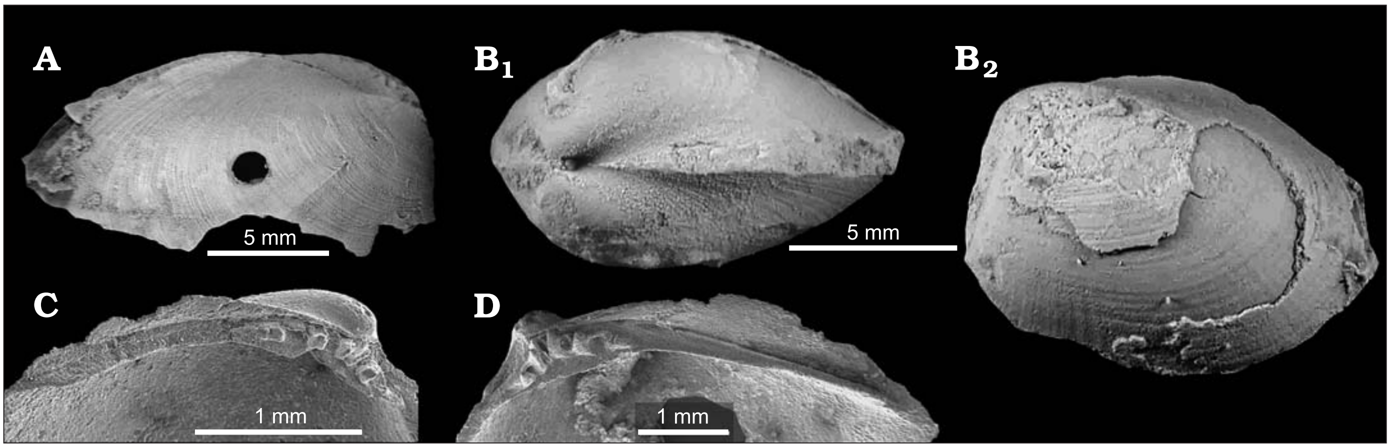

Fig. 3. The protobranch bivalve *Nucinella gigantea* Amano, Jenkins, and Hikida, 2007 from the Cenomanian (Upper Cretaceous) seep carbonate at Kanajirisawa, Obira town, Hokkaido. **A**. Specimen (UMUT MM 29527) with drill hole and a healed shell injury. **B**. Articulated specimen (UMUT MM 29528) in dorsal view (B_1) and right valve showing radial internal striations (B_2). **C**. Hinge of right valve (UMUT MM 29529). **D**. Hinge of left valve (UMUT MM 29530).

valve) of *Nucinella gigantea*. However, the large size, nuculid shell shape and one or two large central teeth allow us to safely identify the specimens as *N. gigantea*.

One specimen has a circular drill hole (outer diameter 1.5 mm; inner diameter 1.4 mm) and a healed shell injury that is commarginal, short, and straight, and resulted in a ridge-like trace in the remainder of the shell, indicating that this injury affected not only the shell but also the shell-forming mantle margin (Fig. 3A). The shape of drill hole is similar to that made by naticids, but naticids have so far not been found at this locality (own observations and Andrzej Kaim, personal communication, 2007). Thus the predator that caused the drill hole is unknown. The sharp injury at the central part of the valve may be attributed to the attack of a crustacean. This is by far the oldest drill hole reported from a seep deposit, being almost two-and-a-half times as old as the naticid drill holes recognized at a Late Eocene cold seep site on Hokkaido (Amano and Jenkins 2007).

Stratigraphic and geographic distribution.—Late Cretaceous (Cenomanian to Campanian), Tenkaritoge and Omagari Formations of the Yezo Group, Hokkaido, Japan.

Family Nuculidae Gray, 1824

Genus *Acila* Adams, 1858

Subgenus *Truncacila* Grant and Gale, 1931

Type species: *Nucula castrensis* Hinds, 1843; Recent, Northeastern Pacific.

Acila (*Truncacila*) *hokkaidoensis* (Nagao, 1932)

Fig. 4A.

1932 *Nucula* (*Acila*) *hokkaidoensis* sp. nov.; Nagao 1932: 28–30, pl. 5: 17, 18.
1936 *Acila* (*Truncacila*) *hokkaidoensis* (Nagao); Schenck 1936: 52.
1938 *Nucula* (*Acila*) *hokkaidoensis* Nagao; Nagao and Otatume 1938: 37, pl. 1: 1.
1941 *Acila* (*Truncacila*) *hokkaidoensis* (Nagao); Nagao and Huzioka 1941: 118–119.
1975 *Acila* (*Truncacila*) *hokkaidoensis* (Nagao); Hayami 1975: 21.
non 1958 *Acila* (*Truncacila*) *hokkaidoensis* (Nagao); Ichikawa and Maeda 1958: 79–80, pl. 3: 9–11, 14.
non 1962 *Acila* (*Truncacila*) *hokkaidoensis* (Nagao); Saito 1962: 59–60, pl. 1: 1.
non 1976 *Acila* (*Truncacila*) *hokkaidoensis* (Nagao); Tashiro 1976: pl. 1: 12–16.
non 2007 *Acila hokkaidoensis* (Nagao); Tsujino and Maeda 2007: figs. 6C, D.

Material.—One specimen from the Omagari seep site, 27 specimens from the Yasukawa seep site (figured: UMUT MM 29531).

Discussion.—Nagao (1932: 29) indicated that *Acila hokkaidoensis* is easily separable from other Recent and fossil species in Japan “in that the line, from which the radial ribs diverge downward, is placed much anteriorly to the median vertical”. This applies not only for the Japanese species but also for most species from the American side of the North Pacific, including the nine species of *Truncacila* reported by Weaver (1942) from the Cenozoic of Oregon and Washington, and the seven Cretaceous species of *Truncacila* described by Squires and Saul (2006) from British Columbia to Baja California. However, Squires and Saul (2006) noted that these North American Cretaceous species were from warm, shallow water sediments and that the deep-water species from the same area need critical evaluation. A specimen with a similar anterior line of divergence was figured as *Acila* (*Truncacila*) *haidana* Packard in Schenck, 1936 from the Redding Fm, Frazier Siltstone Member (Turonian) in northern California (Squires and Saul 2006: fig. 15). The holotype of *Acila* (*Truncacila*) *haidana* figured by Squires and Saul (2006: figs. 13, 14, and 16) has the line of divergence in a central position. The specimen from the Californian Turonian Redding Formation might thus belong to *Acila* (*Truncacila*) *hokkaidoensis*.

Tsujino and Maeda (2007: fig. 6C, D) figured a specimen from the lowermost Campanian of the Upper Haborogawa Formation in west-central Hokkaido as *A*. (*T*.) *hokkaidoensis* which has the line from which the radial ribs diverge in a cen-

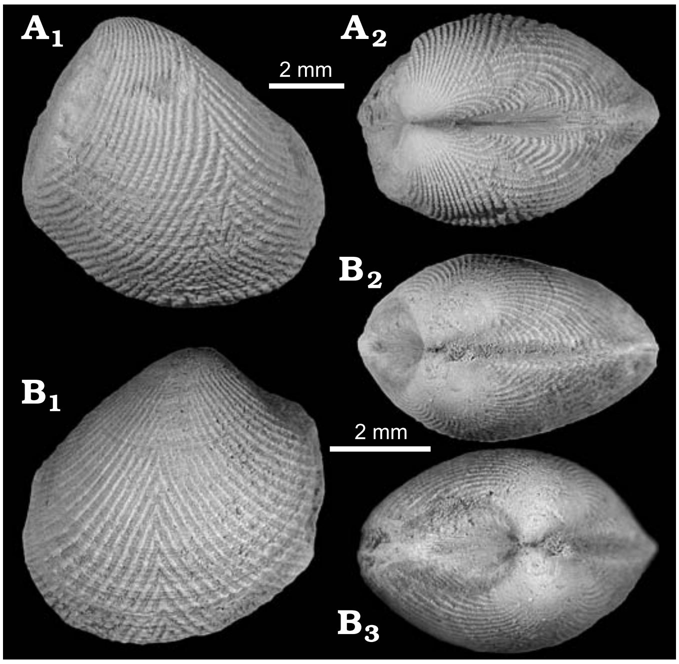

Fig. 4. *Acila* (*Truncacila*) from the Campanian Yasukawa seep site on Hokkaido, Japan. **A**. *Acila* (*Truncacila*) *hokkaidoensis* Nagao, 1932 (UMUT MM 29531), lateral view on left valve (A_1) and dorsal view (A_2). **B**. *Acila* (*Truncacila*) *himenourensis* Tashiro, 1985 (UMUT MM 29532), lateral view on right valve (B_1), dorsal view showing escutcheon (B_2), and dorsal view showing lunule (B_3).

tral position; this specimen most probably belongs to *A*. (*T*.) *himenourensis* Tashiro, 1985 (discussed below).

Stratigraphic and geographic range.—Turonian of California, USA (uncertain); Coniacian to Campanian of the Yezo Group, Japan.

Acila (*Truncacila*) *himenourensis* Tashiro, 1992

Fig. 4B.

1958 *Acila* (*Truncacila*) *hokkaidoensis* (Nagao); Ichikawa and Maeda 1958: 79–80, pl. 3: 9–11, 14.
1962 *Acila* (*Truncacila*) *hokkaidoensis* (Nagao); Saito 1962: 59–60, pl. 1: 1.
1976 *Acila* (*Truncacila*) *hokkaidoensis* (Nagao); Tashiro 1976: pl. 1: 12–16.
1985 *Acila* (*Truncacila*) *himenourensis* sp. nov. (in MS); Tashiro 1985: 56.
1992 *Acila* (*Truncacila*) *himenourensis* Tashiro; Tashiro 1992: 26, pl. 3: 4.
2007 *Acila hokkaidoensis* Nagao; Tsujino and Maeda 2007: fig. 6C, D.

Material.—One specimen from the Kanajirisawa seep site, three from the Yasukawa seep site (figured is UMUT MM 29532).

Original description.—"Shell ovate with short posterior margin and strongly arched ventral margin. Ribs on surface fine, but strong. Lines connecting tops of v-shaped ribs gently sloping anteriorly, attaining to slightly anterior part to center of ventral margin." (translated from the Japanese by KA).

Discussion.—*Acila* (*Truncacila*) *himenourensis* has a narrower umbonal angle than *A*. (*T*.) *hokkaidoensis*, and the line from which the radial ribs diverge is not as far anterior as in the specimen of *A*. (*T*.) *hokkaidoensis* figured by Nagao (1932: pl. 5: 17, 18). *Acila* (*T*.) *picturata* Yokoyama, 1890 from the late Eocene Poronai Formation differs from *A*. (*T*.) *himenourensis* by having a broader apical angle and finer, and more numerous ribs (Yokoyama 1890; own observations). Also *Acila brevis* Nagao and Huzioka, 1941 from the Miocene of Hokkaido has a broader apical angle and finer ribs (Kanno and Ogawa 1964). A similar species from the North American Pacific Coast Cretaceous is *A*. (*T*.) *grahami* Squires and Saul, 2006, which has usually a more elongate shape and thicker ribs with narrower interspaces than *A*. (*T*.) *himenourensis* (Squires and Saul 2006: 95, figs. 27–38).

Stratigraphic and geographic range.—Japan; Cenomanian to Campanian of the Yezo Group, Hokkaido; Coniacian to Santonian of the Futaba Group, northeast Honshu; Campanian part of the Izumi Group, Kinki District of Honshu; Coniacian to Maastrichtian of the Himenoura Group, western Kyushu.

Subclass Heterodonta Neumayr, 1884

Family Thyasiridae Dall, 1901

Genus *Thyasira* Lamarck, 1818

Type species: *Tellina flexuosa* Montagu, 1803; Recent, North Sea.

Discussion.—A Recent molecular analysis using 18S and 28S rRNA sequences showed that *Thyasira* can be subdivided into two clades; the *T. flexuosa* and *T. sarsi* clades (Taylor et al. 2007). Morphologically, the former clade is characterized by having an ovate shell and a deep sulcus in the posterior area while the latter has a subcircular shell as well as a shallow sulcus (Oliver and Killeen 2002).

Thyasira tanabei sp. nov.

Figs. 5A–G, 6A.

1993 *Conchocele*? sp.; Kanie et al. 1993: fig.2.
2008 Thyasirid bivalve; Kiel, Amano et al. in press: fig. 3L, M.

Etymology: For Prof. Kazushige Tanabe (The University of Tokyo), a specialist on ammonoids from Hokkaido, who also brought our attention to several cold seep deposits there.

Type material: Holotype (UMUT MM 29533: articulated specimen, length 10.4 mm, height 10.3 mm, width 6.1 mm) and paratypes (UMUT MM 29534, articulated specimen, length 10 mm, from the Kanajirisawa site; UMUT MM 29535: articulated specimen, length 9.2 mm; UMUT MM 29536: specimen with preserved shell material from the Omagari site, height 11.2 mm; UMUT MM 29537: specimen with preserved hinge; UMUT MM 29539: articulated specimen from the Ponbetsu site, length 7.1 mm).

Type locality: Yasukawa seep site in Nakagawa Town, Hokkaido.

Type horizon: Early Campanian, Omagari Formation, Yezo Group.

Material.—29 specimens from the type locality, five from the Kanajirisawa seep site, nine from Ponbetsu River.

Diagnosis.—Medium-sized *Thyasira* with narrow posterior area and sharp 1st posterior fold.

Description.—Shell moderate size attaining 12.9 mm in length, thin-walled, subcircular, equivalve and inequilateral. Convexity of shell variable, from moderately inflated (Fig.

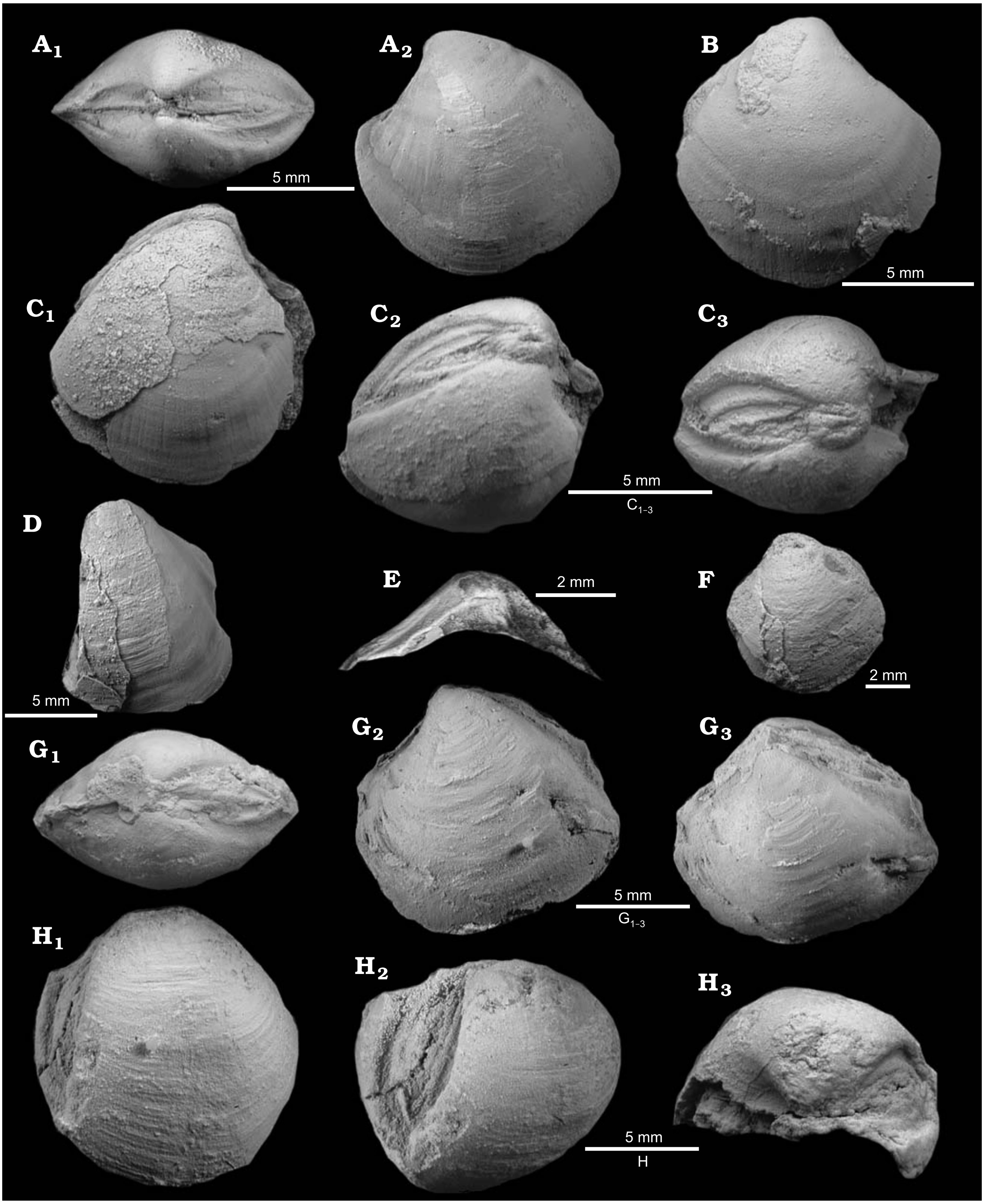

Fig. 5. *Thyasira* spp. from Cretaceous cold seep deposits on Hokkaido, Japan. **A**–**G**. *Thyasira tanabei* sp. nov. **A**. Holotype (UMUT MM 29533) from the Campanian Yasukawa site. **B**. Paratype (UMUT MM 29534) from the Cenomanian Kanajirisawa site. **C**. Paratype (UMUT MM 29535) from the Campanian Yasukawa site; lateral view on right valve (C_1), oblique view on right valve, showing posterior sulcus (C_2), and dorsal view (C_3). **D**. Paratype (UMUT MM 29536) from the Campanian Omagari site. **E**. Paratype (UMUT MM 29537) from the Campanian Yasukawa site showing the hinge. **F**. Small specimen (UMUT MM 29538) from the Campanian Yasukawa site. **G**. Paratype (UMUT MM 29539) from the Albian Ponbetsu site. **H**. *Thyasira* sp. (UMUT MM 29540) from the Cenomanian Kanajirisawa site; lateral view on right valve (H_1), oblique view on right valve showing posterior sulcus (H_2), and dorsal view (H_3).

$5A_1$, G_1) to strongly inflated (Fig. $5C_3$). Beak projecting above dorsal margin, prosogyrate, situated at anterior one-third of shell length. Antero-dorsal margin concave, making right angle with ventral margin at anterior end; ventral margin well rounded. Posterior area narrow; posterior sulcus rather deep, but posterior sinus shallow; 1st posterior fold elevated and sharp, rib-like; submarginal sulcus relatively shallow with very shallow marginal sinus; auricle narrow. Lunule lanceolate, concave, bounded by sharp ridge. Surface sculptured only by growth lines or irregular growth ridges in some specimens. In right valve, no evidence of cardinal tooth (Fig. 5E). Pallial line entire. Anterior muscle scar large, elongate ovate, weakly impressed, separated from pallial line ventrally (Figs. $5A_2$, 6A); posterior muscle scar small, subquadrate, in front of 2nd posterior fold (Figs. 5D, 6A). Radiating interior striae distinct.

Discussion.—Kanie et al. (1993: fig. 2) illustrated a shell silhouette as *Conchocele*? sp. from the Albian Ponbetsu seep site in Mikasa City, central Hokkaido. Their figure of *Conchocele*? sp. does not show a posterior fold and an auricle. However, these features can be seen in several specimens that we collected at this site. Thus we assume that Kanie et al. (1993) overlooked these features and that their *Conchocele*? sp. is in fact *Thyasira tanabei* described herein.

Thyasira tanabei sp. nov. resembles *Thyasira* sp. nov. described by Tashiro (2004) from the Albian to Cenomanian sediments of the Yezo Group in Horokanai Town in its general outline and size. But judging from the figure (Tashiro 2004: pl. 1: 3, 4) the Horokanai specimen seems to lack a posterior fold and auricle. *Thyasira tanabei* also resembles *T. nakazawai* Matsumoto, 1971 from the early Miocene Wappazawa Formation in Shizuoka Prefecture, central Honshu, by having a sharp rib-like 1st posterior fold. However, *T. tanabei* reaches twice the size of *T. nakazawai* (maximum length = 21.0 mm) and the wide posterior part of *T. nakazawai* enables us to separate it from *T. tanabei*. The thyasirids from the Campanian Western Interior Seaway of the USA are different from *T. tanabei* by having a wider posterior area, a shallowly depressed lunule, and a posterior adductor scar astride the posterior sulcus (Kauffman 1967). *Thyasira tanabei* can be distinguished from Recent *Thyasira* species by its narrow posterior area, the posterior adductor scar in front of the posterior sulcus, and the sharp rib-like 1st posterior fold.

Hikida et al. (2003) illustrated two fragmentary specimens from the Campanian Omagari seep site as *Thyasira* sp. Because the type locality and formation of the new *T. tanabei* is the Omagari Formation near their site, these specimens may be identical with *T. tanabei*, but better preserved material from the Omagari seep site is necessary to confirm this suggestion.

Measurements.—See Table 2.

Stratigraphic and geographic range.—Albian to Campanian, Yezo Group, Hokkaido Japan; so far found at the Ponbetsu site (Albian), the Kanajirisawa seep site (Cenomanian), and the type locality (Campanian, Omagari Formation), as well as associated with Coniacian sunken wood in the Nishichirashinai Formation (Kiel, Amano et al. in press).

Thyasira sp.

Fig. 5H.

Material.—One articulated specimen (though most of the left valve is missing) from the Kanajirisawa site in Obira Town; length 11.7 mm, height 12.4 mm, thickness 6.7 mm, UMUT MM 29540.

Description.—Shell moderate size, thick-walled, triangular in shape, swollen and slightly inequilateral. Umbo prominent, beak slightly prosogyrate, situated at central part of shell. Antero-dorsal margin steeply sloping, making angle with well rounded ventral margin. Posterior area wide; 2nd posterior fold very strong, posterior sulcus very deep, but without posterior sinus; 1st posterior fold elevated and sharp, rib-like; submarginal sulcus also deep without marginal sinus; auricle slightly convex and wide. Lunule double; outer lunule wide, bounded by crude ridge; inner lunule small, aubcircular, deeply depressed and bounded by distinct incision. Surface sculptured only by growth lines. Internal features unknown.

Discussion.—This species is unique in having a double lunule, a strongly inflated shell, and a deeply grooved posterior sulcus. These features separate this species from *T. tanabei* sp. nov. found in the same seep site. Because it is only known from a single specimen with an incomplete left valve, we do not establish a new species for it.

Stratigraphic and geographic range.—Known only from the Cenomanian Kanajirisawa seep site.

Family Lucinidae Fleming, 1828

Genus *Nipponothracia* Kanie and Sakai, 1997

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

Discussion.—*Nipponothracia* was initially introduced as a large, potentially symbiont-bearing thraciid from a Miocene

Table 2. Measurements of *Thyasira tanabei* sp. nov.

UMUT MM	Type	Length (mm)	Height (mm)	Width (mm)	Valve	Locality
29533	Holotype	10.4	10.3	6.1	both	Yasukawa
29534	Paratype	10.2	10.8	–	right	Kanajirisawa
29535	Paratype	9.2	10.0	7.2	both	Yasukawa
29536	Paratype	10.3+	11.8	–	left	Yasukawa
29537	Paratype	7.6	8.3	–	right	Yasukawa
29538	–	7.1	7.1	4.8	both	Yasukawa
29539	Paratype	11.7	10.8	6.6	both	Ponbetsu

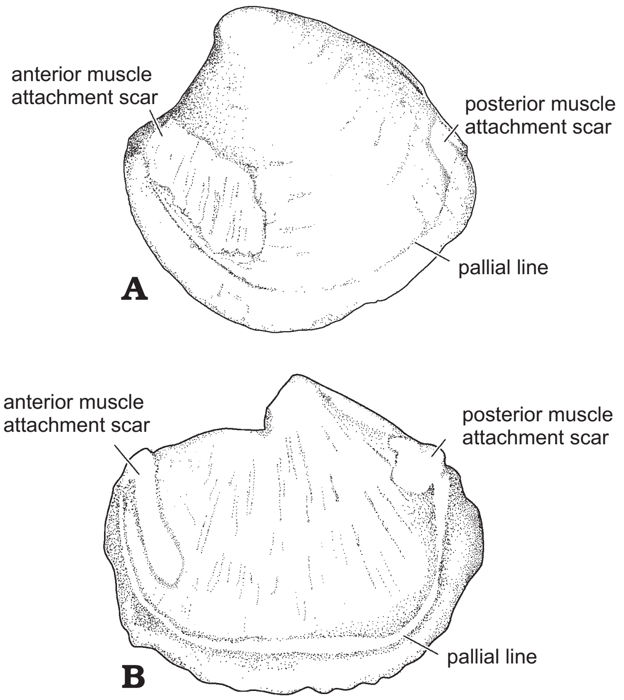

Fig. 6. Outline drawings showing internal features. **A**. *Thyasira tanabei* sp. nov. **B**. *Nipponothracia yezoensis* (Kanie and Kuramochi, 1996). Not to scale.

and an Early Cretaceous methane seep deposit (Kanie and Sakai 1997). Kase et al. (2007) recently documented an elongate anterior adductor muscle scar that is ventrally detached from the pallial line in the Miocene type species, showing that *Nipponothracia* belongs to the Lucinidae rather than the Thraciidae.

Nipponothracia yezoensis (Kanie and Kuramochi, 1996)

Figs. 6B, 7A, B.

1996 *Thracia yezoensis* sp. nov.; Kanie and Kuramochi 1996: 64, fig. 1.

Material.—Several specimens from the type locality at Obira.

Supplementary description.—Hinge plate narrow and smooth; ligament rapidly widening posterior of umbo, supported by narrow nymph. Internal radial striations well developed; pallial line distant from shell margin, marked by a groove; anterior adductor muscle scar elongate, about 1/3 of shell length, tongue-shaped, marked by a groove, ventrally detached from pallial line by a thin margin for about 4/5 of its length; posterior adductor muscle scar less distinct, apparently subcircular with a short ventral protrusion.

Discussion.—Kase et al. (2007) reported that a specimen of *Nipponothracia yezoensis* from the type locality stored in the National Museum of Nature and Science, Tokyo, has "an elongate anterior muscle that is more elongate than the posterior one and seemingly detached from the pallial line". This observation is here confirmed. The anterior muscle scar of *N. yezoensis* is more elongate than that of *N. gigantea*, the posterior muscle scar is more rounded, and the pallial line is more distant from the shell margin than in *N. gigantea* (Fig. 6B). In addition, the hinge plate of *N. gigantea* is deeply excavated below the umbo, a feature not seen in *N. yezoensis*. Thus *N. yezoensis* can clearly be distinguished from the type species. Because no internal features except radial striations are known for *N. ponbetsensis* (see below), the question whether *N. ponbetsensis* and *N. yezoensis* are synonymous remains unresolved.

The Indonesian *Nipponothracia hetzeli* (Martin, 1933) from a late Miocene asphalt deposit at Buton, Indonesia, also has an excavated hinge plate, a more elongate ligament, and a broader nymph than *N. yezoensis* (Beets 1942; Kase et al. 2007; SK, own observations). The same applies to *Cryptolucina elassodyseides* Saul, Squires, and Goedert, 1996 from the Eocene of Washington State, USA. Species of the Recent *Anodontia* clade generally have a long and narrow ligament that slowly tapers toward the umbo (Taylor and Glover 2005). This is in contrast to the ligament of *N. yezoensis* which appears to attain its maximum width just posterior to the umbo.

Stratigraphic and geographic range.—Only known from the Cenomanian type locality on Hokkaido, Japan.

Nipponothracia ponbetsensis Kanie and Sakai, 1997

Fig. 7C.

1993 Thraciidae gen. et sp. indet.; Kanie et al. 1993: 33, fig. 4.

1997 *Nipponothracia ponbetsensis* Kanie and Sakai, 1997: 214, figs. 6, 7.

1997 *Yoldia* (*Megayoldia*) cf. *thraciaeformis* Kanie and Sakai, 1997: 210, fig. 4.

Material.—Several specimens from the Ponbetsu site.

Discussion.—Kase et al. (2007) indicated that *Nipponothracia ponbetsensis* has a long ligamental nymph posterior to the beaks and that it appears to belong to the Lucinidae. Here we document radial internal striations in this species that suggest its position within Lucinidae. The specimen that Kanie and Sakai (1997) figured as *Yoldia* (*Megayoldia*) cf. *thraciaeformis* is clearly a deformed specimen of *N. ponbetsensis*; we have several specimens from the Ponbetsu site that experienced a similar kind of deformation.

Stratigraphic and geographic range.—Only known from the Albian type locality on Hokkaido, Japan.

Lucinidae gen. et sp. indet.

Fig. 7D, E.

Material.—Three specimens from the Kanajirisawa seep site.

Description.—Shell oval in outline, compressed, slightly wider than high, becoming more circular during ontogeny; sculpture of irregular, fine commarginal ribs, fine radial ribs in larger specimens; radial striations on inner side of shell, one anterior lateral tooth; anterior adductor muscle scar very weakly impressed, elongate, tongue-shaped, apparently detached from the pallial line. The smaller of the two figured specimens is 26 mm wide and 21 mm high, the larger one is 43 mm wide, 40 mm high, and a single valve is 8 mm thick.

Discussion.—Fossil bivalves with circular, compressed shells like the one described here have frequently been placed in the

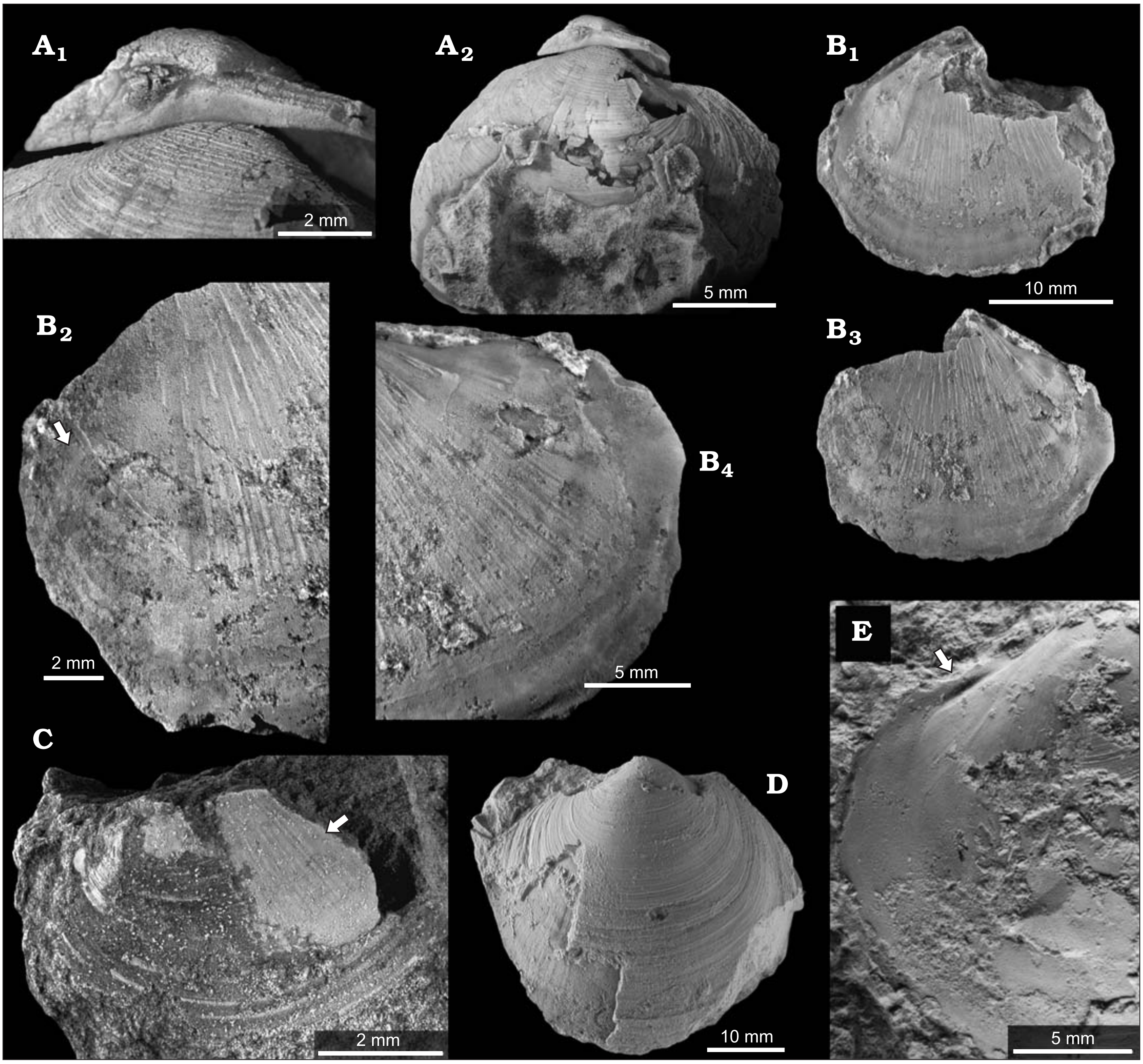

Fig. 7. Lucinidae from Cretaceous seep carbonates on Hokkaido, Japan. **A**, **B**. *Nipponothracia yezoensis* Kanie and Kuramochi, 1996 (Lucinidae) from the Cenomanian Kanajirisawa seep site on Hokkaido, Japan. **A**. Silicified specimen (UMUT MM 29541) showing the broad ligament (A_1) and the edentulous hinge (A_2). **B**. Internal mold (UMUT MM 29542) showing internal features, right and left valves (B_1, B_2), anterior part showing the elongate muscle scar (B_3, arrow), posterior part with muscle scar and pallial line (B_4). **C**. *Nipponothracia ponbetsensis* Kanie and Sakai, 1997, from the Albian Ponbetsu site in Mikasa City; specimen (UMUT MM 29543) showing the radial internal ribs (arrow). **D**, **E**. Indetermined lucinid from the Cenomanian Kanajirisawa seep site. **D**. Large specimen (UMUT MM 29544) with nearly circular outline. **E**. Internal mold (UMUT MM 29545) showing faint radial sculpture, arrow indicates impression of lateral tooth.

genus *Miltha* H. Adams and A. Adams, 1857, without knowledge of internal features like hinge dentition and muscle attachment scars. Chavan (1969), Vokes (1969), and Bretsky (1976) diagnosed that lateral teeth are absent from *Miltha*, hence the Kanajirisawa species can not be placed in this genus. Because other internal features such as the cardinal hinge dentition and the shape of the ligament are not preserved in the available specimens, they are described here only in open nomenclature.

Discussion

The bivalve fauna of the Japanese Cretaceous seep deposits has its own distinctive character that sets it apart from other Cretaceous seep faunas as well as from Cenozoic seep faunas in Japan and elsewhere. Characteristic features are the unique occurrence of large species of the solemyoid *Nucinella*, the common nuculid *Acila* (*Truncacila*), and the high diversity of

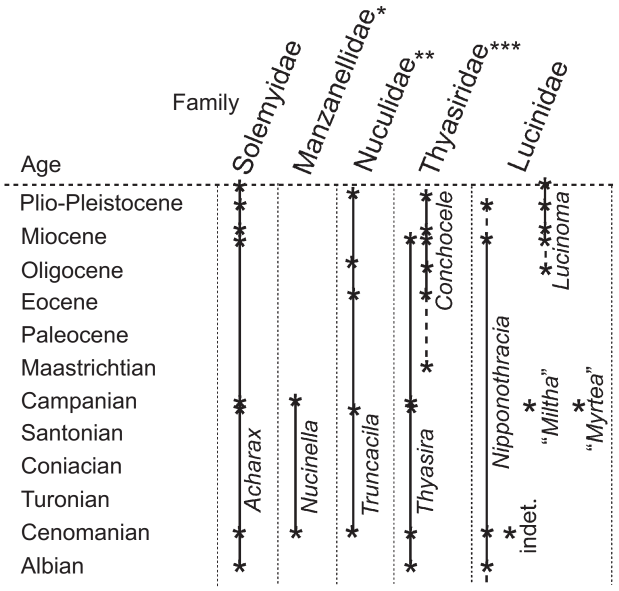

Fig. 8. Geologic ranges of bivalve genera at Japanese seep deposits discussed herein. Dashed lines indicate range extensions outside Japan; *chemosymbiosis uncertain; **non-chemosymbiotic; ***chemosymbiosis only in some species, especially larger ones.

Lucinidae. The nuculid *Acila* (*Truncacila*) occurs throughout the deep-water sediments of the Yezo Group (Nagao 1932; Hayami 1975; Tashiro 1992; Tsujino and Maeda 2007) and is a common "background" taxon in Japanese seeps since the Cenomanian (Majima et al. 2005; and herein), although it has not been reported from the modern vent and seep sites around Japan (cf., Sasaki et al. 2005). Outside Japan the taxon is very rare at fossil seeps; the only other records are from the Oligocene seeps of the Heath Shale in northern Peru (Olsson 1931; Kiel and Peckmann 2007) and from late Oligocene seep deposits in Washington State, USA (SK, own observation).

The genus *Nipponothracia* has now been recognized as a large-sized, seep-restricted lucinid, reaching 10 cm or more in length. It appears to have a world-wide distribution and has a geologic range from the Barremian to the Pliocene (cf. Kase et al. 2007). We found an additional large lucinid taxon at the Kanajirisawa site, and Hikida et al. (2003) and Jenkins et al. (2007b) described several lucinid-like shells as *Miltha* and *Myrtea* from Campanian seep sites on Hokkaido. Unfortunately, these specimens are too poorly preserved for a precise taxonomic identification; however, they most likely belong to three distinct genera. In sum, there probably were four distinct lucinid genera living at Cretaceous seep sites on Hokkaido alone. In contrast, from the relatively well-studied Cretaceous seep deposits of California, only a few specimens questionably assigned to *Lucina* have been reported (Stanton 1895; Campbell 2006; Kiel, Campbell et al. in press). The genus *Lucinoma* that is so common at seeps throughout the Cenozoic apparently did not appear before the Oligocene (Majima et al. 2005; Campbell 2006; Kiel and Little 2006; see Fig. 8).

Previous reports of *Calyptogena* (*Ectenagena*), *Yoldia* (*Megayoldia*), and *Conchocele* from the Albian Ponbetsu seep deposit by Kanie et al. (1993) and Kanie and Sakai (1997) could not be confirmed. The putative *Calyptogena* (*Ectenagena*) is herein identified as *Acharax mikasaensis*; *Yoldia* (*Megayoldia*) is a deformed *Nipponothracia ponbetsensis*; and the *Conchocele* is here described as *Thyasira tanabei*. The only Cretaceous seep-related thyasirid that could indeed belong to *Conchocele* is the large (>10 cm length) "*Thyasira*" *townsendi* from the Maastrichtian Snow Hill Island of Antarctica (Wilckens 1910), where it occurs in a large carbonate body that could be a seep deposit (J. Alistair Crame, personal communication, 2006). Taylor et al. (2007) presented an *Axinus*-like species from Albian shelf deposits in England as oldest thyasirid; however, the Valanginian–Hauterivian "*Lucina*" *rouyana* (d'Orbigny, 1844) from shelf deposits in Europe [in the French Alps (d'Orbigny 1844) and in the Grodziszcze Beds in the Carpatians (Ascher 1906; Oszczypko 2004)] clearly belongs to *Thyasira* and is here considered the oldest thyasirid.

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