

# New and Mesozoic-relict mollusks from Paleocene wood-fall communities in Urahoro Town, eastern Hokkaido, northern Japan

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**Abstract.**—Five species of bivalves and two species of gastropods are described from late Selandian to earliest Thanetian wood-fall communities from the Katsuhira Formation in Urahoro Town, eastern Hokkaido, northern Japan. Three bivalves and two gastropods are new to science: *Thyasira* (*Thyasira*) *oliveri* Amano and Jenkins, new species, *Astarte* (*Astarte*) *paleocenica* Amano and Jenkins, new species, *Poromya katsuhiraensis* Amano and Jenkins, new species, *Neverita majimai* Amano and Jenkins, new species, and *Biplica paleocenica* Amano and Jenkins, new species. *Poromya katsuhiraensis* n. sp. and *Neverita majimai* n. sp. are the earliest records of their genus. *Astarte paleocenica* n. sp. is the last species before the genus disappeared from the northern Pacific region during the Eocene, only to reappear with the opening of the Bering Strait during the latest Miocene. Moreover, two bivalve species and one gastropod genus are Cretaceous relict forms: *Propeamussium yubarensense* (Yabe and Nagao, 1928), *Myrtea ezoensis* (Nagao, 1938), and *Biplica* Popenoe, 1957. These species and other relict protobranch bivalves had wide geographical ranges in the deep sea during the Cretaceous, which helped them to survive the end-Cretaceous mass extinction. The chemosynthesis-based species *Bathyacmaea?* sp., *Myrtea ezoensis*, and *Thyasira oliveri* n. sp. were recovered, but small bathymodioline mussels have not been found. This confirms that the small deep-sea mussels did not appear in the wood-fall communities at least by the earliest Thanetian.

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## Introduction

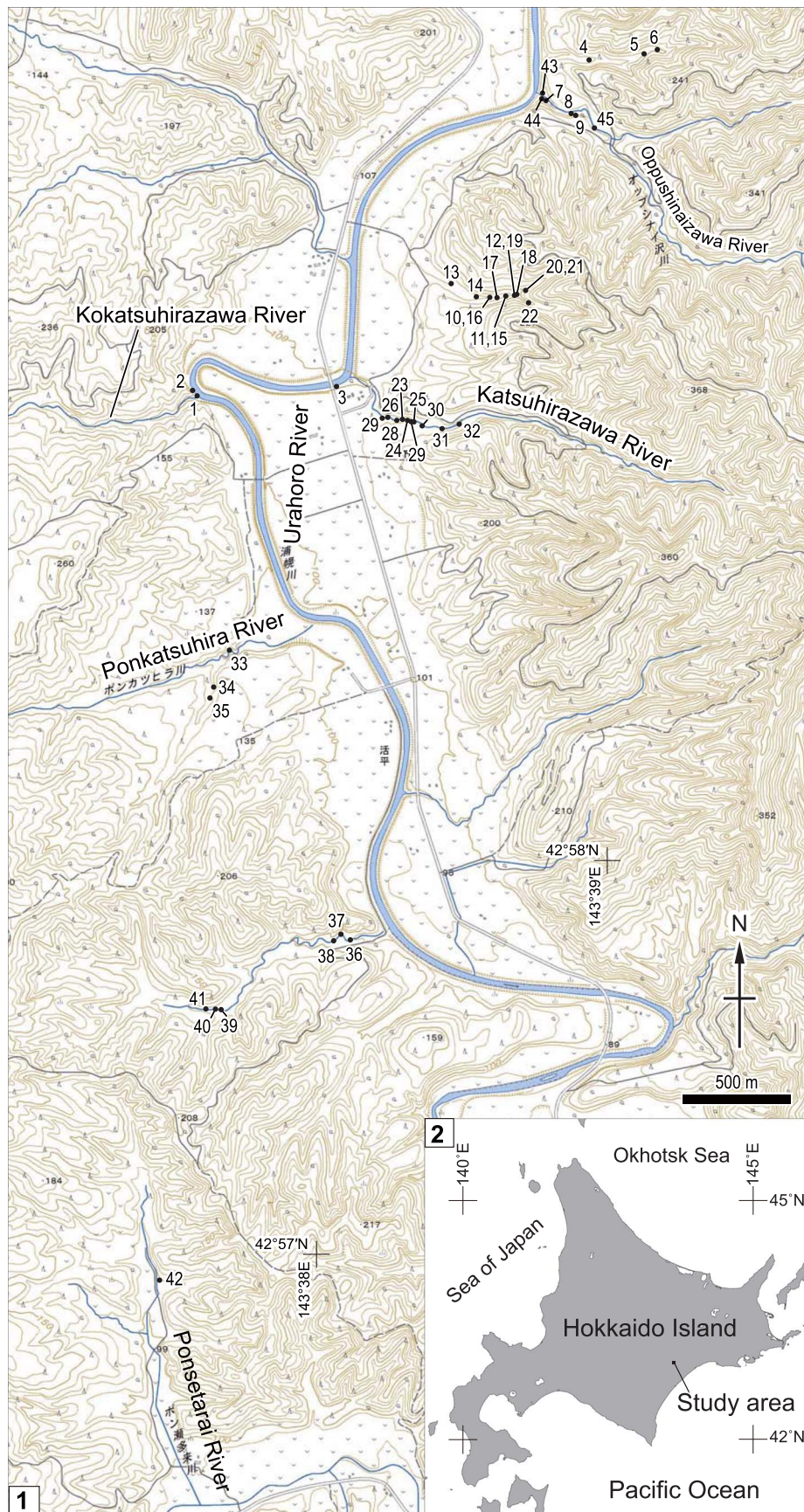
Wood-fall communities are considered an evolutionary first step for shallow-water invertebrates in adapting to vent and seep sites (e.g., Distel et al., 2000; Lorion et al., 2010). Therefore, it is essential to reconstruct the evolution of these communities over geological time, especially for so-called ‘Cenozoic type’ chemosynthetic communities, including the vesicomysids and bathymodiolines, which first appeared in the middle Eocene (Amano and Kiel, 2007; Kiel and Amano, 2013). Although many Cretaceous chemosynthetic communities have been recorded (e.g., Campbell, 2006), only two Paleocene chemosynthetic communities have been reported, from the Panoche Hills in California (Schwartz et al., 2003) and Spitsbergen Island (Hryniewicz et al., 2016). Neither of these communities contained vesicomysids or bathymodiolines.

In Urahoro Town, eastern Hokkaido (Fig. 1), many species of deep-sea mollusks have been recovered from the Paleocene Katsuhira Formation around its type locality (Oda et al., 1959) by the authors and their colleagues (Amano and Jenkins, 2014, 2017; Amano and Oleinik, 2014; Amano et al., 2015a, b, 2016b). These are defined as wood-fall communities because they include some chemosymbiotic species such as limpets, lucinids, and thyasirids, as well as an aporhaid gastropod, a detritus feeder on plant fragments, deposit feeders such as

protobranch bivalves, suspension feeders such as *Bentharca* Verrill & Bush, 1898, and predators such as buccinoideans and cancellariids (Amano et al., 2016a), adding to wood-boring bivalves such as *Xylophaga?* sp. Among the protobranchs, two species and two genera survived the end-Cretaceous mass extinction, but disappeared by the end of the Paleocene (Amano and Jenkins, 2017). Moreover, it has been elucidated that *Bentharca steffeni* Amano, Jenkins, and Nishida, 2015a, *Admete katsuhiraensis* Amano, Oleinik, and Jenkins, 2016b, and *Tindaria paleocenica* Amano and Jenkins, 2017 are the oldest records of their genera worldwide. Thus, in the Paleocene, it is possible that the deep sea in the northwestern Pacific could have acted as a refuge from the end-Cretaceous extinction and as a place of origin of Cenozoic-type mollusks. To address this hypothesis, it is necessary to carry out detailed taxonomic research on the fauna of the Katsuhira Formation. In this paper, we describe some new species and Mesozoic-relict species from the formation in detail.

## Geologic setting

Molluscan fossils were collected by the authors from 45 localities of the Katsuhira Formation (Fig. 1). Stratigraphically, use of the Katsuhira Formation by Kaiho (1984) has caused some confusion. In this paper, we use Katsuhira Formation



**Figure 1.** Map showing the fossil localities: (1) locality map of fossils (base map is from ‘Katsuhira,’ scale 1:25,000; topographical map published by the Geospatial Information Authority of Japan); (2) map showing the study area in eastern Hokkaido.



(>600 m in thickness) according to the original definition by Oda et al. (1959), which corresponds to the 'Katsuhira Mudstone Member' of the Tomikawa Formation by Nishijima (1964). The formation consists of dark gray mudstone frequently yielding calcareous concretions with plant debris (~30 cm in diameter).

The age of the Katsuhira Formation herein, near the boundary with the overlying Tokomuro Formation, was confirmed as Selandian by planktonic foraminifers, and the lower part of the formation also as Selandian by calcareous nannofossils (Kaiho, 1984). However, as a result of our examination of many dinoflagellate cysts from the dark gray mudstone of the middle part of the formation at Loc. 1, from which many molluscan fossils have been collected, the following species were identified: *Senegalinium microspinosum* (Boltenhagen, 1977), *Palaeocystodinium golzowense* Alberti, 1961, *Eisenackia margarita* (Harland, 1979), *Eisenackia* sp., *Glaphyrocysta spineta* (Eaton, 1976), *G. divaricata* (Williams and Downie, 1966), and *Hystrichosphaeridium tubiferum* (Ehrenberg, 1838), as well as the acritarch species *Paralecaniella indentata* (Deflandre and Cookson, 1955). This association indicates that the sediments belong to the *Palaeocystodinium golzowense* Biozone and the *Senegalinium microspinosum* Biozone (Kurita, 2004), ranging from late Selandian to Thanetian (middle to late Paleocene) in age. Furthermore, *Eisenackia margarita* has a narrow stratigraphic range from the late Selandian to the earliest Thanetian (Luterbacher et al., 2004).

## Material and methods

Most specimens were observed by stereoscopic microscope (Olympus SZ-2-W). Because astartid specimens are very small size but paleontologically important (as discussed below), we have observed and photographed them by scanning electron microscopy (JEOL model JSM-6010LV) at Kanazawa University. We also measured the specimens by digital calipers (Mitsutoyo Company, model CD-20) to the first decimal place.

Abbreviations used throughout the text include: AL/L = ratio of anterior length and shell length; D = shell diameter; H = shell height; H/L = ratio of shell height and shell length; L = shell length; SH = spire height; W = shell width; W/L = ratio of shell width and shell length.

*Repositories and institutional abbreviations.*—Type, figured, and other specimens examined in this study are deposited in the following institutions: GMH = Institute of Geology and Mineralogy, Faculty of Science, Hokkaido University, Sapporo; IGPS = Institute of Geology and Paleontology, Faculty of Science, Tohoku University, Sendai; JUE = Joetsu University of Education, Joetsu.

## Systematic paleontology

Class Bivalvia Linnaeus, 1758  
 Subclass Pteriomorpha Beurlen, 1944  
 Order Pectinoida Gray, 1854  
 Family Propeamussiidae Abbott, 1954  
 Genus *Propeamussium* de Gregorio, 1884

*Type species.*—*Pecten (Propeamussium) ceciliae* de Gregorio, 1884 (by original designation); Miocene, Italy, Sicily, Terrebianche.

*Propeamussium yubarensis* (Yabe and Nagao, 1928)  
 Figure 2.1–2.4, Table 1

- 1928 *Pecten (Propeamissium) cowperi* var. *yubarensis* Yabe and Nagao, p. 88, pl. 16, figs. 17–19.  
 1932 *Pecten (Propeamissium) cowperi* var. *yubarensis*; Nagao, p. 38, pl. 6, figs. 7, 8, 12, 13.  
 1938 *Pecten (Propeamissium) cowperi* var. *yubarensis*; Nagao, p. 129, pl. 16, fig. 3.  
 1956 *Pecten (Propeamissium) cowperi* var. *yubarensis*; Amano, p. 73, pl. 1, fig. 12.  
 1976 *Parvamussium cowperi yubarensis*; Tashiro, p. 52, pl. 4, figs. 20–24.  
 1992 *Parvamussium yubarensis*; Tashiro, p. 112, pl. 32, fig. 1.

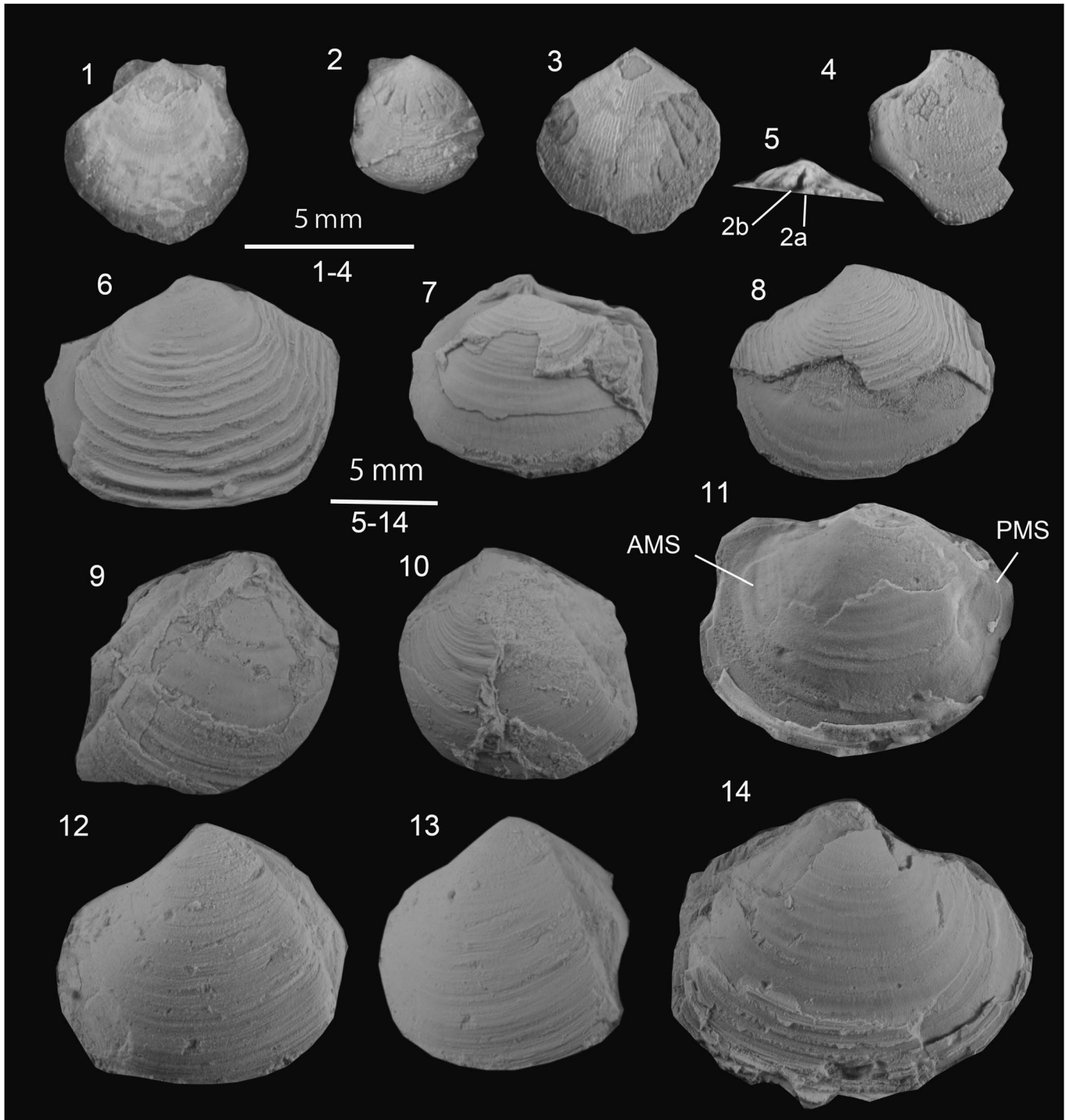
*Type specimen.*—IGPS 22599.

*Occurrence.*—Cenomanian to Campanian formations from Hokkaido to Kyushu; upper Selandian to lowermost Thanetian, Katsuhira Formation, eastern Hokkaido, Japan.

*Original description.*—“Shell very compressed, small, suborbicular, nearly as high as long; subequivalve, almost equilateral, except for the ears; the dorsal third of the disc triangular, with the apical angle about 120°; remaining part of shell semi-circular; antero-dorsal margin almost straight, the postero-dorsal faintly concave, scarcely longer than the anterior; posterior end bluntly angulated. Test thin. Right valve: Posterior ear shorter, with the outer angle slightly obtuse; anterior ear distinctly notched below, with an acute outer angle; both ears ornamented with lines of growth. External surface covered with numerous, fine, equally spaced, concentric lines and numerous very fine radial lines scarcely visible under a lens: inner surface bearing 7 strong, equally spaced round ribs, extending from umbo nearly to the main margin and abruptly truncated at their low ends. Left valve: Ears subequal, with the outer angles slightly obtuse. Outer surface ornamented with numerous, slightly raised, fine radial striae and lines of growth; inner surface bearing strong radial ribs of unknown number” (Yabe and Nagao, 1928, p. 88).

*Materials.*—Six specimens from the floor of Urahoro River at Katsuhira (JUE 16012-1, 16012-2, Loc. 1), Oppushinai-zawa (JUE 16010, Loc. 7; 16013, Loc. 45), Katsuhira-kita-zawa (JUE 16011, Loc. 21), and Ponsetarai-zawa (JUE 16009, Loc. 42); see Table 1 for dimensions.

*Remarks.*—The Katsuhira specimens have a slightly inflated, small, thin shell, to 4.9 mm in length and eight internal radial ribs, not reaching the ventral margin. The shell surface is sculptured with very fine radial threads on the left valve and many distinct commarginal lines on the right valve. The left anterior auricle is slightly larger than the posterior one. From these characters, the Katsuhira species is identified as *Propeamussium*. Tashiro (1976, 1992) allocated this species to *Parvamussium* Sacco, 1897, however, because *P. yubarensis*



**Figure 2.** (1–4) *Propeamussium yubarens* (Yabe and Nagao, 1928): (1) JUE 16009, frontal view of left valve, showing fine radial riblets; (2) JUE 16010, frontal view of right valve, showing distinct growth lines; (3) JUE 16013, frontal view of left valve, showing fine radial riblets; (4) JUE 16011, silicone rubber cast of left valve. (5–8, 11, 14) *Myrtea ezoensis* (Nagao, 1938): (5, 6) JUE 16001, left valve, with view of valve hinge (5) and frontal view (6) showing distinct commarginal ribs; (7, 8) JUE 16003, with right valve and hinge of left valve (7) and left valve (8); (11) JUE 16000-3, interior of the shell; (14) JUE 16000-2, frontal view of right valve. (9, 10, 12, 13) *Thyasira (Thyasira) oliveri* Amano and Jenkins, n. sp.: (9) JUE 15994-1, paratype, frontal view of right valve; (10) JUE 15994-2, paratype, frontal view of left valve; (12, 13) JUE 15993, holotype, left valve, in frontal (12) and oblique (13) views. 2a = anterior hinge tooth of left valve, 2b = posterior hinge tooth of left valve, AMS = anterior muscle scar, PMS = posterior muscle scar.

has the inner ribs not reaching the ventral margin, nearly equal auricles, and no byssal notch, it can be safely included in the genus *Propeamussium*.

*Propeamussium cowperi* Waring, 1917 from the Upper Cretaceous of California can be distinguished from

*P. yubarens* by being larger (24 mm L) and having fewer internal ribs in the left valve (4–8). *Propeamussium kusiroense* (Takeda, 1953) from the Oligocene Nuibetsu Formation is also a closely similar species. However, the latter has a more compressed shell than *P. yubarens*.

**Table 1.** Measurements of *Propeamussium yubarensis* (Yabe and Nagao, 1928). H = height, L = length, – = not available.

Locality	Specimen	L (mm)	H (mm)	Valve
Loc. 42	JUE 16009	4.0	4.4	left
Loc. 7	JUE 16010	3.0	3.3	right
Loc. 21	JUE 16011	–	4.9	left
Loc. 1	JUE 16012-1	3.9	2.9	left
Loc. 1	JUE 16012-2	3.9	2.8	left
Loc. 45	JUE 16013	4.9	5.4	unknown

Order Lucinida Gray, 1854  
 Family Lucinidae Fleming, 1828  
 Subfamily Myrteinae Chavan, 1969  
 Genus *Myrtea* Turton, 1822

*Type species.*—*Venus spinifera* Montagu, 1803 (by original designation); Recent, British Islands.

*Myrtea ezoensis* (Nagao, 1938)  
 Figure 2.5–2.8, 2.11, 2.14, Table 2

- 1890 *Lucina* cf. *fallax* Forbes; Yokoyama, p. 176, pl. 18, fig. 9.  
 1938 *Lucina* (*Myrtea*) *ezoensis* Nagao, p. 136, figs. 4–6.  
 1962 *Lucinoma ezoensis*; Saito, p. 70, pl. 2, fig. 6.  
 1976 *Myrtea* (sensu lato) *ezoensis*; Tashiro, p. 60, pl. 9, fig. 5.

*Type specimen.*—GMH 8234.

*Occurrence.*—Cenomanian to lower Campanian formations from Hokkaido to Kyushu; upper Selandian to lowermost Thanetian, Katsuhira Formation, eastern Hokkaido, Japan.

*Original description.*—“Shell rather small, somewhat pentagonally ovate in outline, slightly longer than high, sub-equilateral, moderately convex from the umbo toward the ventral margin, compressed and attenuated both anteriorly and posteriorly; antero-dorsal margin nearly horizontal, slightly excavated beneath the umbo, convex in the anterior length; postero-dorsal margin straight, inclined backward and downward; ventral margin broadly and evenly curved, passing gradually into the anterior one, which is arcuate and slightly oblique; antero-dorsal end a little produced and rounded along the margin; posterior end vertically truncated by a straight and rather long margin that forms an obtuse angle with the ventral. Umbones small, subcentral, not prominent, with a round posterior umbonal angle running from it to the postero-ventral end, the surface behind this angle compressed and flattened; anterior umbonal angle not well defined, antero-dorsal area bordered by a distinct groove that originates from the umbo and runs to the antero-dorsal end. Lunule small, very short, deep, bounded by sharp ridges. Ligamental groove deeply depressed; escutcheon well defined. Test relatively thin. Surface with numerous, prominent and widely spaced concentric lamellae and flat interspaces in alternation, the latter having a few fine concentric lines. These lamellae prolonged on the ridge at the anterior margin of the escutcheon and also near the antero-dorsal margin. The lamellae and lines distinctly wavy on crossing the groove near the anterior margin. A few specimens have been examined. One from the Obirasibe district in the province of Tesio is well

**Table 2.** Measurements of *Myrtea ezoensis* (Nagao, 1938). H = height, L = length, W = width, – = not available.

Locality	Specimen	L (mm)	H (mm)	W (mm)	Valve
Loc. 1	JUE 16000-1	15.7	13.8	6.1	both
Loc. 1	JUE 16000-2	15.5	12.5	–	right
Loc. 1	JUE 16000-3	13.5	10.8	–	right
Loc. 1	JUE 16001	13.5	11.0	–	left
Loc. 1	JUE 16002	20.8	17.4	7.4	both
Loc. 1	JUE 16004-1	20.3	15.0	–	right
Loc. 1	JUE 16004-2	20.7	16.2	7.3	both
Loc. 1	JUE 16004-3	18.7	14.2	5.7	both
Loc. 3	JUE 16005-1	6.4	5.9	–	both
Loc. 3	JUE 16005-2	4.3	3.9	–	both
Loc. 41	JUE 16003	11.5	9.3	5.0	both

preserved and accordingly selected as the holotype. However, the inner features are not observable in it. One of the two specimens collected in the Abesinai district that are considered conspecific with the holotype, shows, some of the inner features impressed on a cast of the right valve. In this specimen, the lunule is very deeply impressed and very short and the hinge plate narrow, with a distinct and more or less elongated anterior lateral tooth. The posterior cardinal is narrow and slightly oblique backward. The socket in front of the posterior cardinal is also narrow and separates the latter from the anterior margin. The anterior cardinal is apparently obsolete. Anterior adductor muscle scar narrow, elongated, and the pallial line rather distant from the shell margin. The inner margins are smooth. The inner surface has numerous fine radial lines that are distinctly preserved on the cast” (Nagao, 1938, p. 136–137).

*Materials.*—Eight specimens from the floor of Urahoro River at Katsuhira (JUE 16000-1–3, 16001, 16002, 16004-1–3, Loc. 1) and near the Asahi Bridge (JUE 16005-1, 2, Loc. 3), and one specimen from Ponkatsuhira-minami-sawa (JUE 16003, Loc. 41); see Table 2 for dimensions.

*Remarks.*—The maximum size of the collected specimens is 20.8 mm in length. Their shells are longer than high (H/L = 0.76–0.88; type specimens of *M. ezoensis*, 0.79–0.88), weakly inflated (W/L = 0.30–0.39; holotype of *M. ezoensis*, 0.37), subquadrate or quadrate-ovate with a posterior blunt ridge and a subtruncated posterior margin. The beak is pointed and centrally or anteriorly located (AL/L = 0.37–0.57). The surface is sculptured with regular commarginal ribs with fine, weak interstitial riblets. The anterior adductor muscle scar is elongate-ovate in outline, detached from the entire pallial line and larger than the ovate posterior one. The lunule and escutcheon are narrow, sunken, and demarcated by a sharp ridge. In the left valve, the anterior tooth (2a) is thin and vertical whereas the posterior one (2b) is rather thick and inclined posteriorly. Based on these characters, the specimens from the Paleocene Katsuhira Formation can be safely identified as *Myrtea ezoensis*, which was described from the Yezo Group in northern and central Hokkaido and South Sakhalin.

Family Thyasiridae Dall, 1900 (1895)  
 Genus *Thyasira* Lamarck, 1818  
 Subgenus *Thyasira* Lamarck, 1818



*Type species.*—*Tellina flexuosa* Montagu, 1803 (by original designation); Recent, Britain and Ireland.

*Thyasira (Thyasira) oliveri* Amano and Jenkins, new species  
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Figure 2.9, 2.10, 2.12, 2.13, Table 3

2015b *Thyasira* sp.; Amano et al., p. 47, figs. 16–17.

*Type specimens.*—Holotype, JUE 15993, from 550 m upstream of Katsuhira-kita-zawa, Urahoro Town, Hokkaido (Loc. 19); Paratypes, JUE 15994-1–2, from 600 m upstream of Katsuhira-kita-zawa (Loc. 20); Paratype, JUE 15995, from 40 m upstream of Oppushini-zawa (Loc. 44). Type locality: 550 m upstream of Katsuhira-kita-zawa in Urahoro Town, Hokkaido, Japan, 42°59'26"N, 143°38'41"E; Paleocene.

*Diagnosis.*—Small equilateral-ovate *Thyasira* with ridged second posterior fold, rather wide posterior sulcus, and narrow auricle.

*Occurrence.*—Upper Selandian to lowermost Thanetian, Katsuhira Formation, eastern Hokkaido, Japan.

*Description.*—Shell of moderate size (8.1–12.8 mm L), thin, equilateral-ovate, longer than high, rarely higher than long, well inflated ( $W/L = 0.52–0.58$ ). Anterodorsal margin nearly straight; anterior margin subcircular; ventral margin broadly arcuate. Second posterior fold distinct; posterior sulcus rather deep; first posterior fold wide and ridged; submarginal sulcus distinct; auricle narrow, short. No medial flattened area observed. Beak prosogyrate, centrally situated. Surface smooth except for irregular growth lines. Lunule narrow, slightly sunken. Cardinal tooth very weak. Anterior adductor muscle scar quadrate, large; posterior one unknown.

*Etymology.*—Named after Dr. P. Graham Oliver (National Museum of Wales) who has made major contributions to the taxonomy of Recent thyasirids.

*Materials.*—One specimen each from Locs. 10, 19, 29, and 44; two specimens from Loc. 20; see Table 3 for dimensions.

*Remarks.*—*Thyasira (Thyasira) oliveri* n. sp. closely resembles the Cretaceous species *T. (T.) tanabei* Kiel, Amano, and Jenkins, 2008 in having a ridged first posterior fold. However, the new species differs in having a wider first posterior fold than *T. (T.) tanabei*. As discussed by Amano et al. (2015b), both

**Table 3.** Measurements of *Thyasira (Thyasira) oliveri* Amano and Jenkins, n. sp. H = height, L = length, W = width, – = not available; + = dimension in slightly imperfect case.

Locality	Specimen	L (mm)	H (mm)	W (mm)	Valve
Loc. 19	JUE 15993, holotype	10.3	9.0	–	left
Loc. 20	JUE 15994-1, paratype	12.8+	10.3+	–	right
Loc. 20	JUE 15994-2, paratype	10.8	11.2	6.0	both
Loc. 44	JUE 15995, paratype	8.1	7.4	–	right
Loc. 10	JUE 15937	9.7+	9.0	5.0	both
Loc. 29	JUE 15936	10.1+	9.4	5.9	both

*T. (T.) baca* Devjatilova in Devjatilova and Volobueva, 1981 from the Paleocene Getkilninskaya Formation of western Kamchatka (Devjatilova and Volobueva, 1981) and *T. (T.) mironovi* Kalishevich in Kalishevich et al., 1981 from the lower Paleocene Sinegorsk Formation in South Sakhalin are distinguished from the new species in having triangular shells with a narrower posterior area and a wider first posterior fold with an angular ventral end.

Subclass Heterodonta Neumayr, 1884

Order Carditoida Lamarck, 1809

Family Astartidae d'Orbigny, 1844 (1840)

Genus *Astarte* Sowerby, 1816

Subgenus *Astarte* Sowerby, 1816

*Type species.*—*Venus scotica* Maton and Rackett, 1807 (by original designation) = *Pectunculus sulcatus* Da Costa, 1778 var. *scotica* (Maton and Rackett, 1807); Recent, Britain and Ireland.

*Astarte (Astarte) paleocenica* Amano and Jenkins, new species  
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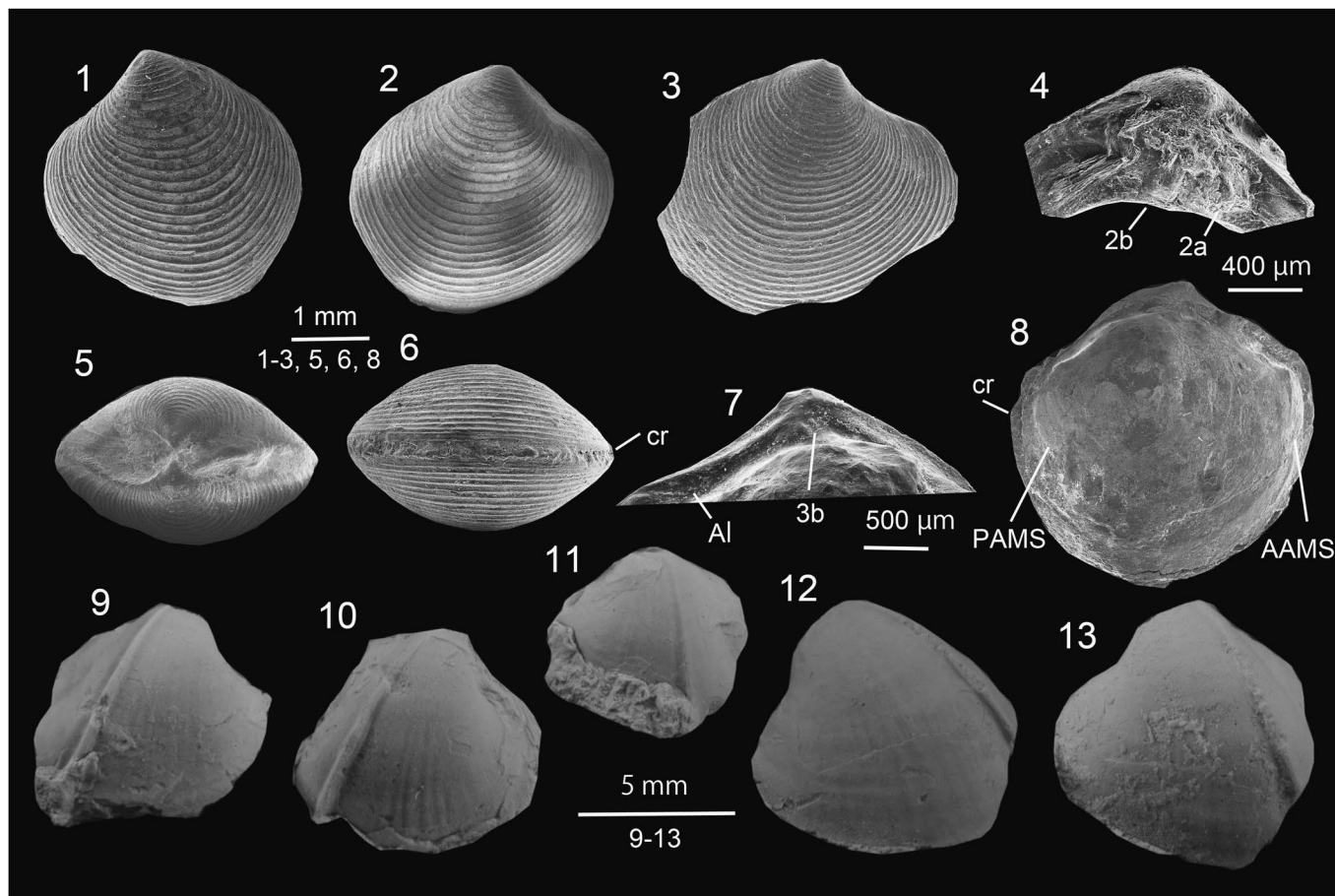
Figure 3.1–3.8, Table 4

*Type specimens.*—Holotype, JUE 15996, from the bank of the Urahoro River at the mouth of Kokatsuhira-zawa, Katsuhira, Urahoro Town, Hokkaido (Loc. 1); paratype, JUE 15997, from Loc. 1; paratype, JUE 15998, from 320 m upstream of Oppushini-zawa (Loc. 45). Type locality: river bank of the Urahoro River at the mouth of Kokatsuhira-zawa, Katsuhira in Urahoro Town, Hokkaido, Japan, 42°59'20"N, 143°38'04"E; Paleocene.

*Diagnosis.*—Very small subquadrate *Astarte* with distinct fine commarginal ribs and a subtruncated posterior margin. Ventral margin finely crenulated. Lunule asymmetrical, narrow, and well demarcated.

*Occurrence.*—Upper Selandian to lowermost Thanetian, Katsuhira Formation, eastern Hokkaido, Japan.

*Description.*—Shell very small (3.3–4.2 mm L), thin, inequilateral, nearly equivalve, subquadrate, slightly longer than high, moderately inflated ( $W/L = 0.63$ ). Anterodorsal margin concave; anterior margin rounded; ventral margin broadly arcuate. Posterodorsal margin nearly straight, gently inclined; posterior margin truncated. Beak prosogyrate, anteriorly situated at two-fifths of shell length. Surface sculptured with regular, fine commarginal ribs. Lunule asymmetrical, left one wider than right, deeply sunken, demarcated by sharp ridge. Escutcheon narrow, flat. Anterior cardinal tooth of right valve (3a) indistinct; posterior cardinal tooth (3b) rather thick, inclined posteriorly; anterior lateral tooth thin. Anterior tooth (2a) of left valve rather thick, divided by groove, inclined anteriorly; posterior tooth (2b) also moderately thick, inclined posteriorly. Anterior adductor muscle scar small, semicircular; posterior adductor muscle scar pear-shaped, rather large. Pallial line entire. Inner ventral margin finely crenulated.



**Figure 3.** (1–8) *Astarte (Astarte) paleocenica* Amano and Jenkins, n. sp.: (1, 2, 5, 6) JUE 15996, holotype, with frontal views of left valve (1) and right valve (2), dorsal view (5) showing distinctly demarcated lunule and escutcheon, and ventral view (6); (3, 7, 8) JUE 15998, paratype, right valve, with frontal view (3), hinge (7), and inner surface (8); (4) JUE 15997-2, paratype, hinge of left valve. (9–13) *Poromya katsuhiraensis* Amano and Jenkins, n. sp.: (9) JUE 16006, holotype, frontal view of right valve; (10) JUE 16007-1, paratype, frontal view of right valve; (11) JUE 16007-4, paratype, frontal view of left valve; (12, 13) JUE 16007-2, paratype, left valve, in oblique (12) and frontal (13) views. 2a=anterior hinge tooth of left valve, 2b=posterior hinge tooth of left valve, 3b=posterior cardinal tooth of right valve, AI=anterior lateral tooth of right valve, AAMS=anterior adductor muscle scar, cr=crenulations, PAMS=posterior adductor muscle scar.

**Table 4.** Measurements of *Astarte (Astarte) paleocenica* Amano and Jenkins, n. sp. H=height, L=length, W=width, –=not available; +=dimension in slightly imperfect case.

Locality	Specimen	L (mm)	H (mm)	W (mm)	Valve
Loc. 1	JUE 15996, holotype	3.3	3.2	2.0	both
Loc. 1	JUE 15997, paratype	4.2	3.7	2.0+	both
Loc. 45	JUE 15998, paratype	3.9+	–	–	right

**Etymology.**—Named after the age of this species.

**Materials.**—Two specimens from the river bank at Katsuhira (Loc. 1); one specimen from 320 m upstream of Oppushinai-zawa (Loc. 45); one specimen (hinge part only) from Loc. 2 (JUE 15999) from the river bank, 100 m north of Loc. 1; see Table 4 for dimensions.

**Remarks.**—*Astarte (Astarte) paleocenica* n. sp. closely resembles *A. (A.) parvula* Kalishevich in Kalishevich et al. (1981) from the Danian and lower Paleocene of southeastern Sakhalin in having a small shell and distinct commarginal ribs. However, the latter species was based on poorly preserved specimens.

The new species is also similar to *A. (A.) trigonula* von Koenen, 1885 from the Paleocene of Copenhagen, Denmark, in its small size (to 7 mm L) and in having distinct commarginal ribs. However, *A. (A.) trigonula* lacks a subtruncated posterior margin and has a centrally situated beak.

Order Pholadomyoidea Newell, 1965  
Family Poromyidae Dall, 1886  
Genus *Poromya* Forbes, 1844

**Type species.**—*Poromya anatinoides* Forbes, 1844 (by original designation) = *Corbula granulata* Nyst and Westendorp, 1839; Recent, Asia Minor and Cyclades.

*Poromya katsuhiraensis* Amano and Jenkins, new species  
urn:lsid:zoobank.org:act:9E236867-FDA1-4EEF-8C96-734328BA71EB

Figure 3.9–3.13, Table 5

**Type specimens.**—Holotype, JUE 16006, from the bank of the Urahoro River at the mouth of Kokatsuhira-zawa, Katsuhira, Urahoro Town, Hokkaido (Loc. 1); paratypes, JUE 16007-1–4,

**Table 5.** Measurements of *Poromya katsuhiraensis* Amano and Jenkins, n. sp. H = height, L = length, W = width, – = not available; + = dimension in slightly imperfect case.

Locality	Specimen	L (mm)	H (mm)	W (mm)	Valve
Loc. 1	JUE 16006, holotype	7.2	6.2	4.7	both
Loc. 1	JUE 16007-1, paratype	7.9	7.0	–	right
Loc. 1	JUE 16007-2, paratype	7.8+	7.5	–	left
Loc. 1	JUE 16007-3, paratype	5.5	5.4	3.7	both
Loc. 1	JUE 16007-4, paratype	5.4	5.0	3.5	both
Loc. 1	JUE 16008	10.8	11.1	–	right

from Loc. 1. Type locality: bank of the Uraho River at the mouth of Kokatsuhira-zawa, Katsuhira in Uraho Town, Hokkaido, Japan, 42°59'20"N, 143°38'04"E; Paleocene.

**Diagnosis.**—Moderate-sized and subquadrate *Poromya* with posterior carina from beak to posteroventral corner and rather deep groove just before posterior adductor muscle scar. Inner surface nacreous, covered with fine radial grooves in anterior disc before carina. Right valve with one cardinal; left valve with one socket.

**Occurrence.**—Upper Selandian to lowermost Thanetian, Katsuhira Formation, eastern Hokkaido, Japan.

**Description.**—Shell of moderate size (to 10.8 mm L), rather thin, inequilateral, equivalve, subquadrate, slightly longer than high or higher than long (H/L = 0.86–1.03), moderately inflated (W/L = 0.65–0.67). Anterodorsal margin concave; anterior margin subcircular; ventral margin broadly arcuated. Posterodorsal margin nearly straight and gently sloping; posterior margin truncated. Beak prosogyrate and anteriorly situated at one-third L. Distinct carina running from beak to posteroventral corner, separating anterior and posterior parts of shell. Rather deep groove just before posterior adductor muscle scar and forming strongly concave posteroventral margin. Outer surface poorly preserved; inner surface nacreous, sculptured by ~10 fine, weak radial grooves behind carina. One cardinal tooth of right valve small, inserting into socket of left valve. Pallial sinus very shallow, small, just before posterior adductor muscle scar. Anterior adductor muscle scar small, subovate; posterior adductor muscle scar of similar size and shape to anterior one.

**Etymology.**—Named after the formation at the type locality.

**Materials.**—Six specimens from the type locality, including one poorly preserved specimen (JUE 16008); see Table 5 for dimensions.

**Remarks.**—*Poromya katsuhiraensis* n. sp. is the oldest species of *Poromya* in the world. It is closely similar to the Recent species *P. carinata* Lan, 2000 from the Dongsha Islands of Taiwan in size (8.8 mm L in *P. carinata*) and in having a prominent carina. However, *P. katsuhiraensis* n. sp. can easily be distinguished from *P. carinata* by its rather deep groove just before the posterior adductor muscle scar, no groove before the carina, and a longer, truncated posterior margin. The prominent carina distinguishes the present species from the two fossil species *P. osawanoensis* Tsuda, 1959, from the uppermost

lower to lowermost middle Miocene Kurosedani Formation in Toyama Prefecture, and *P. yasukana* Nomura and Hatai, 1936 from the upper Miocene Kubota Formation in Fukushima Prefecture.

Class Gastropoda Cuvier, 1795  
 Subclass Caenogastropoda Cox, 1960  
 Order Littorinimorpha Golikov and Starobogatov, 1975  
 Family Naticidae Guilding, 1834  
 Subfamily Polinicinae Finlay and Marwick, 1937  
 Genus *Neverita* Risso, 1826

**Type species.**—*Neverita josephinia* Risso, 1826 (by original designation); Eocene to Holocene, Europe.

*Neverita majimai* Amano and Jenkins, new species  
 urn:lsid:zoobank.org:act:0EA3A33A-4B9F-4A14-A3D6-D13034D25993

Figure 4.1–4.7, Table 6

**Type specimens.**—Holotype, JUE 16018, from 500 m upstream of Katsuhira-kita-zawa, Uraho Town, Hokkaido (Loc. 15); paratypes, JUE 16019-1–2, from the type locality; paratype, JUE 16020, from 480 m upstream of Katsuhira-kita-zawa (Loc. 16); paratype, JUE 16021, from 325 m upstream of Katsuhira-zawa (Loc. 28). Type locality: 500 m upstream of Katsuhira-kita-zawa, Uraho Town, Hokkaido, Japan, 42°59'27"N, 143°38'43"E; Paleocene.

**Diagnosis.**—Small globose *Neverita* with 4.5 whorls including 1.5 whorls of low-spined protoconch, low spire, and large, massive, semicircular umbilical callus, completely covering umbilicus. Umbilical callus sculptured with weak groove in central part and some very weak furrows on both sides of groove. Surface smooth except for weak axial wrinkles in weakly depressed subsutural area on last whorl.

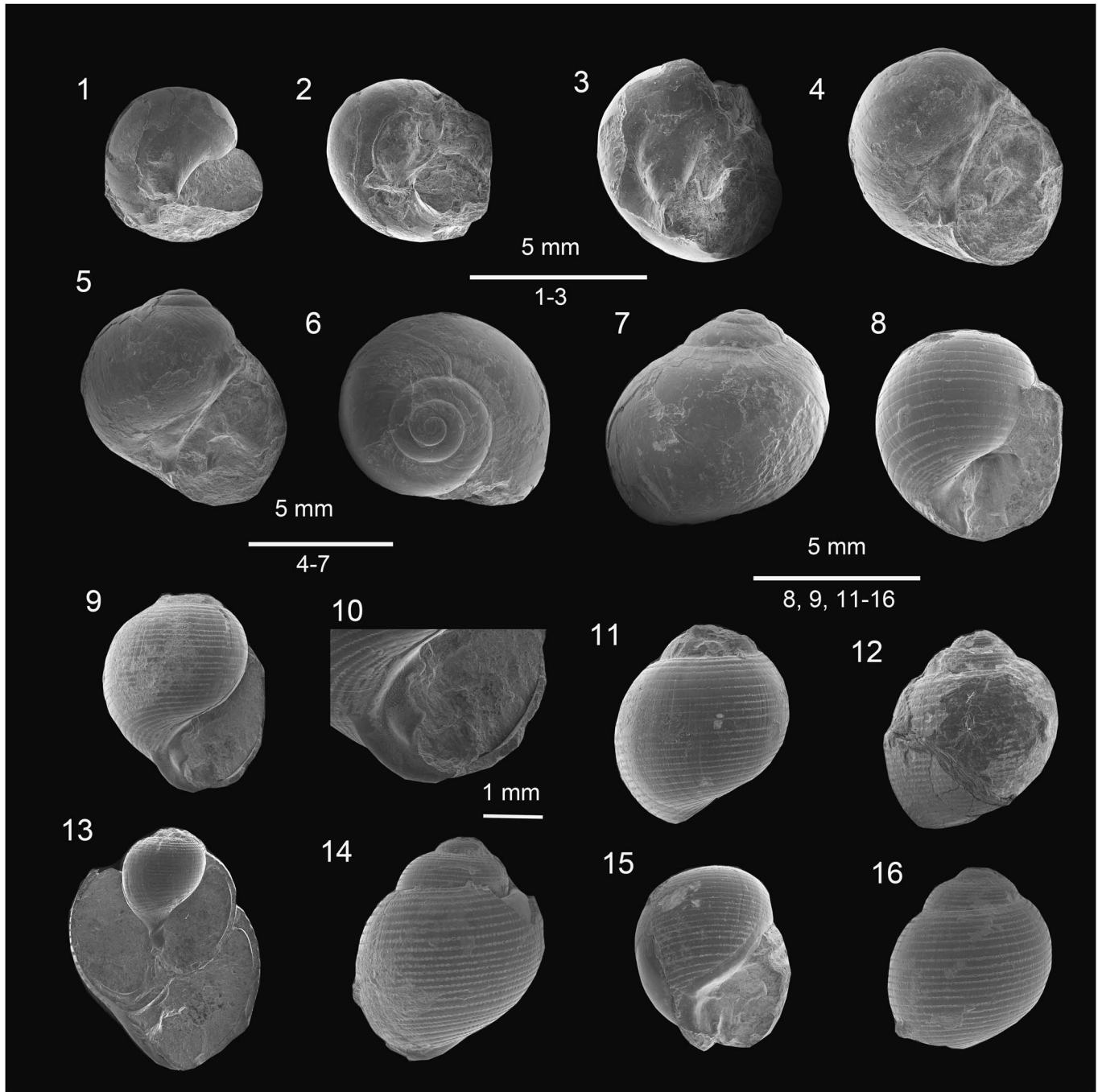
**Occurrence.**—Upper Selandian to lowermost Thanetian, Katsuhira Formation, eastern Hokkaido, Japan.

**Description.**—Shell small for genus (to 11.5 mm H), globose, thin, with low spire; of 4.5 whorls including planispiral protoconch (1.6 mm D) of 1.5 whorls; suture shallow; subsutural area slightly depressed, with weak vertical growth wrinkles; shallow furrow separating substural depressed area on last whorl. Surface smooth except for subsutural wrinkles and growth lines. Parietal callus thin. Umbilicus completely covered with massive semicircular umbilical callus with one weak, central transverse groove; several very weak furrows on both sides of groove. Outer lip thin; interior lip moderately thick.

**Etymology.**—Named after Prof. Ryuichi Majima (Yokoyama National University) who studied the taxonomy of Cenozoic naticids in Japan.

**Materials.**—Five specimens from the type locality (Loc. 15); one specimen from 480 m upstream of Katsuhira-kita-zawa (Loc. 16); four specimens from 325 m upstream of Katsuhira-zawa (Loc. 28); two specimens from 450 m upstream of





**Figure 4.** (1–7) *Neverita majimai* Amano and Jenkins, n. sp.: (1) JUE 16019-2, paratype, umbilical view; (2) JUE 16019-1, paratype, umbilical view; (3) JUE 16021, paratype, umbilical view; (4–7) JUE 16018, holotype, in umbilical (4), apertural (5), apical (6), and abapertural (7) views. (8–16) *Biplica paleocenica* Amano and Jenkins, n. sp.: (8) JUE 16028-1, paratype, apertural view; (9–11) JUE 16027, holotype, in apertural (9) and abapertural (11) views, plus enlargement of basal part of aperture (10); (12) JUE 16029-2, abapertural view; (13, 14) JUE 16028-3, paratype, in apertural (13) and abapertural (14) views; (15) JUE 16028-2, paratype, apertural view; (16) JUE 16029-3, abapertural view.

Katsuhira-kita-zawa (Loc. 10); two specimens from 575 m upstream of Katsuhira-zawa (Loc. 32); two specimens from 250 m upstream of Ponkatsuhira-minami-zawa (Loc. 38); see Table 6 for dimensions.

**Remarks.**—*Neverita majimai* n. sp. is one of the oldest species of this genus. According to Marincovich (1977), *N. globosa* Gabb, 1869 occurs in the upper Paleocene Meganos Formation

in California. However, Squires (2003) dated the ‘Meganos’ stage to the latest Paleocene to early Eocene. It is difficult to be sure whether the Katsuhira Formation or the Meganos Formation is older. *Neverita majimai* n. sp. is closely similar to *N. eocenica* (Nagao, 1928) from the lower Eocene Futagajima Formation in Kyushu in having a small globose shell with a massive umbilical callus. However, it differs from *N. eocenica* in having several very weak furrows on both sides of the

**Table 6.** Measurements of *Neverita majimai* Amano and Jenkins, n. sp. D = diameter, H = height; + = dimension in slightly imperfect case.

Locality	Specimen	D (mm)	H (mm)
Loc. 15	JUE 16018, holotype	7.7	7.3
Loc. 15	JUE 16019-1, paratype	4.9	5.3
Loc. 15	JUE 16019-2, paratype	3.4	3.7+
Loc. 16	JUE 16020, paratype	6.0	5.7
Loc. 28	JUE 16021, paratype	4.0	5.1
Loc. 15	JUE 16022-1	6.4	6.6
Loc. 15	JUE 16022-2	4.9	3.5
Loc. 10	JUE 16023-1	5.1	4.2
Loc. 10	JUE 16023-2	4.3	4.7
Loc. 28	JUE 16024-1	5.7	6.1
Loc. 28	JUE 16024-2	4.1	4.2
Loc. 28	JUE 16024-3	4.6	4.0
Loc. 28	JUE 16024-4	3.3	3.6
Loc. 32	JUE 16025-1	4.1	2.8
Loc. 32	JUE 16025-2	3.9	2.9
Loc. 38	JUE 16026-1	9.0	11.5
Loc. 38	JUE 16026-2	7.6	6.7

transverse groove on the umbilical callus. *Neverita globosa* Gabb, 1869, from the upper Paleocene to upper Eocene in California, has a lower shell and a wider umbilical callus than the new species. Moreover, the transverse groove on the umbilical callus of the Californian species is sometimes recognized but very weak.

Subclass Heterobranchia Burmeister, 1837  
 Family Ringiculidae Philippi, 1853  
 Genus *Biplica* Popenoe, 1957

*Type species.*—*Biplica heteroplicata* Popenoe, 1957 (by original designation); early Senonian?

*Biplica paleocenica* Amano and Jenkins, new species  
 urn:lsid:zoobank.org:act:68D288A8-D9A4-4B8C-A01C-16147F2F9126

Figure 4.8–4.16, Table 7

*Type specimens.*—Holotype, JUE 16027, from 900 m upstream of the small river, 1.5 km south to Ponkatsuhira-zawa, Urahoro Town, Hokkaido (Loc. 40; same as Amano and Olienik, 2014, loc. 1); paratypes, JUE 16028-1–2, from the type locality. Type locality: 900 m upstream of the small river, 1.5 km south to Ponkatsuhira-zawa, Urahoro Town, Hokkaido, Japan, 42°57'37"N, 143°37'41"E; Paleocene.

*Diagnosis.*—Small to moderate-sized ringiculid with smooth interior of outer lip. Spire rather high for genus; suture rather deep. No varix observed at outer lip. Surface sculptured with 18–26 (commonly 23–24) punctate spiral grooves, forming flat-topped spiral ribs between grooves. Inner lip covered with thin callus and two columellar folds.

*Occurrence.*—Upper Selandian to lowermost Thanetian, Katsuhira Formation, eastern Hokkaido, Japan.

*Description.*—Shell small to moderate-sized for genus (to 6.6 mm H), elongate-ovate; spire rather high, occupying 0.10–0.32 of H. Suture rather deep, forming step between penultimate and last whorls. Shell of 3.5 whorls, including 1.5 whorls of smooth, low-spined protoconch. Surface sculptured by

**Table 7.** Measurements of *Biplica paleocenica* Amano and Jenkins, n. sp. D = diameter, H = shell height, NGB = number of grooves on body whorl, SH = spire height (mm), – = not available; + = dimension in slightly imperfect case.

Locality	Specimen	D (mm)	H (mm)	SH	NGB
Loc. 40	JUE 16027, holotype	4.8	5.6	0.8	26
Loc. 40	JUE 16028-1, paratype	5.4	5.9	0.8	18
Loc. 40	JUE 16028-2, paratype	4.3	5.2	0.8	27
Loc. 41	JUE 16029-1	5.3	6.1	0.6	24
Loc. 41	JUE 16029-2	5.5	6.5	1.3	23
Loc. 41	JUE 16029-3	4.5	5.3	0.8	26
Loc. 41	JUE 16029-4	4.9	5.1	1.2	25
Loc. 41	JUE 16029-5	4.5	4.8	0.8	–
Loc. 39	JUE 16030	4.8	5.4	1.0	24
Loc. 7	JUE 16031	2.4	3.2	0.6	23
Loc. 1	JUE 16032-1	4.4	4.5	–	24
Loc. 1	JUE 16032-2	3.7	3.3	0.9	25
Loc. 3	JUE 16033	4.2	5.6	0.9	–
Loc. 30	JUE 16034	4.8	6.3	1.6	–
Loc. 32	JUE 16035-1	5.5	6.4	1.1	24
Loc. 32	JUE 16035-2	5.5	6.6	2.1	–
Loc. 32	JUE 16035-3	4.9	5.8	–	–
Loc. 32	JUE 16035-4	5.0	5.0+	–	–
Loc. 32	JUE 16035-1	5.0	4.8	–	–

18–26 spiral grooves (23–24 in most specimens) with small pits, separating flat-topped spiral ribs. Outer lip of most specimens thin, not dentate. Inner lip covered by thin callus, becoming thicker toward base, reaching posterior end of aperture. Two distinct columellar folds present near base.

*Etymology.*—Named after the age of this species, pointing out that it is the single relict species of this genus from the Paleocene.

*Materials.*—Six specimens from the type locality (Loc. 40); eight specimens from 50 m upstream of the type locality (Loc. 41); four specimens from 25 m downstream of the type locality (Loc. 39); one specimen from 50 m upstream of Oppushinai-zawa (Loc. 7); two specimens from the river bank near Katsuhira (Loc. 1); one specimen from the outcrop below the Asahi Bridge near Katsuhira (Loc. 3); one specimen from 360 m upstream of Katsuhira-zawa (Loc. 29); one specimen from 410 m upstream of Katsuhira-zawa (Loc. 30); six specimens from 575 m upstream of Katsuhira-zawa (Loc. 32); see Table 7 for dimensions of well-preserved specimens among the material.

*Remarks.*—This new species can be distinguished from the Cretaceous species from Hokkaido, *Biplica problematica* (Nagao, 1932), which was originally described under the genus *Avellana* d'Orbigny, 1842. After *Biplica* was established by Popenoe (1957), Poyarkova and Dzhililov (1985) allocated *A. problematica* to *Biplica*. At the same time, they synonymized *B. ovooides* Blank, 1980 from the Maastrichtian deposits in the Koryak Upland with *B. problematica*. The type specimen of *B. problematica* has a very low spire and a very thick callus on the base, and is sculptured with 12 weak spiral grooves on the upper half of the last whorl. *Biplica paleocenica* n. sp. differs from *B. osakaensis* Kase, 1990 from the lower Maastrichtian Shindachi Formation in Osaka Prefecture, Honshu, by having an elongate shell and a step between the last and penultimate whorls, no varix at the outer lip, a higher spire (SH/H = 0.14–0.19 in *B. osakaensis*) although having a similar number of spiral grooves (24–27 in *B. osakaensis*). *Biplica siberica* Kaim

and Beisel, 2005 from the Maastrichtian Gankin Formation in western Siberia is similar to *B. paleocenica* n. sp. in having 24 spiral grooves. However, the lower spire, the outer lip with a varix, and the single columellar fold of *B. siberica* enable us to separate it from *B. paleocenica* n. sp. *Biplica miniplicata* Popenoe, 1957 from the uppermost Cretaceous deposits of California can be easily separated from *B. paleocenica* n. sp. by its more numerous spiral grooves (~30) and single columellar fold.

## Discussion

When Heinberg (1999) compared the Maastrichtian chalk fauna with the fauna from the Danian *Cerithium* Limestone at Stevens Clint in Denmark, he listed 24 common species among a total of 123 species in his table 2. Among these, only three species (12.5%) are protobranch bivalves. However, it is plausible that some Paleocene species might be reworked from the Maastrichtian chalk because, like the chalk, the Paleocene *Cerithium* Limestone was deposited under shallow-water conditions. In contrast, the Katsuhira fauna consists of wood-fall communities and might have lived in deep water during the late Selandian to earliest Thanetian, as mentioned above. Thus, it is very unlikely that any taxa in the Katsuhira Formation were derived from underlying Cretaceous deposits.

As the result of this study, the pectinoidean *Propeamussium yubarense* and the lucinid *Myrtea ezoensis* are newly recognized as surviving the end-Cretaceous mass extinction at the species level (Table 8), in addition to the two protobranchs *Acila (Truncacila) hokkaidoensis* (Nagao, 1932) (Table 8) and *Pristigloma? sachalinensis* (Salnikova, 1987) pointed out by Amano and Jenkins (2017). At the genus level, *Astarte* Sowerby, 1816 and *Biplica* Popenoe, 1957 survived the event but became extinct before the Eocene, as did *Ezonuculana* Nagao, 1938 and *Menneroctenia* Kalishevich, 1973 (Amano and Jenkins, 2017). Moreover, aporrhaid gastropods suffered a severe extinction at the end of the Cretaceous, as pointed out by Roy (1994, 1996). In the northwestern Pacific, the following two aporrhaid species survived the end-Cretaceous extinction:

*Kangilioptera inouei* Amano and Jenkins, 2014 from the Katsuhira Formation, and *Drepanocheilus grammis* Kalishevich in Kalishevich et al., 1981 from the Danian to early Paleocene Sinegorsk horizon in southeastern Sakhalin.

Among these taxa, it is interesting to consider the evolution of astartids from a biogeographical point of view. Marincovich et al. (2002) pointed out that the occurrence of *Astarte parvula* Kalishevich in Kalishevich et al., 1981 from the Danian to lower Paleocene of Sakhalin is the last occurrence of astartids before they disappeared from the Pacific. They then reinvaded the North Pacific region after the opening of the Bering Strait during the latest Miocene (Ogasawara, 1986; Gladenkov et al., 1991; Amano, 1994; Marincovich and Gladenkov, 1999; Marincovich et al., 2002). The occurrence of *A. paleocenica* n. sp. newly described herein reveals that astartids continued to live until at least the late Selandian to earliest Thanetian in eastern Hokkaido.

Among the surviving species, the Cretaceous occurrence of *Acila (Truncacila) hokkaidoensis*, *Propeamussium yubarense*, and *Myrtea ezoensis* have wide occurrences from Kyushu to Hokkaido or from Hokkaido to the Koryak Upland. Such wide geographical distributions possibly helped these species to survive through the extinction event (Jablonski and Raup, 1995; Jablonski and Hunt, 2006; Jablonski, 2008; Robertson et al., 2013; Landman et al., 2014).

Some authors have pointed out the low extinction rate of protobranchs or deposit feeders (Sheehan and Hansen, 1986; Jablonski and Raup, 1995; Jablonski, 1996; Levinton, 1996; Robertson et al., 2013). This trend can be seen in the late Selandian to earliest Thanetian Katsuhira fauna. Among the nine relict Mesozoic taxa described above, four are protobranchs. Although Jablonski and Raup (1995) denied the role of water depth as a cause of a low extinction rate, they only examined the depth range of taxa on the continental shelf, not on slopes or in basins. Based on the Recent bathymetric range of protobranchs, the Katsuhira Formation was deposited in an upper bathyal depth. The end-Cretaceous mass extinction by an asteroid impact is thought to have depended on climatic change (e.g., Kaiho et al., 2016). However, deep-sea benthic

**Table 8.** List of mollusks from the Katsuhira Formation, indicating Mesozoic-relict taxa (Mes. R.) and oldest records as genera and species (Oldest Rec.). \* = chemosynthesis-based species, + = species level, ++ = genus level.

Species	Mes. R.	Oldest Rec.	Reference
<i>Leionucula yotsukurensis</i> (Hirayama, 1955)			Amano and Jenkins (2017)
<i>Acila (Truncacila) hokkaidoensis</i> (Nagao, 1932)	+		Amano and Jenkins (2017)
<i>Ezonuculana</i> aff. <i>obsoleta</i> Tashiro, 1976	++		Amano and Jenkins (2017)
<i>Meganuculana alleni</i> Amano and Jenkins, 2017			Amano and Jenkins (2017)
<i>Malletia poronaica</i> (Yokoyama, 1890)			Amano and Jenkins (2017)
<i>Menneroctenia plena</i> Kalishevich, 1973	+		Amano and Jenkins (2017)
<i>Neilonella alleni</i> Amano and Jenkins, 2017			Amano and Jenkins (2017)
<i>Tindaria paleocenica</i> Amano and Jenkins, 2017		++	Amano and Jenkins (2017)
<i>Pristigloma? sachalinensis</i> (Salnikova, 1987)	+		Amano and Jenkins (2017)
<i>Bentharca steffeni</i> Amano, Jenkins, and Nishida, 2015a		++	Amano et al. (2015a)
<i>Propeamussium yubarense</i> (Yabe and Nagao, 1928)	+		This study
<i>Myrtea ezoensis</i> (Nagao, 1938)*	+		This study
<i>Thyasira (Thyasira) oliveri</i> Amano and Jenkins, n. sp.*			This study
<i>Astarte (Astarte) paleocenica</i> Amano and Jenkins, n. sp.	++		This study
<i>Poromya katsuhiraensis</i> Amano and Jenkins, n. sp.		++	This study
<i>Bathyacmaea? sp.*</i>			This study
<i>Neverita majimai</i> Amano and Jenkins, n. sp.		++	This study
<i>Kangilioptera inouei</i> Amano and Jenkins, 2014	++		Amano and Jenkins (2014)
<i>Urahorosphaera kanekoi</i> Amano and Oleinik, 2014			Amano and Oleinik (2014)
<i>Admete katsuhiraensis</i> Amano, Oleinik, and Jenkins, 2016b		++	Amano et al. (2016b)
<i>Biplica paleocenica</i> Amano and Jenkins, n. sp.	++		This study



foraminifers show a lower extinction rate than shallow-water ones in the end-Cretaceous extinction because of little environmental change (Kaiho, 1994). Consequently, the low extinction rate of protobranchs is attributed to their deposit feeding strategy and preference of dwelling in deep water (e.g., Dame, 1996).

Five of the oldest fossil records of Recent molluscan genera have been found in the Katsuhira Formation: *Tindaria* Bellardi, 1875, *Bentharca*, *Poromya*, *Neverita*, and *Admete* Krøyer in Möller, 1842 (Amano et al., 2015a, 2016b; Amano and Jenkins, 2017; this study; Table 8). Moreover, *Urahorosphaera kanekoi* Amano and Oleinik, 2014 is the one of the oldest records of buccinoids in the Paleocene (Amano and Oleinik, 2014). Some Recent genera of deep-sea chemosynthetic bivalves also originated in the North Pacific after the middle Eocene: *Vulcanidas* Cosel and Marshall, 2010, *Bathymodiolus* Kenk and Wilson, 1985, *Calyptogena* Dall, 1891, and *Archivesica* Dall, 1908 (Kiel and Amano, 2010, 2013; Amano and Kiel, 2010; Amano et al., 2014). It is interesting to note that species of these genera are epifaunal or very shallowly infaunal, regardless of feeding type. However, the exact reason why these Recent genera originated in the North Pacific is unknown. From these, although the Katsuhira fauna includes many Mesozoic-relict taxa as refuges, some Cenozoic species first appeared in this formation.

From the viewpoint of the evolution of wood-fall communities, the fauna of the Katsuhira Formation includes three chemosynthesis-based species: the limpet *Bathyacmaea?* sp., the lucinid *Myrtea ezoensis*, and the thyasirid *Thyasira oliveri* n. sp. Consequently, the Paleocene wood-fall communities from the Katsuhira Formation in Hokkaido and the Basilika Formation in Spitsbergen have no provannid gastropods and no small mussels, compared to the first appearance of provannids in the Upper Cretaceous wood-fall communities (Kiel et al., 2009). Based on the protobranch species from the Katsuhira Formation (Amano and Jenkins, 2017), the paleobathymetry of the formation can be estimated to be between 200 and 500 m in depth. According to Hryniewicz et al. (2016), the Basilika Formation was deposited in an offshore prodelta. On the other hand, most Recent species of *Provanna* Dall, 1918 live deeper than 500 m (see Amano and Little, 2014, table 1). Because the Paleocene wood-fall communities lived in shallower water than the habitat of provannids, they lack provannid gastropods. On the other hand, despite the fact that small mussels can live in shallower water (e.g., Lorion et al., 2010), they have not been found in the Paleocene sites and even in the early to middle Eocene wood-fall communities from Washington State in the US (Kiel, 2008). The oldest record of small mussels from the wood-fall communities has been found from the upper Eocene part of the Lincoln Creek Formation (Kiel and Goedert, 2006). Adding to the previous Paleocene fossil records, this study also confirms that small bathymodioline mussels in the chemosynthetic communities did not appear in the Paleocene.

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