PALEOCENE PROTOBRANCH BIVALVES FROM URAHORO TOWN IN EASTERN HOKKAIDO, NORTHERN JAPAN

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Abstract *Eleven protobranch species are described from deep-sea deposits of the Paleocene Katsuhira Formation. Among them, one new genus and three new species are included; Meganuculana n. gen., M. alleni n. sp., Neilonella alleni n. sp. and Tindaria paleocenica n. sp. Acila (Truncacila) hokkaidoensis, Pristigloma? sachalinensis, Ezonuculana and Menneroctenia survived the End-Cretaceous Mass Extinction and became extinct by the end of Paleocene. Such a pattern of extinction is similar to that of the deep-sea benthonic foraminifers.*

Key words *Paleocene, protobranch bivalves, deep sea, Hokkaido, Japan*

Introducion

Protobranch bivalves include many deep-sea deposit feeders and chemosymbiotic species (e.g. Dame, 1996). By examining their molecular phylogeny, it has been elucidated that they consist of three orders, the chemosymbiotic taxa, Solemyoida Dall, 1889, and the deposit feeders Nuculida Dall, 1889 and Nuculanida Carter, Campbell & Campbell, 2000 (Sharma *et al*., 2013). According to Sharma *et al*. (2013), Nuculida consists of one family, Nuculidae. On the other hand, Nuculanida consists of two superfamilies and nine families, including families Malletiidae H. & A. Adams, 1858, Neilonellidae Schileyko, 1989, Nuculanidae H. & A. Adams, 1858, Tindariidae Verrill & Bush, 1897, and Sareptidae Stoliczka, 1870 treated herein. Sato & Sasaki (2015) supported this classification of higher taxa, based on shell microstructure.

Paleocene fossils have been recorded in the Russian Far East from South Sakhalin, western Kamchatka, the Ilpinskyi Peninsula of eastern Kamchatka, and the Koryak Upland (Dvjatilova & Volobueva, 1981; Kalishevich *et al*., 1981; Volobueva *et al*., 1994; Gladenkov *et al*., 1997). In contrast, there are few Paleocene molluscan records from Hokkaido and Shikoku. Ando *et al.* (2001) and Ando & Tomosugi (2005) recorded only *Glycymeris* sp. from the Paleocene part of the Hakobuchi Formation in the Nakatonbetsu area of northern Hokkaido. Kano *et al.* (2003) listed some protobranchs identified as *Acila* sp., *Nucula* sp. and *Portlandi*a sp. from the Paleocene part of the Domeki Formation in Shikoku. Recently, three new species have been described from the Paleocene Katsuhira Formation in eastern Hokkaido by the authors: the aporrhaid gastropod *Kangilioptera inouei* Amano & Jenkins, the doubtful buccinid *Urahorosphaera kanekoi* Amano & Oleinik and the arcid bivalve *Bentharca steffeni* Amano, Jenkins & Nishida (Amano & Jenkins, 2014; Amano & Oleinik, 2015; Amano *et al*., 2015). They were collected mainly from calcareous concretions with many plant fragments included in mudstone. Many specimens of protobranch bivalves have also been recovered from these concretions and host rock mudstone. In this paper, we describe these protobranchs and discuss their evolutionary significance.

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Material

Many protobranch specimens were recovered at 29 localities in the upper part of the Katsuhira Formation (Oda *et al*., 1959), in eastern Hokkaido, northern Japan (Fig. 1). Eleven species have been identified (Table 1; Figs 2–41). The age of the upper part of the formation was assigned to the early Selandian, based on planktonic foraminifer and calcareous nannofossil biostratigraphy (Kaiho, 1984).

All specimens are stored at the Joetsu University of Education (JUE).

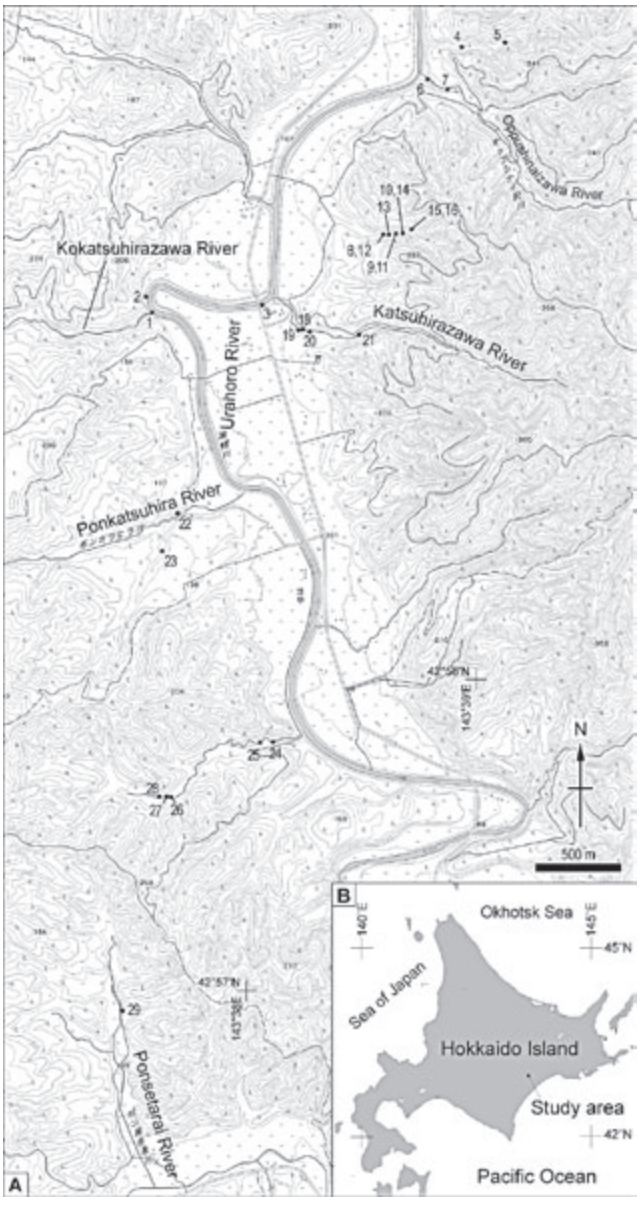


Figure 1 Collection localities for protobranch bivalves (based on the topographical map of "Katsuhira", scale 1:25,000, published by the Geographical Survey Institute of Japan).

Table 1 List of protobranch bivalves from the Katsuhira Formation. Number in the list shows individuals.

Species Loc.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Leionucula yotsukurensis (Hirayama)	12		3	1			1			7	1		2	1	6	1	1	1	1	8	5							
Acila (*Truncacila*) *hokkaidoensis* (Nagao)	11	2	1		2	12			1			1					3				3					1		12
Ezonuculana aff. *obsoleta* Tashiro	2	4																											
Maganuculana alleni sp. nov.										3								1		1				1			2		
Malletiaporonaica (Yokoyama)								1		1																		2	
M. sp.																				2					1				
Mennerocteni a plena Kalishevich	4	6											1							1									2
Neilonella alleni sp. nov.			1																		9								
Pseudoneilonella? sp.																													4
Pristigloma? *sachalinensis* Salnikova																						1		1		1	1		4
Tindaria paleocenica sp. nov.										4												5	3			1		3	4

SYSTEMATICS

Class Bivalvia
Order Nuculida Dall, 1889
Superfamily Nuculoidea Gray, 1824
Family Nuculidae Gray, 1824
Genus ***Leionucula*** Quenstedt, 1930
Type species: *Nucula albensis* d'Orbigny, 1844

Leionucula yotsukurensis (Hirayama, 1958)
Figs 2–4

Nucula ventricosa Hirayama, 1955, p. 77–78, pl. 1, figs. 12–15 (junior homonym).

Nucula yotsukurensis Hirayama, 1958, p. 96.
Ennucula yotsukurensis (Hirayama). Kamada, 1962, p. 43–44; Nemoto & O'Hara, 1979, pl. 1, fig. 1.
?*Leionucula naibensis* Kalishevich, 1969, p. 22–23, pl. 2, fig. 3; Kalishevich *et al.*, 1981, p. 95–96, pl. 12, fig. 5.

Material In total 51 specimens from the following 15 localities: Loc. nos. 1, 3, 4, 7, 10, 11, 13, 14, 15, 16, 17, 18, 19, 20, 21. Of these, 11 specimens are well preserved and could be measured.

Dimensions See Table 2.

Remarks This species was originally described as *Nucula ventricosa* by Hirayama (1955), based on specimens from the lower Oligocene Asagai Formation in the Joban coal field. Later, Hirayama (1958) noticed that this name was preoccupied by many authors and proposed *N. yotsukurensis* as a new name. The present species is characterized by its small to medium size (up to 15mm in length for the type specimens), its trigonally ovate shape, its umbo near the posterior end and its escutcheon demarcated by a rounded ridge. Most specimens obtained from the Katsuhira Formation are small, less than 15mm long like the type specimen, but they attain up to 19.6mm.

Leionucula naibensis Kalishevich, 1969 was proposed from the lower Paleocene Sinegorsk Formation in the area along the Naiba River in South Sakhalin. Kalishevich *et al.* (1981) described this species by reproducing the original picture. This species is probably a synonym of *L. yotsukurensis* because it shares a medium-sized (up to 21mm in length), trigonally ovate shell with a demarcated escutcheon.

Leionucula formosa was originally described by Nagao (1930) as a species of *Nucula* from the Upper Cretaceous Himenoura Group in Kyushu. Topotype specimens were re-examined by Tashiro (1976). Although this species is very similar to *L. yotsukurensis,* it can be distinguished from the latter by having an acute angle at the posterior end and a narrower escutcheon.

Stratigraphic and geographic range Paleocene Katsuhira Formation in eastern Hokkaido and Sinegorsk Formation (?) in South Sakhalin; lower Oligocene Asagai Formation in the Joban coal field.

Genus ***Acila*** H. Adams & A. Adams, 1858
Subgenus ***Truncacila*** Schenck in Grant & Gale, 1931
Type species: *Nucula castrensis* Hinds, 1843

Acila* (*Truncacila*) *hokkaidoensis (Nagao, 1932)
Figs 5–7

Nucula (*Acila*) *hokkaidoensis* Nagao, 1932, p. 28–29, pl. 5, figs. 17, 18; Nagao & Otatume, 1938, p. 37, pl. 1, fig. 1.
Acila (*Truncacila*) *hokkaidoensis* (Nagao). Schenck, 1936, p. 52; Nagao & Huzioka, 1941, p. 118–119; Tashiro, 1976, p. 35–36, pl. 1, fig. 11 (*non* figs 12–15); Hayami, 1975, p. 21; Salnikova, 1987, pl. 20, figs. 5, 6; Tashiro, 1992, p. 24–25, pl.1–11; Kiel *et al*., 2008, p. 529–530, fig. 4A.

Table 2 Dimensions of *Leionucula yotsukurensis* (Hirayama) *PL= posterior length.

Specimens	Length (mm)	Height (mm)	PL*	Width (mm)	Valve	Loc.
JUE no. 15946	19.6	13.9	5.7	8.2	Both	1
JUE no. 15947	7.2	5.5	2.1	–	Left	3
JUE no. 15948–1	11.5	10.9	2.0	–	Both	10
JUE no. 15948–2	10.3	8.4	1.5	5.5	Both	10
JUE no. 15949	11.0	7.7	3.0	–	Right	19
JUE no. 15950–1	13.7	11.0	1.9	6.5	Both	20
JUE no. 15950–2	15.3	11.3	2.9	7.8	Both	20
JUE no. 15950–3	14.1	11.5	1.9	8.0	Both	20
JUE no. 15950–4	9.7+	8.0	–	4.6	Both	20
JUE no. 15950–5	12.6	9.0	2.4	–	Left	20
JUE no. 15951	11.7	8.1	2.2	–	Right	21

Acila (*Truncacila*) *longa* Kalishevich, 1969, p. 28, 31, pl. 1, figs 10–11; Kalishevich *et al*., 1981, p. 102–103, pl. 13, figs. 6, 7.
Acila (*Truncacila*) *pecticostata* Kalishevich, 1969, p. 32–33, pl. 2, figs. 12–14; Kalishevich *et al*., 1981, p. 104, pl. 13, figs. 10–12.
Acila (*Truncacila*) *vereshagini* Kalishevich, 1969, p. 33–35, pl. 2, fig. 15; Kalishevich *et al*., 1981, p. 104–106, pl. 13, figs. 13–14.
Acila (*Truncacila*) *victoriensis* Salnikova, 1980, p. 22–23, pl. 8, figs. 4–9; Salnikova, 1987, pl. 20, figs 7–9.

Material In total 49 specimens from Loc. nos. 1, 2, 3, 5, 6, 9, 12, 17, 21, 27, 29. Among these, four specimens are well preserved and were measured.

Dimensions JUE no. 15952–1, length, 11.5mm, height, 8.6mm; JUE no. 15952–2 length, 11.2mm, height, 7.8mm; Loc. 1. JUE no. 15953, length, 10.9mm, height, 7.8mm; Loc. 9. JUE no. 15954, length, 22.5mm, height, 18.8mm; Loc. 29.

Remarks The present species has been known only from the Upper Cretaceous (Coniacian to Maastrichtian) formations in northern Japan (Nagao & Otatume, 1938; Tashiro, 1992; Kiel *et al*., 2008). As described and discussed in detail by Kiel *et al*. (2008), it is characterized by a medium-sized elongate shell (up to 30mm in length) and by its ribs diverging once near the anterior extremity.

In the Naiba area of South Sakhalin, Kalishevich (1969) proposed *Acila* (*Truncacila*) *longa* and *A.* (*T.*) *pecticostata* from the lower Paleocene Sinegorsk Formation and *A.* (*T.*) *vereshagini* from the Maastrichtian Krasnoyarsk Formation. These species can be synonymized with the present species because they have small to medium-sized shells and ribs diverging once near the anterior end. Moreover, despite its type locality being located nearby in Hokkaido, he did not compare his three species with *A.* (*T.*) *hokkaidoensis*. Salnikova (1980) proposed *A. (T.) victoiensis* from South Sakhalin. She distinguished this species from *A.* (*T.*) *hokkaidoensis* by having a more quadrate outline, and a larger and more inflated shell with the bifurcation of the ribs located closer to the anterior end. However, these differences are included in the variation of *A.* (*T.*) *hokkaidoensis.*

Stratigraphic and geographic range Late Cretaceous (Coniacian to Maastrichtian), Krasnoyarsk Formation in South Sakhalin; Upper Yezo Group and Hakobuchi Formation in Hokkaido; Kuji Group and Sawameguri Formation in Iwate Prefecture; Futaba Group in Fukushima Prefecture. Paleocene Sinegorsk Formation in South Sakhalin and Katsuhira Formation in Hokkaido.

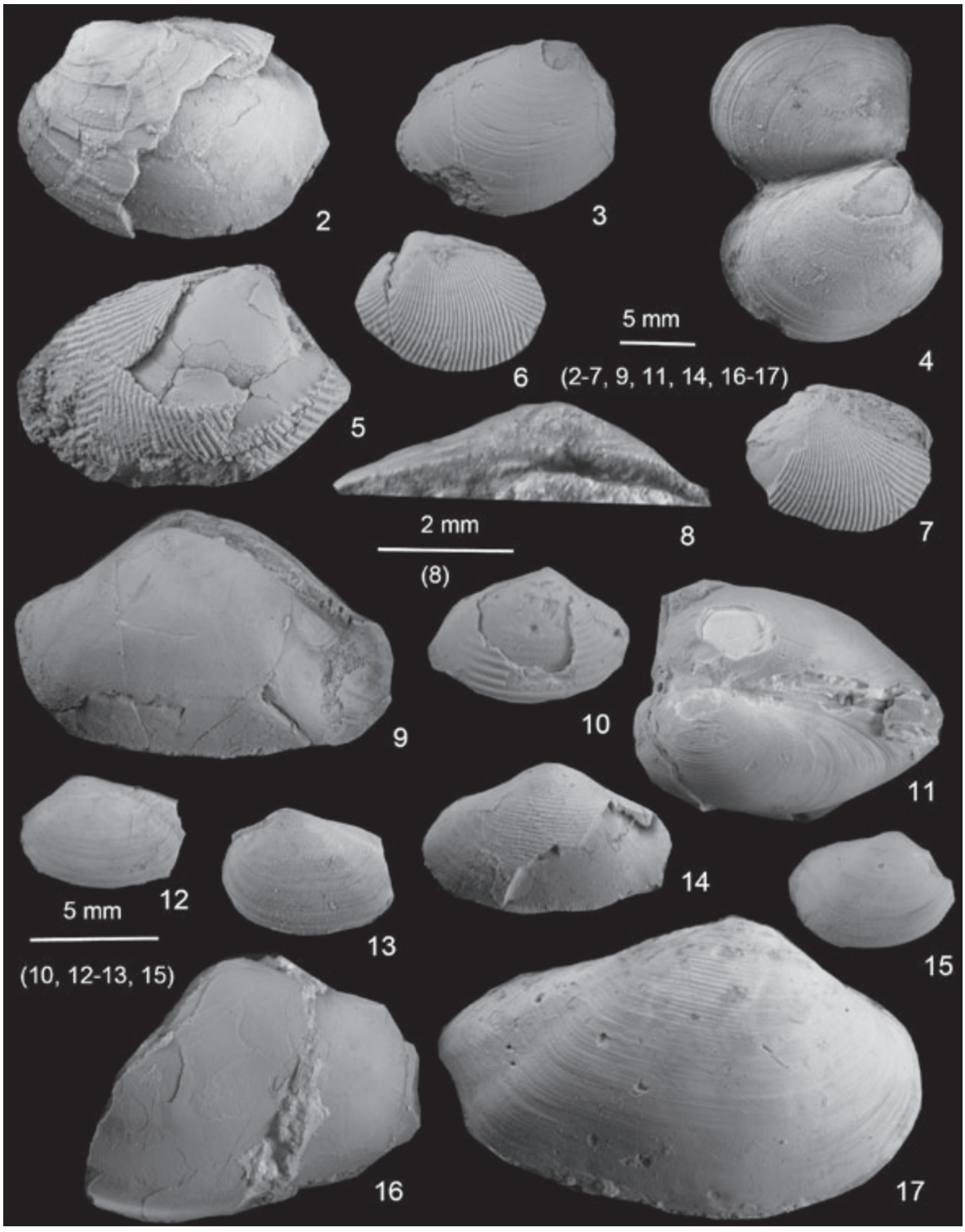
Order Nuculanida Carter, Campbell & Campbell, 2000
Superfamily Nuculanoidea H. & A. Adams, 1858
Family Nuculanidae H. & A. Adams, 1858
Subfamily Nuculaninae H. & A. Adams, 1858
Genus ***Ezonuculana*** Nagao, 1938
Type species: *Nuculana mactraeformis* Nagao, 1932

Ezonuculana aff. ***obsoleta*** Tashiro, 1976
Figs 9, 14

Material Six specimens from Loc. nos. 1, 2. Among them, one specimen is rather well preserved.

Dimensions JUE no. 15955, length, 29.5mm, height, 16.8mm; Loc. 1. JUE no. 15956–1, length, 23.0mm, height, 15.3mm, width, 11.8mm (without shell); JUE no.15956–2 length, 14.2mm, height, 8.9mm; JUE no. 15956–3, length, 5.7mm, height, 3.9mm; Loc. 2.

Description Shell thick, elongate triangular, large for genus (internal mould up to 29.5mm in length), well inflated, equilateral and equivalve. Umbo not very prominent, situated almost in centre of dorsal margin. Antero-dorsal margin nearly straight, continuing to rounded anterior margin; postero-dorsal margin very slightly concave and forming blunt angle with subtruncated posterior margin; ventral margin nearly straight to broadly arched. Blunt ridge running from umbo to posterior corner. Surface smooth except for fine commarginal riblets near umbo. Posterior teeth small, more than 12; more than six anterior teeth, larger than posterior ones; resilium very small and shallow. Anterior adductor muscle scar subquadrate; posterior adductor muscle scar slightly smaller than anterior one, semi-elliptical. Pallial sinus indistinct but shallow. Inner ventral margin smooth.



Figures 2–4 *Leionucula yotsukurensis* (Hirayama); **2.** Right valve, JUE no. 15946, Loc. 1; **3.** Left valve, JUE no. 15950, Loc. 10; **4.** Two valves spread apart, JUE no. 15950, Loc. 20. **Figures 5–7.** *Acila* (*Truncacila*) *hokkaidoensis* (Nagao); **5.** Left valve, JUE no. 15952–3, Loc. 1; **6.** Right valve, JUE no. 15952–1, Loc. 1; **7.** Right valve, JUE no. 15952–2, Loc. 1. **Figures 8, 11–13, 16, 17.** *Meganuculana alleni* sp. nov.; **8.** Hinge of left valve, paratype, JUE no. 15960, Loc. 24; **11.** Dorsal view of anterior part, paratype, JUE no. 15958–1, Loc. 27; **12.** Left valve, paratype, JUE no. 15959, Loc. 20; **13.** Left valve, paratype, JUE no. 15960, Loc. 24; **16.** Posterior part of left valve, paratype, JUE no. 15958–2, Loc. 27; **17.** Right valve, holotype, JUE no. 15957, Loc. 17. **Figures 9, 14.** *Ezonuculana* aff. *obsoleta* Tashiro; **9.** Interior surface of left valve, JUE no. 15956–1, Loc. 2; **14.** Left valve, JUE no. 15956–2, Loc. 2. **Figure 10.** *Pseudoneilonella*? sp. Right valve, JUE no. 15974–1, Loc. 29. **Figure 15.** *Malletia poronaica* (Yokoyama) Right valve, JUE no. 15962, Loc. 28.

Remarks The present species is very similar to *Ezonuculana obsoleta* Tashiro, 1976 from the upper Campanian Member U-IIb of the Himenoura Group in Kyushu. However, the present material is slightly different in having a larger (up to 17.9mm in *E. obsoleta*) and lower shell (H/L=0.57–0.67; 0.66–0.75 for *E. obsoleta*). Although Tashiro (1976) described the pallial sinus of *E. obsoleta* as "pallial line simple" (implying that it probably had no pallial sinus), the paratype specimen KE 2055 has a small pallial sinus in front of the posterior adductor muscle scar. In this character, there is no difference between the Paleocene species and *E. obsoleta*.

Stratigraphic and geographic range Only from Katsuhira Formation in Hokkaido.

Genus ***Meganuculana*** n. gen.
Type species: *Meganuculana alleni* n. sp. (this paper)

Diagnosis Large, moderately inflated, elongate shell sculptured with many fine commarginal grooves on upper half of disc. Two ridges running from umbo to posterior end and to postero-ventral corner. Posterior outline concave. Hinge consisting of two series of taxodont teeth and small resilium. Escutcheon flat, bounded by sharp ridge; lunule slightly depressed, narrow, lanceolate, bounded by blunt ridge. Pallial sinus obscure but seems to be shallow.

Description Shell large, to 32.0mm long, rather thick, elongate, rostrate, with porcellanous inner layer, moderately inflated, equivalve, inequilateral. Antero-dorsal margin broadly arched, continuing to semicircular anterior margin; ventral margin broadly rounded; posterior margin concave, posterior end pointed, continuing to rather straight postero-dorsal margin. Two ridges running from umbo to posterior end and postero-ventral corner; both blunt in holotype but sharp in smaller paratype specimens. Umbo prominent, rather prosogyrate, located at anterior one-third of shell length. Surface sculptured with fine, distinct commarginal grooves; grooves distinct on only upper half of holotype but over whole surface of smaller paratype specimens. Escutcheon flat, bounded by sharp ridge; lunule slightly depressed, narrow, lanceolate, bounded by blunt ridge. Hinge plate narrow with two series of small teeth; 11 anterior teeth; 16 posterior teeth. Posterior adductor muscle scar small, ovate. Pallial sinus obscure but seems to be shallow.

Comparison The present new genus differs from *Nuculana* Link, 1807 in having a large shell with a straight postero-dorsal margin, a broadly arched ventral margin and a concave posterior margin. Some species of the genus *Ledella* Verrill & Bush, 1897 resemble this new genus. However, *Ledella* easily can be distinguished from the present new genus by having a minute shell (a few mm in length), a wider resilium, a pointed posterior end, an opisthogyrate umbo and fewer teeth.

Meganuculana alleni n. sp.
Figs 8, 11–13, 16, 17

Type material Holotype, JUE no. 15957, Loc. 27; Paratype, JUE no. 15958, Loc. 27; Paratype, JUE no. 15959, Loc. 20; Paratype, JUE no. 15960, Loc. 24.

Type locality 0.9km upstream from Ponkatsuhira-minami-zawa (Loc. 27); Katsuhira Formation.

Dimensions Holotype, JUE no. 15957, length, 32.0mm, height, 19.6mm, Loc. 27; Paratype, JUE no. 15959, length, 5.4 mm+, height, 4.9mm, width 3.0mm, Loc.20; Paratype, JUE no. 15960, length, 6.8 mm+, height, 4.7mm, Loc. 24.

Diagnosis & *Description* Same as for the genus.

Etymology Named for John A. Allen (Emeritus Professor of Marine Biology, University of London).

Comparison *Meganuculana alleni* n. sp. can be separated from *Nuculana pernula* (Müller, 1779), the type species of the genus *Nuculana* Link, 1807 by having a larger but less elongate shell with a straight postero-dorsal margin, a weakly pointed posterior end and a shallowly concave postero-ventral margin. The shell outline of *Ledella bernardi* (Dautzenberg & Fischer, 1897) is somewhat similar to that of the present new species. However, *L. bernardi* differs from the present new species in being much smaller (up to 9.4mm; La Perna, 2008), with a less inflated shell, a more produced posterior end, a centrally located opisthogyrate umbo and a wider resilium.

Stratigraphic and geographic range Paleocene Katsuhira Formation in eastern Hokkaido.

Family Malletiidae H. Adams & A. Adams, 1858
Genus ***Malletia*** des Moulins, 1832
Type species: *Malletia chilensis* des Moulins, 1832

Malletia poronaica (Yokoyama, 1890)
Figs 15, 18

Nucula poronaica Yokoyama, 1890, p. 195–196, pl. 25, figs. 3a–c.
Malletia poronaica (Yokoyama). Kanehara, 1937, p. 159, pl. 15, figs.1–4; Uozumi, 1952, p. 20, pl. 16, figs. 122a,b, 123, 124; Takeda, 1953, p. 72, pl. 8, figs. 2–10; Honda, 1989, p. 49, pl. 1, figs. 1, 2, 3, 6; Gladenkov *et al*., 1991, p.150, pl. 28, fig. 19a, b; Amano & Jenkins, 2007, fig. 4C.
Neionella poronaica (Yokoyama). Oyama, 1951, pl. 6, fig. 1; Oyama *et al*., 1960, p. 87–88, pl. 19, figs. 2a–d.
? *Malletia* (*Minormalletia*) *poronaica* (Yokoyama). Shikama & Kase, 1976, p. 15–16, pl. 1, fig. 3.
Malletia (*Malletia*) *poronaica* (Yokoyama). Devyatilova & Volobueva, 1981, p. 20, pl. 18, fig. 5.
Malletia convexa Kalishevich in Kalishevich *et al*., 1981, p. 91–92, pl. 11, figs. 8–12.

Material Four specimens from Loc. nos. 8, 10, 28.

Dimensions JUE no. 15961, length, 6.8 mm+; height, 4.8mm; Loc. 8. JUE no. 15962, length, 6.1mm; height, 4.0mm; Loc. 28.

Remarks Our specimens are characterized by their small, elliptical, moderately inflated shell, the anteriorly situated beak, the subtruncated posterior margin and fine growth lines. They are probably young shells of *Malletia poronaica* (Yokoyama) whose length attains to 20mm in adult. Kalishevich in Kalishevich *et al.* (1981) described and illustrated *Malletia convexa* as a new species from the lower Paleocene middle part of Sinegorsk Horizon in the Naiba and Krasnoyarsk River area, South Sakhalin. Despite the characteristics of his species coinciding exactly with those of the present species, he did not compare *M. convexa* with *M. poronaica*, but only with *M. inermis* (Yokoyama, 1925). Thus, it is possible that *Malletia convexa* is a junior synonym of *M. poronaica*.

Stratigraphic and geographic range Paleocene Sinegorsk Horizon (middle part) in South Sakhalin and Katsuhira Formation in eastern Hokkaido. Upper Eocene Olkhovskya Bed in the Koryak Upland, Poronai and Tappu Formations in central to northwestern Hokkaido. Lower Oligocene Nuibetsu Formation in eastern Hokkaido. ? Early Miocene Morozaki Group (Yamami Formation) in Aichi Prefecture, central Honshu.

Malletia sp.
Fig. 19

Material Three specimens from Loc. nos. 20, 25.

Dimensions JUE no. 15963, length, 10.9mm; height, 6.4mm; Loc. 20. JUE no. 15964, length, 10.4mm; height, 5.5mm; Loc. 25.

Remarks The available specimens differ from *Malletia poronaica* in having a less inflated and lower shell. Although they resemble *Portlandia* in shape, the hinge seems to lack a resilium.

Genus ***Menneroctenia*** Kalishevich, 1973
Type species: *Menneroctenia ornata* Kalishevich, 1973

Cnestriella Tashiro & Otsuka, 1980, p. 47–48.

Remarks This genus was proposed by Kalishevich (1973) based on specimens from the Mastrichtian and Paleocene formations in South Sakhalin. It resembles *Portlandia* Mörch, 1857 in outline but has oblique ridges crossing the growth lines like those of *Cnesterium* Dall, 1898. However, it differs from yoldiids, including *Cnesterium*, by having no resilium under the umbo. Tashiro & Otsuka (1980) proposed *Cnestriella* as a subgenus of *Portlandia*, based on *Portlandia cunesteriata* Ichikawa & Maeda, 1958 from the Maastrichtian part of the Izumi Group. However, Ichikawa & Maeda (1958) did not describe the interior structure. When Tashiro & Otsuka (1980) proposed the new subgenus, they described *P. cunesteriata* from the Maastichtian Himenoura Group in Kyushu. During our examination of the hinge of their specimens, we found two specimens with continuous anterior and posterior teeth series. Judging from this hinge, *Cnestriella* belongs in Malletiidae and is a junior synonym of *Menneroctenia* Kalikevich, 1973. Although Kalishevich *et al.* (1981) considered this genus to be a junior synonym of *Multidentata* Krishtofovich, 1964, the latter "genus" can be separated from the former by having a prominent,

blunt ridge extending from the umbo to the postero-ventral corner and many lamellate commarginal ribs. As shown by Amano *et al*. (2000), *Multidentata* must be treated as a subgenus of *Neilo* A. Adams, 1854.

Menneroctenia plena Kalishevich, 1973
Figs 21, 22, 25, 28

Menneroctenia plena Kalishevich, 1973, p. 25, pl. 1, fig. 4.
Multidentata plena (Kalishevich, 1973). Kalishevich *et al*., 1981, p. 87–88, pl. 10, figs. 8–11.

Material In total thirteen specimens from localities nos. 1, 2, 13, 29. Among these, eight specimens are well preserved and were measured.

Dimensions JUE no. 15965–1, length, 13.9mm, height, 8.5mm; JUE no. 15965–2, length, 20.7mm, height, 12.5mm; JUE no. 15965–3, length, 16.2mm, height, 11.1mm; JUE no. 15965–4, length, 12.9mm, height 7.9mm; Loc. 1. JUE no. 15966–1, length, 15.8mm, height, 9.8mm; JUE no. 15966–2, length, 14.9mm, height, 8.4mm; Loc. 2. JUE no. 15967–1, length, 12.6 mm+, height, 7.9mm; JUE no.15967–2, length, 5.9mm, height, 3.6mm; Loc. 29.

Remarks The species from Katsuhira has a *Portlandia*-like shell with oblique lines crossing the growth lines over the posterior part. The ratio of shell height to length is about 0.61–0.62. The umbo is located at the anterior third of the shell length. The pallial sinus is small but deep. The hinge consists of anterior and posterior taxodont teeth. From these characters, the Katsuhira species can be safely identified as *Menneroctenia plena* Kalishevich, 1973.

Stratigraphic and geographic range Paleocene Sinegorsk Horizon (middle part) in South Sakhalin and Katsuhira Formation in eastern Hokkaido.

Family Neilonellidae Schileyko, 1989
Genus ***Neilonella*** Dall, 1881

Neilonella alleni n. sp.
Figs 20, 23, 24

Type material Holotype, JUE no. 15969; Paratype, JUE nos. 15970–1, 2, 3, 4, Loc. 21.

Type locality 550m upstream of Katsuhira-zawa (Loc. 21=Loc. 6 of Amano and Jenkins, 2014); Katsuhira Formation.

Material examined In total eleven specimens were collected from Loc. 3, 20, 21. Among these, seven specimens are well-preserved and were measured.

Dimensions Holotype, JUE no. 15969, length, 5.4mm, height, 4.0mm; Loc. 21. Paratype, JUE no. 15970–1, length, 6.0mm, height, 4.3mm; JUE no. 15970–2, length, 5.9mm, height, 4.8mm; JUE no.15970–3, length, 5.8mm, height, 4.2mm; JUE no. 15970–4, length, 7.9mm, height, 5.0mm; Loc. 21. JUE no. 15972, length, 5.2mm, height, 4.0mm; Loc. 3. JUE no. 15973, length, 5.5mm, height, 3.9mm; Loc. 20.

Diagnosis Small, moderately inflated, ovate shell sculptured with many fine, flat commarginal riblets. Posterior margin narrowly rounded, not pointed. Hinge consisting of two series of taxodont teeth and no resilium. Pallial sinus shallow, continuing to quadrate anterior adductor scar.

Description Shell small (up to 7.9mm long), ovate, moderately inflated, equivalve. Antero-dorsal margin rather straight, continuing to well-rounded anterior end; postero-dorsal margin straight, gently sloping, making right angle with subtruncated posterior margin; ventral margin broadly arcuate. Umbo located at anterior two-fifth to half of shell length, slightly protruding. Surface of shell sculptured with fine, flat commarginal riblets; riblets distinct on central part, becoming obscure near dorsal margin. Hinge consisting of two taxodont series without resilium; eight anterior teeth, 12 smaller posterior teeth. Pallial sinus shallow, continuing to quadrate posterior adductor scar.

Etymology Named for John A. Allen (Emeritus Professor of Marine Biology, University of London).

Comparison This new species is similar to so-called *Nuculana* (*Borissia*) species from the Russian Far East in having a shorter posterior part than other *Nuculana* species. However, as pointed by Kafanov *et al*. (2000, p. 59), this species group belongs in *Neilonella*. Among them, *Neilonella alferovi* (Slodkewitsch, 1938) most

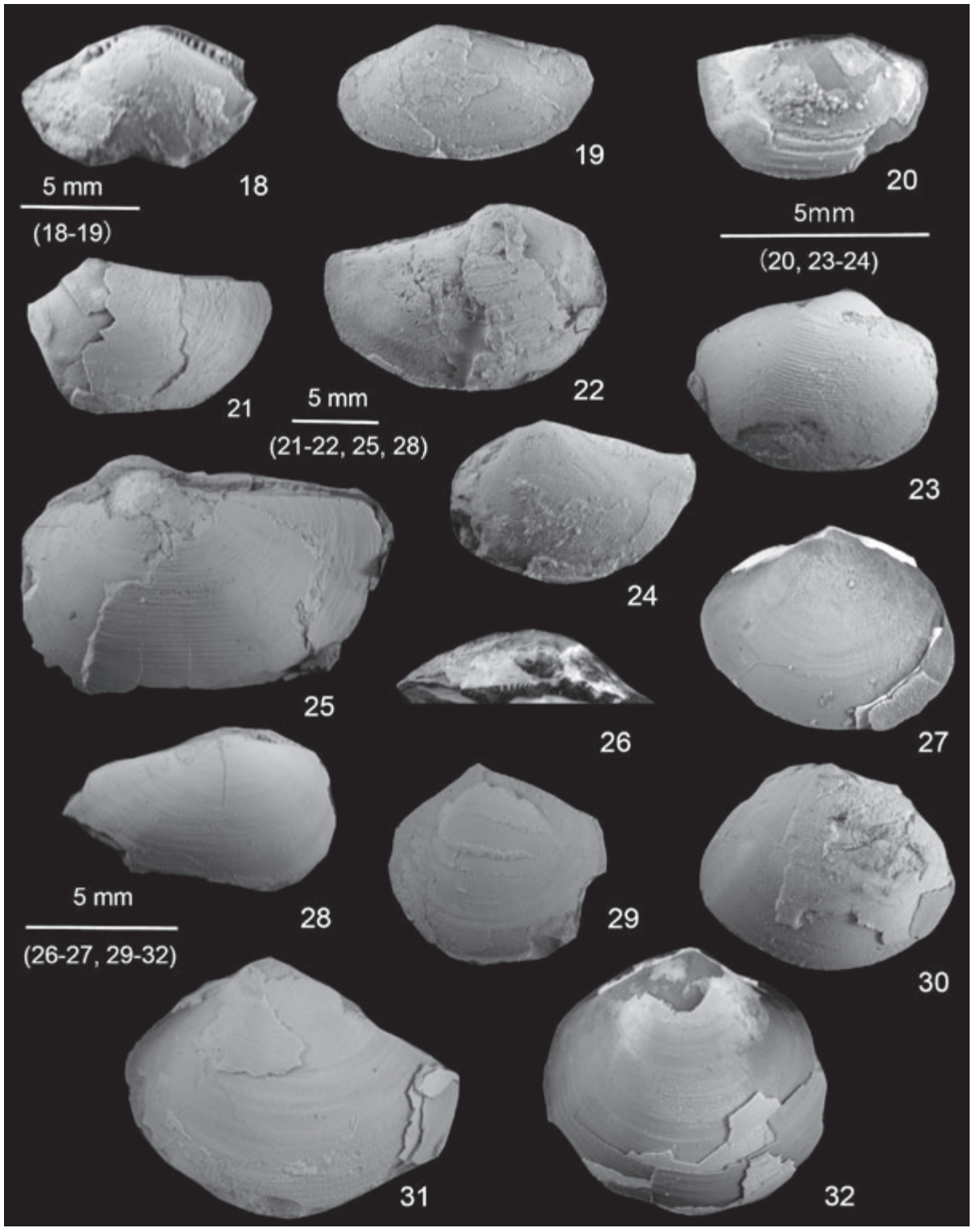


Figure 18 *Malletia poronaica* (Yokoyama) Hinge of left valve, JUE no. 15968, Loc. 10. **Figure 19.** *Malletia* sp. Left valve, JUE no. 15963, Loc. 20. **Figures 20, 23, 24.** *Neilonella alleni* sp. nov.; **20.** Right valve, JUE no. 15972, Loc. 3; **23.** Right valve, holotype, JUE no. 15969, Loc. 21; **24.** Left valve, paratype, JUE no. 15970–2, Loc. 21. **Figures 21, 22, 25, 28.** *Menneroctenia plena* Kalishevich; **21**. Left valve, JUE no. 15965–1, Loc. 1; **22.** Right valve, JUE no. 15965–3, Loc. 1; **25.** Left valve, holotype, JUE no. 15965–2, loc. 1; **28.** Right valve, JUE no. 15967–1, Loc. 29. **Figure 26, 27, 29–32.** *Pristigloma*? *sachalinensis* Salnikova; **26**. Hinge of left valve, **27**. Right valve, **30.** Left valve, JUE no. 15976, Loc. 29; **29.** Left valve, JUE no. 16975, Loc. 24; **31.** Right valve, JUE no. 15977–2, Loc. 29; **32.** Right valve, JUE no. 15977–1, Loc. 29.

closely resembles the new species. *N. alferovi* was described from the uppermost lower to lowest middle Miocene Tjushevskaya Formation in eastern Kamchatka and the lower Miocene Kholmsk and Nevelsk Formations in South Sakhalin. However, *N. alferovi* is larger (more than 10mm in length), with a more protruding umbo and a pointed anterior end.

Neilonella polunini (Devjatilova in Devjatilova & Volobueva, 1981), described from the upper Eocene Unelskaya Formation in Penjinsk Inlet, has a similar small shell and outline to the present new species. Its pointed posterior end, slightly concave posterior margin and produced umbo enable us to separate two species.

Stratigraphic and geographic range Paleocene Katsuhira Formation in eastern Hokkaido.

? Genus ***Pseudoneilonella*** Laghi, 1986
Type species: *Nucula pusio* Philippi, 1844

Remarks According to La Perna (2007), the oldest record of this genus dates back to the middle Miocene. This genus is characterized by a small ovate-trigonal shell with opisthogyrate umbo, a single series of hinge teeth, an opisthodetic ligament and a wide pallial sinus.

Pseudoneilonella? sp.
Fig. 10

Material Four specimens from Loc. no. 29.

Dimensions JUE no. 15974–1, length, 6.1mm, height, 4.2mm; JUE no. 15974–2, length, 7.3mm, height, 5.0mm; JUE no. 15974–3, length, 5.5mm, height, 3.6mm; JUE no. 15974–4, length, 7.5 mm+, height 5.5mm; Loc. 29.

Description Shell large for genus, to more than 7.5mm long, rather thick, elongate triangular, weakly inflated. Antero-dorsal margin broadly arched, with rounded anterior margin; postero-dorsal margin nearly straight; ventral margin broadly arched; posterior margin subtruncated, making obtuse angle with postero-dorsal margin. Blunt ridge running from umbo to postero-ventral corner. Umbo opisthogyrate, located at anterior two-fifth of shell length. Lunule very small, shallow. Surface sculptured with coarse, prominent commarginal ribs, obscure near anterior and posterior margins. Hinge plate narrow, bearing small chevron-shaped teeth without resilium; 15 anterior teeth, more than 15 posterior teeth. Inner ventral margin smooth. Anterior adductor muscle scar triangular, crenulated by fine threads; posterior adductor scar elliptical. Pallial sinus shallow and wide.

Remarks This species has a similar shell outline to *Pseudoneilonella* species. Among these, *P. taurinensis* La Perna, 2007 from the middle Miocene deposits of the Turin Hills, northwestern Italy, is the most closely similar species. However, the present species differs from species of *Pseudoneilonella* by its slightly larger (up to 6.4mm in length for *Pseudoneilonella*) and less inflated shell with coarser commarginal ribs. Added to these differences, the fossil records of *Pseudoneilonella* date back to only the middle Miocene in the Mediterranean area. For these reasons, the present species cannot be definitely classified into *Pseudoneilonella.* Further research on Neilonellidae is required to define the range of *Pseudoneilonella*.

Family Pristiglomidae Sanders & Allen, 1973
?Genus ***Pristigloma*** Dall, 1900
Type species: *Glomus nitens* Jeffreys, 1876

Pristigloma? sachalinensis (Salnikova, 1987)
Figs 26, 27, 29–32

"*Sarepta*" *sachalinensis* Salnikova, 1987, p. 134, pl. 21, figs. 10–13.
"*Sarepta*" *sachalinensis glomusiformis* Salnikova, 1987, p. 134, pl. 21, fig. 11.
"*Sarepta*" *sachalinensis* Salnikova, 1987, p. 134–135, pl. 21, figs. 12.

Material In total eight specimens from localities 22, 24, 26, 27, 29. Among them, three specimens are well preserved and were measured.

Dimensions JUE no. 15975, length, 6.4mm, height, 5.0mm, Loc. 24. JUE no. 15976, length, 7.5mm, height 6.1mm, Loc. 27. JUE no. 15977, length, 8.4 mm+, height, 8.3mm, Loc. 29.

Remarks This species is characterized by its weakly inflated, ovate shell, resembling tellinids. The shell surface is smooth except for fine growth lines. The umbo is located at about the centre of the length or is slightly posteriorly located. The hinge consists of anterior and posterior taxodont teeth series with a small resilium. Both adductor scars are ovate. The pallial line is entire. From

these characters, the Katsuhira species can be identified as *Pristigloma*? *sachalinensis* (Salnikova, 1987), described from Maastrichtian deposits in the Naibuchi area of South Sakhalin. Salnikova (1987) separated the species into two species and one subspecies by their shell outline. However, these differences can safely be included in the variation of one species. Moreover, she described this species doubtfully under the genus "*Sarepta*". *Sarepta speciosa* A. Adams, 1860, the type species of the genus, has a larger shell (maximum shell length 12.4mm), a narrow anterior part, and a very shallow pallial sinus. Both Sakhalin and Hokkaido specimens have a smaller and more rounded shell more nearly resembling those of species of *Pristigloma* Dall, 1900. Although we tentatively include this species in *Pristigloma* rather than in *Sarepta*, some characters of *Pristigloma*, such as its elongate resilium and shallow pallial sinus (see Okutani & Kawamura, 2002), cannot be observed in the present material.

Stratigraphic and geographic range Maastrichtian in South Sakhalin and Paleocene Katsuhira Formation in eastern Hokkaido.

Family Tindariidae Verrill & Bush, 1897
Genus ***Tindaria*** Bellardi, 1875
Type species: *Tindaria arata* Bellardi, 1875

Tindaria paleocenica n. sp.
Figs 33–41

Type material Holotype, JUE no. 15978, Loc. 10. Paratype, JUE no. 15979, Loc. 10; Paratype, JUE nos. 15980–1, 2, 3, Loc. 29.

Type locality 5.5km upstream from Katsuhira-kita-zawa (Loc. 10); Katsuhira Formation.

Dimensions Holotype, JUE no. 15978, length, 6.2mm, height, 5.4mm, Loc. 10. Paratype, JUE no. 15979, length, 6.2mm, height, 5.4mm, Loc. 10. Paratypes, JUE no. 15980–1, length, 5.2mm, height, 3.9mm, width, 2.9mm; JUE no. 15980–2, length, 3.6mm, height, 3.2mm, width, 2.3mm; JUE no. 15980–3, length, 3.2mm, height, 2.9mm, width, 1.9mm; Loc. 29. JUE no. 15981–1, length, 4.6mm, height, 3.4mm; JUE no. 15981–2, length, 4.1mm, height, 3.2mm; Loc. 28.

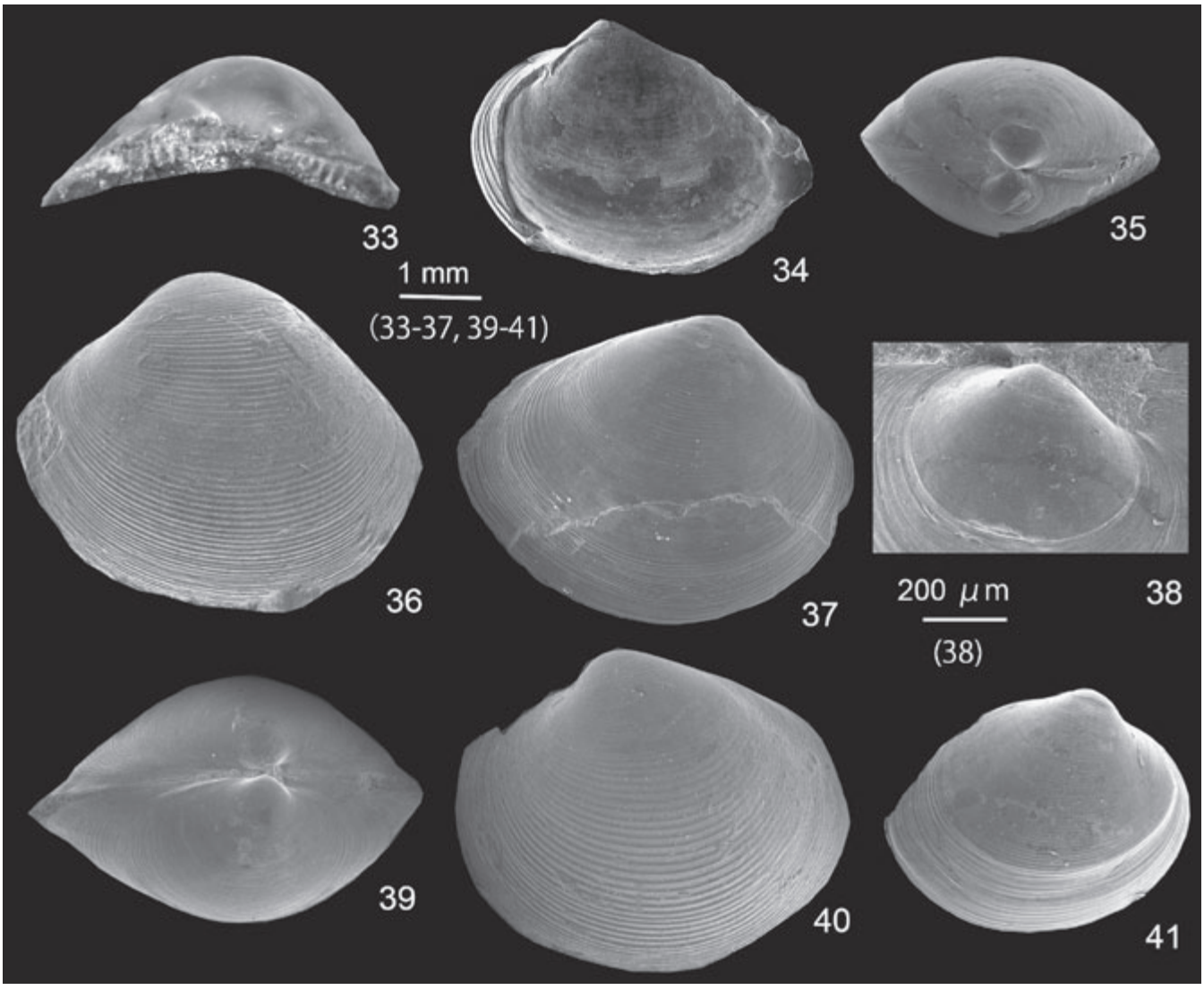
Diagnosis Strongly inflated species of *Tindaria* sculptured with many fine commarginal ribs. Hinge taxodont with no resilium. Pallial line entire.

Description Shell moderate-size for genus, to 6.2mm long, rather thick, nuculid-like, with porcellanous inner layer, well inflated (W/L= 0.56–0.64 for paratype specimens), equivalve, inequilateral. Prodissoconch rather large, attaining about 580μm in length, smooth. Antero-dorsal margin broadly arched, continuing to semicircular anterior margin; ventral margin broadly rounded; posterior end short, subtruncated, continuing to straight postero-dorsal margin. Blunt ridge extending from umbo to postero-ventral corner. Umbo prominent, rather prosogyrate, located at anterior third of shell length to centre of shell (AL/L= 0.35–0.47). Surface sculptured with fine, distinct commarginal ribs; interspaces between commarginal ribs each narrower than one rib. Hinge plate narrow, with two series of small teeth; nine anterior teeth; 15 posterior teeth. Anterior adductor muscle scar small, ovate; posterior adductor scar subquadrate. Pallial line entire.

Etymology From Paleocene, the stratigraphic occurrence of the species.

Comparison The present new species closely resembles the Recent Japanese species *Tindaria soyoae* Habe, 1953 in having a nuculid-like shell and fine commarginal ribs. However, *T. paleocenica* n. sp. differs from the Recent species by its more acute posterior end, fewer teeth (eight to 13 anterior and 14 to 22 posterior teeth of *T. soyoae*) and no pallial sinus (a very shallow sinus has been observed in *T. soyoae*). The outline of *Tindaria*? sp. from the seep site of the upper Oligocene Lincoln Creek Formation described by Kiel (2006) is similar to the present new species. However, the lack of information on its interior structure prevents us from comparing them with each other. Another Recent species, *T. kennerlyi* (Dall, 1897), can be separated from the present species by having a more elongate and less inflated shell.

Remarks According to Moore (1969), the geological range of this genus is Tertiary to Recent. Amano *et al.* (2004) listed *Tindaria* sp. resembling *T. kennerlyi* from the mudstone of the uppermost lower to lowermost middle Miocene Higashibessho Formation in Toyama Prefecture,



Figures 33–41 *Tindaria paleocenica* sp. nov.; **33.** Hinge of left valve, **36.** Left valve, holotype, JUE no. 15978, Loc. 10; **34.** Inner surface of left valve, paratype, JUE no. 15980–2, Loc. 29; **35.** Dorsal view of both valves, **38.** Enlargement of beak, **41.** Right valve, paratype, JUE no. 15980–3, Loc. 29; **37.** Right valve, paratype, JUE no. 15980–4, Loc. 29; **39**. Dorsal view of both valves, **40**. Left valve, paratype, JUE no. 1980–1, Loc. 29.

central Honshu. The geological range of the genus *Tindaria* has been extended back to the late Oligocene by Kiel (2006), as noted above. From the finding of the present new species, it is clear that the genus appeared in the Paleocene.

Stratigraphic and geographic range Paleocene Katsuhira Formation in eastern Hokkaido.

Discussion

Among the 11 species identified here, excluding *Malletia* sp. and *Pseudoneilonella*? sp., the geological range has been examined. As a result, it has become clear that five taxa have survived the mass extinction at the end of Cretaceous: the two species *Acila* (*Truncacila*) *hokkaidoensis*, *Pristigloma*? *sachalinensis*, and the genera *Ezonuculana*, *Menneroctenia* and *Neilonella*. Among these, *Pristigloma*? *sachalinensis* and *Ezonuculana* are recorded here for the first time from Paleocene rocks. In contrast, *Malletia poronaica* and *Leionucula yotsukurensis* appeared in the Paleocene and extended to the Oligocene. The oldest species of *Tindaria* is recorded here, extending the genus back to the Paleocene.

At the K/Pg boundary, mainly shallow-water foraminifers became extinct while deep-water species survived (Kaiho, 1994; Thomas, 2007; Alegret *et al*., 2009). Following this, many deep-water benthonic foraminifers suffered

from extinction at the PETM (Paleocene-Eocene Thermal Maximum). In contrast, few data exist on the extinction of deep-sea molluscan fossils. The survival of *Acila* (*Truncacila*) *hokkaidoensis* and *Menneroctenia* is also recognized in South Sakhalin (Kalishevich *et al.*, 1981). The aporrhaid gastropod *Kangilioptera inouei* demonstrates that the aporrhaid also survived the End-Cretaceous extinction (Amano & Jenkins, 2014). However, *Acila* (*Truncacila*) *hokkaidoensis, Pristigloma*? *sachalinensis*, *Ezonuculana* and *Menneroctenia* became extinct by the end of the Paleocene. These trends are concordant with the extinction pattern of the benthonic foraminifers. Thus, the environmental change at the PETM seems to have severely affected deep-sea benthic animals.

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