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Nuculana onoyamai Otuka as an extinct nuculanid bivalve in the Japan Sea

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Abstract

Nuculana onoyamai Otuka, 1935 is one of the representative extinct species of the Plio-Pleistocene Omma-Manganji fauna in the Japan Sea borderland. Based on 62 specimens herein examined, this species has high shells, a produced umbo above the dorsal margin, a wide and depressed escutcheon with one blunt ridge running from beak to two thirds of escutcheon length, a narrow and shallowly depressed lunule, a subtruncated posterior margin and a thick inner rostral ridge. *Nuculana onoyamai* and its related species first appeared in northernmost Sakhalin in the Early Miocene then migrated to the Japan Sea side of Honshu by the Pliocene. Among the deep-sea Nuculanoidea, a similar evolutionary history is observed in living species such as *Robaia robai* (Kuroda, 1929) and *Megayoldia toyamaensis* (Kuroda, 1929). Among these, the fossil occurrences of *N. onoyamai* and *M. toyamaensis* are restricted to the Japan Sea. *N. onoyamai* flourished in the Pliocene and declined in the Early Pleistocene while *M. toyamaensis* has been recorded mainly from Lower Pleistocene deposits. *Nuculana onoyamai* became extinct by the end of Early Pleistocene due to the deteriorated environment of the Japan Sea while *M. toyamaensis* was able to survive.

Key words: Bivalvia, extinction, Omma-Manganji fauna, Protobranchia, Sakiyama Formation

1. Introduction

Nuculanidae H. Adams and A. Adams, 1858, is a representative family including many genera and species and lives in the deep-water mud and sand bottom (Higo et al., 1999; WoRMS, 2026). In the Pliocene to the Early Pleistocene, the Omma-Manganji fauna (Otuka, 1939) flourished in the Japan Sea borderland and some species became extinct at the end of the Early Pleistocene (0.9 Ma) (Amano, 2024). The following four species of Nuculanidae have been recorded in the Omma-Manganji fauna; *Nuculana pernula* (Müller, 1779), *N. yokoyamai* Kuroda, 1934, *N. onoyamai* Otuka, 1935a and *Robaia robai* (Kuroda, 1929) (e.g. Hatai and Nisiyama, 1952; Masuda and Noda, 1976; Amano and Kanno, 1991; Amano and Narita, 1992). *Leda sadoensis* was described from the Lower Pleistocene Sawane Formation in Sado Island by Yokoyama (1926). After that, this species was sometimes treated as a subspecies of *Nuculana pernula* as proposed by Suzuki and Kanehara (1936). However, it is difficult to separate *sadoensis* from the variation of *N. pernula*. In this paper, I treat it as a synonym of *N. pernula* as did Coan et al. (2000).

Among four nuculanid species, there is no detailed description of *Nuculana onoyamai* because few

specimens could be obtained from each locality. In particular, the inner structure of shells has not been described. When he proposed *N. onoyamai* as a new species, Otuka (1935a) illustrated no inner surface of this species because the type specimens are fragile and attached to the rock (Fig. 1).

Nuculana onoyamai became extinct by the end of the Early Pleistocene (Amano, 2024). In contrast, *Robaia robai* is an endemic species in the Japan Sea and the Sea of Okhotsk that was able to survive the deteriorated environment during the glaciations (Amano and Narita, 1992; Amano, 2024). Moreover, one of the deep-water Nuculanoidea, *Megayoldia toyamaensis* (Kuroda, 1929) also survived (Amano, 1996). However, the reason why these species had different histories has not been discussed.

Many well-preserved specimens were recovered from the Upper Pliocene Sakiyama Formation from which the type specimens were obtained. In this paper, the inner structure and the variation of shells of this species are examined in detail. Moreover, the previous records of this species are re-examined and the causes for extinction are discussed.

Institutional abbreviations: NMNS, Department of Paleontology and Anthropology, National Museum of Nature and Science, Tokyo, Tsukuba, Japan; UMUT, The University Museum, The University of Tokyo, Tokyo, Japan.

2. Materials

I collected 62 specimens from the Upper Pliocene Sakiyama Formation (Ozaki, 2010) in the Noto Peninsula. The fossil site is located at Tonomachi in Nanao City, Ishikawa Prefecture (37°3’6”N, 137°1’21”E), 2.4 km south from the type locality of *Nuculana onoyamai*, Kamiyukawa in Nanao City. At this site, many detached valves and a few conjoined valves of *N. onoyamai* occur densely in the thin sandy siltstone layer (20 cm in thickness) of the Sakiyama Formation. Above this layer, some specimens of *Conchocele* sp. sporadically occurred. Among these specimens of *N. onoyamai*, 30 right valves, 30 left valves and two conjoined valves are well preserved and measured.

Moreover, I also have examined the type specimens (UMUT CM 12630, 12649) stored at University Museum of the University of Tokyo (UMUT) and some specimens including the type of *Nuculana magarikawaensis* Nomura and Zinbo, 1937 (NMNS PM 18503, 22987), stored at National Museum of Nature and Science (NMNS). Among the specimens deposited in NMNS, the following well-preserved specimens were measured; one left valve (NMNS PM 58937) from the Pliocene Yuchi Formation at the upstream of Niju-san-gou River in Teshio Town, norther Hokkaido; four left and two right valves (NMNS PM 52672, 52673) from the Pliocene Kuwae Formation at 430 m upstream from Tsustsumioka-ohashi Bridge in Kurokawa Village, Niigata Prefecture.

3. Systematic Paleontology

Class Bivalvia Linnaeus, 1758
Family Nuculanidae H. Adams and A. Adams, 1858

Genus *Nuculana* Link, 1807

Type species: *Arca rostrata* Bruguière, 1789. Recent, Greenland.

Diagnosis: Shell equivalve, usually rather thick. Posterior end strongly rostrate; rostrum truncated or oblique, not pointed; distinct inner rostral ridge. Surface sculptured by strong to feeble commarginal riblets. Umbones small, opisthogyrate. Escutcheon well developed. Hinge with numerous teeth and with small and oblique resilifer (modified from Coan et al., 2000).

Remarks: *Thestyleda* Iredale, 1929 was frequently used as a “subgenus” of *Nuculana* in Japan (Habe, 1977; Kurozumi and Tsuchida, 2000; Kurozumi et al., 2017). However, only the strong commarginal ribs distinguish the two taxa, casting doubt on the validity of *Thestyleda*. The strength of commarginal ribs varies widely in all species of *Nuculana* (Link, 1807). Thus, I agree with the opinion by Coan et al. (2000) that *Thestyleda* is a junior synonym of *Nuculana*.

Robaia Habe, 1958 can be easily distinguished from *Nuculana* by having a smooth shell and no inner rostral ridge.

Saccella Woodring, 1925 and *Jupiteria* Bellardi, 1875 are distinguished from *Nuculana* by having a pointed posterior end and no inner rostral ridge.

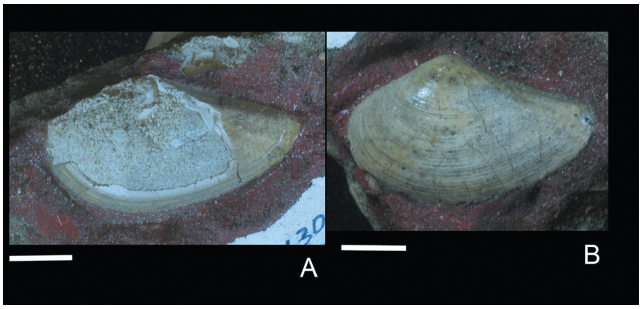


Fig. 1. Type specimens of *Nuculana onoyamai* Otuka. A. Holotype, UMUT CM 12630. B. Paratype, UMUT CM 12649. Scale bar = 5 mm.

***Nuculana onoyamai* Otuka, 1935**

[Japanese Name: Onoyama-roubai]

(Fig. 1, Pls. 1, 2)

Nuculana onoyamai Otuka, 1935a, p. 507–508, figs. 3b, c; Otuka, 1935b, p. 881, pl. 55, figs. 105, 106; Itoigawa, 1958, pl. 1, fig. 2; Iwai, 1960, pl. 4, figs. 2a, b, 3a, b; Iwai, 1965, pl. 14, figs. 3a, b, 4a, b; Matsuura, 1985, pl. 34, fig. 8; Matsuura and Hotta, 1986, p. 7, pl. II-3, fig. 10; Amano and Kanno, 1991, figs. 4-10, 12, 15, 16; Matsuura, 1992, p. 69, pl. V-10(1), fig. 10; Amano, 1994, pl. 1, figs. 2, 11; Matsuura, 2009, p. 106, pl. IV-12, figs. 20–22.

Nuculana magarikawaensis Nomura and Zinbo, 1937, p. 165–166, pl. 22, figs. 3, 4.

Nuculana (*Nuculana*) cf. *onoyamai* Otuka. Masuda et al., 1981, pl. 5, fig. 3.

Sacella (*Costanuculana*) *onoyamai* (Otuka). Matsui, 1985, p. 226–227, pl. 31, figs. 9–11.

Type specimens: Holotype, UMUT CM 12630; Paratype, UMUT CM 12649.

Type Locality: Kamiyukawa, Nanao City, Ishikwa Prefecture; Sakiyama Formation.

Material: Thirty right valves, thirty left valves and two conjoined valves from the Upper Pliocene Sakiyama Formation at Tonomachi, Nanao City in Ishikawa Prefecture.

Dimensions: *see* Tables 1, 2.

Original description: "Shell small, equivalve, inequilateral. Surface sculptured with fine concentric lines. Posterior part relatively long, rostrate and curved upward. Anterior margin rounded; one ridge running from umbo to postero-ventral comer, making depressed area in postero-dorsal side; depressed area sculptured with concentric lines; weak ridge running from beak to central part of postero-dorsal margin and dividing posterior depressed area. Beak not prominent. Hinge teeth v-shaped with small resilifer. Weak ridge horizontally running in posterior end of shell." (in Japanese, translated by the author).

Supplementary description on the Tonomachi specimens: Shell moderate in size, less than 20.3 mm in length, rather thick, high nuculaniform (H/L= 0.58–0.76, avg. 0.68), moderately inflated (T/L= 0.23–0.36, avg. 0.28) (Table 1). Postero-dorsal margin nearly straight. In left valve, narrow and shallow furrow running from beak to ventral margin near anterior end (Plate 1, figs. A, D, H, M, N).

Umbo produced above dorsal margin; beak opisthogyrate, located at posterior three-fifths of shell length (PL/L= 0.45–0.69, avg. 0.57). Escutcheon wide and depressed and one blunt ridge running from beak to two thirds of escutcheon length (Plate 1, figs. B, O); lunule narrow, shallowly depressed, demarcated by edge. Two radial ridges running from umbo to posterior dorsal side and posterior ventral side respectively. Posterior margin acute, short and subtruncated.

Hinge consisting of anterior and posterior arcs, separated by moderate-sized and deep triangular resilifer; anterior v-shaped taxodont teeth 7–15 (avg. 10.9) in number while posterior v-shaped teeth 10-16 (avg. 13.4). Pallial sinus wide and shallow. Anterior adductor muscle scar subquadrate, larger than small elongate posterior adductor muscle scar. Inner rostral ridge thick near ventral side of posterior margin.

Remarks: The type specimens were collected from the Pliocene Sakiyama Formation at Kamiyukawa in Nanao City. Many specimens were newly collected from the same formation at Tonomachi in Nanao Coty, 2.4 km south of the type locality. The anterior part of Holotype (UMUT CM 12630; Fig. 1A) is now destroyed and the paratype (UMUT CM 14649; Fig. 1B) has a lower shell (H/L= 0.58) than the specimens from Tonomachi (avg. H/L= 0.68).

Some specimens from the Pliocene Yuchi and Kuwae formations show usually lower shells than the Tonomachi specimens (H/L= 0.57–0.60) which is similar to the type specimens (Fig. 2). One specimen (Plate 2, fig. M) from the Kuwae Formation has a much higher shell like the Tonomachi specimens. Moreover, these specimens have a weak fine furrow on the anterior part of left valve (Plate 2, figs. A, H) and a weak ridge on the escutcheon (Plate 2, figs. B, C, F) as in the Tonomachi specimens.

Table 1. Measurements of *Nuculana onoyamai* Otuka from the Pliocene Sakiyam Formation. *PL= posterior part of shell length. **AT = number of anterior teeth, ***PT= number of posterior teeth.

No.	Type	Length (mm)	Height (mm)	PL* (mm)	Thickness (mm)	H/L	PL/L	T/L	AT**	PT***	Valve
UMUT CM 12630	Holotype	23.4	13.7	13.5	-	0.59	0.58	-	-	-	left
UMUT CM 12649	Paratype	19.7	11.5	11.9	-	0.58	0.60	-	-	-	left
NMNS PM 69042		19.1	13.6	9.1	6.9	0.71	0.48	0.36	11	15	left
NMNS PM 69043		20.3	14.1	9.1	-	0.69	0.45	-	-	-	left
NMNS PM 69044		18.6	13.4	10.5	-	0.72	0.56	-	-	-	left
NMNS PM 69045		17.7	12.0	9.1	-	0.68	0.51	-	-	-	left
NMNS PM 69046		18.9	13.8	8.4	5.3	0.73	0.44	0.28	11	15	left
NMNS PM 69047		18.8	12.1	11.5	-	0.64	0.61	-	-	-	left
NMNS PM 69048		15.7	10.3	8.6	-	0.66	0.55	-	-	-	left
NMNS PM 69049		19.7	12.9	10.8	-	0.65	0.55	-	-	-	left
NMNS PM 69050		16.8	10.6	11.2	-	0.63	0.67	-	-	-	left
NMNS PM 69051		17.3	10.6	9.7	-	0.61	0.56	-	-	-	left
NMNS PM 69052		16.7	12.6	10.1	4.8	0.75	0.60	0.29	-	16	left
NMNS PM 69053		15.8	10.4	8.6	-	0.66	0.54	-	-	-	left
NMNS PM 69054		16.0	10.2	10.2	4.3	0.64	0.64	0.27	12	-	left
NMNS PM 69055		16.6	9.9	9.4	-	0.60	0.57	-	-	-	left
NMNS PM 69056		14.8	10.2	9.1	-	0.69	0.61	-	-	-	left
NMNS PM 69057		15.1	9.4	9.3	-	0.62	0.62	-	15	-	left
NMNS PM 69058		14.4	9.4	8.3	-	0.65	0.58	-	-	-	left
NMNS PM 69059		13.2	8.0	7.6	-	0.61	0.58	-	-	-	left
NMNS PM 69060		14.0	9.8	7.1	3.3	0.70	0.51	0.24	12	14	left
NMNS PM 69061		11.6	7.9	6.8	-	0.68	0.59	-	-	-	left
NMNS PM 69062		12.7	8.3	6.6	3.5	0.65	0.52	0.28	12	14	left
NMNS PM 69063		12.6	8.5	7.2	3.0	0.67	0.57	0.24	-	-	left
NMNS PM 69064		11.8	8.0	6.5	-	0.68	0.55	-	-	-	left
NMNS PM 69065		11.9	8.3	7.6	-	0.70	0.64	-	-	-	left
NMNS PM 69066		13.0	8.7	7.5	3.8	0.67	0.58	0.29	12	15	left
NMNS PM 69067		11.3	8.1	6.7	-	0.72	0.59	-	-	-	left
NMNS PM 69068		11.5	7.8	7.2	-	0.68	0.63	-	-	-	left
NMNS PM 69069		12.6	7.3	6.2	-	0.58	0.49	-	-	-	left
NMNS PM 69070		11.7	8.5	6.8	-	0.73	0.58	-	-	-	left
NMNS PM 69071		10.1	7.3	5.7	-	0.72	0.56	-	-	-	left
NMNS PM 69072		17.1	12.1	9.8	3.9	0.71	0.57	0.23	11	15	right
NMNS PM 69073		15.8	10.4	9.9	-	0.66	0.63	-	-	-	right
NMNS PM 69074		16.1	11.5	10.1	4.6	0.71	0.63	0.29	13	13	right
NMNS PM 69075		17.4	11.1	10.2	-	0.64	0.59	-	-	-	right
NMNS PM 69076		13.3	9.2	8.2	-	0.69	0.62	-	8	12	right
NMNS PM 69077		16.3	12.4	9.9	-	0.76	0.61	-	-	-	right
NMNS PM 69078		14.1	9.5	8.9	3.8	0.67	0.63	0.27	7	11	right
NMNS PM 69079		17.3	11.8	8.9	-	0.68	0.51	-	-	-	right
NMNS PM 69080		17.1	11.2	10.6	-	0.65	0.62	-	-	-	right
NMNS PM 69081		16.1	11.8	9.6	4.9	0.73	0.60	0.30	-	13	right
NMNS PM 69082		16.0	11.7	8.9	-	0.73	0.56	-	-	-	right
NMNS PM 69083		14.8	9.3	7.9	-	0.63	0.53	-	-	-	right
NMNS PM 69084		13.6	9.8	7.4	-	0.72	0.54	-	-	-	right
NMNS PM 69085		14.9	10.4	8.8	-	0.70	0.59	-	-	-	right
NMNS PM 69086		14.4	10.0	7.4	-	0.69	0.51	-	-	-	right
NMNS PM 69087		13.5	9.0	7.5	-	0.67	0.56	-	-	-	right
NMNS PM 69088		13.7	8.9	7.5	-	0.65	0.55	-	-	-	right
NMNS PM 69089		13.8	9.8	8.7	-	0.71	0.63	-	11	11	right
NMNS PM 69090		11.8	8.6	7.1	-	0.73	0.60	-	-	-	right
NMNS PM 69091		13.2	10.0	7.8	-	0.76	0.59	-	-	-	right
NMNS PM 69092		14.4	8.8	9	-	0.61	0.63	-	-	-	right
NMNS PM 69093		13.9	9.2	8.4	-	0.66	0.60	-	11	12	right
NMNS PM 69094		12.8	8.1	7.2	-	0.63	0.56	-	-	-	right
NMNS PM 69095		13.2	9.1	7.4	-	0.69	0.56	-	-	-	right
NMNS PM 69096		12.0	8.8	6.8	-	0.73	0.57	-	-	15	right
NMNS PM 69097		13.4	9.4	8.2	-	0.70	0.61	-	-	-	right
NMNS PM 69098		12.2	8.1	6.3	-	0.66	0.52	-	-	-	right
NMNS PM 69099		10.5	7.4	7.2	-	0.70	0.69	-	-	-	right
NMNS PM 69100		10.7	7.3	5.8	2.8	0.68	0.54	0.26	7	10	right
NMNS PM 69101		11.3	7.7	6.4	-	0.68	0.57	-	-	-	right
NMNS PM 69040		13.2	-	6.8	-	-	-	-	-	-	right (conjoined)
NMNS PM 69041		12.7+	-	-	-	-	-	-	-	-	right (conjoined)

Table 2. Measurements of *Nuculana onoyamai* Otuka from the Pliocene Yuchi and Kuwae formations. *PL= posterior part of shell length. **AT = number of anterior teeth, ***PT= number of posterior teeth.

No.	Length (mm)	Height (mm)	PL* (mm)	Thickness (mm)	H/L	PL/L	T/L	AT**	PT***	Valve	Formation
NMNS PM 58937	16.9	9.7	10.2	3.3	0.57	0.60	0.20	15	16	left	Yuchi, F.
NMNS PM 52672-1	14.3	8.6	9.5	-	0.60	0.66	-	-	-	left	Kuwae F.
NMNS PM 52672-2	15.0	8.9	7.7	-	0.59	0.51	-	-	-	left	Kuwae F.
NMNS PM 52672-3	16.0	9.5	8.0	-	0.59	0.50	-	-	-	left	Kuwae F.
NMNS PM 52673-1	15.0	9.0	8.1	-	0.60	0.54	-	-	-	right	Kuwae F.
NMNS PM 52673-2	14.2+	9.3	8.5	-	-	-	-	-	-	left	Kuwae F.
NMNS PM 52673-3	14.1+	9.7	7.5+	-	-	-	-	-	-	right	Kuwae F.

Matsui (1985) allocated *Nuculana onoyamai* to the subgenus *Costanuculana* Habe, 1951 of the genus *Saccella* Woodring, 1925. However, as discussed by Amano et al. (2026), it is not necessary to separate *Saccella* and *Costanuculana*. As mentioned above, *Saccella* species lack an inner rostral ridge. On the other hand, *N. onoyamai* has an inner rostral ridge and no pointed posterior end.

Nomura and Zinbo (1937) proposed *Nuculana magarikawaensis* from the Pliocene Hanezawa Formation in Yamagata Prefecture. However, on the original label of this species, two specimens (NMNS PM 18503, 22987; Plate 2, figs. K, L) were once identified with *Nuculana onoyamai* Otuka. The new label of *Nuculana magarikawaensis* is inserted in the same box. According to Nomura and Zinbo (1937), the larger specimen (L= ca. 11. 5 mm; NMNS PM 18503) was assigned to the type. This type corresponds to the holotype while another one (NMNS PM 22987) can be considered as the paratype as pointed out by Hatai and Nisiyama (1952). Nomura and Zinbo (1937) distinguished *N. magariakwaensis* from *N. onoyamai* by having a smaller shell and more distinct concentric sculpture. However, the preservation of the type specimens of *N. magarikawaensis* is so poor that these characteristics cannot be used to separate the species. Therefore, *N. magarikawensis* is herein designated as a junior synonym of *N. onoyamai.*

Comparison: *Nuculana tumiensis* Lautenshläger, 1937 MS was described by Krishtofovich, 1964 from the Lower Miocene of Schmidt Peninsula, northernmost Sakhalin. This species shares a similar shell size (23 mm in shell length), a similar ratio of H/L (0.56–0.66), and a produced umbo above the dorsal margin with *N. onoyamai*. However, *N. tumiensis* lacks a blunt ridge on the escutcheon and has more numerous teeth (anterior arc of teeth, 16–17; posterior arc of teeth, 20–28) than *N. onoyamai.*

Nuculana (*Nuculana*) *karihaensis* Hatai and Nisiyama, 1949 was described from the Upper Miocene Ishiguro Formation (= Teradomari Formation) in Niigata Prefecture. This species is very similar to the lower shell specimens of *N. onoyamai* in having a similar shell size and proportion (21.5 mm in length; 12.6 mm in height; H/L= 0.59) to the type specimens and a subtruncated posterior margin. However, *N.* (*N.*) *karihaensis* differs from *N. onoyamai* in having a narrow escutcheon without any ridge, no shallow furrow on the anterior side of the left valve and a less prominent umbo.

Nuculana minuta (Müller, 1776) from the northern Atlantic Ocean, northeastern and northwestern Pacific Ocean can be separated from *N. onoyamai* by having a lower umbo and coarser commarginal ribs. *Nuculana minuta praecusor* Arnold, 1903 from the Pliocene and Pleistocene Fernando and San Pedro Formations in California shares a relatively high shell with a short rostrum with *N. onoyamai.* However, *N. minuta praecusor* is different from *N. onoyamai* by having coarse commarginal ribs and a truncated posterior end.

Nuculana fossa (Baird, 1863) from the Pliocene to Holocene in California can be distinguished from *N. onoyamai* by its lower shell (H/L= 0.55 by Baird, 1863) with a longer rostrum and no ridge on the escutcheon.

Stratigraphic distribution: Pliocene, Yuchi Formation in Hokkaido (Masuda et al., 1981; this study), Narusawa Formation in Aomori Prefecture (Iwai,

1960, 1965), Tentokuji Formation in Akita Prefecture (Matsui, 1985), Hanezawa Formation in Yamagata Prefecture (Nomura and Zinbo, 1937); Kuwae, Nishiyama, Kurokura and Nadachi formations in Niigata Prefecture (Itoigawa, 1958; Amano and Kanno, 1991; Amano, 1994; this study) and Sakiyama Formation in Ishikawa Prefecture (Otuka, 1935a, b; Matsuura, 1985; Matsuura and Hotta, 1986; Matsuura, 1992; Matsuura, 2009). Early Pleistocene, Sasaoka Formation in Akita Prefecture (Matsui, 1985) (Fig. 2).

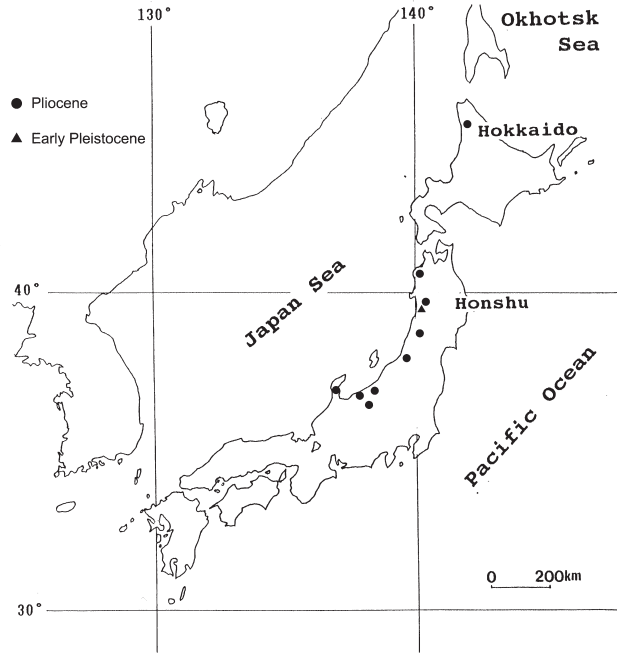


Fig. 2. Distribution of *Nuculana onoyamai* Otuka.

4. Discussion

Four nuculanid species occur in the Plio-Pleistocene Omma-Manganji fauna in the Japan Sea borderland; *Nuculana onoyamai*, *N. pernula*, *N. yokoyamai* and *Robaia robai*. In the superfamily Nuculanoidea including Nuculanidae, *Megayoldia toyamaensis* (Kuroda, 1929) is also recorded from the Omma-Manganji fauna (Amano, 1996).

Of these species, *Nuculana pernula* and *N. yokoyamai* are both extant in the lower to upper bathyal depth of the Pacific Ocean and the Japan Sea (Scarlato, 1981; Higo et al., 1999; Kurozumi and Tsuchida, 2000; Kamenev, 2013; Kurozumi et al., 2017). *Nuculana pernula* is also living in the Arctic Ocean (Bernard, 1979; Coan et al., 2000). Both species have Plio-Pleistocene fossil records on the Pacific Ocean side and the Japan Sea side (Hatai and Nisiyama, 1952; Masuda and Noda, 1976; Baba, 1990; Table 3).

Nuculana onoyamai, *Robaia robai* and *Megayoldia toyamaensis* have a similar history. These or related species appeared in the Miocene formations of northernmost Sakhalin. Then, they migrated to the Japan Sea side of Honshu by the Pliocene (Amano and Narita, 1992; Amano, 1996; this study). However, *Robaia robai* still lives in the Japan Sea, the Sea of Okhotsk and the Pacific side of Northeast Honshu (Scarlato, 1981; Higo et al., 1999; Okutani et al, 2008; Kamenev, 2013; Kurozumi et al., 2017; Lisitsyna and Kamenev, 2024). *Megayoldia toyamaensis* also live and is endemic to the Japan Sea (Higo et al., 1999; Kurozumi and Tsuchida, 2000, 2017; Kamenev, 2013) while *Nuculana onoyamai* became extinct. *Nuculana onoyamai* has been found mainly from the siltstone which might be deposited in the lower sublittoral to upper bathyal silty bottom (Masuda et al., 1981; Matsui, 1990; Amano and Kanno, 1991; Table 3). *Robaia robai* and *Megayoldia toyamaensis* are still extant in the lower sublittoral to upper bathyal silty bottom of the Japan Sea (Scarlato, 1981; Higo et al., 1999; Kurozumi and Tsuchida, 2000; Kamenev, 2013; Kurozumi et al., 2017).

Summarizing the Recent and fossil distributions of the above nuculanid species and *Megayoldia toyamaensis*, the above five species share similar habitats (Table 3). Only the fossil occurrences of *N. onoyamai* and *M. toyamaensis* are restricted to the Japan Sea and differ from the other three species. During the Pleistocene glacial period, the Japan Sea was semi-enclosed and many shallow and deep-water species became extinct because of the brackish surface water and anoxic deep-water (Amano, 1996, 2001, 2004, 2007, 2024). Exceptionally, *R. robai* and *M. toyamaensis* survived such deteriorated environments in the intermediate water of the Japan Sea (Amano and Narita, 1992; Amano, 1996). The exact reason why *N. onoyamai* having similar fossil occurrences with *M. toyamaensis* became extinct is unknown. *N. onoyamai* flourished in the Pliocene and declined in the Early

Table 3. Fossil occurrence and ecology (paleoecology) of Nuculanoidean species in the Omma-Manganji fauna.

Species \ Distribution	Fossil occurrence		Bottom sediment	Depth (m)
	Pacific side	Japan Sea side		
Nuculana pernula (Müller, 1779)	+	+	mud, sandy mud	30–1,600
N. yokoyamai Kuroda, 1934	+	+	mud	50–450
N. onoyamai Otuka, 1935†	-	+	siltstone	lower sublittoral–upper bathyal
Robaia robai (Kuroda, 1929)	+	+	sandy mud	83–2,900
Megayoldia toyamaensis (Kuroda, 1929)	-	+	mud	100–1,475

Pleistocene as described above while *M. toyamaensis* has been recorded mainly from Lower Pleistocene deposits (Amano, 1996). These differences in age possibly affected the survival of *Megayoldia toyamaensis* and the extinction of *N. onoyamai*.

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I am very grateful to Geerat J. Vermeij (University of California at Davis) for his critical review of this manuscript. I thank Paul Valentich-Scott (Santa Barbara Museum of Natural History) for his critical review and many useful suggestions for improving the manuscript. I also thank Takenori Sasaki (UMUT) and Takuma Haga (NMNS) for their help examining the specimens stored at each museum.

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Nuculana onoyamai Otuka as an extinct nuculanid bivalve in the Japan Sea

Kazutaka Amano

Plates 1–2

Plate 1

Figs. A–P. *Nuculana onoyamai* Otuka, 1935 オノヤマロウバイ

All specimens are from the Sakiyama Formation at Tonomachi in Nanao City, Ishikawa Prefecture.

Fig. A. NMNS PM 69043, left valve.

Fig. B. NMNS PM 69040, dorsal view of conjoined valves.

Figs. C, F. NMNS PM 69072, right valve; C, external view; F, inner view.

Fig. D. NMNS PM 69042, left valve.

Figs. E, K. NMNS PM 69046, left valve; E, inner view; K, external view.

Figs. G, N. NMNS PM 69060, left valve; G, inner view; N, external view.

Fig. H. NMNS PM 69049, left valve.

Fig. I. NMNS PM 69073, right valve.

Figs. J, M. NMNS PM 69066, left valve; J, inner view; M, external view.

Fig. L. NMNS PM 69074, right valve.

Fig. O. NMNS PM 69041, dorsal view of conjoined valves.

Fig. P. NMNS PM 69087, right valve.

Abbreviations: aas= anterior adductor muscle scar; dp = deepest point of pallial sinus; irr = inner rostral ridge; pas = posterior adductor muscle scar; re = ridge on the escutcheon. White arrow shows a narrow and shallow furrow running from beak to ventral margin near posterior end in the left valve.

All scale bars show 5 mm.

Plate 1

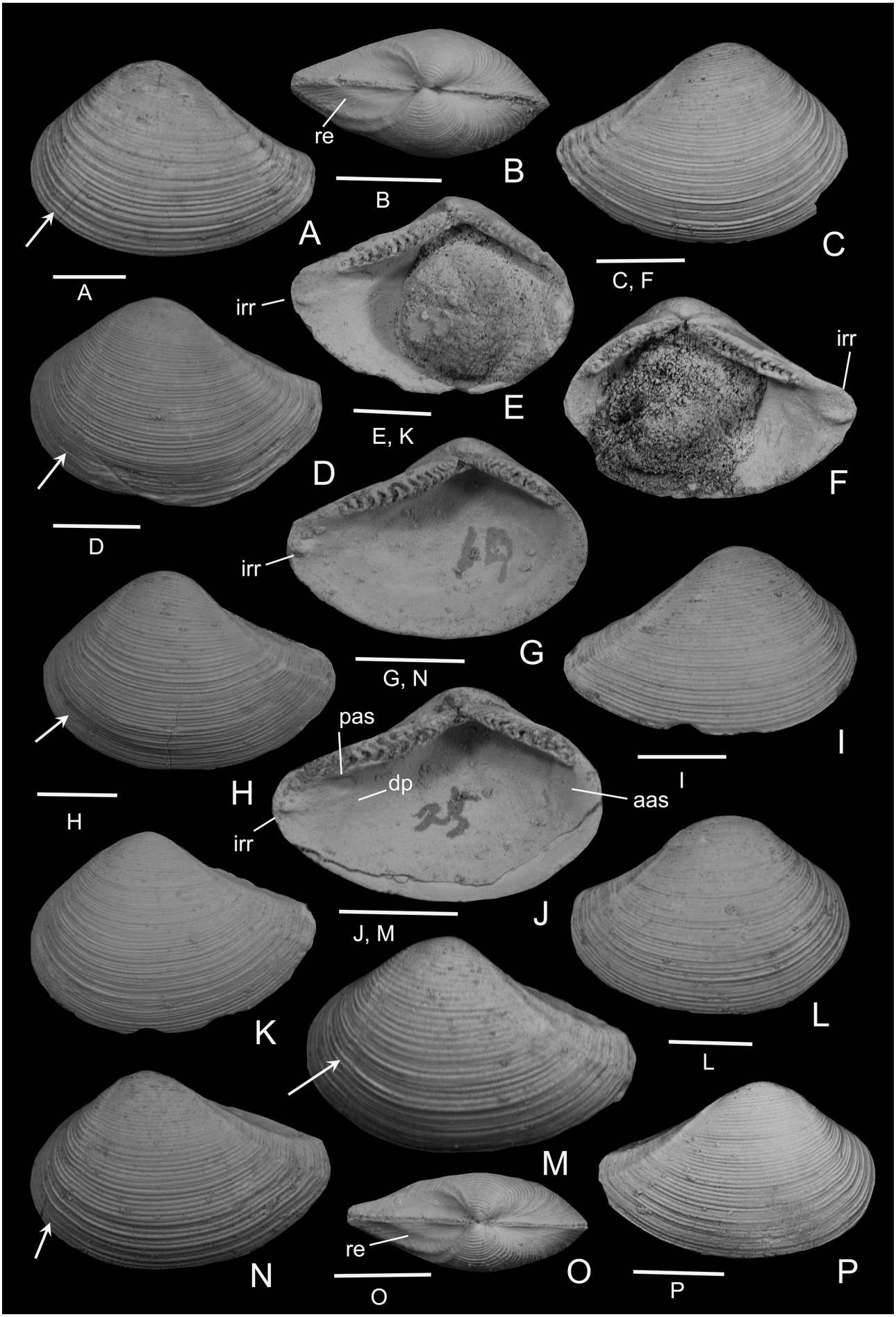

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Plate 2

Figs. A–J, M. *Nuculana onoyamai* Otuka, 1935 オノヤマロウバイ

Figs. A, B, C. NMNS PM 58937, left valve, Yuchi Formation; A, external view; B, dorsal view; C, inner view.

Figs. D, G. NMNS PM 52673-2, left valve, Kuwae Formation; D, dorsal view; G, eternal view.

Figs. E. NMNS PM 52672-1, left valve, Kuwae Formation.

Figs. F, I. NMNS PM 52673-1, right valve, Kuwae Formation; F, oblique dorsal view; I, external view.

Fig. H. NMNS PM 52672-3, left valve, Kuwae Formation.

Fig. J. NMNS PM 52672-2, left valve, Kuwae Formation.

Figs. M. NMNS PM 52673-3, right valve, Kuwae Formation

Figs. K, L. *Nuculana magarikawaensis* Nomura and Zinbo, 1937 [= *N. onoyamai*]

Fig. K. Paratype, NMNS PM 22987, right valve, Hanezawa Formation.

Fig. L. Holotype, NMNS PM 18503, right valve, Hanezawa Formation.

Abbreviations: aas= anterior adductor muscle scar; dp = deepest point of pallial sinus; irr = inner rostral ridge; pas = posterior adductor muscle scar; re = ridge on the escutcheon. White arrow shows a narrow and shallow furrow running from beak to ventral margin near posterior end in the left valve.

All scale bars show 5 mm.

Plate 2

