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New Fossil and Recent *Limopsis* (Bivalvia) from the Northwestern Pacific

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Abstract. *Limopsis* ***satoi,*** sp. nov. and *L.* ***hokkaidoensis,*** sp. nov. are described from Plio-Pleistocene formations in northern Japan. They are members of the Omma-Manganji fauna mainly distributed in the Japan Sea side of Honshu and in southwestern Hokkaido. *Limopsis* ***oliveri,*** sp. nov. is an endemic species living off Iturup Island near Hokkaido, and is most similar to the unique extinct species, *L. adamsiana* Yokoyama, 1920. In the Plio-Pleistocene, the diversity of limopsids extensively increased especially in and around the Japanese Islands, probably due to the speciation by the biogeographical isolation. It has been maintained today by the recruitment of some species including *L.* ***oliveri,*** sp. nov. which might have arisen very recently.

INTRODUCTION

The genus *Limopsis* Sassi, 1827, comprises bivalves mainly living in the lower sublittoral to the upper bathyal zones. Habe (1977) classified the Recent *Limopsis* of Japan into the following six genera: *Limopsis* Sassi, 1827; *Empleconia* Dall, 1908; *Crenulilimopsis* Kuroda & Habe in Kuroda et al., 1971; *Oblimopa* Iredale, 1939; *Nipponolimopsis* Habe, 1951; and *Cyrenolimopsis* Habe, 1953. However, when he studied the functional morphology and evolution of Limopsidae, Oliver (1981) did not subdivide the genera of Limopsidae, but did recognize 13 morphological classes. He also treated *Nipponolimopsis* as a genus of Philobryidae because of the presence of a prodissoconch cap. Thus, in this paper we also treat all limopsid species other than *Nipponolimopsis* as *Limopsis,* based on Oliver (1981).

In recent decades, the senior author has studied the taxodont bivalves of the Plio-Pleistocene Omma-Manganji fauna (Otuka, 1939) in the Japan Sea side of Honshu and southwestern Hokkaido (Amano & Narita, 1992; Amano, 1996). The junior author has studied the Recent boreal bivalves of Far East Russia (Lutaenko, 1999, 2002). We have found two new species of *Limopsis* in the Plio-Pleistocene Omma-Manganji fauna and one new species from the off-shore waters of Iturup Island near Hokkaido. In this paper, we describe these new species and summarize the history of Cenozoic limopsids in the northwestern Pacific.

MATERIALS AND METHODS

Fossil specimens of new species were collected from the following localities (Figure 1):

Loc. 1. 400 m upstream of Tonogedo-zawa, Futatsui Town (40°15′48″N, 140°11′50″E), Akita Prefecture, northernmost Honshu.

Loc. 2. 50 m upstream of small stream at Okawa, Yakumo Town (42°20′18″N, 140°17′00″E), Hokkaido.

These fossil specimens are housed at the Joetsu University of Education (JUE). In addition, we examined fossils stored at Tohoku University (IGPS) and the Museum of the University of Tokyo (UMUT).

Some Recent empty shells of a new species were obtained from the following localities.

Loc. 3. Dobroe Nachalo Bay (44°42′8″N, 147°3′8″E), Okhotsk Sea side of Iturup Island: gravel at the depth of 218 m.

Loc. 4. Dobroe Nachalo Bay (44°43′15″N, 147°7′8″E), Okhotsk Sea side of Iturup Island: gravel at the depth of 54 m.

The type material of Recent specimens is housed at the Zoological Museum, Far East State University (ZMFU). We also examined the Recent specimens at the National Science Museum (NSM) and compared the type specimens with the fossil species *Limopsis adamsiana* Yokoyama, 1920, stored at the Museum of University of Tokyo (UMUT) and with the Recent species *L. brazieri,* Angas, 1871, housed at the British Museum of Natural History (BMNH).

According to the classification of morphological classes by Oliver (1981), we paid special attention to resilifer shape, presence or absence of marginal crenulations, surface sculpture, and presence of cleft. In addition, on the Recent specimens, we carefully examined the type of periostracum as well as ligament type.

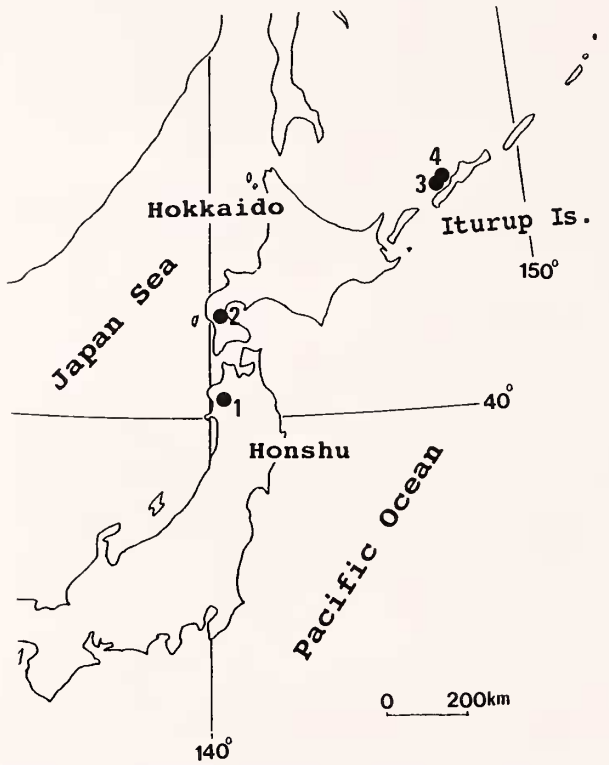


Figure 1. Localities of new species of *Limopsis*. Closed circles with numbers are the localities and the locality numbers.

SYSTEMATICS

Family LIMOPSIDAE Dall 1895

Genus *Limopsis* Sassi, 1827

Limopsis satoi Amano & Lutaenko, sp. nov.

(Figures 2a, b, 3a, b, 4a, b)

Limopsis tokaiensis Yokoyama. Chinzei, 1973: pl. 14, fig. 8.
Non L. tokaiensis Yokoyama, 1910.

Diagnosis: A medium-sized *Limopsis* with thick and subcircular shell and with strong teeth arranged in arcuate series.

Holotype: Length 15.1 mm, height 13.8 mm, width 8.1 mm, both valves, JUE 15736.

Paratypes: Length 15.4 mm, height 15.4 mm, thickness 4.9 mm, right valve, JUE 15737-1; Length 15.7 mm, height 13.5 mm, thickness 4.2 mm, right valve, JUE 15737-2; Length 15.4 mm, height 14.3 mm, thickness 4.4 mm, right valve, JUE 15737-3; Length 12.6 mm, height 11.4 mm, thickness 3.3 mm, right valve, JUE 15737-4; Length 15.3 mm, height 14.2 mm, thickness 4.7 mm, left valve, JUE 15737-5; Length 15.6 mm, height 13.4 mm, thickness 4.9 mm, left valve, JUE 15737-6.

Type locality: 400 m upstream of Tonogedo-zawa, Futatsui Town, Akita Prefecture (40°15′48″N, 140°11′50″E; Loc. 1); very fine-grained sandstone of the upper Pliocene Sasaoka Formation.

Table 1

Associated species of *Limopsis* ***hokkaidoensis*** Amano & Lutaenko, sp. nov. at the type locality (Loc. 2).

Species	Depth (m)*
Limopsis tokaiensis Yokoyama, 1910	—
Monia macroschisma (Deshayes, 1839)	0–60
Chlamys (*Leochlamys*) *tanassevitchi* (Khomenko, 1934)	—
Yabepecten tokunagai (Yokoyama, 1911)	—
Acesta goliath (Sowerby, 1883)	100–1417
Cyclocardia crassidens (Broderip & Sowerby, 1829)	35–360
Tridonta borealis Schumacher, 1817	10–230
T. alaskensis (Dall, 1903)	7–500
Profulvia kurodai (Sawada, 1962)	—
Ezocallista brevisiphonata (Carpenter, 1865)	0–30
Nettastomella japonica (Yokoyama, 1920)	0–300
Puncturella nobilis (A. Adams, 1860)	0–85
Littorina sitkana Philippi, 1846	0
Trichamathina nobilis (A. Adams, 1867)	50–100
Fusitriton oregonensis (Redfield, 1846)	0–420
Boreoscala greenlandica (Perry, 1811)	0–650
Volutopsius middendorffi (Dall, 1891)	22–450
Colus nobilis Dall, 1919	50–100
Volutomitra alaskana (Dall, 1902)	100–200

* After Higo et al. (1999).

Stratigraphic and geographic distribution: Upper Pliocene, Sasaoka Formation; known only from the type locality.

Description: Shell medium in size, thick, compressed, subcircular, equivalve, inequilateral. Antero-dorsal margin broadly rounded, grading into rounded anterior end; ventral margin well rounded; postero-dorsal margin nearly straight, gently sloping into broadly arcuate posterior margin. Umbo partly dissolved, but anteriorly situated at about two-fifths of shell length. Surface sculptured by distinct growth lines as well as very shallow and fine radial grooves. Resilifer triangular and shallow. Hinge plate wide, with strong teeth arranged in arcuate series, seven to 12 in anterior and seven to 11 in posterior series. Heteromyarian condition advanced, posterior adductor muscle scar much larger than anterior one, distinct ridge running behind anterior muscle scar. Inner margin smooth. Inner surface covered by very weak radial striations.

Discussion: This new species was collected from very fine-grained sandstone of the upper Pliocene Sasaoka Formation, in association with *Acila* (*Truncacila*) *insignis* (Gould, 1861), *Limatula* sp., and *Cyclocardia ferruginea* (Clessin, 1888). Based on the depth range of these species

(Higo et al., 1999), *Limopsis* ***satoi*** might have lived in a lower shelf environment.

Chinzei (1973) illustrated a specimen from the Upper Pliocene Sasaoka Formation near the type locality of *Limopsis* ***satoi*** as *L. tokaiensis* Yokoyama, 1920. The type material of *L. tokaiensis* is characterized by rather thin, slightly concave sides of the hinge plate and a wide resilifer (Figure 5). These characters cannot be observed in the Chinzei's specimen. Alternatively, Chinzei's specimen can be identified as *L.* ***satoi*** because of its subcircular shell, continuous large teeth, and relatively wide resilifer. Moreover, *L.* ***satoi*** differs from *L. tokaiensis* in having smaller and higher shells.

This new species belongs to the morphological class IV of Oliver (1981) because of its thick shell, strong teeth, and advanced heteromyarian condition.

Etymology: This species is named after Dr. Tokiyuki Sato, Akita University, who studies calcareous nannofossils and offered the type material to the authors.

Limopsis ***hokkaidoensis*** Amano & Lutaenko, sp. nov.
(Figures 7, 8a, b, 9a, b, 10)

Limopsis tokaiensis Yokoyama. Iwai, 1959: pl. 2, figs. 8a, b (not figs. 9a, b); Hatai et al., 1961: pl. 1, figs. 10a, b; Iwai: 1965, pl. 14, figs. 8a, b (not figs. 9–11). *Non L. tokaiensis* Yokoyama, 1910.

Limopsis (*Empleconia*) *tokaiensis* Yokoyama. Zhikova et al., 1972, pp. 104–105, pl. 31, figs. 2a,b. *Non L. tokaiensis* Yokoyama, 1910.

Limopsis (*Empleconia*) *cumingii* (Adams). Mizuno & Amano, 1988, pl. 14, figs. 2, 3. *Non L. cumingi* (Adams, 1863).

Diagnosis: Large *Limopsis* with thick, compressed, and ovate shell, infolded postero-dorsal margin, and shallow resilifer.

Holotype: Length 26.5 mm, height 24.4 mm, thickness 6.4 mm, left valve, JUE 15739.

Paratypes: Length 26.7 mm, height 22.8 mm, thickness 5.8 mm, right valve, JUE 15740-1; Length 40.9 mm, height 25.3 mm, thickness 7.1 mm, left valve, JUE 15740-2.

Type locality: 50 m upstream of small stream at Okawa, Yakumo Town, Hokkaido (42°20′18″N, 140°17′00″E; Loc. 2); medium-grained sandstone of the lower Pleistocene Setana Formation.

Stratigraphic and geographic distribution: Pliocene Parusnaya Formation of Iturup Island (Zhidkova et al., 1972). Upper Pliocene Kuwae Formation in Niigata Prefecture (this study). Lower Pleistocene Setana Formation in Hokkaido (this study), Hamada (Hatai et al., 1961) and Higashimeya (Iwai, 1959, 1965) formations in Aomori Prefecture and Haizume (this study) and Kota (Mizuno & Amano, 1988) formations in Niigata Prefecture.

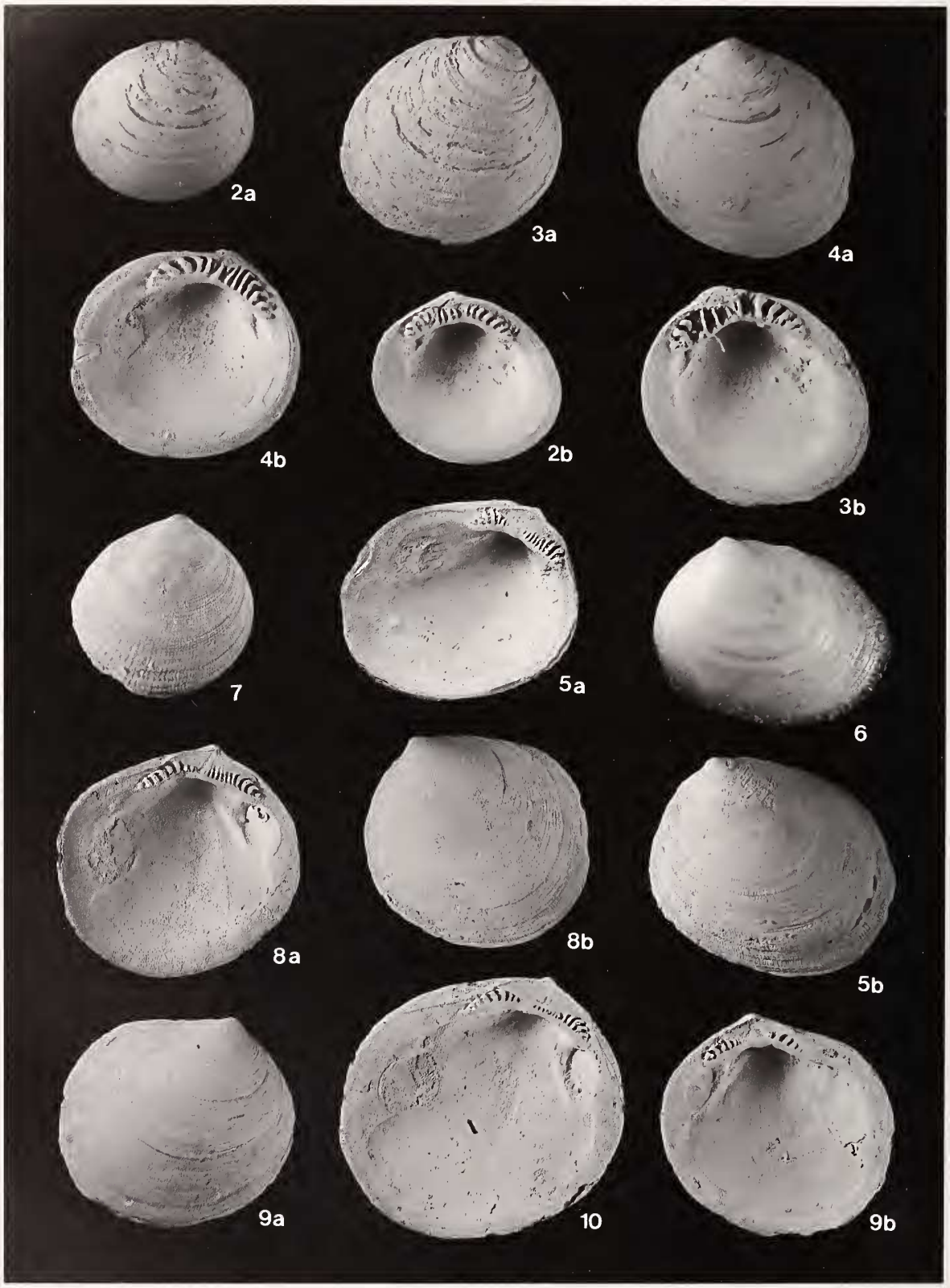
Description: Shell large, compressed, ovate, equivalve, inequilateral. Antero-dorsal margin broadly rounded, grading into well rounded anterior margin; ventral margin well rounded, grading into rounded posterior margin; postero-dorsal margin straight and deeply infolded. Umbo produced, orthogyrate, and situated anteriorly at about one-third of shell length. Surface ornamented with distinct fine growth lines and many fine radial striations. Dorsal area of ligament very wide with oblique, shallow, and narrow resilifer. Hinge plate wide, posterior portion short, with six to 11 anterior teeth and five to eight posterior teeth. Anterior muscle scar orbicular, strongly impressed, with distinct ridge behind; posterior scar subquadrate, larger than anterior and with weak ridge behind. Inner margin smooth. Inner surface covered by very weak radial striation.

Discussion: *Limopsis* ***hokkaidoensis,*** sp. nov. differs from the Recent species, *L. cumingi* (A. Adams, 1863) (Figure 6) by having a larger and higher shell. Moreover, judging from the associated fauna (Table 1), the new species is boreal while *L. cumingi* now lives in warm waters south to Choshi, Chiba Prefecture, central Japan.

Limoposis vaginata Dall, 1891, is another similar species now living in the northern Pacific region. However, it can be easily distinguished from *L.* ***hokkaidoensis*** by its elongate shell with a more deeply infolded dorsal margin and much more difference between the size of anterior and posterior muscle scars.

Iwai (1959, pl. 2, figs. 8a, b; 1965, pl. 14, figs. 8a, b) and Hatai et al. (1961) recorded *Limopsis tokaiensis* Yokoyama, from the lower Pleistocene Higashimeya and Hamada formations, both in Aomori Prefecture, northernmost Honshu. However, the Hamada specimens stored at Tohoku University (IGPS 90510) have large ovate shells with a deeply infolded postero-dorsal margin and short posterior teeth. Moreover, both Higashimeya and Hamada specimens do not have concavities on both sides of the hinge plate or straight dorsal margin which are characteristics of *L. tokaiensis*. Zhidkova et al. (1972) also reported *L.* (*Empleconia*) *tokaiensis* from the Pliocene Parusnaya Formation of Iturup Island. However, this material can be identified as *L.* ***hokkaidoensis*** because it has a large ovate shell with a deeply infolded postero-dorsal margin. The lectotype of *L. tokaiensis* (UMUT CM 20652; Figure 5) has an infolded dorsal margin thus leading to taxonomic confusion. However, adult specimens of *L. tokaiensis* have a weakly infolded postero-dorsal margin at both ends of the hinge plate, sometimes becoming pointed at the base of the ligament, and having a straight dorsal margin as in *L. tajimae* Sowerby, 1914.

Mizuno & Amano (1988) illustrated small subcircular shells from the lower Pleistocene Kota Formation in Niigata Prefecture (Figure 7). Judging from their ratio of length and height, they can be included in *L.* ***hokkaidoensis,*** not in *L. cumingi*. Generally, the shell size of


2a
3a
4a
4b
2b
3b
7
5a
6
8a
8b
5b
9a
10
9b

the southern population collected from Niigata Prefecture is smaller than that of Aomori and Hokkaido populations. Consequently, *L. **hokkaidoensis*** is a characteristic member of the Pliocene to early Pleistocene Omma-Manganji fauna (Otuka, 1939) along the Japan Sea side of Honshu and Southwestern Hokkaido (Figure 11).

This new species belongs to morphological class III of Oliver (1981) because it has a deeply infolded postero-dorsal margin.

Etymology: This species is named after the type locality.

*Limopsis **oliveri*** Amano & Lutaenko, sp. nov.
(Figures 12a, b, 13a, b, 16)

Diagnosis: Small *Limopsis* with a thin and roundly trigonal shell, prosogyrate umbo, and with dorsal margin not infolded.

Holotype: Length 9.2 mm, height 8.3 mm, width 4.6 mm, both valves, ZMFU XII-19680-Bv-2969.

Paratypes: Length 9.0 mm, height 8.5 mm, width 5.2 mm, both valves, ZMFU XII-19681-Bv-2970-1; Length 9.1 mm, height 8.8 mm, thickness 2.8 mm, right valve, ZMFU XII-19681-Bv-2970-2; Length 8.9 mm, height 8.0 mm, thickness 2.3 mm, right valve, ZMFU XII-19681-Bv-2970-3; Length 11.1 mm, height 10.2 mm, thickness 3.0 mm, left valve, ZMFU XII-19681-Bv-2970-4; Length 10.6 mm, height 9.8 mm, thickness 2.8 mm, left valve, ZMFU XII-19681-Bv-2970-5.

Type locality: Dobroe Nachalo Bay (44°42′8″N, 147°3′8″E), Okhotsk Sea side of Iturup Island (Loc. 3); gravel, at 218 m.

Geographic distribution: Dobroe Nachalo Bay, Okhotsk Sea side of Iturup Island; known only from the type locality (Loc. 3) and Loc. 4 near the type locality (ZMFU XII 19682-BV-2971) at depths of 54–218 m.

Description: Shell small, thin, compressed, subtriangular, equivalve, subequilateral. Antero-dorsal margin broadly arcuate, grading into anterior margin; ventral margin broadly arcuate; postero-dorsal margin nearly straight, gently sloping into subtruncated posterior margin. Umbo prosogyrate, produced, situated at two-fifths anteriorly to midpoint of shell length. Surface sculptured by distinct growth lines and faint fine radial striations. Dorsal area short, ligament in shallow and wide resilifer. Hinge plate with five to seven anterior and six to eight posterior teeth. Heteromyarian condition slight, anterior adductor muscle scars being slightly larger. Inner margin smooth. Inner surface covered by distinct radial striations. Long and fine periostracal bristles yellowish brown, lying flat against shell and forming a narrow fringe.

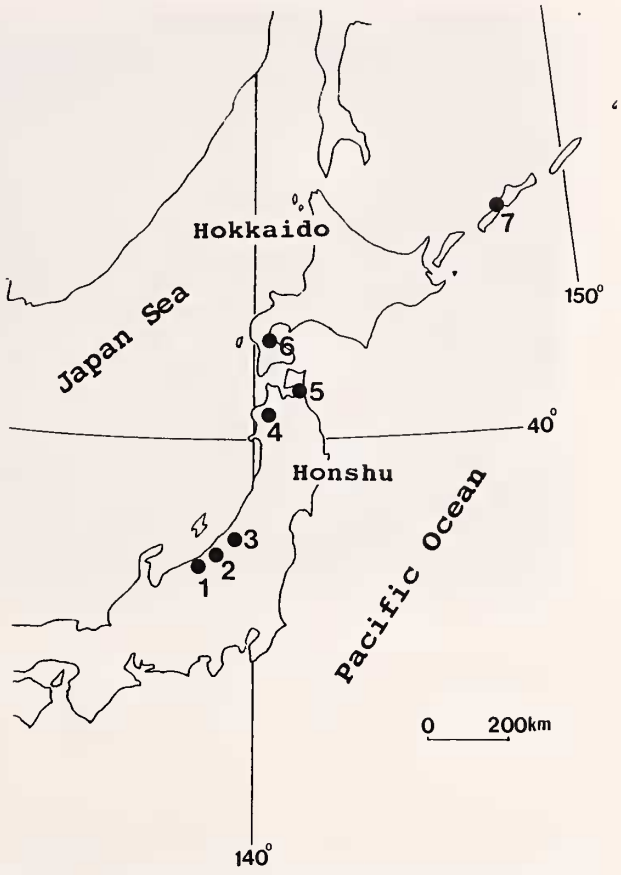


Figure 11. Distribution of *Limopsis **hokkaidoensis*** Amano & Lutaenko, sp. nov. 1. Kota Formation (Mizuno & Amano, 1988). 2. Haizume Formation (this study). 3. Kuwae Formation (this study). 4. Higashimeya Formation (Iwai, 1959, 1965). 5. Hamada Formation (Hatai et al., 1961). 6. Setana Formation (type locality, this study). 7. Parusnaya Formation (Zhidkova et al., 1972).

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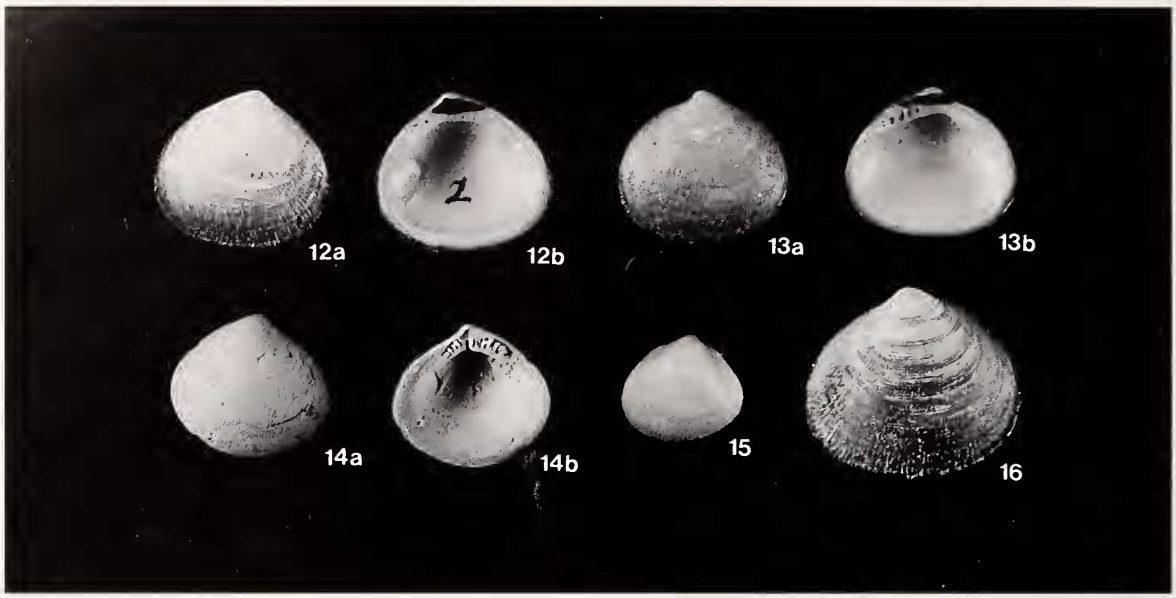
Figures 2–10. Fossil new species of *Limopsis* and their compared species. Figures 2–4. *Limopsis **satoi*** Amano & Lutaenko, sp. nov.. Figures 2a, b. Paratype, length = 12.6 mm, JUE no. 15737-4. Figures 3a, b. Paratype, length = 15.4 mm, JUE no. 15737-3. Figures 4a, b. Holotype, length = 15.1 mm, JUE no. 15736: Loc. 1. Figure 5. Lectotype of *Limopsis tokaiensis* Yokoyama, length = 27.8 mm, UMUT CM 20652, Koshiba, Kanagawa Pref., Japan. Figure 6. *Limopsis cumingi* (A. Adams), length = 15.9 mm, JUE no. 15743, Shionomisaki, Wakayama Pref., Japan. Figures 7–10. *Limopsis **hokkaidoensis*** Amano & Lutaenko, sp. nov.. Figure 7. *Limopsis* (*Empleconia*) *cumingii* (Adams) by Mizuno & Amano (1988), length = 12.6 mm, JUE no. 15085, Joetsu, Niigata Pref., Japan. Figures 8a, b. Holotype, length = 26.5 mm, JUE no. 15739. Figures 9a, b. Paratype, length = 26.7 mm, JUE no. 15740-1: Figure 10. Paratype, length = 40.9 mm, JUE no. 15740-2: Loc. 2.



Figures 12–16. Recent new species of *Limopsis* and its compared species. Figures 12, 13, 16. *Limopsis* ***oliveri*** Amano & Lutaenko, sp. nov.. Figures 12a, b, Paratype, length = 9.1 mm, ZMFU XII-19681-Bv-2970-2. Figures 13a, b. Holotype, length = 9.2 mm, ZMFU XII-19680-Bv-2969. Figure 16. Paratype, length = 11.1 mm, ZMFU XII-19681-Bv-2970-4: Loc. 3. Figures 14a, b. *Limopsis adamsiana* Yokoyama, lectotype, length = 8.2 mm, UMUT CM 20679, Koshiba, Kanagawa Pref. Japan. Figure 15. *Limopsis brazieri* Angas, syntype, length = 5.0 mm, BMNH 1871.7.5.30, Port Jackson, Southeast Australia.

Discussion: *Limopsis* ***oliveri*** is most similar to the extinct species *L. adamsiana* Yokoyama, 1920, which ranges from the Pliocene to middle Pleistocene in Kanto Region, Pacific side of central Honshu. *Limopsis* ***oliveri*** and *L. adamsiana* share such characteristics as small size, prosogyrate umbo, subtriangular shape, subisomyarian muscle scars, and strongly sculptured inner surface. The shell surface of the lectotype of *L. adamsiana* (UMUT CM 20679; Figure 14) from the Pleistocene Koshiba Formation in Kanagawa Prefecture is water worn. However, most specimens from the lower Pleistocene Higashihigasa Formation in Chiba Prefecture housed at Tohoku University (IGPS 25160) have fine and distinct concentric lines as in *L.* ***oliveri.*** *Limopsis* ***oliveri*** slightly differs from *L. adamsiana* in having no infolding at the anterior dorsal margin just anterior the umbo. Although there is no information on the periostracum and ligament of *L. adamsiana,* we believe that the present new species is a descendant form of *L. adamsiana.*

Limopsis brazieri Angas, 1871, living in southeast Australia, was designated as the type species of *Phrynelima* by Iredale (1929). *L. brazieri* is also similar to *L.* ***oliveri*** in its small size, prosogyrate umbo, concentric surface sculpture, and radial striations on the inner surface. However, the syntypes of *L. brazieri* (BMNH 1871.7.5.30; Figure 15) are easily distinguished from *L.* ***oliveri*** in having a smaller shell, a more produced beak, a straight dorsal margin, thin periostracum near ventral margin, subtruncated anterior margin, and narrow triangular ligament.

Limopsis lilliei Smith, 1885, living in the seas around the Antarctic, resembles *L.* ***oliveri*** in its small size, subisomyarian muscle scars, and strongly sculptured inner surface. However, *L. lilliei* has a more tumid shell, a less prosogyrate umbo, a unique ligament (D type of Oliver, 1981), and a pilose periostracum.

This new species belongs to morphological class XII of Oliver (1981) because of its small shell, prosogyrate umbo, and subisomyarian muscle scars.

Etymology: This species is named after Dr. P. Graham Oliver, National Museum of Wales who has contributed to our knowledge of the functional morphology and evolution of *Limopsis.*

HISTORY OF CENOZOIC *LIMOPSIS* IN THE NORTHWESTERN PACIFIC

There is no Paleogene record of *Limopsis* in the northwestern Pacific. *Limopsis* of the northwestern Pacific area diversified somewhat in the early to early middle Miocene. From western and central Honshu, eastern Hokkaido, southwestern Sakhalin, and southern Kurile Islands, the following species have been recorded (Tsuda, 1959; Araki, 1960; Okamoto et al., 1986; Morita et al., 1996; Ilyina, 1954; Zhidkova et al., 1972): *L. osawanoensis* Tsuda, 1959; *L. cuniingi* (A. Adams, 1863); *L.* sp. by Okamoto et al. (1986); *L. tsubetsuensis* Morita & Titova in Morita et al., 1996; *L.* sp. by Ilyina (1954); *L. oblonga* A. Adams, 1860.

In the Plio-Pleistocene, limopsids extensively diversified especially in and around the Japanese Islands. Nine species have been described in and around Japan; *L. tajimae* Sowerby, 1914; *L. uwadokoi* Oyama, 1951; *L. tokaiensis* Yokoyama, 1910; *L. auritoides* Yokoyama, 1920; *L. obliqua* A. Adams, 1863; *L. cumingi* (A. Adams, 1863); *L. oblonga* (A. Adams, 1860); *L. japonica* (A. Adams, 1863); *L. adamsiana* Yokoyama, 1920 (Hatai & Nisiyama, 1952; Zhidkova et al., 1972; Masuda & Noda, 1976). Two new species described here, *L. **satoi*** and *L. **hokkaidoensis*** confined to the Plio-Pleistocene deposits mainly in the Japan Sea borderland, are added to this list. In the Pliocene to early Pleistocene, the Japan Sea became semi-enclosed (Ogasawara, 1994) and enabled many endemic species of Omma-Manganji fauna (Otuka, 1939) including *L. **satoi*** and *L. **hokkaidoensis*** to arise in the Pliocene. However, by the end of early Pleistocene, they became extinct because of environmental deterioration in the Japan Sea after the middle Pleistocene like other deep-water species (Amano et al., 1996).

Some recent species, *L. tajimae, L. uwadokoi, L. obliqua, L. cumingi, L. oblonga,* and *L. japonica* have survived in and around Japanese Islands. Among them, four species (*L. tajimae, L. cumingi, L. oblonga,* and *L. japonica*) are also known from Korea and three species (*L. tajimae, L. oblonga,* and *L. japonica*) are reported from China (Li, 1990; Kwon et al., 2001). Four recent species of the northwestern Pacific, *L. belcheri* (Adams & Reeve, 1850), *L. crassula* Habe, 1953, *L. kurilensis* Scarlato, 1981, and *L. **oliveri*** sp. nov. have no fossil record and might have arisen very recently.

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