

Two warm-water species of Trochoidea (Gastropoda) from Pliocene deposits on the Japan Sea side of Honshu, Japan, with remarks on the influence of the onset of Northern Hemisphere glaciation

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ABSTRACT

Two warm-water trochoidean gastropods are studied. One of them, *Monodonta joetsuensis* new species, is the first Pliocene record of this genus in Japan. Another, *Pomaulax omorii* (Shibata, 1957), is distributed widely along the Japan Sea side of Honshu. In the Japan Sea borderland, both species are confined to late Pliocene deposits and became extinct as a result of cooling at the onset of Northern Hemisphere glaciation near the end of the Pliocene (2.75 Ma). It has become clear that thirteen shallow-water suspension-feeding bivalves, including Miocene relict forms, and eleven grazing or predatory/scavenging gastropods that mostly lived in warm shallow-water disappeared from the Japan Sea during this cooling event.

INTRODUCTION

Many species of trochoidean gastropods live on rocky bottoms (Hickman and McLean, 1990). Fossils of these species are not plentiful, and are usually collected from sandy sediments or turbidites, deeper than their original living habitats. Two extinct species of Trochoidea have been recovered from the upper Pliocene deposits on the Japan Sea side of Honshu. One of them, a small trochid gastropod, is a new species of *Monodonta*, and the other, is a large turbinid gastropod *Pomaulax omorii* (Shibata, 1957). *Pomaulax omorii* was originally described by Shibata (1957) as *Astraea (Pachypoma) omorii* from the lower Pliocene Ochiai Formation in Kanagawa Prefecture, on the Pacific side of Honshu. On the Japan Sea side of Honshu, this species was illustrated as *Astralium (Distellifer) aff. rhodostoma* (Lamarck, 1822) by Amano et al. (2000b) from the upper Pliocene Tentokuji Formation. Fortunately, I collected some well-preserved specimens of *Pomaulax omorii* from the upper Pliocene formations in Niigata.

I describe the new species of *Monodonta*, redescribe the features of *Pomaulax omorii* from the Japan Sea borderland and discuss their paleogeographic significance.

Accordingly, I also discuss the influence of the onset of major Northern Hemisphere glaciation to the molluscan fauna in the Japan Sea borderland.

MATERIALS AND METHODS

Monodonta joetsuensis new species was recovered from an alternation of fine-grained sandstone, yielding pebbles and plant fragments, and dark gray mudstone of the Nadachi Formation, 220 m upstream from a tributary 0.8 km upstream from the Fujikake-dani River in Joetsu City, Niigata Prefecture (Figure 1, Loc. 4). From this locality, 18 species of gastropods and 22 bivalves co-occurred, crowded together (Table 1). Many shallow-water species were carried into deep water by turbidity currents—most bivalves, even the deep-sea bivalve *Calyptogena pacifica* Dall, 1891 are disarticulated at this site. Two warm-water species, *Thais clavigera* (Küster, 1860) and *Veremolpa micra* (Pilsbry, 1904), are associated with many cold-water or endemic extinct species. Calcareous nannofossils from this locality were identified by Tokiyuki Sato (Akita University), who indicated that their ages fall within the lower to middle part of zone NN16 (Martini, 1971; 3.66–2.75 Ma).

Seventeen specimens of *Pomaulax omorii* were obtained from pebble-bearing sandstones of the lower part of the Tentokuji Formation at the large cliff along the Sannai River in Kami-Sannai, Akita City, Akita Prefecture (Figure 1, Loc. 1). This locality corresponds to the fossil locality described by Shimamoto and Koike (1986) and the Loc. 2 of Amano et al. (2000b). The age of the Tentokuji Formation was assigned to the lower to middle zone NN16 (3.85–2.75Ma) via calcareous nannofossils (Amano et al., 2000). Some warm-water species such as *Erronea* sp. and *Oliva mustelina* Lamarck, 1811 were collected with many cold-water mollusks (Amano et al., 2000b; Table 2). One specimen of *Pomaulax omorii* was also collected from a calcareous concretion yielding plant debris included in siltstone of the upper part of the Araya

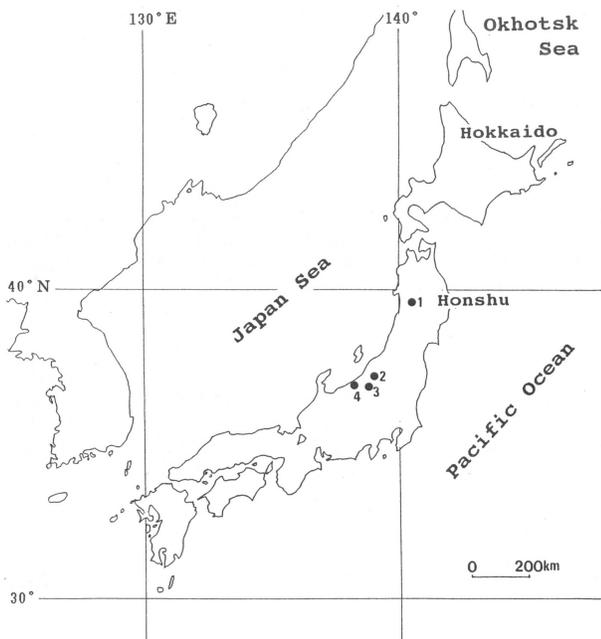


Figure 1. Localities of fossils.

Formation on the bank of the Maekawa River, 600 m south of Kiyamazawa, Nagaoka City, Niigata Prefecture (Figure 1, Loc. 2). The age of the upper part of this formation was assigned to the late Pliocene based on foraminifers by Kobayashi et al. (1991). Other than *Nemocardium samarangae* (Makiyama, 1934), the associated fauna consists of cold-water or extinct endemic species (Table 1). One more well-preserved specimen of *Pomalulax omorii* was collected from sandy siltstone of the Shitoka Formation, 550m upstream in the Shitoka River in Minami Uonuma City, Niigata Prefecture (Figure 1, Loc. 3). The age of the Shitoka Formation was assigned to the late Pliocene based on calcareous nannofossils by Amano et al. (2009). Many cold-water species and one warm-water species, *Nemocardium samarangae* (Makiyama, 1934), are associated with this specimen (Table 2).

I have followed the arrangement in Bouchet et al. (2017). All pictures were taken with the specimens covered with ammonium chloride. All specimens are deposited at the National Museum of Nature and Science, Tsukuba (NMNS PM).

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1797
 Subclass Vetigastropoda Salvini-Plawen, 1980
 Order Trochida Cox and Knight, 1960
 Superfamily Trochoidea Rafinesque, 1815
 Family Trochidae Rafinesque, 1815
 Subfamily Monodontinae Gray, 1857

Genus *Monodonta* Lamarck, 1799

Type Species: *Trochus labio* Linnaeus, 1758 by monotypy.

Remarks: According to Williams et al. (2010), the subfamily Monodontinae includes three genera: *Monodonta* Lamarck, 1799, *Austrocochlea* P. Fischer, 1885 and *Diloma* Philippi, 1845. Based on molecular and morphological data, *Austrocochlea* seems to be very close to *Monodonta* (Donald et al., 2005; Williams et al., 2010). However, *Austrocochlea* has narrower spiral cords without any axial grooves, a weak tooth on the inner lip, and very weak crenulations inside the outer lip. *Diloma* differs from *Monodonta* in having no tooth on the inner lip and no crenulations inside the rather thin outer lip.

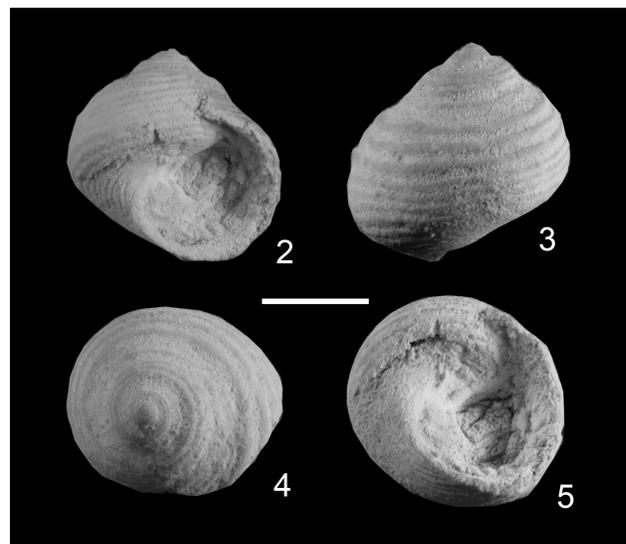
Monodonta joetsuensis new species

(Figures 2–5)

Diagnosis: Small *Monodonta* with 4.25 whorls and rather low spire, sculpture of about 20 spiral cords on last whorl, separated by nearly equal interspaces. Inner lip with prominent basal tooth and eight denticles inside outer lip.

Description: Shell small (9.5 mm in height, 10.4 mm in diameter), rather thick, turbiniform with relatively low spire; protoconch decolated; teleoconch with 4.25 whorls; suture deep. Surface sculptured with growth lines and spiral cords; growth lines distinct, particularly near aperture, and oblique posteriorly; spiral cords separated by nearly equal interspaces, seven on penultimate whorl, twenty on last whorl, cords color alternating light and dark gray; area below substural wide cord concave, sculptured with three fine cords. Aperture circular; columella arched, with prominent basal tooth, deeply notched below; interior of outer lip crenulated by eight denticles.

Holotype: NMNS PM 28267 (9.5 mm in height, 10.4 mm in diameter).



Figures 2–5. *Monodonta joetsuensis* new species, **holotype**, NMNS PM 28267 from the Nadachi Formation. **2.** Apertural view. **3.** Abapertural view. **4.** Apical view. **5.** Basal view. Scale bar = 5 mm.

Table 1. Molluscan fossils associated with *Monodonta joetsuensis* new species from the upper Pliocene Nadachi Formation (Loc. 4 in Figure 1). * warm-water species.

Species
<i>Notoacmaea</i> sp.
<i>Cocculina japonica</i> Dall
<i>Homalopoma noctrum</i> (Gould)
<i>Monodonta joetsuensis</i> new species
<i>Umbinium</i> (<i>Suchium</i>) <i>akitanum</i> Suzuki
<i>Omphalius</i> aff. <i>rusticus</i> (Gmelin)
<i>Bittium</i> sp.
<i>Littorina brevicula</i> (Philippi)
<i>Turritella</i> (<i>Naohaustator</i>) <i>saishuensis motidukii</i> Otuka
<i>Euspira pallida</i> (Broderip and Sowerby I)
<i>Neverita</i> (<i>Glosaulax</i>) <i>vesicalis</i> (Philippi)*
<i>Cryptonatica clausa</i> (Broderip and Sowerby I)
<i>C. janthostoma</i> (Deshayes)
<i>Thais clavigera</i> (Küster)*
<i>Lirabuccinum fuscolabiatum</i> (Smith)
<i>Buccinum</i> sp.
<i>Mitrella bicincta</i> (Gould)
<i>Reticunassa acutidentata</i> (Smith)
<i>Acila</i> (<i>Truncacila</i>) <i>nakazimae</i> Otuka
<i>Leionucula niponica</i> (Smith)
<i>Portlandia</i> (<i>Portlandella</i>) <i>toyamaensis</i> (Kuroda)
<i>Nuculana</i> (<i>Nuculana</i>) <i>onoyamae</i> Otuka
<i>Anadara</i> (<i>Scapharca</i>) <i>ommaensis</i> Otuka
<i>Porterius dalli</i> (Smith)
<i>Glycymeris</i> (<i>Glycymeris</i>) <i>yessoensis</i> (Sowerby III)
<i>Chlamys</i> (<i>Chlamys</i>) <i>cosibensis</i> (Yokoyama)
<i>Anomia chinensis</i> (Philippi)
<i>Felaniella usta</i> (Gould)
<i>Astarte hakodatensis</i> Yokoyama
<i>Tridonta borealis</i> (Schumacher)
" <i>Dinocardium</i> " <i>angustum</i> (Yokoyama)
<i>Macoma</i> (<i>Macoma</i>) <i>calcareae</i> (Gmelin)
<i>Calyptogena pacifica</i> Dall
<i>Pseudamiantis tauyensis</i> (Conrad)
<i>Humularia perlaminosa</i> (Conrad)
<i>Securella</i> sp.
<i>Veremolpa micra</i> (Pilsbry)*
<i>Protothaca tateiwai</i> (Makiyama)
<i>Anisocorbula venusta</i> Gould
<i>Myadora fluctuosa</i> Gould

Type Locality: Small outcrop at 220 m upstream from a tributary 0.8 km upstream from the Fujikake-dani River in Joetsu City, Niigata Prefecture, Japan.

Remarks: This new species can be safely assigned to *Monodonta*, not to *Austrocochlea* nor *Diloma*, because it has a strong basal tooth and strong denticles inside the outer lip. The present species is most similar to the recent *Monodonta australis* Lamarck, 1822, from around the Ogasawara Islands, Okinawa Islands, Mariana Islands, Hawaii, and Australia (Higo et al., 1999) in having a similar number of cords (6–12 on the penultimate whorl and 15–22 on the last whorl) and a similar number of crenulations inside the outer lip (6–13). *Monodonta joetsuensis* new species, however, has narrow spiral cords, as in some species of *Austrocochlea*. In contrast, *M. australis* has flat

spiral cords separated by deep grooves and crossed by vertical grooves near the aperture.

Another recent species, *Monodonta canalifera* Lamarck, 1822, differs from the present species in having fewer (14–18), lower spiral cords.

Etymology: Named after the city name of locality.

Distribution: Late Pliocene, Nadachi Formation in Niigata Prefecture.

Family Turbinidae Rafinesque, 1815

Subfamily Turbininae Rafinesque, 1815

Genus *Pomaulax* Gray, 1850

Type Species: *Trochus japonicus* Dunker, 1844 by subsequent designation.

Remarks: *Astraea* Röding, 1798 previously encompassed species now included in distinct genera such as *Astralium* Link, 1807, *Lithopoma* Gray, 1850, *Megastraea* MacLean, 1970, *Pomaulax* Gray, 1850, and others (see Alf and Kreipl, 2011). This usage is now considered outdated because many paraphyletic clades were included (based on molecular data by Williams (2007, 2012) and Williams et al. (2008)). The type species, *Astraea heliotropium* (Martyn, 1784) is the only living species left in this genus. It is restricted to New Zealand. *Astraea* can easily be distinguished from *Pomaulax* by presence of well-inflated whorls, a very wide umbilicus and many prominent, wide spines at the periphery. *Pachypoma* was established by Gray (1850), based on *Trochus caelatus* Gmelin, 1791 (see Bouchet, 2011). Thus, *Pachypoma* is a junior synonym of *Lithopoma*.

Megastraea, based on *Astraea undosa* (Wood, 1828), most closely resembles *Pomaulax*. *Megastraea* differs from *Pomaulax* by having an operculum with three spiny ridges, and one or two wavy spiral ridges on and above the periphery (see also Alf and Kreipl, 2011). However, recent molecular work shows a close relationship between *Pomaulax* and *Megastraea* (Williams, 2007: 2012).

Lithopoma, from the western Atlantic, is another genus similar to *Pomaulax*. *Lithopoma* can be discriminated from *Pomaulax* in generally having a smaller shell and a periphery with strong axial ridges or with hollow spines (see also Alf and Kreipl, 2011). Molecular data shows a close relationship with *Lithopoma* and *Pomaulax* (Williams, 2007, 2012).

Pomaulax omorii (Shibata, 1957)

(Figures 6–13, 15, 17)

Astraea (*Pachypoma*) *omorii* Shibata, 1957, p. 24, pl. 4, figs. 2a–c.

? *Omphalius pfeifferi* cf. *carpenteri* (Dunker), Ogasawara et al., 1986, pl. 26, figs. 7a–c.

Astralium (*Distellifer*) aff. *rhodostoma* (Lamarck), Amano et al., 2000b, pl. 1, figs. 17a, b.

Astraea omorii Shibata, Matsushima et al., 2003, pl. 4, fig. 1, 2; Shiba et al., 2013, figs. 4.3, 4.4.

?non *Pomaulax omorii* (Shibata), Amano et al., 2011, figs. 5.13, 5.14.

Table 2. Molluscan fossils associated with *Pomaulax omorii* (Shibata) from Loc. 1 (Tentokuji Formation), 2 (Araya Formation), 3 (Shitoka Formation) in Figure 1. * warm-water species.

Species name	Loc.	1	2	3
<i>Puncturella nobilis</i> A. Adams		+		
<i>Lepeta</i> cf. <i>lima</i> Dall		+		
<i>Niveotectura pallida</i> (Gould)		+		
<i>Minolia</i> sp.		+		
<i>Turcica</i> sp.		+		
<i>Littorina</i> sp.		+		
<i>Turritella</i> (<i>Neohaustator</i>) <i>saishuensis</i>		+	+	
<i>saishuensis</i> Yokoyama				
<i>T. (N.) nipponica</i> (Yokoyama)			+	
<i>Erronea</i> sp.*		+		
<i>Neverita</i> (<i>Glossaulax</i>) cf. <i>vesicalis</i>		+		
(Philippi)				
<i>Cryptonatica janthostomoides</i>		+		
(Kuroda and Habe)				
<i>C.</i> sp.				+
<i>Fusitriton izumozakiensis</i> Amano		+	+	
<i>F.</i> aff. <i>oregonensis</i> (Redfield)				+
<i>Mohnia yanamii</i> (Yokoyama)			+	
<i>Neptunea</i> (<i>Neptunea</i>) <i>eos</i> (Kuroda)		+		
<i>N. (N.) insularis</i> (Dall)			+	
<i>N.</i> sp.				+
<i>Buccinum</i> cf. <i>unuscarinatum</i> Tiba			+	
<i>B.</i> sp.		+		+
<i>Oliva mustelina</i> Lamarck*		+		
<i>Fulgoraria prevostiana</i> (Crosse)		+		
<i>F. masudae</i> Hayasaka				+
<i>Propebela</i> sp.				+
<i>Antiplanes contraria</i> (Yokoyama)			+	
<i>Rectiplanes sanctioannis</i> (Smith)			+	+
Conidae gen. et sp. indet.*		+		
<i>Acila</i> (<i>Acila</i>) <i>divaricata</i> (Hinds)		+		
<i>A. (Truncacila) insignis</i> (Gould)		+	+	
<i>A. (T.)</i> aff. <i>castrensis</i> (Hinds)		+		
<i>Leionucula</i> cf. <i>nipponica</i> (Smith)		+		
<i>Malletia inermis</i> Yokoyama		+		
<i>Nuculana</i> (<i>Nuculana</i>) <i>pernula</i> (Müller)				+
<i>Yoldia</i> (<i>Cnesterium</i>) <i>notabilis</i> Yokoyama				+
<i>Y.</i> sp.		+		
<i>Portlandia</i> (<i>Portlandella</i>) <i>japonica</i>		+		
(Adams and Reeve)				
<i>P. (P.) toyamaensis</i> (Kuroda)				+
<i>Arca boucardi</i> Jousseau		+		
<i>Anadara</i> (<i>Anadara</i>) <i>amicula</i> (Yokoyama)		+		
<i>Porterius dalli</i> (Smith)		+		
<i>Glycymeris</i> (<i>Glycymeris</i>)		+		
<i>albolineata</i> (Lischke)				
<i>G. (G.) nipponica</i> (Yokoyama)		+	+	
<i>Limopsis tajimae</i> Sowerby		+		
<i>L.</i> cf. <i>tajimae</i> Sowerby		+		
<i>L. oblonga</i> (A. Adams)			+	
<i>Musculus laevigatus</i> (Gray)		+		
<i>Megacrenella columbiana</i> (Dall)			+	
<i>Chlamys</i> (<i>Chlamys</i>) <i>cosibensis</i> (Yokoyama)		+		
<i>C. (C.) tamurae</i> Masuda and Sawada		+		
<i>Mizuhopecten yokoyamae</i> (Masuda)		+		
<i>M.</i> sp.		+		

(Continued)

Table 2. (Continued)

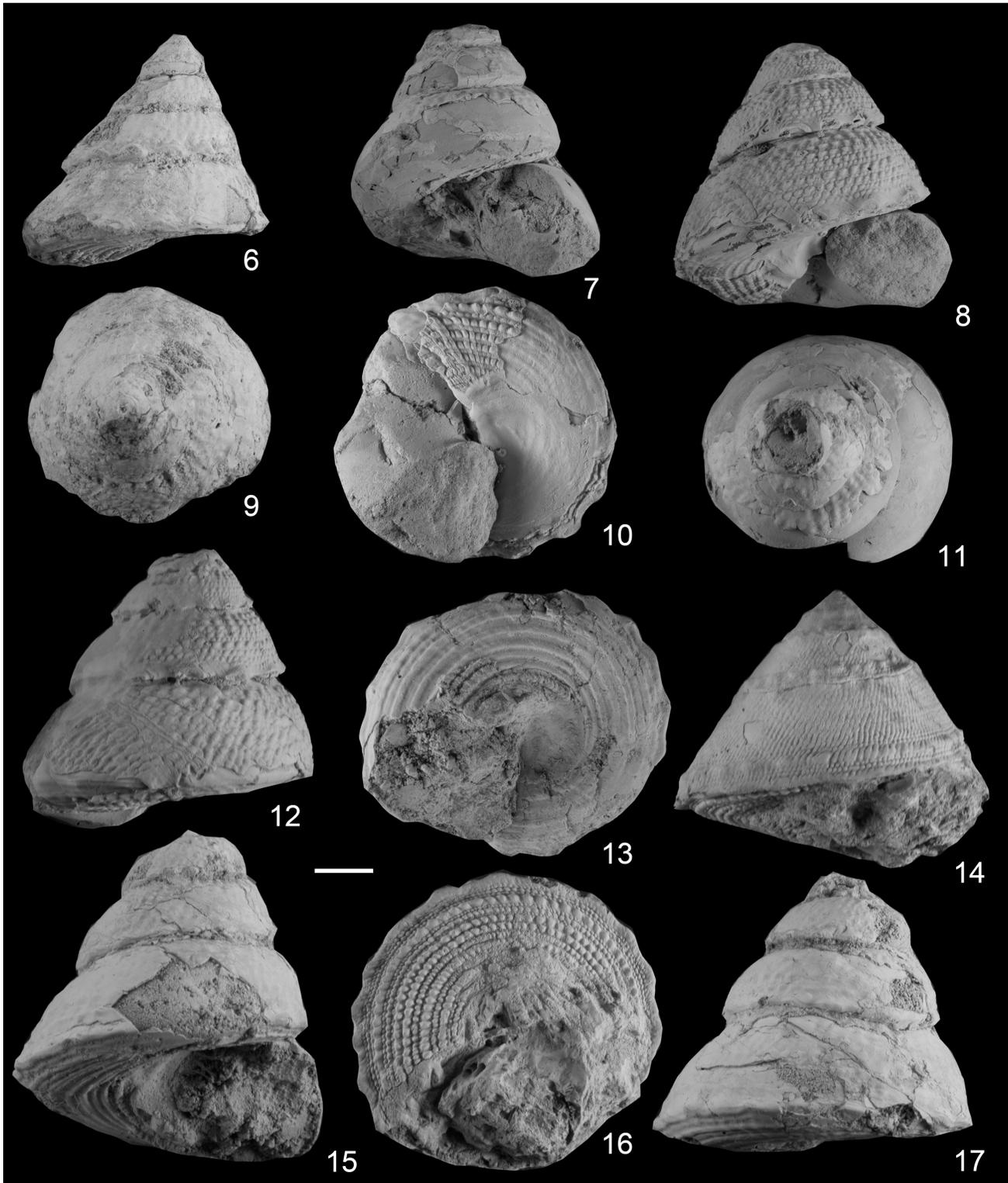
Species name	Loc.	1	2	3
<i>Yabepecten tokunagai</i> (Yokoyama)		+		
<i>Cycladicama cumingii</i> (Hanley)*		+		
<i>Felaniella usta</i> (Gould)		+		
<i>Cardita leana</i> Dunker		+		
<i>C.</i> cf. <i>leana</i> Dunker		+		
<i>Megacardita</i> sp.		+		
<i>Cyclocardia myogadaniensis</i> (Itoigawa)		+		
<i>Tridonta borealis</i> Schumacher		+		
<i>Nemocardium samarangae</i> (Makiyama)*		+	+	+
<i>Clinocardium</i> (<i>Ciliatocardium</i>)		+		
<i>ciliatum</i> (Fabricius)				
<i>Serripes groenlandicus</i> (Bruguière)			+	
<i>Spisula</i> (<i>Mactromeris</i>) <i>voysi</i> Gabb		+		
<i>S. (M.) grayana</i> (Schrenck)		+		
<i>Cadella lubrica</i> (Gould)		+		
<i>Macoma</i> (<i>Macoma</i>) <i>calcareo</i> (Gmelin)		+	+	+
<i>M. (M.) nipponica</i> (Tokunaga)		+		
<i>Securella</i> cf. <i>stimpsoni</i> (Gould)		+		
<i>S. chitaniana</i> (Yokoyama)		+		
<i>Phacosoma tomikawensis</i> (Takagi)		+		
<i>Pseudamiantis</i> cf. <i>tauyensis</i> (Yokoyama)		+		
<i>Pandora wardiana</i> (A. Adams)				+
<i>Entodesma naviculoides</i> Yokoyama		+		

Type Locality: Bank of Hayato River near Ochiai, Kiyokawa Village, Kanagawa Prefecture: Ochiai Formation, Pacific side of central Honshu, Japan.

Original Description: "Shell trochoid, depressed, large, conic-pyramidal, solid, thick, broader than high: surface of whorls flat, declined, sculptured by oblique axial plicae, the plicae weaker on the upper but stronger on the lower where they become somewhat crossed: peripheral margin angulated: on the lower surface sculptured by nine spiral cords, with alternating weak knotted and smooth cords: the columella base somewhat elevated, umbilical area somewhat concave: aperture squarely rounded in outline, outer lip sharply inclined, basal lip thin: columella somewhat concave, smooth, tooth-like swelling on lower part." (Shibata, 1957, p. 24).

Material Examined: Two well-preserved specimens (NMNS PM 28268, 28269) from the Tentokuji Formation, one specimen (NMNS PM 28270) from the Araya Formation, and one well-preserved specimen (NMNS PM 28271) from the Shitoka Formation are examined.

Description of the Specimens from the Japan Sea Side of Honshu: Shell medium in size, attaining 51.8 mm+ in height, 56.8 mm in diameter, rather thick, trochiform with high spire; protoconch decollated; teleoconch of more than five whorls; suture overlapped by periphery of previous whorl. Surface of each whorl rather flat, sculptured by growth lines, axial ribs, and spiral cords; growth lines distinct and very oblique; axial ribs narrow, low, oblique in opposite direction to growth lines, 37 to 42 on penultimate whorl, 35 to 37 on last whorl, becoming more distinct near upper suture; spiral cords 6 to 13 on last



Figures 6–17. Fossil *Pomaulax* species from Japan. **6–13, 15, 17.** *Pomaulax omorii* (Shibata). **6, 9.** NMNS PM 28268. **6.** Abapertural view. **9.** Apical view; Tentokuji Formation. **7, 11.** NMNS PM 28270. **7.** Apertural view. **11.** Apical view; Araya Formation. **8, 10, 12.** NMNS PM 28271. **8.** Apertural view. **10.** Basal view. **12.** Abapertural view; Shitoka Formation. **13, 15, 17.** NMNS PM 28269. **13.** Basal view. **15.** Apertural view. **17.** Abapertural view. **14, 16.** *Pomaulax tyosiensis* (Ozaki), syntype NMNS PM 4257. **14.** Apertural view. **16.** Basal view; Na-Arai Formation. Scale bar = 10 mm.

whorl, forming granulations at intersection with axial ribs. Periphery with undulating carina bearing 14–15 nodes. Base flat, sculptured with five to nine spiral cords. Aperture oblique and squarely rounded in outline; umbilical region covered by rather thick callus.

Remarks: The holotype specimen of *Pomaulax omorii* (Shibata, 1957) attains ca. 61 mm in height and 65 mm in diameter. The topotype specimens illustrated by Matsushima et al. (2003) differ slightly from the holotype by their taller trochiform shape. Matsushima et al. (2003) also pointed out two forms having higher and lower spires.

Amano et al. (2000b) illustrated *Astralium (Distellifer) aff. rhodostoma* (Lamarek, 1822) from the upper Pliocene Tentokuji Formation at Kami-Sannai in Akita City, Akita Prefecture. However, from its size (max. 51.8 mm in shell height, 56.8 mm in diameter) and shell sculpture (37 to 42 axial ribs on the penultimate whorl, 14 to 15 nodes at the periphery, and five to nine spiral cords on the base), this species can be identified as *Pomaulax omorii*.

From the same locality as Amano et al. (2000b), Ogasawara et al. (1986) illustrated a poorly preserved specimen as *Omphalius pfeifferi cf. carpenteri* (Dunker, 1859). Judging from its size, shape and seven spiral cords on the base, this specimen probably can be identified with *Pomaulax omorii*.

Amano et al. (2011) illustrated two specimens as *Pomaulax omorii* from the lowermost Sasaoka Formation at the upstream of Ogurosawagawa River. However, one specimen in their fig. 5.14 has a noded spiral cord above the suture as in species of *Bolma* Risso, 1826.

Pomaulax omorii is closely allied to *P. tyosiensis* (Ozaki, 1954) from the Pliocene Na-arai Formation at Inuwaka in Choshi City, Chiba Prefecture. In the description of *P. tyosiensis*, Ozaki (1954) assigned Nat. Sci. Mus., coll. cat. no. 4257 as the holotype. However, as three specimens are included in the container under no. 4257, they should be considered as syntypes. I have examined all three specimens. *Pomaulax tyosiensis* (Figures 14, 16) differs from *P. omorii* in its two distinct rows of peripheral nodes like those of *Megastraea turbanica* (Dall, 1910), more fine and numerous axial ribs (132 on the last whorl), and more numerous peripheral nodes (13–16).

The Recent species *Pomaulax japonicus* (Dunker in Philippi, 1844) can be easily distinguished from *P. omorii* easily by having a larger and lower shell as well as no spiral cords on the last whorl.

Distribution: On the Pacific side of Honshu, upper Miocene Osozawa Sandstone Member of Iitomi Formation in Yamanashi Prefecture (Shiba et al., 2014) and lower Pliocene Ochiai Formation in Kanagawa Prefecture. On the Japan Sea side of Honshu, upper Pliocene Tentokuji Formation in Akita Prefecture, Araya and Shitoka formations in Niigata Prefecture.

DISCUSSION

Fossils of two species of *Monodonta* have been known from Japan: *M. minuta* Itoigawa and Nishikawa, 1976 and

M. labio (Linnaeus, 1758). The former species has been proposed from the lower Miocene Lower Member of the Bihoku Group in Okayama Prefecture (Itoigawa and Nishikawa, 1976). Nakagawa (2009) reported this species as *M. kanzakii* from the lower Miocene Kohnoura Shale Member of Shimo Formation in Fukui Prefecture. Later, Nakagawa (2018) synonymized *M. kanzakii* with *M. minuta*. The Recent species *M. labio* has been recorded from the middle Pleistocene Sakishima Formation in Mie Prefecture (Itoigawa and Ogawa, 1973), an upper Pleistocene deposit at Akaura in Ishikawa Prefecture (Matsuura, 1977), the Holocene Numa Coral Bed in Chiba Prefecture (Yokoyama, 1924), Holocene deposits at Hachigasaki and Onogi in Ishikawa Prefecture (Matsuura, 1985) and the Holocene Takahama shell bed in Fukui (Nakagawa et al., 1993). All these fossils are associated with warm-water faunas. In conclusion, *Monodonta joetsuensis* new species is the first record of *Monodonta* from the Pliocene in Japan. As mentioned above, two warm-water species are associated with *Monodonta joetsuensis* new species. The warm-water Tsushima current has flowed into the semi-enclosed Japan Sea for the past 4 Ma (Amano et al., 2008; Gallagher et al., 2015). Moreover, the temperature of this thin, in-flowing current in the late Pliocene was 3 to 4 °C higher than that of today (Amano et al., 2008; Amano, 2019). *Monodonta joetsuensis* new species related to *M. australis* possibly appeared along with the inflow of the warm-water current during the late Pliocene.

On the other hand, *Pomaulax omorii* appeared in the late Miocene to early Pliocene warm-water “Zushi-Ochiai type fauna” (Chinzei and Matsushima, 1987) or the “Zushi fauna” (Ozawa and Tomida, 1992) on the Pacific side of central Honshu. In the late Pliocene, this species invaded the Japan Sea to what is now the Akita Prefecture via the warm-water current. The occurrence of this species from the Araya and Shitoka formations seems to be nearly autochthonous. Judging from the habitat depth of living specimens of the associated recent species, the paleodepth of both formations can be estimated as 100–200 m, which is slightly deeper than the Recent Japanese species, *Pomaulax japonicus* (0–100 m; Higo et al., 1999). This estimated paleodepth of *Pomaulax omorii* explains its co-occurrence with some bathyal molluscs from conglomerates of the Ochiai, Iitomi, and Tentokuji formations.

On the Atlantic side of North America and Europe, severe extinction of molluscan species resulted from the cooling event at the onset of major Northern Hemisphere Glaciation (NHG) around the end of the Pliocene (e.g. Stanley and Campbell, 1981; Stanley, 1986; Vermeij, 1991; Vermeij et al., 2008). The end-Pliocene extinction event was also recognized in corals and vertebrates (Woesik et al., 2012; Pimiento et al., 2017). When Sato and Kameo (1996) noticed the drastic change of nanofossils and increase of ice rafted debris (IRD) in the core from North Atlantic Ocean, they named this datum plane as Datum A (2.78 Ma, changed to 2.75 Ma by Sato et al., 2002) indicating the onset of glaciation and traced it in the land deposits in Akita Prefecture. Bailey et al. (2013) considered the onset of NHG at 2.72 Ma (MIS

Table 3. Molluscan species extinct by the end of the Pliocene in the Japan Sea borderland. [○]temperate relict species from the Miocene; * warm-water species.

Species	Formation	Reference
<i>Chlamys ingeniosa tanakai</i> (Akiyama) [○]	Arakurayama F., Ogikubo F.	Amano (1994)
<i>C. insolita</i> (Yokoyama)	Ogikubo F.	Amano (1994)
<i>C. lioica shigaramiensis</i> Amano and Karasawa	Ogikubo F.	Amano and Karasawa (1986)
<i>Mizuhopecten yamasakii</i> (Yokoyama) [○]	Ogikubo F.	Amano (2001)
<i>M. tryblum</i> (Yokoyama) [○]	Ogikubo F., Mita F.	Amano (2001), Amano et al. (2008)
<i>M. naganensis</i> (Masuda)	Joshita F.	Amano and Sato (1995)
<i>Neogenella hokkaidensis</i> (Nomura) [○]	Joshita F.	Amano and Sato (1995)
<i>Kaneharaia ausiensis</i> (Ilyina) [○]	Joshita F., Mita F., Nadachi F.	Amano and Sato (1995), Amano et al. (2008), this study
<i>Protothaca tateiwai</i> (Makiyama) [○]	Joshita F., Tentokuji F., Mita F., Nadachi F.	Amano and Sato (1995), Amano et al. (2000b, 2008), this study
<i>Humilaria perlaminosa</i> (Conrad)	Kuwae F., Nadachi F.	Amano et al. (2000a), this study
<i>Meretrix</i> spp.	Takafu F., Sarumaru F.	Nagamori and Yoshikawa (2019)
<i>Thracia higashinodonoensis</i> Oinomikado [○]	Ogikubo F., Sasaoka F.	Amano (1995), Amano et al. (2011)
<i>Pholadomya kawadai</i> Omori [○]	Tentokuji F.	Amano et al. (2011)
<i>Monodonta joetsuensis</i> new species*	Nadachi F.	this study
<i>Pomaulax omorii</i> (Shibata)*	Tentokuji F., Araya F., Shitoka F.	this study
<i>Vermeijia japonica</i> Amano	Sasaoka F., Kuwae F.	Amano (2019)
<i>Glossaulax didyma coticaeze</i> (Makiyama) [○]	Joshita F.	Amano and Sato (1995)
<i>Ranella yasumurai</i> Amano	Kuwae F.	Amano (1997)
<i>Chicoreus totoniensis</i> (Makiyama)*	Kuwae F.	Amano et al. (2000a)
<i>Babylonia elata</i> (Yokoyama)*	Mita F.	Amano et al. (2008)
<i>Buccinum sinanoense</i> Makiyama	Joshita F.	Amano and Watanabe (2001)
<i>B. shibatense</i> Amano and Watanabe	Kuwae F.	Amano and Watanabe (2001)
<i>Cyllene satoi</i> Amano*	Tentokuji F.	Amano (2019)
<i>Scalptia kurodai</i> (Makiyama)*	Tentokuji F.	Amano et al. (2000b)

G6), based on the abundant IRD deposition in the Nordic Seas and subpolar North Atlantic Ocean. Many cold-water species living now in Hokkaido migrated southward to central Honshu, and some Miocene-type relict mollusks suffered from extinction by the cooling event around 2.75Ma (Amano, 2001, 2007, 2019; Amano et al., 2011). Also, Pacific-type deep-water radiolarians disappeared from the Japan Sea around 2.75 Ma because of the intermittent development of low oxygen conditions in deep water (Itaki, 2016).

The grazers *Monodonta joetsuensis* new species and *Pomaulax omorii* also disappeared at the end of the Pliocene, probably as a result of the cooling event of the NHG. The species that probably became extinct at Datum A in the Japan Sea are shallow-water dwellers (Table 3). They include eight relict bivalves and the naticid *Neverita* (*Glossaurax*) *didyma coticaeze* (Makiyama, 1926) which are temperate-water species that survived from the Miocene, and many warm-water gastropods. Also, it is interesting to note that the extinct species consist of suspension-feeding bivalves and grazing and predatory/scavenging gastropods. When Todd et al. (2002) examined the end-Pliocene extinction of mollusks in the Caribbean region, they found that predatory gastropods and suspension feeding bivalves declined in abundance. This suggests that the nutrient supply changed by the cooling event of the NHG caused the faunal change even in the semi-enclosed Japan Sea.

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