

Two Rare Warm-water Bivalves from the Pliocene Seguchi Formation in Nagano Prefecture, Central Japan

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Abstract: Fossils of *Divalucina soyoae* Habe, 1952 and *Cardilia semisulcata* (Lamarck, 1819) have been recovered from a shallow-water assemblage of the upper Pliocene Seguchi Formation in Nagano Prefecture. The fossils mark the second oldest record of *Divalucina soyoae* and the oldest one of *Cardilia semisulcata*. The oldest fossil record of both species are from the Japan Sea side of Japan, not from the Pacific. Although both species live now in warm waters around Japan, *Divalucina soyoae* has not been found in the Japan Sea today. Moreover, the Pliocene occurrence of *D. soyoae* indicates a shallower habitat than it occupies today.

Keywords: *Divalucina soyoae*, *Cardilia semisulcata*, Pliocene, Seguchi Formation

Introduction

During the Pliocene to early Pleistocene, the Japan Sea became semi-enclosed (*e.g.* Chinzei, 1978; Ogasawara, 1994). As a result, the Omma-Manganji fauna (proposed by Otuka, 1936 as “Manganzian fauna” and renamed as “Omma-Manganzian fauna” by Otuka, 1939; recently used as Omma-Manganji fauna, followed by Chinzei, 1978) which was dominated by cold-water and endemic species, flourished in the Japan Sea (Ogasawara, 1977, 1986; Masuda & Ogasawara, 1981; Amano, 2001, 2007). During the mid-Pliocene warm period (3.264–3.025 Ma), the global mean annual surface temperature was 2.7–4.0°C higher and sea level also was 10–30 m higher than today (Dwyer & Chandler, 2009; Haywood *et al.*, 2013, 2016). This warm climate led to the invasion of warm-water species into the Japan Sea via the Tsushima Strait (Gallagher *et al.*, 2015).

Some warm-water molluscan species have been collected from the upper Pliocene deposits in the Japan Sea side of Honshu (Amano & Karasawa, 1993; Amano *et al.*, 2000a, 2000b, 2008, 2009, 2012). During the Plio-Pleistocene, a large bay existed in northern Nagano and Niigata Prefectures (Kobayashi & Tateishi, 1992; Kosaka *et al.*, 1992). The Pliocene Seguchi Formation is distributed from Iizuna Town in Nagano Prefecture northward to Iiyama City in Nagano Prefecture and to Myoko City in Niigata Prefecture. From the formation both in Iiyama and Myoko Cities, fifty-three species of molluscs were recorded by Nakata & Amano (1991). The molluscan assemblages consist of shallow-water dwellers comprising cold-water species except for the warm-water species *Solamen specitabilis* (A. Adams).

From the Pliocene Seguchi Formation in Iizuna Town, two rare bivalve species, the lucinid *Divalucina soyoae* Habe, 1952 and the cardiliid *Cardilia semisulcata* (Lamarck, 1819) have been recovered in association with some warm-water species. In this paper, I describe these species and discuss the significance of the occurrence of *Divalucina soyoae* and *Cardilia semisulcata*.

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Materials and Methods

Many molluscan fossils have been recovered from the fine-grained sandstone of the Seguchi Formation at the small stream about 1 km southeast of Horikoshi, Iizuna Town, Nagano Prefecture (Fig. 1). As original shell material of all specimens has been dissolved, I made silicone rubber casts for identification. In total, 21 species including *Divalucina soyoae* Habe and *Cardilia semisulcata* can be identified (Table 1). Based on the fission track dating method, the absolute age of the Hiramaru Pumice Tuff, which is intercalated in the Seguchi Formation, was measured as 3.1 Ma (M. Maruyama, pers. comm. in Nakata & Amano, 1991) and 2.9 Ma (Nakamura, 1999). These ages correspond to the mid-Pliocene warm period or slightly later.

I used the ecological data in Higo *et al.* (1999) and Okutani (ed.) (2017) and estimated the depth of each species by using the maximum range in both literatures. All specimens herein treated are stored at the National Museum of Nature and Science, Tsukuba (NMNS).

Taxonomy

Family Lucinidae Fleming, 1828
Subfamily Lucininae Fleming, 1828
Genus *Divalucina* Iredale, 1936

Type species: *Lucina (Cyclas) cumingi* A. Adams & Angas, 1864 (original designation).

Remarks: *Divalucina* can be distinguished easily from *Divaricella* Martens, 1880 by having ribs that do not extend beyond the edge of the shell, a deeply depressed and larger lunule, and a longer anterior adductor muscle scar. *Divalucina* can be separated from *Divalinga* Chavan, 1951 in having a smooth ventral margin and a long anterior adductor muscle scar (see Chavan, 1951, 1969; Dekker & Goud, 1994). *Divalucina* ranges from the middle Eocene to the Recent (Beu & Maxwell, 1990).

Divalucina soyoae Habe, 1952

(Fig. 2A–F)

Divaricella soyoae Habe, 1951: 133, fig. 292 [*nomen nudum*]; Habe, 1977: 129, pl. 25, fig. 1; Baba, 1990: 267–268, pl. 31, fig. 2; Matsukuma, 2000a: 931, pl. 463, fig. 23; Matsukuma, 2017a: 1219, pl. 517, fig. 2.

Divalucina soyoae Habe, 1952b: 160; Habe, 1958: 30, pl. 2, fig. 2; Dekker & Goud, 1995: pl. 2, fig. 19; Huber, 2015: 84, 432.

Divaricella (Divalucina) soyoae – Habe, 1961: 125, pl. 56, fig. 25; Habe, 1964: 183, pl. 56, fig. 25. *non Divaricella soyoae* – Min, 2004: 419, fig. 1361. [= *Petricola divergens* (Gmelin, 1791)]

non Divalucina soyoae – Poppe & Tagaro in Poppe, 2017: pl. 1464, fig. 6. [= *Divaricella ornatissima* (d'Orbigny, 1846)]

Material examined: Six specimens, NMNS PM28231–PM28236.

Description of the Seguchi specimens: Shell small for species (less than 7.4 mm in length), moderately inflated, nearly circular (height/length = 0.77–1.07), equivalve and nearly equilateral. Antero-dorsal margin concave, gradually continuing to subtruncate anterior margin; postero-dorsal margin nearly straight and gently sloping into subtruncate posterior margin; ventral margin broadly arcuate; inner side of ventral margin smooth. Beak low, prosogyrate and centrally located. Lunule deeply depressed and bounded by ridge. Surface ornamented with anteriorly bifurcate oblique ribs

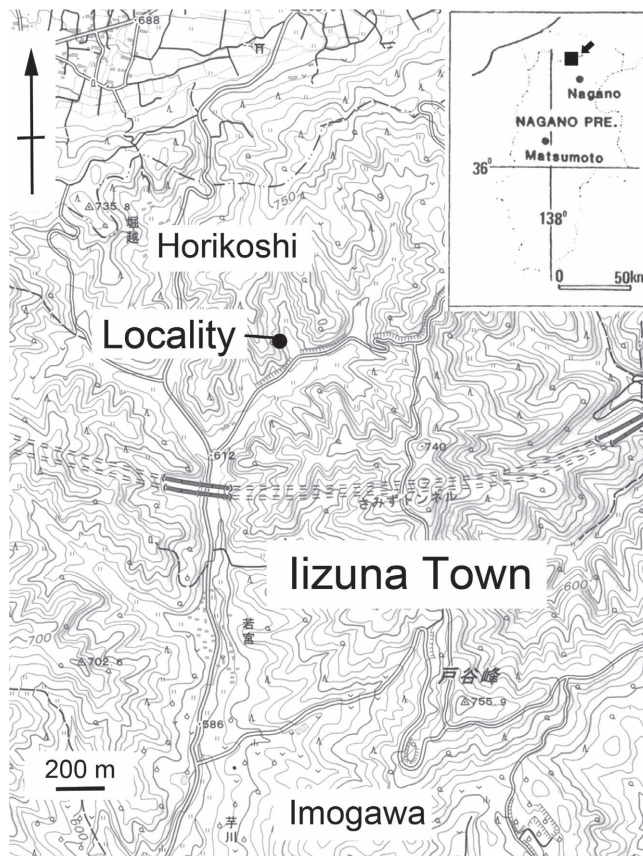


Fig. 1. Map indicating the fossil locality (using the topographical map of “Kaesa”, scale 1:25,000, published by the Geospatial Information Authority of Japan).

with narrower interspaces. Dorsal slope of ribs steep and ventral slope slightly concave. Bifurcation angles ranging from 110° – 135° . Left valve hinge rather narrow, with two cardinal teeth; anterior tooth (2) small and narrow and posterior tooth (4b) relatively thick and not bifid. Posterior lateral tooth of left valve (PII) long, but anterior one unknown. Anterior adductor scar elongated and along entire pallial line; posterior adductor scar ovate. Ventral margin smooth.

Remarks: As already pointed out by Dekker & Goud (1995), although Habe (1951) proposed “*Divaricella soyoae* Habe, n. sp.” for a figure, it is unavailable (under ICZN Art. 13.1.1) because no description of the species was provided. Since Habe (1952b) taxonomically described the same species as “*Divalucina soyoae* (Habe MS) n. sp.”, Habe (1952b) is the author of this species (under ICZN Art. 50.1).

Min (2004) described *Divaricella soyoae* Habe from the Tsushima Strait. However, his citation of an irregular and subquadrate shell with many fine divergent grooves suggests this is probably *Petricola divergens* (Gmelin, 1791).

“*Divalucina soyoae* (Habe)” from the Cuyo Islands in the Philippines (10–25 m) was illustrated by Poppe & Tagaro in Poppe (2017). Some ribs in the posterior part extend beyond the edge of the shell, which is the case in *Divaricella*, and their illustrated specimen is probably *Divaricella ornatissima* (d’Orbigny, 1846).

Divaricella aff. *soyoae* Habe, 1951 was described from the lower Pleistocene Ananai Formation by Okumura & Takei (1993: p. 173–174, pl. 37, fig. 8). As already pointed out by Mimoto (2014),

Table 1. Molluscan fossils from the Seguchi Formation near Horikoshi.

Species	N**	Depth (m)***
<i>Saccella confusa</i> (Hanley)	24	10–60
<i>Glycymeris</i> (<i>Glycymeris</i>) <i>nipponica</i> (Yokoyama)	43	–
<i>Chlamys</i> sp.	1	–
<i>Limaria</i> cf. <i>hakodatensis</i> (Tokunaga)	1	–
<i>Lucinoma annulatum</i> (Reeve)	85	10–670
<i>Pegophysema</i> ? <i>stearnsiana</i> (Oyama)	31	0–20
<i>Divalucina soyoae</i> Habe*	5	90–200
<i>Cycladicama</i> sp.	1	–
<i>Hiatella</i> ? sp.	1	–
<i>Clinocardium</i> sp.	5	–
<i>Placamen tiara</i> (Dillwyn)	3	10–120
<i>Veremolpa micra</i> (Pilsbry)	27	0–20
<i>Callista chinensis</i> (Holten)	6	0–150
<i>Clementia vatheleti</i> Mabille	1	0–20
<i>Tellinides</i> ? sp.	1	–
<i>Nitidotellina</i> sp.	7	–
<i>Macoma</i> (<i>Macoma</i>) sp.	1	–
<i>Siliqua pulchella</i> (Dunker)	1	0–50
<i>Cardilia semisulcata</i> (Lamarck)*	6	5–100
<i>Eunaticina papilla</i> (Gmelin)	3	0–20
<i>Ophiidermella</i> sp.	1	–

* Species described herein. ** Number of individuals. *** Cited from Higo *et al.* (1999) and Okutani (ed.) (2017).

however, the Ananai species and Mimoto's Dainichi species should be included in *Divaricella*, not *Divalucina*, because the ribs extend beyond the edge of the shells.

Divalucina soyoae Habe, 1952 resembles the type species of the genus, *D. cumingi* (Adams & Angas, 1864) from southern Australia and New Zealand. *D. cumingi* has a more inflated shell than *D. soyoae* and a flexure beneath the lunule. *Divalucina euclia* Cotton & Godfrey, 1938 from Southern Australia differs from *D. soyoae* by having a more anteriorly located beak and more wavy ribs.

Measurements (mm):

Specimens	length (L)	height (H)	H/L	angle of ribs (°)	Valve
NMNS PM 28231	7.0	5.7	0.81	135	left
NSMS PM 28232	7.4	7.9	1.07	–	left
NSMS PM 28233	6.2	5.3	0.85	133	left
NSMS PM 28234	6.6	5.1	0.77	110	right

Distribution: Late Pliocene, Mita Formation in Toyama Prefecture (Amano *et al.*, 2008), Seguchi Formation in Nagano Prefecture (this study); Early Pleistocene, Umegase Formation in Chiba Prefecture (Baba, 1990); Recent, Boso Peninsula and southwards, off Kii Peninsula, Tosa Bay, western Kyushu (90–200 m; Higo *et al.*, 1999; Matsukuma in Okutani, 2017).

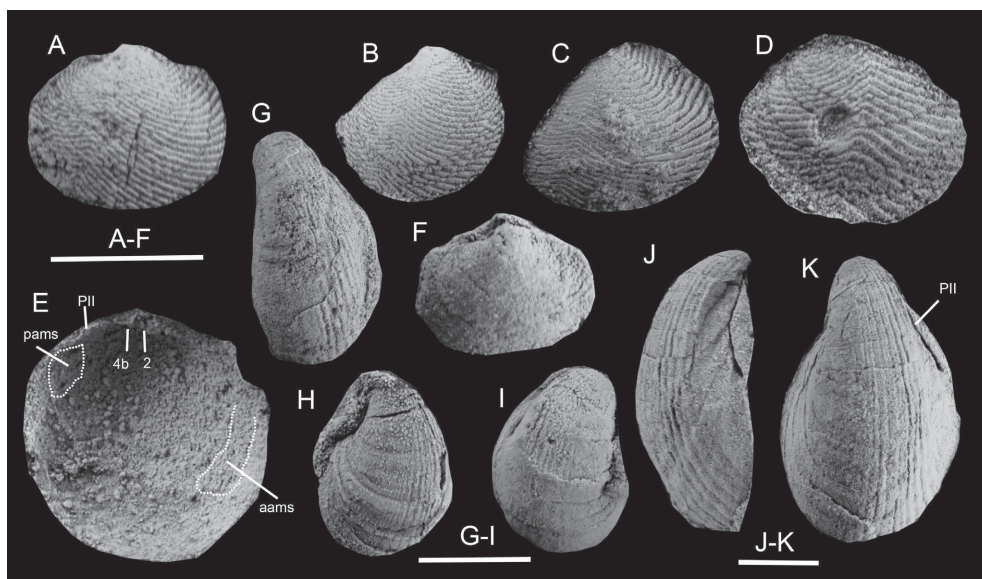


Fig. 2. A–F. *Divalucina soyoeae* Habe; A, left valve, silicone rubber cast, NMNS PM 28231; B, slightly deformed left valve, silicone rubber cast, NMNS PM 28233; C, D, outer surface of parts of left (C) and right (D) valves, silicone rubber casts, NMNS PM 28235, 28236; E, inner surface of slightly deformed left valve, silicone rubber cast, NMNS PM 28232; aams = anterior adductor muscle scar, pams = posterior adductor muscle scar; F, left valve, NMNS PM 28234. G–K. *Cardilia semisulcata* (Lamarck); G, left valve, NMNS PM 28238; H, I, articulated specimen, NMNS PM 28240; J, K, left valve (J, lateral view), NMNS PM 28237. Scale bars show 1 cm.

Family Cardiliidae Fischer, 1887

Genus *Cardilia* Deshayes, 1835

Type species: *Isocardia semisulcata* (Lamarck, 1819) (original designation). Signorelli & Raven (2018) postulated that Deshayes (1835) had placed both *Isocardia semisulcata* and *I. michelini* in his new genus *Cardilia* without type designation and that Deshayes (1844) subsequently had designated *I. semisulcata* as a type species of the genus, following the opinion by Huber (2010). However, Deshayes (1835) originally assigned *Isocardia semisulcata* as the type in a footnote.

Remarks: According to Keen in Moore (1969), the family Cardiliidae consists of *Cardilia* Deshayes, *Cardilona* Marwick, 1943 and *Hemicyclonosta* Deshayes in Blainville, 1827. Signorelli & Raven (2018) claimed that *Hemicyclonosta* is a *nomen nudum* and assigned *Cardilona* to the Lyonsiellidae. Consequently, there is only one genus, *Cardilia*, in Cardiliidae. *Cardilia* ranges from the middle Eocene to the Recent (Signorelli & Raven, 2018).

Cardilia semisulcata (Lamarck, 1819)

(Fig. 2 G–K)

Isocardia semi-sulcata Lamarck, 1819: 32; Deshayes, 1835: 447 [*semisulcata*].

Cardilia semi-sulcata – Deshayes, 1844: 5, pl. 99 [*semisulcata*].

Cardilia semisulcata – Adams & Adams, 1857: 461–462, pl. 112, figs 6, 6a; Sowerby, 1873:

Cardilia, pl. 1, fig. 1; Dunker, 1882: 213–214, pl. 8, figs 1–3; Fischer, 1887: 1120, pl. 18, fig. 18; Bernard, 1895: 150–151, fig. 28; Smith, 1906: 260; Lamy, 1917: 409; Yokoyama, 1927:

428, pl. 48, fig. 16; Habe, 1951: p. 99–100, figs 16–19; Habe, 1952a: 199, figs 473–480; Taki & Oyama, 1954: 46, pl. 45, fig. 16; Habe, 1961: 134, pl. 60, fig. 13; Habe, 1964: 195, pl. 60, fig. 13; Ito, 1967: 69; Kuroda *et al.*, 1971: 673 (in Japanese), 440 (in English), pl. 97, figs 11, 12; Oyama, 1973: 109, pl. 49, fig. 9; Habe, 1977: 190, pl. 37, figs 3–6; Nunomura, 1997: 92; Lamprell & Healy, 1998: 246, fig. 747; Healy & Lamprell, 1998: 340, fig. 8.24; Matsukuma, 2000b: 969, pl. 482, fig. 1; Kawabe, 2006: 85; Robba *et al.*, 2007: 16, fig. 7-l, m; Xu & Zhang, 2008: 169, fig. 510; Huber, 2010: 454; Poppe in Poppe, 2011: pl. 1187, figs 3a–3f; Nevesskaja *et al.*, 2013: figs 152–10a, b; Matsukuma, 2017b: 1268, pl. 561, fig. 6; Signorelli & Raven, 2018: 132, 134, figs 1.1–1.8.

Material examined: Six specimens, NMNS PM28237–PM28242.

Description of the *Seguchi* specimens: Shell rather small (less than 15.0 mm in height), strongly inflated (width/length = 0.84–1.24), ovate to vertically elongate (height/length = 0.97–1.75), equivalve and nearly equilateral. Umbones well produced above dorsal margin; beak strongly prosogyrate. Antero-dorsal margin slightly concave, continuing to broadly arched anterior margin; postero-dorsal margin broadly arcuate; ventral margin subcircular. Surface of central part of shell usually sculptured by 12 flat radial ribs, but rarely 7 to 8 ribs in small specimens; anterior half and posterior extremity smooth, without growth lines. Anterior lateral tooth short; posterior lateral tooth long and distinct.

Remarks: *Cardilia toyamaensis* Tsuda, 1959 from the uppermost lower Miocene Kurosedani Formation in Toyama Prefecture differs from this species by having a smaller shell (maximum height 12.7 mm) and fewer radial ribs (8–9). “*Cardilia*” *yudaensis* Otuka, 1934 from the uppermost lower Miocene Kadonosawa Formation in Iwate Prefecture is similar in having 12 radial ribs, but can be separated from this species by its inequivalve shell.

Measurements (mm):

Specimens	length (L)	height (H)	width (W)	H/L	W/L	Valve
NMNS PM 28237	9.7	15.0	–	1.55	–	left
NMNS PM 28238	6.2	10.5	7.7	1.64	1.24	left
NMNS PM 28239	4.4	7.7	4.8	1.75	1.09	right
NMNS PM 28240	6.2	6.0	5.2	0.97	0.84	right
NMNS PM 28241	6.9	6.8	6.8	0.99	0.99	left

Distribution: Late Pliocene, Seguchi Formation in Nagano Prefecture (this study); Latest middle–Late Pleistocene, Tokyo Formation in Tokyo Metropolis; Recent, Boso Peninsula and southwards, Japan Sea (Toyama Bay and southwards), East China Sea, South China Sea, southeast Asia, Andaman Islands, Persian Gulf, off Oman, Fiji, New Caledonia and northern Australia (5–100 m; Nunomura, 1997; Higo *et al.*, 1999; Signorelli & Raven, 2018).

Discussion

In the assemblage that includes *Divalucina soyoae* Habe and *Cardilia semisulcata* (Lamarck), numerous articulated specimens of the lucinids *Lucinoma annulatum* (Reeve) (Fig. 3 J, L) and *Pegophysema? stearnsiana* (Oyama) (Fig. 3K) also occurred, together with mostly disarticulated specimens of *Saccella confusa* (Hanley) (Figs 3B, C), *Glycymeris (Glycymeris) nipponica* (Yokoyama) (Figs 3A, G) and *Veremolpa micra* (Pilsbry) (Fig. 3I) (Table 1). These disarticulated specimens are not abraded nor fragmented. Moreover, almost all the species in this assemblage nowadays live in the same sandy bottoms that are the origin of the host matrix of the fossils. From this we propose that the disarticulated specimens were not far from their habitat. This assemblage

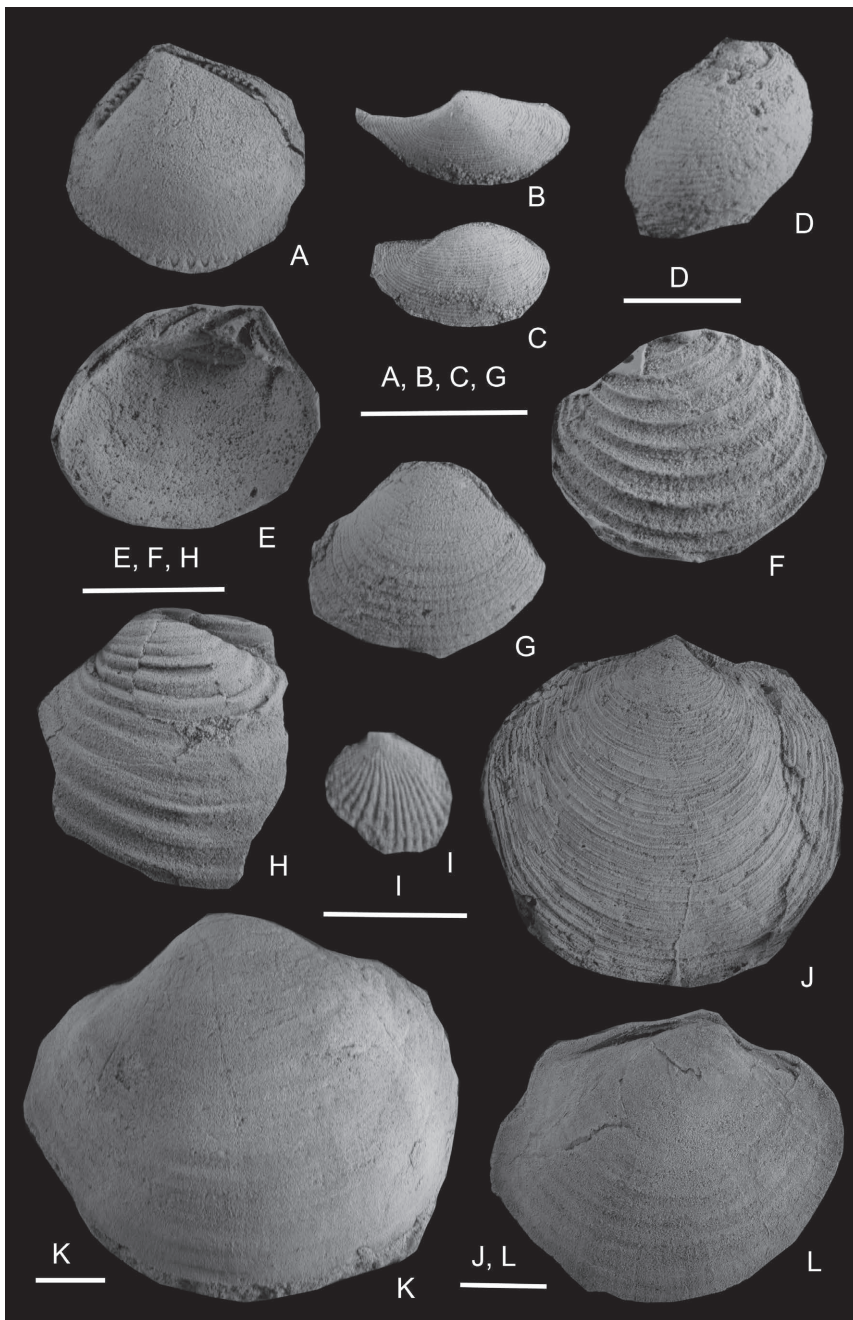


Fig. 3. Associated species with *Divalucina soyoae* and *Cardilia semisulcata*. **A, G.** *Glycymeris* (*Glycymeris*) *nipponica* (Yokoyama); **A**, left valve, NMNS PM 28245; **G**, right valve, silicone rubber cast, NMNS PM 28246. **B, C.** *Saccella confusa* (Hanley); silicone rubber casts of right valve, NMNS PM 28243, 28244. **D.** *Eunaticina papilla* (Gmelin); silicone rubber cast, NMNS PM28253. **E, F.** *Placamen tiara* (Dillwyn); **E**, inner surface of left valve, silicone rubber cast, NMNS PM28250; **F**, outer surface of left valve, silicone rubber cast, NMNS PM28250. **H.** *Clementia vatheleti* Mabilie; NMNS PM28252. **I.** *Veremolpa micra* (Pilsbry); silicone rubber casts of left valve, NMNS PM 28251. **J, L.** *Lucinoma annulatum* (Reeve); **J**, silicone rubber casts of right valve, NMNS PM 28248; **L**, right valve, NMNS PM 28249. **K.** *Pegophysema?* *sternsiana* (Oyama); left valve, NMNS PM28257. Scale bars for **D** and **I** show 5 mm. Other ones show 1 cm.

includes many warm-water species such as *Saccella confusa* (Hanley), *Divalucina soyoae* Habe, *Placamen tiara* (Dillwyn) (Fig. 3E, F), *Veremolpa micra* (Pilsbry), *Clementia vatheleti* Mabilie (Fig. 3H), *Cardilia semisulcata* (Lamarck) and *Eunaticina papilla* (Gmelin) (Fig. 3D). Except for the extinct species *Glycymeris nipponica*, most live in the upper sublittoral depth (Table 1). The *Anadara-Dosinia* assemblage, indicating deposition in the upper sublittoral zone, has also been recorded from the Seguchi Formation in the Tomikura area around the boundary between Nagano and Niigata Prefectures (Nakata & Amano, 1991).

Divalucina soyoae from the Seguchi Formation is the second-oldest record of this species as a fossil. It now lives in the lower sublittoral zone (90–200 m) only in the East China Sea and on the Pacific side of southwestern Honshu, as above described, and is not known from the Japan Sea. The oldest fossil record is from above the MT1 tuff (3.5 Ma; Goto *et al.*, 2014) of the Mita Formation (Amano *et al.*, 2008, Localities 11, 12), where it was densely present in the shell beds. Judging from the associated species at both localities, the beds were deposited in the upper to lower sublittoral depth (Table 2 of Amano *et al.*, 2008). Goto *et al.* (2014) reported many open-water and upper to lower sublittoral ostracods from the horizons above the MT1 tuff. Considering the occurrence of the fossils, *D. soyoae* possibly lived also in shallower water during the Pliocene than it does today.

Cardilia semisulcata from the Seguchi Formation is the oldest record of this species. Up to this time, there was one fossil record from the uppermost middle–upper Pleistocene Tokyo Formation in Tokyo Metropolis (Yokoyama, 1927; Taki & Oyama, 1954; Oyama, 1973), which was overlooked by Signorelli & Raven (2018). This species lives in shallow water (5–100 m) and is very widely distributed in southern Japan, Southeast Asia to Oman, and in northern Australia.

Divalucina soyoae and *Cardilia semisulcata* possibly appeared first in the semi-enclosed Japan Sea with the inflow of the warm-water Tsushima Current during the late Pliocene and spread rapidly to other areas after the early Pleistocene.

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長野県の鮮新統堰口層より産出した稀産暖流系二枚貝 2 種

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要 約

長野県の鮮新世中期の堰口層の浅海域の群集中に現生種であるセワケツキガイとキサガイの化石が認められた。セワケツキガイは 2 番目に古く、キサガイは最古の化石記録であり、両種とも最古の化石記録は太平洋側でなく、日本海側にあることが判明した。両種は日本付近の暖流域に生息するが、セワケツキガイは現生では日本海からの報告はない。さらに、セワケツキガイは現在よりも浅海域にも生息していた可能性があることも明らかとなった。