

The overlooked diversity: occurrence of a microscopic gastropod *Pelycidion* (Mollusca: Caenogastropoda: Pickworthiidae) from the Middle Pleistocene Toyohashi Formation, Atsumi Group, central Honshû, Japan

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渥美層群豊橋層産の微小巻貝ハマケシツボ属
(軟体動物門：新生腹足類：ソビエツブ科) 化石

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Introduction

The genus *Pelycidion* P. Fischer in de Folin and Périér, 1873 is a small caenogastropod group proposed monotypically for the Recent species *P. venustum* de Folin and Périér, 1873, and is currently assigned to the subfamily Pelycidiinae Ponder and Hall, 1983 of the family Pickworthiidae Iredale, 1917. The genus is characterized by a tall cylindrical minute shell which does not exceed 2 mm in length and 1 mm in width, and was considered by Habe (1961) to be the smallest gastropods (as the genus *Nannoteretispira*). The genus was reviewed taxonomically for the first time by Ponder and Hall (1983), who regarded two genera, *Allixia* Cossmann, 1913 and *Nannoteretispira* Habe, 1961 as its synonyms, and recognized six Recent and one fossil valid species in the genus. Subsequent descriptions of new species and reviews of existing taxa resulted in the increase of the number of the Recent species to 11 (Bouchet, 2015; Table 1). They are found intertidally or from shallow marine bottoms in tropic to warm temperate waters. Regarding fossil taxa, *Pelycidion* has a long

fossil history since the Paleocene, and comprises 17 nominal species (Table 1), with the highest diversity in the Recent. The stratigraphically oldest species of the genus, *Pelycidion longula* (Briart and Cornet, 1887), is known from the Danian (Early Paleocene) of Belgium, and during the Paleogene, the genus is recorded only from the western part of the Tethys region (Table 1). Lozouet (2014) recorded an unnamed species of the genus from the Oligocene–Miocene of the Paris Basin, and Lozouet et al. (2001) listed *Pelycidion acicularis* (Cossmann and Pissarro, 1913) from the Aquitanian (earliest Early Miocene) of France. From the Middle Miocene onward, however, fossil records are very limited: only two valid species are independently known from the middle Pliocene of Tunisia and the east coast of North America (Table 1), and no examples have been known thereafter leaving a hiatus of approximately 3.5 Myr.

During a recent field survey at the Middle Pleistocene Toyohashi Formation of the Atsumi Group distributed in the Atsumi Peninsula in Aichi Prefecture, central Honshû, Japan, single microscopic gastropod shell was discovered, and after

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原稿受付 2017 年 2 月 23 日. Manuscript received Feb. 23, 2017.

原稿受理 2017 年 3 月 1 日. Manuscript accepted Mar. 1, 2017.

Key words : micromolluscs, molluscan fauna, *Pelycidion japonicum*, species diversity, warm water.

キーワード : 種多様性, 暖水, 軟体動物相, ハマケシツボ, 微小貝.

Table 1. List of the possibly valid species of the genus *Pelycidion*.

Species	Age	Locality	Reference
<i>Pelycidion longula</i> (Briart and Cornet, 1887)	Early Paleocene (Danian)	Belgium	Gilbert (1973)
<i>Pelycidion mimiola</i> (Cossmann and Pissarro, 1913)	Early Eocene (Ypresian)	Paris Basin	Cossmann (1913); Cossmann and Pissarro (1913)
<i>Pelycidion persitratum</i> (Gougerot, Fekih and Le Renard, 1977)	Middle Eocene (Lutetian)	Paris Basin	Gougerot et al. (1977)
<i>Pelycidion acicularis</i> (Cossmann and Pissarro, 1913)	Middle Eocene (Lutetian)	Paris Basin	Cossmann (1913); Cossmann and Pissarro (1913)
	Early Miocene (Aquitanian)	Paris Basin	Lozouet et al. (2001)
<i>Pelycidion posticum</i> (Gougerot, Fekih and Le Renard, 1977)	middle Pliocene	Tunisia and Italy	Gougerot et al. (1977); Ceregato et al. (2004)
<i>Pelycidion matthewi</i> Campbell, 1993	middle Pliocene	Virginia and South Carolina, USA	Campbell (1993)
<i>Pelycidion japonicum</i> (Habe, 1961)	Middle Pleistocene Recent	this study Japan	- Hasegawa (2000, 2017); Sasaki (2008)
<i>Pelycidion venustum</i> P. Fischer in de Folin and Périer, 1873	Recent	West Africa	Ponder and Hall (1983); Stephens and Vafiadis (2013)
<i>Pelycidion africanum</i> (Bartsch, 1915)	Recent	South Africa	Ponder and Hall (1983); Stephens and Vafiadis (2013)
<i>Pelycidion xanthias</i> (Watson, 1886)	Recent	Indo-Pacific	Ponder and Hall (1983); Stephens and Vafiadis (2013)
<i>Pelycidion habe</i> (Kay, 1979)	Recent	Hawaii	Severns (2011)
<i>Pelycidion kelseyi</i> (Bartsch, 1911)	Recent	Eastern Pacific	Ponder and Hall (1983); Stephens and Vafiadis (2013)
<i>Pelycidion megalomastomus</i> (Olsson and McGinty, 1958)	Recent	Caribbean	Ponder and Hall (1983); Stephens and Vafiadis (2013)
<i>Pelycidion eukyrios</i> Stephens and Vafiadis, 2013	Recent	Australasia	Stephens and Vafiadis (2013)
<i>Pelycidion caperovertex</i> Stephen and Vafiadis, 2013	Recent	Australasia	Stephens and Vafiadis (2013)
<i>Pelycidion kratycylindros</i> Stephens and Vafiadis, 2013	Recent	Australasia	Stephens and Vafiadis (2013)
<i>Pelycidion meizonarchei</i> Stephen and Vafiadis, 2013	Recent	Australasia	Stephens and Vafiadis (2013)

the careful comparison it was identified with a poorly known extant species *Pelycidion japonicum* (Habe, 1961). The Recent *P. japonicum* is known to distribute temperate to subtropic shallow waters in Japan (Hasegawa, 2000, 2017; Sasaki, 2008) but very few examples have so far been recorded due to its rare occurrence (e.g., Sasaki, 2008). The discovery of *P. japonicum* from the Toyohashi Formation is the first record of this species as a fossil. Here, we give a detailed description of this specimen and briefly discuss the significance of this discovery.

Collecting site and geological setting

A specimen described in this paper was collected from an outcrop exposed at a sea cliff in Hane, southeastern part of Takamatsu-chô, Tahara City, southeastern part of Aichi Prefecture, Pacific side of central Honshû, Japan (34.621499° N, 137.243894° E) on July 27, 2014 by the first author (T.H.). The collecting site is identical with the studied site “Loc. 2” in Nakashima et al. (2010: 63).

The collecting site is referable to the *Tonna* Bed (*sensu* Oinomikado, 1933) of the Takamatsu Muddy Sand Member (Nakashima et al., 2008a, 2008b), Toyohashi Formation, Atsumi Group. The Atsumi Group (Kuroda, 1958) is widely distributed in the Tempakubara Upland, a zone extending from the western part of Lake Hamana to Atsumi Peninsula, and composed partly of shallow marine sediments deposited during glacio-eustatic sea-level changes in the Middle Pleistocene (Nakashima et al., 2010 and references therein). The group comprises three formations: Futagawa, Tahara, and Toyohashi Formations in ascending stratigraphic order (Sugiyama, 1991; Nakashima et al., 2008a, 2008b, 2010). Nakashima et al. (2008a) demonstrated that the age of the Toyohashi Formation is referable to Marine Isotope Stage 9 (= Ionian) based on his tephra correlation. The Takamatsu Muddy Sand Member (TMSM, hereafter) of the Toyohashi Formation only exposes along the coastline near Takamatsu-chô, stretching approximately 2 km-wide, with more than eight meters thick, and its sedimentary environment is estimated to be a dissected valley which had transited from river mouth into full marine conditions during the sea level rise (Nakashima et al., 2010).

The TMSM is very fossiliferous and consists of four major shell-bearing horizons: *Batillaria* Bed, *Dosinia* Bed, *Mya* Bed and *Tonna* Bed in ascending order (Oinomikado,

1933; Hayasaka, 1961; Nakashima et al., 2010). Depositional paleoenvironments of the TMSM were interpreted to be river mouth or shallow inshore marine in an embayment for the lower *Batillaria* and *Dosinia* Beds, and relatively deeper marine in an embayment influenced by coastal/oceanic waters for the upper *Mya* and *Tonna* Beds (Oinomikado, 1933; Tsuchi, 1960; Shibata and Ujihara, 1983; Shibata et al., 2006; Nakashima et al., 2010; Kawase et al., 2015). The TMSM possesses a rich fauna (see Nakashima et al., 2010; Kawase et al., 2015), including molluscs (Hayasaka, 1962; Shibata and Ujihara, 1983; Shibata et al., 2006; Kawase et al., 2015) and decapod crustaceans (Karasawa et al., 2014) with thermophile elements reflecting strong influence of the Kuroshio Current. The TMSM displays the highest species richness of molluscs within the Atsumi Group (Kawase et al., 2015).

Method

The single specimen examined in this study was obtained by drying and disaggregating fossiliferous sediment rocks in tap water, then picked out under a binocular microscope. The specimen was thoroughly cleaned in distilled water using a fine point brush with plastic hairs under the microscope. The specimen was then observed and photographed without coating on a scanning electron microscope (SEM), JCM-6000 (Benchtop SEM; JEOL Ltd., Tokyo), at the Toyohashi Museum of Natural History (TMNH: Toyohashi City, Aichi Prefecture) under low-vacuum mode. Measurements were obtained digitally on a “digital measurement” packaged in an operating software of the SEM.

The voucher specimen is housed in the Paleontology Collection of TMNH with a prefix TMNH-10102.

Systematic paleontology

Family Pickworthiidae Iredale, 1917

Subfamily Pelycidiinae Ponder and Hall, 1983

Remarks: The Pelycidiinae was originally proposed as a distinct family of the vetigastropod superfamily Trochoidea by Ponder and Hall (1983), but its systematic position has been controversial due to the lack of anatomical data except for the radula (see Ceregato et al., 2004 and Stephens and Vafiadis, 2013 for the detail). It was retained in the Trochoidea by several subsequent authors (e.g. Ponder, 1985; Vaught,

1989; Rolán and Ryall, 2003) because of the possession of the rhipidogossate-like radula, but transferred by others to caenogastropod superfamilies Cerithioidea (Pacaud and Le Renard, 1995), Littorinoidea with probably close relation to (or even synonymous with) the family Pickworthiidae (Bouchet and Le Renard, 1998) or Rissooidea (Lozouet et al., 2001). Most recently in a comprehensive framework of gastropods, Bouchet and Rocroi (2005) regarded the group as the subfamily of the Pickworthiidae, which comprises superficially heterogeneous species inhabiting submarine caves and other cryptic environments. Recent molecular phylogenetics upon hypsogastropods including both pickworthiids and an unnamed *Pelycidion* strongly supported this assignment (Takano and Kano, 2014). Although Bouchet (2015) again recognized the Pelycidiidae as a full family, we retain it at the subfamily level based on the molecular phylogenetic result by Takano and Kano (2014).

Genus *Pelycidion* P. Fischer in de Folin and Périer, 1873

Allixia Cossmann, 1913, p. 141. Type species: *Allixia acicularis* Cossmann and Pissarro, 1913, by original designation.

Nannoteretispira Habe, 1961, p. 270. Type species: *Nannoteretispira japonica* Habe, 1961, by original designation.

Type species: Pelycidion venustulum P. Fischer in de Folin and Périer, 1873, by monotypy, from the Bay of Levrier, Senegal, West Africa, Recent. Original designation. See Ponder and Hall (1983) and Stephens and Vafiadis (2013) for the authorship and the type locality.

Pelycidion japonicum (Habe, 1961)

[Japanese name: Hama-keshi-tsubo]

(Figure 1)

Nannoteretispira japonica Habe, 1961, p. 270, text-fig. 2.

Pelecydion [sic] *japonica*. Hasegawa, 2000, p. 146–147, pl. 73, fig. 1; Tachikawa, 2011, p. 3, unnumbered figure, lower left.

Pelycidion japonica. Ikebe, 2011, p. 14, fig. 2; Hasegawa,

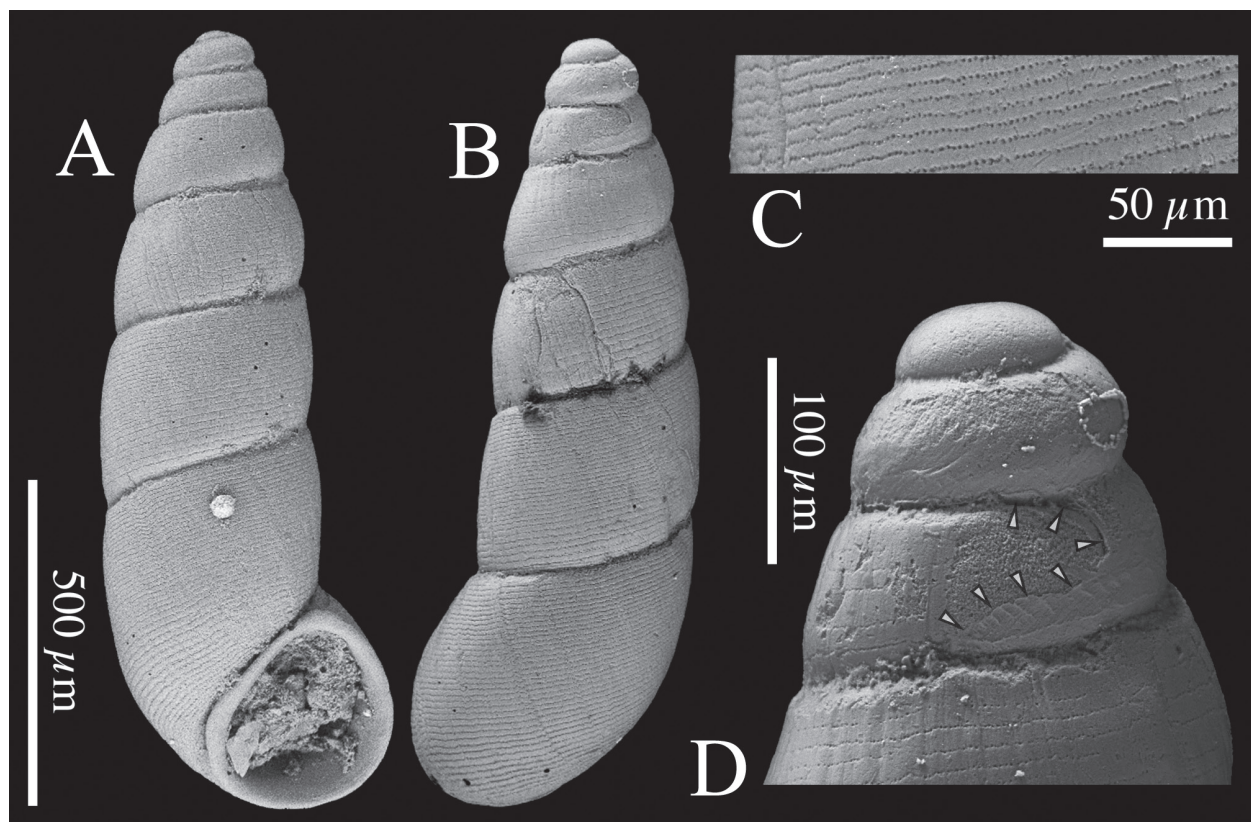


Figure 1. Scanning electron micrographs of the shell of *Pelycidion japonicum* (Habe, 1961) recovered from the Middle Pleistocene Takamatsu Muddy Sand Member, Toyohashi Formation, Atsumi Group, central Honshū, Japan. TMNH-10102. A. Ventral view. B. Dorsal view. C. Microscopic sculptures on the external surface of the teleoconch. D. Protoconch. Arrowheads indicate the boundary between the teleoconch and protoconch.

2017, p. 111, pl. 67, fig. 5, p. 800.

Description: Shell minute, elongate pupoid, tapering towards apex, consisted of ca. 7 whorls including protoconch (Fig. 1A, B). Aperture prosocline, D-shape, widened laterally (Fig. 1A). Peristome smooth, slightly thickened (Fig. 1A). Umbilical groove narrow but clear (Fig. 1A). Surface of teleoconch sculptured with rather regularly spaced spiral grooves composed of microscopic dots (Fig. 1C) that particularly densely arranged in last two whorls (Fig. 1A, B). Protoconch paucispiral consisting of ca. 3 whorls, sculptured with reticulate threads but indistinct except in last whorl due to erosion in specimen at hands (Fig. D). Nucleus cap apparently smooth but detail unknown due to erosion. Margin of last whorl of protoconch having wide sinus at shoulder, slightly flared, demarcated from teleoconch by sigmoidal incision (Fig. 1B, D).

Material examined: TMNH-10102. Shell length: 1.13 mm, shell width: 0.41 mm, protoconch height: ca. 175 μ m.

Remarks: Two Recent species has been recognized in this genus in Japanese waters: *P. japonicum* and “*Pelycidion habei* Kay, 1975”. *Pelycidion habei* was originally described from Hawaii, and first reported in Japanese waters from off Zenisu submarine bank in the northern Izu Islands by Tsuchida et al. (1993). It has since been known under the Japanese name “Seno-keshi-tsubo” in Japanese literature. Hasegawa (2000: pl. 73, fig. 2) put the identification in doubt and depicted it to be *Pelecydion* [sic = *Pelycidion*] sp. “Seno-keshi-tsubo” is characterized by having an uncolored and smooth paucispiral protoconch and rather small aperture in circular shape with thickened peristome (Tsuchida et al., 1993; Hasegawa, 2000, 2017). Sasaki (2008: fig. 8D) also illustrated an unidentified *Pelycidion* (as *Pelecydion* sp.) from Omurodashii submarine bank in the northern Izu Islands, but it considerably differs from the specimens figured by Hasegawa (2000, 2017) and Tsuchida et al. (1993) in the number of the protoconch whorls, convexity of the teleoconch whorls, and the shape of aperture, and may represent another undescribed species as pointed out by Stephens and Vafiadis (2013). Regardless of the taxonomic confusion of the “Seno-keshi-tsubo”, *P. japonicum* is safely separated from it because it has a distinctly sculptured multispiral protoconch (ca. 3 whorls) of brown in color when fresh, punctate surface in the teleoconch, and oval aperture (Hasegawa, 2000, 2017). Although Ponder and Hall (1983) suggested a possibility that *P. japonicum* is a junior synonym

of *Pelycidion xanthias* (Watson, 1886) occurring widely in the tropical Indo-Pacific, it is rather tentatively regarded herein as a distinct species according to the opinion of Bouchet (2015). A more detailed taxonomic revision is needed for *Pelycidion* found not only in Japanese waters, but also in the tropical Indo-West Pacific to solve the taxonomic problems.

Discussion

The discovery of *P. japonicum* from the Tonna Bed of the TMSM, Toyohashi Formation, Atsumi Group is noteworthy, because it represents not only the first fossil record of the subfamily in Japan but also the first Pleistocene record in the world, as far as we know. We assume that the diversity of both fossil and Recent species of *Pelycidion* is underestimated because of their microscopic size as well as their rarity mentioned in several works both for the fossil (e.g., Cossmann, 1921; Lozouet et al., 2001) and the Recent (e.g., Ponder and Hall, 1983; Sasaki, 2008) species. Despite its rarity, species of *Pelycidion* can serve as an index of the influence of warm waters because members of extant *Pelycidion* are generally thought to be tropic to warm temperate full marine elements (e.g., Ponder and Hall, 1983; Bouchet and Le Renard, 1998; Stephens and Vafiadis, 2013), and fossil species of *Pelycidion* are also known to occur together with molluscs having tropic to warm temperate distributions (Campbell, 1993; Lozouet et al., 2001; Ceregato et al., 2004). Extant individuals of *P. japonicum* have actually been recovered only from coasts influenced by the Kuroshio Current and its branches in Japanese waters (Hasegawa, 2000, 2017). The occurrence of *P. japonicum* in the TMSM therefore provides further evidence to support the interpretation that the TMSM was deposited under the influence of the Kuroshio Current during a Middle Pleistocene interglacial (Hayasaka, 1962; Shibata and Ujihara, 1983; Shibata et al., 2006; Karasawa et al., 2014; Kawase et al., 2015).

The discovery of this microscopic species sheds new light on the recognition of the diversity of the Middle Pleistocene molluscan fauna of the Toyohashi Formation. Kawase et al. (2015) recently catalogued 470 molluscan species including many micromolluscs from the TMSM, and demonstrated the highest species richness in the Atsumi Group. However, the present discovery of *P. japonicum* implies the presence of further overlooked micromolluscs in the TMSM, suggesting a possibility that its molluscan fauna is more diverse than

previously thought. Micromolluscs have generally been overlooked and poorly recorded in faunal catalogues of fossil assemblages primarily due to the difficulty in handling (e.g., collection, identification, etc.), and they are regarded as rather “useless or even hampered” for faunal analyses. However, Lozouet (2014) demonstrated the importance of micromolluscs in analyzing the dynamic faunal succession in the Eocene–Miocene European realm. He utilized a dataset of more than 10,000 molluscan species including a large number of micromolluscs, and first showed a clear trend towards homogenization appeared in the Late Oligocene which leads to the development of a vast biogeographical region of Euro-West Africa. The present finding suggest that the Toyohashi Formation may also have a high diversity of unrevealed micromolluscs, and become a good model to reconstruct the history of faunal formation in Japanese waters. More detailed field studies and scrutiny upon museum collections focusing on micromolluscs are indispensable to testify this possibility.

Acknowledgements

We are grateful to Drs. Tsuyoshi Takano and Yasunori Kano (both Atmosphere and Ocean Research Institute, The University of Tokyo) to the access to the literatures. Dr. Keiji Matsuoka and Mr. Hiroaki Yoshikawa (both TMNH) are thanked for their constructive comments on the manuscript. This study was partly funded by a grant-in-aid to T.H. from the Research Institute of Marine Invertebrates (Chuô-ku, Tokyo) (no. Ko-29) in 2014.

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(要 旨)

芳賀拓真・長谷川和範：渥美層群豊橋層産の微小
巻貝ハマケシツボ属（軟体動物門：新生腹足類：
ソビエツブ科）化石

Pelycidion ハマケシツボ属は、殻長 2 mm 以下の微小な殻をもつソビエツブ科の巻貝の一群である。本属の最古の化石記録はテチス海西部の始新世ダン階まで遡り、以後鮮新世までいくつかの化石種が知られるものの、更新世からは全く記録がなかった。本論では、本州中部に分布する渥美層群豊橋層高松泥質砂部層から得られた現生種 ハマケシツボ *Pelycidion japonicum* (Habe, 1961) の化石を記録した。これは本属の日本における初めての化石記録であるとともに、更新世の化石記録として世界初となる。この発見は、高松泥質砂部層が暖流の強い影響下にあったとする古環境についてのこれまでの解釈を補強する証拠ともなる。また、このような微小な腹足類の発見は、豊橋層産の化石種の多様性を明らかにし、ひいては日本の軟体動物相成立の歴史を理解するうえで、微小種を対象としたさらなる精査が必要であることを示している。