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Paleocene and Miocene Thyasira (s. s.) (Bivalvia) from chemosynthetic communities from Japan and New Zealand

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ABSTRACT

A new species of bivalve, Thyasira (Thyasira) beui, is described from lower to middle Miocene hydrocarbon seep deposits from the North Island of New Zealand. T. (T.) nakazawai Matsumoto, 1971 is redescribed from lower Miocene seep deposits in central Honshu of Japan, and T. (T.) sp. from Paleocene wood-fall communities in eastern Hokkaido is described as the first Thyasira (s. s.) in Japan of this age. As the genus Conchocele replaced the niche of Thyasira (s. s.) at seep sites from the Eocene in Japan, the occurrence of T. (T.) nakazawai is an exceptional occurrence of this genus at younger seeps in Japan. In contrast, Conchocele disappeared from New Zealand waters from the end of the Paleocene, leaving Thyasira (s. s.) as the sole thyasirid taxon at New Zealand Cenozoic seep sites.

Key Words: hydrocarbon seep, Thyasira (s. s.), Conchocele, New Zealand, Japan

INTRODUCTION

Bivalves within the family Thyasiridae today inhabit reduced environments from intertidal mudflats to deep-sea hydrothermal vents. Some thyasirid species host chemoautotrophic bacteria in their gills, particularly those towards the larger end of the size range of thyasirids, and some do not (Dufour, 2005; Oliver and Levin, 2006; Taylor and Glover, 2010). Most species within the genus Thyasira have two demibranchs and symbionts (Oliver and Killeen, 2002; Dufor, 2005). Such chemosymbiotic thyasirids are deep burrowers and mine sulfide deeply using their vermiform foot (Dando and Southward, 1986; Seilacher, 1990; Oliver and Killeen, 2002; Dufour and Felbeck, 2003). Thyasirid species can extend their foot up to 30 times that of shell length (Dufour and Felbeck, 2003).

The oldest currently known thyasirid, Cretaxinus hurumi Hryniewicz, Little and

Nakrem, 2014, comes from uppermost Jurassic to lowermost Cretaceous seeps in Svalbard. As noted by Kiel et al. (2008), Thyasira rouyana (d' Orbigny, 1844) from Lower Cretaceous (Valangian-Hauterivian) rocks in Europe is the oldest species of Thyasira (s. s.). By the late Early Cretaceous (Albian), species within this subgenus appeared in seep and wood-fall sites in Hokkaido, northern Japan (Kiel et al., 2008, 2009).

Several species of Thyasira (s. s.) have been reported from Cenozoic deposits around the Pacific Rim (Table 1), including Thyasira (s. s.) from Paleocene carbonates with plant debris in eastern Hokkaido, Japan, Thyasira nakazawai from Miocene accretionary-prism deposits in central Honshu, Japan (Matsumoto, 1971), and Thyasira sp. from Miocene seep deposits of North Island, New Zealand (Campbell et al., 2008).

Here we formally describe Thyasira (s. s.) fossils from the Paleocene and Miocene of Japan and the Miocene from New Zealand. They extend knowledge of the fossil species of Thyasira (s. s.) in hydrocarbon seep and wood-fall communities from the Pacific Rim.

MATERIAL

The fossils used in this study were collected from two Paleocene sites in Japan and from two Miocene localities in New Zealand. We also examined some Miocene specimens from New Zealand housed at the University of Auckland and one Miocene species described by Matsumoto (1971), which is stored at National Museum of Nature and Science, Tokyo. Details of localities and associated faunas are as follows.

Eastern Hokkaido, Japan. — All specimens were collected from two carbonate float blocks from the Katsuhira-zawa (K1) and Katsuhira-kita-zawa (K2) localities of Urahoro Town, Eastern Hokkaido, Japan (Figure 1). The upper part of the Katsuhira Formation crops out in this area and consists of mudstones yielding carbonates that contain many plant fragments. The carbonates containing the thyasirid fossils have probably been eroded out from the mudstones of this formation, the age of which has been assigned to the Paleocene (early Selandian) (see Amano and Jenkins, 2014). In addition to the thyasirid bivalves the carbonates also contain specimens of a provannid?,

a limpet and Bentharca sp. nov. (Amano et al., accepted). The taxonomic composition of this fauna suggests that its primary energy source was the degradation products derived from sunken wood, which was probably bored by xylophagain bivalves.

Central Honshu, Japan. — Thyasira nakazawai Matsumoto, 1971 was the name proposed for specimens collected from limestone lenses or calcareous mudstones within turbidites of the Wappazawa Formation (Setogawa Group) on a branch of the Hakkou River, 1600 m west of Matsushita, Shimada City (S1) and at Nakadaira, Shimada City (S2) (Figure 1). The age of the Wappazawa Formation has been assigned to the early Miocene (Watanabe, 1988). From the formation, molluscan fossils have been recovered only from the limestone lenses and calcareous mudstones (Matsumoto, 1971). Thyasira nakazawai was collected with Saxolucina (Megaxinus) matsushitai Matsumoto, 1971 and Pitar matsuraensis (Nagao, 1928) [= Pliocardia? sp.]. Based on the fauna and lithofacies of the limestone lenses and calcareous mudstones, the taxa from these localities probably inhabited hydrocarbon seeps.

North Island, New Zealand. — Thyasira beui sp. nov. specimens were collected from hydrocarbon seep carbonates from the Moonlight North (MN), Bexhaven (BX) and Turihaua (TH) localities, north of Gisborne, North Island, New Zealand (Figure 1). The deposits belong to the Bexhaven Limestone, which is assigned to the early to middle Miocene (Campbell et al., 2008). From MN, Amano et al. (2014) described the vesicomyid species Notocalyptogena neozelandica and Pliocardia? sp. Saether et al. (2010) described the bathymodioline mussels, Bathymodiolus (s. 1.) heretaunga, from BX and MN, and Gigantidus coseli from BX, MN and TH.

We describe the Thyasira species in this study using the terminology of Kauffman (1967) and Oliver and Killeen (2002). All figured and supplementary specimens are catalogued at the University of Auckland (UOA L), Joetsu University of Education (JUE) and the National Museum of Nature and Science (NSM).

SYSTEMATICS

Family Thyasiridae Dall, 1900 (Dall, 1895)Genus Thyasira Lamarck, 1818Subgenus Thyasira Lamarck, 1818

Type species: Tellina flexuosa Montagu, 1803

Remarks: The subgenus Parathyasira Iredale, 1930 differs from Thyasira (s. s.) by having no auricle. Most historical and some recent literature has treated the taxon Conchocele as a subgenus of Thyasira (e.g. Yabe, H. and S. Nomura, 1925; Grant and Gale, 1931; Krishtofovich, 1936; Slodkewitsch, 1938; Weaver, 1942; Hickman, 1984; Matsui, 1985; Moore, 1988; Matsui, 1990). However, Conchocele Gabb, 1866 attains a large size (max. 165.4 mm in length; Kamenev et al., 2001), has a thick shell, and lacks an auricle. Therefore, we regard Conchocele as a genus distinct from Thyasira.

Thyasira (Thyasira) nakazawai Matsumoto, 1971

(Figures 2–7)

Thyasira nakazawai Matsumoto, 1971: 665–666, pl. 3, fig. 15–18, Amano, 2014: 7, fig. 1.

Type Material: Holotype, NSM PM-16922a. Paratypes, NSM PM-16923, NSM PM-16924, NSM PM-16925.

Material examined: Eleven specimens including the type specimens.

Measurement: See Table 2.

Original description: "Shell medium in size, thin trigonal oval, nearly long as high, strongly inflated. Antero-dorsal border strongly concave, sharply turned to broadly curved, subangular ventral border forming almost a right angle; postero-dorsal long, faintly arched passing into the ventral border forming an obtuse angle. Beak small, strongly curved forwards and situated at about the middle of the shell. Surface of the

shell ornamented with fine and concentric, but somewhat irregular growth-lines. Posterior surface depressed from the upper side of the postero-ventral corner making oblique ridge. A central part of the shell faintly ridged from the beak to middle of the ventral border."

Complementary description: On examination of the material we found that there are some elements of the original description of the species that are incorrect. We therefore offer here more accurate and complementary morphological information.

Shell rather large for the genus (maximum 28.3 mm in length), thin, ovate, slightly longer than high (height/length ratio = 0.85–0.97; exceptionally 1.03), well inflated (width/length ratio = 0.70). Anterodorsal margin short, strongly concave; anterior margin subcircular and graduating into arched ventral margin. Second posterior fold distinct, but not stronger than first posterior fold; posterior sulcus rather shallow and narrow; first posterior fold strong and ridged; submarginal sulcus distinct; auricle narrow but extending total length of submarginal sulcus. Lunule moderately depressed. Beak prominent, prosogyrate, situated at about one-third of shell length. Shell surface ornamented with fine growth lines. Anterior adductor scar elongate quadrate and attached to pallial line; posterior adductor scar indistinct. Inner surface of shell crenulated by many fine radial lines.

Comparison: Thyasira (Thyasira) nakazawai is similar to T. (T.) tanabei Kiel, Amano and Jenkins, 2008 from the Upper Cretaceous formations in Hokkaido, sharing a strongly concave anterodorsal margin and strong and ridged posterior fold. However, T. (T.) nakazawai differs from the latter species by having a larger (maximum length of T. (T.) tanabei = 13.5 mm) and more inflated shell with a smaller anterior adductor scar.

Distribution: Lower Miocene Wappazawa Formation of the Setogawa Group from the Shizuoka Prefecture, central Honshu, Japan.

Thyasira (Thyasira) beui new species

(Figures 8–15)

Thyasira sp. Campbell et al., 2008: 90. Thyasira sp. nov. Saether, 2011: 135–138, Fig. 5-19.

Diagnosis: Medium-sized Thyasira with suborbicular shell, shallow lunule, and small auricle. Ventral end of first posterior fold occasionally angulated.

Description: Shell up to 13.8 mm in length, rather thin, moderately inflated (width/length ratio = 0.58-0.91), suborbicular (height/length ratio = 0.90-1.17), equivalve and inequilateral. Antero-dorsal margin broadly arched and continuing to rounded anterior margin; ventral margin broadly arched. Auricle small, extending in length two-thirds along marginal sulcus; first posterior fold sharp, with ventral end occasionally angulated; posterior sulcus very shallow; second posterior fold less distinct than first posterior fold. Beak prominent, prosogyrate and located around two-fifths of shell length (i.e., at 36–44% of shell length from anterior margin). Lunule shallow and demarcated by very shallow groove. Shell surface with fine growth lines. Inner shell surface ornamented by many fine radial grooves. Pallial line entire, starting from midpoint of ventral side of anterior adductor scar. Anterior adductor scar elongate quadrate shape; posterior adductor scar very small and ovate.

Holotype: UOA L4626 from MN (Y16/f1054), collection AU 15844.

Paratypes: UOA L4627 from MN (Y16/1033), collection AU 19618; UOA L4628 from MN (Y16/f1174), collection AU 19923; UOA L4629 and L4630 from MN (Y16/1059), collection AU 19982; UOA L4631 from BX (Y16/1032), collection AU 19617.

Type locality: Moonlight North seep carbonates, north of Gisborne, North Island, New Zealand.

Material Examined: Twenty-two specimens from three localities (Loc. MN, BX, TH in Figure 1).

Measurements: See Table 3.

Remarks: Thyasira (Thyasira) beui is the same as Thyasira sp. in the compilation of molluscan fossils (in part taken from Beu and Maxwell (1990)) from New Zealand hydrocarbon seep carbonates in Campbell et al. (2008). Saether (2011) described and illustrated this species as Thyasira sp. nov. in his unpublished Ph.D. thesis.

Comparison: Thyasira (Thyasira) beui shares a prominent beak and a moderately inflated shell with T. (T.) motutaraensis Powell, 1935 from the lower Miocene Motutara deposit west of Auckland, North Island, New Zealand (see also Beu and Maxwell, 1990). However, T. (T.) motutaraensis can be separated from the new species by its smaller and higher triangular shell (length = 7.4 mm, height/length ratio = 1.14). T. (T.) planata Marwick, 1926 [This name was preoccupied by Jeffreys, 1882. Moreover, there is no junior synonym of the species. Thus, according to ICZN Art.23.3.5, we proposed T. (T.) marwicki as a new name herein.] from upper Miocene deposits in the western part of North Island, New Zealand, can be distinguished from T. (T.) beui by having a wider posterior area, a longer marginal sulcus, and a narrower auricle than that of the new species. T. (T.) mironovi Kalishevich from the Paleocene of South Sakhalin (Klishevich et al. 1981) is similar to T. (T.) beui in having a first posterior fold with angular ventral end. However, T. (T.) mironovi can be separated from T. (T.) beui by having a less inflated shell, a wider posterior fold and a weak medial flattened area. Another species from the Paleocene of South Sakhalin, T. (T.) uncinata Kalishevich, can be easily distinguished from T. (T.) beui by having an elongate shell with posteriorly situated beak. T. (T.) bartrumi Powell, 1935 from the lower Miocene Motutara deposit is distinctly different from T. (T.) beui by having a Conchocele-like shell with beak at anterior one-seventh of shell length and a medial flattened area. The Recent New Zealand species, T. (T.) peregrina Iredale, 1930 differs from T. (T.) beui by its smaller shell (maximum length = 10.4 mm), which is higher than long, and by having a medial flattened area.

Distribution: Lower to middle Miocene Bexhaven Limestone, north of Gisborne, North Island, New Zealand.

Etymology: Named after Dr. Alan G. Beu who has made significant contributions to studying the taxonomy of Cenozoic fossil faunas from New Zealand.

Thyasira (Thyasira) sp.

(Figures 16–17)

Material examined: Two articulated but imperfect specimens (JUE nos. 15936, 15937).

Description: Shell rather small in size (9.7-10.1 mm + in length), thin, ovate shape, longer than high, well inflated (width/length ratio = 0.52-0.58). Anterodorsal margin short, nearly straight; anterior margin subcircular. Second posterior fold distinct; posterior sulcus rather deep; first posterior fold wide and ridged; submarginal sulcus distinct; auricle narrow and short. Beak prosogyrate. Inner structure of shell not preserved.

Comparison: Thyasira (Thyasira) sp. is similar to the Cretaceous species, T. (T.) tanabei Kiel, Amano and Jenkins, 2008 by having a ridged first posterior fold. However, the wide posterior area of our specimens enables us to separate T. (T.) sp. from T. (T.) tanabei. T. (T.) xylodia Kiel and Goedert, 2007 comes from latest Eocene and early Oligocene wood-fall communities in Washington State, USA and can be distinguished from T. (T.) sp. by its larger size (21 mm in length), deeply concave antero-dorsal margin and narrower posterior area. T. (T.) baca Devjatilova from the Paleocene Getkilninskaya Formation of western Kamchatka (Devjatilova and Volobueva 1981) differs from T. (T.) sp. by having a triangular shell and narrower posterior area. T. (T.) sp. by having its ventral end to the ventral margin of main disc.

Distribution: Paleocene upper part of the Katsuhira Formation, eastern Hokkaido, Japan.

DISCUSSION

Several Recent species of Thyasira (s. s.) have been recorded from hydrocarbon seep or hydrothermal vent sites (Table 4; Clarke, 1989; Dando et al., 1994; Oliver and Killeen, 2002; Olu et al., 2004; Oliver and Sellanes, 2005; Oliver and Holmes, 2006; Rodrigues et al., 2008). Based on recent molecular analysis of nuclear 18S rRNA and 28S rRNA, the subgenus Thyasira (s. s.) is divided into two clades (Taylor et al., 2007). T. (T.) sarsi (Philippi, 1845b) and T. (T.) methanophila Oliver and Sellanes, 2005, from hydrocarbon seeps, form a monophyletic clade. T. sarsi itself is an opportunistic species which is also able to live in sediments with low organic content, and at relatively low densities (Keuning et al., 2011). Another clade includes T. (T.) flexuosa (Montagu, 1803), T. (T.) gouldii (Philippi, 1845a) and T. (T.) polygonata (Jeffreys, 1864), none of which have been recorded from seep and vent sites. Morphologically, the T. (T.) sarsi-T. (T.) methanophila clade differs from the T. (T.) flexuosa-T. (T.) gouldii-T. (T.) polygonata clade by having larger (more than 20 mm in length), subcircular or a slightly longer shells, without a medial flattened area. Other Thyasira species found in seep and vent sites, such as T. (T.) southwardae Oliver and Holmes, 2006, T. (T.) vulcolutre Rodrigues and Oliver in Rodrigues et al., 2008 and T. (T.) oleophila Clarke, 1989, also have similar shell characteristics to the T. (T.) sarsi-T. (T.) methanophila clade.

Payne and Allen (1991) and Dufour (2005) have shown that in thyasirids demibranch number is related to body size, because asymbiotic thyasirids with only one demibranch only have access to a small amount of nutrients at bathyal depths. All the species discussed above have two demibranchs and chemosynthetic bacteria (Dufour, 2005; Oliver and Sellanes, 2005; Oliver and Holmes, 2006; Rodrigues and Oliver, 2008). Almost certainly because of the abundant supply of hydrogen sulfide at seep and vent sites, thyasirids living there can grow to large sizes relative to thyasirids inhabiting other environments. However, the reason that the thyasirids living in chemosynthetic environments have subcircular or longer shells, without a medial flattened area, is unknown. There are exceptions, as T. (T.) striata (Sturany, 1896), found at a Mediterranean seep by Olu et al. (2004), is characterized by a rather small (ca. 7.5 mm) and higher shell with a medial flattened area. This morphological information from Recent seep and vent Thyasira (s. s.) can be used to infer the paleoecology of fossil Thyasira (s. s.) taxa.

As shown in Table 1, T. (T.) nakazawai has a large (length = 28.3 mm) and longer shell (height/length ratio = 0.85-0.97) without a medial flattened area, compared to Thyasira (s. s.) species from Cenozoic deposits around the Pacific Rim. Because of this we speculate that T. (T.) nakazawai might have lived in cold seep areas. In contrast, T. (T.) minoensis Itoigawa, 1960 was collected from non-seep sandstones of the lower Miocene Oidawara Formation; it has a smaller (length = 14.1 mm) and higher shell (height/length ratio = 1.08) and with a distinct medial flattened area. While the maximum size of T. (T.) beui sp. nov. is not large (length = 13.8 mm), the species has a suborbicular shell (height/length ratio = 0.90-1.17) without a medial flattened area. The carbonates and associated fauna (see also Campbell et al., 2008) indicate this species also thrived at fossil seep sites. Judging from the lithofacies and the associated fauna of limpets and provannids, the Paleocene T. (T.) sp. collected from eastern Hokkaido might have been a member of a fossil wood-fall community. Despite the small size of T. (T.) sp. (length = 9.7-10.1 mm) compared with other seep species, it also is longer than high and has no medial flattened area. Such small thyasirid species also have been recognized in Late Cretaceous wood-fall communities with limpets and provannids by Kiel et al. (2009). In the northern Pacific area, Thyasira (s. s.) occurred in hydrocarbon seeps and wood-fall sites during the Late Cretaceous (Kiel et al., 2008, 2009). The eastern Hokkaido Paleocene Thyasira (s. s.) sp. might have lived in wood-fall communities. The first large thyasirid, Thyasira townsendi (White, 1890) (almost certainly a species of Conchocele) appeared in Maastrichtian seep deposits of Snow Hill Island, Antarctica (Kiel et al., 2008; Little et al. 2015). The second oldest large thyasirid species, C. aff. conradi (Rosenkrantz, 1942), is from the Danian Kangilia Formation of western Greenland (Rosenkrantz, 1970; Amano, 2014). From North Island, New Zealand, one specimen of Conchocele sp. has been recorded from Paleocene deposits at Angora Road, south of Wimbledon (Beu and Maxwell, 1990; Beu, 2014 personal communication). Another Paleocene Conchocele specimen up to 70 mm in length was collected from 1 km south of Te Kaukau Point, White Rock, South Wairarapa coast (Beu, 2014 personal communication). So far, no fossil Conchocele has been recorded from Paleocene deposits in the northern Pacific area.

Since the Eocene, the genus Conchocele seems to have replaced the niche of Thyasira (s. s.) in the northern Pacific. Lots of literature has described the flourishing of Conchocele in Eocene to Recent times in this region (e.g. Yabe and Nomura, 1925; Grant and Gale, 1931; Krishtofovich, 1936; Slodkewitsch, 1938; Weaver, 1942; Hickman, 1984; Moore, 1988; Kamenev et al., 2001). Conchocele was also found from Eocene to Holocene seep sites and in Oligocene to Miocene whale-fall sites (Goedert et al., 1995; Majima et al., 2005; Amano et al., 2007; Kiel and Goedert, 2006). Thus the occurrence of Thyasira (Thyasira) nakazawai from lower Miocene seep deposits is an exceptional post-Eocene occurrence of Thyasira (Thyasira) species in the northern Pacific area. In contrast, in Zealand T. (T.) beui occurs in lower to middle Miocene seep sites, in the absence of Conchocele from the region.

Conchocele might have migrated from western Greenland to the northern Pacific area (including Japan) by the Eocene (Amano and Jenkins, 2014), and once there to have replaced Thyasira (s. s.) because of its tolerance to lower oxygen environments. In New Zealand waters, in contrast, Conchocele did not invade hydrocarbon seep sites and had disappeared from the region by end of the Paleocene. Thyasirids [probably Thyasira (s. s.)] from New Zealand Cretaceous seep deposits (Kiel et al., 2013) show that small sized thyasirids have flourished in the area since that time period.

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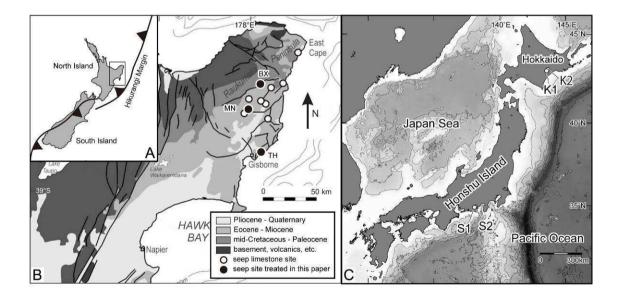
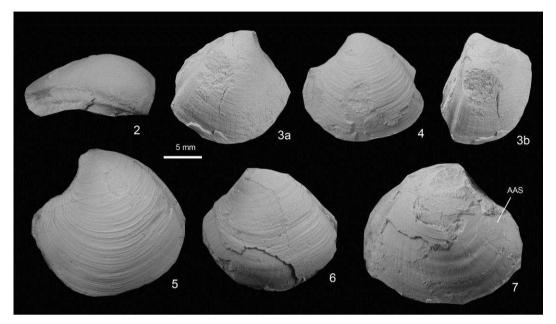
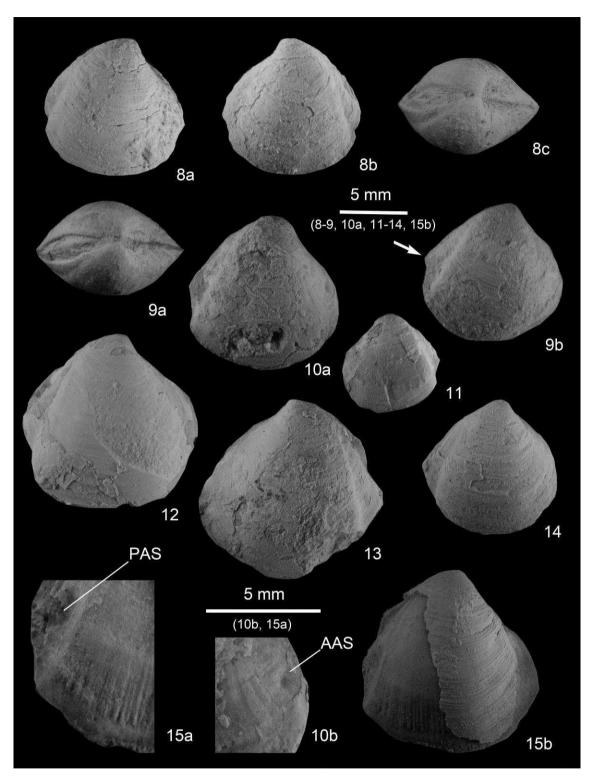


Figure 1. Localities of the fossil Thyasira (s. s.) described herein.

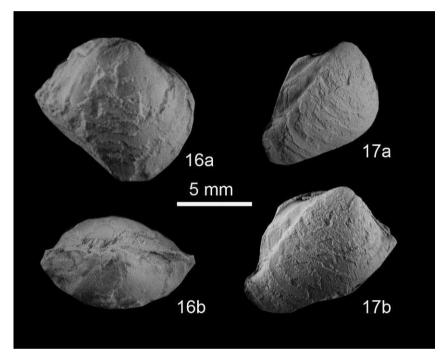


Figures 2–7. Thyasira (Thyasira) nakazawai Matsumoto. 2. Dorsal view of posterior part of left valve; Paratype; NSM PM-16924; Loc. S1. 3a, b. Frontal and oblique view of right valve; NSM PM-16910; Loc. S2. 4. Frontal view of left valve; Paratype; NSM PM-16923; Loc. S1. 5. Frontal view of left valve; Holotype; NSM PM-16922a; Loc. S1.
6. Frontal view of left valve; NSM PM-16905; Loc. S1. 7. Inner surface of right valve; AAS, anterior adductor scar; NSM PM-16909; Loc. S1.



Figures 8–15. Thyasira (Thyasira) beui new species. All specimens except for one illustrated in Figure 15a, b are from the type locality (Moonlight North; MN). One specimen of Figure 15a, b is from Bexhaven (BX). 8a–c. Frontal and dorsal views of both valves; Paratype, UOA L4629. 9a, b. Frontal view of right valve and dorsal view

of both valves; Holotype; UOA L4626; white arrow showing an angulated ventral end of first posterior fold. **10a, b.** Inner surface of right valve and its enlargement of the area around AAS (= anterior adductor scar); Paratype; UOA L 4630. **11.** Frontal view of left valve; Paratype; UOA L 4628. **12.** Frontal view of right valve; UOA L4638. **13.** Frontal view of left valve; left valve; UOA L 4640. **14.** Frontal view of right valve; UOA L 4627. Inner surface of right valve showing PAS (= posterior adductor scar) and its enlargement; Paratype; UOA L 4631.



Figures 16–17. Thyasira (Thyasira) sp. 16a, b. Frontal view of right valve and dorsal view of both valves; JUE no. 15936; Loc. K1. 17a, b. Frontal and oblique view of right valve; JUE no. 15937; K2.

Species		Country,	Age	Μ	L>	MF	Data source
		District		ax	\mathbf{H}^{**}	***	
				\mathbf{L}^{*}			
Thyasira	(Thyasira)	Hokkaido,	Paleocen	10	+	—	This study
sp.		Japan	e	.1			

T. (T.) mironovi S Kalishevich, 1981 S T. (T.) uncinata S Kalikevich, 1981 S R T. (T.) xylodia Kiel V	Russia South Sakhalin, Russia South Sakhalin, Russia Washington, USA	e Paleocen e Paleocen e Latest EocE. Oligoc.	12 14 21	+		Volobueva (1981) Kalishevich et al. (1981) Kalishevich et al. (1981) Kiel and Goedert
Kalishevich, 1981 T. (T.) uncinata Kalikevich, 1981 S R T. (T.) xylodia Kiel	Sakhalin, Russia South Sakhalin, Russia Washington, USA	e Paleocen e Latest EocE.	14	+		Kalishevich et al. (1981) Kalishevich et al. (1981)
Kalishevich, 1981 T. (T.) uncinata Kalikevich, 1981 S R T. (T.) xylodia Kiel	Sakhalin, Russia South Sakhalin, Russia Washington, USA	e Paleocen e Latest EocE.	14	+		(1981) Kalishevich et al. (1981)
RT. (T.) uncinataKalikevich, 1981RT. (T.) xylodia Kiel	Russia South Sakhalin, Russia Washington, USA	Paleocen e Latest EocE.			-	Kalishevich et al. (1981)
T.(T.)uncinataSKalikevich, 1981SRT.(T.)xylodiaKiel	South Sakhalin, Russia Washington, USA	e Latest EocE.			_	(1981)
Kalikevich, 1981 R T. (T.) xylodia Kiel V	Sakhalin, Russia Washington, USA	e Latest EocE.			_	(1981)
RT. (T.) xylodia Kiel	Russia Washington, JSA	Latest EocE.	21	?	_	
T. (T.) xylodia Kiel V	Washington, JSA	EocE.	21	?	_	Kiel and Goedert
	USA	EocE.	21	?	-	Kiel and Goedert
and Goedert, 2007 U						
	Domy	Oligoc.				(2007)
	Jama	-				
T, (T.) peruviana P	Peru	Oligocen	25	<u>+</u>	_	Olsson (1931)
Olsson, 1931		e				
T. (T.) nakazawai c	central	E.	28	+	—	Matsumoto
Matsumoto, 1971 H	Honshu,	Miocene	.3			(1971)
Ja	apan					
T. (T.) minoensis c	central	E.	14	_	+	This study
Itoigawa,1960 H	Honshu,	Miocene	.1			
Ja	apan					
T. (T.) motutaraensis N	North Is.,	E.	6.	_	—	Powell (1935)
Powell, 1935	New Zealand	Miocene	5			
T. (T.) bartrumi N	North Is.,	E.	15	+	+	Powell (1935)
Powell, 1935	New Zealand	Miocene				
T. (T.) beui sp. nov. N	North Is.,	ЕМ.	13	+	—	This study
N	New Zealand	Miocene	.8			
T. (T.) nana K	Kamchatka,	М.	6	+	—	Krishtofovich
Krishtofovich, 1929 S	Sakhalin,	Miocene				(1929)
R	Russia					
T. (T.) marwicki N	North Is.,	L.	10	+	-	Marwick (1926),
nom. nov. N	New Zealand	Miocene				as Thyasira

						planata
T. (T.) tokunagai	Japan	E.	13	_	+	This study
Kuroda and Habe,		Miocene-	.6			
1951		Rec.				
T. (T.) gouldii	California,	Pliocene-	12	_	+	Ockelman
(Philippi, 1845)	USA	Rec.				(1958), Coan et
						al. (2000)
T. (T.) peregrina	New Zealand	Pliocene-	10	_	+	This study
(Iredale, 1930)		Rec.	.4			
T. (T.) ozawai	Japan	E.	15	_	+	This study
(Yokoyama, 1926)		Pleistoce	.3			
		ne				

Number	of	Туре	Length(Height	Width	H/L	W/L	Valve
specime	ns		mm)	(mm)	(mm)			
NSM	PM-	Holotype	20.6	19.1	-	0.93	-	left
16922a								
NSM	PM-	Paratype	14.9	13.1	-	0.88	-	left
16923								
NSM	PM-	Paratype	15.5+	13.8	-	-	-	left
16924								
NSM	PM-	Paratype	18.5	16.9	-	0.91	-	right
16925								
NSM	PM-		16.2	16.7	-	1.03	-	right
16905								
NSM	PM-		22.0	20.1	15.5	0.91	0.70	both
16906								
NSM	PM-		17.9	17.5	-	0.98	-	left
16908								
NSM	PM-		20.4	17.3	-	0.85	-	right

16909						
NSM PM-	21.0	18.4	-	0.88	-	left
16910-1						
NSM PM-	16.0	15.5	-	0.97	-	right
16910-2						

Table 3. Measurements of Thyasira (Thyasira) beui new species.

Number	Туре	Lengt	Heig	Widt	H/L	W/L	Valv	Collectio	Localit
of		h(mm	ht	h			e	n	У
specimen)	(mm	(mm				Number	Numbe
s))					r
UOA	Holot	10.2	9.6	6.6	0.94	0.65	both	AU1584	Y16/f10
L4626	ype							4	54
UOA	Paraty	10.3	10.2	6.6	0.99	0.64	both	AU1961	Y16/f10
L4627	pe							8	33
UOA	Paraty	7.2	7.4	-	1.03	-	left	AU1992	Y16/f11
L4628	pe							3	74
UOA	Paraty	9.5	10.4	7.1	1.09	0.75	both	AU1998	Y16/f10
L4629	pe							2	59
UOA	Paraty	10.4	10.3	7.0	0.99	0.67	both	AU1998	Y16/f10
L4630	pe							2	59
UOA	Paraty	12.4	12.9	9.3	1.04	0.75	both	AU1961	Y16/f10
L4631	pe							7	32
UOA		14.8	14.7	10.7	0.99	0.72	both	AU1584	Y16/f10
L4632								4	54
UOA		10.5	11.3	7.3	1.08	0.70	both	AU1584	Y16/f10
L4633								4	54
UOA		12.7	13.4	9.7	1.06	0.76	both	AU1584	Y16/f10
L4634								4	54
UOA		9.2	9.1	-	0.92	-	left	AU1987	Y16/f10
L4635								2	48

UOA	11.2	11.0	7.9	0.98	0.71	both	AU1992	Y18/f65
L4636							2	7
UOA	11.1	10.0	8.0	0.90	0.72	both	AU1992	Y18/f65
L4637							2	7
UOA	12.9	12.5	-	0.97	-	right	AU1992	Y16/f11
L4638							3	74
UOA	9.0	8.1	-	0.90	-	right	AU1992	Y16/f11
L4639							3	74
UOA	13.8	12.7	-	0.92	-	left	AU1998	Y16/f10
L4640							2	59
UOA	10.7	10.9	7.4	1.02	0.69	both	AU1998	Y16/f10
L4641							2	59
UOA	10.2	11.9	9.3	1.17	0.91	both	AU1998	Y16/f10
L4642							2	59
UOA	12.0	12.1	7.9	1.01	0.66	both	AU1998	Y16/f10
L4643							2	59
UOA	12.6	12.3	9.2	0.98	0.73	both	AU1998	Y16/f10
L4644							2	59
UOA	7.6	7.7	4.6	1.01	0.61	both	AU1998	Y16/f10
L4645							2	59

Table 4. Morphology of recent species of Thyasira (s. s.). * maximum length (mm); **Length>Height; + distinctly longer than high, \pm subcircular, - distinctly higher thanlong; *** Medial flattened area.

Species	sites	Max	L>H	MF*	Data source
		L*	**	**	
Thyasira (Thyasira) sarsi	seep	25	<u>+</u>	_	Dando et al.
(Philippi, 1845)					(1994), Oliver and
					Killeen (2002)
T. (T.) methanophila Oliver and	seep	29.7	+	—	Oliver and Sellanes

Sellanes, 2005					(2005)
T. (T.) southwardae Oliver and	vent	16.7	+	-	Oliver and Holmes
Holmes, 2006					(2006)
T. (T.) vulcolutre Rodrigues and	seep	17.2	±	-	Rodrigues et al.
Oliver, 2008					(2008)
T. (T.) oleophila Clarke, 1989	seep	ca.2	<u>+</u>	_	Clarke (1989)
		3			
T. (T.) striata (Sturany, 1896)	seep	ca.7.	_	+	Olu et al. (2004)
		5			
T. (T.) tokunagai Kuroda and	non-	13.6	_	+	This study
Habe, 1951	seep				
T. (T.) gouldii (Philippi, 1845)	non-	12	_	+	Killeen and Oliver
	seep				(2002b)
T. (T.) polygonata (Jeffreys,	non-	9	-	+	Killeen and Oliver
1864)	seep				(2002a)
T. (T.) flexuosa (Montagu, 1803)	non-	12	_	+	Oliver and Killeen
	seep				(2002)