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A new Miocene *Yabepecten* (Bivalvia: Pectinidae) from the Hongô Formation in northeast Japan

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Abstract. *Yabepecten ogasawarai* sp. nov. is proposed from the Hongô Formation in Yamagata Prefecture, northeastern Honshû, Japan. Its occurrence is inferred to be of early late to middle late Miocene age, which makes *Y. ogasawarai* sp. nov. the oldest *Yabepecten* in the northwestern Pacific. *Yabepecten* was derived from *Patinopecten* in the northeastern Pacific, and migrated into the northwestern Pacific by the early late Miocene. From the early late Miocene onward, *Yabepecten* followed different evolutionary histories on both sides of the North Pacific. *Yabepecten* became extinct in the northeastern Pacific by the end of the early late Miocene. However, *Yabepecten* flourished in the northwestern Pacific from the late Pliocene to early Pleistocene, only becoming extinct at the beginning of the middle Pleistocene, along with many other species of the Omma-Manganji Fauna.

Key words: evolutionary history, late Miocene, northwestern Pacific, *Yabepecten*, *Yabepecten ogasawarai* sp. nov.

Introduction

Yabepecten is a pectinid genus typified by *Pecten tokunagai* Yokoyama, 1911, which was originally described from the lower Pleistocene Koshiba Formation on the Miura Peninsula, Kanagawa Prefecture, central Honshû, Japan (Masuda, 1963). The type species is peculiar for northwestern Pacific pectinids in having auricular crura with distal denticles. This character is common in *Patinopecten* Dall, 1898 (*Patinopectininae sensu* Kafanov, 1986a, b) in the northeastern Pacific, but is entirely absent in *Mizuhopecten* Masuda, 1963, and related genera (*Fortipectininae sensu* Masuda, 1963, and Kafanov, 1986a, b) in the northwestern Pacific.

Yabepecten tokunagai has mainly been found in upper lower Pliocene to lower Pleistocene deposits from central Honshû to southern Hokkaidô (e.g., Masuda and Ogasawara, 1981; Uozumi *et al.*, 1986a; Matsui, 1990; Ogasawara, 1996). The oldest record of *Yabepecten* in the northwestern Pacific was from uppermost Miocene or lowest Pliocene deposits on Hokkaidô (Uozumi *et al.*, 1986a). However, *Yabepecten condoni* (Hertlein, 1925) occurs in the upper Miocene Montesano Formation of Washington, U.S.A. (Masuda and Addicott, 1970), where its oldest occurrence has been dated as of early late Miocene age, based on diatoms and magnetostratigraphic data (Barron, 1981a;

Prothero and Lau, 2001). This occurrence is much earlier than in the northwestern Pacific. The origin and migration of *Yabepecten* have been discussed from the viewpoints of chronologic and geographic distribution patterns (e.g., Masuda and Addicott, 1970; Masuda, 1986; Uozumi *et al.*, 1986a; Amano and Karasawa, 1988).

In the course of examining collections in the Museum of Natural History, Tohoku University (abbreviated as IGPS), I found a new late Miocene *Yabepecten* from northeastern Japan (Figure 1). This is the first record of *Yabepecten* from lower upper or middle upper Miocene deposits in the northwestern Pacific. I propose *Yabepecten ogasawarai* sp. nov. and discuss its paleobiogeographic implications.

Systematic description

The terminology used herein for cardinal properties is principally from Waller (1991) (Figure 2). Right and left valves are abbreviated as RV and LV, respectively. A new term, *inner dorsal flexure (idf)*, refers to a rounded radial flexure on the inner side of both antero- and posterodorsal parts of the disc (Figure 2.1b, 2.2b).

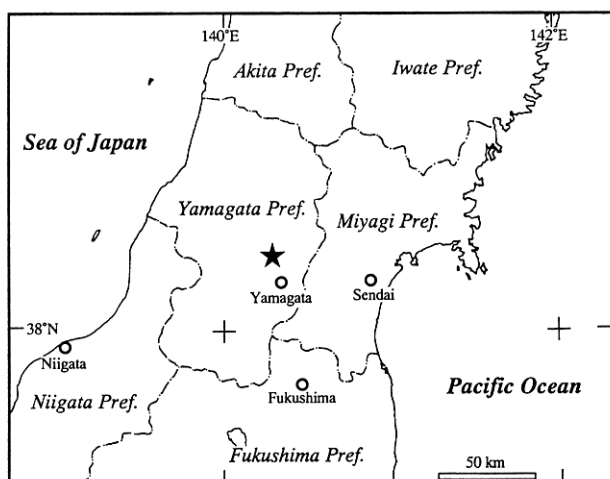


Figure 1. Location of type locality (after Ogasawara *et al.*, 1985; black star).

Family Pectinidae Wilkes, 1810
Subfamily Chlamydinae von Teppener, 1922
Tribe Chlamydini von Teppener, 1922
Genus *Yabepecten* Masuda, 1963

Type species.—*Pecten tokunagai* Yokoyama, 1911, by original designation. Koshiha Formation, early Pleistocene.

Emended diagnosis.—Chlamydini with a circular, compressed, rather thin shell; RV generally more inflated than LV; RV radial costae low, flat-topped or rounded, irregular, broader or narrower than interspaces; LV concave or weakly inflated, sculptured by very fine to fine, low radial costae and strong shagreen microsculpture; LV generally lacking costae in interspaces; auricles rather small; byssal notch very shallow; resilifer small; auricular crura distinct, with a denticle on distal end; dorsal teeth strong; inner dorsal flexures distinct on both RV and LV.

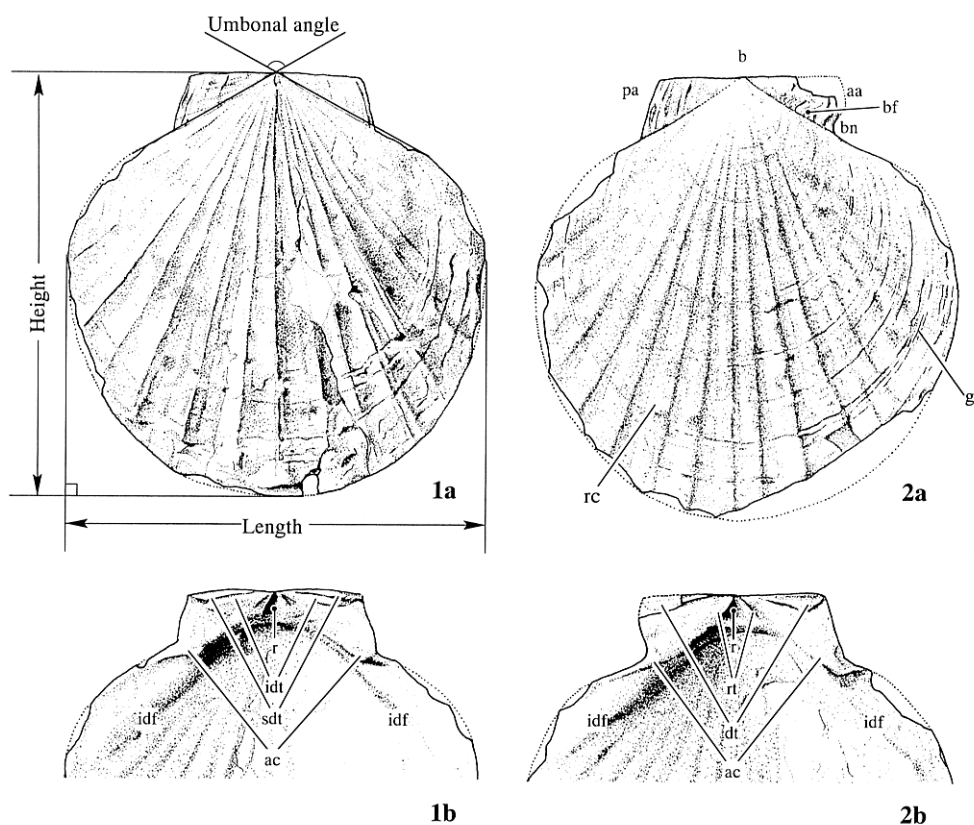


Figure 2. Measurement position and terminology. **1a.** External view of LV with measured position. **1b.** Internal view of LV. IGPS 98911-2 (paratype). **2a.** External view of RV. **2b.** Internal view of RV. IGPS 98911-1 (holotype). Abbreviations: aa: anterior auricle; ac: auricular crura; b: beak; bf: byssal fasciole; bn: byssal notch; dt: dorsal teeth; gl: growth line; idf: inner dorsal flexure; idt: infra-dorsal teeth; pa: posterior auricle; r: resilifer; rc: radial costae; sdt: supra-dorsal teeth.

Discussion.—The taxonomic status of *Yabepecten* is controversial. Masuda (1963) considered this genus phylogenetically close to *Patinopecten* and *Pecten* Müller, 1776 rather than to *Mizuhopecten* and related genera (*Fortipecten* Yabe and Hatai, 1940, *Masudapekten* Akiyama, 1962, *Kotorapekten* Masuda, 1962, and *Nipponopecten* Masuda, 1962) in the northwestern Pacific, because the auricular crura with denticles on the distal end are shared by *Yabepecten*, *Patinopecten* and *Pecten*. Based on this difference, Masuda (1963) referred *Yabepecten* and *Patinopecten* to the subfamily Pectininae, and the above northwestern Pacific genera except for *Yabepecten* to the Fortipectininae. Masuda (1963) stated that the five genera in the Fortipectininae are distinguished from *Patinopecten* in having rounded radial costae in the RV, a very shallow byssal notch and larger auricles in addition to the absence of auricular crura with denticles. In contrast, Hertlein (1969) regarded *Yabepecten* as a member of the *Pecten* (*Patinopecten*) subgroup of the *Pecten* group and used it as a subgenus of *Pecten*. He questionably considered the northwestern Pacific *Masudapekten*, *Kotorapekten* and *Mizuhopecten* as synonyms of *Patinopecten*. Habe (1977) revised Hertlein's (1969) classification and treated *Mizuhopecten*, *Yabepecten* and *Kotorapekten* as subgenera of *Patinopecten*, and grouped them into the single subfamily Patinopectininae "Masuda, 1962" [sic] (see Kafanov, 1986a, b for discussion on the exact author).

Kafanov (1986a, b) revised Masuda's (1963) classification system and referred the northwestern Pacific genera *Mizuhopecten*, *Fortipecten*, *Masudapekten*, *Kotorapekten* and *Nipponopecten* to the subfamily Fortipectininae, as done by Masuda (1963), and the northeastern Pacific genus *Patinopecten* and its subgenera [*Patinopecten* s.s., *Lituyapekten* MacNeil, 1961, and "split-ribbed" *Patinopecten* (= *Blanckenhornia* von Teppener, 1922)], and tentatively the genus *Vertipecten* Grant and Gale, 1931, to the subfamily Patinopectininae, based on the morphological differences and inferred independent evolutionary histories since the early Miocene. Kafanov (1986a, b) considered *Yabepecten* referable to neither Patinopectininae nor Fortipectininae.

Waller (1991, 1993) proposed a new classification system for Pectinidae primarily on the basis of external microsculpture and cardinal properties rather than external macrosculpture. He pointed out that the external shell microsculpture and internal shell characters, including the cardinal structure of *Mizuhopecten* and *Patinopecten*, are coincident with those of the *Chlamys* group rather than the *Pecten* group. Waller (1991) observed that auricular crura, with or without denticles on the distal end, appear repeatedly in many clades of Pectinoidea, and therefore cannot be used as a uniquely derived character for distinguishing *Patinopecten* from *Mizuhopecten*. He concluded that

Mizuhopecten and *Patinopecten* are members of the subfamily Chlamydinae, and considered that these two genera may be referable to distinct subtribes of a single tribe. Following Waller's (1991) opinion, Kafanov and Lutaenko (1998) reduced the rank of the subfamily Fortipectininae to a tribe in the subfamily Chlamydinae, and referred the extant genera *Patinopecten* and *Mizuhopecten* to the tribe Fortipectinini.

Recently, Matsumoto and Hayami (2000) strongly bolstered Waller's (1991, 1993) classification system, based on molecular phylogenetic analysis of extant pectinids using mitochondrial cytochrome *c* oxidase subunit I. Their results include *Mizuhopecten* in the same clade as *Chlamys* [Röding, 1798], *Swiftopecten* Hertlein, 1936 and *Azumapekten* Habe, 1977 (= *Leochlamys* MacNeil, 1967). However, the phylogenetic relationship between this group of genera and *Patinopecten* remains obscure.

In my opinion, *Yabepecten* is a member of the tribe Chlamydini, as are *Patinopecten* and *Mizuhopecten*, based on the presence of shagreen microsculpture on the LV, and on the cardinal properties. The auricular crura with denticles on the distal end, which were considered to be a significant character of Pectinidae by Masuda (1963, 1971), are not useful for subfamily-level classification, as noted by Waller (1991). However, this feature is useful for separating the northeastern Pacific *Patinopecten* and the northwestern Pacific *Mizuhopecten*, *Fortipecten*, *Masudapekten*, *Kotorapekten* and *Nipponopecten*, given the morphological differences that have resulted from their separate evolutionary histories on either side of the North Pacific since the early Miocene (Masuda, 1963, 1971; Kafanov, 1986a, b). Consequently, I consider that *Yabepecten* was derived from *Patinopecten* and migrated westward into the northwestern Pacific by the early late Miocene.

Masudapekten, based on *Patinopecten* (*Masudapekten*) *masudai* Akiyama, 1962, from the lower middle Miocene Sugota Formation in Akita Prefecture, northeastern Japan, closely resembles *Yabepecten*. Similarities include having the LV sculptured by stringy radial costae and shagreen microsculpture, at least on immature shells. However, *Masudapekten* lacks auricular crura with denticles, and has less developed inner dorsal flexures. In addition, this genus has several striated threads in the interspaces of radial costae on the LV, and finely sulcated radial costae on the RV. *Patinopecten* differs from *Yabepecten* in having stouter LV radial costae, very high and squarish RV radial costae, larger auricles and a deeper byssal notch.

Yabepecten ogasawarai sp. nov.

Figures 2, 3, 4.2, 4.4, 4.6a–b

?*Mizuhopecten paraplebejus murataensis* Masuda and Takegawa. Ogasawara, 1983, p. 61–62, pl. 6–1, figs. 1, 2.



Mizuhopecten paraplebejus murataensis Masuda and Takegawa. Ogasawara *et al.*, 1985, p. 31, pl. 2, figs. 5, 7, pl. 3, figs. 1, 5. [not of Masuda and Takegawa, 1965].

Type specimens.—Holotype: IGPS 98911-1; paratypes: IGPS 98911-2, 98911-3, 98911-4 and 98911-5. These are specimens of *Mizuhopecten paraplebejus murataensis* figured by Ogasawara *et al.* (1985). There should be another figured specimen in the IGPS collection (Ogasawara *et al.*, 1985, pl. 2, fig. 5: IGPS 98911), but it was not found when I visited the Natural History Museum, Tohoku University.

Type locality, formation and age.—"Bed of the Sagae River, about 250 m downstream of 'Uwano O-hashii' ['Uwano big bridge'] over the Sagae River and about 500 m south-southwest of the hamlet of Uwano, Sagae City, Yamagata Prefecture" (Ogasawara *et al.*, 1985, p. 7), Ôya Tuffaceous Sandstone Member of the Hongô Formation, late Miocene.

Diagnosis.—*Yabepecten* with moderate-size, moderately thick shell; LV rather inflated; auricles small; byssal fasciole weakly flexed, rather broad; RV radial costae 18, low, broad, flat-topped, round-edged; LV radial costae 18–20, fine, tending to become weakly bi- or tripartite with shell growth; dorsal and inner dorsal teeth strong.

Description.—Shell moderate in size, moderately thick, circular, slightly longer than high, compressed, nearly equilateral except for auricles; apical angle about 120°; both antero- and postero-dorsal margins gape.

RV rather inflated compared to LV; radial costae 18, low, flat-topped, rather irregular, indistinctly defined from interspaces, rarely dichotomous owing to a very shallow median groove; interspaces shallow, somewhat narrower than costae; commarginal growth lines rather distinct, fine to coarse, irregular; auricles small; byssal fasciole broad, very weakly flexed, sculptured by fine to coarse, irregular growth lines; byssal notch very shallow; hinge line very bluntly v-shaped; resilifer moderate in size, moderately concave; resilifer teeth rather strong, with anterior tooth stronger than posterior tooth; dorsal teeth strong; anterior auricular crus indistinct; posterior auricular crus weakly elevated; inner dorsal flexures distinct; thin, foliated calcite layer inside of pallial line; adductor muscle scar indistinct except for dorsal part, reentered by foliated calcite layer; internal disc very weakly folded in concert with radial costae.

LV weakly inflated; radial costae 18–20, fine, tending to become weakly bi- or tripartite with shell growth; faint costae rarely present in interspaces; shagreen microsculp-

ture on entire external shell; commarginal growth lines indistinct; interspace of costae shallow, slightly round-bottomed; auricles small, sculptured by irregular, rather widely spaced growth lines and fine, low, radial costae; hinge line nearly straight; resilifer same as that of RV; sockets of resilifer teeth distinct, especially the anterior one; infradorsal teeth strong; supradorsal teeth very narrow; sockets of dorsal teeth rather deeply concave; anterior auricular crus distinct, with a low distal denticle; posterior auricular crus indistinct, but with a distal denticle; dorsal flexures distinct; foliated calcite layer inside of pallial line, very thin; other internal features same as RV.

Etymology.—This species is named in honor of Prof. Kenshiro Ogasawara of the Institute of Geoscience, the University of Tsukuba.

Discussion.—The type specimens of this new species were once referred to as *Mizuhopecten paraplebejus murataensis* Masuda and Takegawa, 1965, which was originally described from the upper Miocene Fukuda Formation in Miyagi Prefecture, northeastern Japan (Ogasawara *et al.*, 1985). The most significant difference between the two taxa is the mode of the auricular crura. The present new species has auricular crura with rather distinct denticles on the distal end, whereas *M. paraplebejus murataensis* has less developed crura that lack denticles, as seen in other members of *Mizuhopecten*. In addition, *M. paraplebejus murataensis* has much larger auricles, a more inflated RV with more distinct radial costae, and an LV with stouter radial costae and less developed shagreen microsculpture (Fig. 4.2, 4.4, 4.6a–c). The other significant difference is the mode of development of the inner dorsal flexures. The flexures are well developed in the LV of the Hongô specimens, whereas they are indistinct in *M. paraplebejus murataensis*. Taking account of these characters, the Hongô specimens are assigned to *Yabepecten* rather than *Mizuhopecten*.

The specimens illustrated by Ogasawara (1983) as *M. paraplebejus murataensis* from the Hashigami Sandstone Member of the Hongô Formation is probably referable to the present new species, although a definite assignment cannot be made because the specimens are not preserved well.

The present new species closely resembles *Yabepecten condoni* (Hertlein, 1925), from the lower upper Miocene Montesano Formation of Washington, in having a weakly inflated LV. However, it differs from that species by having a larger shell with smaller auricles and stronger shagreen microsculpture. *Y. ogasawarai* sp. nov. is also similar to the "smooth form" of *Patinopecten* (*Patinopec-*

◀ **Figure 3.** *Yabepecten ogasawarai* sp. nov. All figures natural size. **1a–c.** Right valve. IGPS 98911-1 (holotype). 1a. Internal view. 1b. External view. 1c. Apical view. **2a–c.** Left valve. IGPS 98911-2 (paratype). 2a. Internal view. 2b. External view. 2c. Apical view.

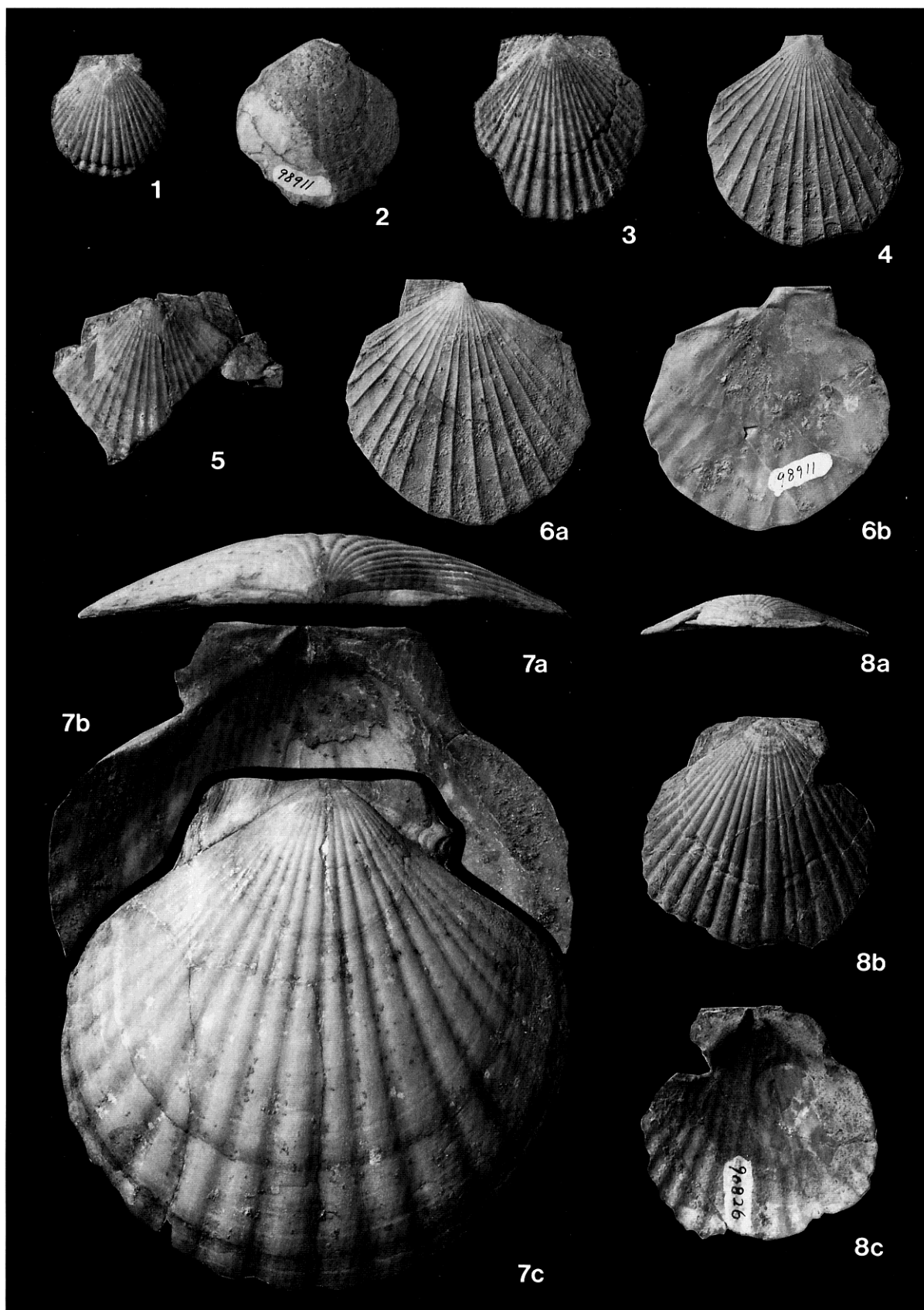


Table 1. Measurements of *Yabepecten ogasawarai* sp. nov.

Specimen	Length	Height	Convexity	Umbonal angle	Number of radial costae	Valve
IGPS 98911-1 (holotype)	82.9 mm	86.1 mm+	8.6 mm	120°	18	Right
IGPS 98911-2 (paratype)	80.7 mm	82.5 mm	8.6 mm	122°	18	Left
IGPS 98911-3 (paratype)	45.1 mm	45.6 mm	4.1 mm	123°	20	Left
IGPS 98911-4 (paratype)	36.1 mm+	39.0 mm	3.6 mm	112°	19	Left
IGPS 98911-5 (paratype)	30.4 mm	31.3 mm	4.1 mm	119°	?18	Right

ten) *healeyi* (Arnold, 1906) of Moore (1979), from Pliocene strata in California, but the latter species has a nearly smooth RV shell surface near the umbo. *Yabepecten tokunagai* (Yokoyama, 1911) clearly differs from the present new species by having a larger shell with an almost flat or weakly concave LV sculptured by much finer and lower radial costae. *Miyagipecten alaskensis* MacNeil, 1967, from the upper Miocene upper part of the Yakataga Formation in south-central Alaska differs in having a smaller shell with more irregular, distinct LV intercalary costae. Masuda and Addicott (1970) tentatively synonymized this species with *Yabepecten condoni* (Hertlein). The nearly smooth RV shell surface and the LV sculptured by fine, stringy radial costae and shagreen microsculpture indicate that *M. alaskensis* probably belongs in *Yabepecten*, as was done by Masuda and Addicott (1970), Uozumi *et al.* (1986a) and Matsubara (1996). The holotype and paratype of *M. alaskensis* are too fragmentary to evaluate thoroughly, and additional material is needed to determine its precise taxonomic position. *Miyagipecten saromensis* Hasimoto and Kanno, 1958, from the Miocene Chirai Formation of northern Hokkaidô, is easily distinguished from *Y. ogasawarai* sp. nov. by a narrower umbonal angle, stouter and very irregular radial costae on the LV, and less distinct radial costae on the RV. Amano and Karasawa (1988) tentatively referred this species to *Yabepecten*, based on the characters of the auricles, umbonal angle and RV sculpture. Unfortunately, the precise generic position of *M. saromensis* is uncertain, because its detailed LV microsculpture and cardinal properties are unknown.

Measurements.—Table 1.

Distribution.—Ôya Tuffaceous Sandstone Member of the Hongô Formation, early late or middle late Miocene; ?Hashigami Sandstone Member of the Hongô Formation, early late or middle late Miocene.

Evolutionary history of *Yabepecten*

The oldest known species of *Yabepecten* is *Y. condoni* (Hertlein) from the upper Miocene Montesano Formation of Washington along the northeastern Pacific margin (Loc. 22 in Figure 5). This species has been cited as an index fossil for the Graysian Stage (Addicott, 1976, 1977, 1984). According to Barron (1981a) the diatom assemblages of the Montesano Formation are referred to subzone b of the XV-XVI to XIII-XIV zones of Barron (1976). These zones correspond to Subzone d of the *Denticulopsis hustedtii*-*Denticulopsis lauta* Zone and Subzone a of the *Denticulopsis hustedtii* Zone of Barron (1981b), which implies an early late Miocene age. Prothero and Lau (2001) recently examined the magnetostratigraphy of the Montesano Formation. Although their recognition of the lower limit of the type Graysian Stage differs from Addicott (1976), this stage can be correlated with chrons C4Ar2r to C4Ar1r (9.584–9.025Ma; Cande and Kent, 1995; Berggren *et al.*, 1995b). *Yabepecten* in the northeastern Pacific is known only in the Graysian Stage (Addicott, 1976, 1977, 1984) and is considered to have become extinct by the end of the early late Miocene.

In contrast, the oldest species of *Yabepecten* in the northwestern Pacific is *Y. ogasawarai* sp. nov. from the Ôya Tuffaceous Sandstone Member of the Hongô Formation in northeastern Honshû, Japan (Loc. 10 in Figure 5). Diatom assemblages from this member indicate that its horizon is somewhere between the *Denticulopsis katayamae* and the lowest part of *Rouxia californica* Zones of Akiba (1986) (Akiba, 1983; Takahashi *et al.*, 1986; Maruyama, 1993; Kanamori *et al.*, 1996). According to Motoyama and Maruyama (1998) and Yanagisawa and Akiba (1998), these zones range from 9.2 or 9.1 to 7.4 or 7.3 Ma, following the magnetostratigraphy of Cande and Kent (1995) and Berggren *et al.* (1995b). This age is slightly younger than

◀ **Figure 4.** *Mizuhopecten paraplebejus murataensis* Masuda and Takegawa, 1965 and *Yabepecten ogasawarai* sp. nov. All figures natural size. 1, 3, 5, 7a–c, 8a–c. *Mizuhopecten paraplebejus murataensis* Masuda and Takegawa, 1965. 1. Right valve. IGPS 90826-4 (paratype). 3. Left valve. IGPS 90826-3 (paratype). 5. Left valve. IGPS 90826-5 (paratype). 7a–c. Right valve. IGPS 90826-1 (holotype). 7a. Apical view. 7b. Internal view. 7c. External view. 8a–c. Right valve. IGPS 90826-2 (paratype). 8a. Apical view. 8b. External view. 8c. Internal view. Shown for comparison. 2, 4, 6a–b. *Yabepecten ogasawarai* sp. nov. 2. Right valve. IGPS 98911-5 (paratype). 4. Left valve. IGPS 98911-4 (paratype). 6a–c. Left valve. IGPS 98911-3 (paratype). 6a. External view. 6b. Internal view.

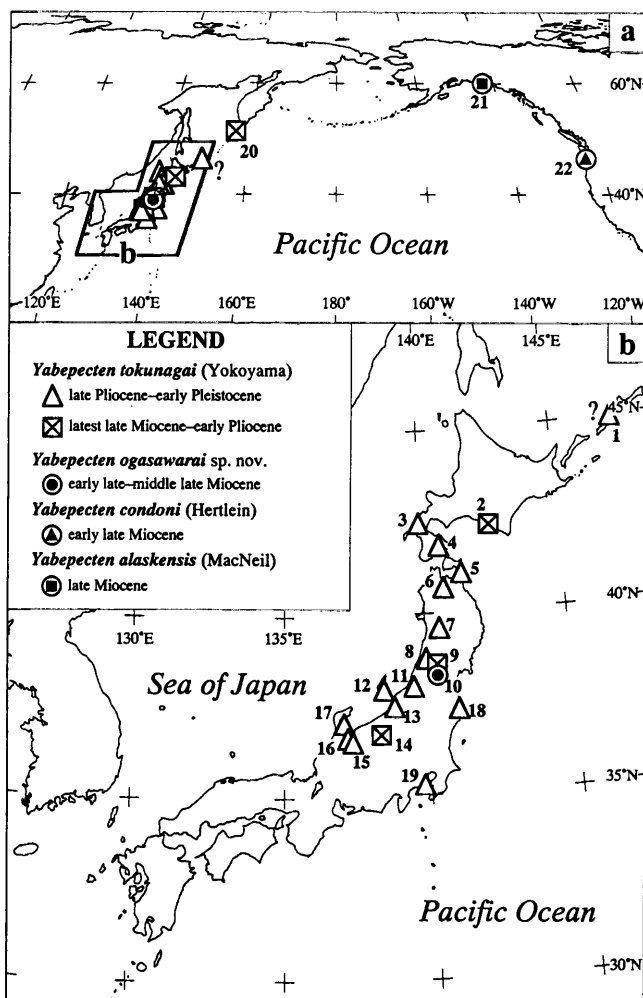


Figure 5. Distribution of *Yabepecten*. **A.** Records from North Pacific. Area shown in Figure 5.B is also indicated. **B.** Records from Japan. See appendix for data sources.

the first appearance of the northeastern Pacific *Y. condoni*.

Masuda and Addicott (1970) and Masuda (1986) speculated that *Yabepecten* originated in the Arctic Ocean or high-latitude northern Pacific. However, the earliest appearances of *Yabepecten* in both the northeastern and northwestern Pacific predate the earliest opening of the Bering Strait (Marincovich and Gladenkov, 1999; Marincovich *et al.*, 2002), and there is no fossil record of *Yabepecten* in its ostensible region of origin.

Yabepecten tokunagai has generally been reported in upper Pliocene to lower Pleistocene strata from southern Hokkaido and the Sea of Japan side of central Japan (Figure 5), and is a representative species in the Omma-Manganji Fauna (Masuda and Ogasawara, 1981; Ogasawara, 1981, 1986, 1996). The oldest record of this species

is from the uppermost Miocene–lower Pliocene Atsuga Formation of Hokkaido (Loc. 2 in Figure 5). Uozumi *et al.* (1986a) cited and figured *Yabepecten* cf. *condoni* (Hertlein) from this formation, and believed that the Atsuga specimens are much more similar morphologically to *Y. condoni* than to *Y. tokunagai*. However, *Y. tokunagai* exhibits a wide range of variation in the height and width of RV radial costae and LV convexity (e.g., Amano and Karasawa, 1988). Consequently, I consider that *Y. cf. condoni* of Uozumi *et al.* (1986a) is included within the intraspecific variation of *Y. tokunagai*. A latest late Miocene to earliest Pliocene age for the Atsuga Formation is indicated by radiometric and diatom data (Uozumi *et al.*, 1986b; Sagayama *et al.*, 1992). Although Amano and Karasawa (1988) inferred that *Y. tokunagai* was derived from *Y. condoni*, the occurrence of *Y. ogasawarai* sp. nov. from upper Miocene strata of northeastern Japan implies that this species is more directly ancestral to *Y. tokunagai*.

There have been only a few records of *Yabepecten tokunagai* from lower Pliocene deposits, one of them being in the Arakurayama Pyroclastic Member of the Shigarami Formation in central Japan (Amano and Karasawa, 1988; Loc. 14 in Figure 5). Amano and Karasawa (1993) reported fission-track ages of 4.6 ± 0.2 and 4.7 ± 0.2 Ma (error: 1σ), indicating an early Pliocene age for this member. Tsuchi and Ibaraki (1988) referred the Ogikubo Sandstone and Siltstone Member of the Shigarami Formation, which overlies the Arakurayama Pyroclastic Member, to planktonic foraminiferal zone N21 of Blow (1969), of late Pliocene age (3.35–2.0 Ma; Berggren *et al.*, 1995a).

Another early Pliocene record of *Y. tokunagai* may be from the Nakawatari Formation in Yamagata Prefecture, northeastern Honshu (Loc. 9 in Figure 5; Ogasawara *et al.*, 1984). However, this formation contains few planktonic microfossils (Maruyama, 1998; Aita *et al.*, 1999), and age estimates based on biostratigraphic and radiometric data are not in agreement (Sato, 1986; Nagasawa *et al.*, 1998, 1999), so further chronostratigraphic study is needed.

Occurrences of *Y. tokunagai* from the “upper Miocene to lower Pliocene” Okurglovskaya Formation on Paramushir Island in the Kurile Islands, northwestern Pacific [Zhidkova *et al.* (1972) described as *Mizuhopecten* cf. *subyessoensis* (Yokoyama); Masuda, 1986; Amano and Karasawa, 1988; Loc. 20 in Figure 5], may be as old as those from the Shigarami and Nakawatari Formations. However, the precise geological age of the Okurglovskaya Formation is unknown, since there are no accompanying radiometric data or planktonic microfossils.

Yabepecten tokunagai flourished in southern Hokkaido and the Sea of Japan side of central and northeast Honshu during the late Pliocene and early Pleistocene, as noted by many workers (Masuda and Ogasawara, 1981; Masuda, 1986; Uozumi *et al.*, 1986a; Amano and Karasawa, 1988;

Figure 5). These occurrences were in a mild- to cold-temperate marine climate somewhat colder than today's (Ogasawara, 1994; Amano, 1994). It subsequently became extinct by the beginning of the middle Pleistocene, along with many other taxa in the Omma-Manganji Fauna.

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Appendix. Distribution of *Yabepecten*

Locality numbers are the same as in Figure 5.

1. Parusnaya Formation (Zhidkova *et al.*, 1972, as *Mizuhopecten* cf. *subyessoensis*), presumably late Pliocene; 2. Atsunai Formation (Uozumi *et al.*, 1986a, as *Yabepecten* cf. *condoni*), earliest Pliocene (Uozumi *et al.*, 1986b; Sagayama *et al.*, 1992); 3. Setana Formation (Sawada, 1962, from Nakanokawa and Chinkope Formations; Uozumi *et al.*, 1986a), early Pleistocene (Nojo *et al.*, 1999); 4. Tomikawa Formation (Sakagami *et al.*, 1966; Uozumi *et al.*, 1986a), early Pleistocene (Nemoto, 1997); 5. Hamada Formation (Hatai *et al.*, 1961; Akiyama, 1962, as *Patinopecten* (*Masudapecten*) *plebejus*; Masuda, 1962, 1963, 1986; Masuda and Ogasawara, 1981; Matsui, 1990), early Pleistocene (Sugawara *et al.*, 1992); 6. Daishaka Formation (Nomura and Hatai, 1935, as *Pecten* (*Patinopecten*) *plebejus*), early–earliest middle Pleistocene (Nemoto and Chida, 1994; Nemoto, 1997); 7. Tentokuji and Sasaoka Formations (Takayasu *et al.*, eds., 1986; Amano *et al.*, 2000b), late Pliocene (Sato *et al.*, 1988); 8. Kannonji Formation (Ogasawara and Naito, 1983), late Pliocene (Okada, 1982; Ogasawara and Naito, 1983); 9. Nakawatari and Sakegawa Formations (Masuda, 1962; Ogasawara *et al.*, 1984), early Pliocene (Okada, 1982; Sato, 1986; Nagasawa *et al.*, 1998, 1999); 10. Hongô Formation (this study), early late–middle late Miocene (Akiba, 1983; Takahashi *et al.*, 1986; Maruyama, 1993; Kanamori *et al.*, 1996); 11. Kuwae Formation (Amano and Kaetsu Gr. Soc. Earth Sci. Ed. Niigata Pref., 1989; Amano *et al.*, 2000a), latest early–early late Pliocene (Hiramatsu and Miwa, 1998; Amano *et al.*, 2000a); 12. Sawane Formation (Yokoyama, 1926, as *Pecten plebejus* Yokoyama; Masuda, 1962; Omori, 1977), early Pleistocene (Okubo *et al.*, 1995); 13. Haizume Formation (Kobayashi *et al.*, 1986), early Pleistocene (Sato *et al.*, 1987); 14. Arakurayama Member of the Shigarami Formation (Amano and Karasawa, 1988), early Pliocene (Tsuchi and Ibaragi, 1988; Amano and

Karasawa, 1993); 15. Mita Formation (Fujii and Shimizu, 1988), early Pliocene–early Pleistocene (Fujii and Shimizu, 1988); 16. Zukawa Formation (Matsuura, 1985), late Pliocene–earliest Pleistocene (Ohkubo, 1999; Ohkubo *et al.*, 2000); 17. Sakiyama and Kojima Formations (Matsuura, 1985), late Pliocene (Matsuura, 1985); 18. Tomioka Formation of the “Taga Group” (O’Hara and Nemoto, 1988), late Pliocene (Taketani *et al.*, 1986); 19. Koshiba Formation (Yokoyama, 1911, 1920), early Pleistocene (Eto *et al.*, 1987); 20. Okruglovskaya Formation (Zhidkova *et al.*, 1972, as *Mizuhopecten* cf. *subyessoensis*; Masuda, 1986; Amano and Karasawa, 1988), late Miocene–early Pliocene (Zhidkova *et al.*, 1972); 21. Upper part of Yakataga Formation (MacNeil, 1967; Masuda and Addicott, 1970), late Miocene (Marincovich, 1984, 1990); 22. Montesano Formation (Hertlein, 1925; Masuda and Addicott, 1970), early late Miocene (Barron, 1981a; Prothero and Lau, 2001).

Comment 1.—Uozumi *et al.* (1986a, fig. 2) cited the occurrence of *Y. tokunagai* in the Plio-Pleistocene Kakegawa Formation [sic; = Kakegawa Group] of central Japan. Nobuhara (1993) also reported this species in the upper Pliocene–lower Pleistocene Ukari Formation of the Kakegawa Group. These records are excluded from Figure 5, because the occurrences are unverified due to the lack of figured specimens. If this record were true, it would be the only record from the late Pliocene–early Pleistocene subtropical realm.

Comment 2.—*Pecten* (*Patinopecten*) *plebejus* of Kubota (1950, p. 13–14, pl. 9, fig. 61) in the Setana Formation, *Yabepecten tokunagai* of Iwai (1965, p. 30–31, pl. 15, fig. 14) in the Daishaka Formation, and *Yabepecten tokunagai* of Shimamoto and Koike (1986, p. 36–37, pl. 5, fig. 12) in the Tentokuji Formation, are referable to *Mizuhopecten yessoensis* (Jay, 1857) or its subspecies, as noted by Masuda and Noda (1976), Takayasu *et al.* (1986) and Amano and Karasawa (1988).