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# The mode of life and taxonomic relationship of a Japanese Miocene pectinid bivalve *Nanaochlamys notoensis*

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Abstract. The mode of life of the Japanese Miocene bizarre pectinid *Nanaochlamys notoensis* (Yokoyama, 1929) is postulated on the basis of functional morphologic and biometric examinations of a large sample from the Middle Miocene Moniwa Formation in northern Japan. This species exhibits a remarkable ontogenetic change of shell morphology; *i.e.*, the weight of valves becomes negatively allometric to the cube of shell size, indicating relative thinning of the shell with growth. Following this allometric change, the umbonal angle increases, the auricles become symmetrical, and the ctenolium disappears. Comparison of shell morphology with Recent pectinids strongly suggests that the present species changed its life style from byssally attached to free-living during ontogeny. This pectinid probably could swim in the later growth stage, but its swimming ability appears to have been poor in view of the high convexity of the left valve. Secondary flaring of the shell and splitting of the first-order plicae are apomorphic features in *N. notoensis*, suggesting that this species is not a direct ancestor of the extant North Pacific pectinid *Swiftopecten swiftii*, with seemingly similar overall shell morphology.

Key words: allometry, evolution, functional morphology, Miocene pectinid, mode of life, Nanaochlamys notoensis

#### Introduction

The Pectinidae is one of the most diverse epifaunal bivalve families in the modern marine environment. They survived in Cenozoic shallow seas under high predation pressure after the "Mesozoic marine revolution" (Vermeij, 1977) by acquiring swimming, byssally attached, and cemented modes of life. A semi-infaunal reclining mode of life is also suggested for the Pliocene pectinid *Fortipecten takahashii* from the northwestern Pacific (Hayami and Hosoda, 1988). These various life styles in the pectinids are well reflected in their shell morphology (e.g., Stanley, 1970; Gould, 1971; Waller, 1984; Hayami and Hosoda, 1988; Hayami, 1991), so that this family is suitable for a study of functional shell morphology.

The pectinid bivalve *Nanaochlamys notoensis* (Yokoyama, 1929) treated in this paper is known to occur in the marine Miocene sediments of central Japan (Nomura, 1940; Hatai and Masuda, 1953; Masuda, 1960, 1962; Sato, 1982, 1991). This species exhibits a marked ontogenetic change in shell convexity and ornamentation of the left valve, whereas the right valve retains a constant shell morphology (Sato, 1982, 1991). However, the marked ontogenetic change of shell morphology in this species has not yet been considered from a functional morphologic point of view, except for Sato (1991). In this paper, we consider this aspect on the basis of qualitative and quantitative examinations of a large sample and comparison of shell morphology with extant pectinids, the modes of life of which are known. We also comment on the taxonomic relationship of *N. notoensis* with the extant north Pacific pectinid *Swiftopecten swiftii*, which was previously interpreted as the direct descendant of the former species by Masuda (1960).

#### Materials and methods

A total of 152 specimens (one articulated shell, 76 right valves and 75 left valves) of *Nanaochlamys notoensis* were utilized. They were recovered from the poorly sorted, coarse- to medium-grained tuffaceous sandstone of the Moniwa Formation at the roadside cliff near Kumanodo, Natori City, Miyagi Prefecture, northeast Honshu (lat.38° 12' 12"N, long. 140° 50' 28"E: WGS B4 geodetic system; same locality as L1 of Sato, 1982, fig. 9). The Moniwa Formation is a



**RIGHT VALVE** 

Figure 1. Diagrams showing the measurements. Abbreviations. U: umbonal angle, H: shell height, D: shell depth,  $E_1$ : length of anterior auricle,  $E_2$ : length of posterior auricle.

constituent of the Natori Group, which represents a standard section of the Miocene deposits in the Pacific coastal region of northeast Japan (Hanzawa *et al.*, 1953). According to the microfossil biostratigraphy by Oda and Sakai (1977), this formation is correlated to Blow's (1969) planktonic foraminiferal zone N.9 of early Middle Miocene age, on the basis of the characteristic occurrence of *Praeorbulina*.

For biometric analysis, the following shell dimensions were measured on each specimen using a slide caliper (accuracy  $\pm 0.05$  mm; see Figure 1). Abbreviations are given in parentheses. 1) shell height (H): distance between umbo and the ventral margin of the valve, measured in the direction perpendicular to the outer ligament (or hinge axis), 2) shell length (L): maximum length of the disc, measured in the direction parallel to the outer ligament, 3) shell depth (D): maximum convexity of the valve, measured in the direction perpendicular to the commissure plane, 4) auricle lengths  $(E_1, E_2)$ : lengths of the anterior auricle  $(E_1)$ and of the posterior one  $(E_2)$ , 5) umbonal angle (U): the angle (in degrees) between two lines from the umbo to the anterodorsal and posterodorsal shoulders of the disc, as defined by Stanley (1970, p. 20). Only left valves were used for measurements of H, L, U,  $E_1$  and  $E_2$ , and D was measured on both left and right valves. In addition, we weighed a left valve (W) using an automatic balance (accuracy  $\pm 10$  mg). In this study, the reduced major axis (Kermack and Haldane, 1950) is used to express allometric relationships between a pair of measurements.

For morphological comparison, we have also examined the umbonal angle and the posterior and anterior auricle lengths in the samples of ten extant pectinid species, mainly from Japanese waters, whose modes of life are known (see Appendix).

The specimens examined are housed in the University Museum, University of Tokyo (UMUT) and the National Science Museum, Tokyo (NSM) (without registered numbers for those of Recent pectinids).

#### Notes on taxonomy and general shell morphology

Nanaochlamys notoensis was first described by Yokoyama (1929) as Pecten notoensis from the Middle Miocene beds in the Nanao area, Noto Peninsula, central Japan. Hatai and Nishiyama (1952) noted that the type specimens of Pecten notoensis Yokoyama, 1929 were lost, but the eight specimens figured by Yokoyama (1929) are actually reposited at the University Museum of Tokyo, with registered numbers UMUT CM25506-CM25513. These specimens are all considered as syntypes by the International Code of Zoological Nomenclature, because Yokoyama (1929) did not designate a holotype and paratypes. Later, Sato (1982) designated CM25509 as the lectotype and CM25510 as a paralectotype.

As shown in Figure 2, this species has a circular shell outline. Radial ribs are rounded, solid and smooth, and increase in number ventrally by bifurcation on both valves. Prominent ribs occur on the shells; the number is six on the right valve and five on



**Figure 2.** *Nanaochlamys notoensis* (Yokoyama, 1929). A-G. Frontal (A, C, E, G) and anterolateral (B, D, G) views of left valves, H-M. Frontal (H, K, L) and posterolateral (I, M) views, and the anterior portion of the inner shell surface with ctenolium (pointed by an arrow) (J) of right valves. All the specimens from the locality L1. A-B. UMUT CM 29042-1. C-D. UMUT CM 29042-2. E. UMUT CM 29042-3. F-G. UMUT CM 29042-4. H-I. UMUT CM 29042-5. J. UMUT CM 29042-6. K. UMUT CM 29042-7. L-M. UMUT CM 29042-8. ×0.5 for A-I, K-M and ×1.0 for J.

the left valve in the juvenile stage, but it increases as the shell grows by the insertion of the secondaries and tertiaries on both valves. This species is inequivalved; the left valve is slightly concave and abruptly bends at a distance from the beak so as to form a flat platform (Figure 2B, D, G), but such ontogenetic change of valve convexity does not occur in the right valve (Figure 2I, M).

#### Functional morphologic analysis

Shell convexity.—The relation of shell convexity to swimming ability in pectinids has been discussed by several authors (Waller, 1969; Kauffman, 1969; Stanley, 1970; Gould, 1971; Hayami and Hosoda, 1988; Morton, 1996). Judging from the remarkable variability of shell form in free-living species involving leftconvex, equiconvex, right-convex and concavo-convex shapes, the mode and extent of shell convexity are not necessarily decisive factors for swimming of living bivalves, even though they are intimately related to swimming orientation (Waller, 1967; Stanley, 1970).

The characteristic morphologic feature of the left valve with an apparent flat early shell portion suggests that the growth of shell depth (D) versus shell height (H) changes from negative allometry to positive allometry at  $H \approx 45$  mm (see Figure 2B, D and G). If only large specimens are considered, the convexity of the left valve is stronger than that of the right one, although the growth of D against H is positively allometric in both valves (Figure 3). This condition is advantageous for obtaining lift according to Bernoulli's Theorem (Stanley, 1970). Namely, the distance of water flow is longer over the more convex upper valve



Figure 3. Average relative growth of shell depth (D) against shell height (H) for left and right valves. The slope shows positive allometry for both valves.

than beneath the less convex lower valve; accordingly, this flow pattern must result in lower water pressure on the upper valve than on the lower valve, providing lift.

Stanley (1970) postulated that the upper-convex species, *Placopecten magellanicus*, achieved mobility in this manner, but according to Hayami's (1991) experimental study, the lift produced by this effect may be negligible in comparison with the underwater gravity. Rather, it is considered that the lift is obtained by swimming with a certain attack angle.

Shell weight.—Because isometric growth of shell weight in a living bivalve must result in a steady decrease of the lift/gravity ratio (Gould, 1971), relative thinning of the shell will be particularly effective in maintaining swimming ability of a pectinid bivalve until the later stage. Owing to the difficulty of measuring the shell thickness, the allometric relationship between linear shell size (height in this case) and shell weight in each valve is examined. As weight is proportional to the cube of size, isometric growth will be accomplished by a weight growth ratio of 3.

The relative growth of shell weight against shell height in *Nanaochlamys notoensis* can be regarded as diphasic in both valves (Figure 4). Though the calculated growth ratios are larger than 3 (3.319 in left valve, 3.301 in right valve) in the early stage (H < 50 mm), relative thinning of the shell seems to occur in the later stage (H > 50 mm), that is, it turns to negative allometry (2.875 in left valve, 2.884 in right valve).

Umbonal angle.—Stanley (1970) pointed out that free-living pectinids are generally characterized by a broader shell and a larger umbonal angle than byssate pectinids. In his interpretation a larger umbonal angle is advantageous for a swimming motion, because the currents expelled from the gapes of the anterodorsal and posterodorsal margins pass more directly to the dorsal direction, so that the resultant propelling force increases. Moreover, by the analogy with a hydrofoil, he supposed that the broader disc must produce a greater ratio of lift/drag.

In this study, the ontogenetic relationship between



**Figure 4.** Average relative growth of shell weight (W) against shell height (H) for left and right valves. The growth of both valves changes from positive allometry to negative allometry during ontogeny.

the umbonal angle (U) and shell height (H) of N. notoensis and several extant pectinids is examined (Figure 5). The mean umbonal angle in the early stage of N. notoensis is nearly the same as those of byssate pectinids. However, it becomes larger with increasing shell size, and the angles of most specimens in the stage larger than 60 mm in shell height are similar to those of free-living pectinids. In contrast, the umbonal angle of an early Pliocene pectinid Fortipecten takahashii, which is inferred to be a recliner, becomes smaller with increasing shell size (Hayami and Hosoda, 1988, text-fig. 2). This trend is completely opposite to the byssate and free-swimming pectinids.

*Posterior/anterior auricle ratio.*—Elongation of the anterior auricle is advantageous for byssal attachment of a living pectinid on the substratum or on other objects (shells) by acting as a support to prevent over-turning of the shell (Stanley, 1970). The shell would be susceptible to overturning along the antero-ventral



**Figure 5.** Scatter plots of umbonal angle (U) against shell height (H) for the examined samples of *N. notoensis* and eight extant pectinid species. In *N. notoensis*, the mean umbonal angle in the early stage is nearly the same as those of extant byssate species (more densely dotted area), but it becomes larger with increasing shell size and the angle in the later stage is similar to those of extant free-living species (less densely dotted area). BA: byssally attached species, FL: free-swimming species.



**Figure 6.** Scatter plots of posterior/anterior auricle ratio against shell height (H) for the examined samples of *N. notoensis* and 11 extant pectinid species and subspecies. The 11 extant pectinids examined can be roughly classified into a byssally attached group with smaller posterior/anterior auricle ratios (more densely dotted area) and a free-living one with larger ratios (less densely dotted area). The specimens of *N. notoensis* are plotted near the boundary between the spectra of the two groups. BA: byssally attached species, FL: free-swimming species.

margin by a weak upward force acting on the posterior part of the shell. By the presence of auricle and sinus, two points along the shell margin, one on either side of the byssus, act as a fulcrum, and this fulcrum shifts distally from the byssus. The greater the distance from byssal notch to fulcrum for a given shell size, the greater the leverage against an overturning force. The functional meaning of auricles in nonbyssate pectinids is poorly known, but symmetry of auricles may be required for swimming straight forward. For this reason, the degree of auricle symmetry is examined in this study. The ratios of lengths of posterior auricles versus anterior ones in specimens of 12 pectinid species and subspecies are shown in Figure 6. The examined species can be classified into the byssally attached group with the smaller ratios and the free-living one with the large ratios. The specimens of N. notoensis examined are distributed near the critical boundary between the areas shared by the two groups.

Ctenolium.—The ctenolium strengthens byssal attachment by spreading byssal threads where they pass over the disc flank (Waller, 1984). A well developed ctenolium indicates the presence of a byssus. *N. notoensis* has the ctenolium on the right valve in the younger stage (see Figure 2J), but it disappears in larger specimens. The largest specimen with a ctenolium is 53 mm in height, and specimens larger than this size lack a ctenolium. The teeth of the ctenolium are small and do not change in absolute size with increasing shell size. A similar ontogenetic disappearance of the ctenolium is observable in an extant freeliving pectinid, *Patinopecten yessoensis*, that has a small ctenolium only in the younger stage (H < 30 mm).

These features cannot be seen in extant byssally attached pectinids. Such species possess a ctenolium throughout their life and the teeth increase in size with growth.

### Discussion

#### Inferred mode of life

Extant byssally attached pectinids have characteristic shell features such as byssal notch, ctenolium, elongation of anterior auricle, inequivalve condition and so on (Waller, 1984). *N. notoensis* has a ctenolium and a deep byssal notch in the early growth stage, both of which reflect a byssally attached mode of life. This species exhibits a remarkable ontogenetic change of several shell features; namely, with increasing shell



**Figure 7.** Phylogenetic relationships of *Nanaochlamys* and related genera and/or species postulated by Masuda (1960) (A) and Waller (1991) (B).

size, the umbonal angle becomes larger and the weight of the shell is negatively allometric to shell size (Figures 4, 5). Relative lightening of the shell in this species is advantageous for swimming, and the auricles approximating symmetry are also advantageous for swimming. This interpretation is also supported by the presence of a large muscle scar (Sato, 1982, p. 48). Moreover, adult specimens larger than 50 mm high have a smaller byssal notch than younger ones, and lack a ctenolium. These characteristic shell features can also be observed in the extant free-living scallop *Patinopecten yessoensis*. Therefore, this species presumably changed its life style from a byssal-attached life to a free-living one during ontogeny.

Prior to this work, Sato (1982, 1992) noticed that in *N. notoensis*, adult specimens have a smaller byssal notch and a more poorly developed ctenolium than in juvenile specimens. Based on these observations, Sato (1992, p. 69) suggested that this species changed its life habit from fixosessile with a firm byssus to liberosessile with free swimming. The results of this study strongly support Sato's (1992) interpretation.

The high shell convexity in the later growth stage of this species, however, seems to be disadvantageous for fast swimming, because at a given attack angle, the convex valves produce a higher drag coefficient than the slender valves (see Hayami, 1991, figs. 1, 3). Indeed, such a convex shell feature occurs in the Pliocene recliner *Fortipecten takahashii* and certain Recent byssate pectinids (e.g., *Swiftopecten swifti*, *Decatopecten striatus*). For this reason, *N. notoensis* might be a poor swimmer, even if it acquired some swimming ability in the later growth stage.

In S. swifti, periodic increase of shell convexity during ontogeny occurs in association with gonad development (I. Hayami, pers. comm.). Therefore, there is a possibility that the abrupt allometric change in shell convexity of the left valve in N. notoensis might occur with sexual maturation.

#### Comparison with Swiftopecten swiftii

Masuda (1960) interpreted the extant north Pacific pectinid Swiftopecten swiftii as a direct descendant of N. notoensis because of the similarity of shell morphology in younger stages and the evidence of the fossil record (Figure 7A). According to him, the former is similar to the latter in both form and sculpture, and the latter is restricted to the early Miocene, when the former appeared. On the other hand, Sato (1982) briefly noted that Swiftopecten is not a direct descendant of Nanaochlamys, because N. notoensis otutumensis, a chronological subspecies of N. notoensis, cooccurs with S. swiftii in the middle Miocene Otsutumi Formation in Miyagi Prefecture, northeast Honshu. More recently, Waller (1991) proposed a similar view that Nanaochlamys and Swiftopecten independently evolved from a common ancestor, forming a single clade (Figure 7B). According to him, this clade is defined by sharing the following synapomorphies; reduction in the number of secondary first-order ribs and their arrangement in a specific pattern, and development of the larger scale ledging, with ledging amplitude greater on the left valve than on the right. The apomorphic features observed in Nanaochlamys are secondary flaring of the shell and splitting of the firstorder plicae, whereas in Swiftopecten frequent ledging during ontogeny is apomorphic.

S. swiftii and N. notoensis share similar shell features such as the shagreen microsculpture throughout ontogeny and the prominent primary radial ribs, numbering five on the left valve and six on the right one. However, these two species are distinguished by the differences in the allometric change of the umbonal angle versus shell height (Figure 5). Interestingly, the mode of ribbing on the left and right valves in the juvenile stage of N. notoensis is fairly similar to that in the adult stage of S. swiftii. This fact suggests to us a possibility that the latter species arose from the former species by neoteny. If neoteny actually occurred, the allometric trend of shell convexity in S. swiftii should resemble that in the early stage of N. notoensis. However, such a phenomenon is not observed in the two species, and the allometric trend of S. swiftii resembles that in the later stage of N. notoensis instead of the early stage. This fact strongly supports Waller's (1991) opinion in which the two species are regarded as constituting sister groups.

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#### References

- Blow, W. H., 1969. Late Middle Eocene to Recent planktonic foraminiferal biostratigraphy. *In*, Bronnimann, P. and Renz, H. H. eds., *Proceedings of the First International Conference on Planktonic Microfossils, Geneva, 1967*, vol. 1, p. 199–422.
- Gould, S. J., 1971. Muscular mechanics and the ontogeny of swimming in scallops. *Palaeontology*, vol. 14, p. 61–94.
- Hanzawa, S., Hatai, K., Iwai, K., Kitamura, J. and Shibata, T., 1953. The geology of Sendai and its environs. *Science Report of Tohoku University, 2nd Series (Geology)*, vol. 25, p. 1–50. (*in Japanese with English abstract*)
- Hatai, K. and Masuda, K., 1953. On the Pecten notoensis (Yokoyama). (On the Miocene Pectinidae from the environs of Sendai, Part 2). Transactions and Proceedings of the Palaeontological Society of Japan, New Series, no. 11, p. 75–85.

- Hatai, K. and Nishiyama, S., 1952. Check list of Japanese Tertiary Mollusca. Science Report of Tohoku University, 2nd Series (Geology), special vol. 3, p. 1–464.
- Hayami, I., 1991. Living and fossil scallop shells as airfoils: an experimental study. *Paleobiology*, vol. 17, p. 1–18.
- Hayami, I. and Hosoda, I., 1988. Fortipecten takahashii, a reclining pectinid from the Pliocene of north Japan. Palaeontology, vol. 31, p. 419–444.
- Kauffman, E.G., 1969. Form, function, and evolution. In, Moore, R.C. ed., Treatise on Invertebrate Paleontology, Part N, Volume 1 (of 3), Mollusca 8 Bivalvia, p. N130– N205. Geological Society of America and University of Kansas Press, Lawrence.
- Kermack, K. A. and Haldane, J. B. S., 1950. Organic correlation and allometry. *Biometrika*, vol. 37, p. 30–41.
- Masuda, K., 1960. On morphogenesis of Nanaochlamys. Science Report of Tohoku University, 2nd Series (Geology), special vol. 4 (Hanzawa Memorial Volume), p. 371–383.
- Masuda, K., 1962. Tertiary Pectinidae of Japan. Science Report of Tohoku University, 2nd Series (Geology), vol. 33, no. 2, p. 117–238.
- Morton, B., 1996. The biology and functional morphology of *Minnivola pyxidatus* (Bivalvia: Pectinidae). *Journal of Zoology*, vol. 240, 735–760.
- Nomura, S., 1940. Molluscan fauna of the Moniwa shell beds exposed along the Natori-Gawa in the vicinity of Sendai, Miyagi Prefecture. Science Report of Tohoku University, 2nd Series (Geology), vol. 21, p. 1–46.
- Oda, M. and Sakai, T., 1977. Microbiostratigraphy of the lower to middle part of the Hatatate Formation, Sendai, Japan. *In*, Takayasu, T. *et al. eds.*, Prof. Hujioka Memorial Volume, pp. 441–456. (*in Japanese with English abstract*)
- Sato, Y., 1982. Redescription of Nanaochlamys notoensis (Yokoyama) and Nanaochlamys notoensis otutumiensis (Nomura and Hatai) (Paleontological study of the molluscan fauna from the Moniwa Formation Part-1) Saito Ho-on Kai Museum, Research Bulletin, no. 50, p. 37–60.
- Sato, Y., 1991. Paleontological study of the molluscan fauna from the Moniwa Formation, Northeast Japan and description of their Pectinidae. *Bulletin of the Geological Survey of Japan*, no. 272, p. 1–249.
- Stanley, S. M., 1970. Relation of shell form to life habits in the Bivalvia (Mollusca). *Memoirs of the Geological Society of America*, no. 125, p. 1–296.
- Vermeij, G., 1977. The Mesozoic marine revolution: Evidence from snails, predators and grazers. *Paleobiology*, vol. 3, p. 245–258.
- Waller, T. R., 1969. The evolution of the Argopecten stock (Mollusca, Bivalvia) with emphasis on the Tertiary and Quaternary species of eastern North America. Paleontological Society Memoir, no. 3 (Journal of Paleontology, vol. 43, supplement to no. 5), p. 1–125.
- Waller, T. R., 1984. The ctenolium of scallop shells: Functional morphology and evolution of a key family-level character in the Pectinacea (Mollusca: Bivalvia). *Malacologia*, vol. 25, p. 203–219.
- Waller, T. R., 1991. Evolutionary relationships among commercial scallops (Mollusca: Bivalvia: Pectinidae). *In*, Shumway, S. E. *ed.*, *Scallops: Biology, Ecology and Aquaculture*, p. 1–73. Elsevier, Amsterdam.
- Yokoyama, M., 1929. Pliocene shells from near Nanao, Noto. Imperial Geological Survey of Japan. Report, no. 104, p. 1–7.

## Appendix

List of material of 11 extant pectinid species and subspecies for functional morphologic comparison. Abbreviations: BA, byssally attached, FL, free-living, NSM, National Science Museum, UMUT, University Museum, University of Tokyo, MS, Michiko Saito's private collection.

- 1. *Swiftopecten swiftii* (Bernardi), BA, Wakkanai, northern Hokkaido, N = 74, NSM.
- 2. *Chlamys islandica* (Müller), BA, Wakkanai, northern Hokkaido, N = 34, MS.
- 3. Chlamys farreri akazara (Kuroda), BA, Hokkaido (N = 9), and Hachinohe (N = 6) and Hitachi (N = 13), northern Honshu (N = 6), NSM and UMUT.
- Chlamys farreri nipponensis (Kuroda), BA, Sagami Bay (N = 27), Boshu (N = 18), and Amahimeyama (N = 2), UMUT.
- 5. Chlamys nobilis (Reeve), BA, Sagami Bay (N = 5) and Misaki (N = 2), central Honshu, and Genkainada, north Kyushu (N = 1), UMUT.

- 6. Chlamys irregularis (Sowerby), BA, unknown (N = 12), Tosa Bay (N = 8), Boshu (N = 1) and Misaki (N = 1), Honshu, UMUT.
- 7. Pecten albicans (Schröter), FL, Kesennuma, northern Honshu (N = 2), Sagami Bay (N = 13), Misaki (N = 13), Choshi (N = 1), Noto Peninsula (N = 2), central Honshu, unknown (N = 3), Miyajima, west Honshu (N = 1), Tsuyazaki, northern Kyushu (N = 33), and Kagoshima, southern Kyushu (N = 1), UMUT.
- 8. Argopecten irradians (Linnaeus), FL, Atlantic coast, U.S.A. (N = 16), UMUT.
- 9. Decapecten striatus (Schumacher), FL, Misaki, central Honshu (N = 8) and unknown (N = 3), UMUT.
- 10. Patinopecten yessoensis (Jay), FL, Aomori, northern Honshu (N = 7) and unknown (N = 70), UMUT.
- 11. Amusium japonicum (Gmelin), FL, Tosa Bay, Shikoku (N = 3), Kagoshima, Kyushu (N = 3), Misaki (N = 1) and Boshu (N = 1), central Honshu, and unknown (N = 3), UMUT.