

A new Miocene *Scutellastra* (Patellidae: Gastropoda: Mollusca) from the Izu Peninsula, Japan, and the paleobiogeographic significance of the molluscan fauna of the Yugashima Group

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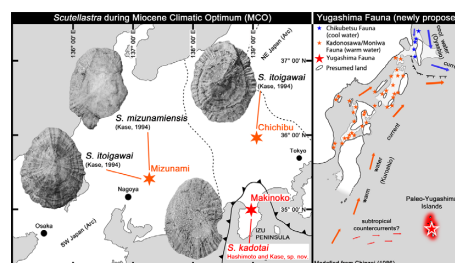
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ABSTRACT

The Izu Peninsula of central Japan is a volcanic block that originated far to the south and was transported to its current location by the northward migration of the Philippine Sea Plate. Several small limestone bodies within the upper Lower to lower Middle Miocene volcanoclastic Yugashima Group on the Izu Peninsula contain a molluscan fossil assemblage associated with coral reefs. This assemblage provides insights into the shallow-water diversity of tropical oceanic islands on the eastern margin of the Philippine Sea Plate during the Miocene. Here, a new species of patellid limpet, *Scutellastra kadotai* sp. nov., is described based on specimens from the Makinoko Limestone in the Shuzenji area of the Izu Peninsula. This new species is distinct from *Scutellastra mizunamiensis* and *Scutellastra itoigawai* from contemporaneous strata in the Mizunami and Chichibu basins on the Honshu Arc of mainland Japan. The molluscan assemblage of the upper Lower to lower Middle Miocene limestone bodies on the Izu Peninsula differs in species composition from those of the nearly contemporaneous Kadonosawa/Moniwa faunas of the Honshu Arc. The discovery of a new *Scutellastra* species provides additional evidence that the late Early to early Middle Miocene fauna of the Izu Peninsula was distinct from those of the Honshu Arc. We propose the new faunal name “Yugashima Fauna” for the molluscan assemblage found within the limestone bodies of the Yugashima Group and discuss its paleobiogeographic significance.



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Keywords: Izu Peninsula, Makinoko Limestone, Miocene, Patellogastropoda, *Scutellastra*, Yugashima Fauna

Introduction

The Izu Peninsula in central Japan occupies the northern margin of the Philippine Sea Plate. It is the northernmost extent of a volcanic arc that has been colliding with the Honshu Arc (i.e., the Southwestern and Northeastern

Japan arcs) since the Late Miocene (Hirooka *et al.*, 1985; Koyama, 1991, 1994; Niitsuma and Koyama, 2006). The contemporaneous Miocene volcanoclastic Sakurada and Kadono formations of the Yugashima Group on the Izu Peninsula contain several meter-scale limestone bodies. These include the Shikura, Ena, and Shirakawa limestones in the Matsuzaki area and the Makinoko Limestone in the Shuzenji area. These limestone bodies were deposited far south of their present location and contain a diverse assemblage of marine fossils, including corals, mollusks, and calcareous algae, which are exotic to the Miocene

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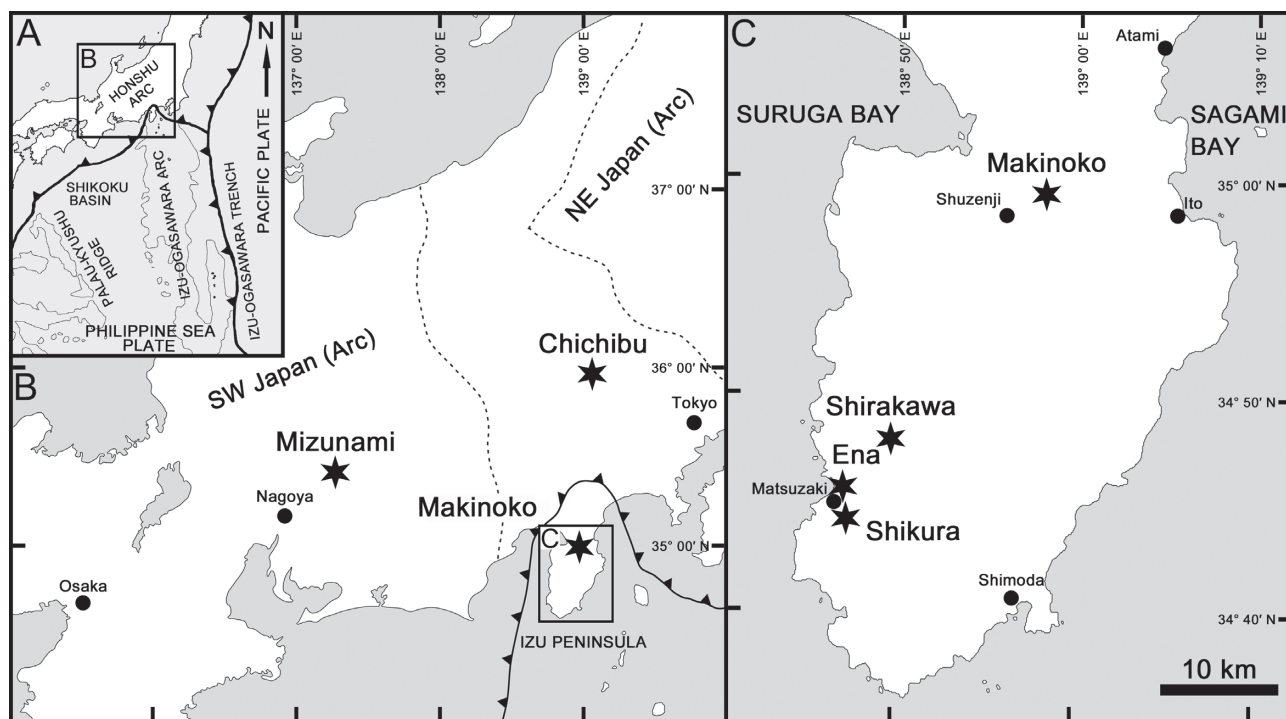


Figure 1. A, Map showing the tectonic framework of the Izu Peninsula; B, Map showing the three localities of the specimens discussed in this paper; C, Map showing the locations of mollusk-bearing limestone bodies in the Izu Peninsula. For detailed information on these localities, see Tomida and Kadota (2012b, 2014) and Kase *et al.* (2020).

fauna and flora of the Japanese archipelago (Ishijima, 1967, 1968; Kase and Katayama, 1981; Tomida and Kadota, 2012a, b, 2014; Tomida *et al.*, 2013, 2017, 2021, 2022; Kadota, 2015; Kase *et al.*, 2020). These fossils therefore provide further evidence of the gradual northward movement of the Philippine Sea Plate and offer a rare insight into the little-known Miocene shallow marine biotas of tropical oceanic islands in the northeastern Philippine Sea (Tomida and Kadota, 2012a, b, 2014; Tomida *et al.*, 2013, 2021; Kadota, 2015).

The Makinoko Limestone (Makinoko Limestone in previous studies) is a limestone body of the Yugashima Group and is interbedded within the Kadono Formation. Eleven species of calcareous algae and three mollusks have been reported (Ishijima, 1968; Kase and Katayama, 1981; Majima, 1994; Kase *et al.*, 2020). Our research on the Makinoko Limestone has led to the discovery of over 70 species of fossil mollusks. However, the taxonomic study of these species is still in progress. Here, we describe a new species of the patellogastropod genus *Scutellastra* from the Makinoko Limestone. For comparison, two species of *Scutellastra* previously described from the Miocene of the Japanese archipelago were reexamined based on the type series and other referred specimens. We also review the molluscan fauna of the Yugashima Group

and discuss its paleobiogeographic characteristics.

Institutional abbreviations.—IGUT, Institute of Geoscience, the University of Tsukuba, Tsukuba, Ibaraki, Japan; MFM, Mizunami Fossil Museum, Mizunami, Gifu, Japan; NMNS, Department of Paleontology and Anthropology, National Museum of Nature and Science, Tsukuba, Ibaraki, Japan; SMNH, Saitama Museum of Natural History, Nagatoro, Saitama, Japan.

Notes on the Makinoko Limestone

The Makinoko Limestone is exposed in a small valley approximately 1.5 km east of Makinoko Station in Shuzenji Town, in the north-central part of the peninsula (Figure 1). This small outcrop is located along a path heading east and was measured by Kadota *et al.* (1985) to be 2 m × 5 m. It consists of massive, friable, and pinkish limestone, mostly composed of massive biomicrite with minute grains of oxidized dacite, limonitic ooids, and abundant algal-coated andesite cobbles (Kase and Katayama, 1981). The stratigraphic relationship between this limestone body and the surrounding volcanic sediments is unknown owing to poor exposure.

Ishijima (1968) described the circumstances surrounding the discovery of the Makinoko Limestone and its

fossil content. Before 1968, Mr. Morita, the landowner and proprietor of Numazu Fossil Crafts Co., donated several fossiliferous rocks to Hiroshi Ozaki of the National Science Museum, Tokyo (now the National Museum of Nature and Science, Tokyo). Under Morita's guidance, Ishijima visited the site, collected samples, and studied the calcareous algae (Ishijima, 1968). The limestone was likely being commercially quarried at that time. Although Ishijima (1968) did not provide details about the size and distribution of the limestone body, he noted that it is rich in gastropod, coral, and bryozoan fossils, which are quite conspicuous even to the naked eye.

Since 1980, the second author (T. K.) has visited this site several times to collect fossil mollusks. Several mollusks have been reported from the locality, including the pleurotomariid gastropod *Entemnotrochus ozakii*, the clavigellid bivalve *Humphreyia (Nipponoclava) gigantea*, and the turbinid gastropod *Turbo (Marmarostoma) izuensis* (Kase and Katayama, 1981; Majima, 1994; Kase *et al.*, 2020). These reports noted that the currently exposed limestone body contains abundant calcareous algae but relatively few mollusks.

The mollusks reported here were collected from cobble- to boulder-sized limestone debris accumulated in a creek adjacent to the outcrop. We infer that the limestone beds bearing these mollusks are now buried under the soil and vegetation but were previously exposed on the ridge slope above the current limestone outcrop. Kase and Katayama (1981) estimated that the limestone-bearing beds were almost 50 m thick; however, they provided no evidence to support this estimate.

Although the Makinoko Limestone lacks reliable index fossils, the Kadono Formation, which includes this limestone, has been correlated with the upper Lower to lower Middle Miocene Sakurada Formation in the Matsuzaki area (Niitsuma and Koyama, 2006). A recent study integrating microfossil biostratigraphy and strontium isotopic data correlated the Ena limestone of the Sakurada Formation with the nannofossil CN3 zone and Blow's planktonic foraminiferal N7–8 zones (Yagi *et al.*, 2018). Kase *et al.* (2020) reported *T. (M.) izuensis* from both the Makinoko and Ena limestones, and here, we report four gastropod species shared by the two limestones (Table 1). We therefore consider these limestones to be contemporaneous and assign them to the late Early to early Middle Miocene.

Systematic paleontology

(Kairu Hashimoto and Tomoki Kase)

Family Patellidae Rafinesque, 1815

Genus *Scutellastra* H. Adams and A. Adams, 1854

Type species.—*Patella plicata* Born, 1778 (= *Patella barbara* Linnaeus, 1758), Recent, South Africa and Namibia; subsequent designation by Wenz (1938).

Remarks.—Kase (1994) described *Patella mizunamiensis* and *Patella itoigawai* from the lower Middle Miocene beds of the Mizunami Basin in Gifu Prefecture and *Patella yajimai* from the lower Pliocene Ochiai Formation of the Tanzawa Mountains in central Japan. This generic allocation was based on MacClintock's (1967) classification using a shell-layering combination of the four basic structure types. In the two species, the outer shell of the two shell layers above the myostracum (m+2 layer; MacClintock, 1967) consists of a radial crossed-foliated structure and classified into MacClintock's (1967) shell structure Group 10, whereas ten species of the genus *Scutellastra* (including the type species) possessing an additional crossed-foliated layer above the m+2 layer were classified into Group 9. However, subsequent studies failed to confirm the presence of the m+3 layer in Group 9, making it difficult to distinguish between the two groups (Ridgway *et al.*, 1998; Fuchigami and Sasaki, 2005). Ridgway *et al.* (1998) clarified that the presence of an outermost radial crossed-foliated layer is a synapomorphy of the genus *Scutellastra*. Hence, we here reallocate *P. mizunamiensis* and *P. itoigawai* to *Scutellastra*. In accordance with this change of the definition of the genus, we also reallocate *Patella yajimai* to *Scutellastra*. Three comprehensive molecular phylogenetic studies have shown *Scutellastra* to be a paraphyletic group closely related to the genera *Cymbula* and *Helcion* (Koufopanou *et al.*, 1999; Lindberg, 2007; Nakano and Ozawa, 2007).

Scutellastra mizunamiensis (Kase, 1994)

Figure 2A–D

Penepatella cf. *stellaeformis* (Reeve). Itoigawa *et al.*, 1974, p. 114, pl. 36, fig. 15; Itoigawa *et al.*, 1981, pl. 24, fig. 13; Itoigawa *et al.*, 1982, p. 128.

Patella mizunamiensis Kase, 1994, p. 58, fig. 3c, d.

Type.—Holotype, MFM 10095, length 27.9 mm, width 20.1 mm, height 7.1 mm.

Type locality.—Bed of the creek Hiyoshigawa in Shukubora, Mizunami, Gifu, Japan (35°24'40.7"N, 137°15'53.2"E); locality 18 in Itoigawa *et al.* (1974) (Figure 1).

Type horizon and age.—Shukunohora Formation; lower part of Blow's (1969) planktonic foraminiferal zone N8 (Ibaraki, 1981; Itoigawa, 1989; Irizuki and Hosoyama, 2006).

Other material examined.—Four specimens, MFM 13080–13083; two specimens, NMNS PM69337, coll. T. Kaede, from the type locality.

Table 1. Mollusk species of the Yugashima Fauna from the Makinoko Limestone in the Shuzenji area and the Ena Limestone in the Matsuzaki area of the Izu Peninsula, central Japan. Two species marked with an asterisk are unpublished. The right column lists taxa that are congeneric or consubgeneric with taxa from the Kadonosawa/Moniwa faunas.

YUGASHIMA FAUNA	Makinoko Limestone in Shuzenji area	Ena Limestone in Matsuzaki area	KADONOSAWA/MONIWA FAUNA
<i>Scutellastra kadotai</i> Hashimoto and Kase, sp. nov.	○		<i>Scutellastra mizunamiensis</i> (Kase) ¹² <i>Scutellastra itoigawai</i> (Kase) ¹²
<i>Entemnotrochus ozakii</i> Kase and Katayama ¹	○		none
<i>Turbo</i> (<i>Marmarostoma</i>) <i>matsuzakiensis</i> Tomida and Kadota ²		○	<i>Turbo</i> (<i>Marmarostoma</i>) <i>ozawai</i> Otuka ¹³
<i>Turbo</i> (<i>Marmarostoma</i>) <i>ishidai</i> Tomida, Sano and Kase ³		○	<i>Turbo</i> (<i>Marmarostoma</i>) <i>tochiyensis</i> Kanno ¹³
<i>Turbo</i> (<i>Marmarostoma</i>) <i>izuensis</i> Kase, Tomida, Inoue and Kadota ⁴	○	○	
<i>Turbo</i> (<i>Marmarostoma</i>) <i>yoshiharuyabei</i> Tomida and Kadota ⁵	○	○	
<i>Turbo</i> (<i>Marmarostoma</i> ?) <i>sanoi</i> Tomida and Kadota ⁵		○	
<i>Turbo</i> (<i>Turbo</i>) <i>hosodai</i> Tomida and Kadota ⁵		○	none
<i>Astralium ena</i> Tomida, Inoue and Kase ⁶	○	○	<i>Astralium hayakawai</i> (Kanno) ⁶
<i>Tectus</i> aff. <i>pyramis</i> (Born) ⁷		○	<i>Tectus</i> (<i>Rochia</i>) <i>japonicus</i> Horikoshi ¹⁴
<i>Campanile</i> sp. ^{8*}	○	○	none
<i>Chavanicerithium</i> sp. ^{8*}	○		<i>Chavanicerithium kannoi</i> (Nakagawa) ^{8, 14}
<i>Strombus</i> (<i>Tricornis</i>) sp. ⁹		○	none
<i>Tutufa</i> (<i>Tutufa</i>) sp. ¹⁰		○	none
<i>Humphreyia</i> (<i>Nipponoclava</i>) <i>gigantea</i> (Sowerby) ¹¹	○		<i>Humphreyia</i> (<i>Nipponoclava</i>) <i>kanazawensis</i> (Omura) ¹¹

References: ¹Kase and Katayama (1981); ²Tomida and Kadota (2012b); ³Tomida *et al.* (2021); ⁴Kase *et al.* (2020); ⁵Tomida and Kadota (2014); ⁶Tomida *et al.* (2022); ⁷Tomida *et al.* (2017); ⁸unpublished data; ⁹Tomida and Kadota (2012a); ¹⁰Tomida *et al.* (2013); ¹¹Majima (1994); ¹²this study; ¹³Kase *et al.* (2023); ¹⁴Nakagawa (2009).

Distribution.—Known only from the type locality.

Remarks.—This species was described based solely on the holotype specimen (Figure 2A). We reexamined the holotype and five additional specimens from the type locality (Figure 2B–D). The shell is small (up to 28 mm) and depressed with the apex slightly anterior to the middle. The aperture is an elongated oval and is not stellate, and its anterior margin is more narrowly rounded than its posterior margin. The sculpturing consists of thick primary ribs arranged like a six-pointed asterisk, thin secondary ribs developed between them, and four to six slender ribs (varying in protrusion) positioned between the primary and secondary ribs. Itoigawa *et al.* (1974, 1981, 1982) compared this taxon with the Recent *Penepatella stel-laeformis* Reeve, 1842 [a junior synonym of *Scutellastra flexuosa* (Quoy and Gaimard, 1834)]. However, *S. mizu-*

namiensis has a smaller shell size relative to *S. flexuosa* and is also characterized by a more elongated and non-stellate aperture and six-pointed asterisk-like primary ribs. Additionally, the radial ribs are rather smooth in *S. mizunamiensis*, whereas they are scaly in *S. flexuosa*.

Scutellastra itoigawai (Kase, 1994)

Figures 3A, B; 4A–C

Diodora aff. *sieboldii* (Reeve). Kanno, 1960, p. 329, pl. 46, fig. 4a, b.
“*Acmaea*” sp. 4. Itoigawa *et al.*, 1981, pl. 24, fig. 9a–c; Itoigawa *et al.*, 1982, p. 128.

Patella itoigawai Kase, 1994, p. 58, fig. 3a, b.

Type.—Holotype, MFM 10096, fragmentary specimen, length 27.2 mm, width 17.1 mm, height 15.0 mm.

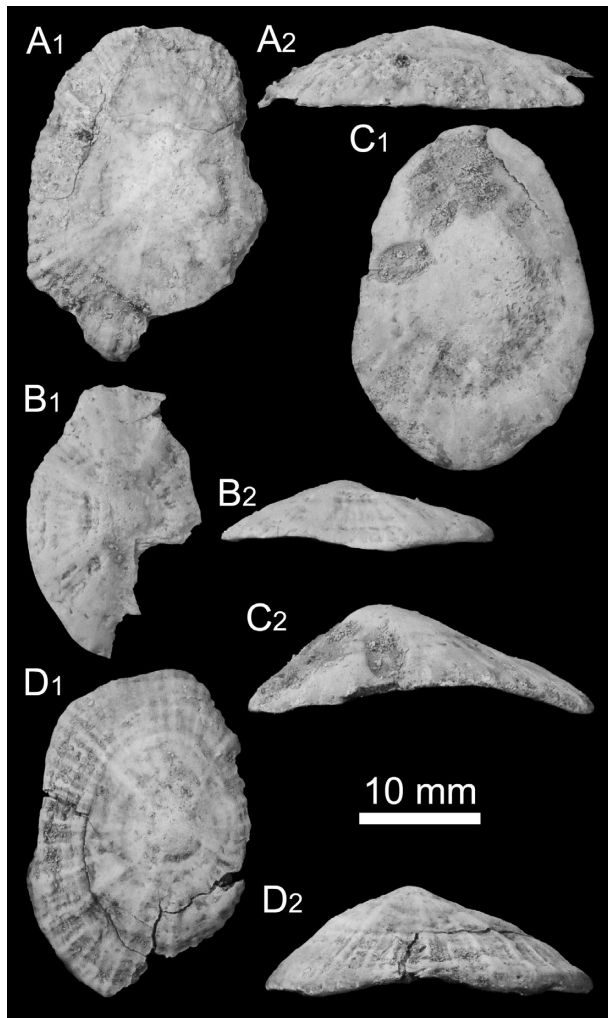


Figure 2. *Scutellastra mizunamiensis* (Kase, 1994) from the lower Middle Miocene Shukunohora Formation of the Mizunami Basin in Akatsukibora, Mizunami, Gifu, Japan. **A**, holotype, MFM 10095; dorsal (A1) and lateral (A2) views, length 27.9 mm, width 20.1 mm, height 7.1 mm; **B**, MFM 13080; dorsal (B1) and lateral (B2) views, length 22.6 mm, width 14.4 mm, height 6.1 mm; **C**, MFM 13081; dorsal (C1) and lateral (C2) views, length 28.6 mm, width 20.1 mm, height 9.2 mm; **D**, MFM 13082; dorsal (D1) and lateral (D2) views, length 27.2 mm, width 18.6 mm, height 9.2 mm.

Type locality.—Akatsukibora, Hiyoshi-cho, Mizunami, Gifu, Japan (Figure 1).

Type horizon and age.—Shukunohora Formation; late Early to early Middle Miocene (Ibaraki, 1981; Itoigawa, 1989; Irizuki and Hosoyama, 2006).

Other material examined.—MFM 11048, a complete specimen from the type locality. IGUT 6172, a cast of a specimen from the Hiranita Formation (currently considered part of the Chichibumachi Formation: Takahashi, 2008), bed of the river Arakawa in Hiranita, Chichibu, Saitama, Japan (Locality 813 of Kanno [1960];

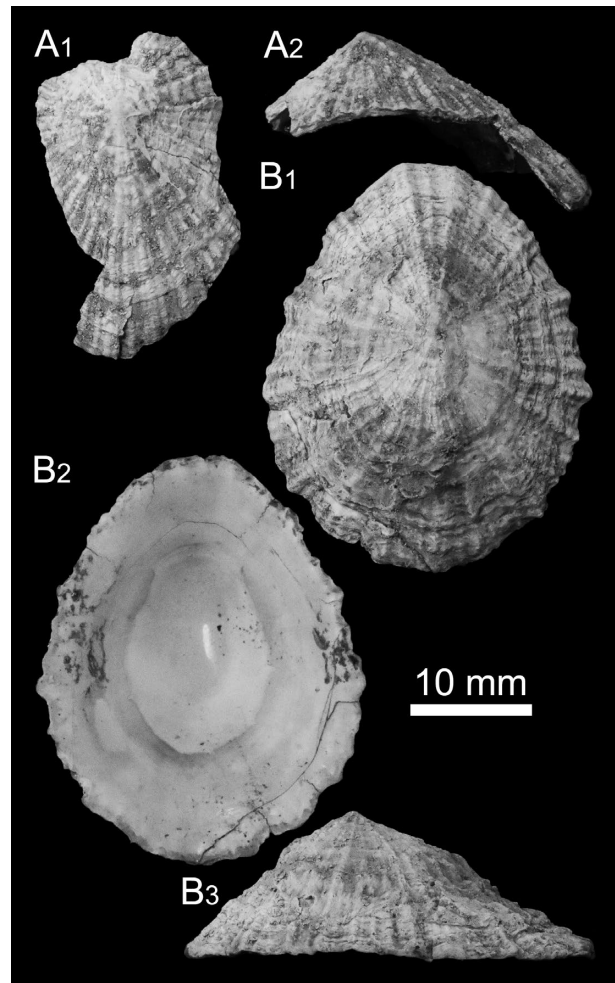


Figure 3. *Scutellastra itoigawai* (Kase, 1994) from the lower Middle Miocene Shukunohora Formation of the Mizunami Basin in Akatsukibora, Mizunami, Gifu, Japan. **A**, holotype, MFM 10096; dorsal (A1) and lateral (A2) views, length 27.2 mm, width 17.1 mm, height 15.0 mm; **B**, complete specimen, MFM 11048; dorsal (B1), ventral (B2) and lateral (B3) views, length 34.0 mm, width 27.3 mm, height 12.6 mm.

35°57'54.4"N, 139°02'33.8"E). SMNH-MoF3234, SMNH-MoF3235–3239, specimens from the S. Horiguchi collection; SMNH-MoF3240–3249, specimens from the K. Yajima collection; NMNS PM69035; NMNS PM69036, coll. Y. Kurihara, all of which are from the Hiranita Formation at locality 813 of Kanno (1960) or nearby sites.

Distribution.—Mizunami and Chichibu basins (Figure 1).

Remarks.—This species was described by Kase (1994) based on a fragmentary specimen from the Shukunohora Formation in the Mizunami Basin (Figure 3A). He also referred an intact specimen from the type locality to this species, which was illustrated by Itoigawa *et al.* (1981, pl. 24, fig. 9) as “*Acmaea*” sp. 4. This specimen is in the

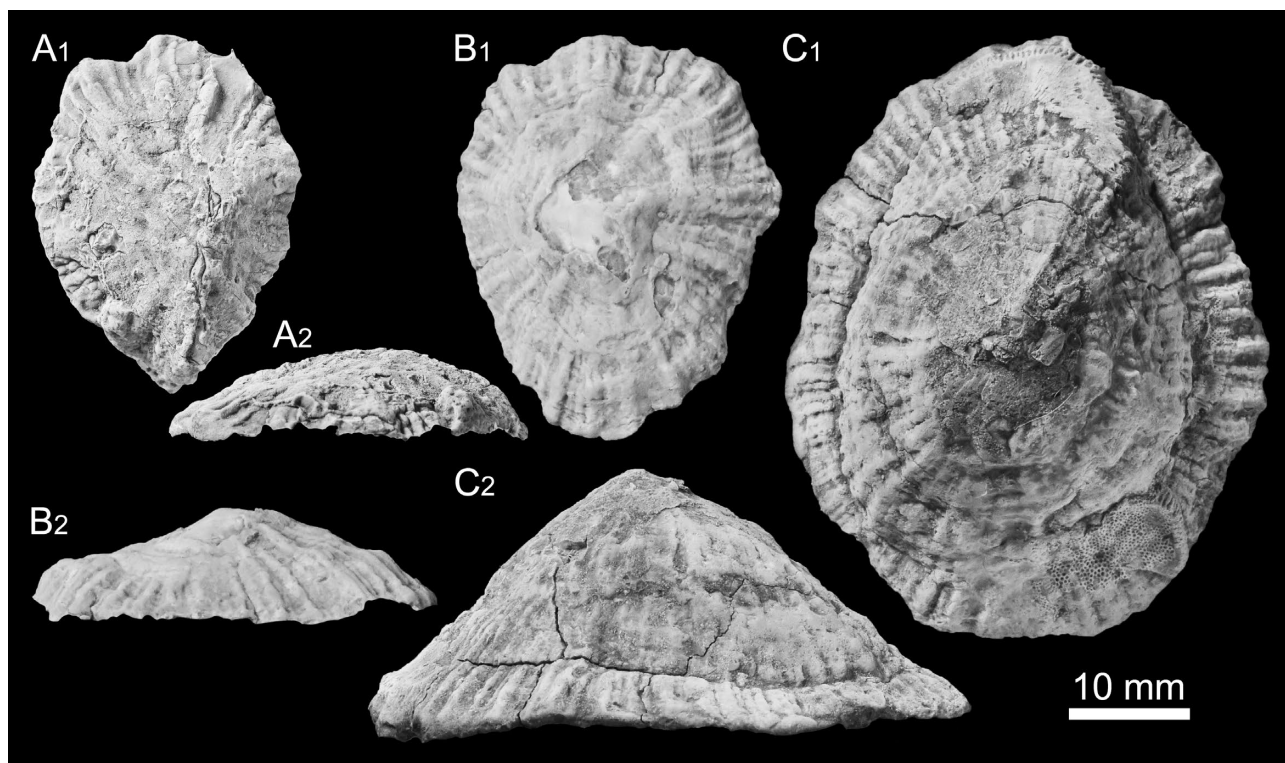


Figure 4. Specimens tentatively identified as *Scutellastra itoigawai* (Kase, 1994) from the lower Middle Miocene Hiranita Formation of the Chichibu Basin in Hiranita, Chichibu, Saitama, Japan. **A**, IGUT 6172, cast originally referred as *Diodora* aff. *sieboldii* (Reeve) by Kanno (1960, pl. 46, fig. 4a, b); dorsal (A₁) and lateral (A₂) views, length 29.7 mm, width 22.3 mm, height 7.9 mm; **B**, dorso-ventrally compressed specimen, NMNS PM69035; coll. Y. Kurihara; dorsal (B₁) and lateral (B₂) views, length 33.6 mm, width 27.0 mm, height 9.7 mm; **C**, largest specimen, coll. S. Horiguchi, SMNH-MoF3234; dorsal (C₁) and lateral (C₂) views, length 50.0 mm, width 40.2 mm, height 22.8 mm.

collection of the Mizunami City Fossil Museum and is figured here (Figure 3B; MFM 11048). This species is characterized by a thin, high-conical shell outline, non-stellate apertural margin, and weak and not scaly major radial ribs. The shell characteristics of this species suggest that it is not closely related to *Scutellastra flexuosa* and *Scutellastra optima* (Pilsbry, 1927) living in the Western Pacific, or to any other known living species of this genus in other oceans outside the Pacific.

Here, we tentatively refer the specimens from the lower Middle Miocene Hiranita Formation in the Chichibu Basin in central Japan to *S. itoigawai* (see Figure 4B, C). These specimens, which are found in the K. Yajima and S. Horiguchi collections of the Saitama Prefectural Museum of Natural History, were collected from granule- to pebble-sized conglomerate beds along the river Arakawa at Site 813 of Kanno (1960) and nearby sites. One specimen from Site 813 identified by Kanno (1960) as *Diodora* aff. *sieboldii* (Reeve) is actually *S. itoigawai* (Figure 4A). This specimen is a modeling cast obtained from an incomplete external mold, so the stellate apertural margin does not reflect the original shape. All specimens from

the Hiranita Formation are markedly deformed and have conical shells flattened to varying degrees. However, the largest specimen from the S. Horiguchi collection is an exception (Figure 4C). This specimen is highly conical in shape and has many radial ribs of varying strengths. Additionally, this specimen exhibits a prominent crack running along the growth lines; this shows that the anterior margin is narrowly rounded, whereas the posterior margin is broadly rounded. Hence, this specimen is quite similar to the complete specimen of *S. itoigawai* (MFM 11048) from the Mizunami Basin, except that its radial ribs are smoother in comparison. The Hiranita Formation specimens were collected from the conglomerates. The smooth shell sculpture likely resulted from abrasion that occurred during transport from high-energy environments to the final depositional sites.

***Scutellastra kadotai* Hashimoto and Kase, sp. nov.**

Figure 5A–C

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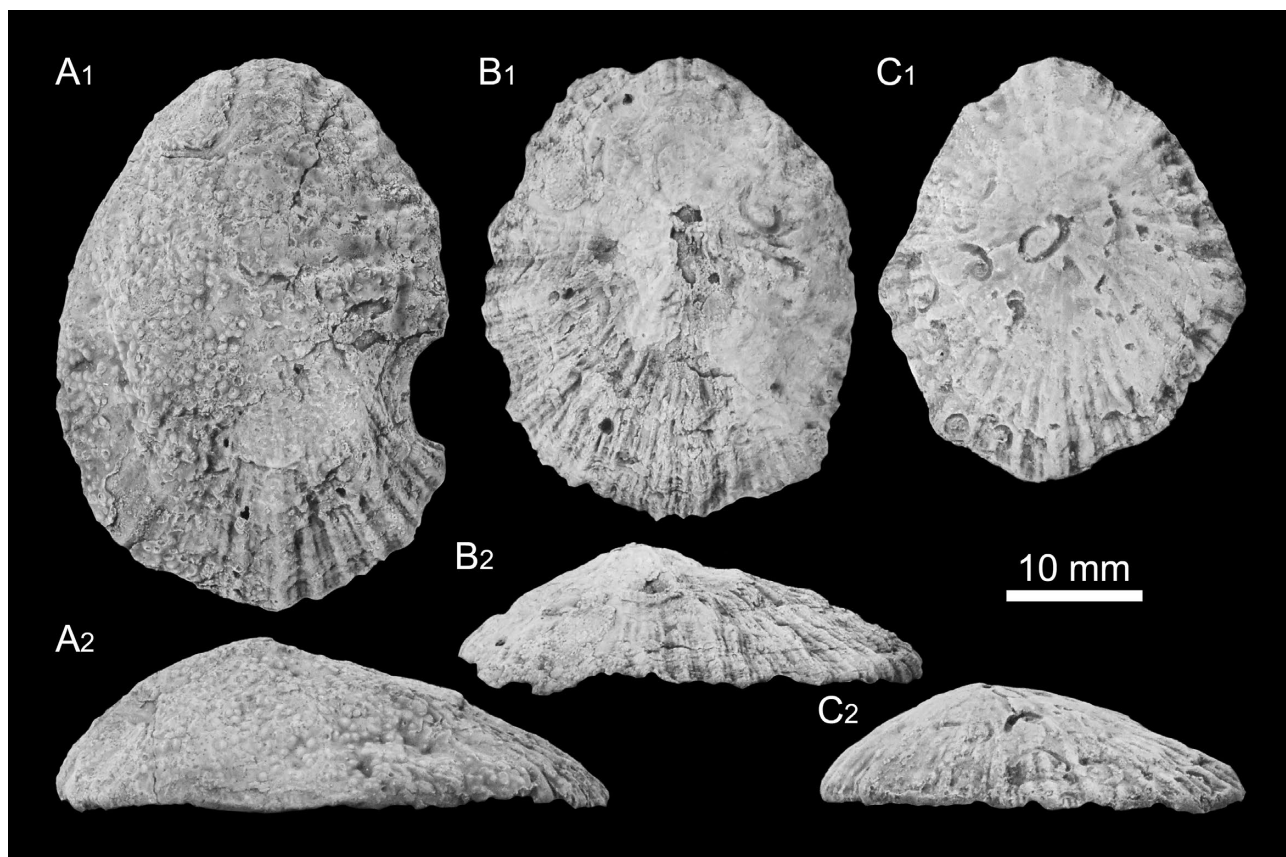


Figure 5. *Scutellastra kadotai* Hashimoto and Kase, sp. nov. from the lower Middle Miocene Makinoko Limestone of Makinoko, Izu, Shizuoka, Japan. **A**, holotype, NMNS PM65189; dorsal (A₁) and lateral (A₂) views, length 40.7 mm, width 29.0 mm, height 13.1 mm, apical part is covered with limonitic ooids-bearing limestone matrix. **B**, paratype, NMNS PM65190; dorsal (B₁) and lateral (B₂) views, length 34.2 mm, width 27.6 mm, height 11.3 mm. **C**, paratype, NMNS PM65191; dorsal (C₁) and lateral (C₂) views, length 31.4 mm, width 27.1 mm, height 9.7 mm.

Etymology.—The specific epithet honors the late M. Kadota, who contributed greatly to the study of fossil corals in the Tanzawa Mountains and on the Izu Peninsula.

Type material.—Holotype, NMNS PM65189; paratypes, NMNS PM65190, NMNS PM65191, NMNS PM65192.

Type locality.—Tashirozawa, 2.8 km ENE of Makinoko Station, Makinoko, Izu, Shizuoka, Japan.

Type horizon and age.—Makinoko Limestone, late Early or early Middle Miocene.

Distribution.—Known only from the type locality.

Dimension.—Holotype, NMNS PM65189, length, 40.7 mm; width, 29.0 mm; height, 13.1 mm.

Diagnosis.—Shell moderate in size, low cap-shaped, with elongate oval apertural margin. Shell surface covered with approximately ten major ribs composed of fine and dense radial ribs mostly lacking scales.

Description.—Shell low cap-shaped, moderately thick, length to 40.7 mm, with height/length ratio of 0.3

and width/length ratio of 0.7. Apex obtuse, situated 1/3 length from anterior end, anterior slope gently convex, whereas posterior slope nearly straight. Aperture elongate oval, anterior margin narrowly rounded, posterior margin broadly arched. Shell surface sculptured with fine, dense secondary radial ribs mostly lacking spines, several of which come together to form approximately ten thicker primary ribs, which project only slightly beyond apertural margin.

Remarks.—In the three specimens shown in Figure 5, the shell slope becomes steeper at the apertural margin. Such changes have sometimes been observed among fully grown specimens of the extant *S. flexuosa*. We therefore interpret all specimens of *S. kadotai* sp. nov. as being ontogenetically mature.

This new species has a more anteriorly situated apex, irregularly appearing major radial ribs, and thinner, sharper secondary ribs compared with *S. mizunamiensis*. Compared with *S. itoigawai*, it has a lower conical shell

outline and denser and sharper secondary ribs.

Of the 19 living species currently recognized in the genus *Scutellastra* (MolluscaBase eds., 2025), the most likely candidates for comparison with this new species are *S. flexuosa* and *S. optima*. By using morphological and molecular phylogenetic analyses, these two species were found to form a clade within the genus *Scutellastra* (Ridgway *et al.*, 1998; Koufopanou *et al.*, 1999; Nakano and Ozawa, 2007; Sung *et al.*, 2025). *Scutellastra flexuosa* is a variable and widely distributed species throughout the Indo-West Pacific Ocean, with eight synonyms (Powell, 1973). However, molecular phylogenetic studies have shown that it forms a species complex and indicated the presence of several cryptic species (Paulay and Meyer, 2002; Sung *et al.*, 2025). *Scutellastra flexuosa* is characterized by a circular-to-ovate aperture and fewer than ten broad, scalloped major radial folds that give rise to lobes of varying prominence at the apertural margin (Cernohorsky, 1972; Powell, 1973; Herbert, 1991; Wilson, 1993; Sasaki *et al.*, 1994; Bosch *et al.*, 1995; Sasaki, 2000; Poppe, 2008). In contrast, the new species has a non-stellate aperture, less prominent major radial folds, and denser and finer secondary radial ribs on its shell surface compared with *S. flexuosa*.

Scutellastra kadotai sp. nov. most closely resembles *S. optima*, which is distributed separately on Torishima and the Tokara Islands (type locality) in the northwestern Pacific and Hainan Island in the South China Sea (Sasaki *et al.*, 1994; Sasaki, 1998; Sung *et al.*, 2025). Pilsbry (1927) described this species as a race of *Patella stellaeformis* (= *S. flexuosa*), whereas Powell (1973) classified it as a subspecies of *S. flexuosa*. However, morphological and molecular studies have shown *S. flexuosa* and *S. optima* to be distinct species (Sasaki *et al.*, 1994; Nakano and Ozawa, 2007; Sung *et al.*, 2025). The new species has a non-stellate ovate aperture, similar to that of *S. optima*; however, *S. optima* has an apertural diameter that exceeds 90 mm in adults (Sasaki *et al.*, 1994), which is more than twice that of *S. kadotai* sp. nov. Unlike mature specimens, young specimens of *S. optima*, which are approximately the same size as the holotype of the new species, mostly have stellate apertures similar to those of *S. flexuosa*. Both species have fine secondary radial ribs on the shell surface; however, the secondary ribs of *S. kadotai* sp. nov. are composed of three much thinner ribs, a feature not observed in *S. optima*. Considering the differences in shell size and sculpture, as well as the age difference of more than 15 million years, we consider these two distinct species.

Paleobiogeographic consideration

Owing to its complex volcanic composition, the Izu

Peninsula is among the areas of the Japanese archipelago with the poorest fossil record. However, although limited in quantity, the fossil assemblages discovered on the peninsula offer a glimpse into the little-known Neogene biotas that inhabited the tropical shallow waters of the Philippine Sea far south of the present-day location of the peninsula. On the Izu Peninsula, fossil mollusks are found in the Lower Pliocene Harada Formation of the Shirahama Group and the upper Lower to lower Middle Miocene Sakurada Formation and its contemporaneous Kadono Formation of the Yugashima Group. Nomura and Niino (1932) were the first to study the fossil mollusks of the Izu Peninsula. They reported 28 species from the Shirahama and Yugashima groups. Most specimens were incomplete and required reexamination based on thoroughly preserved specimens. Although eight species were reported from the Yugashima Group, our preliminary literature survey suggests that all eight species were actually collected from the Shirahama Group rather than the Yugashima Group.

Fossil mollusks are fairly common in the Pliocene Harada Formation of the Shirahama Group on the coasts of Shirahama, Shimoda and Imaiama, Kawazu Town in the southeastern part of the Izu Peninsula (Nomura and Niino, 1932; Utagawa *et al.*, 2015; Tomida *et al.*, 2016). It was once thought that only a few species are common between the Zushi Fauna and the assemblage of the Shirahama Group (Tomida, 1996; Matsushima *et al.*, 2003). However, Tomida *et al.* (2016) reported 14 gastropod species and 20 bivalve species from the Imaiama site, of which 21 were extant species and 10 were extinct species; the remaining three could only be identified at the genus level. The fossil assemblage consists of a mixture of intertidal to subtidal rocky/gravelly bottom species, such as *Turbo* (*Batillus*) *priscus* and *Omphalius pfeifferi*, and lower sublittoral to bathyal species, such as *Xenophora tenuis* and *Acesta goliath*. Of the 34 species, 18 were shared with the Zushi Fauna, a warmer-water shallow marine molluscan fauna that flourished on the coasts from the Kanto region of Honshu to Kumejima Island of Okinawa during the latest Miocene to the Early Pliocene (Ozawa and Tomida, 1992; Tomida, 1996; Tomida *et al.*, 2016). This strongly suggests that the Izu Peninsula was influenced by the same ocean currents as the southwestern coast of the Honshu Arc during the Pliocene (Ozawa and Tomida, 1992; Tomida, 1996; Tomida *et al.*, 2016). Paleomagnetic studies have suggested that the Izu Peninsula was situated somewhere between a paleolatitude of around 30° N and its current position during the deposition of the Harada Formation (e.g. Hirooka *et al.*, 1985; Koyama *et al.*, 1992). The fossil assemblage of the Shirahama Group includes species that are not found in the Zushi Fauna of the Honshu

Arc but whose living or congeneric species are found in the subtropical Ryukyu Islands and tropical seas further south. These species include *Bolma tamikoeae*, *Okina-wastraena nakamineae*, *Chama lazarus*, and the extinct *Comptopallium tayamai* (Nomura and Niino). Tomida *et al.* (2016) therefore inferred that the Izu Peninsula was located considerably farther south than it is today during the Pliocene.

The fossil mollusks from the Yugashima Group are found in the Ena, Shikura, and Shirakawa limestones of the Sakurada Formation in the Matsuzaki area and the Makinoko limestone of the Kadono Formation in the Shuzenji area. This fossil assemblage contains tropical taxa, including diverse reef-building corals, calcareous algae, and large foraminifera (Ishijima, 1967, 1968; Matsumaru, 1971; Kadota, 2015). The age of this fauna is not well constrained. However, the available evidence suggests that it dates to the late Early to early Middle Miocene, as discussed above. A comprehensive taxonomic inventory of fossil mollusks contained within these limestones has not been completed. To date, the species that have been studied or definitively identified, or those identified but yet to be published, include 14 gastropod species and one bivalve species (Table 1). Highly diverse warm- and shallow-water mollusks approximately the same age as the Yugashima molluscan assemblage were widely distributed across the Honshu Arc, from western Honshu to central Hokkaido. This fauna was initially referred to as the Kadonosawa Fauna (e.g. Otuka, 1939; Chinzei, 1978, 1986) and is a local representation of the global warming interval known as the Miocene Climatic Optimum (MCO) (e.g. Holbourn *et al.*, 2015; Kochhann *et al.*, 2016). The Kadonosawa Fauna is now subdivided into the Kadonosawa Fauna *sensu stricto* and the slightly younger Moniwa Fauna (Kurihara *et al.*, 2003; Ogasawara *et al.*, 2008; Kase *et al.*, 2023; Irizuki *et al.*, 2025). These two faunas correspond to the two warming peaks of the MCO, which are separated by a positive oxygen stable isotope excursion called Miocene isotope event 2 (e.g. Irizuki *et al.*, 2025). The Kadonosawa Fauna *sensu stricto* is distinguished by its shallow-water, soft-bottom species and was dated to approximately 17.0–16.7 Ma (Yanagisawa and Watanabe, 2017). This fauna is typically found in the Kurosedani Formation in the Yatsuo area of Toyama, central Japan, and the fauna-bearing beds are widely distributed across the Honshu Arc south of Hokkaido (see Table 1 in Kase *et al.*, 2020). On the other hand, the Moniwa Fauna, represented primarily by fossils from the Moniwa Formation in the Moniwa area of northeast Japan and the Hiranita Formation in the Chichibu Basin, primarily comprises intertidal and subtidal hard-bottom dwellers and was dated to approximately 15.3–14.7 Ma (Kurihara *et al.*, 2003; Yanagisawa, 2012). To date, no common spe-

cies have been identified between the molluscan assemblages of the Yugashima Group and the Kadonosawa/Moniwa faunas (Table 1). Six species of the genus *Turbo* were found on the Izu Peninsula, four of which were characterized by the large size, with shell heights exceeding 100 mm. This contrasts with the two small species of *Turbo* (*Marmarostoma*) from the Kadonosawa/Moniwa faunas, *Turbo* (*Marmarostoma*) *ozawai* and *Turbo* (*Marmarostoma*) *tochiyensis*, which do not exceed 40 mm in shell height (Tomida and Kase, 2022; Kase *et al.*, 2023).

The absence of species common to both the Yugashima Group and the Kadonosawa/Moniwa faunas is likely attributable to their geographic separation, their contrasting depositional settings, and differences in the water masses or oceanic currents that influenced their habitats. On continental islands, such as the Honshu Arc, the influx of rivers causes extensive continental shelves, thereby creating diverse environments, including inner bays and tidal flats. Conversely, the coastlines of volcanic oceanic islands, such as the Izu–Ogasawara–Northern Mariana Arc, are characterized by precipitous slopes that face the sea directly. This leads to the formation of narrow intertidal zones and limited coral reef development, even in tropical regions. There is no consensus on the precise location of the late Early to early Middle Miocene volcanic island group on the Philippine Sea Plate that would become the Izu Peninsula, but it is generally considered to have been situated in the eastern Philippine Sea far south of the current location of the Izu Peninsula (somewhere around 20°–30°N latitude: Seno and Maruyama, 1984, 1985; Hirooka *et al.*, 1985; Koyama *et al.*, 1992; Wu *et al.*, 2016).

We infer that the molluscan assemblages of the Yugashima Group and the Kadonosawa/Moniwa faunas inhabited different water masses. This is extrapolated from previous studies of the Recent molluscan faunas of mainland Japan (Honshu, Kyushu, Shikoku, and Hokkaido) and the Ogasawara Islands, located approximately 1,000 km south of Honshu. A total of 817 gastropod species have been documented from the Ogasawara Islands, although this likely includes many records of rare species resulting from death migration or abortive migration (Fukuda, 1995b). Many of these species are shared with the Ryukyu, Mariana, and Philippine islands, whereas only approximately 5% are shared with mainland Japan (Fukuda, 1993, 1994, 1995a). This difference stems from the distinct ocean current systems around the Pacific coast of the Honshu Arc and Ogasawara Islands (e.g. Fukuda, 1993; Asakura, 2003). The Pacific coast of the Honshu Arc is influenced by the Kuroshio Current, which originates near the Philippines, whereas the Ogasawara Islands receive little direct influence from the Kuroshio Current. Instead, they are influenced by weak currents,

such as the Subtropical Countercurrent, which flows eastward from a branch of the Kuroshio Current, and a branch of the North Equatorial Current. This system of currents hinders faunal dispersal between mainland Japan and the Ogasawara Islands.

It has been hypothesized that the configuration of continents and islands in the northwestern Pacific during the late Early to early Middle Miocene did not differ substantially from the present configuration (Hall, 1998). Consequently, the ocean current systems in this region are inferred to have been similar to those of the present. We hypothesize that the volcanic island(s) on which the Yugashima Group was deposited were located within a tropical water mass in the eastern Philippine Sea and were unaffected by the warm southwesterly ocean currents that influenced the Honshu Arc. As the Philippine Sea Plate gradually migrated northward, the volcanic islands that would become the Izu Peninsula were also carried northward. By the Early Pliocene, when the Harada Formation was deposited, these islands were influenced by warm ocean currents that also supported the Zushi Fauna along the Pacific coast of the western Honshu Arc. Kitazato (1987) presented a similar scenario based on the geographic distribution of benthic foraminifera in the South Fossa Magna region of central Japan.

The discovery of *S. kadotai* sp. nov. in this study provides an additional example of the characteristics of the shell fossil fauna of the Yugashima Group. Testing the above hypothesis will require a comprehensive understanding of the entire fossil fauna of the Yugashima Group. Although currently represented by relatively few species, the Yugashima fossil assemblage is distinctive in terms of both its species composition and biogeographic origin. We therefore propose the name “Yugashima Fauna” for this unique fossil assemblage to facilitate future discussion and comparison.

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Author contributions

KH and TK initiated the study, drafted the manuscript, and were responsible for the taxonomic description and discussion. All authors contributed to the faunal discussion.