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# New species of *Turbo* (*Marmarostoma*) (Gastropoda, Turbinidae) from the Miocene limestone in central Japan: a window into the Miocene marine biodiversity in the northeastern Philippine Sea

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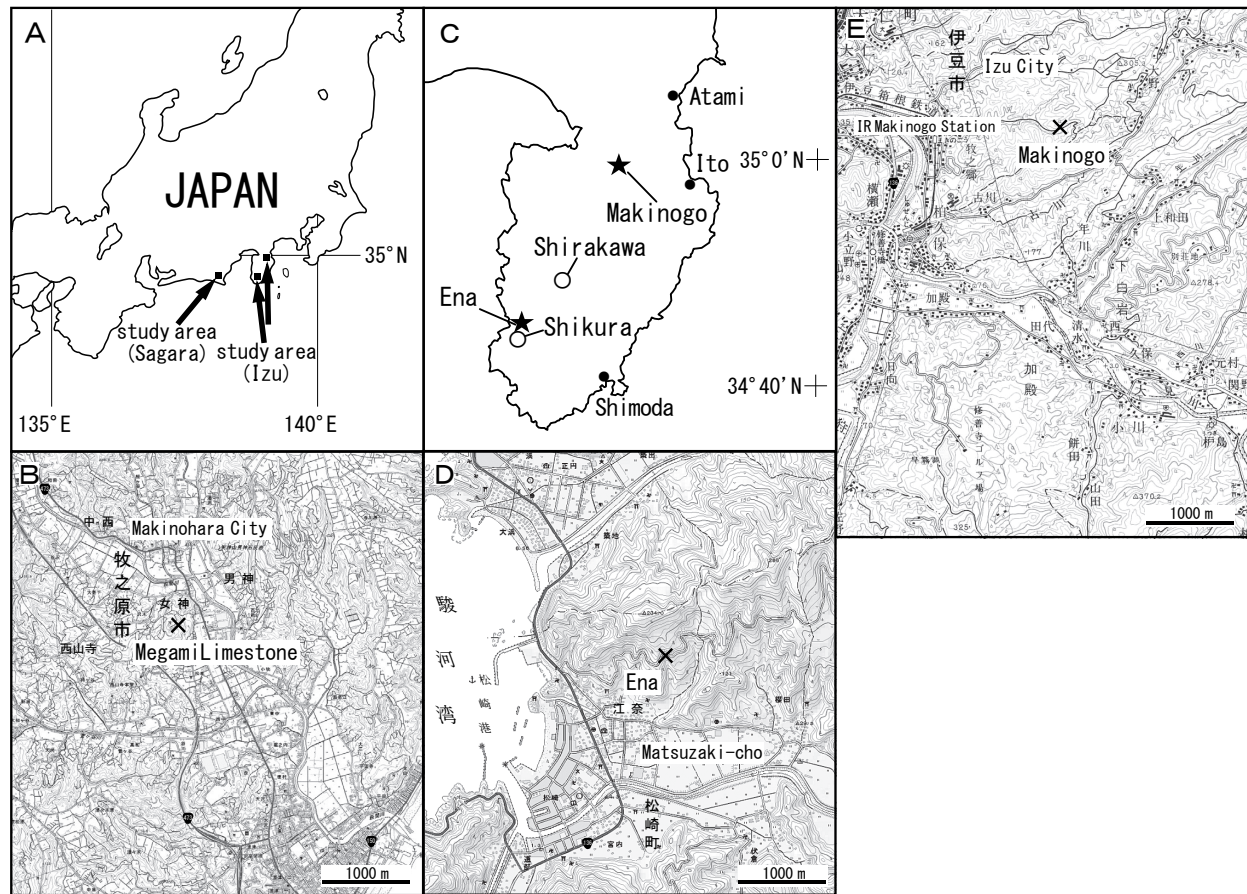
**Abstract.** The late early to middle Miocene limestone bodies in the Sagara and Izu Peninsula areas of central Japan are reefal deposits that were deposited under a tropical climate and provide a window into the paleodiversity of tropical volcanic islands in the northeastern Philippine Sea Plate. Specimens from the early middle Miocene Megami Limestone in the Sagara area and from the middle Miocene limestone blocks within the Yugashima Group on the Izu Peninsula are described as *Turbo* (*Marmarostoma*) *histrioides* sp. nov. and *Turbo* (*Marmarostoma*) *izuensis* sp. nov., respectively. Discovery of these two new species raises the number of *Marmarostoma* species from four to six in the Sagara and Izu Peninsula areas, demonstrating that the subgenus was more diverse in the northeastern Philippine Sea Plate during the middle Miocene than it is today. In particular, there are double the number of *Marmarostoma* species (four species) from the middle Miocene in the Izu Peninsula compared with the modern fauna on the tropical islands of the Izu-Ogasawara Arc. The highest richness of modern species of *Marmarostoma* is found in the central Indo-West Pacific, where molecular phylogenetic studies have suggested that the subgenus rapidly diversified in the late Oligocene or early Miocene. Nevertheless, Miocene species of this subgenus are sparse in the central IWP, being incongruent to the diversity pattern expected from the molecular studies. The findings reported herein provide an insight into the origin of the central IPW biodiversity hotspot.

**Key words:** central Japan, *Marmarostoma*, Miocene, paleobiogeography, Philippine Sea, Turbinidae

## Introduction

This paper provides descriptions of two new species of the turbinid gastropod genus/subgenus *Turbo* (*Marmarostoma*) from the middle Miocene limestone bodies in central Japan: one from the Megami Limestone in the Sagara area and the other from the Kadono/Sakurada formations of the Yugashima Group on the Izu Peninsula (Figure 1). These limestone bodies contain abundant reef-building corals and coralline algae, representing reef deposition under a tropical climate (Makiyama, 1963; Hamada, 1975; Kase and Katayama, 1981; Konishi *et al.*, 1988; Nakamori *et al.*, 1991; Tomida and Kadota, 2012, 2014). The middle Miocene Megami Limestone is an

allochthonous limestone body considered to have been deposited on a volcanic seamount in the Shikoku Basin of the northeastern Philippine Sea Plate in the middle Miocene, and it is now part of an accretional complex in the Honshu Arc (Sugiyama, 1992; Ozawa *et al.*, 1995). In contrast, the limestone blocks of the Izu Peninsula are within the middle Miocene Sakurada Formation (Tomida and Kadota, 2014; Tomida and Hosoda, 2015) and its equivalent Kadono Formation (Kase and Katayama, 1981). Paleomagnetic evidence suggests that the peninsula was positioned at a low latitude, further south than the present position on a volcanic island(s) along the Izu-Ogasawara Arc in the northeastern Philippine Sea Plate (Hirooka *et al.*, 1985; Koyama, 1991, 1994; Niitsuma



**Figure 1.** A, maps showing study areas in central Japan; B, details of collecting site (×) of *Turbo* (*Marmarostoma*) *histrioides* sp. nov. in Sagara area, Makinohara City, Shizuoka Prefecture; C, locations of Ena and Makinogo limestone bodies (★) on Izu Peninsula; D, details of collecting site (×) of *Turbo* (*Marmarostoma*) *izuensis* sp. nov. from Ena Limestone, Matsuzaki-cho, Shizuoka Prefecture; E, details of collecting site (×) of *Turbo* (*Marmarostoma*) *izuensis* sp. nov. from Makinogo Limestone, Izu City, Shizuoka Prefecture. Topographic maps adapted from 1:25,000-scale ‘Sagara’ (B), ‘Shimoda’ (D) and ‘Shuzenji’ (E), published by Geospatial Information Authority of Japan.

and Koyama, 2006). Previous studies have recorded molluscan fossils in these areas including Nishiwada (1894), Nomura and Niino (1932), Kase and Katayama (1981), Majima (1994), Ozawa *et al.* (1995), and Tomida and Kadota (2012, 2014). These studies offer a glimpse into the poorly known middle Miocene shallow marine fauna of the northeastern Philippines Sea Plate.

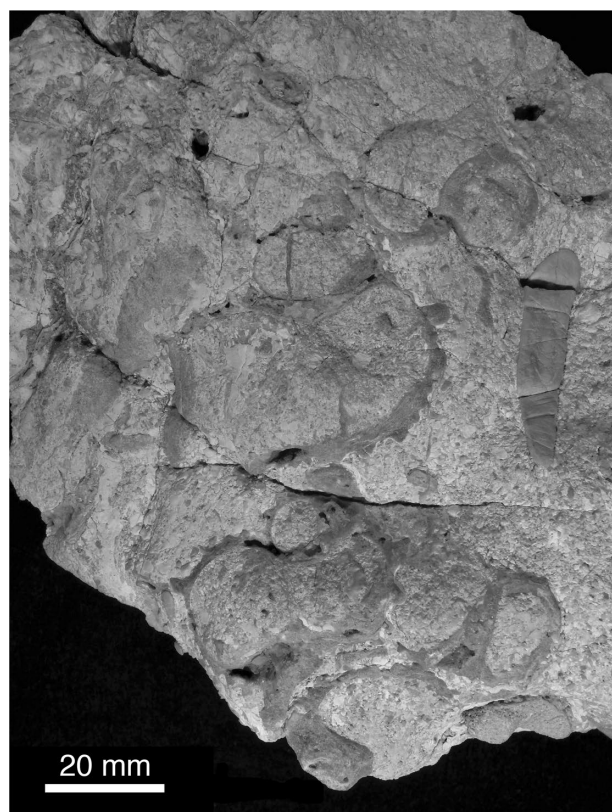
### Geological outline and collection localities

The geology and fossil content of the Megami Limestone and other nearby limestone bodies (e.g. the Ogami Limestone and the Ebie Limestone) in the Sagara area have been studied to elucidate Neogene stratigraphy and marine sedimentary environments in this district (e.g. Nishiwada, 1894, 1895; Saito, 1963; Oda, 1971; Ujiie, 1975; Nakamori *et al.*, 1991; Sugiyama, 1992; Ozawa *et al.*, 1995). The upper Neogene system in the Sagara

area is divided into the Megami Formation and the Sagara Group, with the latter divided into the Sugegaya Formation overlaid by the Sagara Formation. The Megami Limestone, striking N35°E, dipping 30°E and overturned, is an allochthonous limestone body within the Megami Formation, and is in contact with the middle to upper Miocene Sugegaya Formation by NE–SW directed faults in the north and south and with the lower Pliocene Sagara Formation with a NE–SW directed fault in the northeast (Nakamori *et al.*, 1991; Ozawa *et al.*, 1995).

The specimens of *Turbo* (*Marmarostoma*) *histrioides* sp. nov. were recovered from the limestone exposed in the northeastern corner of the Megami Limestone body (Figure 1A, B). Our field study revealed that *T. (M.) mekamiensis* and *T. (M.) histrioides* sp. nov. do not occur together: *T. (M.) mekamiensis* occurs sporadically in the upper part of the Megami Limestone whereas *T. (M.) histrioides* sp. nov. forms a shell bed in the lower part (Fig-





**Figure 2.** A limestone slab (NUM-Fa225) showing aggregated mode of occurrence of *Turbo (Marmarostoma) histrioides* sp. nov. in the Megami Limestone.

ure 2). *Turbo (Marmarostoma) histrioides* sp. nov. occurs in association with some shallow warm-water molluscs such as *Cypraea* sp., *Conus* sp., *Spondylus* sp., and *Peryglypta* sp., and also with cobble-sized broken colonies of reef-building corals, abundant coralline algae and the larger foraminifer *Nephrolepidina japonica*. Approximately 17 species of coral, including *Heliopora coerulea* (Pallas) and *Millepora* sp., were obtained from the Megami Limestone (Kadota and Misawa, 2005). These two taxa are presently distributed widely in the tropical Indo-West Pacific (IWP) and are indicative of tropical to subtropical marine climates during the late early to middle Miocene (Kadota and Misawa, 2005). The Megami Formation has been assigned to Blow's (1969) zone N8 (–N9) (16.38–14.24 Ma: Gradstein *et al.*, 2012) on the basis of the planktonic foraminifers (Saito, 1963; Oda, 1971; Ujiie, 1975), and the calcareous nannofossil assemblages from the Megami Limestone and the Megami Formation are referable to zones CN3–4 of Okada and Bukry (1980) (17.95–13.53 Ma: Gradstein *et al.*, 2012) (Nakamori *et al.*, 1991). In conclusion, the age of the Megami Lime-

stone has been constrained to 17–16 Ma (late early to early middle Miocene) (Nakamori *et al.*, 1991).

Specimens of *Turbo (Marmarostoma) izuensis* sp. nov. were obtained from a limestone block (Makinogo Limestone) exposed in a valley approximately 1.5 km east of Makinogo, Shuzenji Town in the north-central Izu Peninsula (Figure 1C, E). The limestone is within the volcanic sediments of the middle Miocene Kadono Formation but the contact between the limestone and surrounding volcanic sediments has not been observed. Kase and Katayama (1981) described the lithology and fossil content of this limestone in detail, and found that it mostly comprises massive biomicrite with minute grains of oxidized dacite and limonic ooids. Coralline algae are common, and several species were described by Ishijima (1968). Molluscs occurs sporadically, and other than *T. (M.) izuensis* sp. nov., rocky-shore patellogastropods such as *Cellana* and *Patella* are common, and subtidal species such as *Nipponoclava gigantea* and *Entemnotrochus ozakii* are also found (Kase and Katayama, 1981; Majima, 1994). Most of these molluscs as well as the volcanic cobbles are encrusted with coralline algae. Kase and Katayama (1981) suggested that the limestone was deposited under a shallow, nearshore environment with high energy wave action.

Three specimens referable to *T. (M.) izuensis* sp. nov. were also obtained by Y. Sano and E. Hosoda from the Ena Limestone within the Sakurada Formation in the Nishi-izu area of the Izu Peninsula (Figure 1C, D). The Ena Limestone is composed of allochthonous rock bodies consisting of yellowish white limestone: the larger body is ca. 10 m in length and ca. 0.8 m in thickness, and the smaller one ca. 7 m in length and ca. 1.2 m in thickness. For detailed description of the lithology and age of the Ena Limestone, see Tomida and Kadota (2014).

### Systematics

**Repository.**—The materials described herein are housed at Nagoya University Museum (NUM), Kanagawa Prefectural Museum of Natural History (KPM), and the Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba (NMNS PM).

Order Vetigastropoda Salvini-Plawen and Haszprunar, 1987

Family Turbinidae Rafinesque, 1815

Genus *Turbo* Linnaeus, 1758

Subgenus *Marmarostoma* Swainson, 1829

**Type species.**—*Turbo chrysostomus* Linnaeus, 1758 (by original designation).

**Remarks.**—The Megami and Izu species exhibit a rela-

tively high-conical turbiniform shell outline, they have spiny or non-spiny spiral cords crossed by axial striae over the shell surface and an outwardly much thickened operculum. These shell characters are common among species of *Turbo* (*Marmarostoma*). Alf and Kreipl (2003) compiled and illustrated 35 nominal species of *Turbo* (*Marmarostoma*) from the Indo-Pacific. The molecular phylogenetic study by Williams (2007), however, demonstrated that the species of the subgenus *Marmarostoma* listed by Alf and Kreipl (2003) do not form a monophyletic clade. For example, *Turbo* (*Marmarostoma*) *squamiger* Reeve, 1843, *Turbo* (*Marmarostoma*) *haynesi* (Preston, 1914) and *Turbo* (*Marmarostoma*) *heterocheilus* Pilsbry, 1889 were placed far outside the subgenus *Marmarostoma*. In addition, *Turbo* (*Marmarostoma*) *jonathani* Dekker *et al.*, 1992 and *Turbo* (*Marmarostoma*) *radiatus* Gmelin, 1791 are sister to each other and were placed in an undescribed subgenus distinct from *Marmarostoma*. These analyses suggest that *Marmarostoma* cannot be diagnosed by shell morphology alone. We refer the Megami and Izu species to the subgenus *Marmarostoma* in the broad sense, as is the case for other fossil species of *Turbo* (*Marmarostoma*) discussed herein.

***Turbo* (*Marmarostoma*) *histrioides* sp. nov.**

Figure 3A–N

**Diagnosis.**—Shell medium in size, similar to *T. (M.) histrio*, but with less angulated whorls in younger growth stage.

**Material.**—Seven specimens; holotype, NUM-Fa199; paratypes: NUM-Fa203, NUM-Fa204, NUM-Fa208, NUM-Fa209, NMNS PM28032, KPM-NN0026298. All of the specimens discussed in this paper were prepared by using a vibro-tool, and the holotype was further cleaned by soaking in 10% hydrochloric acid.

**Type locality.**—Megami, Sagara-cho, Makinohara City, Shizuoka Prefecture; late early to early middle Miocene Megami Limestone.

**Etymology.**—The specific epithet is derived from its superficial resemblance to the modern species *Turbo* (*Marmarostoma*) *histrio*.

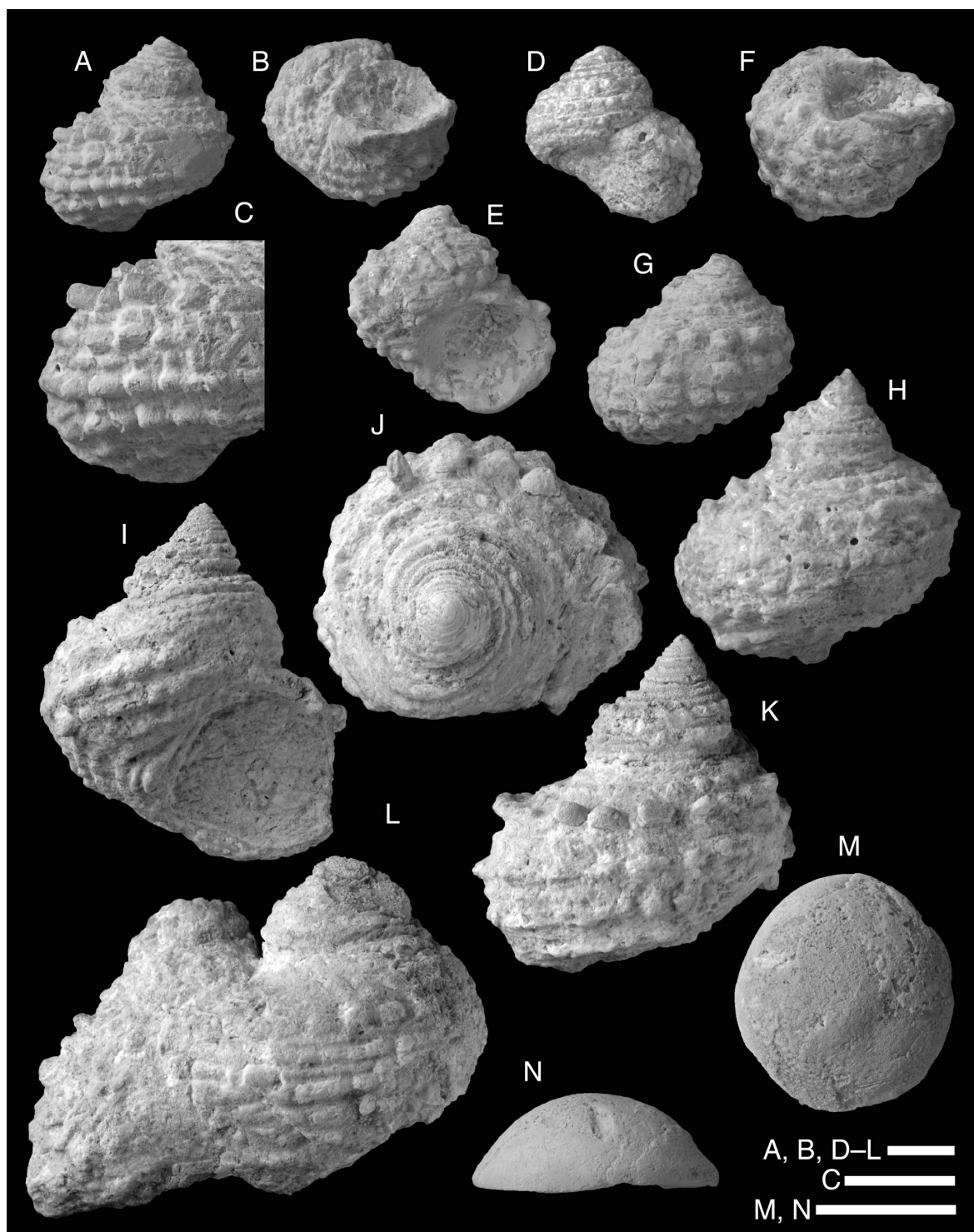
**Description.**—Shell medium-sized, rather thick, solid and turbiniform with spire as tall as or slightly taller than wide. Protoconch missing by erosion. Teleoconch roundly convex throughout, with deeply impressed suture. Subsutural ramp gently inclined, with strong spiral cord at ramp angle, bearing hollow spines and numerous tiny erect scales. Shoulder weakly angled. Last whorl inflated, with height/width ratio ranging from 1.1 to 1.3, ornamented with rather strong primary and weak secondary spiral cords, and interstitial threads; most adapical primary spiral cord located at ramp angle, second one

weak and at whorl periphery, and third one weak and at basal periphery; spines on shoulder strongest, rather densely arranged, 15 to 20 in number on last whorl, short and prominent hollow spines on all primary spiral cords (*ca.* 2 mm thick); ornamentation consisting of numerous tiny erect scales or sometimes short hollow spines on the secondary spiral cords (*ca.* 1.5 mm thick), and interstitial threads, crossing fine axial growth threads. Base slightly inflated and covered with three or four rather strong spiral cords with short hollow spines and numerous tiny erect scales. Columella smooth and evenly curved. Aperture rounded. Umbilicus closed. Operculum round and thick, strongly convex outside and flat inside; exterior surface partly preserved with granules; interior surface with 2.5 to three volutions.

**Discussion.**—Four species of *Marmarostoma* have previously been documented in the study areas, one from the Megami Limestone in the Sagara area (Nishiwada, 1894; Ozawa *et al.*, 1995) and three from the middle Miocene of the Izu Peninsula (Tomida and Kadota, 2012, 2014; Tomida and Hosoda, 2015; Table 1). *Turbo* (*Marmarostoma*) *mekamiensis* Nishiwada, 1894 from the Megami Limestone clearly differs from *T. (M.) histrioides* sp. nov. because the former species has a shallow suture and non-spiny thick and flat-topped spiral cords over the shell surface. Ozawa *et al.* (1995) suggested that *T. (M.) mekamiensis* is closely related to the modern species *T. (M.) setosus* Gmelin, 1791. *Turbo* (*Marmarostoma*) *matsuzakiensis* Tomida and Kadota, 2012 from the middle Miocene Shikura Limestone in the Izu Peninsula resembles *T. (M.) histrioides* sp. nov. in having a similar shell profile, shell size and spiny primary spiral cords. *Turbo* (*Marmarostoma*) *matsuzakiensis* differs from *T. (M.) histrioides* sp. nov., however, in having angular whorls and fewer primary spiral cords. In addition, the hollow spines are sparse and developed only on the primary spiral cords at the ramp and basal angles in *T. (M.) matsuzakiensis*, as opposed to being densely distributed and developed on all of the primary spiral cords in *T. (M.) histrioides* sp. nov. Even considering the large intraspecific variation in the development of spines in *Turbo* (*Marmarostoma*), the above-described difference in these forms is not known among modern species. We therefore consider that *T. (M.) histrioides* sp. nov. is not a spiny form of *T. (M.) matsuzakiensis*.

*Turbo* (*Marmarostoma*) *yoshiharuyabei* Tomida and Kadota, 2012 from the middle Miocene Ena Limestone in the Izu Peninsula has a well inflated whorl profile similar to *T. (M.) histrioides* sp. nov. and has four thick and slightly spiny primary spiral cords between the ramp and basal angles on the last whorl. Between the primary spiral cords, two or more fine interstitial spiral cords are present in *T. (M.) yoshiharuyabei*, while only one, thicker and





**Figure 3.** *Turbo (Marmarostoma) histrioides* sp. nov., from Megami Limestone in Sagara area. **A–C**, NUM-Fa208, paratype, adapertural and basal views, and enlarged view of sculpture, shell height 31.9 mm, shell width 28.4 mm; **D**, NUM-Fa209, paratype, apertural view, shell height 27.1 mm, shell width 25.8 mm; **E–G**, NUM-Fa204, paratype, apertural, basal and adapertural views, shell height 31.9 mm, shell width 29.5 mm; **H**, NUM-Fa199, holotype, adapertural view, shell height 44.3 mm, shell width 40.5+ mm; **I–K**, NMNS PM28032, paratype, apertural, apical and adapertural views, shell height 53.4 mm, maximum shell width 47.7 mm; **L**, KPM-NN0026298, adapertural view, shell height 43.3 mm, shell width 49.2 mm; **M, N**, NUM-FA203, outer and lateral views of operculum, maximum diameter 17.3 mm, maximum thickness 7.2 mm. Scale bars represent 10 mm.

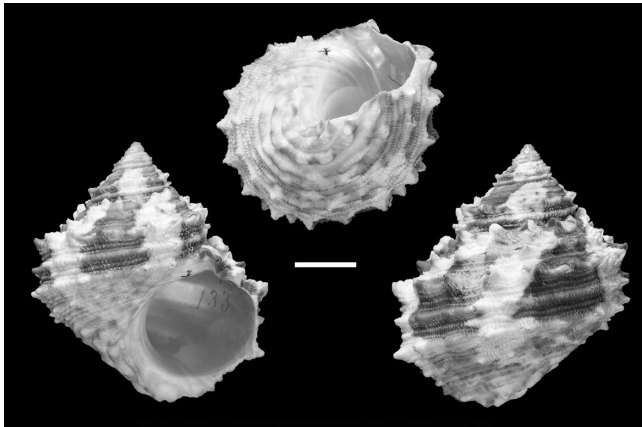
**Table 1.** List of Miocene species of *Turbo* (*Marmarostoma*).

Area	Species	Age	Locality	References
Sagara and Izu Peninsula, central Japan	<i>T. (M.) mekamiensis</i> Nishiwada	late early to early middle Miocene	Sagara	Nishiwada (1894, 1895); Ozawa <i>et al.</i> (1995)
	<i>T. (M.) histrioides</i> sp. nov.	late early to early middle Miocene	Sagara	This study
	<i>T. (M.) matsuzakiensis</i> Tomida & Kadota	middle Miocene	Izu Peninsula	Tomida and Kadota (2012), Tomida and Hosoda (2015)
	<i>T. (M.) sanoii</i> Tomida & Kadota	middle Miocene	Izu Peninsula	Tomida and Kadota (2014)
	<i>T. (M.) yoshiharuyabei</i> Tomida & Kadota	middle Miocene	Izu Peninsula	Tomida and Kadota (2014)
	<i>T. (M.) izuensis</i> sp. nov.	middle Miocene	Izu Peninsula	This study
Honshu, Japan	<i>T. (M.) ozawai</i> Otuka	late early to early middle Miocene	Shobara and Fukui	Otuka (1938), Nakagawa (2018)
	<i>T. (M.) parvuloides</i> Nomura	early middle Miocene	Sendai	Nomura (1940)
	<i>T. (M.) tochiyensis</i> Kanno	middle Miocene	Chichibu	Kanno (1958)
	<i>T. (M.) minoensis</i> Itoigawa	early middle Miocene	Mizunami	Itoigawa (1960)
Tropical Western Pacific islands	<i>T. (M.)</i> sp.	early Miocene	Fiji	Ladd (1966)
Java and Borneo, Indonesia	<i>T. (M.) pamotanensis</i> Martin	early Miocene	Remban, central Java	Martin (1905); Leloux and Wesselingh (2009)
	<i>T. (M.) djunggranganensis</i> Martin	early Miocene	Progo Mountain, central Java	Martin (1916); Leloux and Wesselingh (2009)
	<i>T. (M.) ruttenei</i> Beets	late Miocene	Kalimantan Timur, Borneo	Beets (1942, 1984)

scaly interstitial spiral cord is present in *T. (M.) histrioides* sp. nov. (see Tomida and Kadota, 2014, fig. 2). *Turbo* (*Marmarostoma*) *histrioides* sp. nov. has a wider shell profile and larger pleural angle than *T. (M.) yoshiharuyabei*. *Turbo* (*Marmarostoma*?) *sanoii* Tomida and Kadota, 2014 from the Ena Limestone differs from *T. (M.) histrioides* sp. nov. by its much larger shell size and stronger but fewer spiral cords without sculpture between them. Thus, *T. (M.) histrioides* sp. nov. is easily distinguished from the above two species.

Three more middle Miocene species are known from the Japanese islands outside the Sagara and Izu Peninsula areas. These species were warm-water shallow marine

inhabitants during the Mid-Neogene Climatic Optimum. *Turbo* (*Marmarostoma*) *ozawai* Otuka, 1938 is commonly found in the lower to middle Miocene Uchiura Group in Fukui, western Japan (Ozawa *et al.*, 1986; Nakagawa, 2018). *T. (M.) minoensis* Itoigawa, 1960 from the lower middle Miocene Shukunohara Formation in Gifu Prefecture, central Japan, and *Turbo parvuloides* Nomura, 1940 from the lower middle Miocene Moniwa Formation in Sendai, northern Japan, all from non-calcareous clastic sediments. *Turbo* (*Marmarostoma*) *minoensis* and *T. (M.) ozawai* are easily distinguished from *T. (M.) histrioides* sp. nov. in having much finer spiral cords and an obtusely spiny spiral cord, if present, only on the shoulder angle.



**Figure 4.** Syntype of *Turbo histrio* Reeve, 1848, NHMUK1968713-1, from Amirante Island, Indian Ocean, in Hugh Cumming collection of Natural History Museum, London (courtesy of A. Salvador). Scale bar represents 10 mm.

*Turbo parvuloides* is a poorly known species and clearly differs from *T. (M.) histrioides* sp. nov. by its non-spinose primary and finer secondary spiral cords.

Among the modern species from the Indo-Pacific, three species should be compared with *T. (M.) histrioides* sp. nov. *Turbo (Marmarostoma) histrioides* sp. nov. most resembles *T. (M.) histrio* Reeve, 1848, an endemic species in the Amirante Islands and Rodrigues Island in the western Indian Ocean (Alf and Kreipl, 2003, p. 33; Figure 4). Adults of both species have almost the same shell size and profile, and spiny spiral cords over the shell surface. We consider that they are not conspecific because in *T. (M.) histrioides* sp. nov. the early whorls are more rounded and the shoulder is less well developed than in *T. (M.) histrio*. The two species are also geographically and temporally distant.

*Turbo (Marmarostoma) histrioides* sp. nov. also resembles *T. (M.) argyrostomus* Linnaeus, 1758 and *T. (M.) radiatus* Gmelin, 1791. *Turbo (Marmarostoma) argyrostomus* is widely distributed in the Indo-Pacific and is highly variable regarding the development of the spines on the spiral cords. In particular, *T. (M.) histrioides* sp. nov. resembles a spiny form which Alf and Kreipl (2003, pl. 17) classified as '*T. (M.) argyrostomus argyrostomus* forma *carduus* Fischer, 1873' from the Philippines and Queensland, Australia, but it is primarily distinguished from this and other forms of *T. (M.) argyrostomus* in having far fewer granules found only marginally on the outer surface of the operculum instead of having a dense coverage of granules over the whole outer surface as seen in the latter form. In addition, *T. (M.) histrioides* sp. nov. differs from *T. (M.) argyrostomus* in having spiny spiral cords all over the teleoconch whorls while they are mostly on the

last whorl in the latter. *Turbo (Marmarostoma) radiatus*, known from the western Indian Ocean to Western Australia, is characterized by a prominent spiny spiral cord at the shouldered angle and basal periphery, and a rather flattened outer whorl surface and base. In contrast, all of the spiral cords are spiny and the outer whorl surface and base are rather inflated in *T. (M.) histrioides* sp. nov.

### *Turbo (Marmarostoma) izuensis* sp. nov.

Figure 5A–H

**Material.**—A total of 20 specimens; 17 specimens from the Kadono Formation; holotype: NMNS PM28021; 16 paratypes: NMNS PM28022–28024, 28025 (operculum), 28026 (operculum), 28027–28031, 28035–28038, 28039 (operculum), and 28040 (operculum). Three specimens from the Ena Limestone; one unregistered specimen held by the Matsuzaki Visitor Center, Matsuzaki, Izu Peninsula, two specimens NMNS PM28033 and 28034.

**Type locality.**—Small exposure in a valley approximately 1.5 km east of Makinogo, Shuzenji Town, Shizuoka Prefecture, in the north-central Izu Peninsula; middle Miocene Kadono Formation.

**Etymology.**—Named after the Izu Peninsula.

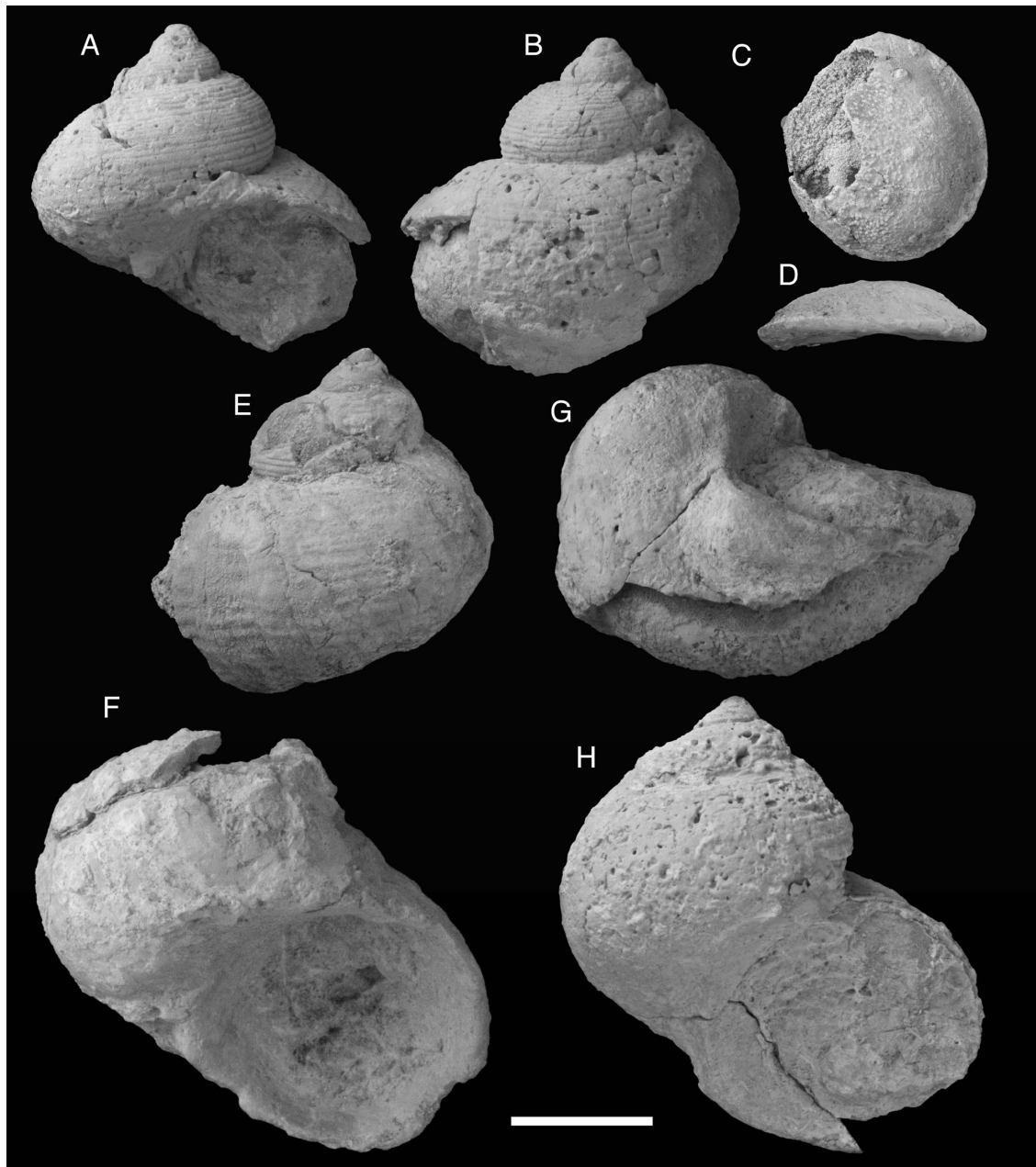
**Diagnosis.**—Large species characterized with rounded whorls and fine, non-spinous spiral ribs. Umbilicus closed. Operculum not so thickened like most species of *Turbo (Marmarostoma)*, with outlining thin peripheral zone, covered with fine granules centrally.

**Description.**—Shell moderately large, reaching 65 mm in width, thick, as high as wide, with pleural angle around 85°. Spire elevated, occupying almost half of shell height. Protoconch unknown. Teleoconch whorls well inflated and rounded, separated by impressed suture; early teleoconch whorls subangulated at shoulder edge, basal periphery and middle of outer whorl surface each with slightly thicker spiral cord, further ornamented with finer spiral cords six on ramp and five on outer whorl surface; subangulation obsoleting gradually through growth. Penultimate and last whorls rounded, ornamented with 13 finer spiral cords on surface above basal periphery in holotype. Base not well preserved in all specimens, seemingly also covered with finer spiral cords. Umbilicus closed. Aperture imperfect. Operculum less thickened, peripherally flattened, covered with many granules centrally.

**Discussion.**—The specimens from the type locality described herein were all covered with thick coral-line algae and were incomplete. The shell surface is best observed in the holotype, but the basal area and aperture are poorly preserved. The closed umbilicus is well observable in NMNS PM28023 (Figure 5G).

Although all available specimens of *T. (M.) izuensis* sp. nov. are incomplete, the holotype and some other speci-





**Figure 5.** *Turbo (Marmarostoma) izuensis* sp. nov. **A, B**, NMNS PM28021, holotype, apertural and adapertural views, shell height 48.4 mm, maximum shell width 48.6 mm+, from Kadono Formation; **C, D**, NMNS PM28025, paratype, outer and lateral views of operculum, maximum diameter 34.3 mm, maximum thickness 10.6 mm, from Kadono Formation; **E**, NMNS PM28033, adapertural view, shell height 48.5 mm, from Ena Limestone; **F**, unregistered specimen held by Matsuzaki Visitor Center, Matsuzaki, Izu Peninsula, shell width 64.8 mm, from Ena Limestone; **G, H**, NMNS PM28023, paratype, basal and apertural views, shell height 64.0 mm, shell width 58.3 mm, from Kadono Formation. Scale bar represents 20 mm for all specimens.

mens preserve enough shell characters to make informative comparisons with other species. Among the six fossil species from the Sagara and Izu Peninsula areas discussed above, *T. (M.) yoshiharuyabei* is the only species that resembles *T. (M.) izuensis* sp. nov. The largest specimen

of *T. (M.) yoshiharuyabei* is 92.7 mm wide (Tomida *et al.*, 2019), and the penultimate and last whorls are ornamented only by spiral cords the same as *T. (M.) izuensis* sp. nov. Those spiral cords, however, are of almost the same strength in *T. (M.) izuensis* sp. nov. while they are

composed of three major, often somewhat nodulous spiral cords and finer interstitial ones in *T. (M.) yoshiharuyabei*. Although the relationships among *T. (M.) minoensis*, *T. (M.) ozawai* and *Turbo parvuloides* need further examination, they are all different from *T. (M.) izuensis* sp. nov. in the presence of three stronger spiral cords on the ramp angle and basal periphery and at the mid-whorl. In addition, the spiral cords on the ramp angle are often spiny in *T. (M.) minoensis* and *T. (M.) ozawai*.

*Turbo sondeianus* Martin, 1905 from the Pliocene of Sonde in central Java, Indonesia has a shell shape and shell surface sculpture almost the same as *T. (M.) izuensis* sp. nov. The holotype of *T. sondeianus* appears to be an adult and is approximately 50 mm in shell height. The holotype and six specimens of *T. sondeianus* in the collection of NMNS from the Sonde area have a characteristic open and deep umbilicus that is surrounded by a thick and noded spiral cord, while the umbilicus is totally closed in *T. (M.) izuensis* sp. nov. The beds yielding *T. sondeianus* in the Sonde area have been assigned to a time interval between 3.95 Ma and 3.58 Ma (Kase *et al.*, 2008), which is more than 10 my younger than the age of *T. (M.) izuensis* sp. nov. We therefore consider that *T. sondeianus* and *T. (M.) izuensis* sp. nov. are similar but different species.

## Discussion

Paleomagnetic evidence has shown that during the middle Miocene the Izu Peninsula consisted of volcanic islands on the Izu-Ogasawara Arc located at low latitude, and drifted to the present position due to the northward drift of the Philippine Sea Plate (Hirooka *et al.*, 1985; Koyama, 1991, 1994; Niitsuma and Koyama, 2006). In contrast, the Megami Limestone is considered to have formed on a hotspot seamount in the northeastern Philippine Sea Plate and accreted allochthonously at the continental margin of the Eurasian Plate (Ogawa and Taniguchi, 1989; Sugiyama, 1992; Ozawa *et al.*, 1995). Although the limestone bodies in the Sagara and Izu Peninsula areas might have been deposited in geographically distant locations, they provide a window into the shallow marine paleodiversity on the oceanic islands at the eastern margin of the Philippine Sea Plate.

Modern species of *Turbo (Marmarostoma)* exhibit the highest species maximum in the Indo-West Pacific (or the Indo-Australian Archipelago) region delimited by the Philippines, Indonesia and Papua New Guinea, as do some corals, other molluscs and fishes (e.g. Briggs, 1974; Paulay, 1997; Williams and Duda, 2008; Hoeksema, 2007; Tittensor *et al.*, 2010; Bellwood *et al.*, 2012; Jablonski *et al.*, 2013). Previous authors have hypothesized that this high diversity in the IWP originated in the late Oligocene or early Miocene and was the result of an increase in shal-

low marine habitats, the length of the coastline, and habitat complexity due to the collision of the Indo-Australia plate with the Eurasian plate (e.g. Williams and Duda, 2008; Williams, 2007; Renema *et al.*, 2008; McMonagle *et al.*, 2011), or that the diversity increase occurred in the Pliocene (for ostracods; Yasuhara *et al.*, 2017; Shin *et al.*, 2019). Williams and Duda (2008) enumerated 16 species of *Marmarostoma* in this region, a richness that decreases both latitudinally and longitudinally, and their molecular phylogenetic studies demonstrated that the rate of cladogenesis in this subgenus increased in the late Oligocene or early Miocene (Williams, 2007; Williams and Duda, 2008). From these studies, the occurrence of many fossilized *Turbo (Marmarostoma)* species in tropical Southeast Asia is expected, for example, from the shallow marine beds found in the Indonesia and Philippine archipelagos.

The present study brings the total species number of *Turbo (Marmarostoma)* to six in the Sagara and Izu Peninsula areas (Table 1). Given the incompleteness of the fossil record and the very limited distribution of the fossil-bearing beds in the Sagara and Izu Peninsula areas, it is possible that species richness in these areas was higher, but it is just not being picked up by the fossil record. In the tropical sea along the Izu-Ogasawara Arch to the Northern Mariana Islands, only two species of *T. (M.)* have been recorded: *T. (M.) argyrostomus* and *T. (M.) setosus* (Fukuda, 1993; Kurozumi and Asakura, 1994; Smith, 2003). Species of *T. (M.)*, therefore, were more diverse in this region during the middle Miocene than they are today.

Despite the rich molluscan record in the Indonesian and Philippine archipelagos of the central IWP, the fossil record indicates that Miocene species of *T. (M.)* are sparse, with only three species known (Table 1). Also, Ladd (1966) recorded only one undetermined species of *T. (M.)* from the Miocene deposits in the tropical Western Pacific islands encompassing the Mariana Islands, Palau, Vanuatu, Tonga and Fiji (Table 1). In the Indonesian and Philippine archipelagos, however, *T. (M.)* species have been collected from clastic sediments, whereas all known specimens from the Sagara and Izu Peninsula areas were collected from calcareous sediments. All modern species of *Marmarostoma* inhabit mostly intertidal to shallow subtidal rocky shores or carbonate platforms in the tropical Pacific (Hickman, 1998; Hickman and McLean, 1990). The sparsity of *T. (M.)* species in the central IWP, therefore, is likely to be explained by collection biases because fossil molluscs from the carbonate sediments have not been extensively explored in the Indonesian and Philippine archipelagos. Nevertheless, turbinid gastropods are sometimes commonly found locally in younger Cenozoic clastic sediments (e.g. Hickman and McLean, 1990; Williams, 2007; Nehm and Hickman, 2008), prob-

ably due to postmortem transportation by water currents and/or hermit crabs. This is the same even in Cenozoic strata in Java and the Philippines (TK, unpublished). It is therefore still uncertain whether or not the low species-richness of *Marmarostoma* in the central IWP Miocene shallow marine sediment is due to mere imperfection of the fossil record. For understanding the paleodiversity in the central IWP, rigorous taxonomic study of and search for turbinid fossils, as well as the age refinements of fossil-bearing beds, are strongly required.

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#### Author contributions

S. Tomida, K. Inoue and M. Kadota collected the material from the Megami and Ena limestone, and T. Kase the material from the Makinogo Limestone. All authors contributed to the writing of the paper.