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Revision of four species of *Turbo* (*Marmarostoma*) (Gastropoda: Turbinidae) from the lower-middle Miocene of Japan

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Abstract. The turbinid gastropod species *Turbo* (*Lunella*) *ozawai* Otuka, 1938 was described based on two opercula from the lower to middle Miocene Korematsu Formation in Southwest Japan. This inadequate proposal of the new species without the shell character information has confused subsequent taxonomic and faunal studies on the early to middle Miocene species of *Turbo* in Japan. For the first time, we clarify the shell characters of *T.* (*M.*) *ozawai* based on the type series and newly obtained materials from the Korematsu Formation in the Shobara area, Hiroshima Prefecture, and the Yoshino Formation in the Tsuyama area, Okayama Prefecture, Southwest Japan. The clarification of the shell and opercular characters of *T.* (*M.*) *ozawai* has enabled a taxonomic revision of the previously described four nominal species from early to middle Miocene species of *Turbo* (*Marmarostoma*) from the Honshu Arc of the Japanese Islands. Consequently, these four species are reclassified into two species, *T.* (*M.*) *ozawai* and *T.* (*M.*) *tochiyensis* Kanno, 1958; *T.* (*M.*) *parvuloides* Nomura, 1940 and *T.* (*M.*) *minoensis* Itoigawa, 1960 are junior synonyms of *T.* (*M.*) *ozawai* and *T.* (*M.*) *tochiyensis*, respectively. Both species are rare examples of mollusks that thrived along the Honshu Arc throughout the Miocene Climatic Optimum (~16.9 to 14.7 Ma). The species richness of *Turbo* (*Marmarostoma*) is similar to that of the modern species in the warm water region of the Japanese Islands.

Keywords: Japanese Islands, Miocene, Miocene Climatic Optimum, paleobiodiversity, *Turbo* (*Marmarostoma*) *ozawai*

Introduction

Turbo (*Lunella*) *ozawai* Otuka, 1938 (currently referred to the subgenus *Marmarostoma* Swainson, 1829) was proposed based only on two opercula from the lower–middle Miocene Korematsu Formation (Bihoku Group) in Shobara City of Hiroshima Prefecture, Southwest Japan, (Figure 1A). Because the opercular characters are not always diagnostic for taxonomic identification at the species-level in the subgenus *Marmarostoma*, this inadequate proposal of the new species has caused confusion in the subsequent identification of the early to middle Miocene specimens of *Turbo* (*Marmarostoma*) from the Japanese Islands. Since then, the taxonomic and/or faunal studies of *Turbo* (*Marmarostoma*) species from the Bihoku Group and its almost contemporaneous strata in Southwest Japan have been referred to and/or listed in one of the three ways: i) *T.* (*M.*) *ozawai* when the opercula are examined (Taguchi, 2002); ii) *Turbo* (*Marmarostoma*) *minoensis* Itoigawa, 1960 when the shells are examined (e.g. Itoigawa and Nishikawa, 1976; Taguchi *et al*., 1979; Taguchi, 2002); iii) *T.* (*M.*) *ozawai* when both shells and opercula are examined; moreover, *T.* (*M.*) *minoensis* has been regarded as a junior synonym of the former species (Oyama *et al*., 1994; Nakagawa, 2018; Amano and Aida, 2020). To resolve this confusion, a clarification of the shell character of *T.* (*M.*) *ozawai* is required.

This study first considers the clarification of shell char-

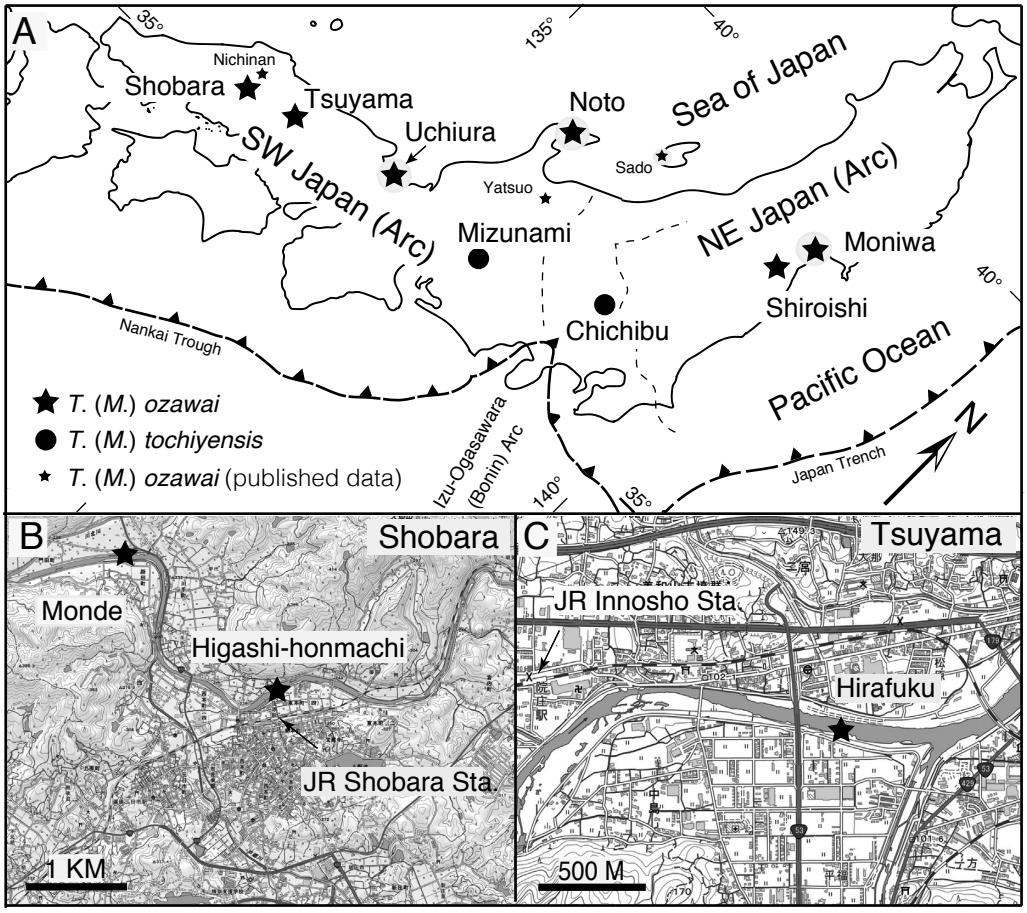

Figure 1. Localities of the specimens. **A**, Map showing the positions of fossil collection; **B**, **C**, Collecting sites (★) in the Shobara area in Hiroshima Prefecture (B) and in the Tsuyama area in Okayama Prefecture (C). The base map is the "Shobara" topographic maps (1:50,000 scale) and "Western part of Tsuyama-seibu" topographic maps (1:25,000 scale), respectively, obtained from the website of the Geospatial Information Authority of Japan (http://maps.gsi.go.jp/).

acters of *T*. (*M*.) *ozawai* based on the type specimens and newly obtained materials from the Korematsu Formation in the Shobara area and the Yoshino Formation in the Tsuyama area, Okayama Prefecture. Secondly, it considers a taxonomic revision of the four nominal species of *Turbo* (*Marmarostoma*) from the lower–middle Miocene in the Honshu Arc (Southwest and Northeast Japan Arcs; Takahashi, 2006) of the Japanese Islands based on the examination of the type series of all the species as well as additional specimens. These species are *T*. (*M*.) *ozawai*; *Turbo minoensis* Itoigawa, 1960 from the Mizunami basin in Gifu Prefecture, Southwest Japan; *Turbo tochiyensis* Kanno, 1958 from the Chichibu Basin in Saitama Prefecture, Southwest Japan; and *Turbo parvuloides* Nomura, 1940 from the Moniwa Formation in the Moniwa area, Sendai, Northeast Japan (Figure 1A). This paper reports the reclassification of the aforementioned four species into two species: *Turbo* (*Marmarostoma*) *ozawai* and *Turbo* (*Marmarostoma*) *tochiyensis*. *Turbo parvuloides* and *T*. (*M*.) *minoensis* were regarded as junior synonyms of *T*. (*M*.) *ozawai*, and *T*. (*M*.) *tochiyensis*, respectively.

Materials

Species and materials examined in this study are shown in Table 1. The geologic time scale adopted herein is the astronomically tuned Neogene time scale ATNTS2012 Gradstein *et al*., 2012). The ages of the Miocene planktonic microfossil datum planes follow Yanagisawa and Watanabe (2017). The materials used in this study are housed at the Hiwa Museum for Natural History, Shobara (HMN); Fukui City Museum of Natural History, Fukui (FCMNH); Masutomi Museum of Geology, Kyoto (MMG); Nagoya University Museum, Nagoya (ESN); Institute of Geoscience, the University of Tsukuba, Tsukuba (IGUT); National Museum of Nature and Sci-

Table 1. Species and specimens examined in this study. Taxonomic assignments in this study are indicated in bold or brackets.

Species	Locality	Formation/Group	Associated fauna
***Turbo* (*Marmarostoma*) *ozawai* Otuka, 1938**			
	Higashi-honmachi, Shobara City, Hiroshima Prefecture, Southwest Japan[1]	Korematsu Formation, Bihoku Group	Kadonosawa[12]
	Monde, Shobara City, Hiroshima Prefecture, Southwest Japan	Korematsu Formation, Bihoku Group	Kadonosawa[12]
	Tari, Nichinan City, Tottori Prefecture, Southwest Japan[2]	Tari Formation	Kadonosawa[2]
	Hirafuku, Tsuyama City, Okayama Prefecture, Southwest Japan	Yoshino Formation, Katsuta Group	Kadonosawa[12]
	Ogurui, Takahama Town, Fukui Prefecture, Southwest Japan[3]	Shimo Formation, Uchiura Group	Kadonosawa[12]
	Matsunagi and Konami, Suzu City, Ishikawa Prefecture, Southwest Japan[4]	Higashi-Innai Formation	Kadonosawa[12]
	Kakuma, Suzu City, Ishikawa Prefecture, cenral Japan[5]	Higashi-Innai Formation	Kadonosawa[12]
	Ikuridani, Yatsuo, Toyama City, Toyama Prefecture, Southwest Japan[6]	Kurosedani Formation	Kadonosawa[12]
	Kougasezaeki, Sado City, Niigata Prefecture, central Japan[7]	Orito Formation	Kadonosawa[7]
	Float in Akabira River near Akabira Bridge, Ogano Town, Saitama Prefecture, Southwest Japan	Chichibumachi Formation, Akahira Goup	?
Turbo (*Marmarostoma*) *parvuloides* Nomura, 1940 [=*T*. (*M*.) *ozawai* Otuka, 1938]			
	Minami- and Kita-akaishi, and Oide, Sendai City, Miyagi Prefecture, Northeast Japan[8]	Moniwa Formation, Natori Group	Moniwa[13]
	Akaihata, Shiroishi City, Miyagi Prefecture, Northeast Japan[9]	Akaibata Formation	Moniwa[14]
***Turbo* (*Marmarostoma*) *tochiyensis* Kanno, 1958**			
	Tochiya, Chichibu City, Saitama Prefecture, Southwest Japan[10]	Chichibumachi Formation, Akahira Goup	Moniwa[15]
Turbo (*Marmarostoma*) *minoensis* Itoigawa, 1960 [=*T*. (*M*.) *tochiyensis* Kanno, 1958]			
	Akatsukibora and Shukubora, Mizunami City, Gifu Prefecture, Southwest Japan[11]	Shukunohora Formation, Mizunami Group	Kadonosawa[12]
	Sakurado, Nataki, Hongo, Tsukiyoshi, Kawaishizugabora, and Garaishi-shita, Mizunami City, Gifu Prefecture, Southwest Japan[11]	Oidawara Formation, Mizunami Group	Reworked?[16]

References: [1]Loc. 1 (Suketo) of Otuka (1938); [2]Yamana (1997); [3]Nakagawa (2009, 2018); [4]Locs. 32 and 35 of Masuda (1966a, b); [5]Loc. Kakuma (37°28′14″N, 137°08′26″E); [6]Kaneko and Goto (1992); [7]Amano and Aida (2020); [8]Locs. Minami- and Kita-akaisi of Nomura (1940) and Loc. Oide, almost the same as Loc. 3002 of Nomura and Maeda (2008); [9]Loc. 3 of Hatai *et al*. (1970); [10]Loc. 801 of Kanno (1960); [11]Itoigawa *et al*. (1974, 1981); [12]Itoigawa (1987), Matsubara (1995); [13]Sato (1991), Kurihara *et al.* (2003); [14]Amano (1983), Kitamura (1988); [15]Y. Kurihara (unpublished data); [16]Itoigawa (1974), Seto (1992)

ences, Tsukuba (NMNS); Mizunami Fossil Museum, Mizunami (MFM); the University Museum, the University of Tokyo, Tokyo (UMUT); and the Tohoku University Museum, Sendai (IGPS).

Turbo (*Marmarostoma*) *ozawai*.—Otuka (1938) reported that the type locality of *T. ozawai* was "Suketô, 200 m northeast of Syôbara [= Shobara] railway station." This site is a riverbed of the Saijo River located in

4-chome, Higashi-honmachi of Shobara City in terms of the current location (Otuka, 1938; Oyama *et al.*, 1994; Kaikiri and Nishimoto, 1995; Figure 1A, B). In addition to the two syntypes, we examined 3 shells and 2 opercula from this site. We also examined 2 shells from the contemporaneous shell-bearing beds exposed at Monde, another riverbed site of the same river, about 2 km northwest from the type locality (Figure 1A, B). The beds exposed in these sites are mapped as Shinjo Sandstone Member of the Korematsu Formation; this formation, with a thickness of about 60 m, is the lower unit of the Bihoku Group (Ueda, 1986, 1989). Yamamoto (1999) dated the Korematsu Formation around 16 Ma based on his nannofossil analysis with the data obtained from the age analysis of planktonic foraminifers by Okamoto (1992). The fossil shells and opercula from these two sites were obtained from sandstone and siltstone beds, and associated with intertidal to subtidal soft-bottom mollusks (Otuka, 1938; Furukawa *et al*., 2010). We assume that the shells and opercula of *T*. (*M*.) *ozawai* were transported from the nearby hard bottom habitats into this shallow marine bottom by water currents.

We also examined 27 shells and 14 opercula from the Yoshino Formation collected at Hirafuku in Tsuyama City, Okayama Prefecture, Southwest Japan (Figure 1A, C). The Yoshino Formation is the middle unit of the three formations of the Katsuta Group (Kawai, 1957; Taguchi, 2002). These fossils were obtained from a 0.5–1 m thick and *ca.* 3 m long lenticular conglomeratic sandstone body within the grayish-brown tuffaceous siltstone bed, and associated with the mixed assemblage of tidal to subtidal mollusks. Watanabe *et al*. (1999) assigned the overlying Takakura Formation to the upper part of *Crucidenticula kanayae* zone (NPD 3A, 17.0–16.6 Ma), or the lower part of the *Denticulopsis praelauta* zone (NPD 3B, 16.6–15.9 Ma) according to the diatom biostratigraphy by Akiba (1986). The fission track dating of the Kanoko Tuff within the Yoshino Formation is 17.9±2.1 Ma (Suzuki *et al*., 2003). Therefore, the Yoshino Formation is contemporaneous with the Korematsu Formation in the Shobara area.

To determine the morphological variability and spatiotemporal distribution of the species, we further examined the shell and opercular specimens collected from the Shimo Formation (Uchiura Group) at Ogurui in Fukui Prefecture, which are housed in FCMNH and NMNS, and those collected from the Higashi-innai Formation in Noto Peninsula, Southwest Japan as described by Masuda (1966a), which are housed in the collection of IGPS and NMNS. In addition, we examined specimens collected from a Miocene float rock on the Akabira River in the Chichibu Basin of Saitama Prefecture, Southwest Japan, which are housed in the collection of NMNS. The float rock consists of a fossiliferous granule conglomerate that contains the trochid gastropod *Protorotella hayashii* Kanno. Judging from the occurrence of *P. hayashii* and the geologic map, the source of the float rock was likely the Nagura Formation (Kanno, 1960), which is currently a part of the Chichibumachi Formation (Takahashi, 2008). The Chichibumachi Formation has been correlated to the upper part of Blow's (1969) planktonic foraminiferal zone N8, of early middle Miocene age as mentioned above (see Takahashi, 2008 for detailed discussion).

Turbo (*Marmarostoma*) *parvuloides*.—*Turbo parvuloides* was described by Nomura (1940) from the Miocene Moniwa Formation exposed on riverbeds of the Natori River at Minami-akashi in the Moniwa area, *ca.* 10 km west of Sendai City proper, Miyagi Prefecture, Northeast Japan (Figure 1A). We examined the holotype and 22 fragmental paratypes in the collection stored at NMNS and five specimens collected by the last author (Y. T.). The latter five specimens were from the basal calcareous conglomerate beds of the Moniwa Formation at Kita-akashi, which is the riverbank on the other side of the type locality. Nomura and Maeda (2008) have shown that the beds were deposited in open-coast shoreface with strong current or wave action. The Moniwa Formation has been correlated to the upper part of Blow's (1969) planktonic foraminiferal zone N8 and N9 (Oda and Sakai, 1977; Kitamura *et al*., 1986; Yanagisawa, 2012), of early middle Miocene age.

We also examined a large shell and three opercula collected by the last author (Y. T.) from the Akaihata Formation in Shiroishi City of Miyagi Prefecture. These specimens were informally identified as *T.* (*M.*) *pauvuloides* by the late K. Masuda (Miyagi University of Education, Sendai). Hatai *et al*. (1970) reported the occurrences of 55 molluscan species from three localities. The Akaihata Formation has been correlated to the Moniwa Formation in Sendai (e.g. Kitamura and Fukudome, 1979; Amano, 1983; Kitamura, 1988).

Turbo (*Marmarostoma*) *tochiyensis*.—The holotype and two paratypes of *T. tochiyensis* Kanno, 1958 in the IGUT collection were examined. These are from the Hiranita Formation [currently part of the Chichibumachi Formation (Takahashi, 2008)] exposed at Amago-iwa, a small exposure about 70 m upstream of Shimizu bridge, Tochiya (Chichibu City) in the Chichibu basin, Saitama Prefecture, Southwest Japan (Kanno, 1958, 1960; Figure 1A). We also examined eight specimens from the type locality in the NMNS collection. Although poorly preserved, this species was found in abundance at the type locality together with rocky shore mollusks and reef coral rubbles. The Chichibumachi Formation has been correlated to the upper part of Blow's (1969) planktonic foraminiferal zone N8, of early middle Miocene age (Makimoto and Takeuchi, 1992; Takahashi, 1992, 2008).

Turbo (*Marmarostoma*) *minoensis*.—We examined 7 shells and a total of 266 opercula in the collection of MFM and one shell in the collection of NMNS, all from the Mizunami Group in the Mizunami basin, Gifu Prefecture, Southwest Japan (Figure 1A). The Mizunami Group is composed of five units: the Toki, Hongo, Akeyo, Shukunohora and Oidawara formations in ascending order (Irizuki and Hosoyama, 2006). These specimens were from two units: 6 shells and 164 opercula were from the Shukunohora Formation (localities Akatsukibora and Shukubora), and 2 shells and 102 opercula were from the Nataki Conglomerate Member of the Oidawara Formation (localities Sakurado, Nataki, Hongo, Tsukiyoshi, Kawaishizugabora and Garaishi-shita). At the Akatsukibora site, well-preserved shells and opercula of *T*. (*M*.) *minoensis* were found, which were associated with diverse mixed assemblages of tidal to subtidal (~ 20 m) mollusks in conglomerate beds unconformably overlying the Cretaceous Nohi Rhyolite. The Shukunohora Formation has been correlated to the lower part of Blow's (1969) planktonic foraminiferal zone N8 (Ibaraki, 1981; Itoigawa, 1989; Irizuki and Hosoyama, 2006). The Nataki Conglomerate Member is a 0.5–2 m-thick, basal conglomerate bed of the Oidawara Formation that unconformably overlies the Shukunohora Formation. However, the fossils from the Nataki Conglomerate Member are believed to be derived mostly from the underlying Shukunohora Formation (Itoigawa, 1974, p. 22; Seto, 1992).

Systematic description

(Tomoki Kase, Yukito Kurihara and Susumu Tomida)

Family Turbinidae Rafinesque, 1815
Genus ***Turbo*** Linnaeus, 1758
Subgenus ***Marmarostoma*** Swainson, 1829

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

Remarks.—The subgenus *Marmarostoma* is tropical to subtropical Indo–West Pacific in distribution and includes approximately 20 species (Williams, 2008; Williams and Duda, 2008). We assign the two species described below to *Marmarostoma*. They are characterized by the presence of thick spiral cords, two of which are prominent on the shouldered angle and at the basal periphery of the last whorl, and the thick opercula sculptured with fine granules on the outer surface. These characters are common in many species of this subgenus (Williams, 2008).

Turbo (***Marmarostoma***) ***ozawai*** Otuka, 1938

Figures 2–4

Turbo (*Lunella*) *ozawai* Otuka, 1938, p. 36, pl. 3, figs. 22–24 (operculum).
Turbo parvuloides Nomura, 1940, p. 35, pl. 3, fig. 12a, b.
Turbo (*Marmarostoma*) cf. *ticaonica* Reeve. Horikoshi in Kobayashi and Horikoshi, 1956, p. 49, pl. 4, fig. 1a, b.
Turbo (*Marmorostoma* [sic]) *ozawai* Otuka. Masuda, 1966b, p. 333–335, pl. 36, figs. 18a–22c; Nakagawa and Takeyama, 1985, pl. 23, fig. 3a, b; Ozawa *et al*., 1986, pl. 13, fig. 1; Masuda and Sasaki, 1987, p. 5, pl. 1, figs. 3a–6b; Nakagawa, 2009, pl. 1, figs. 6a–8; Nakagawa, 2018, p. 17, pl. 2, figs. 3–5.
Turbo ozawai Otuka. Masuda, 1969, pl. M-6, figs. 6a–7b; Taguchi *et al*., 1979, pl. 3, figs. 19, 20; Masuda, 1982, p. 252, pl. 126, figs. 1197–1199b; Michinoku Amateur Paleontologists' Club, 1991, pl. 2, figs. 34a–35c; Kaneko and Goto, 1992, p. 18, pl. 9, fig. 4a, b; Yamana, 1997, pl. 37, figs. 9–14; Taguchi, 2002, pl. 6, fig. 7; Matsuura, 2009, pl. IV-2(1), fig. 3.
Turbo (*Marmorostoma* [sic]) *minoensis* Itoigawa. Taguchi, 2002, pl. 6, figs. 5, 6.
Turbo (*Marmarostoma*) *ozawai* Otuka. Amano and Aida, 2020, p. 5, figs. 2–4, 7, 8.
non *Turbo* (*Marmorostoma* [sic]) *ozawai* Otuka. Itoigawa *et al*., 1981, p. 147, pl. 27, fig. 13; Itoigawa *et al*., 1982, p. 147.

Types.—Otuka (1938, p. 36) described *Turbo* (*Lunella*) *ozawai* based on two opercula (formerly Reg. No. 10018-No. 1 and -No. 2 in Geological Institute, Faculty of Science, Imperial University of Tokyo), and designated both specimens as "syntypes" in the text. In the figure caption of his plate 3, however, he erroneously indicated "holotype" for a specimen in figure 22, and "paratype" for the outer and lateral views of the same specimen in figures 23 and 24, respectively. In this study, these two specimens were regarded as syntypes, and UMUT CM12744) (formerly Reg. No. 11018-No. 1) was designated as **lectotype** (Otuka, 1938, pl. 3, figs. 22–24; Figure 2H, I) and UMUT CM12765 (formerly Reg. No. 11018-No. 2) as paralectotype. *Turbo parvuloides* Nomura, holotype, NMNS PM 19283 (formerly Saito Ho-on Kai Mus. Coll. Reg. 19877).

Other materials examined.—Korematsu Formation in the Shobara area: 5 shells, HMN-F11702-S893, HMN-F-06704-SKS-T0003, HMN-F-06705-SKS-T-0001, from the type locality; HMN-11721-N5800 and HMN-11721-N6257, from Monde, and 1 operculum, HMN-F-06706-S-1344, from the type locality. Yoshino Formation in the Tsuyama area: 6 shells, MMG-F19001–19006, and 14 opercula, MMG-F19007, 19008, NMNS PM 28487, 28488, all from loc. Hirafuku. Uchiura Group in Fukui: 11 shells, FCMNH 9584–9586, 6502, NMNS PM 28489 and 9 opercula, FCMNH 6503, 7986–7990, 7993, 7995, 9587, 9588, from loc. Ogurui. Higashi-innai Formatin in the Noto Peninsula area: 4 shells and 17 opercula, IGPS 90687, from loc. Konami; 3 shells, NMNS PM 28473–282475, from loc. Kakuma. Chichibumachi Formation in Chichibu basin: 3 shells, NMNS PM 28484–28486. Moniwa Formation in Sendai: 11 shells, NMNS PM

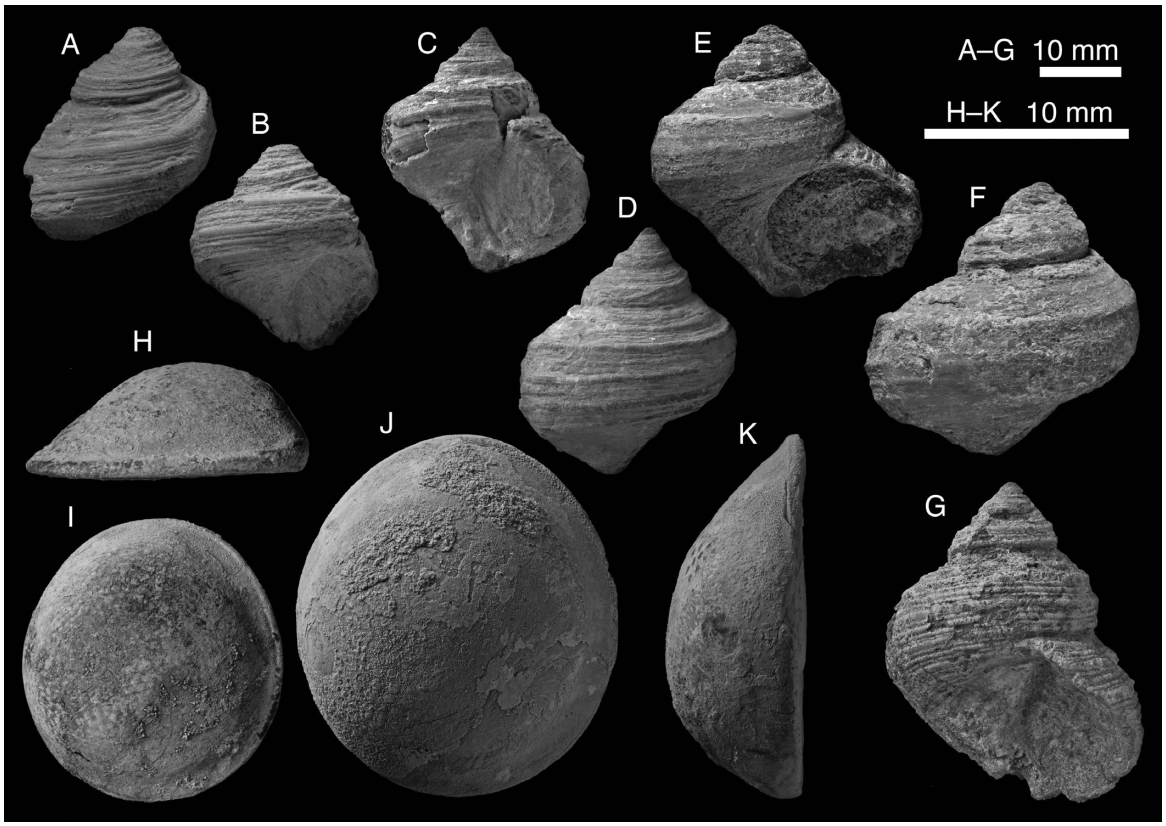

Figure 2. *Turbo* (*Marmarostoma*) *ozawai* Otuka. **A–D,** Specimens from Korematsu Formation, Bihoku Group, loc. Monde in Shobara City, and **E–K,** Specimens from Korematsu Formation, Bihoku Group, loc. Suketo (type locality) in Shobara City, Hiroshima Prefecture; A, B, adapertural and apertural views, HMN-11721-N5800, height 22.9 mm, width 21.2 mm; C, D, apertural and adapertural views, HMN-11721-N6257, height 25.8 mm, width 21.7 mm; E, F, apertural and adapertural views, HMN-F-06705-SKS-T-0001, height 33.6 mm, width 30.6 mm; G, apertural view, HMN-F-06704-SKS-T-0003, height 38.6 mm, width 32.1 mm; H, I, lateral and outer views, UMUT CM12744, max. diameter 15.2 mm, min. diameter 14.1 mm, thickness 6.0 mm; J, K, outer and lateral views HMN-F-06706-S-1344, max. diameter 17.9 mm, min. diameter 15.9 mm, thickness 7.0 mm.

28479–28483, 29493 and 7 opercula, NMNS PM 29495, 28496, from loc. Minami-akaishi. Akaihata Formation in Shiroishi: 1 shell, NMNS PM 28498 and 4 opercula, NMNS PM 28496, 28497, from loc. Akaihata.

Diagnosis.—*Turbo* (*Marmarostoma*) less than 40 mm in height, slightly higher than wide. Surface covered with thick spiral cords in last whorl, with interstitial secondary cords and with or without much finer threads, all crossed by fine, not lamellate axial threads. Umbilicus closed. Columella evenly curved, with weak anterior extension. Outer surface of operculum covered with granules or pustular granules in most part, very finely granulated or smooth at margin.

Description of shell and opercula from Korematsu and Yoshino formations.—Shell deformed variably through sediment compaction, up to 35 mm in height, more or less higher than wide, moderately thick. Protoconch missing. Teleoconch up to four whorls, more or less inflated. Suture shallowly impressed in early whorls, slightly channeled in last whorl. Sculpture consisting of thick primary spiral cords with weaker secondary spiral cords and even much weaker spiral threads between them, and crossed by fine growth lines, giving fine pustular appearance. Five primary cords present on last whorl; one on shouldered angle, at basal periphery, in middle between these angles, in middle of subsutural ramp, and just below suture; one on shoulder angle thicker than others, sometimes becoming rope-shaped due to crossing by fine growth lines. Base weakly convex, covered by less than nine secondary spiral cords with one or two spiral threads in interspaces. Columella evenly curved, with almost flat surface, slightly extending downward and reflected. Umbilicus totally closed. Operculum very thick, slightly oval, covered with granules or pustules in most part, very finely granulated or smooth along outer margin.

Discussion.—In fossil turbinid gastropods, the shells

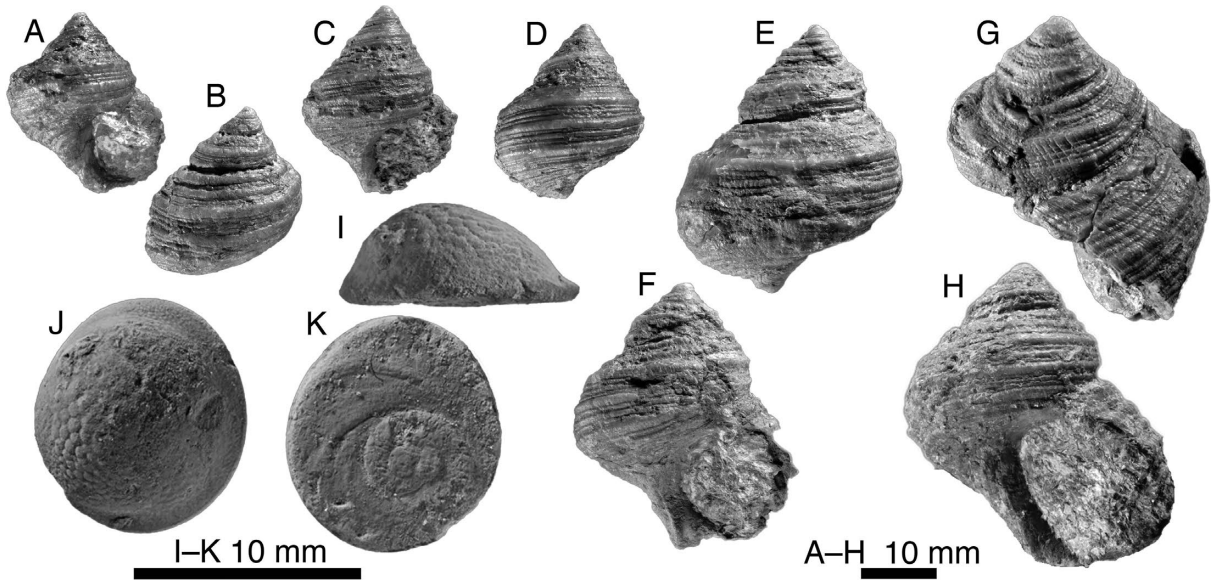

Figure 3. *Turbo* (*Marmarostoma*) *ozawai* Otuka. **A–K,** Specimens from Yoshino Formation, Katsuta Group, loc. Hirafuku in Tsuyama City, Okayama Prefecture; A, B, apertural and adapertural views, MMG-F19006, height 20.4 mm, width 16.6 mm; C, D, apertural and adapertural views, MMG-F19005, height 21.0 mm, width 16.8 mm; E, F, adapertural and apertural views, MMG-F19004, height 30,1 mm, width 24.6 mm; G, upper lateral view, MMG-F19001, height 32.4 mm, width 27.2 mm; H, apertural view, MMG-F19003, height 30.2 mm, width 25.4 mm; I–K, lateral, outer and inner views, NMNS PM 28487, max. diameter 10.5 mm, min. diameter 9.5 mm, thickness 4.5 mm.

and calcified opercula usually occur separately; the opercula, in general, have a higher preservation potential because their microstructural compositions are more durable than shells (Hickman, 1992, 1998). This is the case of fossil *Turbo* (*Marmarostoma*), where the opercula are more frequently preserved than the shells (e.g. Nehm and Hickman, 2008). For such isolated shells and opercula found in the same bed, either or both can be referred to more than one species judging from their morphologies, it is difficult to determine which operculum belongs to which shell or vice versa unless otherwise the opercula are preserved *in situ* in the shells. In contrast, when both isolated shells and opercula associated in the same bed are thought to belong to a single species, respectively, it is highly convincing that the opercula and shells belong to a single species. As described above, both the shells and opercula from the Korematsu and the Yoshino formations have the same characters and are considered to belong to a single species, respectively. Therefore, it is highly convincing that the shells from these formations are referred to *T*. (*M*.) *ozawai*.

This identification of the shells and opercula of *T*. (*M*.) *ozawai* can be more convincing if the same association is found in beds of other remote sites. Such associations were recognized in the fossil molluscan assemblages from the Shimo Formation (Uchiura Group) at Ogurui of Fukui Prefecture and the Higashi-innai Formation in the Noto Peninsula, Ishikawa Prefecture, Central Japan. The shell and opercular specimens from these two formations are well preserved (Figure 4D–I, N, M), and have been assigned to *T*. (*M*.) *ozawai* (Masuda, 1966b; Nakagawa and Takeyama, 1985; Ozawa *et al*., 1986; Nakagawa, 2009, 2018). We concur with the species assignment by these authors because the specimens from these formations have shell and opercular characters that are similar to those from the Korematsu and Yoshino formations in Southwest Japan, except for some specimens from the Higashi-innai Formation, as discussed below.

Masuda (1966b) noted that the shells of *T*. (*M*.) *ozawai* from the Higashi-innai Formation varied in morphology and surface sculpture from site to site, while the opercula did not. For example, the shells collected from his collecting locality 32 (Masuda, 1966b, pl. 36, fig. 19a, b; Figure 4A) exhibited a slightly higher shell profile and thicker primary spiral cords than those collected from his collecting locality 35 (Masuda, 1966b, pl. 36, fig. 18a, b; Figure 4J–L). In addition, the finer spiral threads between the primary and secondary spiral cords are absent in the shells from the locality 32, while four shells from locality 35 have tuberculated spiral cords and fine interstitial spiral threads. These shells from locality 35 appear quite different from those of the Korematsu and Yoshino formations and some large-sized specimens from Ogurui in Fukui Prefecture (Figure 4H, I). However, there are specimens that have intermediate shell profiles and sculpture patterns in the Uchiura Group and the Higashi-innai

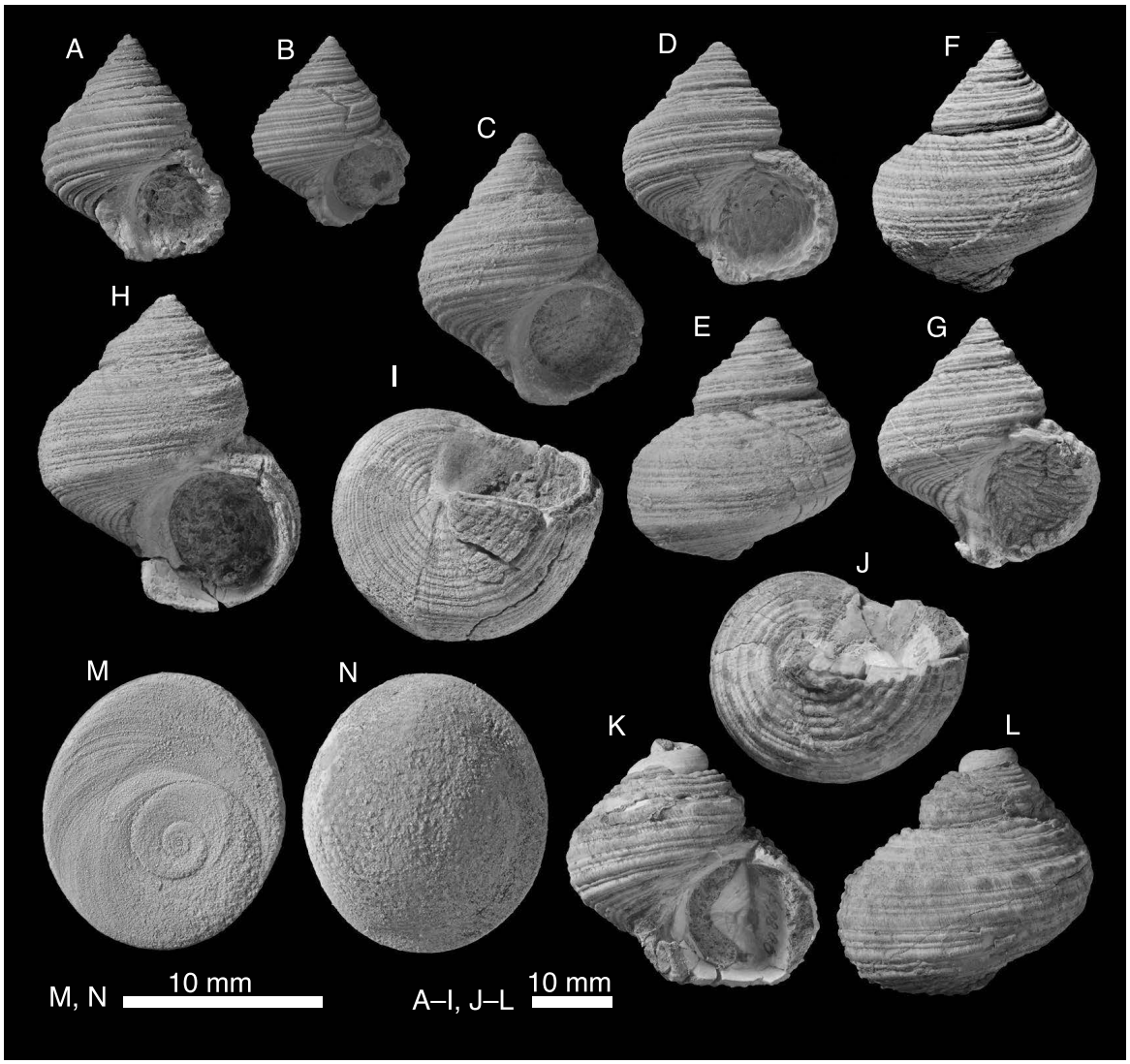

Figure 4. *Turbo* (*Marmarostoma*) *ozawai* Otuka. **A–C, J–L,** specimens from Higashi-innai Formation in Noto Peninsula; A, apertural view, IGPS 90853, illustrated in Masuda (1966b, pl. 36, fig. 19), height 30.0 mm, width 25.0 mm; B, apertural view, NMNS PM 28473, height 24.4 mm, width 20.5 mm; C, apertural view, NMNS PM 28474, height 34.9 mm, width 28.8 mm; J–L, basal, apertural and adapertural views, IGPS 90867, illustrated in Masuda (1966b, pl. 36, fig. 18), height 34.3 mm, width 32.9 mm; **D–I, M, N,** Specimens from Uchiura Group, loc. Ogurui, Fukui Prefecture; D, E, apertural and adapertural view, FCMNH-GF9685, height 31.7 mm, width 28.4 mm; F, G, adapertural and apertural views, FCMNH-GF9586, height 32.1 mm, width 28.0 mm; H, I, apertural and basal views, FCMNH-GF6502, height 40.5 mm, width 33.2 mm; M, N, inner and outer view of operculum, FCMNH-GF6503, height 114.3 mm, width 12.5 mm.

Formation (Figure 4B–G). Therefore, we concur with Masuda (1966b) that such nodulous specimens are a type of morphological variation in *T*. (*M*.) *ozawai.*

We consider *Turbo parvuloides* Nomura, 1940 as a junior synonym of *T*. (*M*.) *ozawai* (Figure 5). Nomura (1940) did not compare his species with *T*. (*M*.) *ozawai* based on the shell morphology, because the shell of the latter species was not obtained at the time. Several authors distinguished *T*. (*M*.) *parvuloides* from *T*. (*M*.) *ozawai* by i) its smaller shell size and lower number of spiral threads (Masuda, 1966b), ii) fewer, coarse and not spinous spiral cords as well as the presence of faint tubercles on the outer surface of operculum (Masuda and Sasaki, 1987), iii) finer and not spinous spiral cords (Michinoku Amateur Paleontologists' Club, 1991), and iv) the less prominent spiral cords (Amano and Aida, 2020). However, a fragmentary paratype of *T*. (*M*.) *parvuloides*, with a complete shell, may reach 40 mm in width, which is almost the same as the largest known specimen of *T*. (*M*.) *ozawai*. The holotype and some additional specimens

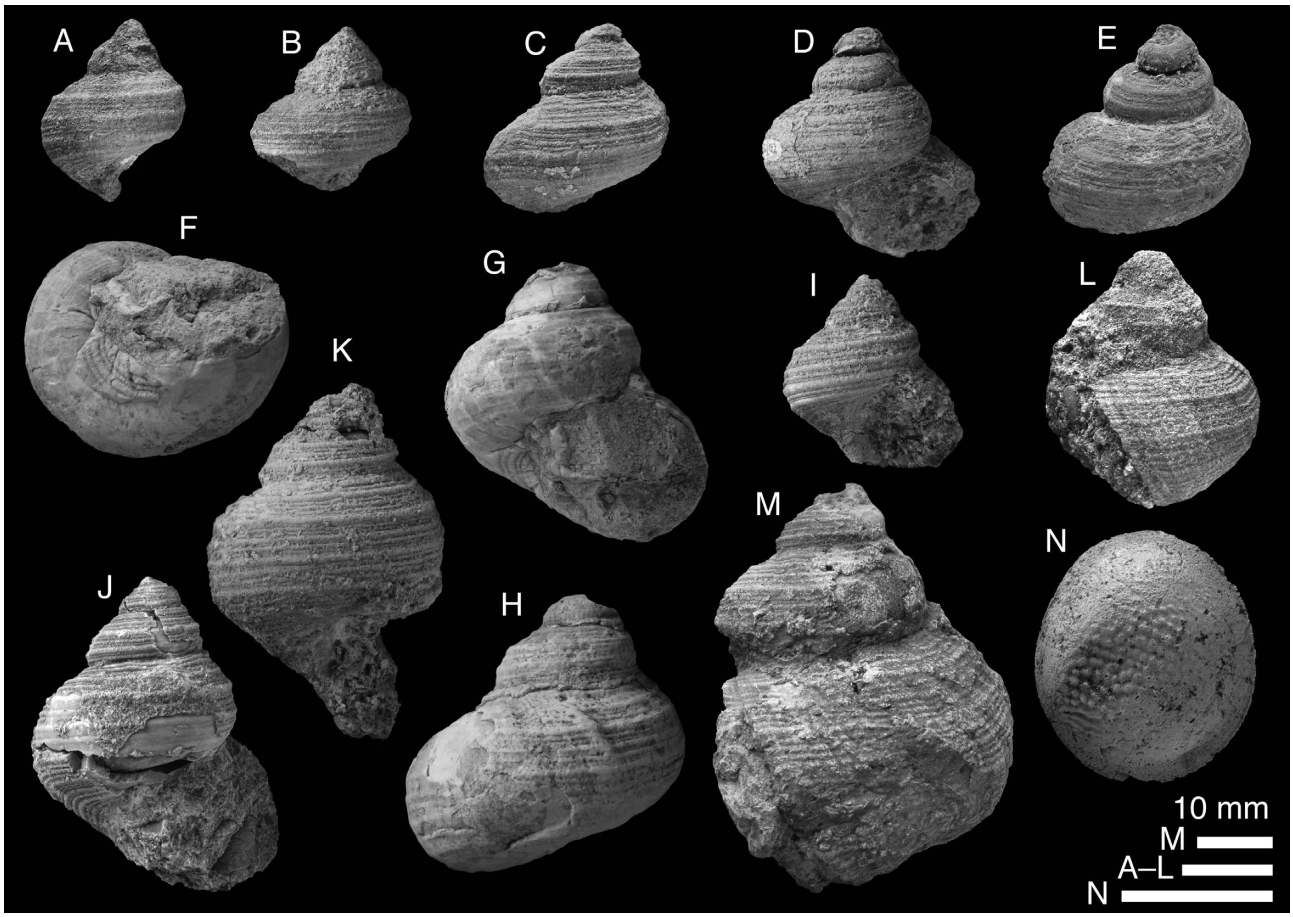

Figure 5. *Turbo* (*Marmarostoma*) *ozawai* Otuka. **A–H, L,** from Moniwa Formation, Sendai; A, apertural view, NMNS PM 28479, loc. Kita-akaishi, height 23.0 mm; B, adapertural view, NMNS PM 28480, loc. Kita-akaishi, height 21.0 mm, width 20.8 mm; C, adapertural view, NMNS PM 28481, loc. Kita-akaishi, height 23.8 mm, width 23.0 mm; D, E, apertural and slightly oblique apertural view, NMNS PM 28482, loc. Kita-akaishi, height 28.6 mm, width 25.6 mm; F–H, basal, apertural and adapertural views, holotype of *Turbo parvuloides* Nomura, 1940, NMNS PM 19283, loc. Minami-akaishi, height 31.4 mm, width 29.5 mm; L, lateral view, NMNS PM 28483, loc. Kita-akaishi, height 28.7 mm; **I–K,** specimens from Chichibumachi Formation, loc. float in Akabira river, Chichibu basin; I, apertural view, NMNS PM 28484, height 21.4 mm, width 19.0 mm ; J, apertural view, NMNS PM 28485, height 39.6 mm; K, apertural view, NMNS PM 28486, height 35.1 mm; **M, N,** specimens from Akaihata Formation, loc. Akaihata, Shiroishi; M, lateral view, NMNS PM 28498, height 54.2 mm; N, outer view of operculum, NMNS PM 28497, height 16.8 mm, width 14.7 mm.

show that the last whorl has three thick spiral cords: at the shouldered angle, at the periphery of the whorl, and in the middle of the ramp. The interstitials of these cords are three or four finer spiral cords/threads of variable strength (Figure 5A–I). Thus, the sculpture patterns of the spiral cords are not different between *T*. (*M*.) *parvuloides* and *T*. (*M*.) *ozawai*. Certainly, some specimens from the Moniwa Formation have thinner spiral cords than in *T*. (*M*.) *ozawai* (Figure 5A, B). This is probably because of the modification of the original shell material by severe diagenetic alteration. Some specimens from the Moniwa Formation have three thick spiral cords as do those from the Higashi-innai and Shimo formations (compare Figures 4B, F and 5C, D).

One poorly preserved shell from the Akaihata Formation attains about 54 mm in height (Figure 5M), and four opercula found in the same bed have a granulated outer surface (Figure 5N). These shells and opercula have the same characters as those of *T*. (*M*.) *ozawai*, except that the shell is large.

A specimen from the Uchiura Group was once referred to as *Turbo* cf. *ticaonica* Reeve, 1848 by Horikoshi in Kobayashi and Horikoshi (1956), but later reassigned to *T*. (*M*.) *ozawai* (Oyama *et al*., 1994; Kaikiri and Nishimoto, 1995; Nakagawa, 2018; Amano and Aida, 2020). *T. ticaonica* is a modern species, and has been synonymized with *Turbo* (*Marmarostoma*) *bruneus* (Röding, 1798) (e.g. Habe and Kosuge, 1966; Cernohorsky, 1972).

T. (*M*.) *bruneus* and *T*. (*M*.) *ozawai* almost have the same shell profile and sculpture pattern of the spiral cords; however, the former clearly differs from the latter in the presence of characteristic lamellar growth striae. None of the specimens we examined had such growth striae.

Stratigraphic and geographic distribution.—See Table 1.

Turbo* (*Marmarostoma*) *tochiyensis Kanno, 1958

Figure 6

Turbo (*Marmarostoma*) *parvuloides* Nomura. Watanabe *et al*., 1950, pl. 5, figs. 12–14. [not Nomura, 1940]

Turbo (*Batillus*) *cornutus* Solander. Watanabe *et al*., 1950, pl. 5, fig. 15 (paratype, IGUT 5887, of *Turbo* (*Marmorostoma* [sic]) *tochiyensis* Kanno, 1958).

Turbo (*Marmorostoma* [sic]) *tochiyensis* Kanno, 1958, p. 206, pl. 6, figs. 13–15; Kanno, 1960, p. 343, pl. 47, figs. 4–8.

Turbo (*Marmorostoma* [sic]) *minoensis* Itoigawa, 1960, p. 278, pl. 4, figs. 2, 3; Itoigawa *et al*., 1974, p. 125, pl. 38, figs. 13a–15; Itoigawa and Shibata, 1977, p. 66, pl. 29, figs. 11–13; Itoigawa *et al*., 1981, pl. 27, fig. 12a, b; Itoigawa *et al*., 1982, p. 146.

Turbo minoensis Itoigawa. Itoigawa, 1970, N-10, figs. 10, 11.

Turbo ozawai Otuka. Itoigawa *et al*., 1974, p. 125, pl. 38, figs. 17a–18b; Itoigawa *et al*., 1981, pl. 27, fig. 13a, b; Itoigawa *et al*., 1982, p. 147.

Turbo (*Marmarostoma*) *minoensis* Itoigawa. Horikoshi, 1983, p. 112, fig. H (reproduction from Itoigawa *et al*., 1981).

?*Turbo* (*Marmorostoma* [sic]) *tochiyensis* Kanno, 1958, p. 206, pl. 6, figs. 17, 18 (poorly preserved operculum); Hirayama, 1973, p. 176, pl. 15, fig. 28.

Types.—*Turbo* (*Marmarostoma*) *tochiyensis* Kanno, holotype, IGUT 5886, from the Chichibumachi Formation (late early to early middle Miocene) in the Chichibu Basin, Saitama Prefecture (Figure 6C). *Turbo* (*Marmarostoma*) *minoensis* Itoigawa, holotype, ESN-20044, from the Shukunohora sandstone (late early to early middle Miocene) in the Mizunami Basin, Gifu Prefecture.

Type locality.—Amagoiwa, a small exposure along Yokose River, about 70 m upstream from Shimizu bridge, Tochiya in Chichibu City, Saitama Prefecture.

Other material examined.—Chichibumachi Formation in the Chichibu basin: three paratypes, IGUT 5887 (two shells) and 6184 (one operculum), from the type locality (Figure 6A, B, D); two shells, NMNS PM 28477, 28478, from the type locality (Figure 6E–G). The Shukunohora Formation in the Mizunami Basin: 1 shell, MFM 13024 (Figure 6H), 1 shell, MFM 13025 (Figure 6I–K), 1 shell, MFM 11077 (Figure 6L), Akatsukibora; 2 shells, MFM 13026, Shukubora; 1 shell, NMNS PM 28476; Akatsukibora (Figure 6M); 1 operculum, MFM 11078, Akatsukibora (Figure 6N); 103 opercula, MFM 13027, Akatsukibora; 60 opercula, MFM 13028, Shukubora; 2 opercula, MFM 13029, Tsukiyoshi. Nataki Conglomerate Member of the Oidawara Formation in the Mizunami Basin: 31 opercula, MFM 13030, Sakurado; 22 opercula, MFM 13031, Nataki; 22 opercula, MFM 13032, Hongo; 2 fragmentary shells and 5 opercula, MFM 13033, Garaishishita; 20 opercula, MFM 13034, Kawai-shizugabora.

Diagnosis.—*Turbo* (*Marmarostoma*) reaching 40 mm in height, with constricted whorls. Shell surface densely covered with unraised spiral cords, thicker one at shoulder angle, basal periphery and in middle of them, all incised by axial striae in early whorls; often with scaly semitubular protrusions at shoulder angle and basal periphery. Umbilicus completely closed. Columella shallowly depressed medially, with slightly extended anterior edge. Parietal area covered with thin callus extended from upper part of columella. Operculum covered with pustules or pustular granules in center, becoming finer toward margin.

Discussion.—The type series of *T*. (*M*.) *tochiyensis* consists of the holotype and three paratypes. These specimens are all incomplete and very poorly preserved, and none preserves a whole shell. The holotype preserves the adapertural side of whorls better than the apertural side (Figure 6C). Although the shell surface is very rough due to the poor state of preservation, the sculptural pattern is basically almost the same as that of *T*. (*M*.) *ozawai*, with three slightly thicker and a few finer interstitial spiral cords on the last whorl. The sculptural pattern of this species is more evident in one of the paratypes, which shows that the last whorl has a subangulated shoulder and basal periphery with a row of scaly semitubular protrusions, three thicker spiral cords and interstitial, wavy finer ones (Figure 6A). The holotype, two paratypes (IGUT5887), and one specimen from the type locality bear scaly protuberances on the last whorl, which are more prominent at the shouldered angle than at the basal periphery (Figure 6A, C, D, G). One additional fragmentary specimen from the type locality, without such protuberance, is most probably a non-spiny form of this species because other sculptural characters are the same (Figure 6E). A unique character of this species is the presence of thin callus deposit that spreads on the parietal area of the aperture (Figure 6F, K).

We consider that *T*. (*M*.) *minoensis* is a junior synonym of *T*. (*M*.) *tochiyensis*. Itoigawa (1960) described *Turbo* (*Marmarostoma*) *minoensis* Itoigawa, 1960 based on at least two shells from the Shukunohora sandstone (equivalent to the Shukunohora Formation in this study) in the Mizunami Basin. The shells of *T*. (*M*.) *minoensis*, which we examined in this study, are all well preserved with uncrystallized original shell material (Figure 6H–M), and one specimen preserves even the original color markings (Figure 6M). The shells were collected together with many opercula and they exhibit the same morphological characters, respectively; hence, the opercula can quite convincingly be referred to *T*. (*M*.) *minoensis*. The scaly

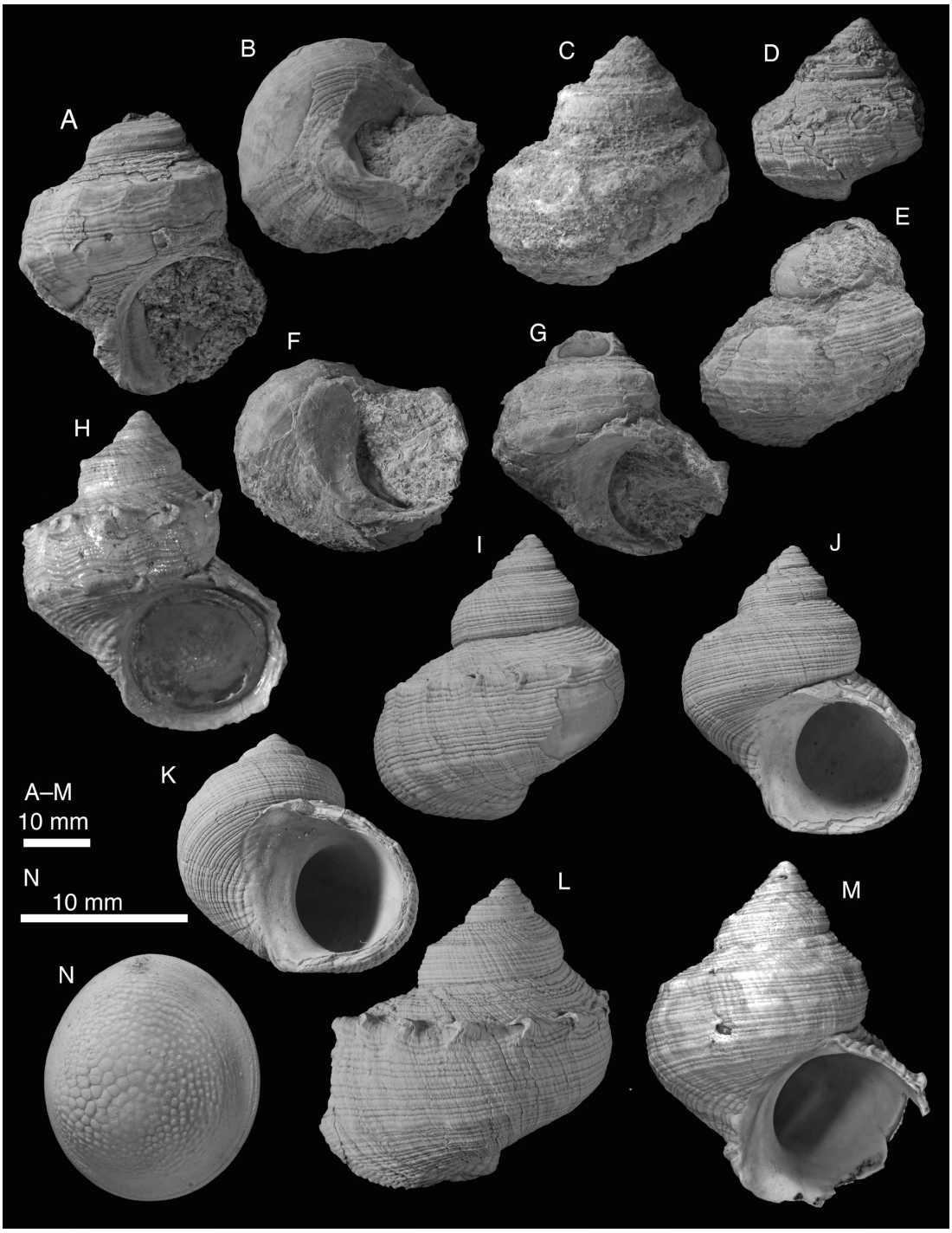

Figure 6. *Turbo* (*Marmarostoma*) *tochiyensis* Kanno. **A–G,** Chichibumachi Formation, loc. Amagoiwa, Tochiya, Chichibu basin; A, B, apertural and basal view of paratype, IGUT 5887, height 42.6 mm, width 37.3 mm; C, adapertural view of holotype, IGUT 5886, height 40.4 mm, width 37.3 mm; D, adapertural view of paratype, IGUT 5886, height 27.9 mm, width 27.3 mm; E, adapertural view, NMNS PM 28477, height 34.8 mm, width 37.0 mm; F, G, basal and apertural views, NMNS PM 28488, height 35.0 mm, width 36.3 mm. **H–N,** specimens previously referred to *Turbo* (*Marmarostoma*) *minoensis* Itoigawa from Shukunohora Formation, loc. Akatsukibora, Mizunami basin; H, apertural view, replica cast, MFM 13024, height 49.2 mm, width 40.5 mm, (photograph courtesy of Y. Ando of Mizunami Fossil Museum); I–K, adapertural, apertural and oblique basal views, MFM 13025, height 42.2 mm, width 38.3 mm; L, adapertural view of MFM 11077, height 47.0 mm; M, apertural view of NMNS PM 28476, showing color marking, height 43.4 mm, width 35.4 mm; N, outer view of operculum, MFM 11078, height 14.9 mm, width 13.0 mm.

semitubular protrusions at the shouldered angle and basal periphery in most specimens are developed only on the last whorl of large specimens; these protrusions are quite variable in prominence and almost absent in some specimens (Itoigawa *et al*., 1981, pl. 27, figs. 12a, b). The callus deposit extended to the parietal area is also present in the Mizunami specimens (Figure 6K). The synonymy of *T*. (*M*.) *minoensis* within *T*. (*M*.) *tochiyensis* is primarily based on the fact that a strongly spiny form of the former species has the same shell profile and sculpture pattern as that of the best preserved paratype of the latter one (Figure 6A, H).

Itoigawa (1960) distinguished *T*. (*M*.) *minoensis* [= *T*. (*M*.) *tochiyensis* in this paper] from *Turbo* cfr. *ticaonica* sensu Horikoshi in Kobayashi and Horikoshi (1956) [= *T*. (*M*.) *ozawai* in this paper] from the Uchiura Group in having a larger number of interstitial spiral cords. He was also aware of the close resemblance in opercular morphology between *T*. (*M*.) *minoensis* and *T*. (*M*.) *ozawai*, and stated that both species are conspecific if the opercula of the latter species were found together with the shell of the former species. Indeed, several authors synonymized *T*. (*M*.) *minoensis* with *T*. (*M*.) *ozawai* (Oyama *et al*., 1994; Kaikiri and Nishimoto, 1995; Nakagawa, 2018; Amano and Aida, 2020). We consider that *T*. (*M*.) *minoensis* with *T*. (*M*.) *ozawai* can definitely be separated into independent species. *T*. (*M*.) *minoensis* differs from *T*. (*M*.) *ozawai* in that the teleoconch whorls are more inflated, and therefore, more constricted by the presence of the sutures that are more deeply impressed. Moreover, the interstitial finer spiral cords are less variable in thickness; the protrusions at the shouldered angle are more prominent and scaly, instead of being knobs; and the parietal callus extends more widely at the base.

Stratigraphic and geographic distribution.—See Table 1.

Discussion

Japanese paleontologists have been paying attention to the occurrence of remarkable warm-water faunas in the lower–middle Miocene of Japan since the 1930's (e.g. Makiyama, 1932; Otuka, 1938; Oyama, 1950; Chinzei, 1986). This warming event was named the Mid-Neogene Climatic Optimum (Tsuchi, 1987) or the Miocene Tropical Spike (Itoigawa, 1989). Today, the early to middle Miocene transition is known as the globally warmest time interval during the Neogene, which is called the Miocene Climatic Optimum (MCO) (e.g. Holbourn *et al*., 2015; Kochhann *et al*., 2016). Kochhann *et al*. (2016) estimated the time interval of MCO as ~16.9 to 14.7 Ma. During this time interval, two stratigraphically and paleoecologically distinct warm-water molluscan faunas, the lower, or the Kadonosawa Fauna and the upper, or the Moniwa Fauna, have been widely recognized in the Honshu arc (e.g. Kurihara *et al*., 2003; Ogasawara *et al*., 2008). The Kadonosawa Fauna is typically characterized by intertidal sandy-mud and subtidal sandy bottom associations, and rocky and gravelly bottom associations are sporadic (Chinzei, 1981, 1986). In contrast, the Moniwa Fauna is characterized by open-marine subtidal rocky and gravelly bottom associations dominated by pectinid bivalves (Sato, 1991; Kurihara *et al*., 2003). These faunas usually occur from nearshore deposits, from which few age-diagnostic microfossils occur. However, the ages of the mollusk-bearing horizons have been well controlled by microfossil biostratigraphy and radiometric dating of under- and overlying deposits. The age of the Kadonosawa and Moniwa faunas is estimated as ~17.0–16.7 Ma (Yanagisawa and Watanabe, 2017) and ~15.3–14.7 Ma (Kurihara *et al*., 2003; Yanagisawa, 2012), respectively. Most of the lower to middle Miocene warm-water molluscan faunas in Honshu Arc have been referred to either the Kadonosawa or Moniwa faunas, but an assignment of those in the Chichibu Basin remains unclear. We referred herein the molluscan fauna of the upper part of the Chichibumachi Formation [= Hiranita Formation of Kanno (1960)] to the Moniwa Fauna on the basis of the occurrence of *Nanaochlamys notoensis* (Yokoyama), the characteristic pectinid of that fauna (Y. Kurihara, unpublished data). This assignment is compatible with the planktonic foraminiferal data of the upper part of the Chichibumachi Formation (upper part of Blow's (1969) zone N8; Takahashi, 2008).

This study demonstrated that both *T*. (*M*.) *ozawai* and *T*. (*M*.) *tochiyensis* are present during the MCO in the Honshu Arc, and that both are in common between the Kadonosawa and Moniwa faunas (Table 1). Although the geographic and stratigraphic ranges of these species are almost the same, they do not occur together in the same locality. This may suggest that their habitat preference differed from one another.

Modern species of *Turbo* (*Marmarostoma*) are intertidal to shallow subtidal, rocky, or carbonate bottom dwellers in the tropical Indo-Pacific region (Hickman and McLean, 1990; Hickman, 1998; Alf and Kreipl, 2003). They exhibit a biodiversity hotspot in the central Indo-West Pacific bounded by the Philippines, Indonesia and Papua New Guinea, where 16 species have been identified (Williams and Duda, 2008). The species number declines sharply toward the north in the northwestern Pacific, and only three species, *T.* (*M.*) *argyrostoma*, *T.* (*M.*) *setosus* and *T.* (*M.*) *stenogyrus*, extend their distribution to the subtropical or warm-temperate realms in the Japanese Islands (Sasaki, 2000).

Recently, a total of seven species of *Turbo* (*Marma-*

rostoma) have been reported in the four late early to early middle Miocene reefal limestone bodies in the Izu Peninsula and Sagara areas, central Japan (Tomida and Kadota, 2012, 2014; Tomida and Hosoda, 2015; Kase *et al*., 2020; Tomida *et al*., 2021). These species were dwellers in reefal environments around the volcanic islands of the Izu–Ogasawara (Bonin) Arc, which were thought to be positioned further south of the present locations (Hirooka *et al*., 1985; Koyama, 1994), or somewhere in a tropical domain both in the northeastern part of the Philippine Sea Plate (Ozawa *et al*., 1995) during the late early to early middle Miocene. Kase *et al*. (2020) and Tomida *et al*. (2021) have shown that, during that time period, *Turbo* (*Marmarostoma*) was more diverse in the northeastern Philippine sea more than today's hotspot in the central Indo–West Pacific, where only two species have been heretofore known. This paper discusses the reclassification of four nominal species of *Turbo* (*Marmarostoma*) from the lower to middle Miocene of Honshu Arc in the Japanese Islands into two species. In addition, the habitats of their modern relatives, as well as the sedimentological and associated faunal evidences, suggest that these two species were warm-water dwellers in non-carbonate, rocky shores along the Honshu Arc roughly at the same position today. This study also shows that the current biodiversity pattern in the central Indo-West Pacific is different from that in the early to middle Miocene time, providing a new insight into the shallow marine biodiversity history of this bioprovince.

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Author contributions

T. K. and S. T. mainly designed and performed this study, and T. K., Y. K. and S. T. contributed to the writing the manuscript. M. T., T. Y., Y. I., H. O. collected the materials from the Yoshino and Korematsu formations, Y. K. from the Nagura and Hiranita formations, and Y. T. from the Moniwa and Akaihata formations. All authors gave final approval for publication.