First *Strebloceras* (Mollusca: Gastropoda: Caecidae) from the middle Pleistocene of Japan

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中部更新統渥美層群豊橋層産ミジンギリギリツツガイ科（軟体動物門：腹足綱）の１新種

芳賀拓真*

（Abstract）

A caecid gastropod of the small genus *Strebloceras* recovered from the middle Pleistocene Toyohashi Formation, Atsumi Group, was newly described as *S. kobayashii* n. sp. It is the first record of the genus in Japan and is the geochronologically youngest fossil that fills a large time gap of approximately 5 Myr after the middle Miocene. *Strebloceras kobayashii* n. sp. is characterized as having a large shell that is up to approximately 5 mm long and a dorsally or ventrally depressed teleoconch. It is interpreted to be a rare, extinct fossil species that lived exclusively in the warm-temperate conditions during interglacial periods in the middle Pleistocene. Although the geochronological occurrence of *Strebloceras* apparently matches well with the hypothesis of the eastward migration from the Tethys to the Pacific in Miocene times, the origins of the Pacific members may be explainable by overlap of both the Tethys and original Pacific lineages.

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Introduction

Members of the family Caecidae Gray, 1850 are small to minute caenogastropods with characteristically tusk-shaped to tubular or depressed trochiform to almost planispiral shells (e.g., Ponder and de Keyzer, 1998). They are found worldwide in tropical to temperate marine waters from the intertidal to upper subtidal zones, and rarely in the deep sea down to approximately 1,000 meters (e.g., Pizzini et al., 2013). Their habitats vary but are essentially epibenthic or interstitial in shallow marine bottoms (e.g., Bandel, 1996). These habitats include the surfaces of substrata such as algae and rocks, gravels (e.g., Ponder and de Keyzer, 1998), underneath pebbles (Tatara, 2011), and underneath rocks and wood in sulphide-rich reducing environments (Kano and Haga, 2011).

The Caecidae comprises three subfamilies: Caecinae Gray, 1850, Ctiloceratinae Iredale and Laseron, 1957 (= Pedumicrinae Iredale and Laseron, 1957; Watsoniinae Iredale and Laseron, 1957; Parastrophiinae Hinoide and Habe, 1978), and Strebloceratinae Bandel, 1996 (Bandel, 1996; Bouchet et al., 2017; MolluscaBase, 2019). Over 150 nominal species from ten genera are known (MolluscaBase,
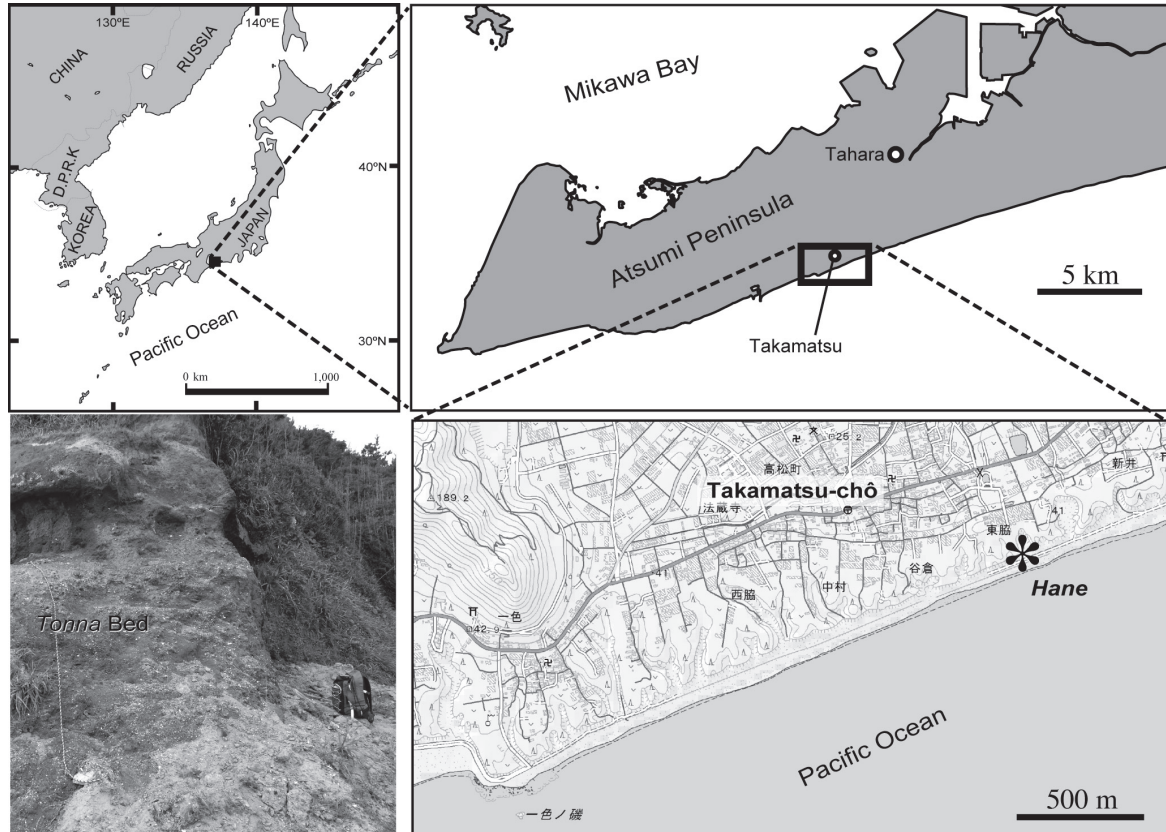
Figure 1. Locality map and image of outcrop at Hane, the type locality, where *Strebloceras kobayashii* n. sp. has been collected. Asterisk indicates the type locality at Hane. Photograph of the outcrop was taken on 27 July 2014. The locality map at the lower right was produced based on 1:25,000 scale topographic map of the Geospatial Information Authority of Japan.

2019). The three subfamilies are discerned primarily based on protoconch and teleoconch morphologies (e.g., Bandel, 1996; Pizzini et al., 2013). The Caecinae has a planispirally coiled protoconch, which is discarded during ontogeny, to produce a tube-like teleoconch whose posterior end is sealed with a septum in a fully-grown individual. The Ctiloceratinae features an "uncoiled" protoconch of which earlier portions are planispirally coiled. The protoconch permanently attaches to the teleoconch throughout the lifetime. Finally, the Strebloceratinae retains a trochospirally coiled protoconch attached to an uncoiled teleoconch thorough the lifetime. The Caecidae is suggested to have originated in the Cretaceous period based on the fossil records of alleged sister groups (Ponder, 1988; Bandel, 1996), whereas the oldest caecid fossils are represented by early Eocene (Ypresian) examples: two species of the genus *Caecum* in the Caecinae from the northwestern United States (Goedert and Raines, 2016) and an undescribed Strebloceratinae species from the South Island of New Zealand (Beu and Maxwell, 1990; Beu and Raines, 2009).

The genus *Strebloceras* Carpenter, 1859 of the subfamily Strebloceratinae is a monotypic genus previously composed of only eight species. Of these, seven are considered to be valid and one is unnamed through the Cenozoic, since the early Eocene (Vannozzi, 2016; MolluscaBase, 2018; Vannozzi, 2019a, b; Table 1). The oldest recorded species of the genus is from the early Eocene (Ypresian) in New Zealand, and from the European Tethys realm during the Paleogene to earliest Miocene (Aquitanian) (Table 1). In the Neogene, in contrast, *Strebloceras* is recorded exclusively in the Pacific region, and the highest species diversity is observed in the Recent tropical Indo-Pacific, particularly in West Pacific waters (Table 1). A single species, *Strebloceras hinemoa* Finlay, 1931, is recorded from Miocene sediments of New Zealand as well as from modern Pacific waters of New Caledonia and Mariana Islands (Table 1). There is a hiatus of the fossil record of *Strebloceras* between the last occurrence in the late middle Miocene of New Zealand and Recent (Pizzini et al., 2013; Vannozzi, 2016; Vannozzi, 2019b; Table 1).

Recent field surveys and curatorial works of paleontological

collections have discovered gastropod shells referable to the genus *Strebloceras* from the middle Pleistocene (Chibanian) Toyohashi Formation of the Atsumi Group, the Pacific side of central Honshû, Japan. These gastropod shells, once labeled as the ctiloceratine caecid *Parastrophia japonica* Hinoide and Habe, 1978 in Kawase et al. (2015: pl. 6, fig. G59, left and right), were suggested by Vannozzi (2016: 111) to be an undescribed species of *Strebloceras sensu lato*. This discovery represents the first record of the genus in Japan as well as the geologically youngest fossil of the genus that fills a time gap of approximately 5 Myr after the middle Miocene. Here, I describe this fossil species as *S. kobayashii* n. sp. and discuss the significance of its discovery.

***Abbreviations used in the text*:** AH—apertural height; IWP—Indo-West Pacific; MFM—Mizunami Fossil Museum, Mizunami, Gifu, Japan; NMNS—National Museum of Nature and Science, Tokyo, Tsukuba, Ibaraki, Japan; TMSM—Takamatsu Muddy Sand Member; TMNH—Toyohashi Museum of Natural History, Toyohashi, Aichi, Japan; SL—shell length; SW—shell width (= maximum width of the teleoconch).

Materials and Geological Setting

A total of eight well-preserved specimens of the present new species were recovered from an outcrop exposed at a sea cliff at Hane, Takamatsu-chô, Tahara City, located in the southeastern part of Aichi Prefecture in central Japan (34º37'17.4" N, 137º14'38.0" E: Fig. 1), which represents the surveyed site "Loc. 2" in Nakashima et al. (2010: 63). This outcrop was recently covered during revetment related shoreline preservation. Three paratype specimens were acquired from the collection of late Mr. Shûji Ugai. The collection, now kept at the Mizunami Fossil Museum (MFM), was amassed during long-term field sampling from 1973 to 2005 (see Kawase, 2013: 44; Kawase et al., 2015: 51–53).

The collection site represents the *Tonna* Bed of the Takamatsu Muddy Sand Member (TMSM: Nakashima et al., 2008a, b; Fig. 1, lower left), Toyohashi Formation, Atsumi Group. The Atsumi Group (Kuroda, 1958) is widely distributed in the Tempakubara Upland located in a zone extending from the west of Lake Hamana to Atsumi Peninsula on the Pacific side of central Japan. It is composed of shallow marine sediments deposited during glacio-eustatic sea level

changes in the middle Pleistocene (Nakashima et al., 2010 and references therein). The group comprises the Futagawa, Tahara, and Toyohashi Formations in ascending stratigraphic order (Sugiyama, 1991; Nakashima et al., 2008a, b, 2010). The TMSM is exposed along the coastline. It is approximately 2 km wide near Takamatsu-chô and over 8 m thick. Its sedimentary environment is likely a dissected valley (e.g., Hayasaka, 1961; Nakashima et al., 2010). Nakashima et al. (2008b) demonstrated Marine Isotope Stage 9 (= Chibanian) of the Toyohashi Formation on tephra correlation. The TMSM is very fossiliferous, with four major shell-bearing horizons in ascending order: *Batillaria* Bed, *Dosinia* Bed, *Mya* Bed and *Tonna* Bed (Oinomikado, 1933; Hayasaka, 1961; Nakashima et al., 2010). The sedimentary basin of this member was likely a bay environment that had transited from the river mouth or inner part of the bay to full marine conditions receiving coastal/oceanic waters during the sea level rise (Oinomikado, 1933; Tsuchi, 1960; Shibata and Ujihara, 1983; Shibata et al., 2006; Nakashima et al., 2010; Kawase et al., 2015). Kawase et al. (2015) subdivided the *Tonna* Bed into two horizons comprising the *Ruditapes* Bed for the lower part and the *Tonna* Bed for the upper. However, I treat those two horizons as the *Tonna* Bed according to previous interpretations (Oinomikado, 1933; Hayasaka, 1961; Nakashima et al., 2010).

Rich invertebrate fauna indicative of shallow marine condition have been reported from this member. The fauna include foraminifera (Makiyama and Nakagawa, 1940), ostracodes (Yajima, 1987; Wakamatsu, 1988), barnacles (Kobayashi et al., 2008) decapod crustaceans (Karasawa and Tanaka, 1994; Karasawa and Goda, 1996; Kobayashi et al., 2008; Karasawa et al., 2014; Ando et al., 2016) as well as molluscs (Oinomikado, 1933; Tsuchi, 1960; Hayasaka, 1961; Shibata and Ujihara, 1983; Matsuoka and Goda, 1996; Kawase, 2002, 2013; Kawase et al., 2015; Shibata et al., 2006; Shimamoto et al., 1994). Molluscan (Hayasaka, 1962; Shibata and Ujihara, 1983; Shibata et al., 2006; Kawase et al., 2015; Haga and Hasegawa, 2017) and decapod crustacean (Karasawa et al., 2014) fauna recognized from this member, including a warm-temperate element, indicate the strong influence of the Kuroshio Current. Kawase et al. (2015) recorded a total of 470 molluscan species from the TMSM in which the highest species diversity was found in the *Tonna* Bed *sensu* Oinomikado (1933), Hayasaka (1961) and Nakashima et al. (2010).

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Table 1. A summary of fossil records of *Strebloceras*, arranged in geologic order.

Species	Geologic age (Stage)	Formation	Distribution	Biogeographic Region	Apertural morphology	Reference / Voucher
S. sp. †	early Eocene (Late Ypresian)	Kauru Formation	South Island, New Zealand	A	circular	Beu and Maxwell (1990); Beu and Raine (2009)
S. bezanconi (Cossmann, 1888) †	middle Eocene (Lutetian–Bartonian)	calcaires lutétiens	Paris Basin	T	circular	Deshayes (1861–1864); Cossmann (1888); Morellet and Morellet (1945); Gougerot (1975); Vannozzi (2016); MNHN (2020: MNHN.F.A29177)
S. cornuoides Carpenter, 1859 †	middle Eocene (Lutetian)	Bracklesham Beds	Southern England			Wrigley (1934)
	middle Eocene (Lutetian) –late Eocene (Priabonian)	Barton Beds	Southern England			Carpenter (1858–1859); Newton (1891)
	early Oligocene (Rupelian)	"Hempstead Beds" (= Bouldnor Formation)	Southern England	T	circular	Carpenter (1858–1859); Newton (1891) MNHN (2020: MNHN.F.J12110)
	early Oligocene (Rupelian)	-	Paris Basin			
	early Oligocene (Rupelian)	Bouldnor Formation	Southern England			Munt and Barker (1996)
	early Oligocene (Rupelian)	Borgloon Formation	Belgium			Marquet et al. (2008)
	middle Eocene (Lutetian)	calcaire grossier d'Etrechy	Paris Basin			Deshayes (1861–1864)
	late Eocene (Priabonian) –late Oligocene (Chattian)	"Magdeburg Greensand"	Central Germany			Müller (2008, 2011)
S. edwardsi (Deshayes, 1861) †	early Oligocene (Rupelian)	-	Paris Basin	T	circular	Cossmann (1912); Gilbert (1962); Lozouet and Maestrati (2012); Vannozzi (2016); MNHN (2020: MNHN.F.A42236, MNHN.F.J12109)
	early Oligocene (Rupelian)	Danismen Formation	NW of Turkey			Lebküchner (1974); Islamoğl et al. (2010)*; Harzhauser et al. (2016)
	earliest Early Miocene (Aquitanian)	-	Aquitaine, France			Bandel (1996)
S. hinemoa Finlay, 1931	late early Miocene (Burdigalian) –late middle Miocene (Serravallian)	Mount Harris Formation	South Island, New Zealand	A	circular	Finlay (1931); Gage (1957); Beu and Maxwell (1990)
	Recent	-	-17 m, Loyalty Islands, New Caledonia and Saipan of Northern Mariana Islands	CIP	circular	Pizzini et al. (2013); Vannozzi (2016)
S. kobayashii n. sp. †	middle Pleistocene (Chibanian)	Toyohashi Formation	central Japan	NIP	oval	this study
S. subannulatum de Folin, 1880	Recent	-	beach drift and subtidal, Hawaii	EIP	circular	de Folin (1880); de Folin (1886); Lightfoot (1992); Pizzini and Raines (2011); Severns (2011); Pizzini et al. (2013); Vannozzi (2016)
	Recent	-	French Polynesia		circular	Shasky (1989); Tröndlé and Boutet (2009); Pizzini and Raines (2011); Vannozzi (2016)
	Recent	-	Easter Island			Raines and Pizzini (2005)
	Recent	-	Mariana Islands	CIP		Smith (2003)**; Pizzini et al. (2013); Vannozzi (2016)
S. pizzinii Vannozzi 2016	Recent	-	-80–120 m, Bohol Sea, Philippines	CIP	circular	Vannozzi (2016); Vannozzi (2017)
S. oliverioi Vannozzi 2019	Recent	-	-60 m, Sudan, Red Sea	WI	circular	Vannozzi (2016); Vannozzi (2019b)

†, fossil species; *, cited as S. cf. *edwardsi*; **, cited as S. cf. *subannulatum*.
Abbreviations of biogeographic region: A, Australasia; CIP, central Indo-Pacific; EIP, eastern Indo-Pacific; NIP, northern part of Indo-Pacific; T, Tethys realm; WI, western Indian Ocean.

Methods

All specimens described in this study were primarily obtained by drying and disaggregating fossiliferous sediment samples in tap water, and collecting materials from washed residues using binocular microscopy by the author, the late S. Ugai, and by Mr. N. Kobayashi (see Kawase et al., 2015 on methodological detail for paratypes 1–3). Specimens were then processed by the author. This involved thorough cleaning in distilled water using a fine point brush with plastic hairs under binocular microscopy. The inside of the shell of the specimen was cleaned by using a hair cut from a Dîpu Kurîn (= Deep Clean) "normal" toothbrush (Kao Co., Tokyo), air-dried then photographed under a binocular microscope. Scanning electron microscopy (SEM) images were directly acquired using a JCM-6000 benchtop instrument (JEOL Ltd., Tokyo) at TMNH in the low-vacuum mode without coating. Measurements were primarily made using Vernier calipers together with the "digital measurement" package in the microscope's operating software for the protoconch.

Specimens used in this study are housed in a Paleontology Collection, TMNH (TMNH-10101, 10758–10760), a collection at MFM (MFM 110117–110119), and a Paleontology Collection of Cenozoic Molluscs at NMNS (NMNS PM 28402).

I followed Vannozzi (2016), MolluscaBase (2018), and Vannozzi (2019a, b) concerning the systematics of the Strebloceratinae. Terminology of conchological characters followed Vannozzi (2016).

Systematic Paleontology

Class Gastropoda Cuvier, 1797
Family Caecidae Gray, 1850
Subfamily Strebloceratinae Bandel, 1996
Genus *Strebloceras* Carpenter, 1859

Type species: *Strebloceras cornuoides* Carpenter, 1859, by subsequent designation, Finlay, 1931: 20.
Remarks: The genus *Strebloceras* characteristically features a trochospirally coiled protoconch permanently attached to the teleoconch throughout the life, unlike the genus *Caecum*, and never undergoes an uncoiled stage, like *Parastrophia*. The teleoconch is uncoiled and tube-like, being a lightly curved or twisted, with a diameter that gradually increases anteriorly. A boundary between the protoconch and teleoconch is obvious

and marked with an incised line. The surface of the teleoconch is usually smooth or sculptured with fine collabral rings.

***Strebloceras kobayashii* n. sp.**
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(Figs. 2–4)
Creseis virgula (Rang, 1828). Kawase, 2013: 50 (not figured).
Parastrophia japonica Hinoide and Habe, 1978. Kawase et al., 2015: 55, 74, pl. 6, fig. G59.

Diagnosis: Shell large for genus, horn- or claw-like, reaching approximately 5 mm in length. Teleoconch dorso-ventrally depressed, rather thin, slightly incurved to right, may slightly kink either dorsally or ventrally at mid-shell length. Aperture laterally oblong, oval. Protoconch large for genus, constitutes approximately 2.1 whorls.
Description:

Shell (Teleoconch)—Shell large for genus attaining approximately 5 mm in length including protoconch (average: 4.96 mm, $n = 5$ for fully-grown intact specimens), rather thin but solid, vitreous translucent, shiny in excellently preserved specimens (Figs. 2. A–D, F–H; 4. A–C). Surface of teleoconch rather smooth, marked only with irregular growth lines (Figs. 2; 3. A, D; 4). Teleoconch horn- or claw-like, dorso-ventrally depressed (Figs. 2. C, D, H; 3. D; 4. B, C, G, E, I), slightly curved rightward (Figs. 2. A, B, E, F, G, I; 4. A, F, D, H). Teleoconch abruptly expands towards aperture in early portion but expansion rate may decrease at approximate anterior two thirds (Figs. 2; 3. D; 4). Teleoconch dorso-ventrally straight but may bend dorsally or ventrally near mid-shell length when grown (see under *Variations*). Aperture thin, simple, not thickened, elliptical, inclined ventrally (Figs. 2; 3. A, D; 4). Apertural height occupies approximately 0.65% of apertural width.

Protoconch—Low trochospiral, mutispirally coiled (Figs. 3. B–F; 4. A–C, D, E, H, I), approximately 2.1 whorls (Figs. 3. B, E; 4. D), 407.98 μm in width (range: 393.27–415.68 μm, $n = 3$) and 213.87 μm ($n = 1$) in height. Umbilicus obvious, narrow (Figs. 3. C; 4. H). Surface smooth, marked with blunt growth lines (Fig. 3. B, C, E, F); earlier whorl partly marked with minute honeycomb-like sculptures (Fig. 3. B). Growth lines in early portion of last whorl comprise deep sinuses in both apical and abapical sides like sinusigera, whereas sinuses obscured towards aperture, being straight
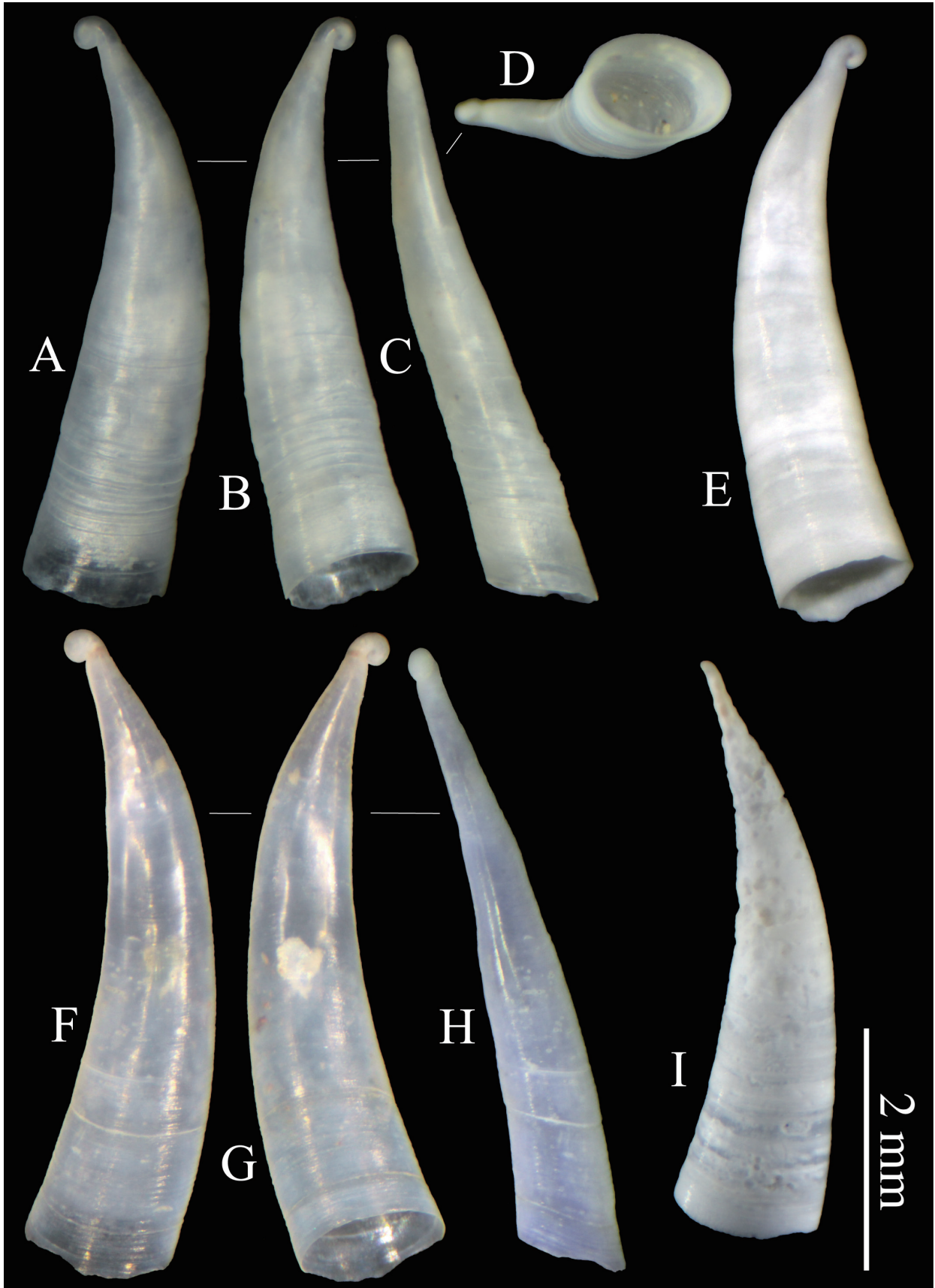
Figure 2. *Strebloceras kobayashii* n. sp. A–D. Holotype, TMNH-10101, dorsal, ventral, right lateral, apertural views, respectively. E. Paratype 1, MFM 110117, ventral view. F–H. Paratype 2, MFM 110118, dorsal, ventral, right lateral views, respectively. I. Paratype 3, MFM 110119, dorsal view.
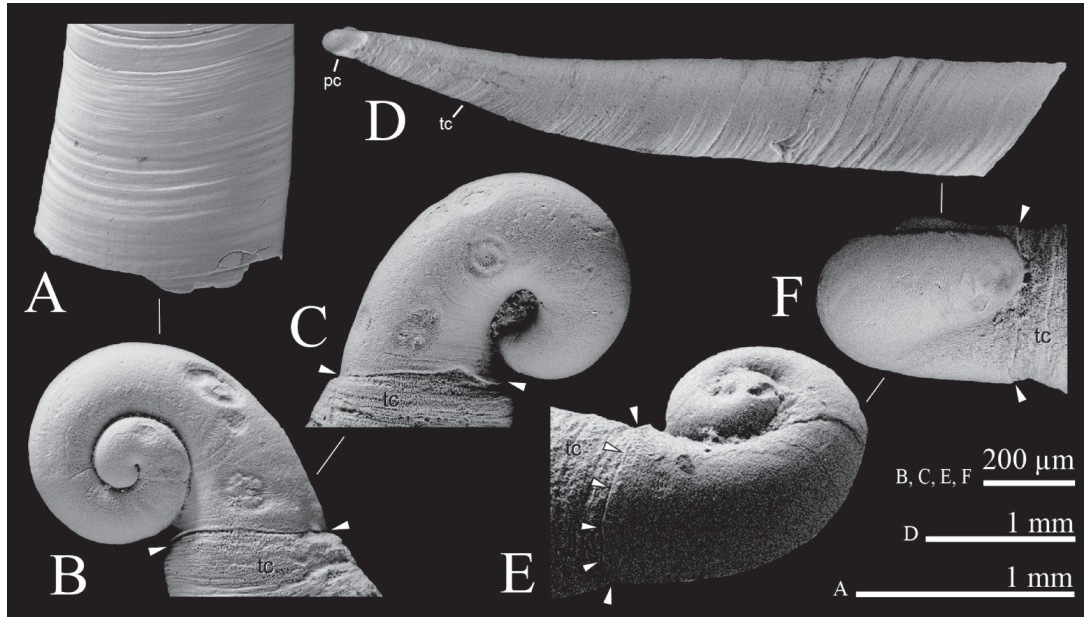
Figure 3. Scanning electron microscopy images of *Strebloceras kobayashii* n. sp. A–C. Paratype 1, MFM 110117, dorsal apertural surface, dorsal view of protoconch, ventral view of protoconch, respectively. D–F. Holotype, TMNH-10101, right lateral view of whole shell, dorso-lateral view of protoconch, right lateral view of protoconch, respectively. Arrowheads indicate boundary between protoconch and teleoconch. Abbreviations: pc, protoconch; tc, teleoconch.

lines (Fig. 3. B, C). Last whorl abruptly expands to form flared apertural lip, slightly projecting from earlier whorls (Figs. 3. B, C, E, F; 4. D, E). Boundary between protoconch and teleoconch clearly demarcated by incised line (Fig. 3. B, C, E, F: arrowheads; Fig. 4).

Types: Holotype (Figs. 2. A–D, 3. D–F), TMNH-10101, SL = 4.90 mm, SW = 1.25 mm, AH = 0.85 mm, an intact specimen preserved with a protoconch, 27 June 2014, leg. T. Haga; paratype 1 (Figs. 2. E; 3. A–C), MFM 110117, SL = 4.90 mm, SW = 1.20 mm, AH = 0.80 mm, an intact but whitish weathered specimen preserved with a protoconch; paratype 2 (Fig. 2. F–H), MFM 110118, SL = 5.25 mm, SW = 1.25 mm, AH = 0.75 mm; an intact specimen preserved with a protoconch; paratype 3 (Fig. 2. I), MFM 110119, SL = 4.80 mm, SW = 1.25 mm, AH = 0.80 mm, an intact but a protoconch and a posterior portion eroded with secondary lining formed; paratype 4 (Fig. 4. A–C), NMNS PM 28402, SL = 4.95 mm, SW = 1.25 mm, AH = 0.85 mm, an intact specimen preserved with a protoconch; paratype 5 (Fig. 4. D, E), TMNH-10758, SL = 1.75 mm, SW = 0.75 mm, AH = 0.47 mm, an intact young specimen preserved with a protoconch. All the types were collected from the type locality. Paratypes 1–3 were collected by the late S. Ugai from 1973 to 2005, and paratypes 4 and 5 by N. Kobayashi from 2017 to 2019.

Paratypes 1–3 are voucher specimens previously identified as *Creseis virgata* (Rang, 1828) in Kawase (2013: 50). Paratypes 1 and 3 are also the figured vouchers of *Parastrophia japonica* Hinoide and Habe, 1978 in Kawase et al. (2015: 55, 74; pl. 6, fig. G. 59, right and left, respectively). See *Remarks* below for the detail.

Other material examined: TMNH 10760, SL = 4.70 mm, SW = 1.35 mm, AH = 0.85 mm, a full-grown specimen whose protoconch is missing (Fig. 4. F, G); TMNH 10759, SL = 1.65 mm, SW = 0.75 mm, AH = 0.35 mm, a young slightly damaged specimen preserved with a protoconch (Fig. 4. H, I). Both specimens were collected from the type locality by N. Kobayashi from 2017 to 2019.

Type locality: A sea cliff at Hane, Takamatsu-chô, Tahara City, Aichi Prefecture, central Japan (34º37'17.4" N, 137º14'38.0" E: Fig. 1).

Occurrence: The *Tonna* Bed of the TMSM, Toyohashi Formation, Atsumi Group, at the type locality; middle Pleistocene, Chibanian.

Etymology: Named for Mr. Nobuaki Kobayashi of Gamagôri City, Aichi Prefecture, who has long been collecting fossils from the Atsumi Group and who has provided important research material to us, including specimens were used to describe the present new species.
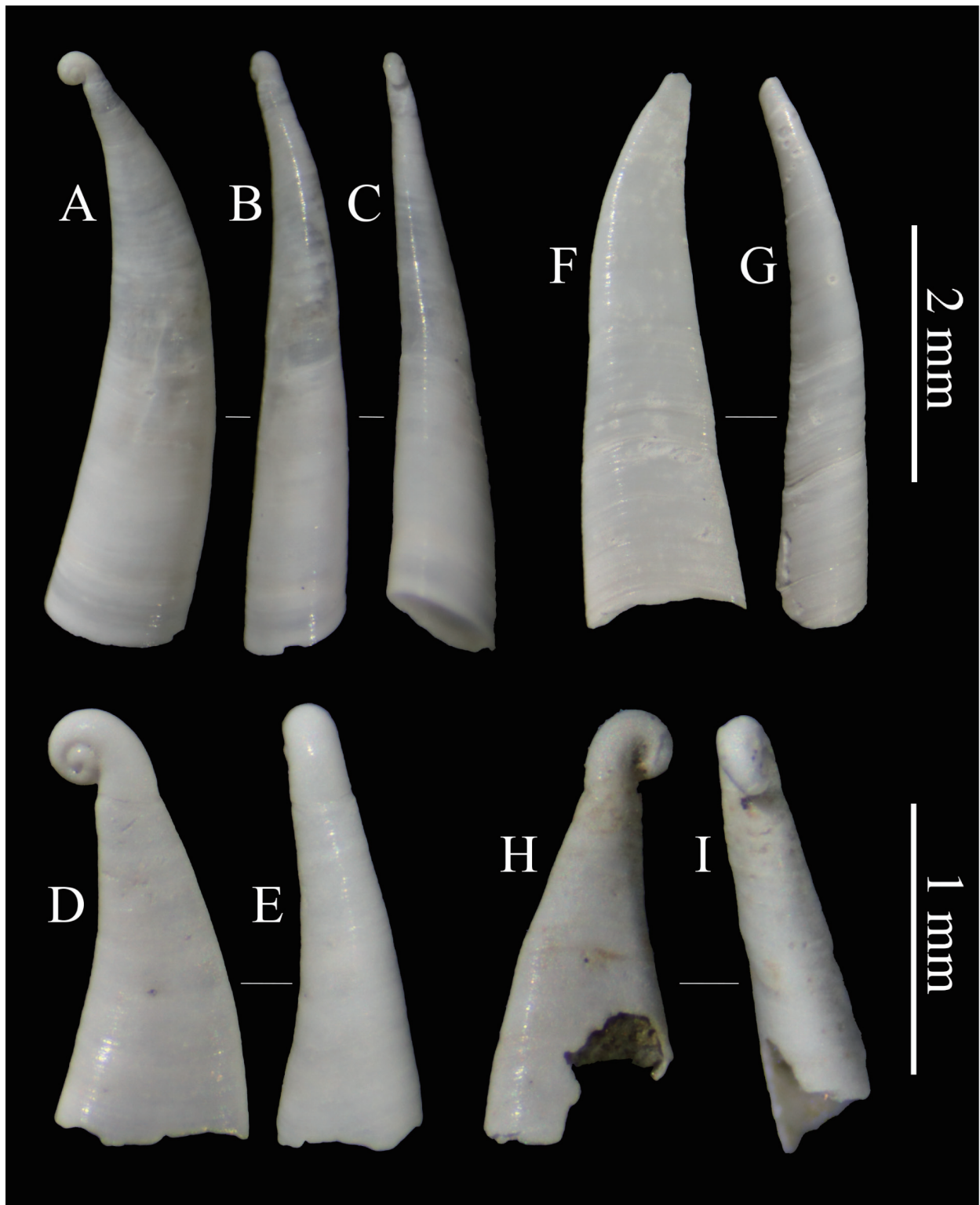
Figure 4. *Strebloceras kobayashii* n. sp. A–C. Paratype 4, NMNS PM 28402, dorsal, left lateral, right lateral views, respectively. D, E. Paratype 5, TMNH-10758, dorsal and left lateral views, respectively. F, G. TMNH-10760, ventral and left lateral views, respectively. H, I. TMNH-10759, ventral and right lateral views, respectively.

***Variations*:** Major variations are observed in the shell profile at the fully-grown stage. The teleoconch tends to bend dorsally or ventrally when grown. Of six full-grown specimens, three were bent dorsally (Figs. 2. C; 4. C, G), one ventrally (Fig. 2. H) and two were almost straight with an unbent anterior portion (Fig. 2. E, I). The expansion rate of the teleoconch towards the anterior also varies and two types are observed: some specimens have a regularly increase diameter (Figs. 2. F–H; 2I) whereas the expansion tapers off in some specimens (Figs. 2. A–C, E; 4. A–C, F, G).

***Remarks*:** The new species is the largest species of those previously known in the genus, and is clearly distinguishable from all other species, both fossil and extant, previously reported by a large shell that can be up to approximately 5 mm in length and a dorso-ventrally depressed teleoconch whose aperture is elliptical in shape. All congeners have smaller shells in size (approximately < 3 mm SL) and circular apertures (Table 1). The abruptly expanded early teleoconch is also diagnostic for the new species.

Irrespective of the presence of unique diagnostic characteristics of new species, correct identification is tricky due to the analogous morphologies with phylogenetically unrelated gastropod taxa of pteropods. The present new species had previously been identified as a holoplanktonic pteropod, *Creseis virgula* (Rang, 1828), of the family Creseidae Rampal, 1973 (Kawase, 2013: 50). The identification was based on a slightly incurved and unexpanded anterior portion of the teleoconch recall species in the genus *Creseis* Rang, 1828, particularly when the original trochospiral protoconch is eroded or missing, as seen in paratype 3 (Fig. 2. I) and in another specimen (Fig. 4. F, G). However, creseids characteristically have a barrel-like protoconch and a rather symmetrical, smooth teleoconch and aperture (e.g., van der Spoel, 1987; Gasca and Janssen, 2014). Thus, the combination of the trochospiral protoconch, asymmetrical aperture and teleoconch marked with ventrally inclined growth rings in the present new species are not referable to the creseids. Based on taxonomic scrutiny of previously collected specimens (Kawase, 2013), Kawase et al. (2015) subsequently identified and depicted the present new species as a ctiloceratine caecid *Parastrophia japonica* Hinoide and Habe, 1978 (Kawase et al., 2015: pl. 6, fig. G59, left and right). Members of the genus *Parastrophia* characteristically feature a protoconch that is permanently attached to a very loosely twisted teleoconch, and a coiled protoconch followed by an uncoiled tube-like stage in the last whorl (e.g., Habe, 1978a; Hinoide and Habe, 1978; Bandel, 1996; Pizzini et al., 2013). These diagnostic characters do not match with those of the present new species. Thus, the present new species is not a member of the genus *Parastrophia*.

The new species also resembles Neogene fossils of freshwater gastropods in gross morphology. The planorbiid genus *Orygoceras* Brusina, 1882 found in middle to late Miocene rocks of central Europe (e.g., Brusina, 1882; Harzhauser et al., 2002; Neubauer et al., 2011, 2013, 2016), and late Pliocene to early Pleistocene deposits in the northwestern United States (e.g., Dall, 1924; Yen, 1944; Taylor, 1966), is comparable with *S. kobayashii* n. sp. because of its relatively large shell size (up to 10 mm SL), rapid teleoconch expansion rate, and non-circular aperture. European *Orygoceras tropidophorum* Brusina, 1902 and North American *Orygoceras tricarinatum* Yen, 1944 in particular exhibit extreme similarity with *S. kobayashii* n. sp. in their depressed teleoconch with uneven growth rate, and their unusual curvature (Yen, 1944; Neubauer et al., 2016). However, members of *Orygoceras* share a paucispiral (approximately 1 whorl), planispirally coiled small protoconch whose surface is marked with spiral lirae (e.g., Harzhauser et al., 2002; Neubauer et al., 2011, 2013, 2016). The teleoconch of *Orygoceras* is more or less marked with spiral threads, often with macrosculptural development such as longitudinal carina and widely spaced concentric ribs (Dall, 1924; Yen, 1944; Hershler and Longley, 1986; Harzhauser et al., 2002; Neubauer et al., 2011, 2013, 2016). These features in *Orygoceras* safely rule out their attribution to the genus *Strebloceras*.

Discussion

Strebloceras kobayashii n. sp. as an extinct species in the Pleistocene Japanese waters

Most members of Pleistocene marine molluscs still survive today. Only a few have become extinct. A total of 470 marine molluscan species have been identified from the TMSM of the Toyohashi Formation, Atsumi Group (Kawase et al., 2015). Of these, 21 (14 in Gastropoda excluding the present new species, and seven in Bivalvia), representing approximately 4.5% of the total, are extinct fossil species (summed by T.H., based on Kawase et al., 2015). This level of extinction is consistent with the background extinction rates of Pleistocene

molluscan fauna of both sides of the temperate Pacific (e.g., Stanley and Campbell, 1981; Valentine and Jablonski, 1991; Kase et al., 2013).

Whether *S. kobayashii* n. sp. is an extinct fossil species or a yet undiscovered Recent species is an intriguing question. Although modern caecids are well catalogued in Japanese waters (Sasaki, 2008) mostly because of the contribution by enthusiastic amateur shell collectors (e.g., Kato, 1990, 2000; see also Habe, 1978a, b), *S. kobayashii* n. sp. has never appeared in the Recent records. In addition, irrespective of its extraordinary large shell size of up to approximately 5 mm in SL for the genus, *S. kobayashii* n. sp. has, to my knowledge, never been recovered from Pleistocene beds, except the Toyohashi Formation, or from Recent Japanese waters in a numbers of inventories. Thus, it is reasonable to assume that *S. kobayashii* n. sp. is an extinct fossil species in the Pleistocene.

Of the eight specimens of the present new species used in this study, three were collected by late S. Ugai. He sampled a total of 122 kg dry weight of sediments recovered from a collection site, the type locality of *S. kobayashii* n. sp., on the coast of Takamatsu-chô (Kawase, 2013; Kawase et al., 2015), from which these specimens were collected. Despite more than two years of careful and meticulous sorting of the sampled sediments at the type locality by N. Kobayashi, only four specimens were obtained. The low frequency of occurrence probably reflects the biological rarity of *S. kobayashii* n. sp. Pizzini et al. (2013) showed in his systematic synthesis of caecids from the South-West Pacific that many represent only by empty shells occurring in a few localities. Ponder and de Keyzer (1998) mentioned that nearly all Australian caecid species have never been collected alive. Bouchet et al. (2002) amassed an extensive inventory of 2,738 marine molluscs from a 295-km^2 site on the west coast of New Caledonia. The authors reported that rare species made up a considerable portion of the fauna, comprising 32% species collected at a single station and 20% represented by a singleton. Caecids are the major representatives of this faunal proportion (Pizzini *in* Bouchet et al., 2002: appendices 1 and 2). Among these, members of the Recent *Strebloceras* are the most remarkable example of such a biological rarity. Out of five species of Recent *Strebloceras*, *Strebloceras subannulatum* de Folin, 1880 is exceptional due to the presence of a relatively large number of available specimens especially from Easter Island (Raines and Pizzini, 2005) and from Tahiti (Vannozzi, 2016), but until now only three living individuals

(de Folin, 1880, 1886) have been recovered from reefs off Honolulu, Hawaii. Very few specimens represented only by empty shells are available for other Recent species (Lightfoot, 1992; Pizzini et al., 2013; Vannozzi, 2016; Vannozzi, 2017; Vannozzi, 2019b). There are also few specimens of fossil species (see references in Table 1). These have been recognized as rare, such as the Eocene species from France (Gougerot, 1975). The fossilization process may bias the total number of successfully preserved fossils due to the minuteness of the shell. However, *Caecum* spp. congeners were unearthed together with a *Strebloceras* fossil in the Eocene of France (Gougerot, 1975). The same can be said for the collection site of this study, where many *Caecum* species co-occurred with *S. kobayashii* n. sp. (Kawase et al., 2015; T.H., personal observation). Considering these facts and in the context of the probable biological rarity of both modern and fossil *Strebloceras* species as discussed above, it is reasonable to interpret that *S. kobayashii* n. sp. was a rare species with a small population size.

Strebloceras kobayashii n. sp. as a thermophile element

All four members of Recent *Strebloceras* exclusively occur in tropical waters in the Pacific: *S. subannulatum* in both the central Indo-Pacific and the eastern Indo-Pacific, *S. hinemoa* and *S. pizzinii* Vannozzi, 2016 in the central Indo-Pacific; and *S. oliverioi* Vannozzi, 2019 in the Red Sea of western Indo-Pacific (Table 1). Three fossil *Strebloceras* species—*S. bezanconi* (Cossmann, 1888), *S. cornuoides* Carpenter, 1859 and *S. edwardsi* (Deshayes, 1861)—thrived in the middle Eocene–earliest early Miocene of the European Tethys realm (Table 1). They are also interpreted to be a thermophile element, as the European Tethys at that time likely had a tropical to warm-temperate climate (e.g., Lozouet, 2014; Harzhauser et al., 2016). Two other fossil members from New Zealand, an unidentified species from the early Eocene and *S. hinemoa* from the Miocene (Table 1), co-occurred with molluscs indicative of tropical and/or warm-temperate waters (Beu and Maxwell, 1990). Considering the occurrence of *Strebloceras* from a tropical or warm waters setting, it is reasonable to assume that *S. kobayashii* n. sp. is also a thermophile element. This interpretation is strengthened by previous descriptions that the TMSM comprises warm-water fauna that thrived under the strong influence of the Kuroshio Current during the middle Pleistocene interglacial periods (Hayasaka, 1962;
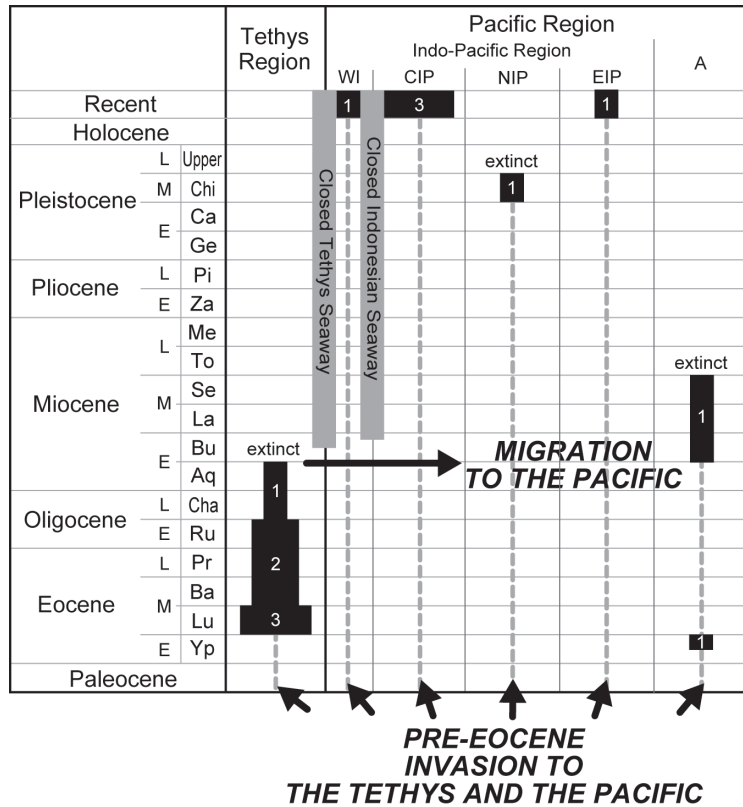
Figure 5. The geochronologic occurrence of *Strebloceras* produced from a data given in Table 1. Numbers in black box denote the number of species recorded. Arrows indicate probable events of migration. Broken lines trace hypothetical occurrence of undiscovered fossils in the regions. The highest species diversity of the genus is observed in the Recent Indo-Pacific region, whereas Paleogene paleodiversity is high in the Tethys region. Although this pattern of geochronological occurrence recalls eastward migration from the Tethys to the Pacific by the Miocene, another equivocal hypothesis is that Pacific members have long survived from the early Eocene to the Recent. The origin of Pacific *Strebloceras* may be explained by overlap of the Tethyan and Pacific stocks.

Shibata and Ujihara, 1983; Shibata et al., 2006; Karasawa et al., 2014; Kawase et al., 2015; Haga and Hasegawa, 2017).

Monophyly of *Strebloceras* revisited

The monophyly of the genus *Strebloceras* has been questioned because there are gaps in morphology and in geochronological and geographical occurrence between Recent and fossil taxa. Pizzini et al. (2013) and Vannozzi (2019b) have suggested that Recent species are phylogenetically unrelated to fossil species, and their similar shell shape is the result of convergence. This is because Recent species more or less have sinusigera in the last whorl of the protoconch, whereas fossil species have a simple protoconch without sinusigera. The geographically distant occurrence of fossil species, and a geochronological gap in occurrence after the middle Miocene may also support this hypothesis. Although compelling evidence is needed to assess the monophyly of *Strebloceras*, at this time, I favor the view that *Strebloceras* has a single lineage throughout the Cenozoic, as they share a rather conservative protoconch morphology (except for the presence/absence of sinusigera) that features a low trochospiral shape with approximately 2 whorls. Modern *S. subannulatum* have a deep sinusigera notch rimmed with prominent crenation (Raines and Pizzini, 2005; Pizzini et al., 2013; Vannozzi, 2016), but the remaining three Recent species (*S. hinemoa*, *S. pizzinii*, and *S. oliverioi*) possess sinusigera without clear crenation that gradually become shallower towards their aperture (Pizzini et al., 2013; Vannozzi, 2016; Vannozzi, 2017; Vannozzi, 2019b). Based on the protoconch morphology of *S. kobayashii* n. sp., having the sinusigera-like deep sinuses that become shallower and feebler towards the aperture in the last protoconch whorl, it is likely that *S. kobayashii* n. sp. represents an evolutionary intermediate form between fossil members and extant ones. The geographic and geochronologic occurrences of *S. kobayashii* n. sp. from the middle Pleistocene of the Pacific region, filling in these gaps, may support a view of the monophyletic origin of *Strebloceras*. On the other hand, the familial/generic assignment of *S. bezanconi* is questionable as it has a small paucispiral protoconch with an average of 1 whorl (Vannozzi, 2016; Vannozzi, 2019b), displaying similarity for example with the phylogenetically unrelated, freshwater-dwelling planorbiid *Orygoceras* or even the phreatic hydrobiid *Phreatoceras* Hershler and Longley, 1987. Morphological scrutiny of the protoconch of *S. bezanconi* thus enables us to unveil its identity.

Tethyan origin of Pacific *Strebloceras*?

The tropical Indo-West Pacific (IWP) harbors the Earth's greatest biodiversity of marine organisms. This marine biodiversity hotspot likely originated from the Tethys via the Tethys Seaway during the Miocene or a much earlier period on the basis of fossil records (e.g., Wallace and Rosen, 2006; Harzhauser et al., 2007; Yamaguchi et al., 2012) and molecular phylogenetic evidence (e.g., Meyer, 2003; Williams and Reid, 2004; Frey and Vermeij, 2008; Malaquias and Reid, 2009; Ozawa et al., 2009; Liu et al., 2018) of various invertebrate groups. The center of global marine biodiversity was observed in the Tethys realm from the Cretaceous to Eocene, but shifted to the Arabian Peninsula and western Indian Ocean during the late Eocene–Oligocene, and finally into Indonesia as far east as in the Fiji Islands in the IWP by the early Miocene (e.g., Briggs, 1999; Renema et al., 2008; Leprieur et al, 2016). Active tectonic events in the IWP region accelerated speciation and isolation, and resulted in the establishment of the highest concentration of species by the late Miocene in the IWP (Leprieur et al, 2016).

Assuming the genus *Strebloceras* is monophyletic, the pattern of geochronologic occurrence of *Strebloceras* (Fig. 5) is apparently best explained by the ˮTethys originˮ hypothesis because of the transition in the diversity from the Tethys to the Pacific region during the early Miocene (Aquitanian–Burdigarian). In the Tethys realm, three species (*S. bezanconi*, *S. cornuoides* and *S. edwardsi*) have been recorded from the early middle Eocene. Subsequently, the diversity gradually decreased, with two species (*S. bezanconi* and *S. cornuoides* in the Bartonian, and *S. cornuoides* and *S. edwardsi* in the Priabonian–Rupelian) in the late middle Eocene (Bartonian)–early Oligocene (Rupelian) and finally just *S. edwardsi* surviving in the late Oligocene–earliest early Miocene (Aquitanian). The fossil record demonstrates that *Strebloceras* in the Tethys realm had disappeared by the beginning of the late early Miocene (Burdigalian). The timing of disappearance of Tethyan *Strebloceras* is coeval with the loss of tropic biota in the Tethys realm, which was most likely caused by a climate shift to a colder temperature in the late Oligocene (e.g., Briggs, 1999; Zachos et al., 2001). During much of the same time, *S. hinemoa* appeared in the fossil record of late early (Burdigarian) to late middle Miocene (Serravallian) of New Zealand, representing the first fossil record of *Strebloceras* in the Neogene of the Pacific.

However, considering the oldest fossil of *Strebloceras*, *Strebloceras* sp. (ˮ*Strebloceras* n. sp.ˮ in Beu and Maxwell, 1990 and Beu and Raine, 2009) recorded from the Kauru Formation in South Canterbury, South Islands, New Zealand, representing the oldest fossil of the genus, this ˮTethys originˮ must be revisited. The geologic age of the *Strebloceras*-yielding lower horizon of Kauru Formation was given as early Eocene (Ypresian). However, it may be much older, possibly going back to the late Paleocene (Beu and Maxwell, 1990). During much of the same time, the oldest fossil of the Caecinae of the family Caecidae, *Caecum benhami* Goedert and Raines, 2016 and another unidentified *Caecum*, were recorded from the middle early Eocene (Ypresian) of the Crescent Formation in Washington States of the United States (Goedert and Raines, 2016). Goedert and Raines (2016), suggesting that the Caecidae had already diversified into two subfamilies, Caecinae and Strebloceratinae, and inhabited both the northeastern Pacific and southern Pacific by the early Eocene. These early Eocene caecids fossils having slight conchological difference with living species provide evidence that the Caecinae and Strebloceratinae were already present in Paleocene time, as estimated by Bandel (1996). Divergence of the common ancestor of the Caecidae and its sister group are suggested to have occurred as far back as the Late Cretaceous (Ponder, 1988; Bandel, 1996; Ponder and de Keyzer, 1998). Ponder (1988) inferred that they presumably migrated to the west coast of the Americas from the Tethyan realm by at least the Late Cretaceous. Considering the oldest fossil records of caecids and the previous assumptions concerning the time of divergence of caecids, I suggest that it is likely that *Strebloceras* was already widely distributed in Eocene tropical and subtropical waters of the Pacific, as well as the Tethyan realm, although no fossils have yet been discovered from the Paleocene–early Eocene Tethys realm.

The origin of *Strebloceras* in the Neogene Pacific region is controversial due to incomplete fossil records. However, I suggest that probable origins of the Pacific *Strebloceras* may be explained by the overlap of the Tethyan and original Pacific lineages. As presented above, the eastward migration from the Tethys into the Indo-Pacific via the Tethyan Seaway by the end of late early Miocene is very likely. As New Zealand has received a large number of thermophile genera from warmer areas (Kohn, 1990), presumably under Tethyan or even Indo-Pacific influence (Fleming, 1967; Beu and Maxwell, 1990) during the late Oligocene–early Miocene, the occurrence of *S. hinemoa* in Miocene rocks of New Zealand appears to

exemplify the eastward migration of *Strebloceras* into the Indo-Pacific region. However, *S. hinemoa* became extinct in New Zealand waters by the late middle Miocene, probably due to a cooling event that gradually eliminated warm-water taxa (Beu and Maxwell, 1990). On the other hand, I favor the view that the Pacific lineage has survived somewhere in the tropical to warm-temperate Pacific waters from the late Paleocene to the present. The sparse fossil record of *Strebloceras* in the Pacific, except for New Zealand and Japan, is likely due to the extreme rarity and small shell size that hinders successful preservation and collection. In the Pacific region, well-preserved warm-water shallow marine molluscan fossils of Paleogene times are very rare (Ogasawara, 2002 for Japan; Kase and Aguilar, 2014 for Indonesia and Philippines). Furthermore, even in highly fossiliferous Neogene beds, micromolluscan fauna are still largely masked because few studies have assessed such fossils. In the case of New Zealand *Strebloceras*, I assume that they persisted, but have not yet been discovered, from the middle Eocene to early Miocene, since New Zealand was likely a tropical to warm-temperate marine setting during that period (e.g., Beu and Maxwell, 1990). However, I suggest that migration from New Zealand into other Pacific regions by Miocene times is unlikely because, as far as I know, no such examples exist.

The discovery of *S. kobayashii* n. sp. from the middle Pleistocene Toyohashi Formation in central Japan is remarkable, as this finding clearly demonstrates that the genus *Strebloceras* had once occurred in Japanese waters. The timing of invasion into Japan is unclear, but I assume *Strebloceras* had arrived after the early Miocene and before the Pleistocene. After the remarkable faunal transition from warm-water to temperate or cool-water molluscs in the late Eocene to the early Oligocene, warm-water molluscs have repeatedly flourished in Japanese Neogene sediments corresponding with global Neogene climatic optima. Warm-water molluscan faunas are prominent in the early Miocene (the subtropical Akeyo-Kunugidaira Fauna), late early Miocene–early middle Miocene (the tropical to subtropical Yatsuo-Kadonosawa Fauna), middle to late Miocene (the tropical to warm-temperate Kukinaga Fauna, the warm-temperate Old Shiobara-Yama Fauna, the subtropical to warm-temperate Fujina Fauna), late Miocene to early Pliocene (the tropical to warm-temperate Zushi Fauna), late Pliocene to early Pleistocene (subtropical to warm-temperate Kakegawa Fauna), despite the fact that the Neogene is an era of cooling from its early to late stages, and that the overall faunal composition of molluscs have been accordingly changed from warmer to cooler waters (e.g., Chinzei, 1986; Ozawa et al., 1995; Ogasawara, 2002; Ogasawara et al., 2008). Ogasawara et al. (2008) inferred that the closure of the Indonesian Seaway during the late early to early late Miocene influenced the equatorial current system in the Pacific, which may have resulted in the formation of the Paleo-Kuroshio Current reaching the coast of Japanese archipelago, and allowed tropical/subtropical molluscs indicative of the Yatsuo-Kadonosawa Fauna to invade Japanese archipelago. Considering the thermophile nature of *Strebloceras*, it is reasonable to assume that they had reached Japanese waters somewhere in correspondence with the Neogene influx of warm-water taxa into Japan, that they disappeared in the middle Pleistocene. Although Neogene marine sediments rich in molluscs are common in Japan and numerous faunistic studies have been carried out, micromollusks have been very little studied even if successfully collected. Thus, I suggest that scrutiny of Neogene micromollusks may discover further *Strebloceras* fossils in the IWP.

Acknowledgements

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（要　旨）

芳賀拓真：中部更新統渥美層群豊橋層産ミジンギリギリツツガイ科（軟体動物門：腹足綱）の1新種

　愛知県田原市の太平洋岸に分布する中部更新統渥美層群豊橋層高松泥質砂部層から得られたミジンギリギリツツガイ科の *Strebloceras* 属　ミジンネジレヅノ属（新称）の1新種を，*Strebloceras kobayashii* n. sp. として新種記載した．本新種は中期更新世間氷期の温暖環境下に棲息した絶滅種であると考えられる．これは，現生，化石ともに本属の日本における初めての記録であり，後期中新世以降の化石記録の空白を埋める記録でもある．ミジンネジレヅノ属はこれまで8種が知られ，化石記録はニュージーランドの下部始新統に遡る．以降，テチス海域の中部始新統〜下部中新統に3種が，ニュージーランドの下部〜中部中新統に1種が，そしてインド - 太平洋域に4種の現生種が知られてきたが，後期中新世以降は化石記録が皆無であった．ミジンネジレヅノ属の時空分布は，多くの海生無脊椎動物において一般的に信じられているように，テチス海からインド - 太平洋域へと祖先種が移住したことを示唆する．しかし最古の化石記録ならびに新第三紀の化石記録は，本属が太平洋域に古くから分布していたことを示している．よって，現生種の起源は，もともと太平洋域にあった系統とテチス海域のものが重複したことに求められると考えられよう．

Strebloceras kobayashii n. sp.
　コバヤシミジンネジレヅノ（新種・新称）
　殻はやや薄質半透明，角状で太く，胎殻を含めて殻長約5 mm に達する．殻表はほぼ平滑で，不規則な成長脈のみ刻まれる．後成殻は背腹に潰れ，巻き方向に僅かに捻れ，中央部付近で腹側もしくは背側に曲がる．殻口は左右に長い楕円形．胎殻は殻長408 μm ほどの低い螺旋形で，およそ2.1 巻，後成殻との境界は明確に刻まれる．大きな殻サイズと背腹に潰れた後成殻の特徴により，他の既知種の全てから容易に区別される．殻長4.90 mm，殻幅（殻口幅）1.25 mm（ホロタイプ）.

タイプ産地：愛知県田原市高松町羽根の海食崖 (34º37'17.4" N, 137º14'38.0" E).

分布：タイプ産地の中部更新統豊橋層高松泥質砂部層の *Tonna* Bed からのみ知られる.

種小名は，豊橋層はじめ中部地方の化石を精力的に収集され，本新種の発見にも甚だ貢献された小林伸明氏（愛知県蒲郡市）に因む.

なお，ミジンネジレヅノ属のタイプ種 *Strebloceras cornuoides* Carpenter, 1859（ヨーロッパ西部の中部始新統〜下部漸新統の化石種）にはミジンネジレヅノの新称を与える.