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Authors: Isaji, Shinji, Haga, Takuma, and Kashiwagi, Kenji

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Early Cretaceous small-sized gastropods from the shallow marine deposits of the Kimigahama Formation, Choshi Group, Japan

SHINJI ISAJI[1], TAKUMA HAGA[2] AND KENJI KASHIWAGI[3]

[1]*Natural History Museum and Institute, Chiba, 955-2 Aoba-cho, Chuo-ku, Chiba, Chiba 260-8682, Japan*
[2]*National Museum of Nature and Science, Tokyo, 4-1-1, Amakubo, Tsukuba, Ibaraki 305-0005, Japan*
[3]*Graduate School of Science and Engineering for Research, University of Toyama, 3190 Gofuku, Toyama, Toyama 930-8555, Japan*
(e-mail: isaji@chiba-muse.or.jp)

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Abstract. Twelve species of small gastropods are extracted using the sodium tetraphenylborate method from the strongly lithified shallow marine deposits of the Barremian (Lower Cretaceous) Kimigahama Formation of the Choshi Group, central Japan. They belong to the following families and subfamilies; Eudaroniidae, Pseudomelaniidae, Ampezzopleurinae, Metacerithiidae, Procerithiidae, Nystiellidae, Metaxiinae, Stuoraxidae and Ebalinae, including six new species and one new genus. *Pseudomelania yamadai* sp. nov., *Ampezzopleura barremica* sp. nov., *Choshipleura striata* gen. et sp. nov., *Metacerithium boshuae* sp. nov., *Antiphora aurora* sp. nov. and *Stuoraxis kasei* sp. nov. are described as new species. *Pseudomelania yamadai*, *Metacerithium boshuae* and *Cirsocerithium subspinosum* are closely related to or identical with the species from the Lower Cretaceous in western Europe. *Ampezzopleura barremica* and *Choshipleura striata* are the first Cretaceous records of the subfamily Ampezzopleurinae that has hitherto been limited to the Triassic deposits. *Antiphora aurora* is the first record of the family Triphoridae from Mesozoic deposits, suggesting that the sinistral triphorids originated from the dextral ancestor. *Stuoraxis kasei* is the youngest occurrence of the heterostrophan family Stuoraxidae that has hitherto been reported from the Permian to Middle Jurassic deposits. The sodium tetraphenylborate method for finding the small molluscs from the strongly lithified deposits is an effective tool with which to reveal the true diversity of the fossil molluscan fauna.

Keywords: Cretaceous, Japan, shallow marine, small gastropod, sodium tetraphenylborate

Introduction

Investigation of small molluscs, including larval shells, is required to reveal the true diversity of local molluscan fauna. Such materials are expected to provide clues related to taxonomy and evolutionary history not only in malacology but also in paleontology. The use of such materials in the latter field usually depends on the ease of extraction of well-preserved small fossils from rocks, especially those in Paleozoic and Mesozoic deposits. Concerning gastropod fossils, previous studies employing microscopic observations using scanning electron microscopy (SEM) were performed mainly in well-preserved fossil assemblages found in Europe, North America, China and Australia. A large number of contributions have resulted in marked progress in taxonomy, evolutionary history and paleobiogeography (e.g. Yoo, 1988, 1994; Bandel, 1991, 1993, 1994, 1995, 2006; Dzik, 1994; Pan, 1997; Frýda, 1998; Nützel, 1998, 2014; Kiel, 2001; Nützel and Mapes, 2001; Bandel *et al*., 2002; Pan and Erwin, 2002; Kaim, 2004; Gründel and Kaim, 2006). In most of these studies, the deposits are loosely lithified, except for the altered carbonate rocks; thus, small fossils could be easily extracted with excellent preservation.

In Japan, it is generally not easy to extract small molluscan fossils from Paleozoic and Mesozoic clastic rocks since the deposits tend to be strongly lithified due to solid cementation by diagenetic processes. Therefore, previous researchers have focused on large-sized molluscan fossils more than centimeter-scale (see Hayami and Kase, 1977); thus, minute molluscan fossils have often been overlooked. Some examples are known to occur in Paleozoic shallow marine limestones and Mesozoic cold-seep limestones as silicified or chloritic replacements (Kaim *et al*., 2008; Isaji and Okura, 2014, 2020). In contrast, microshells preserved with calcium carbonate do not commonly

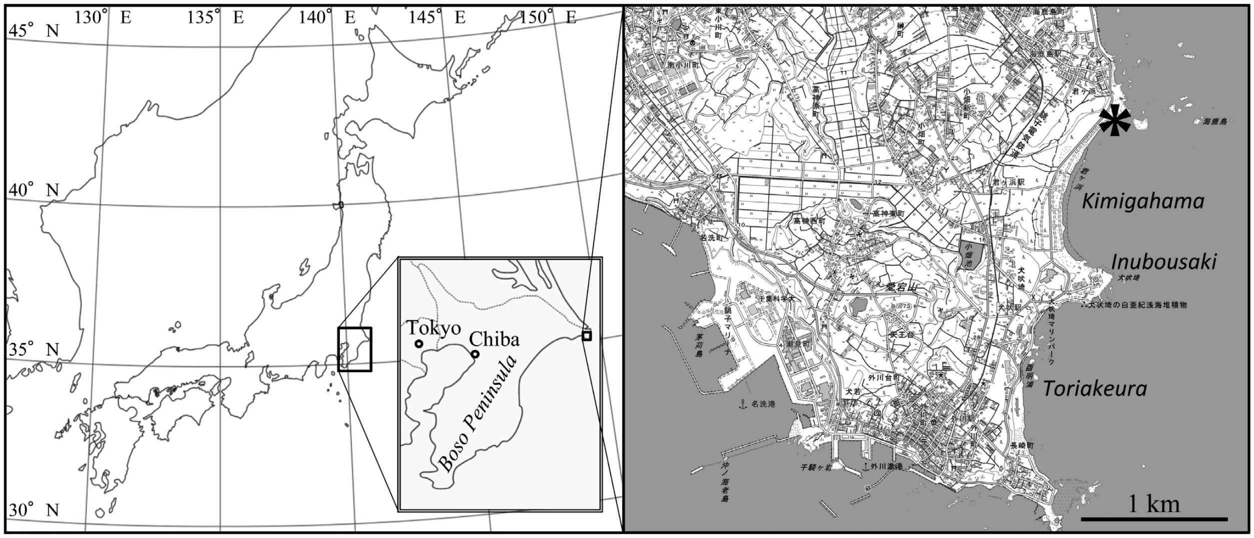

Figure 1. Map showing the fossil locality (asterisk; 35°43.04' N, 140°52.11' E) on 1:25,000 scale topographic map of the Geospatial Information Authority of Japan (GSI).

occur in sandy or muddy clastic rocks, and few related studies have been carried out. (e.g. Nakazawa, 2007; Isaji, 2010; Nützel and Nakazawa, 2012). Some were discovered during the extraction of microfossils such as radiolarians (e.g. Kashiwagi *et al*., 2007; Kashiwagi and Hirasawa, 2010).

The Choshi Group in Japan includes Early Cretaceous shallow marine deposits that contain well-preserved molluscan fossils. The normally large-sized molluscan species more than 10 mm diameter from the Choshi Group were studied by previous researchers, revealing at least 36 species of bivalves (Shikama and Suzuki, 1972; Hayami and Oji, 1980), 12 species of gastropods (Kase and Maeda, 1980), and 35 species of ammonoids (Obata and Matsukawa, 2009). Kase (1984) pointed out that the small number of gastropods may be due to the difficulty of collecting well-preserved materials in non-calcareous clastic rocks showing complex geologic structures. On the other hand, several benthic foraminifer tests were discovered from the weakly-weathered mollusc-bearing clastic rocks; thus, the ability to collect the materials seemed to depend on the degree of weathering of the rocks (Obata *et al*., 1982). According to these previous studies, small-sized species are potentially preserved within these fossiliferous rocks.

We aimed to extract small molluscan fossils less than 10 mm diameter from the shell-bearing sandstones and mudstones of the Barremian (Lower Cretaceous) Kimigahama Formation of the Choshi Group, using the sodium tetraphenylborate method to decompose the rock-fabrics into grains and minerals, resulting in the discovery of numerous gastropod fossils. This paper describes newly found small gastropods, including six new species and one new genus. Discussions of the taxonomy of each species and faunal comparisons with other areas are also provided.

Geological setting

The Choshi Group outcrops in the coastal area at the eastern end of the Choshi Peninsula, which is located in the northeastern part of the Chiba Prefecture, Japan (Figure 1). The Choshi Group is subdivided into five lithostratigraphic units, i.e., the Ashikajima, Kimigahama, Inubouzaki, Toriakeura and Nagasakihana formations, in ascending order (Obata *et al*., 1975; stratigraphy reinterpreted by Obata *et al*., 1982). The formations are assumed to have formed in a storm-dominated shallow marine environment (Katsura *et al*., 1984). Of the formations, the Kimigahama Formation is characterized by inner shelf sediments (Katsura *et al*., 1984; Ishigaki and Ito, 2000) and is assigned to the Barremian in age based on the occurrence of 14 species of ammonoids and 12 species of benthic foraminifera (Obata *et al*., 1982; Obata and Matsukawa, 2009). Recently, palynofloras from the Ashikajima and Kimigahama formations were revealed (Legrand *et al*., 2011).

At the locality examined in this study, the alternating beds of hummocky, cross-stratified, fine-grained sandstone and dark gray mudstone were exposed. An abundant mollusc-bearing lenticular sandstone bed is also intercalated within the alternations (Figures 1, 2A). The stratigraphic position of this locality is approximately 50 m above the base of the Kimigahama Formation

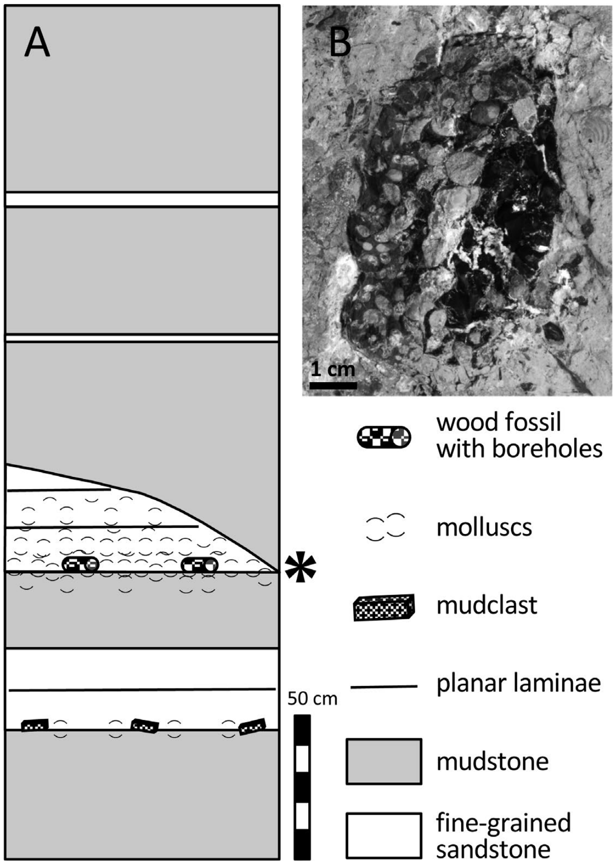

Figure 2. Detail of the lithofacies of the Kimigahama Formation at the studied locality. **A**, columnar section with mollusc-bearing horizons, asterisk indicating the horizon of gastropod fossils. **B**, a wood fossil with numerous boreholes produced by pholadoidean bivalves in the same horizon indicated by asterisk in 2A.

(Obata *et al*., 1982). Presence of the mollusc-rich horizon shows that this locality appears to be identical to the locality examined in previous studies, such as Loc. 09 in Shikama and Suzuki (1972), Loc. 7316 in Obata *et al.* (1975) and Loc. 2 in Kase and Maeda (1980). In these studies, nine gastropods and 14 bivalves were found at this locality (Hayami and Oji, 1980; Kase and Maeda, 1980; Kase, 1984). Compared with other Mesozoic mollusc assemblages in Japan, the bivalve assemblage of the Kimigahama Formation has several elements in common with the Ishido Formation of the Sanchu Group in central Honshu and the lower Monobegawa Group in middle Kyushu (Hayami and Oji, 1980). In contrast, the gastropod assemblage is quite different from other Early Cretaceous gastropod assemblages, such as those of the Ishido Formation in central Honshu and the Miyako Group in northern Honshu, except for the co-occurrence of related taxa at the generic level, such as *Perissoptera* from the Ishido Formation and *Ataphrus* from the Miyako Group (Kase and Maeda, 1980; Kase, 1984). On the other hand, the gastropod composition of the Kimigahama Formation is similar to that of the Tethyan region. For example, *Vanikoropsis decussata* (Deshayes *in* Leymerie, 1842), *Hayamia rex* Kase, 1980 (in Kase and Maeda, 1980), *Ceratosiphon densestriatus* Kase, 1980 (in Kase and Maeda, 1980) and *Perissoptera elegans* Kase, 1980 (in Kase and Maeda, 1980) are identical or closely related to species from the Lower Cretaceous in western Europe (Kase and Maeda, 1980; Kase, 1984).

Materials and methods

All the examined specimens were obtained from a cuboidal, fine-grained sandstone boulder (40 × 36 × 49 cm), which was collected by Katsuhiko Yamada on May 5, 1998, in the northern part of Kimigahama coast, Choshi City (35°43.04' N, 140°52.11' E, Figure 1). A lenticular mollusc-rich sandstone bed, which is very similar to the examined rock, is currently intercalated in the outcrop of the locality (Figure 2A). Therefore, it is safe to assume that the examined rock was not transported from another place but was found *in situ* in the outcrop. The molluscan fossils are well-preserved and aggregated in a fine-grained layer in the middle to basal part of the sandstone (Figure 2A). Infaunal bivalves are the most dominant elements, including *Nuculopsis* (*Palaeonucula*) *ishidoensis* (Yabe and Nagao, 1926), *Portlandia sanchuensis* (Yabe and Nagao, 1926) and *Grammatodon* (*Nanonavis*) *yokoyamai* Yabe and Nagao, 1926 which are usually articulated, whereas rocky bottom bivalves are absent. Wood-boring pholadoidean bivalves occurr *in situ* in the boreholes of a wood fossil (Figure 2B). These pholadoidean bivalves are assigned to the Mesozoic genus *Turnus*; details will be given in a separate paper in the near future. Gastropods are common and are characterized by the abundant number of juvenile to adult specimens of *Cirsocerithium subspinosum* (Deshayes *in* Leymerie, 1842), *P. elegans*, *Calliostoma*? *ojii* Kase, 1980 (in Kase and Maeda, 1980) and *Ataphrus* (*Ataphrus*) *nipponicus* Kase, 1980 (in Kase and Maeda, 1980). Dentaliids are also common. Ammonoids are rare. The molluscan assemblage is associated with a wide variety of bioclastic fragments or individuals, such as echinoids, asteroids, ophiuroids, annelids, foraminiferans, radiolarians, ostracods, decapods, fish otoliths and shark teeth. The Barremian age is suggested by the three co-occurring ammonoid species, *Karsteniceras obatai* Matsukawa, 1987, *Crioceratites* (*Crioceratites*) *emerici* Léveillé, 1837 and *Calliphylloceras tsudai* Obata and Matsukawa, 2007, and a benthic foraminiferan *Lenticulina heiermanni* Bettenstaedt, 1952 (Obata *et al*., 1982; Obata and Matsukawa, 2007).

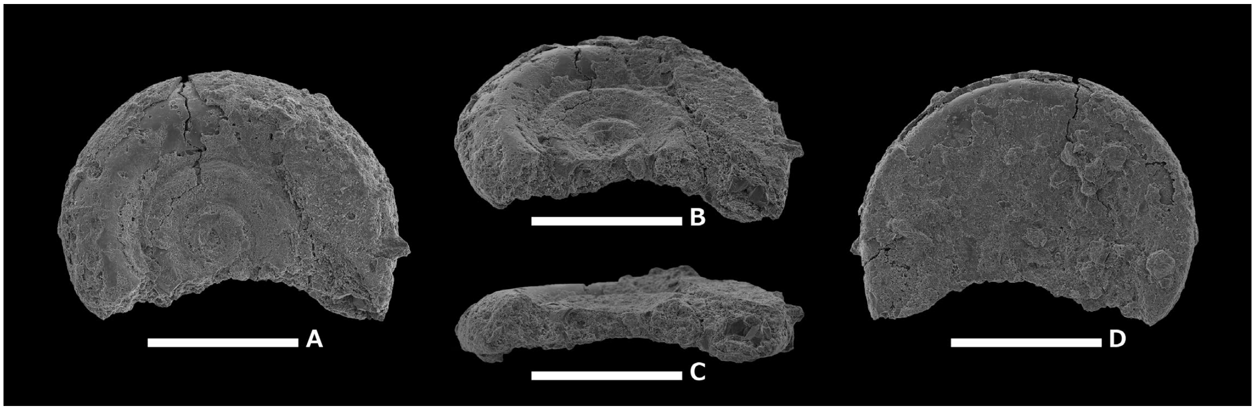

Figure 3. Eudaroniid gastropod from the Barremian Kimigahama Formation, Choshi Group, Japan. **A–D**, CBM-PS 6441; A, apical view; B, oblique view of apical side; C, lateral view; D, umbilical view. All scale bars = 0.5 mm.

The gastropod fossils examined here were extracted in the following manner according to the technique by Hanken (1979), Yasuda *et al*. (1985) and Noda and Jin (2004). Well-weathered parts (approximately 1500–2000 cm^3) were taken from the examined boulder surface. The deposits were cut into small pieces, immersed in sodium tetraphenylboron (0.2 N NaTPB-1 N NaCl) and kept at low temperature in a refrigerator for several days. After decomposing the deposits, the residues were washed and sorted using sieves (ø 40, 100, 500 and 1000 µm). The sorted residues were dried and selected under a binocular microscope. Over 1000 small gastropod fossils less than *ca.* 10 mm diameter were collected. Images were obtained using a Hitachi S-800 scanning electron microscope at the Natural History Museum and Institute, Chiba. The specimens were numbered with the prefix CBM-PS and stored at the Natural History Museum and Institute, Chiba.

Abbreviations for shell dimensions.—*D*, diameter; *H*, height; *W*, width.

Systematic description

(By S. Isaji except the genus *Stuoraxis*)

Systematic descriptions basically follow the classification by Bouchet *et al*. (2017). The type locality and horizon of new species are all from northern part of Kimigahama coast, Choshi City, Chiba Prefecture, central Japan; Kimigahama Formation of Choshi Group, Lower Cretaceous (Barremian: Obata *et al*., 1982). All taxa are listed in Table 1, which includes the previously described species by Kase and Maeda (1980).

Class Gastropoda Cuvier, 1795
Subclass Vetigastropoda Salvini-Plawen, 1980

Superfamily Seguenzioidea Verril, 1884
Family Eudaroniidae Gründel, 2004
Gen. et sp. indet.

Figures 3A–D

Material.—Single specimen; CBM-PS 6441.

Description.—The shell is small and discoidal in shape. The spire side is slightly concave and the umbilical side is broadly concave and planar. The protoconch is not observable. The teleoconch whorl increases gently in diameter and is convex with impressed sutures on the spire side. The whorl of the umbilical side seems to be flattened with flush sutures. The whorl has a shoulder and marked peripheral angulation, and the spaces between them are flat. The surface of the teleoconch is not covered by marked sculptures. The aperture is unknown.

Dimensions (in mm).—CBM-PS 6441: *D* = 1.13. *H* = 0.20+.

Remarks.—The spire side of the present specimen is similar to that of *Eudaronia pusilla* (Gründel, 2000) from Middle Jurassic deposits of Podlasie and Częstochowa region, Poland (Kaim, 2004, figs. 2B, C), but the present specimen differs in having a flattened outline and a planar umbilical side. Such a concave planar shell is not observed in the extant *Eudaronia* and closely related *Adeuomphalus* (e.g. Kaim, 2004; Kano *et al.*, 2009). Therefore, this specimen is tentatively assigned as an indeterminant species of family Eudaroniidae of the Seguenzioidea (Bouchet *et al*., 2017).

A heterostrophan *Amphitomaria dockeryana* Kiel and Bandel, 2001 from the Campanian of Torallola, Spain (Kiel and Bandel, 2001, pl. I, figs. 9–12), resembles this specimen in its disk-shaped shell with a concave and planar base but differs in having flattened spire with flush sutures and a strongly angulated shoulder. The present specimen is also similar to the genus *Stuoraxis* of the

Table 1. List of the gastropod fossils reported from the Kimigahama Formation of the Choshi Group. All species except *Oolitica* and *Amberleya* were found from the same locality and horizon studied in this paper.

Taxa	References
Calliostoma? *ojii* Kase	Kase and Maeda (1980)
Ataphrus (*Ataphrus*) *nipponicus* Kase	Kase and Maeda (1980)
Hayamia rex Kase	Kase and Maeda (1980)
Hayamia choshiensis Kase	Kase and Maeda (1980)
Oolitica sp.	Kase and Maeda (1980)
Amberleya (*Eucyclus*) *japonica* Kase	Kase and Maeda (1980)
Perissoptera elegans Kase	Kase and Maeda (1980)
Pietteia cretacea Kase	Kase and Maeda (1980)
Ceratosiphon densestriatus Kase	Kase and Maeda (1980)
Vanikoropsis decussata (Deshayes)	Kase and Maeda (1980)
Eriptycha japonica Kase	Kase and Maeda (1980)
Eudaroniidae gen. et sp. indet.	This paper
Pseudomelania yamadai Isaji sp. nov.	This paper
Ampezzopleura barremica Isaji sp. nov.	This paper
Choshipleura striata Isaji gen. et sp. nov.	This paper
Ampezzopleurinae gen. et sp. indet.	This paper
Metacerithium boshuae Isaji sp. nov.	This paper
Cirsocerithium subspinosum (Deshayes)	This paper
Nystiellidae gen. et sp. indet.	This paper
Antiphora aurora Isaji sp. nov.	This paper
Knightella sp.	This paper
Stuoraxis kasei Isaji and Haga sp. nov.	This paper
Ebala sp.	This paper

superfamily Omalogyroidea, which is similar in shell size and discoidal morphology, but differs in having a planar base.

Occurrence.—Single specimen from the studied locality.

Subclass Caenogastropoda Cox, 1960
Superfamily Pseudomelanoidea Hörnes, 1884
Family Pseudomelaniidae Hörnes, 1884
Genus **Pseudomelania** Pictet and Campiche, 1862

Type species.—*Pseudomelania gresslyi* Pictet and Campiche, 1862, Early Cretaceous, Sainte-Croix, Switzerland.

Remarks.—Pseudomelaniidae is a problematic group based on the genus *Pseudomelania*, which includes small- to large-sized species with slender conical teleoconchs with a smooth or with inconspicuous sculptures (e.g. Gründel, 2001; Kaim, 2004; Ferrari, 2013; Cataldo, 2017). However, the holotype of the type species *P. gresslyi* is an indeterminable intenal mould (Kaim, 2004). Therefore, Kaim (2004) indicated that most of the known species included in *Pseudomelania* have an unknown protoconch shape and are potentially members of the eulimids, zygopleurids or other groups.

Pseudomelania yamadai Isaji sp. nov.

Figures 4A–G

Etymology.—In honor of Katsuhiko Yamada who collected the fossil-bearing block studied in this paper and donated it to the Natural History Museum and Institute, Chiba.

Types.—Holotype, CBM-PS 6442; three paratypes, CBM-PS 6443–6445.

Diagnosis.—The shell is small and slender conical. The protoconch I is smooth, and the protoconch II bears a subsutural spiral ridge on third whorl, ornamented with fine, deeply opisthocyrtic growth lines. The teleoconch shell is thick and glossy, ornamented with orthocline growth lines.

Description.—The shell is small and turritelliform. The protoconch is high-spired and conical in shape and consists of approximately 3.5 whorls, reaching 0.40 mm width and 0.47 mm height. The demarcation between the protoconch I and II is visible. The protoconch I is smooth and consists of one whorl, reaching approximately 0.14 mm in diameter. The whorls of protoconch II increase gently in diameter and are convex with shallow impressed sutures. The protoconch II bears a subsutural spiral ridge on the third whorl, which disappears gradually towards the termination of the protoconch whorl (Figure 4F, G). The surface of protoconch II is glossy and ornamented with fine, deeply opisthocyrtic growth lines (Figure 4F). The termination of the protoconch is not clearly demarcated from the teleoconch (Figure 4F). The teleoconch consists of more than 10 whorls. The spire angle is approximately 25°. The whorls increase isometrically in diameter and are almost flat with shallow sutures. The shell is thick and glossy, ornamented with orthocline growth lines. The periphery is situated in the lowermost part of the whorl, just above the suture. The base is smooth and broadly arcuate, forming an obtuse angle with the periphery. The aperture is rectangular and siphonostomatous, occupying approximately 30% of the

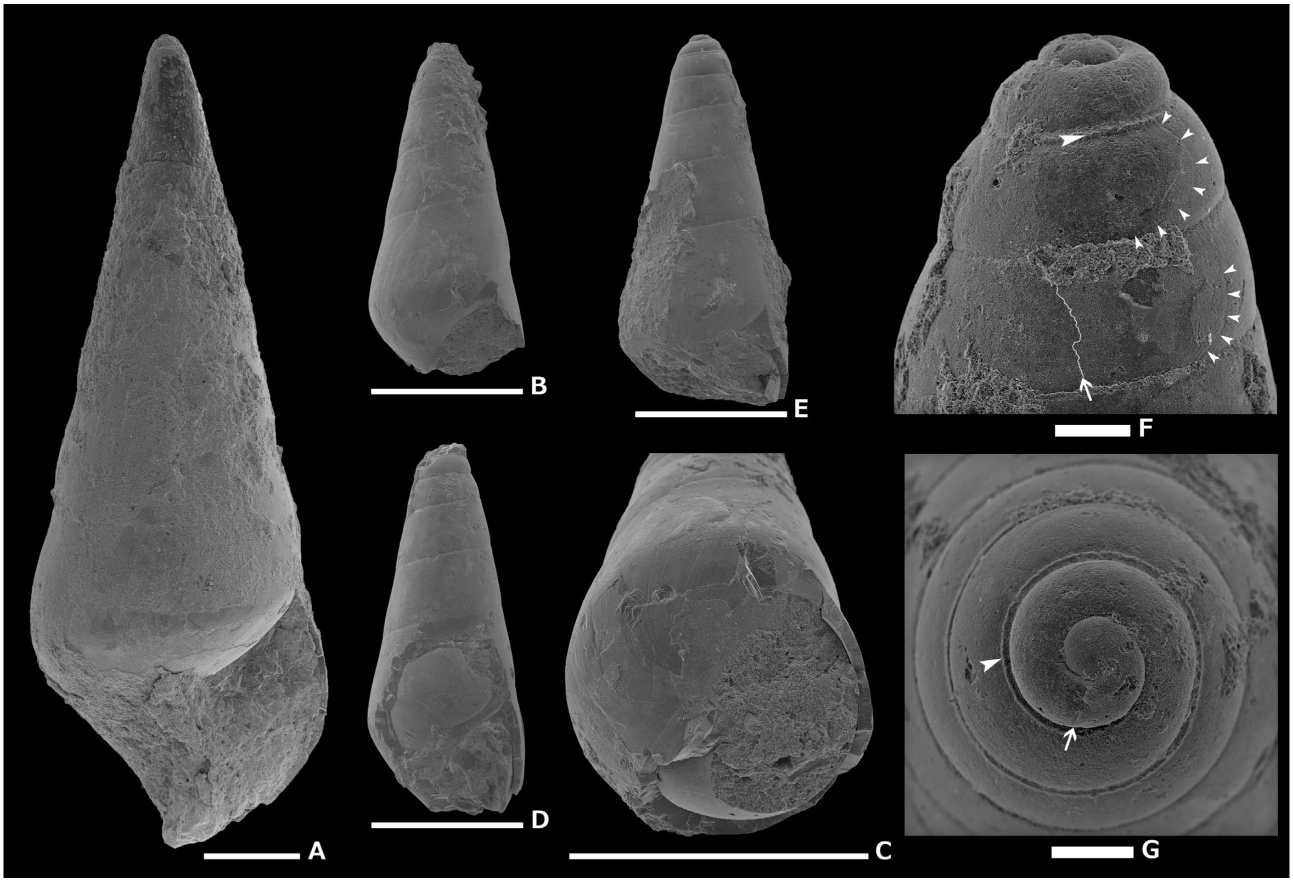

Figure 4. *Pseudomelania yamadai* sp. nov. from the Barremian Kimigahama Formation, Choshi Group, Japan. **A**, CBM-PS 6443, paratype, apertural view; **B**, **C**, CBM-PS 6444, paratype; B, apertural view of juvenile shell; C, oblique basal view; **D**, CBM-PS 6445, paratype, apertural view of juvenile shell; **E–G**, CBM-PS 6442, holotype; E, apertural view of juvenile shell; F, enlarged oblique view of protoconch, small white arrowheads indicating deeply opisthocyrtic growth lines, large white arrowhead indicating a subsutural spiral ridge, white line (white arrow) indicating a possible growth line of early teleoconch; G, apical view of protoconch, white arrow indicating the demarcation between protoconch I and protoconch II, white arrowhead indicating a subsutural spiral ridge. Scale bars = A–E: 1 mm; F, G: 0.1 mm.

total shell height.

Dimensions (in mm).—CBM-PS 6442: *H* = 2.45+, *W* = 1.13+. CBM-PS 6443: *H* = 8.50, *W* = 3.12. CBM-PS 6444: *H* = 2.21+, *W* = 1.04+. CBM-PS 6445: *H* = 2.46+, *W* = 1.05.

Remarks.—The protoconch of the present specimen is easily observable and it is sufficient to establish a new taxon. Compared with the unveiled protoconch of known *Pseudomelania*, the protoconch of the present species has striking differences in having a subsutural spiral ridge and deeply opisthocyrtic growth lines. *Pseudomelania trochiformis* (Piette, 1857) from the Valanginian of Wąwał, southern Mazowsze, Poland (Kaim, 2004, fig. 77) is similar to this species in size and the morphology of protoconch I but differs in having a protoconch II with orthocline growth lines. *Pseudomelania paucispira* Kaim, 2004 (Kaim, 2004, fig. 78) also differs from the present species in having a high-spired, paucispiral protoconch.

The large (over 120 mm height) species, *Pseudomelania elegantula* Nagao, 1934 from the Aptian to Albian Hiraiga Formation in the Miyako area, Iwate Prefecture, Japan (Nagao, 1934, pl. 37, figs. 1–9; Kase, 1984, pl. 16, figs. 1–4), is easily distinguished from the present species by its shell size and tear-shaped holostomatous aperture; hence, the latter species seems to be assignable to another unrelated family.

Occurrence.—This species is relatively common from the studied locality.

Superfamily Pseudozygopleuroidea Knight, 1930
Family Zygopleuridae Wenz, 1938
Subfamiliy Ampezzopleurinae Nützel, 1998
Genus ***Ampezzopleura*** Bandel, 1991

Type species.—Ampezzopleura tenuis Nützel, 1998, Carnian (Late Triassic), Cassian Formation, Campo near

Cortina d'Ampezzo, Italy.

*Remarks.—*Ampezzopleurinae is erected as a subfamily of the Zygopleuridae by having a larval shell with collabral axial ribs (Nützel, 1998). The overall protoconch morphology of the Ampezzopleurinae is strikingly reminiscent of many fossil and recent nystiellids (Epitonioidea) such as *Ageria*, *Gibboscala*, *Eccliseogyra*, *Narrimania* and *Opaliopsis* (e.g. Nützel, 1998; Tracey, 2010; Pimenta *et al*., 2017). However, there is distinct difference between them, that is, the spiral fine threads appear on the protoconch of nystiellids, while it is absent in the Ampezzopleurinae. The axial ribbed protoconch seems to indicate the close relationships of the ampezzopleurines and nystiellids and is suggestive of the polyphyletic origin of the Zygopleuridae.

Ampezzopleura barremica Isaji sp. nov.

Figures 5A–G

Etymology.—From the Barremian Kimigahama Formation, Choshi Group.

Types.—Holotype, CBM-PS 6446; three paratypes, CBM-PS 6447–6449.

Diagnosis.—The shell is very slender turritelliform for *Ampezzopleura*. The protoconch is high-spired and pupiform, ornamented by axial ribs. The teleoconch is ornamented by axial and spiral ribs, forming nodes at the intersections between them.

Description.—The shell is small and slender turritelliform. The protoconch is high-spired and pupiform. It consists of approximately four whorls, reaching 0.38 mm width and 0.63 mm height. The protoconch I is round and smooth, and is approximately 0.20 mm in diameter. The protoconch II is ornamented by sharp and prominent axial ribs (approximately 20 ribs per whorl), which are slightly narrower than their interspaces. Some ribs are connected abapically and adapically to other ribs, the others occur independently in a whorl. The demarcation between the protoconch and teleoconch is not sharp and obscure since the axial ribs disappear gradually towards the teleoconch (Figure 5D, F). The teleoconch consists of more than 11 whorls, which are as wide as they are tall. The spire angle is approximately 14° in the early teleoconch, which decreases to approximately 8° in the mature teleoconch. The whorls are slightly convex to straight sided. The suture is represented by an indistinct narrow groove, and the areas just above and below the suture are slightly swollen in the later whorls (Figure 5B). The teleoconch whorls are ornamented by axially elongated narrow but strong ribs (six ribs per whorls) that extend from suture to suture. The axial ribs are opisthocline on the first three teleoconch whorls and orthocline on the later whorls. The axial ribs are relatively prominent on the early four teleoconchs, giving the whorls a convex appearance (Figure 5C). The teleoconch whorls also have spiral sculptures. They are very weak or absent on the early teleoconch whorls (Figure 5C), become more developed with ontogeny, and increase in strength on the mature whorls (Figure 5A). The flank above the suture is concave, where two weak spiral striae exist. There are seven prominent spiral ribs on the mature whorls, forming the weak nodes at the intersections of the spiral and axial ribs (Figure 5B). Among the spiral ribs, the first and sixth are markedly slender, and the seventh is the stoutest. The aperture is not preserved in the examined specimens.

Dimensions (in mm).—CBM-PS 6446: H = 10.7+, W = 2.21. CBM-PS 6447: H = 2.20, W = 0.69. CBM-PS 6448: H = 1.44, W = 0.54. CBM-PS 6449: H = 1.31, W = 0.50.

Remarks.—Nützel (1998) described two genera for the subfamily Ampezzopleurinae based on the presence or absence of spiral sculptures on the teleoconch, i.e., the spirally sculptured *Striazyga* and smooth *Ampezzopleura*. However, Kiel *et al*. (2008) questioned the validity of the genus *Striazyga* since the type species of *Ampezzopleura*, *A. tenuis*, has weak spiral sculptures, as Nützel (1998) described. The present species has spiral sculptures that are very weak or absent on the early teleoconch and become stronger as the shell grows (Figure 5C). Therefore, in this paper, *Striazyga* is treated as the junior synonym of the genus *Ampezzopleura*, and the present species is described as a new species under *Ampezzopleura*.

All species hitherto placed within the genus *Ampezzopleura* have been collected from the Triassic deposits of Europe (Zardini, 1985; Nützel, 1998; Kaim *et al*., 2006), USA (Batten and Stokes, 1986; Nützel and Erwin, 2004; Nützel and Schulbert, 2005), China (Stiller, 2001), and Vietnam (Kaim *et al*., 2014). Thus, *Ampezzopleura barremica* sp. nov. is the youngest species of *Ampezzopleura*. The present species is very similar to *Striazyga zardinii* Nützel, 1998 from the Carnian (Upper Triassic) Cassian Formation, Italy (= *Zygopleura cylindrica* Zardini, 1978, in Zardini, 1985, table 3, fig. 21; Nützel, 1998, abbildung 24), in having a highly turriculate shell with axial and spiral sculptures but differs in having a higher profile of the teleoconch whorls. *Striazyga angusta* Nützel, 1998 (Nützel, 1998, tafel 25, N–Q) and *Striazyga armata* (Zardini, 1980) (Nützel, 1998, tafel 25R–U), both from the Cassian Formation, differ from the present species in having many more strong axial ribs. *Ampezzopleura barremica* is also similar to *Ampezzopleura tenuis* Bandel, 1991 (Nützel, 1998, tafel 24E–M) from the Cassian Formation in having a turriculate teleoconch with axially elongated ridges but differs in having a narrower spire angle and many fewer axial ribs. Another species of *Ampezzopleura*

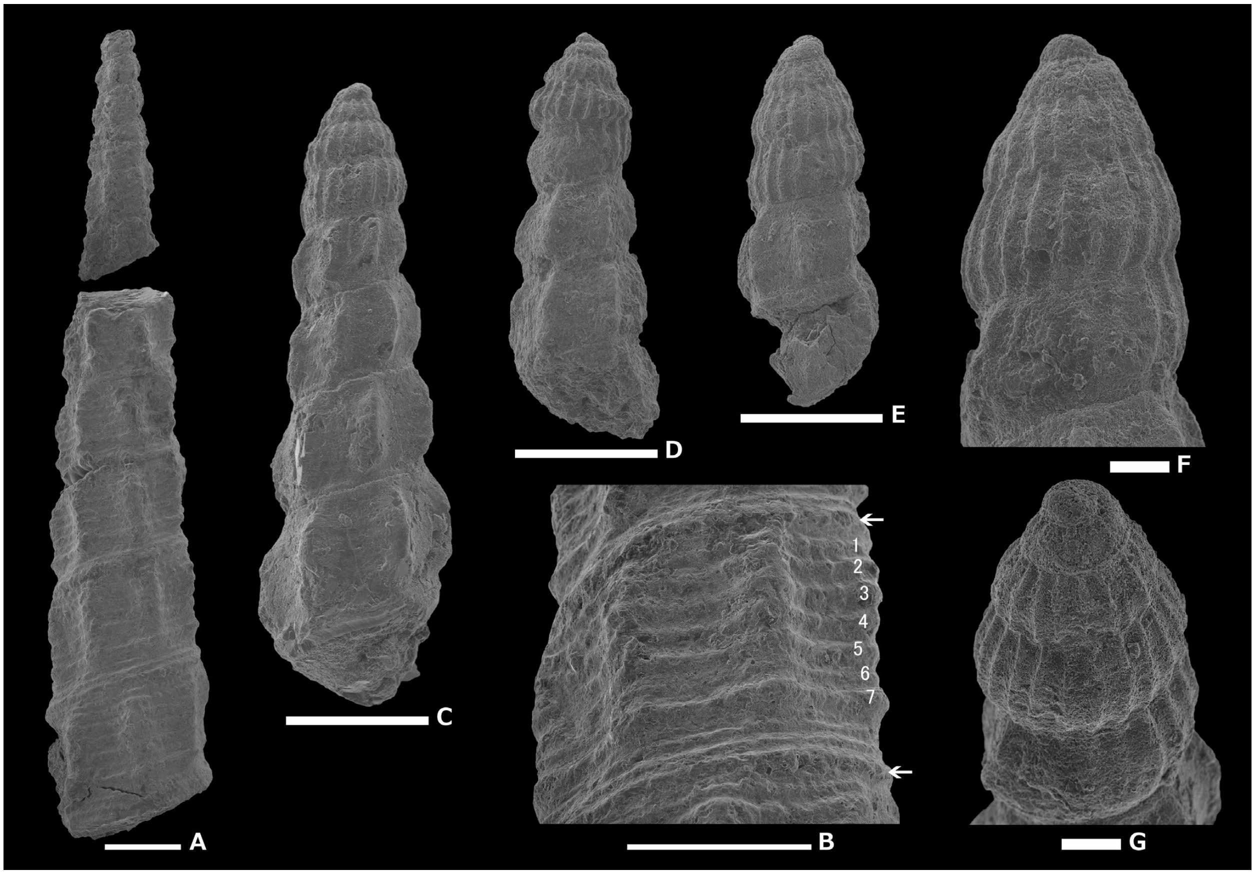

Figure 5. *Ampezzopleura barremica* sp. nov. from the Barremian Kimigahama Formation, Choshi Group, Japan. **A**, **B**, CBM-PS 6446, holotype; A, lateral view; B, enlarged oblique view of mature whorls, white numbers indicating the major seven spiral ribs, and white arrows indicating the sutures; **C**, CBM-PS 6447, paratype, lateral view of juvenile shell; **D**, CBM-PS 6448, paratype, lateral view of juvenile shell; **E**–**G**, CBM-PS 6449, paratype; E, lateral view of juvenile shell; F, enlarged lateral view of protoconch; G, oblique apical view of protoconch. Scale bars = A, B: 1 mm; C–E: 0.5 mm; F, G: 0.1 mm.

illustrated in Nützel (1998; *Ampezzopleura bandeli* Nützel, 1998, tafel 24N–R; *Ampezzopleura hybridopsis* Nützel, 1998, tafel 25A–L; *Ampezzopleura mammilata* Nützel, 1998, tafel 25M) differ from the present species in having broader shells without spiral ribs. *Ampezzopleura rugosa* (Batten and Stokes, 1986, figs. 24, 25; Nützel and Schulbert, 2005, figs. 11D, I) from the Early Triassic Sinbad Limestone, Utah, USA, differs in having more inflated teleoconch whorls and numerous axial wrinkles instead of ribs. *Ampezzopleura slovenica* Kaim *et al.*, 2006 (Kaim *et al.*, 2006, figs. 4A–D) from the Carnian (Upper Triassic) Raibl Beds of the Mežica region in the Karavanke Mountains, Slovenia, differs in having third and fourth teleoconch whorls ornamented by broad and round axial ribs.

Occurrence.—This species is relatively common from the studied locality.

Genus ***Choshipleura*** Isaji gen. nov.

Type species.—*Choshipleura striata* Isaji sp. nov.

Etymology.—After Choshi City.

Diagnosis.—The shell is conical. The protoconch is ornamented by axial ribs, and demarcated by sculptural discontinuity from the teleoconch. The teleoconch is sculptured by a subsutural spiral groove and numerous spiral striations, which are not observed in other species of the Ampezzopleurinae.

Choshipleura striata Isaji sp. nov.

Figures 6A–D

Types.—Holotype, CBM-PS 6450; single paratype, CBM-PS 6451.

Diagnosis.—As for the genus.

Description.—The shell is small and conical. The protoconch is high-spired and consists of approximately four whorls, reaching 0.60 mm width and 0.66 mm height. The protoconch I is not ornamented, consists of approxi-

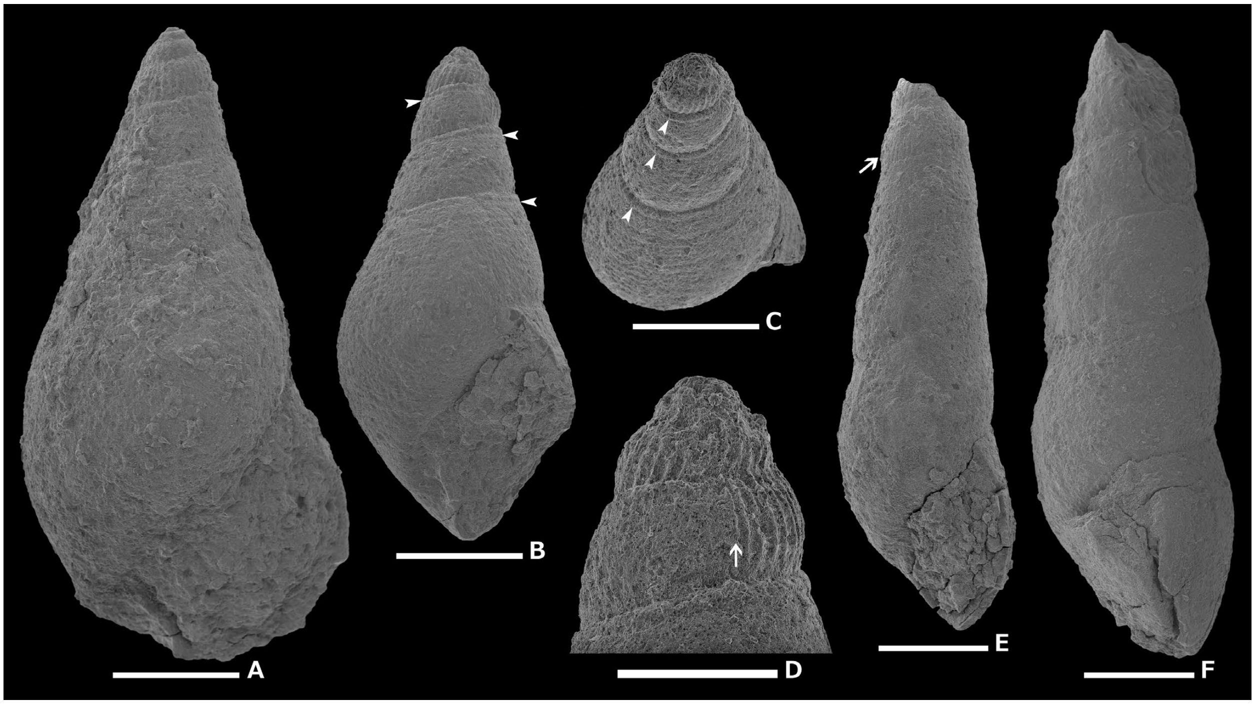

Figure 6. Zygopleurid gastropods from the Barremian Kimigahama Formation, Choshi Group, Japan. **A**–**D**, *Choshipleura striata* gen. et sp. nov.; A, CBM-PS 6451, paratype, apertural view; B–D, CBM-PS 6450, holotype; B, apertural view; C, oblique apical view, white arrowheads indicating subsutural spiral grooves; D, enlarged lateral view of protoconch, white arrow indicating the demarcation between protoconch and teleoconch; **E**, **F**, Ampezzopleurinae gen. et sp. indet.; E, CBM-PS 6452, apertural view, white arrow indicating the last whorl of protoconch sculptured by axial ribs; F, CBM-PS 6453, apertural view. Scale bars = A–C, E, F: 1 mm; D: 0.5 mm.

mately 2.5 whorls and reaches 0.36 mm in diameter. The protoconch II is ornamented by sharp axial ribs, which are slightly narrower than their interspaces, and clearly demarcated by sculptural discontinuity from the smooth teleoconch (Figure 6D). The teleoconch consists of approximately four whorls. The whorls increase rapidly in diameter and are convex with shallow sutures. The spire angle is approximately 34–38°. The teleoconch whorls are sculptured by a subsutural spiral groove and numerous spiral striations, which are clearly visible on the upper half of the mature whorls but faint on the early two teleoconch whorls (Figure 6B, C). The whorl profile between sutures is rather straight in early whorls and slightly round in later whorls. The periphery is situated just above the suture. The base is smooth and broadly arcuated. The aperture is tear-shaped and holostomatous and occupies approximately 45% of the total shell height. The inner lip is slightly reflected.

Dimensions (in mm).—CBM-PS 6450: *H* = 3.80, *W* = 1.90+. CBM-PS 6451: *H* = 5.03+, *W* = 2.62.

Remarks.—It is plausible to assign the present species to the subfamily Ampezzopleurinae based on shell features such as an axially ribbed protoconch and a simple holostomatous aperture without an anterior siphonal canal. However, the teleoconch whorls of the genera of ampezzopleurines are normally sculptured with axial ribs (Nützel, 1998). The gross morphology of *Ampezzopleura slovenica* Kaim *et al.*, 2006 (Kaim *et al.*, 2006, figs. 4A–D) from the Carnian (Upper Triassic) Raibl Beds of the Mežica region in the Karavanke Mountains, Slovenia is similar to that of the present species, but the former differs in having broad and rounded axial ribs in the third and fourth teleoconch whorls. The zygopleurid species *Omphaloptychia hormolira* Batten and Strokes, 1986 from the middle Scythian (Lower Triassic) Moenkopi Formation, Utah, USA (Batten and Stokes, 1986, figs. 41–43), and from the lower Dienerian (Lower Triassic) of Far East Russia (Kaim, 2009, fig. 143) have an axially ribbed protoconch, hence, *O. hormolira* appears to be placed in the Ampezzopleurinae based on the definition by Nützel (1998). Although *O. hormolira* has smooth teleoconch whorls without axial ribs like *C. striata* but differs in having a higher protoconch, well-rounded teleoconch whorls with well-defined sutures and no spiral ornamentation and much more inflated body whorls. Therefore, it is reasonable to establish a new genus of the subfamily Ampezzopleurinae for the present species.

Occurrence.—Two specimens from the studied locality.

Gen. et sp. indet.

Figures 6E, F

Material.—Two specimens; CBM-PS 6452, 6453.

Description.—The shell is small and slenderly fusiform. The early whorls of the protoconch are not observed in the examined specimens. The last whorl of the protoconch is ornamented by weak axial ribs, and it is not clearly demarcated by sculptural discontinuity from the smooth teleoconch (Figure 6E). The teleoconch consists of approximately five whorls. The whorls increase gently in diameter and are widely convex with shallow sutures. The whorl profile between sutures is rather straight in early whorls and slightly round in later whorls. The spire angle is approximately 16–19°. The base is smooth and broadly arcuated. The aperture is tear-shaped and holostomatous.

Dimensions (in mm).—CBM-PS 6452: $H = 5.00+$, $W = 1.65$. CBM-PS 6453: $H = 5.70+$, $W = 1.87$.

Remarks.—The axially ribbed protoconch and the simple holostomatous aperture indicate that this species belongs to the Ampezzopleurinae. However, this species has no axial ribs on the teleoconch whorls, which is usually found in known genera of Ampezzopleurinae (Nützel, 1998), as well as the *Choshipleura* gen. nov. described in this paper. On the other hand, *Choshipleura striata* differs from this species by having a spiral groove and many striations on the teleoconch. Therefore, this paper tentatively assigns this species as an indeterminant species of subfamily Ampezzopleurinae.

Occurrence.—Two specimens from the studied locality.

Superfamily Campaniloidea Douvillé, 1904
Family Metacerithiidae Cossmann, 1906
Genus ***Metacerithium*** Cossmann, 1906

Type species.—Cerithium trimonile Michelin, 1838, Albian (Early Cretaceous), France, by original designation (Cossmann, 1906).

Remarks.—Two and a half smooth and globular protoconch whorls that are terminated by a distinct varix are observed in *Metacerithium ponsi* Kiel and Bandel, 2000 (in Kiel *et al*., 2000, pl. 2, figs. 1, 2) from the Campanian Vallcarga Formation of Torallola, Spain. Kiel *et al*. (2000) suggested that the protoconch of *M. ponsi* is similar to that of *Campanile houbricki* Kiel and Perrilliat, 2000 (in Kiel *et al*., 2000, pl. 1, fig. 1) from the Maastrichtian Mexcala Formation of Mexico. Based on this similarity in the protoconch, Kiel *et al.* (2000) placed *Metacerithium* in the Campaniloidea. A comparable protoconch is also reported in the type species *Metacerithium trimonile* Michelin, 1838 from the Albian Gault Clay of Folkestone, Kent, England (Tracey, 2010, pl. 21, fig. 11) and in *Metacerithium* aff. *trimonile* from the Albian, Mahajanga Basin, Madagascar (Kiel, 2006, figs. 3.6, 3.9). The protoconch and juvenile teleoconch of *Campanile* sp. from the Mid-Eocene of Gan, France, by Bandel (2006, pl. 10, figs. 10–12) are also comparable in size, morphology and sculpture with those of *C. houbricki*, *M. ponsi* and *M. trimonile*. However, the assignment of *Metacerithium* to the Campaniloidea by Kiel *et al*. (2000) is doubted based on considerable differences in teleoconch morphology between the Metacerithiidae and the Campanilidae (Kollmann, 2005; Gründel and Kollmann, 2013). Considering these kinds of arguments, Bouchet *et al*. (2017) followed Kiel *et al*. (2000) and Bandel (2006) in classifying Metacerithiidae as a family of Campaniloidea.

Metacerithium boshuae Isaji sp. nov.

Figures 7A–F

Etymology.—In honor of Fumiko Boshu who has collected numerous fossils from the Choshi area and has made contributions as a field guide of the Choshi Geopark.

Types.—Holotype, CBM-PS 6454; four paratypes, CBM-PS 6455–6458.

Diagnosis.—The shell is turritelliform and small for the genus. The protoconch is smooth and globular, and terminates at a varix. The teleoconch is ornamented by two tuberculate ridges; the upper one is a subsutural row of numerous weak tubercles, the lower one is a row of strong tubercles.

Description.—The shell is small and turritelliform. The protoconch is smooth and globular and consists of approximately 2.2 convex whorls. The initial whorl of the protoconch is approximately 0.05 mm in diameter. It reaches an approximately 0.30 mm width and 0.31 mm height and terminates at a varix (Figure 7F). The teleoconch consists of at least ten whorls. The spire angle is approximately 24°. The teleoconch whorls increase isometrically in diameter and are slightly convex with weakly grooved sutures. The teleoconch whorls are sculptured by two tuberculate ridges. The upper ridge is a subsutural row of numerous weak tubercles (24 tubercles on the last whorl) that are not observable on the first five teleoconch whorls (Figure 7E). The lower ridge is a row of strong tubercles (16 tubercles on the last whorl) at the mid-whorls or somewhat below, forming an angular periphery of whorls (Figure 7A–D). The basal edge of the mature whorl bears a weak keel, which is usually covered by the succeeding whorls. The base is smooth and flatly concave and gradually curves towards the columella. The aperture is poorly preserved in the examined specimens; it seems to be rectangular and siphonostomatous, occupying approximately 25% of the total shell height.

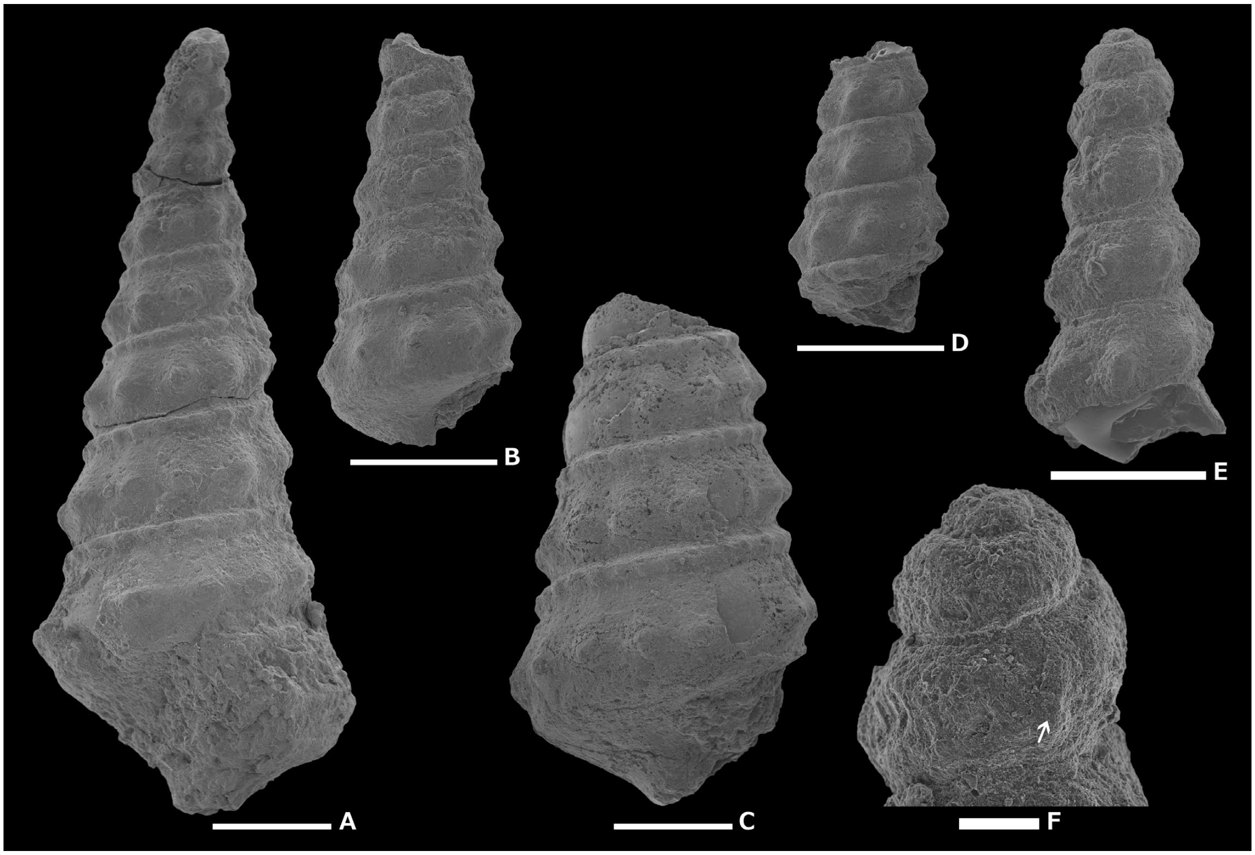

Figure 7. *Metacerithium boshuae* sp. nov. from the Barremian Kimigahama Formation, Choshi Group, Japan. **A**, CBM-PS 6454, holotype, lateral view; **B**, CBM-PS 6455, paratype, lateral view; **C**, CBM-PS 6456, paratype, lateral view; **D**, CBM-PS 6457, paratype, lateral view; **E**, **F**, CBM-PS 6458, paratype; E, lateral view of juvenile shell with protoconch; F, enlarged oblique apical view of protoconch, white arrow indicating a terminated varix of protoconch. Scale bars = A–D: 1 mm; E: 0.5 mm; F: 0.1 mm.

Dimensions (in mm).—CBM-PS 6454: $H = 6.66+$, $W = 2.75$. CBM-PS 6455: $H = 2.83+$, $W = 1.41+$. CBM-PS 6456: $H = 4.33+$, $W = 2.61+$. CBM-PS 6457: $H = 2.00+$, $W = 1.10+$. CBM-PS 6458: $H = 1.40+$, $W = 0.66+$.

Remarks.—The protoconch morphology of *Metacerithium boshuae* sp. nov. seems to match that of other described *Metacerithium*. In contrast, the teleoconch features are considerably different from those known species of *Metacerithium*. The gross shell morphology of *Metacerithium trimonile* (Michelin, 1838) from the Albian Gault, Folkestone, Kent (Abbass, 1973, pl. 4, figs. 2, 3, 7, 8, 10), the Albian Gault of France (d'Orbigny, 1842), the Albian Losenstein Formation of Upper Austria (Kollmann, 1979, tafel 2, figs. 16–20), and the Albian Mahajanga, Madagascar (Kiel, 2006, fig. 10), is similar to that of *M. boshuae* but differs in having three rows of many tubercles and smaller tubercles on the basal ridge. *Metacerithium turriculatum* (Forbes, 1845) from the Atherfield Clay Formation of the Lower Greensand Group in the Isle of Wight, which includes the holotype designated by Abbass (1973, pl. 5, fig. 10), is similar to the present species in its early teleoconch but differs in having small and many tubercles on the mature whorls, where the tubercles decrease gradually in prominence and tend to be axially elongated ridges. Cataldo and Lazo (2016, fig. 6) reported on the ornament variation of *M. turriculatum* from the Lower Cretaceous Agrio Formation, Neuquén Basin, west-central Argentina. In those specimens, the gradual transformation of the shell ornaments could be seen, especially the tubercles tending to disappear more than in the European specimens, even on the middle teleoconch whorls.

Metacerithium ornatissimum (Deshayes in Leymerie, 1842) from the Albian to Cenomanian of Europe (Leymerie, 1842; Abbass, 1973, pl. 4, figs. 5, 12; Kollmann, 2005, pl. 18, fig. 8) differs from *M. boshuae* in having two spiral rows of nodes adjacent to the sutures and flat-sided whorls. *Metacerithium rikuchuense* Nagao, 1934 (Nagao, 1934, pl. 35, figs. 4–7) from the Aptian

Hiraiga Formation in the Miyako area, Iwate Prefecture, Japan was transferred to *Trypanotrochus rikuchuensis* (Nagao, 1934) by having a deep umbilicus (Kase, 1984, pl. 11, figs. 1–5). *Metacerithium ponsi* Kiel and Bandel, 2000 (in Kiel *et al*., 2000, pl. 2, figs. 1–4) differs in having many strong tubercles on the early teleoconch that decrease the strength ontogenically. *Metacerithium coquandi* (Pictet and Campiche, 1863) from the Barremian of Serre de Bleyton, Drôme, France (Gründel and Kollmann, 2013, pl. 5, figs. 16, 17) differs in having three spiral rows of many small tubercles.

Occurrence.—This species is rare from the studied locality.

Order Cerithimorpha Golikov and Starobogatov, 1975
Taxa of uncertain position (Bouchet *et al*., 2017)
Family Procerithiidae Cossmann, 1906
Genus ***Cirsocerithium*** Cossmann, 1906

Type species.—Cerithium? *subspinosum* Deshayes in Leymerie, 1842 by original designation; Early Cretaceous, France.

Cirsocerithium subspinosum (Deshayes in Leymerie, 1842)

Figures 8A–F

Cerithium? *subspinosum* Deshayes in Leymerie, 1842, p. 14, pl. 17, figs. 12a, b.

Cerithium subspinosum Deshayes, d'Orbigny, 1843, p. 364, pl. 229, figs. 4–6; Pictet and Campiche, 1864, p. 304; Wollemann, 1903, p. 32, pl. 4, figs. 11, 11a; Wollemann, 1906, p. 290, pl. 10, figs. 2–3.

Cirsocerithium subspinosum (Deshayes in Leymerie, 1842), Cossmann, 1906, p. 50–52, pl. 7, figs. 1–3; Wenz, 1940, p. 733, 734, fig. 2125; Pcelincev and Korobkov, 1960, p. 153, 154; Abbass, 1973, p. 119, 120, pl. 2, figs. 1, 2; Kase, 1984, p. 130, 131, pl. 20, figs. 10, 11; Tracey, 2010, p. 116, pl. 21, figs. 3, 4).

Material.—Three specimens; CBM-PS 6459–6461.

Description.—The shell is high-spired and turbiniform. The protoconch is conical in shape and consists of approximately six whorls. It reaches an approximately 0.77 mm width and 1.30 mm height and is separated from the teleoconch by an axial rib (Figure 8C, D). The protoconch I is smooth and approximately 0.10 mm in diameter. The protoconch II is ornamented by four spiral sculptures (Figure 8E). The uppermost one is a subsutural row of tubercles (approximately 0.01 mm in diameter), which are regularly arranged with interspaces of similar width (Figure 8E). Two spiral keels are located at the flank, of which the lower keel appears first on the second protoconch whorl and is situated at the periphery. The upper keel starts to appear on the third protoconch whorl and is situated on the shoulder. The basal keel appears belatedly on the later protoconch whorls. The basal keel is slender and situated just above the suture, often covered by the succeeding whorl. The teleoconch consists of at least seven whorls. The spire angle is approximately 40°. The teleoconch whorls increase isometrically in diameter and are convex with impressed sutures. The whorls are ornamented by thick axial ribs (12–14 ribs per whorl), which protrude at the middle of the flank, giving the whorls an angular appearance. The axial ribs are slightly opisthocline on the early teleoconch whorls and become orthocline to slightly prosocline on the later whorls. The whorls are also ornamented by spiral cords. They are nine in number in the early teleoconch (Figure 8B) and inserted by a fine spiral cord between each of the preceding spiral cords in the mature whorls (Figure 8A). The base is shallowly concave, ornamented by approximately nine spiral striations. The aperture is subcircular and siphonostomatous, occupying approximately 35% of the total shell height. The anterior canal is short and moderately wide grooved (Figure 8A). The columella and inner lip are smooth and callused. The outer lip is angulated above to form a posterior canal. The inside of the outer lip bears at least eight denticles, the most adaxially situated of which is approximately two times larger than the others (Figure 8A). The outside of the outer lip is thickened by a varix.

Dimensions (in mm).—CBM-PS 6459 : H = 11.20+, W = 6.18. CBM-PS 6460 : H = 3.12, W = 1.90. CBM-PS 6461 : H = 1.48+, W = 0.92+.

Remarks.—*Cirsocerithium subspinosum* (Deshayes in Leymerie, 1842) is widely distributed in the late Early Cretaceous. It has hitherto been reported from the Albian Gault of Yonne, Bourgogne, France (Cossmann, 1906; Wenz, 1940; Kollmann, 2005), the Lower Gault of Saint-Martin-le-Hortier, Pays de Bray, France (Tracey, 2010), the Albian Gault of Algermissen, North Germany (Wollemann, 1903, 1906), the Albian Gault of Folkestone, Kent, England (Abbass, 1973; Tracey, 2010), and the Aptian Tanohata Formation in the Miyako area, Iwate Prefecture, Japan (Kase, 1984).

Cerithium subspinosum from the Lower Cretaceous in Madagascar described by Collignon (1949) was transferred to *Cirsocerithium collignoni* Kiel, 2006 (Kiel, 2006, figs. 11–14) as a new species based on its thicker spiral cords and many axial ribs (14–16 ribs per whorl). The specimens of *C.* cf. *subspinosum* from the Albian Losenstein Formation of Upper Austria (Kollmann, 1979, tafel 3, figs. 21–24) differs in having a large number of axial ribs, and their poor preservation does not allow distinct generic determination. The other specimen of *C. subspinosum* from the Lower Aptian of Sokolovaya gora, Saratov, Russia (Golovinova and Guzhov, 2009, pl. 2, fig. 7a, b) differs from European specimens in having coarser and many spiral cords, more spiny axial ribs, a broader inhalant siphonal groove and a wider spire angle of the

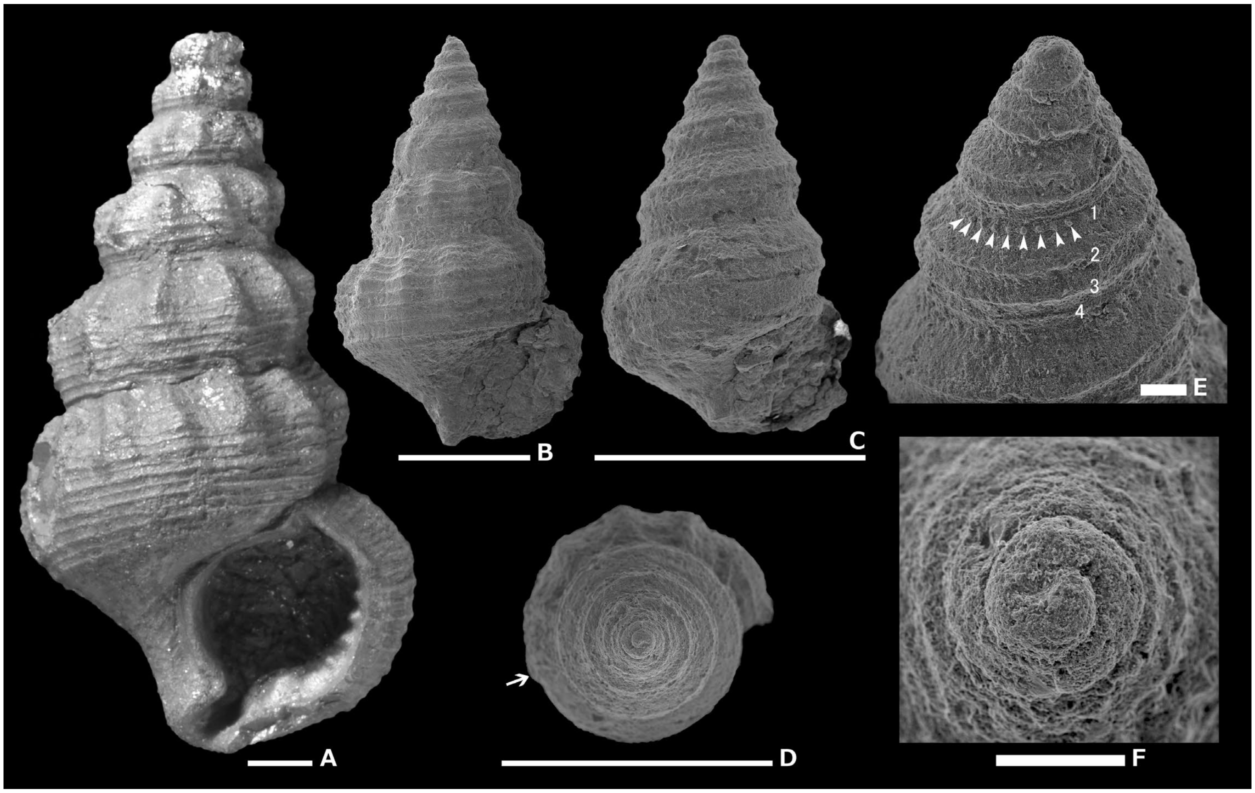

Figure 8. *Cirsocerithium subspinosum* (Deshayes in Leymerie, 1842) from the Barremian Kimigahama Formation, Choshi Group, Japan. **A**, CBM-PS 6459, apertural view of adult shell; **B**, CBM-PS 6460, lateral view of juvenile shell; **C**–**F**, CBM-PS 6461, C, lateral view of juvenile shell; D, apical view of juvenile shell, white arrow indicating a first axial rib of the teleoconch; E, enlarged oblique apical view of protoconch; white numbers indicating four spiral sculptures and white arrowheads indicating tubercles; F, apical view of protoconch showing a smooth protoconch I. Scale bars = A–D: 1 mm; E, F: 0.1 mm.

shell. Therefore, it is likely that the latter two specimens are separated from *C. subspinosum*.

Compared with known specimens of *C. subspinosum*, the present specimens agree well with the European specimens in shell size and teleoconch ornamentation illustrated by Abbass (1973, pl. 2, figs. 1, 2), Kollmann (2005, p. 159–160, pl. 17, figs. 25a–c) and Tracey (2010, p. 116, pl. 21, fig. 3). The present specimens also resemble the Miyako specimens figured in Kase (1984, pl. 20, figs. 10a, b), although the larger specimens having more spiny axial ribs occur from the same locality (Kase, 1984, pl. 20, figs. 11a, b).

The protoconch of *C. subspinosum*, including that of the type specimens, has not yet been described in detail. Some juvenile shells with a protoconch of the European specimens were illustrated by Abbass (1973) and Tracey (2010), but the low magnification of the photographs does not allow a precise comparison with the Kimigahama and European specimens. This paper revealed the details of the protoconch of *C. subspinosum* from the Kimigahama Formation as described above. These features are very similar to those of *C. collignoni* (Kiel, 2006, figs. 12–14), but the latter species differs in having two tuberculate keels and a large larval hook. These differences might be enhanced by the preservation or abrasion of fossils since some of the Kimigahama specimens examined seem to have very weak tubercles on the spiral keel at the shoulder.

Occurrence.—More than 600 specimens which are composed mostly of early juveniles were collected. This species is the most common element of the gastropod assemblage at the studied locality.

Superfamily Epitonioidea Berry, 1910
Family Nystiellidae Clench and Turner, 1952
Gen. et sp. indet.

Figures 9A–D

Material.—Three specimens; CBM-PS 6462–6464.

Description.—The shell is slender and turriculate. The protoconch is missing. The teleoconch whorls increase gradually in diameter and are convex with impressed

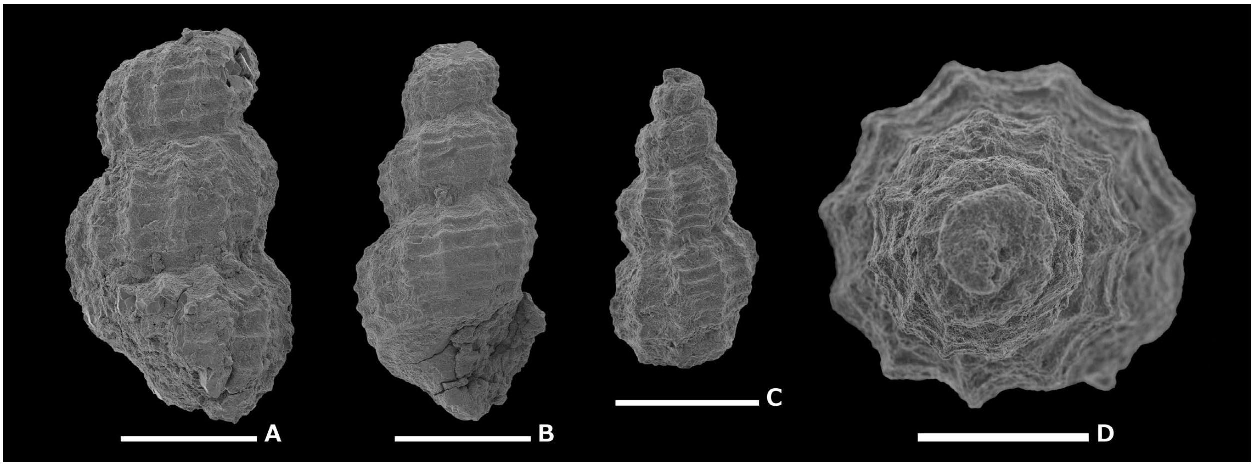

Figure 9. Nystiellid gastropod from the Barremian Kimigahama Formation, Choshi Group, Japan. **A**, CBM-PS 6462, lateral view; **B**, CBM-PS 6463, lateral view; **C**, **D**, CBM-PS 6464; C, oblique lateral view; D, apical view. Scale bars = A–C: 1 mm; D: 0.5 mm.

sutures. The preserved teleoconch whorls form a spire angle of approximately 30°. The shell surface is ornamented with axial ribs and spiral cords, which form nodes at the intersections between them. The axial ribs (12–14 ribs per whorl) are prominent and stout, are one third as wide as their interspaces, and extend from suture to suture. Six spiral cords are almost equal in strength. They are evenly spaced from the shoulder to the suture, and the lowest one is covered by the succeeding whorl. The base is slightly concave with a weak spiral cord. The aperture is not preserved.

Dimensions (in mm).—CBM-PS 6462: H = 2.91+, W = 1.68. CBM-PS 6463: H = 2.80+, W = 1.43+. CBM-PS 6464: H = 2.10+, W = 1.03+.

Remarks.—The present specimens closely resemble *Opaliopsis* aff. *dupinianum* (d'Orbigny, 1842) from the Albian of Mahajanga, Madagascar (Kiel, 2006, figs. 5.1, 5.3). However, the inflated teleoconch whorls ornamented by equally strong axial and spiral sculptures of both the present specimens and *O.* aff. *dupinianum* by Kiel (2006) are diagnostic characters of some other genera of nystiellids such as *Narrimania* and *Papuliscala* (Pimenta *et al*., 2017). The present specimens also resemble a provannid *Desbruyeresia kanajirisawensis* Kaim, Jenkins and Warén, 2008, which is a member of chemosynthesis-based community, from the Cenomanian cold seep in Hokkaido, Japan (Kaim *et al*., 2008, figs. 2A–C, G, H, P, S, 3A). Both the nystiellids and provannids have characteristic larval shells, i.e., the former having a high spired and axially ribbed protoconch, and the latter having a decollate protoconch and a calcareous plug filling the top of the second larval whorl. Unfortunately, the present specimens lack the protoconch data. The early whorl of a specimen (Figure 9C, D) might be a part of protoconch, however, the sculpture of the whorl surface is too ambiguous. Consequently, the present specimens are tentatively assigned as an indeterminant species of family Nystiellidae based on the close similarity of teleoconch features. However, the discovery of new specimens with well-preserved protoconch is needed for the taxonomic determination of this species in a future study.

Occurrence.—This species is rare from the studied locality.

Superfamily Triphoroidea Gray, 1847
Family Triphoridae Gray, 1847
Subfamily Metaxiinae Marshall, 1977
Genus ***Antiphora*** Nützel, 1998

Type species.—*Cerithiopsis discreta* Gougerot and Le Renard, 1981, by original designation; Eocene, Parisians Basin.

Antiphora aurora Isaji sp. nov.

Figures 10A–H

Types.—Holotype, CBM-PS 6465; five paratypes, CBM-PS 6466–6470.

Diagnosis.—The shell is small and slender turriteliform. The protoconch is ornamented by two spiral sculptures and prosocline liner axial ribs. The end of the protoconch shows a sinusigera. The teleoconch is ornamented by three spiral tuberculate cords. Each of the spiral cords and tubercles are weaker than those of *Antiphora ganensis*.

Description.—The protoconch is high-spired and conical and consists of approximately five whorls. It reaches an approximately 0.40 mm width and 0.80 mm height and

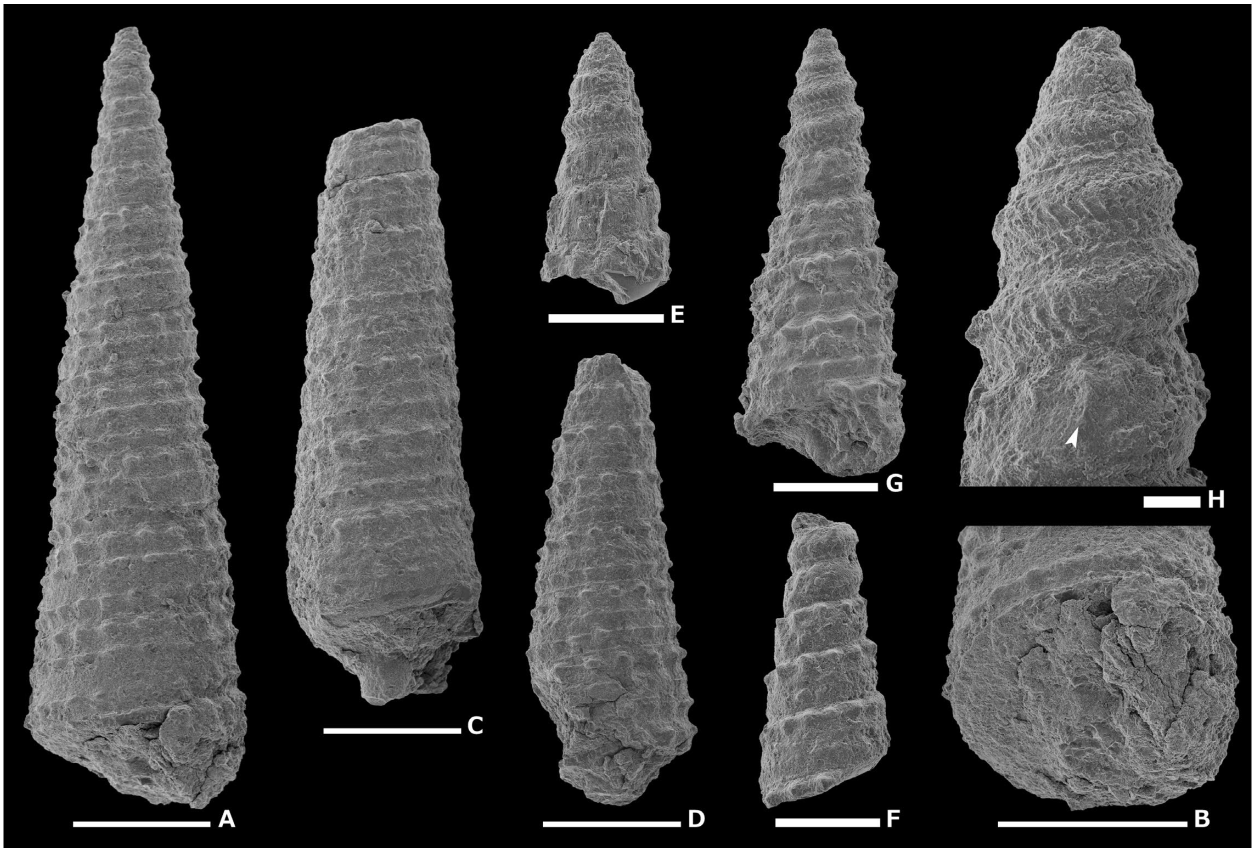

Figure 10. *Antiphora aurora* sp. nov. from the Barremian Kimigahama Formation, Choshi Group, Japan. **A**, **B**, CBM-PS 6465, holotype; A, lateral view; B, oblique basal view; **C**, CBM-PS 6466, paratype, lateral view; **D**, CBM-PS 6467, paratype, lateral view; **E**, CBM-PS 6468, paratype, lateral view of juvenile shell with protoconch; **F**, CBM-PS 6469, paratype, lateral view of juvenile shell; **G**, **H**, CBM-PS 6470, paratype; G, lateral view of juvenile shell with protoconch; H, enlarged view of protoconch, white arrowhead indicating a sinusigera of protoconch. Scale bars = A–D: 1 mm; E–G: 0.5 mm; H: 0.1 mm.

seems to terminate at a varix with a sinusigera (Figure 10H). The early protoconch whorls are poorly preserved. The initial whorl is less than 0.10 mm in diameter and has no marked sculptures. The later protoconch whorls are ornamented by two spiral sculptures, i.e., an upper strong spiral rib and a lower weak spiral thread. The lower half of whorls also has thin, prosocline, and linear axial ribs that extend from the upper strong spiral rib to the suture, forming tubercles at the intersections of the lower spiral thread (Figure 10H). The teleoconch consists of at least 12 whorls. The spire angle is approximately 14°. The teleoconch whorls increase isometrically in diameter. The early third to fourth teleoconch whorls have angulated shoulders with grooved sutures (Figure 10F, G), whereas the later whorls are straight sided with flushed sutures. The teleoconch whorls are sculptured by three spiral tuberculate cords (20–24 tubercles per mature whorl) (Figure 10A, C, D). The upper spiral cord is thick and starts on the early teleoconch, accompanied by conspicuous tubercles. The middle and lower ones are somewhat narrow and appear on the later whorls, accompanied by weak tubercles. The tubercles become almost equal in size and regularly placed in each of the three spiral ribs on mature teleoconch whorls. The interspaces between the upper and middle spiral cords are narrower than those between the middle and lower spiral cords. The base is flatly concave, and lies at a sharp angle to the periphery. A spiral keel exists on the adaxial edge of the base at the suture of the succeeding whorl (Figure 10B). The aperture is poorly preserved on the examined specimens; it seems to be rhombic or rounded rhombic. The columella is stout but poorly preserved.

Dimensions (in mm).—CBM-PS 6465: $H = 5.71+$, $W = 1.63+$. CBM-PS 6466: $H = 4.27+$, $W = 1.45+$. CBM-PS 6467: $H = 3.30+$, $W = 1.26+$. CBM-PS 6468: $H = 1.19+$, $W = 0.57+$. CBM-PS 6469: $H = 1.42+$, $W = 0.62+$. CBM-PS 6470: $H = 2.16+$, $W = 0.82+$.

Remarks.—The slender turriculate teleoconch with spiral tuberculate cords of the present species is similar to those of *Cryptaulax* and *Procerithium*, but those of the last two genera differ in having a bicarinate larval shell typical of the Cerithioidea (e.g. Kaim, 2004). The present species is also similar to the eumetulid *Cosmocerithium antiquum* (Gründel, 2001) from the Bathonian, Gnaszyn, Częstochowa region, Poland (Kaim, 2004, fig. 39), but the latter differs in having strong and collaboral axial riblets on the protoconch and sharp-edged axial ribs on the teleoconch. Alternatively, the present species closely resembles *Antiphora ganensis* Nützel, 1998 from the Eocene, Cuisium of Gan near Pau, France (Nützel, 1998, tafel 18C, D) in having a high-spired protoconch with a smooth initial whorl, a thick spiral rib, thin and prosocline axial ribs and a varix at the termination (Figure 10H) but differs from *A. ganensis* in having thin spiral cords and small tubercles in the teleoconch. Therefore, this paper designates the present species as a new species of the genus *Antiphora*.

The presence of prosocline axial ribs on the lower surface of the protoconch whorl (Figure 10H) is shared by the present species and extant *Metaxia* spp. (Metaxiinae) (e.g. Marshall, 1983; Fernandes and Pimenta, 2011; Romani *et al*., 2018). However, most *Metaxia* are lecithotrophic and have a large paucispiral protoconch I, whereas the present species seems to be planktotrophic, according to its small protoconch I.

Occurrence.—This species is relatively common from the studied locality.

Caenogastropods of uncertain family
Genus ***Knightella*** Longstaff, 1933

Type species.—*Knightia irregularis* Longstaff, 1933, by original designation; Carboniferous, Scotland.

Knightella sp.

Figures 11A–E

Material.—Four specimens; CBM-PS 6471–6474.

Description.—The shell is high-spired and conical. The protoconch is blunt and low-spired with smooth and convex whorls, and it is not clearly demarcated from the teleoconch (Figure 11C). The initial whorl of the protoconch is less than 0.10 mm in diameter. The teleoconch consists of at least four whorls. The teleoconch whorls rapidly increase in height and are well inflated with impressed sutures. The shell surface is smooth with slightly opisthocyrtic growth lines. The base is slightly convex and ornamented by spiral threads (Figure 11E). The aperture is tear-shaped, occupying approximately 50% of the total shell height, and interrupted by the base of the previous whorl. The peristome is thin and sharp. The columellar lip is faintly reflected. The umbilicus is closed.

Dimensions (in mm).—CBM-PS 6471: $H = 1.57$, $W = 0.90+$. CBM-PS 6472: $H = 1.71$, $W = 0.94+$. CBM-PS 6473: $H = 1.90$, $W = 0.97$. CBM-PS 6474: $H = 2.16+$, $W = 1.07$.

Remarks.—Kaim (2004) treated the genus *Knightella* as a member of Rissoidea according to its cylindrical protoconch with a dome-shaped apex. Nützel and Nakazawa (2012) included *Knightella* in the Orthonematidae. However, the protoconch of *Knightella* shows no distinct sinusigera, which is characteristic of the Orthonematidae (Nützel and Bandel, 2000). Here, we adopted an uncertain family of Caenogastropoda as the systematic position of *Knightella* proposed by Kaim (2008).

The present specimens are similar to *Knightella baluki* Kaim, 2004 from the Upper Valanginian (Lower Cretaceous) of Wąwał, Poland (Kaim, 2004, fig. 75), but differ in having a large body whorl. *Knightella* sp. from the Callovian (Middle Jurassic) of Łuków (block in glacial drift), Poland, (Kaim, 2004, fig. 76) also resembles but is smaller than our specimens, and the aperture is unknown. One of the specimens reported as *Knightella* sp. from the Permian Akasaka Limestone, Japan (Nützel and Nakazawa, 2012, figs. 21E, F), is similar to the present specimens but differs in having slender teleoconch whorls.

Occurrence.—This species is relatively common from the studied locality.

Informal group "Lower Heterobranchia", Bouchet and Rocroi, 2005
Superfamily Omalogyroidea Sars, 1878
Family Stuoraxidae Bandel, 1996
Genus ***Stuoraxis*** Bandel, 1996
(by S. Isaji and T. Haga)

Type species.—*Stuoraxis lehmanni* Bandel, 1996, early Carnian (Late Triassic), Italy.

Remarks.—Bandel (1996) stated that the Stuoraxidae is distinguished by the presence of axially ornamented protoconch from the other small, planispiral "lower heterobranch" gastropods such as Omalogyridae, Hyalogyrinidae and Xylodisculidae. Later, Kaim (2004) claimed that the status of Stuoraxidae remains unclear because similar ornamented protoconch are also present among other heterobranch groups, e.g. the omalogyrids and even the mathildids. In this paper, the Bandel (1996)'s opinion is adopted.

The systematic position of the Stuoraxidae in the "Lower Heterobranchia" is also still ambiguous. The Stuoraxidae was originally included in the superfamily Architectonicoidea (Bandel, 1996). Later, the Stuoraxidae was placed as a member of the superfamily Omalo-

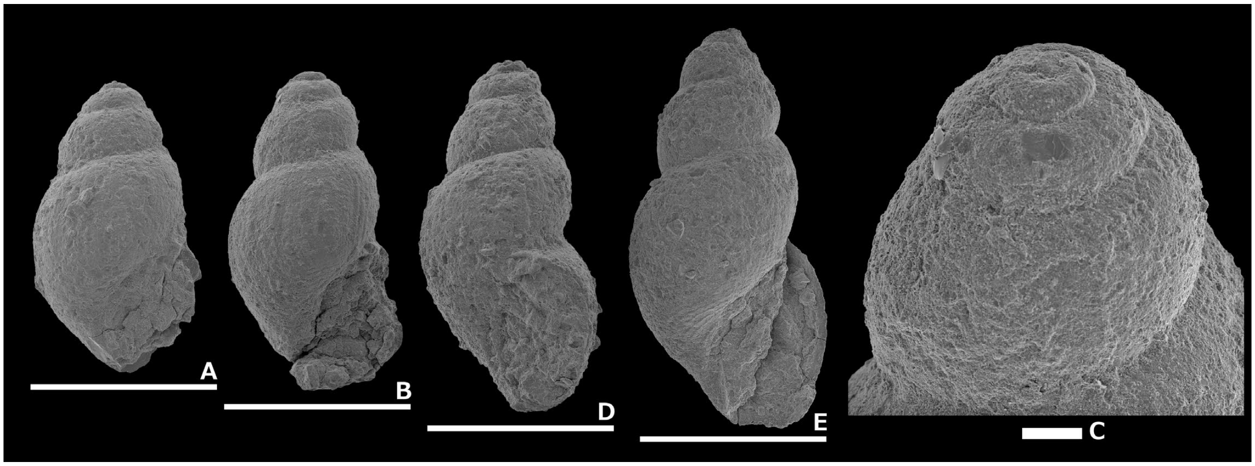

Figure 11. *Knightella* sp. from the Barremian Kimigahama Formation, Choshi Group, Japan. **A**, CBM-PS 6471, apertural view; **B**, **C**, CBM-PS 6472; B, apertural view; C, enlarged oblique apical view showing blunt protoconch; **D**, CBM-PS 6473, apertural view; **E**, CBM-PS 6474, apertural view. Scale bars = A, B, D, E: 1 mm; C: 0.1 mm.

gyroidea (Bouchet and Rocroi, 2005; Gründel, 2007; Bouchet *et al*., 2017).

Stuoraxis kasei Isaji and Haga sp. nov.

Figures 12A–J

Etymology.—In honor of Tomoki Kase of the Kanagawa University who has studied Japanese Mesozoic gastropod fossils and has made great contributions to progress on recent and fossil malacological research in Japan.

Types.—Holotype, CBM-PS 6475; two paratypes, CBM-PS 6476, 6477.

Diagnosis.—The shell is very small and almost planispiral. The protoconch is ornamented by 5–11 axial folds, which are weakest among *Stuoraxis*.

Description.—The shell is almost planispiral and consists of about 3 whorls. The spire is almost flat and the underside is very widely umbilicate. The protoconch consists of about 1.2 whorls, measuring approximately 0.19 mm in diameter. The tip of the protoconch is hyperstrophic, hence, it is visible from the umbilicus (Figure 12I, J). The surface of protoconch I is smooth. The protoconch II is ornamented by approximately 5–11 axial folds, which become weaker and flattened toward the periphery (Figure 12E). The end of the protoconch has an apertural rim that demarcates it from the teleoconch (Figure 12E, J). The teleoconch whorls increase gently in diameter and are moderately convex with tightly impressed sutures. The whorls have an indistinct shoulder and weak peripheral angulation, and the spaces between them are flat. The base is moderately flattened and becomes rounded toward the umbilicus. The aperture is roundly ovate, occupying approximately 35% of the total shell diameter and is not interrupted by the previous whorl. The plane of the aperture is oriented slightly prosocline to the axis. The umbilicus occupies approximately 40% of the total shell diameter.

Dimensions (in mm).—CBM-PS 6475: $D = 0.92$, $H = 0.33$. CBM-PS 6476: $D = 1.27$, $H = 0.50$. CBM-PS 6477: $D = 0.66+$.

Remarks.—Five species hitherto placed in the genus *Stuoraxis* were collected from the late Permian to Middle Jurassic deposits. Thus, Early Cretaceous *Stuoraxis kasei* sp. nov. is the youngest species of *Stuoraxis*. The overall shell shape of *S. kasei* is similar to that of *Stuoraxis wareni* Kaim, 2004 from the Bathonian (Middle Jurassic) of Częstochowa region, Poland (Kaim, 2004, fig. 124, C1–5), but differs from the latter in having weaker axial folds on the protoconch. *Stuoraxis kasei* has fewer axial folds on the protoconch than *Stuoraxis lehmanni* Bandel, 1996 (number of axial folds = *ca.* 12–20) from the lower Carnian (Upper Triassic) of Dolomites, Italy (Bandel, 1996, figs. 12a–d, p. 348, figs. 13c–f), *Stuoraxis angulata* Gründel, 2007 (number of axial folds = *ca.* 20) from the upper Toarcian and the lower Aalenian (Middle Jurassic) in Germany (Gründel, 2007, figs. 3H–J), and *Stuoraxis parvula* Gründel, 1998 (number of axial folds = *ca.* 30) from the Bathonian–middle Callovian (Middle Jurassic) in Germany (Gründel, 1998, pl. 4, figs. 47–51). *Stuoraxis minutus* (Pan and Erwin, 2002, figs. 10.6–10.8) from the lower Changhsingian (upper Permian) of South China, differs from *S. kasei* in that it has a more concave upper side of the shell and an absence of axial folds on the late larval shell.

Occurrence.—This species is rare from the studied locality.

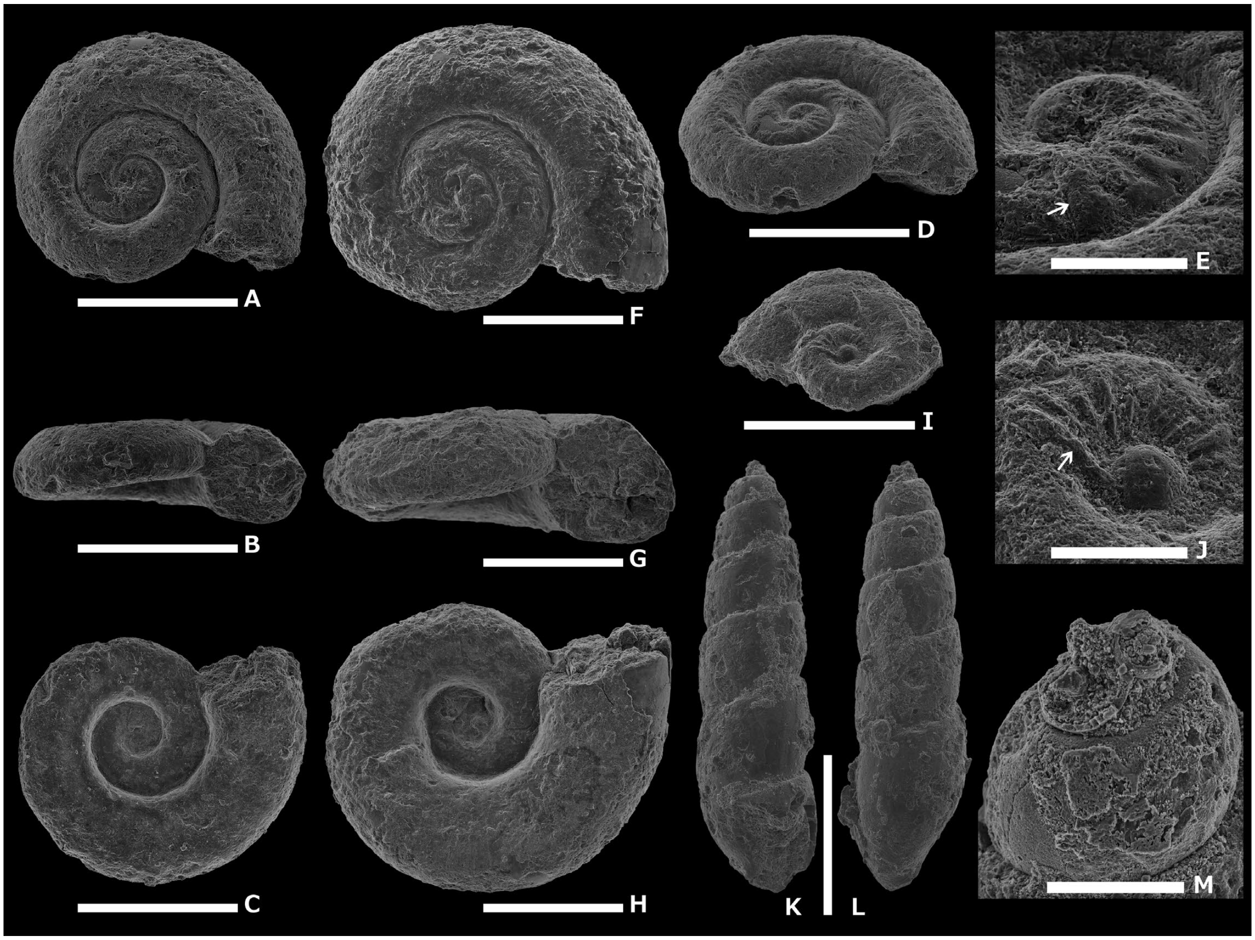

Figure 12. "Lower Heterobranch" gastropods from the Barremian Kimigahama Formation, Choshi Group, Japan. **A–J**, *Stuoraxis kasei* sp. nov.; A–E, CBM-PS 6475, holotype; A, apical view; B, lateral view; C, umbilical view; D, oblique view of apical side; E, enlarged view of protoconch; white arrow indicating the demarcation between protoconch and teleoconch, F–H, CBM-PS 6476, paratype; F, apical view; G, lateral view; H, umbilical view; I, J, CBM-PS 6477, paratype; I, oblique view of umbilical side; J, enlarged view of protoconch; white arrow indicating the demarcation between protoconch and teleoconch; **K–M**, *Ebala* sp., CBM-PS 6478; K, apertural view; L, abapertural view; M, enlarged oblique apical view showing fractured surface of heterostrophic protoconch. Scale bars = A–D, F–I, K, L: 0.5 mm; E, J, M: 0.1 mm.

Superfamily Murchisonelloidea Casey, 1904
family Murchisonellidae Casey, 1904
Subfamily Ebalinae Warén, 1995
Genus *Ebala* Leach in Gray, 1847

Type species.—Turbo nitidissima Montagu, 1803, by original designation; Recent.

Ebala sp.

Figures 12K–M

Material.—Single specimen; CBM-PS 6478.

Description.—The shell is small and cylindrical in shape. The protoconch is heterostrophic but poorly preserved in the examined specimens; its axis seems to form a moderate angle with the coiling axis of the teleoconch (Figure 12M). The teleoconch consists of at least five whorls that increase slowly in diameter, and are broadly convex with inclined sutures and narrow shoulders. The teleoconch surface is smooth with faintly opisthocyrtic growth lines. The aperture seems to be elliptical with a slightly flared basal lip and occupies approximately 20% of the total shell height.

Dimensions (in mm).—CBM-PS 6478: $H = 1.35+$, $W = 0.37$.

Remarks.—*Ebala* is usually found in Mesozoic marine deposits and the morphology has changed little since the Triassic (e.g. Schröder, 1995; Bandel, 1996, 2005; Kaim, 2004). The shell profile of the present specimen is similar to those of some Mesozoic species, such as *Ebala cas-*

siana Bandel, 1996 from the lower Carnian (Upper Triassic) St. Cassian Formation, Italy (Bandel, 1996, figs. 1g–1i) and *Ebala gruendeli* Kiel, 2001 from the Campanian (Upper Cretaceous) of Torallola in north-eastern Spain (Kiel and Bandel, 2001, pl. I, figs. 15–17) in having a slender cylindrical shell.

Occurrence.—This species is rare from the studied locality.

Discussion

Our approach using the sodium tetraphenylborate method appears to be effective for extracting small molluscan fossils from strongly lithified deposits of the Barremian Kimigahama Formation of the Choshi Group, Japan. This study revealed the first occurrence for the following families and subfamilies; Eudaroniidae, Pseudomelaniidae, Ampezzopleurinae, Metacerithiidae, Procerithiidae, Nystiellidae, Metaxiinae, Stuoraxidae and Ebalinae. Among these taxa, six new species, including one new genus, have been described. Details of the fossil gastropod composition are listed in Table 1. Of these newly described species, three species are identical or closely related to the species from the Lower Cretaceous in Western Europe. *Metacerithium boshuae* sp. nov. is closely related to *M. turriculatum* from the Lower Greensand of England. The specimens of *Cirsocerithium subspinosum* (Deshayes in Leymerie, 1842) are indistinguishable from those of the Albian Gault of France, North Germany and England. *Pseudomelania yamadai* sp. nov. seems to be related to *P. trochiformis* and *P. paucispira* from the Valanginian of Poland. Thus, the above three species are considered as constituents of a widely distributed gastropod assemblage during the Early Cretaceous period as well as to have co-occurred with larger gastropods from the Kimigahama Formation, such as *V. decussata*, *H. rex*, *C. densestriatus* and *P. elegans* which were previously pointed out as close relationships with the Early Cretaceous European species (Kase and Maeda, 1980).

On the other hand, the gastropod assemblage of the Kimigahama Formation also contains anachronistic taxa, which have not yet been found in the other Lower Cretaceous deposits. The species of subfamily Ampezzopleurinae have hitherto been limited to those in the Triassic deposits (Zardini, 1985; Batten and Stokes, 1986; Nützel, 1998; Stiller, 2001; Nützel and Erwin, 2004; Nützel and Schulbert, 2005; Kaim *et al.*, 2006; Kaim *et al.*, 2014). *Ampezzopleura barremica* sp. nov. is the first record of occurrence of this genus from the Cretaceous deposit. *Choshipleura striata* gen. et sp. nov. is also first identified as a new genus of the Ampezzopleurinae from the Kimigahama Formation. Consequently, it is probable that *A. barremica* and *C. striata* were relict species of the Ampezzopleurinae in the far eastern Tethyan region in Early Cretaceous period.

The above consideration may be applied to the youngest occurrence of the genus *Stuoraxis*, which has hitherto been reported from the Permian to Middle Jurassic deposits (Bandel, 1996; Gründel, 1998, 2007; Pan and Erwin, 2002; Kaim, 2004). In this case, it is noteworthy that the genus *Stuoraxis* shifted the habitat from shallow marine to deep sea during Permian–Jurassic interval (Figure 13; Bandel, 1996; Gründel, 1998, 2007; Pan and Erwin, 2002; Kaim, 2004). The oldest known early Changhsingian (late Permian) *S. minutus* occurs in siliceous limestone, deposited in muddy–sandy tidal flats (Pan and Erwin, 2002). Early Carnian (Late Triassic) *S. lehmanni* occurs from marl which seems to have been deposited in shallow, warm, carbonate lagoons (Bandel, 1996). In contrast, late Early to Middle Jurassic species, such as *S. angulata*, *S. wareni* and *S. parvula*, occur in claystones suggesting open sea or offshore environments of greater depth (Gründel, 1998, 2007; Kaim, 2004). This presumption regarding the habitat shift indicates that *Stuoraxis* adapted to deep-sea environments by the late Early Jurassic, possibly by increasing tolerance of anaerobic conditions.

In contrast to the Jurassic species, *S. kasei* occurred in the inner shelf deposits of shallow marine environments (Figure 13; Katsura *et al*., 1984; Ishigaki and Ito, 2000). More noteworthy is that *S. kasei* is often found together with a wood fossil with boreholes generated by pholadoidean bivalves of a probable member of the genus *Turnus* on the same bedding plane (Figure 2B). The associated bivalves were most likely xylophagous because their boreholes could be assigned to the trace fossil of *Teredolites longissimus* Kelly and Bromley, 1984 (Kelly, 1988a, 1988b; Haga and Kase, 2011). Research on extant deep-sea food chains shows that xylophagous pholadoidean bivalves play a major role in the foundation of sunken wood ecosystems because animals and their carcasses serve as a food source for predators and scavengers in the communities (Turner, 1978). Importantly, they also provide stable reducing microenvironments in and around boreholes, where chemosynthetic microbial and invertebrate communities develop (Bienhold *et al*., 2013; Nishimoto *et al*., 2015). Thus, the appearance of pholadoidean bivalves with xylophagy, combined with a long and winding borehole, is a probable index of local, chemosynthesis-based environments in sunken wood.

In our study, the evidence of local reducing environments is confirmed by the presence of pyrite in the borehole of the wood fossil. These points of view allow us to imagine that *S. kasei* might be a member of a chemosynthesis-based community that lived around or in the bore-

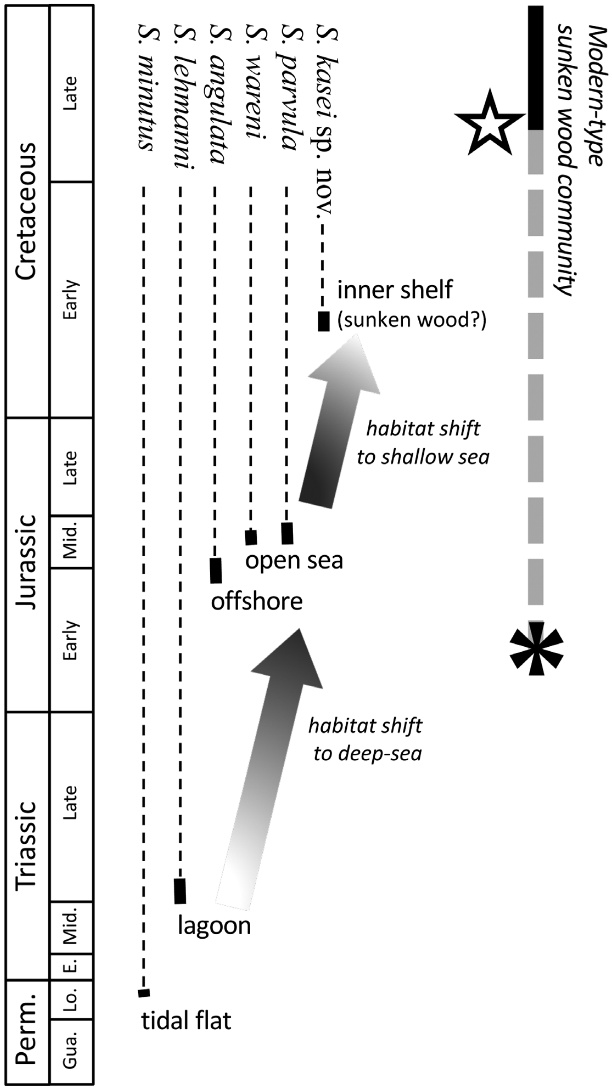

Figure 13. Schematic diagram showing habitat shift of the species of *Stuoraxis* through geologic time. White star indicates the oldest fossil record of the modern-type sunken wood molluscan assemblage (Kiel *et al*., 2009). Asterisk indicates the establishment of the groundwork for the chemosynthesis-based sunken wood communities (Haga and Kase, 2011).

holes of the sunken wood. However, *S. kasei* has not been observed *in situ* around or in the boreholes of the wood fossils due to the use of a sodium tetraphenylborate-based extraction method. On the other hand, Kaim (2011) examined the Middle Jurassic sunken wood association of the Częstochowa Ore-bearing Clay Formation, Poland, in which *Stuoraxis* was not found although *S. wareni* was known from coeval deposits of Częstochowa (Kaim, 2004). Therefore, the assumption of the chemosynthesis-based mode of life for *S. kasei*, however, must be examined further by detailed observations of the *in situ* mode of occurrence and/or geochemical approaches.

The oldest record of a lineage in the gastropod assemblage is also from the Kimigahama Formation. *Antiphora aurora* sp. nov. described here represents the first record of the Triphoridae from Mesozoic deposits, which expands the first appearance datum to the Early Cretaceous. Nützel (1998) regarded *A. ganensis* from the Eocene as a member of subfamily Metaxiinae of the Triphoridae, with *A. ganensis* differing from typical triphorids only by coiling, and then he suggested that the sinistral triphorids originated from the dextral forms like *A. ganensis.* However, this idea appears to be inconsistent with the occurrence of the oldest typical sinistral triphorids from the Lower Paleocene Faxe Formation, Denmark reported by Ravn (1933) and Nützel (1998) as pointed out by Guzhov (2002). Therefore, Early Cretaceous *A. aurora* seems to support the idea that the sinistral triphorids originated from the Mesozoic dextral forms. It is also inferred that triphorids have originated in the far eastern Tethyan region during the Early Cretaceous period.

Concluding remarks

Small molluscan fossils are usually difficult to extract from the strongly consolidated clastic rocks of Mesozoic and Paleozoic deposits in Japan. This might have resulted in collection bias in previous studies, which seemed to reveal only part of the faunal diversity. Most recognized assemblages are based mainly on the fossil record of large animals. Small gastropods have often been overlooked; thus, little has been discovered regarding historical changes in the small-sized gastropod fauna, despite their importance as basal components of marine molluscan ecosystems. At present, this type of small shell-bearing facies is found nowhere else in the Choshi Group, occurring only at a locality in the Kimigahama Formation. Even here, it has been overlooked for many years, despite the first discovery of molluscan fossils made at the locality in 1972. As shown in this study, the sodium tetraphenylborate method is an effective tool with which to reveal the true diversity of the fossil molluscan fauna. It is worth testing this method at other localities and for other deposits. Finally, the findings of this study remind us that we must look more carefully into the composition of oft-ignored “hidden” small-sized gastropod assemblages to obtain a fuller understanding of the molluscan fauna.

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Author contributions

S. I. initiated the study and was primarily responsible for the taxonomic aspects. T. H. was responsible for a part of Taxonomy. K. K. carried out the microfossil analysis. All authors contributed to the writing of the paper.