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Nipponomaria, a new pleurotomarioidean gastropod genus (Mollusca) from the Permian Akasaka Limestone, central Japan

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Abstract. ***Pleurotomaria yokoyamai*** **Hayasaka is a remarkably large gastropod commonly found in the middle Permian allochthonous Akasaka Limestone of central Japan. Its supraspecific systematics have however been unsettled. Examination of a museum collection and newly obtained material reveal previously unreported shell characteristics such as the presence of a long labral slit in the outer lip and a slit-like umbilicus surrounded by an accretionally growing callus pad. On the basis of these and previously known shell characters, a new genus *Nipponomaria* is proposed. We include *Pleurotomaria*? *anatolica* Enderle from the Permian anthracolithic limestone of northwestern Turkey as a member of this new genus.**

Key words: Akasaka Limestone, Gastropoda, *Nipponomaria*, Permian, systematics

Introduction

The Permian Akasaka Limestone in central Japan has long been known for its rich invertebrate fossils, including extraordinary large-sized molluscs such as *Bellerophon*, *Naticopsis* and the alatoconchid bivalve *Shikamaia* (e.g. Hayasaka and Hayasaka, 1953; Ozaki, 1968; Isozaki and Aljenović, 2009). Although gastropods from the Akasaka Limestone have been the subjects of descriptive studies for over a century (e.g. Hayasaka, 1925, 1938, 1939, 1943, 1955; Koizumi, 1995; Nützel and Nakazawa, 2012), many species have not yet been described in museum collection and the suprageneric systematics of some previously named taxa are not well understood. *Pleurotomaria yokoyamai* Hayasaka, 1943 is a remarkable species in the Akasaka Limestone in terms of its extraordinary large shell size (250 mm high and 200 mm wide in the largest specimen), and its familial and/or generic positions are still dubious mainly owing to the absence of information on the labral slit in the outer lip and selenizone (Isozaki and Kase, 2014). This paper is concerned with a redescription of *P. yokoyamai* with special reference to the labral slit and selenizone based on the collections in the National Museum of Nature and Science, Tsukuba (NMNS) and newly obtained material from the Akasaka Limestone. Here we propose a new genus, *Nipponomarina*, for this species.

Material

The Permian Akasaka Limestone, exposed on Mt. Kinshozan in Ogaki City, Gifu Prefecture, central Japan, is an allochthonous limestone body within the Jurassic accretionary complex of the Mino-Tanba Belt in Southwest Japan (e.g. Isozaki, 1997; Isozaki and Ota, 2001; Ota and Isozaki, 2006). It originated on a low-latitude paleo-atoll in the Panthalassan sea (e.g. Zaw Win, 1999; Ota and Isozaki, 2006; Kasuya *et al.*, 2012; Isozaki and Kase, 2014). The Akasaka Limestone consists of four units: the Lower, Middle, Upper and Uppermost members (or Ichihashi Formation: Kani *et al.*, 2013), ranging in age from the uppermost Cisuralian (lower Permian) to the lowermost Lopingian (upper Permian) (e.g. Ozawa and Nishiwaki, 1992; Zaw Win, 1999). Fifteen specimens discussed in this paper were from the black limestone beds of the Middle and Upper members, ranging from the *Neoschwagerina* Zone to the *Yabeina globosa* Zone, Guadalupian (Roadian to Capitanian) in age (Ozawa,

1927; Ozawa and Nishiwaki, 1992; Zaw Win, 1999; Ota and Isozaki, 2006; Nishiwaki *et al*., 2011; Kani *et al*., 2013; Nishiwaki *et al.*, 2014). Ozawa and Nishiwaki (1992) have shown that the Middle to Upper members were deposited in an open lagoonal environment under gentle water movement.

All specimens described in this paper are housed in the Department of Geology and Paleontology, the National Museum of Nature and Science (NMNS), Tsukuba. The morphologic terminology adopted here follows Cox (1960, fig. 1).

Systematic paleontology

Subclass Vetigastropoda von Salvini-Plawen, 1980
Order Pleurotomariina Cox and Knight, 1960
Superfamily Pleurotomarioidea Swainson, 1840
Family Eotomariidae Wenz, 1938
Subfamily Eotomariinae Wenz, 1938
Genus: ***Nipponomaria*** Asato and Kase, gen. nov.

Type species.—*Pleurotomaria yokoyamai* Hayasaka, 1943 from the middle Permian of Japan.

Diagnosis.—Very large, thick and trocho-turbiniform shell characterized by having step-like ramp, angular ramp angle at middle and almost vertical outer face of whorl. Base smooth, weakly convex, separated from outer whorl face with obtusely peripheral bulge. Umbilicus slit-like, surrounded by accretionally growing callus pad. Aperture subcircular with inner lip thickened by inductura. Labral slit extending about 1/4 length of whorl from outer lip. Selenizone very narrow, deep, defined by sharp spiral ridges and lying on ramp angle. Shell surface ornamented with fine sharp spiral cords of variable strength on ramp and outer face of whorl and abaxially fading subsutural collabral folds.

Etymology.—The generic name is a combination of *Nippon* (meaning Japan) and *maria*; gender feminine.

Nipponomaria yokoyamai (Hayasaka, 1943)

Figures 1–5

Pleurotomaria yokoyamai Hayasaka, 1943, p. 28, pl. 2, fig. 1, text-fig. 1; Shikama, 1952, p. 180, pl. 52, fig. 2; Hayasaka and Hayasaka, 1953, p. 39; Shikama, 1964, p. 98, pl. 26, fig. 5.

"*Pleurotomaria*" *yokoyamai* Hayasaka. Masutomi and Hamada,1966, p. 71, pl. 36, fig. 4; Koizumi, 1995, p. 104, pl. B, pl. C, fig. 1, pl. 27, figs 1, 2; Isozaki and Kase, 2014, p. 253, fig. 3.

Bathrotomaria? *yokoyamai* (Hayasaka). Hayami and Kase, 1977, p. 32, pl. 3, figs. 6, 7.

Zhonghuaspira yokoyamai (Hayasaka). Nützel and Nakazawa, 2012, p. 111–113, figs. 8P, Q, 9A.

Type and material.—Holotype (Hayasaka, 1943, pl. 2, fig. 1). The holotype and at least two paratypes appear to have been in the collection of Taiwan National University, Taipei when Hayasaka (1943) described this species, but a coauthor (T. K.) could not locate them in 1984. The specimens examined and discussed in this study are all in the collection of the Department of Geology and Paleontology, National Museum of Nature and Science with the registration numbers NMNS PM: 15 specimens, NMNS P1-1054, P1-1068, P1-4719, PM12417, PM13147, PM25826, PM25827, PM26953–26958, PM26977, and PM26979. PM26953 and PM26954 are polyester resin casts taken from the specimens in the collection of M. Hori of Ogaki City.

Diagnosis.—Same as for the genus.

Description.—Shell very large, trocho-turbinifom, around 250 mm high and wide in largest specimen, as high as wide, thick but becoming thinner rather abruptly after final 1/4 volution of last whorl. Spire occupying about half length of shell height, with spire angle 90°–100°. Spire whorls step-like, with weakly inclined ramp, almost vertical outer face of whorl and rectangular ramp angle located at mid-whorl, whereas in axial section whorl interior is subcircular. Shallowly depressed ramp and ramp angle gradually becoming flat and obsolete toward last whorl, respectively. Suture adpressed. Last whorl wider than high, occupying about half of shell height, with almost vertical outer face of whorl. Base abruptly constricted anteriorly, weakly inflated without any spiral sculpture, and angulated peripheral bulge gradually becoming rounded toward aperture. Aperture subcircular, continuous except for parietal area; outer lip thin, rounded, and inner lip thick and covered with inductura. Labral slit narrow and extending 1/4 length of whorl from outer lip. Umbilicus slit-like and surrounded with accretionally growing callus pad. Ramp and outer face of whorl sculptured with fine and sharp spiral cords of variable strength: ramp ornamented by 12 to 14 abaxially fading collabral subsutural folds. Selenizone at ramp angle very narrow, concave and bordered by sharp spiral cords, probably with fine lunules. Growth line prosocline and opisthocyrt on ramp, while opisthocline and opisthocyrt on outer face of whorl below selenizone.

Remarks.—To the best of our knowledge, NMSN PM26953 (Figure 1A) is the largest specimen that preserves an almost complete shell. However, a fragmentary specimen in the collection of M. Hori approximates 250 mm in shell width, so that this species reaches a much larger size than NMSN PM26953. The detailed characteristics of the shell base and inner lip of the aperture are clarified for the first time, based on NMNS PM25826 (Figure 1B, C), and the abrupt thinning of the shell thickness near the aperture is clearly seen in this specimen.

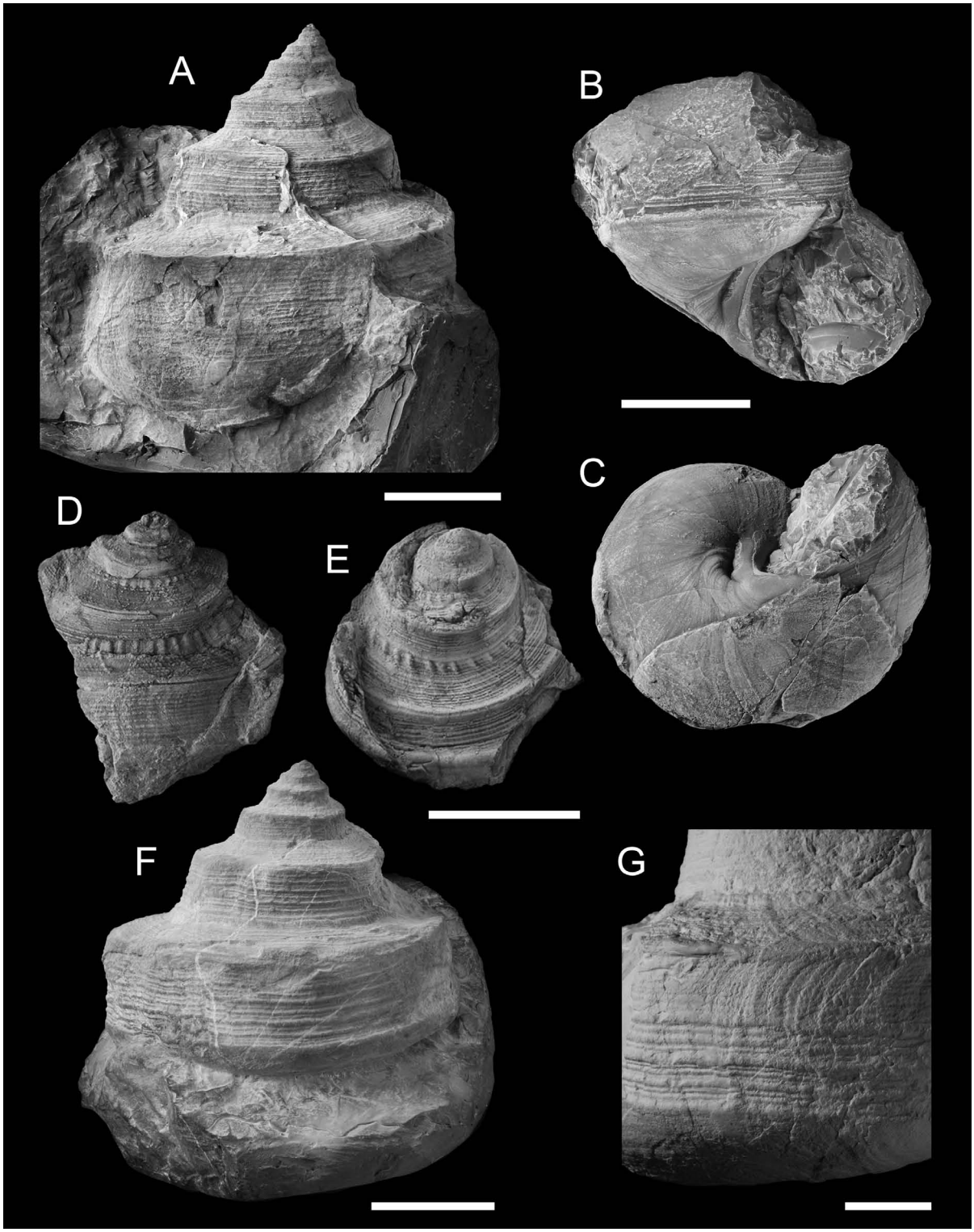

Figure 1. *Nipponomaria yokoyamai* (Hayasaka, 1943). **A**, NMNS PM26953 (cast), shell width 141.2 mm; **B**, **C**, NMNS PM25826, shell width 132 mm; B, apertural view; C, basal view; **D**, NMNS PM25827, shell width 62 mm; **E**, NMNS PM26956, shell width 65 mm; **F**, NMNS PM26954 (cast), shell width 151.4 mm; **G**, NMNS PM26979, shell width 160 mm. All specimens are from the Akasaka Limestone, Gifu Prefecture, Japan. Scale bars, A–C and F, 50 mm; D, E, 30 mm; G, 20 mm.

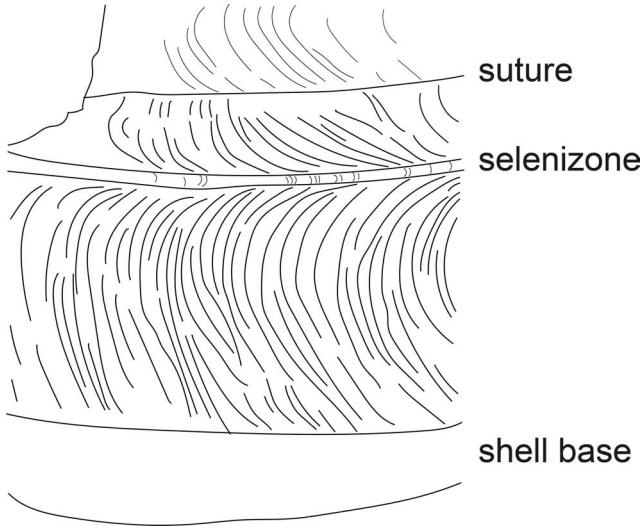

Figure 2. Schematic sketch of the last whorl surface of *Nipponomaria yokoyamai* (Hayasaka, 1943) in NMNS PM26979. Note that the growth lines are prosocline and prosocyrt above and below the selenizone, respectively.

Discussion

Observation of selenizone and labral slit.—Hayasaka (1943) assumed that the selenizone might be located on the ramp angle of the whorls, but he could not observe it in the specimens that he examined. In contrast, Koizumi (1995) believed that the selenizone was absent, and he allocated this species to the family Trochonematidae, where the growth lines form shallow V-shaped sinuses above the mid-whorl (Knight *et al*., 1960). Isozaki and Kase (2014) were the first to recognize the selenizone correctly at the ramp angle. This was based upon the fact that there is a very narrow and deep spiral zone at the ramp angle where the prosocline growth lines on the ramp and the prosocyrt growth lines on the outer face of the whorl join, forming acute V-shaped sinuses in this region (Figure 1D, E, G). They considered the selenizone to be a very narrow and deep spiral zone delimited by two sharp spiral cords (Figure 1D, E). In this study, we found some additional specimens that clearly show this structure (Figures 1G, 2). However, the characteristics of the labral slit in the outer lips still remains unknown, owing to the absence of specimens with a complete outer lip.

In order to clarify the characteristics of the labral slit in this species, we used two methods for the two newly obtained specimens (NMNS PM25826 and PM26958; Figures 3, 4). These specimens have a complete columellar lip covered with a thick inductura (Figures 1B, C, 4A–C). Judging from the extension of this columellar lip, these specimens are likely to preserve the outer lip. Nonetheless, the labral slit is not seen in these specimens because the shell is very thin in this area and the distinction between the shell and limestone matrix is not clear even under a binocular microscope. For NMNS PM25826, we used sandpaper for gradually grinding and polishing the shell surface around the ramp angle in the last 1/4 whorl (Figure 3). In this method, the labral slit, if any, is recognized by the black limestone matrix always exposed on the polished surface in an area of the slit, whereas the selenizone is recognized by the presence of the shell material extending continuously from the upper to the outer whorl surfaces. This method demonstrated the presence of a short labral slit that extends for a quarter volution back from the outer lip in NMNS PM25826 (Figure 3).

The second method is to cut the shell serially along its shell axis in the later part of the last whorl (Figure 4). If the cutting plane crossed the selenizone, the presence or absence of the labral slit and selenizone can be recognized such that the shell is continuous on the ramp to the outer face of the whorl (Figure 4D). However, it is discontinuous if the cutting plane crossed the slit (Figure 4D). This method confirms the presence of a labral slit with a length almost the same as that from the first method, in the case of NMNS PM25826.

Generic comparison.—Here we propose the new genus *Nipponomaria* for *Pleurotomaria yokoyamai* as the type species as discussed below. Hayasaka (1943) referred *N. yokoyamai* to the genus *Pleurotomaria* Defrance, 1826 but suggested that this species might belong to a new genus. He did not propose a new genus as he possibly lacked information on the labral slit and selenizone at that time. *Pleurotomaria* is a genus ranging from the Jurassic to Early Cretaceous, and its type species *P. anglica* (Sowerby, 1818) resembles *N. yokoyamai*, although clearly differing from the latter primarily in having a selenizone positioned well below the ramp angle. It is very likely that Hayasaka did not consider the close affinity between *N. yokoyamai* and *P. anglica*. He thus followed the traditional generic assignment at that time, which meant assigning Paleozoic slit-bearing gastropods to *Pleurotomaria* if the shells were trochoturbiniform while they were referred to as *Murchisonia* d'Archiac and de Verneuil, 1841 if the shells were elongate.

Hayasaka (1943) extensively discussed the affinity of *Nipponomaria yokoyamai* by comparing the following five species: *Pleurotomaria multicarinata* Mansuy, 1912 from the Carboniferous of eastern Yunnan in China, *Pleurotomaria loatienensis* Mansuy, 1914 from the Carboniferous of eastern Yunnan in China, *Pleurotomaria*

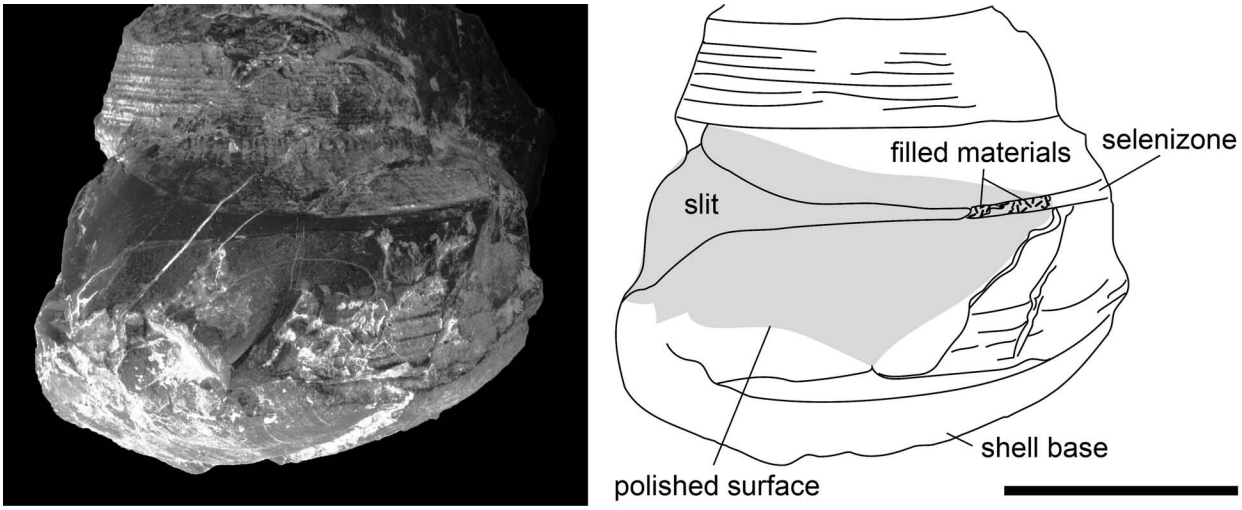

Figure 3. Labral slit of *Nipponomaria yokoyamai* (Hayasaka, 1943) in NMNS PM25826. The polished surface of NMNS PM25826 (left) and its schematic sketch (right). The presence of the labral slit is observable as a line of demarcation between the shell and the black limestone fill within the whorl. Scale bar is 50 mm.

conglobata Wanner, 1922 from the Permian of Timor, *Pleurotomaria* (*Worthenia*) *haydeni* Reed, 1925 from the upper Carboniferous in Chitral, Pakistan and *Pleurotomaria*? *anatolica* Enderle, 1900 from the middle Permian in Turkey. We consider that these species are not closely related to and are not congeneric with *N. yokoyamai* except for *P.*? *anatolica*. Delpey (1942) and Batten (1972, 1989) reallocated *P. multicarinata* to *Worthenia* de Koninck, 1883, whereas Pan (1985) referred it to *Baylea* de Koninck, 1883. Wagner (2013; online supplement) listed *P. conglobata* in the genus *Ananias* Knight, 1945. The illustrated holotype of *P. loatienensis* (Mansuy, 1914, pl. 1, fig. 15) is a trochiform gastropod, whose whorls are turreted and ornamented only by spiral cords, with an indistinct selenizone located at the peripheral bulge of the tabulated whorl. Although its apertural and basal characters are not known, we consider this species to belong to *Baylea* de Koninck, 1883. The single known specimen (holotype) of *P.* (*W.*) *haydeni* is a large trochiform gastropod characterized by tabulate whorls with an angular ramp angle, an almost vertical outer face of the whorl, and a slightly convex shell base. The shell surface sculpture is characteristic as the ramp and outer whorl surfaces are ornamented by thick spiral cords, while the shell base has numerous tuberculated axial ribs. Although the characteristics of the aperture, umbilicus and selenizone are not known, these shell features suggest that this species is a member of the genus *Worthenia* as originally assigned to it as a subgenus of *Pleurotomaria* by Reed (1925).

Pleurotomaria? *anatolica* Enderle, 1900 from the Permian anthracolithic limestone from Balia Maaden (= Balya Maden) in northwestern Turkey, has a shell profile and surface sculpture similar to *Nipponomaria yokoyamai*. According to Enderle (1900), his species was described on the basis of seven fragmentary specimens, at least four of which are now stored in the Geological Survey of Austria, Vienna. The largest specimen (GBA 1900/004/0008; Enderle, 1900, pl. 5, fig. 4a; Figure 6B–E) attains 101 mm in shell height, is worn and does not preserve the last whorl, so that the shell may have been larger than the size given by Enderle. Indeed, Enderle (1900, p. 53) stated that this species might have achieved a much larger shell size as he had an incomplete fragmental specimen of the same (or a closely related) species consisting of only two whorls, whose axial length was almost the same as that of the largest syntype specimen mentioned above. Thus, the shell size of *P.*? *anatolica* (or another similar species) is very large like *N. yokoyamai*. Enderle (1900) did not mention the selenizone. However, a narrow groove delimited by two sharp spiral keels at the ramp angle is clearly visible in one of the syntypes (GBA1900-004-0011; Figure 6D, E). It is highly likely that this groove is the selenizone of *P.*? *anatolica*.

Enderle (1900) placed his species in the genus *Pleurotomaria* with a query, and was inclined to establish a new genus for it owing to the peculiarity of the anterior margin of the shell aperture. He observed that the inner lip is thickened, the columellar lip extends anteriorly form-

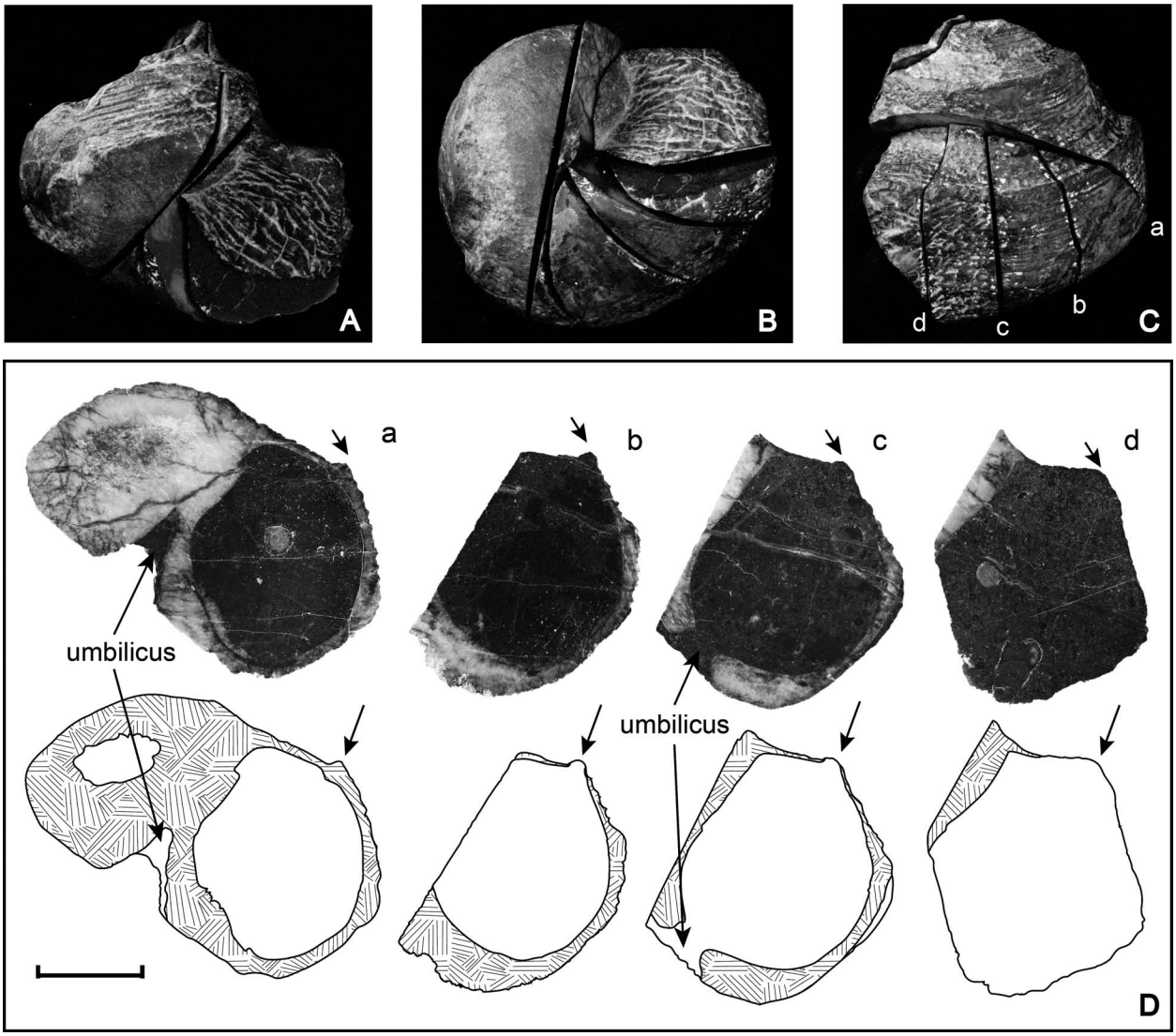

Figure 4. Serial sectioning of NMNS PM26958. **A**, apertural view; **B**, basal view; **C**, lateral view showing positions of sectioning at a to d; **D**, Polished surfaces of each cutting position at a to d. Arrows indicate position of ramp angle. Note that the labral slit is present between the cutting positions a and b. Scale bar is 20 mm.

ing a spout-like projection, and the umbilicus is slit-like (Figure 6). However, such a spout-like projection is not peculiar in imperfect trochiform shells lacking the outer and basal lip of the last whorl, particularly if the shell base is inclined anteriorly (i.e., shell is more elongate) more than in the case of *Nipponomaria yokoyamai*. Therefore, the basal character is quite similar both in *P.*? *anatolica* and *N. yokoyamai*, although it is not known whether the former species, due to poor preservation, has the characteristic callus pad around the umbilicus as seen in the latter. It is likely that the both species are congeneric. *P.*? *anatolica* differs from *N. yokoyamai* in its higher shell profile, the absence of the subsutural short axial ribs and the presence of indistinct spiral cords on the shell base.

Hayami and Kase (1977) allocated *Nipponomaria yokoyamai* to the genus *Bathrotomaria* Cox, 1956 without discussion. *Bathrotomaria* is a Mesozoic genus ranging from the Early Jurassic to the Late Cretaceous (Knight *et al*., 1960), and shows a trochiform to depressed trochiform shell profile; it has a widely open to closed umbilicus and a selenizone at the ramp angle (e.g. Cox, 1960; Das *et al*., 2005). In particular, *Bathrotomaria reticulata* (Sowerby, 1821) from the Kimmerid-

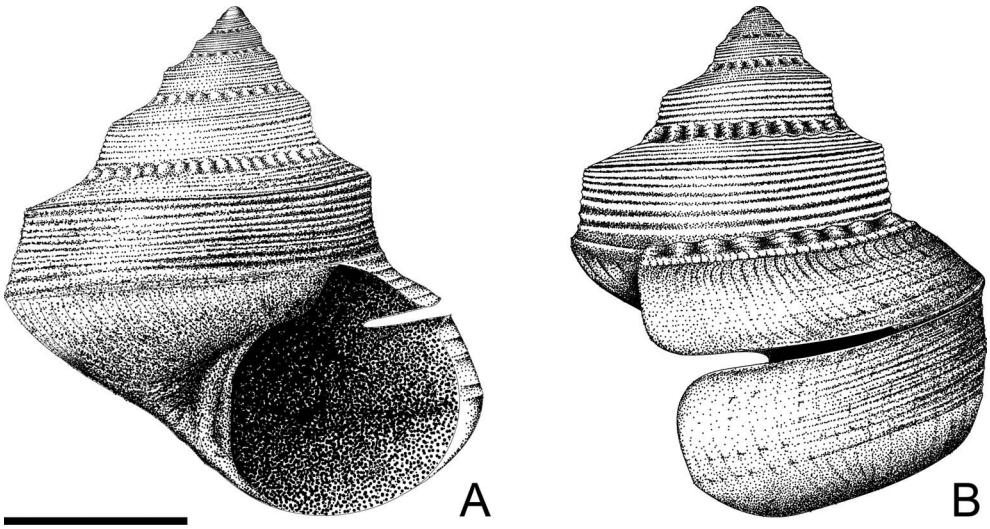

Figure 5. Schematic reconstruction of *Nipponomaria yokoyamai* (Hayasaka, 1943) based mainly upon NMNS PM25826. **A**, apertural view; **B**, right lateral view. Scale bar is 50 mm.

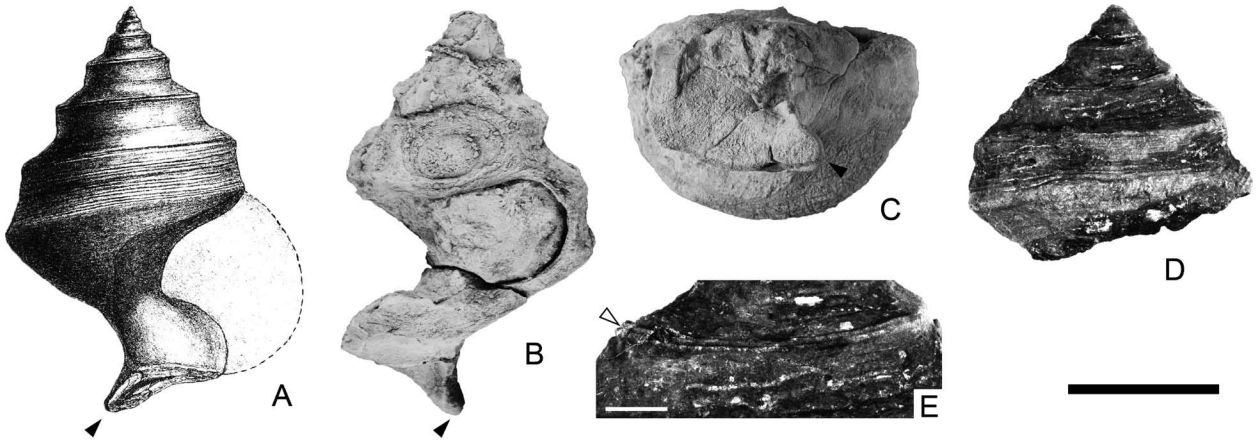

Figure 6. Syntypes of *Pleurotomaria*? *anatolica* Enderle, 1900 in the collection of the Geological Survey of Austria, Vienna. **A–C**, GBA 1900/004/0008; A, hand drawing of *P*?. *anatolica*, showing the thick inner lip and spout-like projection (marked with black and white arrows) of columellar lip (after Enderle, 1900, pl. 4, fig. 4); B, C, adapertural and basal views, showing the spout-like projection of the columellar lip (marked with black arrows) (courtesy of I. Zorn, Geological Survey of Austria); **D**, adapertural view; **E**, closeup of D showing the narrow selenizone (marked with white arrows) (courtesy of I. Zorn, Geological Survey of Austria). Scale bars are 50 mm for A–D and 10 mm for E.

gian of England superficially resembles *N. yokoyamai*. However, the surface sculpture is reticulated or beaded and the selenizone is flush to convex with threads or lunules in *Bathrotomaria*, while the sculpture is only of fine spiral cords (but with short subsutural ribs in *N. yokoyamai*) and the selenizone is deep and delimited by sharp cords in *Nipponomaria* gen. nov. In addition, there is a time gap of over 60 million years between the occurrences of the two genera. More recently, Nützel and Nakazawa (2012) reallocated *N. yokoyamai* to *Zhonghuaspira* Pan and Erwin, 2002 from the upper Permian of South China. *Zhonghuaspira* heretofore accommodates only the type species of the genus, *Zhonghuaspira gibbicircelloides* (Wang, 1982). *Zhonghuaspira gibbicircelloides* has a narrow and deep selenizone at the ramp angle and sculpture in the ramp and the outer whorl face

that are quite similar to those of *N. yokoyamai*. It clearly differs in having an open and deep umbilicus and a more steeply inclined ramp in addition to its much smaller shell size.

The Carboniferous and Permian genus *Baylea* de Koninck, 1883 (Raphistomatidae; Knight *et al*., 1960) resembles *Nipponomaria* gen. nov. in having a turreted trochiform shell and spiral sculpture, with one or two rows of axially elongated subsutural nodes in some species (e.g. Weller, 1929). However, it differs from the new genus in having a much smaller shell size, a narrowly phaneromphalous umbilicus and a shallow selenizone located at the peripheral bulge. Knight (1941, p. 51) suggested that the selenizone is very short in *B. yvani* (Léveillé, 1835), the type species of the genus, while it is quite long in the new genus.

The late Permian genus *Guizhouspira* Wang in Wang and Xi, 1980 from Guizhou Province of China has a sculpture pattern in the ramp and a convex base as in *Nipponomaria* gen. nov. However, in *Guizhouspira* the selenizone is wider and shallower, the peripheral bulge in the last whorl is more angulated, and the ramp is more steeply inclined as compared with *Nipponomaria* gen. nov. *Worthenia* exhibits a similar shell profile but is easily separated from *Nipponomaria* gen. nov. since the selenizone is convex and crenulated within.

Nipponomaria gen. nov. differs from the late Carboniferous to Early Triassic genus *Ananias* Knight, 1945 (type species *Phanerotrema*? *welleri* Newell, 1935 from the upper Carboniferous of Kansas) in having a lower shell profile, a larger pleural angle, a more gently inclined ramp and a narrower and deeper selenizone in addition to the much larger shell size.

Here we follow Knight *et al*. (1960) in the familial classification of Pleurotomarioidea and classify *Nipponomaria* gen. nov. into the subfamily Eotomariinae (Eotomariidae).

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