

Upper Jurassic Pleurotomariidae (Gastropoda) from southwestern Madagascar

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ABSTRACT

This paper describes four new species of Upper Jurassic Pleurotomariidae from southwestern Madagascar: *Obornella thompsonorum*, *Bathrotomaria annejoffeae*, *Bathrotomaria bedetteae*, and *Leptomaria takahashii*. In addition, the previously described *Leptomaria texta* Delpy, 1948, is reassigned to the genus *Obornella*. Comparison of this fauna with that of the geographically proximal Kutch region of northwestern India reveals it to consist of representatives of wide-ranging Tethyan genera, but also to exhibit strong endemism at the species level.

INTRODUCTION

A substantial number of well preserved Upper Jurassic pleurotomariid gastropods have recently been uncovered as a byproduct of commercial mining for ammonites in southwestern Madagascar. Six specimens, representing four species, were kindly made available to us for study by Mr. Chris Takahashi. The pleurotomariids and ammonites were dug by villagers from pit quarries near the town of Zakaraha, in southwestern Madagascar.

A survey of the literature on the Mesozoic gastropod fauna of Madagascar (e.g., Delpy, 1948; Collignon, 1949; Collignon, 1959; Kiel, 2006) revealed the majority of pleurotomariid species known from Madagascar to be of Cretaceous age, with only a single species, *Leptomaria texta* Delpy, 1948, reported from Jurassic strata. Although the sample available to us is of limited size and stratigraphic range, it expands our insight into the Jurassic pleurotomariid fauna of Madagascar. Like the well documented Jurassic pleurotomariid fauna of the Kutch (also spelled Kachchh) region of western India (Jaitley et al., 2000; Das, 2002; Das et al., 2005), the Madagascar fauna reveals Tethyan affinities at the generic level, yet exhibits endemism at the species level. Both faunas

evolved an increasing endemism within the Indo-Madagascan faunal province that was formed as the Tethys Ocean widened between Laurasia and eastern Gondwana, and a seaway started to develop between East and West Gondwana in the latest Jurassic (Tithonian) (Hay et al., 1999; Shome et al., 2004).

The scope of the present study is to review the Oxfordian (Upper Jurassic) pleurotomariid fauna of Madagascar, describe five species, four of them new, and to review the relationships and biogeography of these pleurotomariids.

GEOLOGICAL SETTING

Rifting between Africa and Madagascar produced three large sedimentary basins along the west coast of Madagascar. These are, from North to South, the Ambilobe (or Diego), Mahajanga (also spelled Majunga), and Morondava basins. Sedimentation in this region commenced in the Carboniferous with the deposition of the Gondwanan Karoo sequences and equivalents. The first marine deposits resulting from the break-up of the Gondwana supercontinent are of Toarcian (late Lower Jurassic) age. From then on, alternating shallow marine, brackish, and fluvial sediments were deposited in these basins. The pleurotomariids described here are from the Morondava basin, the southernmost of the three basins. Bio- and lithostratigraphic work in this basin is difficult because outcrops are few, index fossils are often not available, and measurable sections are usually short and difficult to correlate with each other. Consequently, only few lithostratigraphic units have been given formation names so far (Besairie and Collignon, 1972; Luger et al., 1994; Geiger and Schweigert, 2006).

The quarries that produced the specimens described here are located to the west of the town Zakaraha (also

spelled Sakkara), one of them north of the Fiherenana River, the other to the south of it (Figures 1, 2). The fossiliferous layers are thin and consist of pink-yellow iron-oolithic limestones, and are overlain by grey mudstones (K. Bandel, pers. comm., 2007). The southern locality is very close, if not identical, with the “Amparambato section (VIb)” of Geiger and Schweigert (2006: 99) which was characterized by them as “a highly fossiliferous iron-oolithic limestone and sandstone bed with thin mud-stone interlayers.” Accordingly, the oolitic limestones contain an abundant ammonite fauna; the overlying mudstones contain nodosariid Foraminifera and ostracods (Geiger and Schweigert, 2006). The northern quarry is geographically close to the “Middle-Upper Oxfordian Ankilimena section (XI)” of Geiger and Schweigert (2006). This section is characterized by recurrent iron-oolithic limestones, which contain ammonites, rhynchonellids, bivalves, belemnites, echinoderms, and wood debris (Geiger and Schweigert, 2006: 103). Although Geiger and Schweigert (2006) did not report

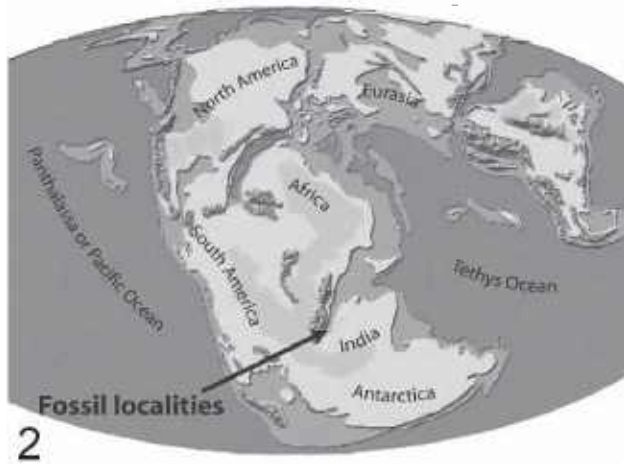
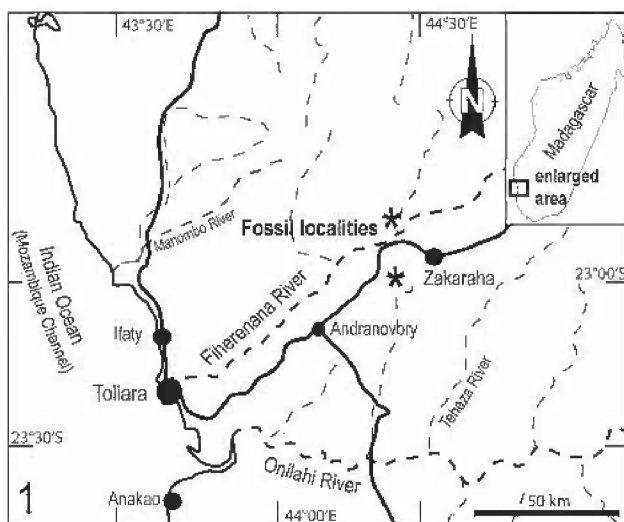
pleurotomariids or other gastropods from these sections, the remaining fossil content, their geographic position, and their lithology agrees well with that observed at the ammonite quarries visited by K. Bandel (pers. comm., 2007).

The ammonite fauna of these two localities, especially the presence of *Dhosaites* cf. *primus* Collignon, 1959, suggests a ‘middle to upper Argovian (early Oxfordian)’ age (Collignon, 1959; H. Kenpp, pers. comm., 2004). The term ‘Argovian’ has been abandoned due to its inconsistent usage, but largely falls within the range of the Oxfordian (Zeiss, 2003). The sediments considered as ‘Argovian’ by Besairie and Collignon (1972) correlate with those mapped as late Callovian–early Oxfordian by Geiger and Schweigert (2006). Thus, the pleurotomariids described here are most probably of Oxfordian (Upper Jurassic) age.

SUPRASPECIFIC CLASSIFICATION WITHIN PLEUROTOMARIIDAE

The number of genera and subgenera currently recognized within the family Pleurotomariidae (Appendix 1) has nearly doubled since the family was reviewed in the *Treatise of Invertebrate Zoology* (Knight et al., 1960). Of the 21 genera and subgenera now recognized (Figure 3), 16 are Mesozoic. Of these, five are restricted to the Triassic, three to the Jurassic, and only a single subgenus to the Cretaceous. At present, *Leptomaria* and *Conotomaria* are the only genera that are recognized as having survived from the Mesozoic into the Cenozoic. Of the seven Cenozoic genera, four survive in the Recent fauna. According to the literature surveyed, there is no chronological overlap between the Mesozoic genera and the Cenozoic genera.

As noted by a number of researchers (e.g., Hickman, 1976: 1094; Szabó, 1980: 49; Das, 2002: 99) fossil pleurotomariids are difficult to classify objectively, since the criteria upon which fossil pleurotomariid genera are defined differ conspicuously from those applied to Cenozoic genera. The monophyly and phylogenetic relationships of the surviving Cenozoic genera have been confirmed using molecular data from living representatives (e.g., Harasevych et al., 1997; Harasevych, 2002). By contrast, the relationships of Mesozoic genera and the species assigned to them are far less certain, as generic classification tends to be based on relatively few conspicuous morphological features (Table 1) especially those that are most easily derived from poorly preserved specimens and external or internal molds, while other characters are unconstrained and may vary widely. Szabó (1980: 49) commented that “almost all genera can be identified with certainty” on the basis of the shape of the whorl section and the surface of the whorls, as well as the position and width of the selenizone. Conti and Szabó (1987: 43) raised a question as to the significance of the presence or absence of an umbilicus in pleurotomariid



Figures 1, 2. Location of collection sites. **1.** Detailed map of two localities in southwestern Madagascar. **2.** Location of sites on a map of land masses during the Late Jurassic.

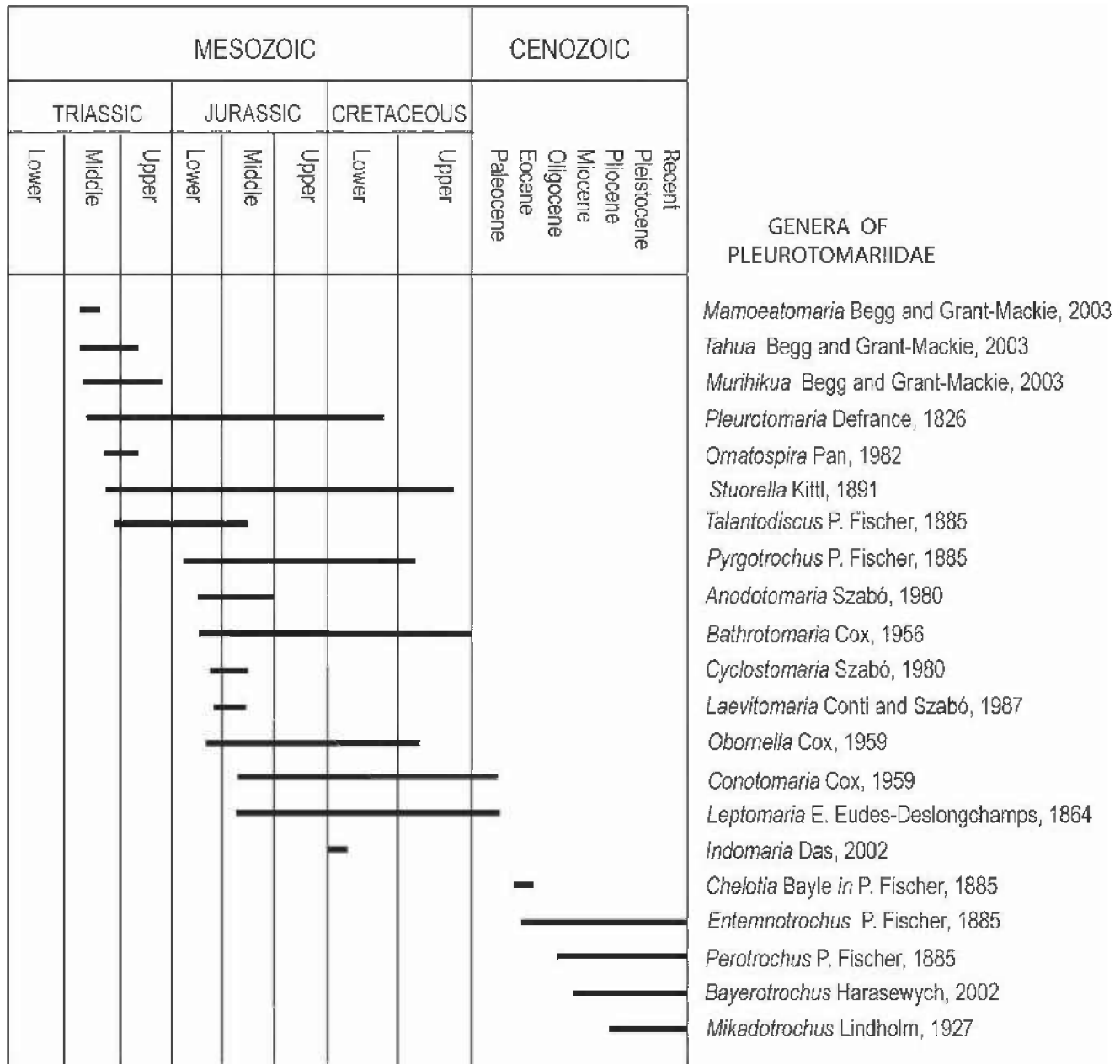


Figure 3. Geological ranges of the genera and subgenera within the family Pleurotomariidae, arranged by first occurrence in the fossil record.

classification. The presence or absence of an umbilicus is sufficient to distinguish the most basal dichotomy among living Pleurotomariidae, yet this feature remains unconstrained and may vary widely within most Mesozoic genera and even within some “species” as they are currently diagnosed. It is therefore not surprising that fossil species are frequently reassigned from one genus to another (e.g., *Pyrgotrochus* to *Laevitomaria* Conti and Szabó, 1987: 46; *Perotrochus* to *Leptomaria*, see Das et al., 2005: 331), especially as more numerous and better preserved specimens become available.

SYSTEMATICS

Family Pleurotomariidae Swainson, 1840
 Genus *Obornella* Cox, 1959
Obornella Cox, 1959: 238.

Type Species: *Pleurotomaria plicopunctata* J. A. Eudes-Deslongchamps, 1849 (By original designation). Bajocian (Middle Jurassic) of France.

Diagnosis: The genus *Obornella* is characterized by a shell that is low turbiniform to sublenticular, with a nar-

Table 1. Genera and subgenera currently recognized within the family Pleurotomariidae and the characters used in the literature to define them.

GENUS	Spire	Whorl profile	Selenizone	Axial shoulder sculpture	Nodes along periphery	Umbilicus	Suture	Base	Peripheral bulge	Slit	Surface sculpture
<i>Pleurotomaria</i>	Graduate	5-sided	Below shoulder	Nodes	Present/absent	Present/absent	Abutting	Convex	Present or absent	Broad, shallow	Spiral cords and nodes
<i>Anodontomaria</i>	Graduate	5-sided	Below shoulder	Absent	Absent	Present/absent	Abutting	Convex	Weak or absent	Broad	Spiral cords and threads
<i>Bathrotomaria</i>	Graduate	5-sided	Along shoulder	Absent	Absent	Present/absent	Abutting	Convex	Weak or absent	Narrow	Spiral or cancellate
<i>Talantodiscus</i>	Planispiral	5-sided	Below shoulder	Nodes	Present	Present	Grooved	Flat	Present	Broad, shallow	Spiral threads and nodes
<i>Cyclostomaria</i>	Low turbiniiform	Oval	Above periphery	Absent	Absent	Wide	Weakly cancellate	Strongly convex	Absent	Narrow	Spiral cords, axial rib
<i>Indomaria</i>	Low turbiniiform	5-sided	Above periphery	Absent	Absent	Always present	Abutting	Convex	?	Broad	Spiral cords, weak axial ribs
<i>Murihikua</i>	Graduate	5-sided	Below shoulder	Axial ribs	Absent	?	Abutting	?	Absent	Narrow	Spiral cords
<i>Mameoatomaria</i>	Graduate	5-sided	Below shoulder	Nodes reduced/absent	Absent	?	Grooved	?	Weak or absent	Narrow	Cancellate
<i>Tahua</i>	Conical	4-sided	At mid-whorl	Absent	Present/absent	Absent	Below periphery	Strongly convex	Absent	Narrow	Cancellate
<i>Ornatospira</i>	Low conical	4-sided	At mid-whorl	Absent	Absent	Wide	Abutting	Nearly flat	Absent	Narrow	Cancellate, axial dominant
<i>Pyrgotrochus</i>	Conical	4-sided	Below mid-whorl	Nodes present	Present	Absent or narrow	Flush	Flat	Present, nodose	Broad	Spiral cords, nodose bands
<i>Stuorella</i>	Conical	4-sided	Just above periphery	Absent	Present	Absent or narrow	Flush	Flat	Present, nodose	Narrow	Axial costae, spiral threads
<i>Laevitomaria</i>	Conical	4-sided	Below mid-whorl	Absent	Absent	Wide	Impressed	Flat	Weak or absent	Narrow	Spiral cords
<i>Obornella</i>	Conical	4-sided	Near periphery	Absent	Present	Present	Abutting	Strongly convex	Weak or absent	Narrow, shallow	Cancellate, costae dominant
<i>Conotomaria</i>	Conical	5-sided	At or above mid-whorl	Absent	Absent	Absent to wide	Flush	Flat	Present	Narrow, deep	Spiral cords
<i>Leptomaria</i>	Conical	4-sided	At mid-whorl	Absent	Absent	Absent to wide	Abutting	Strongly convex	Weak or absent	Narrow, shallow	Spiral cords cancellate
<i>Chelolita</i>	Conical	4-sided	Above mid-whorl	Absent	Absent	Wide	Flush	Flat	Weak or absent	Narrow, deep	Nodose spiral cords
<i>Entennotrochus</i>	Conical	4-sided	Above mid-whorl	Absent	Absent	Wide	Flush	Flat	Weak or absent	Narrow, deep	Spiral threads and cords
<i>Petrotrochus</i>	Conical	4-sided	Just below mid-whorl	Absent	Absent	Absent	Abutting	Convex	Weak or absent	Broad, shallow	Spiral cords fine or nodose
<i>Mikadotrochus</i>	Conical	4-sided	Below mid-whorl	Absent	Absent	Absent	Abutting	Convex	Weak or absent	Broad, shallow	Nodose spiral cords
<i>Bayerotrochus</i>	Conical	4-sided	Above mid-whorl	Absent	Absent	Absent	Abutting	Strongly convex	Weak or absent	Broad, shallow	Spiral cords and threads

rowly open umbilicus and a strongly convex base. Surface sculpture consists of closely spaced collabral costellae (usually dominant) and spiral threads. The periphery is commonly crenate. The selenizone is narrow, smooth, often projecting onto the upper whorl face near the periphery. The labral slit is short.

Remarks: *Obornella* is known from strata of Toarcian (Lower Jurassic) to Oxfordian (Upper Jurassic) age (183 Ma to 156 Ma). Greatest diversity has been documented from Europe (see Gründel, 2003; Hägele, 2003), and this genus has also been reported from northeastern Iran (Majidifard, 2003) and the Kutch region of western India (Jaitley et al., 2000; Das et al., 2005).

Obornella texta (Delpy, 1948)

(Figure 4, reproduced from Delpy, 1948: pl. 2, fig. 1)

Leptomaria texta Delpy, 1948: 9, pl. 2, fig. 1.

Original Description (Translated): “(Height: 25 mm; diameter 31.5 mm; number of whorls: 5). The strip [selenizone] is anterior, wide relative to the last turn, and develops/changes normally until the multicarinate stage, becoming a little convex. The sculpture is latticed. An umbilicus obscured by a lamina pierces the convex base.

It is similar to *Pleurotomaria cudora* d’Orbigny, 1850, but the selenizone of this Oxfordian species is concave between two carinae, which is noticeably different from the Malagasy form. Argovian of Ankirijy (coll. Hourcq).”

Remarks: Unfortunately, Delpy did not specify where her type material was deposited. Inquiries at the Muséum national d’Histoire naturelle in Paris as well as the Université de Paris revealed that the specimens are not deposited in their collections. The description is minimal, and the illustration of the single, partial specimen (Figure 4) is poor, showing a specimen in which the selenizone runs along the shell periphery, with the suture

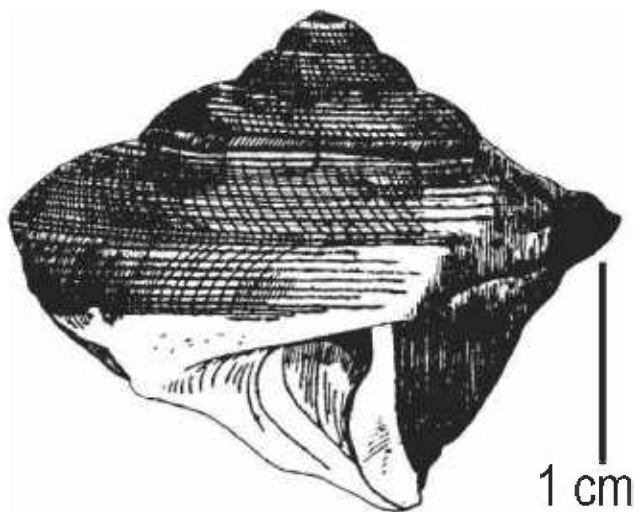


Figure 4. *Obornella texta* (Delpy, 1948). Reproduction of original illustration (Delpy, 1948: pl. 2, fig. 1, as *Leptomaria texta*).

addressed along the lower edge of the selenizone. These features preclude the inclusion of this species in *Leptomaria* E. Eudes-Deslongchamps, 1864, which is characterized by convex whorls, with the selenizone at mid-whorl. It is more likely that this taxon is referable to the genus *Obornella*, in which the selenizone is situated closer to the periphery. Delpy’s illustration resembles the partial specimen (Jaitly et al. 2000: 39, pl. 2, figs. 8A, B) from the contemporary Dhosa Oolite Member of the Kutch region of India that was identified as *Obornella* aff. *granulata* (J. Sowerby, 1818). Delpy’s taxon is here transferred to *Obornella*, but its generic affinities remain obscure until the type, which is the only known specimen, is located.

Obornella thompsonorum new species.

(Figures 5–12)

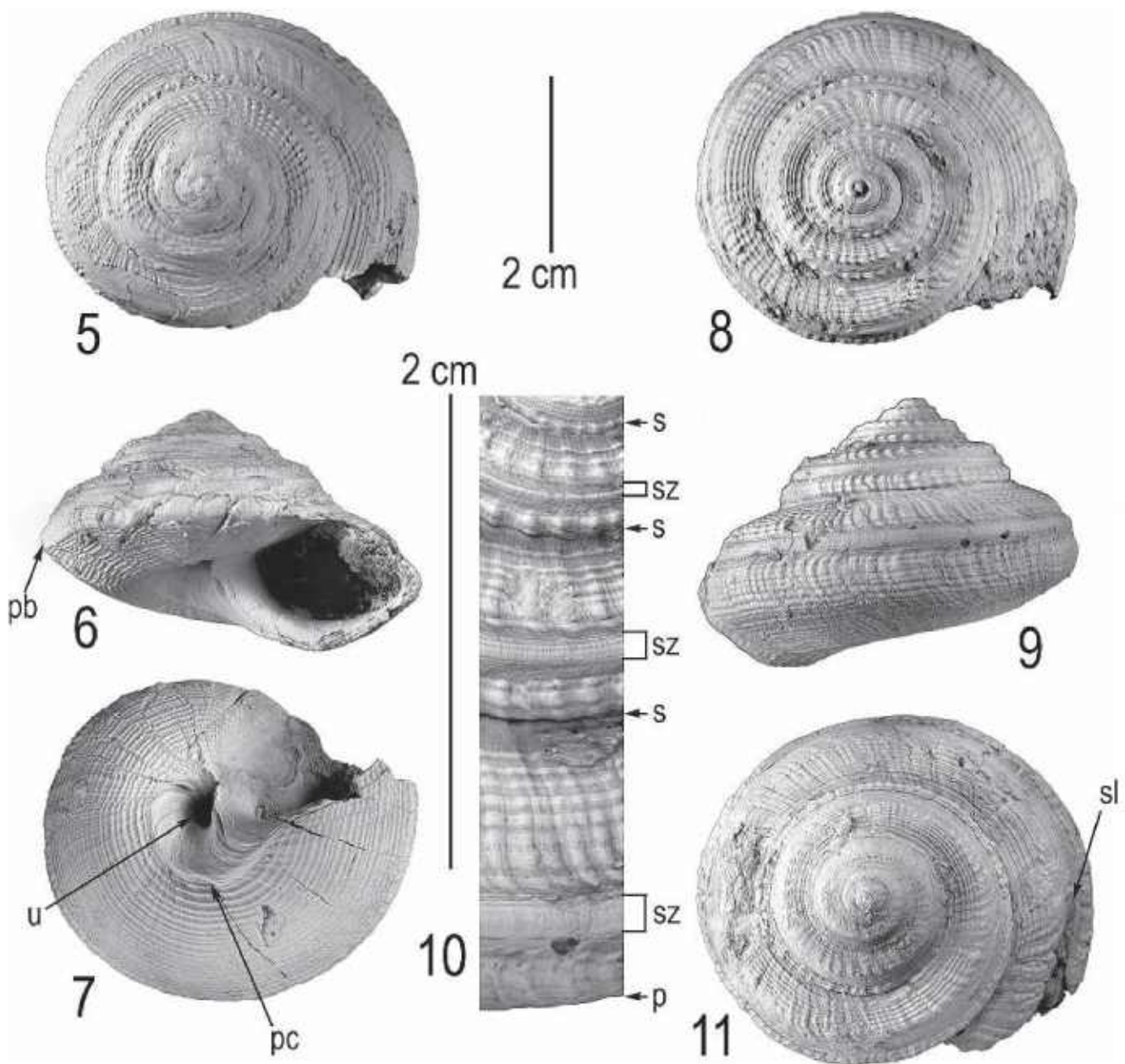
Description: Shell (Figures 5–12) small (holotype maximum diameter 42.2 mm, minimum diameter 34.6 mm, height 26.4 mm) low, turritiform, consisting of approximately 7 teleoconch whorls. Base moderately convex, with narrow umbilicus (Figure 7, **u**). Spire angle 103–106°. Spire slightly convex in profile. Suture adpressed, joining previous whorl at or just below peripheral bulge (Figure 6, **pb**). Protoconch and first 3–5 teleoconch whorls eroded, only final 2–4 teleoconch whorls well preserved. Weak shoulder present on whorls 3–5, becoming convex, rounded in final two whorls. Axial sculpture of oblique radial costae most pronounced on whorls 3–5 (40–50 per whorl), weaker on subsequent whorls (80–108 per whorl), producing cancellate granules at intersections with spiral cords, especially at peripheral bulge and on either side of selenizone (Figure 10, **sz**). Number of strong, simple spiral cords 7–9 between suture and selenizone, 0–3 on selenizone, 2–4 between selenizone and peripheral bulge, 21–22 along base, between peripheral bulge and broad parietal callus (Figure 7, **pc**). Selenizone (Figure 10, **sz**) narrow, convex, with 0–3 spiral cords, and numerous strong to weak lunulae, situated just above peripheral bulge. Aperture ovate, roughly perpendicular to coiling axis. Outer lip smooth, portion below slit offset from portion above slit by 39°. Slit narrow (~2.5 mm), extending posteriorly 62° from end of suture. Lip thickest in columellar and basal region, forming broad parietal callus that partly overlaps the umbilicus.

Type Locality: Zakaraha, near Toliara (also spelled Tnlear), southwestern Madagascar. 6–7 m below surface on plateau cut by river.

Type Material: Holotype, USNM 534480; paratype 1, USNM 534481; paratype 2 USNM 534482, all from the type locality.

Age: Oxfordian (Upper Jurassic).

Etymology: This new species honors Jon and Beverly Thompson for their many contributions and years of service to The Bailey-Matthews Shell Museum in Sanibel, Florida.



Figures 5–11. *Obornella thompsonorum* new species. **5.** Apical, **6.** apertural, and **7.** basal views of the holotype, USNM 534480. **8.** Apical and **9.** dorsal views of paratype 1, USNM 534481. **10.** Details of sculpture between suture and periphery on last three dorsal whorls of paratype 1. **11.** Apical view of paratype 2, USNM 534482. Abbreviations: **p**, periphery; **pb**, peripheral bulge; **pc**, parietal callus; **s**, suture; **sl**, posterior limit of slit; **sz**, selenizone; **u**, umbilicus.

Remarks: The assignment of this new species in the genus *Obornella* is provisional. The type species of *Obornella*, *Pleurotomaria plicopunctata* J. A. Eudes-Deslongchamps, 1849, from the Bajocian (Middle Jurassic) of France and England, is near one end of a morphological spectrum (see Hägele, 2003: fig. 10) that is distinguished by a low, conical spire and conspicuous axial fluting along the shell periphery and base. The other end of this morphological spectrum is characterized by shells with a higher, stepped spire, a rounder

aperture, and spiral cords along the base, features reminiscent of the genus *Pleurotomaria*. *Obornella thompsonorum* more closely resembles *O. trapeza* (Hudleston, 1895: pl. 40, figs. 5a, b) and the “elevated variety” of *O. granulata* (Sowerby, 1818) illustrated by Hudleston (1895: pl. 40, figs. 1a, b) as *Pleurotomaria granulata* var. *ecelata* Deslongchamps, 1848, but differs in having a less pronounced, more rounded peripheral bulge, a spire that is stepped along intermediate whorls, and strongly beaded sculpture along both sides of the selenizone. Two

European species of *Obornella* had been reported from the Kutch fauna (Jaitly et al., 2000; Das, et al., 2005). *Obornella wuerttembergensis* (Sieberer, 1908) from Lower Jurassic [upper Bathonian] strata, is much flatter, lacks a parietal callus, and has a far broader umbilicus than *O. thompsonorum*. Specimens of *Obornella granulata* (Sowerby, 1818) from the Dhosa oolite member of the Chari Formation [Oxfordian] of Kutch (Jaitly et al., 2000; pl. 1, figs. 5–7) resemble *O. thompsonorum* in overall proportions, but have more convex whorls between suture and periphery, far weaker axial sculpture, a broader umbilicus, and lack the distinctive parietal callus. *Obornella thompsonorum* may be distinguished from *Obornella texta* (Delpey, 1948), the only previously described plenrotomariid from the Jurassic of Madagascar, by the position of the selenizone above rather than along the periphery, and by having more prevalent sculpture, especially adjacent to the selenizone.

The shell microstructures found in *Obornella thompsonorum* (Figure 12) are similar to those of plenrotomariids from the Carboniferous (Batten, 1972), Triassic (Bandel, 1991), Jurassic (Bøggild, 1930), Cretaceous (Kiel, 2006), and Recent (Harasewych, 2002), indicating that shell microstructure is a very conservative character in this group.

Genus *Bathrotomaria* Cox, 1956

Type Species: *Trochus reticulatus* J. Sowerby, 1821. (By original designation). Kimmeridgian (Upper Jurassic) of England.

Diagnosis: *Bathrotomaria* can be distinguished by its usually large (to 130 mm), trochiform shell with a spire that may be elevated to depressed. The umbilicus may be broad to entirely absent. The whorl profile is usually angulate and non-tuberculate, with a broad ramp and a second carina or angulation, just overlapped on the spire.

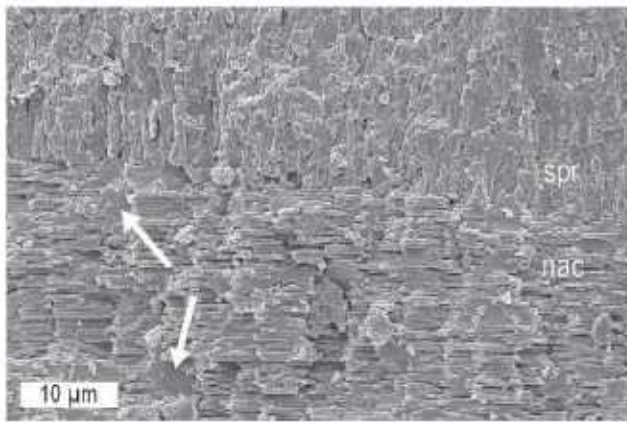


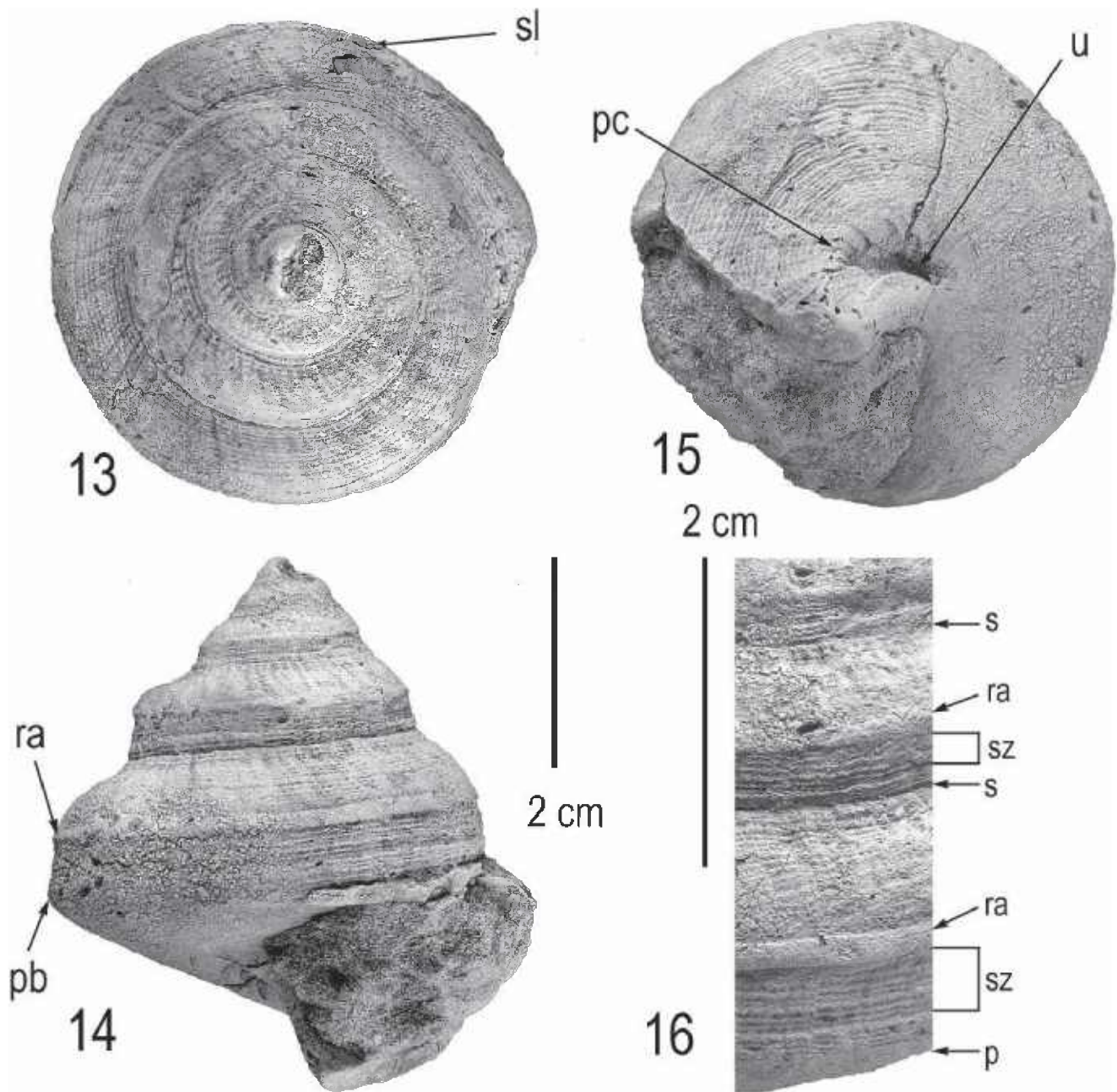
Figure 12. SEM image of a fracture surface of the shell of *Obornella thompsonorum* new species at the aperture just below the slit, showing the transition from the simple prismatic outer layer to the nacreous inner layer. The arrows indicate areas with recrystallized shell material. Abbreviations: **Nac**, nacre; **spr**, simple prismatic crystals.

The selenizone is situated below the ramp angle. Surface sculpture of spiral cords and threads, commonly cancellate at intersection with collabral threads. The selenizone is moderately broad, the labral slit short.

Remarks: The oldest member of this genus is *Bathrotomaria paipotensis* Gründel, 2001, from the Sinemurian (Lower Jurassic) of northern Chile. The selenizone is narrow for the genus and the spiral sculpture is faint compared to other species. During the Middle and Upper Jurassic the genus was diverse and widely distributed from Peru (Cox, 1956) to Europe, India, and the Afro-Arabian East coast (Cox, 1960, 1965; Howarth and Norris, 1998; Das et al., 2005), and possibly also New Zealand (Gardner and Campbell, 1997), although the New Zealand record was not figured and needs confirmation. A number of species were reported from the Lower Cretaceous of the Tethyan realm, including the largest species with 130 mm diameter (Das, 2002; Kollmann, 1982, 2002). From the Cenomanian (lower Upper Cretaceous) Kiel and Bandel (2004) reported four species of *Bathrotomaria* from an intertidal rocky shore setting in Germany, the highest diversity at any Cretaceous locality. Further Upper Cretaceous records are few; the last record is from the lower Maastrichtian of France (Kollmann and Odin, 2001).

Bathrotomaria annejoffeae new species
(Figures 13–16)

Description: Shell (Figures 13–16) small for genus (holotype maximum diameter 47.7 mm, minimum diameter 43.8 mm, height 50.2 mm), with a tall, conical, strongly gradate spire, consisting of 6+ teleoconch whorls. Base weakly but evenly convex, with very narrow umbilicus (Figure 15, **u**). Spire angle 72°. Spire very slightly convex in profile. Suture weakly adpressed, joining previous whorl at or above peripheral bulge (Figure 14, **pb**). Protoconch and approximately first 2 teleoconch whorls missing. Subsequent early whorls with straight to weakly convex ramp between suture and ramp angle (Figure 14, **ra**) that becomes more inflated, convex on body whorl. Shell surface with broad, uneven, undulating rugae most evident near the suture. Axial sculpture of evenly spaced, weak axial costae (about 120 on body whorl) that produce weakly cancellate sculpture at intersections with spiral cords. Spiral sculpture (Figure 16) dominant, of 10–12 narrow, nearly abutting spiral cords between suture and ramp angle (comprised of single, smooth broad cord), 0–2 spiral cords between ramp angle and selenizone, 6–7 along selenizone, 3–4 between selenizone and peripheral bulge. Base with 36–38 spiral cords that are twice as broad as intervening spaces. Selenizone (Figure 16, **sz**) broad, weakly convex, nearly abutting ramp angle, spanning slightly more than half the distance between ramp angle and peripheral bulge. Aperture elongate, roughly pentagonal, long axis nearly perpendicular to the coiling axis. Outer lip broken. Slit broad (~3.8 mm), extending posteriorly 117° from the end of the suture. Lip thick along columellar region, with



Figures 13–16. *Bathrotomaria annejoffeae* new species. **13.** Apical, **14.** apertural, and **15.** basal views of the holotype, USNM 534483. **16.** Details of sculpture between suture and periphery on last three dorsal whorls of the holotype. Abbreviations: **p**, periphery; **pb**, peripheral bulge; **pc**, parietal callus; **ra**, ramp angle; **s**, suture; **sl**, posterior limit of slit; **sz**, selenizone; **u**, umbilicus.

narrow, weakly reflected parietal fold that forms a narrow parietal callus that partially occludes the umbilicus.

Type Locality: Zakaraha, near Toliara, southwestern Madagascar, 6–7 m below surface on plateau cut by river.

Type Material: Holotype, USNM 534483, from the type locality.

Age: Oxfordian (Upper Jurassic).

Etymology: This new species honors Anne Joffe in

recognition of her many contributions and long service to the field of malacology, particularly to the American Malacological Union (now American Malacological Society) and most recently to The Bailey-Matthews Shell Museum in Sanibel, Florida.

Remarks: *Bathrotomaria* was among the most widespread and diverse of the pleurotomariid genera throughout the Middle and Upper Jurassic and Cretaceous. This is particularly true of the Jurassic fauna of the

Kutch region, from which ten species have been reported (Maithani, 1967; Jaitly et al., 2000; Das et al., 2005). Of these, five are of Oxfordian age. From its contemporary congeners within the Indo-Madagascan province, *Bathrotomaria annejoffeae* is readily distinguished from *B. tewarii* (Maithani, 1967), *B. buddhai* Das et al., 2005, *B. prasantai* Das et al., 2005, and *B. dhosaensis* Das et al., 2005 in having a proportionally taller, more gradate spire and a narrower umbilicus. In shell profile, *B. annejoffeae* more closely resembles specimens of *B. reticulata* (Sowerby, 1821) (Das et al., 2005: figs. 4, A–G) and *B. siebereri* (Jaitly et al., 2000: pl. 3, figs. 2–3) both from the Bathonian of Kutch, and the Oxfordian *B. millepunctata* (Endes-Deslongchamps, 1849) (Jaitly et al., 2000: pl. 3, fig. 4), but lacks granular whorl angulations of *B. siebereri* and *B. reticulata* (see Das et al., 2005:334). Das et al. (2005: 334) also noted that the Kutch specimens of *B. reticulata* lack an umbilicus (present in *B. annejoffeae*), whereas the suture of *B. siebereri* is deeply canalculated, unlike that of *B. annejoffeae*. *Bathrotomaria annejoffeae* can also be recognized on the basis of the columellar portion of the aperture being long, straight, and nearly co-axial.

Bathrotomaria bedetteae new species.
(Figures 17–20)

Description: Shell (Figures 17–20) small for genus (holotype maximum diameter 65.0 mm, minimum diameter 58.8 mm, height 47.5 mm), with a short, broad, weakly gradate spire, consisting of 5+ teleoconch whorls. Base weakly but evenly convex, lacking an umbilicus (Figure 19). Spire angle 92°. Spire weakly convex in profile. Suture weakly adpressed, joining previous whorl at or above peripheral bulge (Figure 18, **pb**). Protoconch and approximately first 3 teleoconch whorls missing. Subsequent early whorls gradate, with straight ramp between suture and ramp angle (Figure 18, **ra**) that becomes more inflated, convex with increasing whorl number. Axial sculpture of broad, low, closely spaced, axial costae (about 56 on body whorl) that produce a coarsely cancellate sculpture at intersections of spiral cords, including weakly beaded ramp angle and peripheral bulge. Spiral sculpture codominant, of 3–4 low, broad, cords between suture and ramp angle, 0–1 spiral cords between ramp angle and selenizone, 0–1 between selenizone and peripheral bulge. Base with 17–19 finer spiral cords that are 2–4 times as broad as intervening spaces. Selenizone (Figure 20, **sz**) broad, weakly convex, nearly abutting peripheral bulge, spanning slightly more than half the distance between ramp angle and peripheral bulge. Surface without spiral cords, sculpture limited to strong lunulae. Aperture elongate, weakly pentagonal, long axis deflected from the coiling axis by 103°. Outer lip damaged, slit morphology not known. Inner lip thickest along columellar region.

Type Locality: Zakaraha, near Toliara, southwestern Madagascar, 6–7 m below surface on plateau cut by river.

Type Material: Holotype, USNM 534484, from the type locality.

Age: Oxfordian (Upper Jurassic).

Etymology: This new species honors the late Barbara A. Bedette, whose 52 years of service to molluscan paleontology at the National Museum of Natural History has benefited a multitude of researchers.

Remarks: *Bathrotomaria bedetteae* may be readily distinguished from *B. annejoffeae*, with which it co-occurs, on the basis of its lower, broader shell, with a weaker, more rounded ramp angle, by its coarser and more prominent cancellate sculpture that extends onto the ramp angle and peripheral bulge, and by the absence of an umbilicus. *Bathrotomaria bedetteae* is similar in profile to *B. tewarii*, *B. prasantai*, and *B. dhosaensis*, all from contemporary strata in Kutch, but differs in having a more gradate spire and a pronounced peripheral band, and in lacking an umbilicus.

Genus *Leptomaria* E. Endes-Deslongchamps, 1864.

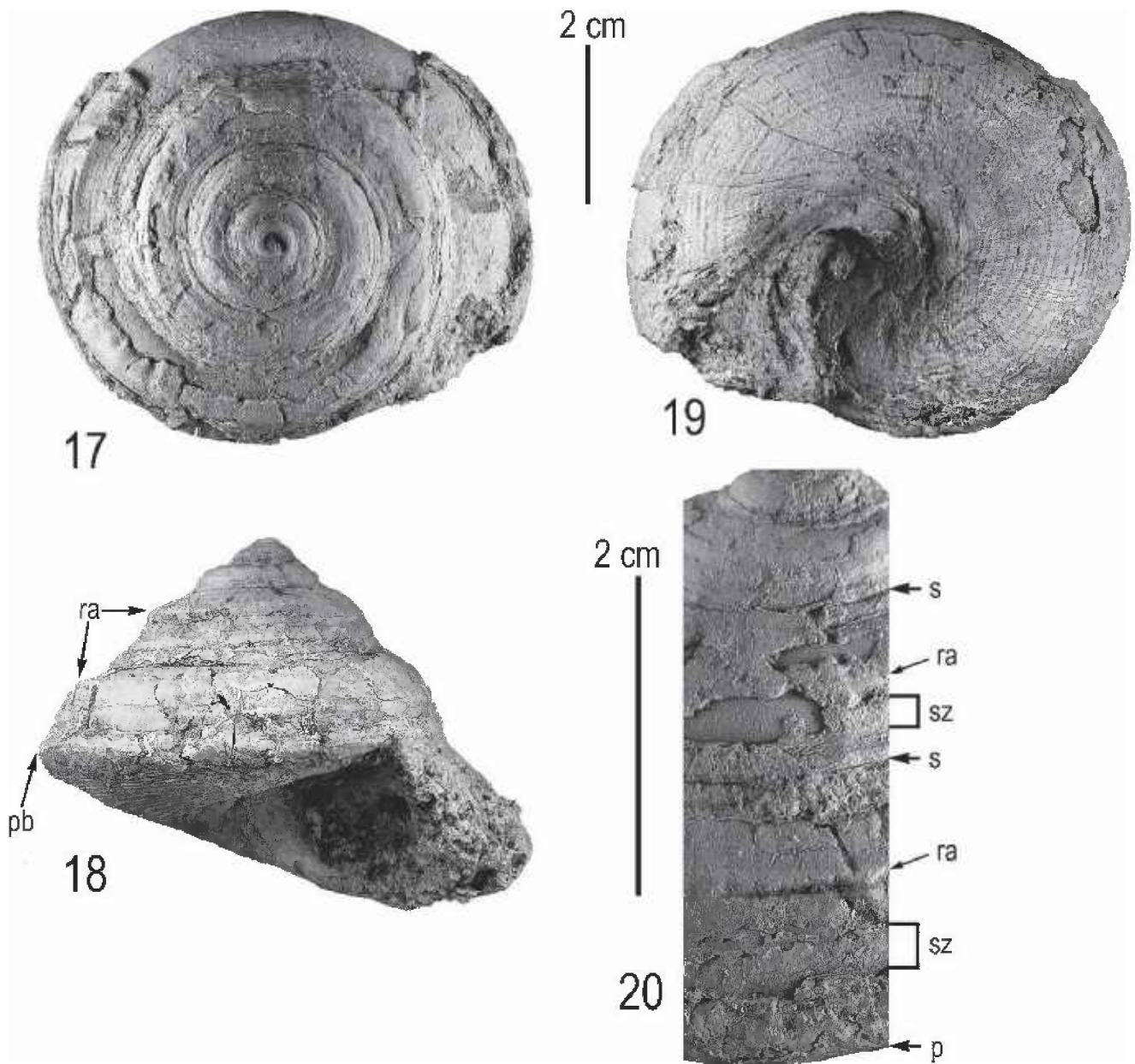
Type Species: *Pleurotomaria amoena* J. A. Endes-Deslongchamps, 1849. (By original designation). Bajocian (Middle Jurassic) of France.

Diagnosis: Species of *Leptomaria* can be recognized on the basis of their large, turbiniform shells with low to moderately high spires and weakly to strongly rounded whorls. The umbilicus may range from broad to entirely absent. The whorl profile is rounded, lacking an angulate shoulder. The selenizone is situated at mid-whorl. Surface sculpture consists primarily of narrow spiral threads with finer axial threads forming weakly cancellate sculpture in some species.

Remarks: *Leptomaria* has been reported from strata ranging in age from Bajocian (Middle Jurassic, Knight et al., 1960) to Selandian (Paleocene, Kollmann and Peel, 1983). Hickman (1976) suggested that even some Eocene species may be included. Not surprisingly, the genus had a cosmopolitan distribution, with diverse faunas ranging from England (Cox, 1960) to New Zealand (Hudson, 2003). *Leptomaria* has been previously reported from Cretaceous deposits of NW Madagascar (Delpey, 1948; Collignon, 1949; Kiel, 2006). It is represented in the Jurassic fauna of Kutch (Jaitly et al., 2000; Das et al., 2005) but is not as diverse as the genera *Bathrotomaria* or *Pleurotomaria*.

Leptomaria takahashii new species
(Figures 21–24)

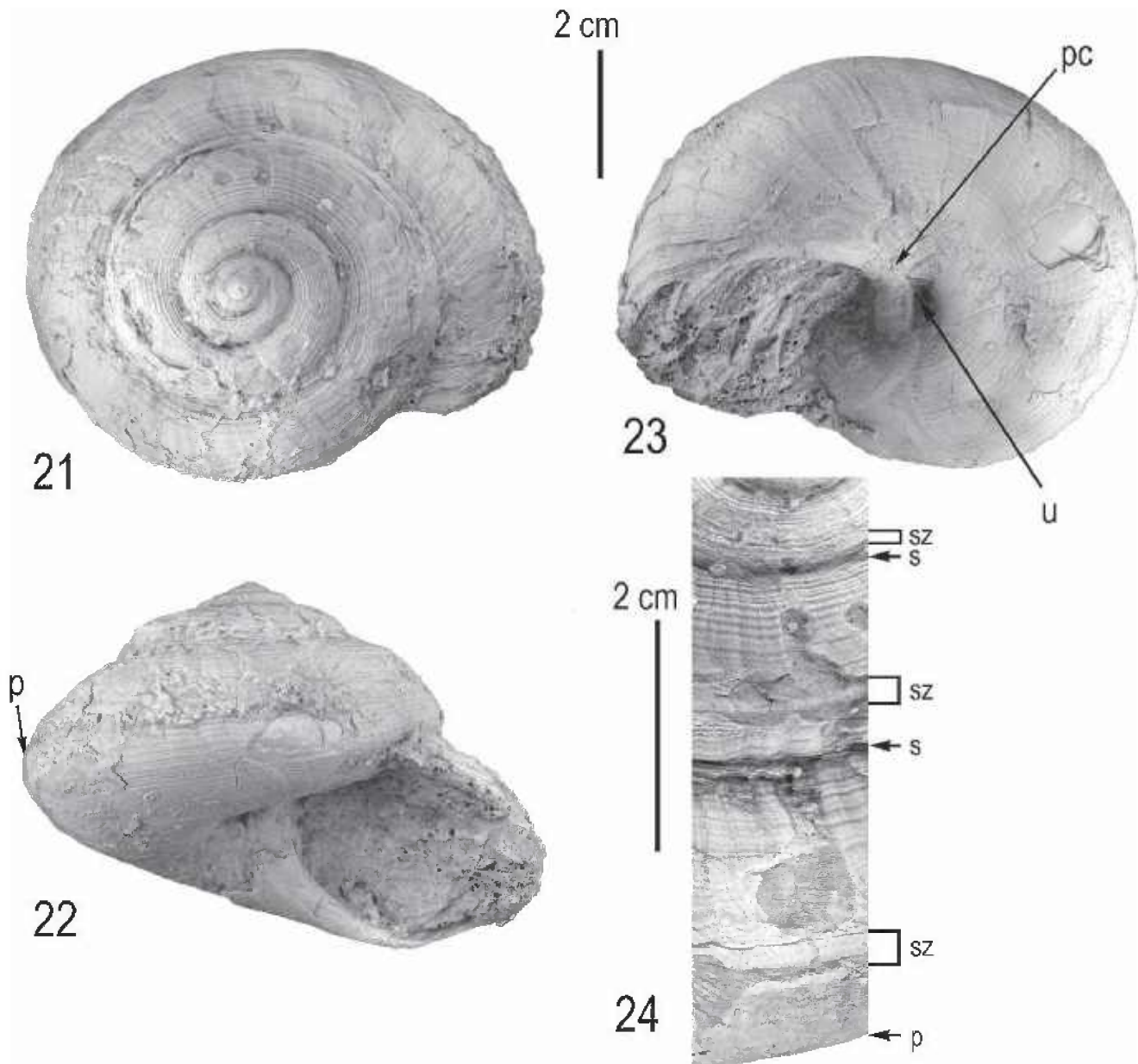
Description: Shell (Figures 21–24) moderately large for the genus (holotype maximum diameter 82.4 mm, minimum diameter 67.23 mm, height 57.3 mm) low, turbiniform, consisting of approximately 6 teleoconch whorls. Base broadly and evenly convex, with very narrow umbilicus (Figure 23, **u**). Spire angle 109°. Spire strongly convex in profile. Suture (Figure 24, **s**) abutting,



Figures 17–20. *Bathrotomaria bedetteae* new species. **17.** Apical, **18.** apertural, and **19.** basal views of the holotype, USNM 534484. **20.** Details of sculpture between suture and periphery on last three dorsal whorls of the holotype. Abbreviations: **p**, periphery; **pb**, peripheral bulge; **ra**, ramp angle; **s**, suture; **sl**, posterior limit of slit; **sz**, selenizone.

joining previous whorl just below selenizone (Figure 24, **sz**) in early whorls, at or below periphery (Figure 22, 24, **p**) in later whorls. Protoconch and part of first teleoconch whorl eroded. Early teleoconch whorls (whorls 2–4) evenly rounded, later whorls (whorls 5–6) becoming more gradate, but evenly rounded, lacking an angular shoulder. Axial sculpture of numerous fine growth striae that produce a strongly reticulate pattern most evident between adjacent cords in region between suture and selenizone of early whorls, and broader low, axial costae that form a weakly cancellate pattern at intersections with the spiral cords. Spiral sculpture dominant, with 10

strong, closely spaced cords between suture and selenizone, 7–9 cords between selenizone and periphery, and 29–32 cords along base. Spiral cords may become broader and less distinct with increasing whorl number. Selenizone (Figure 24, **sz**) narrow, convex, situated just above periphery, with a single, median spiral cord present in early whorls, absent in later whorls, and numerous strong to weak lunulae throughout its length. Aperture evenly ovate, long axis forming an angle of 103° with coiling axis. Outer lip smooth, portion below slit offset from portion above slit by 30° . Slit narrow (~3.3 mm), extending posteriorly 81° from end of suture. Lip



Figures 21–24. *Leptomaria takahashii* new species. **21.** Apical, **22.** apertural, and **23.** basal views of the holotype, USNM 534485. **24.** Details of sculpture between suture and periphery on last three dorsal whorls of the holotype. Abbreviations: **p**, periphery; **pc**, parietal callus; **s**, suture; **sl**, posterior limit of slit; **sz**, selenizone; **u**, umbilicus.

thickest in columellar and basal region, forming narrow parietal callus that partly overlaps the umbilicus.

Type Locality: Zakaraha, near Toliara, southwestern Madagascar, 6–7 m below surface on plateau cut by river.

Type Material: Holotype, USNM 534485, from the type locality.

Age: Oxfordian (Upper Jurassic).

Etymology: This new species honors Mr. Chris Takahashi of Honolulu, Hawaii, in recognition of his many contributions to the study of living and fossil mollusks.

Remarks: *Leptomaria daityai* Das et al., 2005 (Callovian to Oxfordian of Kutch, India) occurs in coeval deposits, and most closely resembles *L. takahashii* in terms of size and general profile, but *L. takahashii* has a shorter spire, more rounded whorls, and has a very narrow rather than a wide umbilicus. Although the genus *Leptomaria* is well represented in the Jurassic fauna of the Indo-Madagascar region, most published records are either from Bathonian and Callovian strata of Kutch, or from Cretaceous deposits of Madagascar. Older taxa, including *L. fraga* (J. A. Eudes-Deslongchamps, 1849), *L. simplex* Jaitly et al., 2000, *L. pseudoumbilicata* Jaitly et al.,

2000 (transferred to *Bathrotomaria* by Das et al., 2005: 340) are easily distinguished as they are smaller, and have a tall, conical whorl profile. Although the Bathonian *L. asurai* Das et al., 2005, is of comparable size, it differs in also having a tall conical profile and lacks an umbilicus.

DISCUSSION

The species most similar to those described herein occur in contemporaneous fossil deposits of northwestern India. This is not surprising considering that the Madagascar species lived near the southern tip of a long and narrow embayment between East and West Gondwana, while northwestern Indian species lived at the northern tip of this embayment, where it opened to the Tethys Ocean (Figure 2). Although Recent pleurotomariids are restricted to hard substrates along the outermost continental shelf and upper continental slope, Mesozoic pleurotomariids inhabited sublittoral depths along the continental shelf. Studies of Upper Jurassic phytogeography have indicated that southern Madagascar was part of a warm temperate biome, while northern Madagascar and northwestern India were part of a warmer, subtropical biome (Rees et al., 2000: fig. 7C). Based on analyses of stable isotope compositions of the ammonite *Perisphinctes* (*Dichotomoceras*), Lécuyer and Bucher (2006: 7, fig. 3) reported seawater temperatures ranging from 21.5°C to 24.1°C in the Morondava Basin of southwestern Madagascar, during the Oxfordian stage of the Upper Jurassic.

Extensive studies of Jurassic pleurotomariid faunas within this Indo-Madagascan Province (e.g., Cox, 1965; Jaitly et al., 2000; Das, 2005) have documented the presence of the genera *Bathrotomaria*, *Leptomaria*, *Obornella*, *Pleurotomaria*, *Anodomaria*, and *Pyrgotrochus*, the first three by far the most diverse. As additional specimens from the Jurassic of Madagascar become available, it is likely that the generic composition and diversity of this fauna will mirror that of the Kutch region of northwestern India.

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Appendix I. Supraspecific taxa included in the family Pleurotomariidae, listed in the order in which they were proposed. Their type species are provided, as are known stratigraphic ranges, and geographical distributions.

- Pleurotomaria* Defrance, 1826 – Type species, *Trochus anglicus* J. Sowerby, 1818. Middle Triassic (Anisian; range extended by Begg and Grant-Mackie, 2003: 259) to Lower Cretaceous (Aptian). Cosmopolitan.
- Leptomaria* E. Eudes-Deslongchamps, 1864 – Type species, *Pleurotomaria amoena* J. A. Eudes-Deslongchamps, 1849. Middle Jurassic (Bajocian) to Paleocene (Danian). Cosmopolitan.
- Talantodiscus* Fischer, 1885 – Type species, *Pleurotomaria mirabilis* Deslongchamps, 1848. Middle Triassic (Kaihikuan; range extended by Begg and Grant-Mackie, 2003: 259) to Middle Jurassic (Bajocian). Europe and New Zealand. Knight et al. (1960: 1214) included this genus in the family Porcellidae Broili, 1924. Subsequent authors (e.g., Szabó, 1980: fig. 3; Begg and Grant-Mackie, 2003: 229) included this genus within Pleurotomariidae.
- Pyrgotrochus* P. Fischer, 1885 – Type species, *Pleurotomaria bitorquata* J. A. Eudes-Deslongchamps, 1849. Lower

- Jurassic to Upper Cretaceous (Cenomanian). Cosmopolitan.
- Perotrochus* P. Fischer, 1885 – Type species, *Pleurotomaria quoyana* Fischer and Bernardi, 1856. Oligocene to Recent. Cosmopolitan.
- Chelotia* Bayle in P. Fischer, 1885 – Type species, *Pleurotomaria concava* Deshayes, 1832. Eocene. Europe.
- Entemnotrochus* P. Fischer, 1885 – Type species, *Pleurotomaria adansoniana* Crosse and Fischer, 1861. Eocene to Recent. Cosmopolitan.
- Stuorella* Kittl, 1891 – Type species, *Trochus subconcauus* Münster, 1841. Middle Triassic (Ladinian) to Upper Cretaceous (Campanian; range extended by Kiel and Bandel, 2000). Europe.
- Mikadotrochus* Lindholm, 1927 – Type species, *Pleurotomaria beyrichii* Hilgendorf, 1877. Western Pacific, Pliocene to Recent.
- Bathrotomaria* Cox, 1956 – Type species, *Trochus reticulatus* J. Sowerby, 1821, by original designation. Lower Jurassic to Upper Cretaceous (Senonian). Cosmopolitan.
- Conotomaria* Cox, 1959 – Type species, *Pleurotomaria mailleana* d'Orbigny, 1843. Middle Jurassic (Bajocian) to Paleocene (Danian; range extended by Pacaud, 2004). Cosmopolitan.
- Obornella* Cox, 1959 – Type species, *Pleurotomaria plicopunctata* J. A. Endes-Deslongchamps, 1849. Lower Jurassic (Toarcian) to Upper Jurassic (Oxfordian) Cosmopolitan.
- Anodotomaria* Szabó, 1980 [described as a subgenus of *Pleurotomaria*] – Type species *Pleurotomaria scacchi* Gemmellaro, 1874. Lower Jurassic (Pliensbachian) to Middle Jurassic (Callovian; range extended by Jaitly et al., 2000: 36). Europe to northwestern India.
- Cyclostomaria* Szabó, 1980 – Type species, *Pleurotomaria suessi* Hörnes, 1853. Lower Jurassic (Pliensbachian) to Middle Jurassic. Europe.
- Ornatospira* Pan, 1982 – Type species *Ornatospira mirifira* Pan, 1982. Triassic, China.
- Laevitomaria* Conti and Szabó, 1987 – Type species, *Pyrgotrochus? problematicus* Szabó, 1980. Lower Jurassic (Pliensbachian) to Middle Jurassic (Bajocian) Europe. Questionably included in Pleurotomariidae by the authors.
- Indomaria* Das, 2002 [described as a subgenus of *Pleurotomaria*] – Type species, *Pleurotomaria (Indomaria) umiensis* Das, 2002. Lower Cretaceous (Berriasian). Northwestern India.
- Bayerotrochus* Harasewych, 2002 – Type species, *Pleurotomaria midas* Bayer, 1964. Miocene to Recent. Cosmopolitan.
- Murihikua* Begg and Grant-Mackie, 2003 – Type species, *Murihikua tuhawaiki* Begg and Grant-Mackie, 2003, Middle Triassic (Anisian) to Upper Triassic (Norian). New Zealand.
- Tahua* Begg and Grant-Mackie, 2003 – Type species, *Tahua waipiro* Begg and Grant-Mackie, 2003 Middle Triassic (Anisian) to Late Triassic (Norian). New Zealand.
- Mamoeatomaria* Begg and Grant-Mackie, 2006 (new name for *Mamoea* Begg and Grant-Mackie, 2003) – Type species, *Mamoea wairakiensis* Begg and Grant-Mackie, 2003. Middle Triassic (Anisian to Ladinian). New Zealand.