

An updated generic classification of Cenozoic pleurotomariid gastropods, with new records from the Oligocene and early Miocene of India

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Abstract.—Although taxonomically distinct, the Cenozoic pleurotomariids are the bottlenecked remnants of the Mesozoic members of the family in terms of morphology, with only conical forms surviving the end-Cretaceous mass extinction. Here, we propose an updated classification scheme for the Cenozoic representatives of this group, based on data from the entire Cenozoic pleurotomariid fossil record. We consider all conventional as well as several new characters so that this scheme can readily help to distinguish Cenozoic pleurotomariid genera. Following the new classification scheme, a revision of the generic status of Cenozoic species previously assigned to ‘*Pleurotomaria*’ Defrance, 1826 is presented.

Only a few Cenozoic pleurotomariid gastropods have been reported from the Indian subcontinent. Here we report four species from the Oligocene of the Kutch Basin and the early Miocene (Burdigalian) of the Dwarka Basin of Gujarat, western India, of which two are described as new: *Perotrochus bermottensis* n. sp., *Entemnotrochus kathiawarensis* n. sp., *Entemnotrochus* cf. *E. bianconii*, and *Entemnotrochus?* sp. 1.

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Introduction

The family Pleurotomariidae Swainson, 1840 is a moderately large clade of marine gastropods (24 genera) that ranges from the Middle Triassic onwards (Begg and Grant-Mackie, 2003; Harasewych and Kiel, 2007; Pieroni and Nützel, 2014; Monari et al., 2018; Szabo et al., 2019). This is the only family within the superfamily Pleurotomarioidea Swainson, 1840 that survived the end-Cretaceous mass extinction (Harasewych, 2002). The family is characterized by a conispirally coiled shell having a trochiform shape with a remarkable emargination or slit along its outer lip that produces a selenizone. The body plan of the pleurotomariids is constrained by the occurrence of homeomorphism with regard to several morphological attributes (e.g., gross shell form, surface ornamentation, presence/absence of umbilicus, and nature and position of selenizone). The recurrence of these attributes with time may reflect strong selective pressure as well as evolutionary limitations in shell geometry (Das, 2002). As a result, this particular group of gastropods has generated considerable scientific interests for decades (e.g., Goldfuss, 1841–1844; Eudes-Deslongchamps, 1849; d’Orbigny, 1850; Huddleston, 1887–1896; Hickman, 1976, 1984, 1998; Szabo, 1980; Fischer and Weber, 1997; Harasewych et al., 1997; Jaitley et al., 2000; Das, 2002; Harasewych and Kiel, 2007).

Pleurotomariids, after their origin in the Middle Triassic, became biogeographically widespread, proliferated quite

rapidly in diversity, and reached their acme during the Middle Jurassic (~11 genera reported; Harasewych and Kiel, 2007, p. 78, fig. 3; Szabo et al., 2019). However, during the Cretaceous, diversity gradually decreased and only three genera remained in the Maastrichtian—*Bathrotomaria* Cox, 1956; *Leptomaria* Eudes-Deslongchamps, 1864; and *Conotomaria* Cox, 1959 (Harasewych and Kiel, 2007). However, while *Leptomaria* and *Conotomaria* survived the K-Pg mass extinction, *Bathrotomaria* succumbed (Harasewych and Kiel, 2007) (Fig. 1). This diversity decline in the Cretaceous happened at all taxonomic levels, hence Cenozoic fossil pleurotomariids are rare. In addition to that, the habitat shift to deeper water and rocky substrate in submarine volcanic settings certainly contributes to their scarce in Cenozoic fossil record (Hickman, 1976).

Mesozoic pleurotomariids were part of shallow marine faunas, whereas extant pleurotomariids are found in deeper waters (i.e., in the bathyal zone), with depths ranging from 100–1000 m (Yonge, 1973; Harasewych, 2002). The bathymetric distribution of pleurotomariids during the Cenozoic still remains uncertain, and several workers have given varied opinions of their distribution. Hickman (1976) and Das (2002) emphasized that the bathymetric distribution shift occurred at the transition from the Mesozoic to the Cenozoic. However, several Oligocene and Miocene pleurotomariids were reported from shallow marine deposits (Kase and Katayama, 1981; Tomida and Sako, 2016). Kanno (1961) suggested that juveniles preferred shallow waters and migrated to a deep-sea habitat after maturing to adults.

Pioneering studies on Cenozoic pleurotomariids were performed by Fischer (1885), who proposed three genera—

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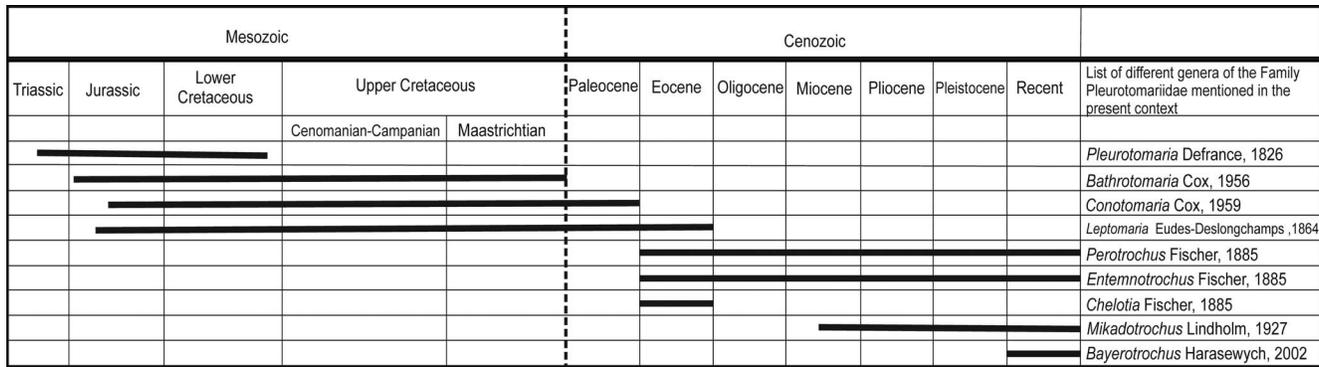


Figure 1. Temporal ranges (time units not up to scale) of pleurotomariid genera mentioned in the present context (adopted from Harasewych and Kiel, 2007). The dotted line represents the K-Pg boundary. The figure portrays the temporal range of the genus *Pleurotomaria* as ranging up to the Lower Cretaceous whereas only two genera have crossed the K-Pg boundary, i.e., *Leptomaria* and *Conotomaria*.

Perotrochus, *Entemnotrochus*, and *Chelotia*. Later, Lindholm (1927) described another new genus, *Mikadotrochus*. Kuroda (1955) was the first to express the need to discriminate the Cenozoic pleurotomariids from those that occurred during the Mesozoic. He concluded that *Perotrochus*, *Entemnotrochus*, and *Mikadotrochus* are the only extant genera strictly occurring in the Cenozoic (Lin, 1975). Later, a new extant genus, *Bayerotrochus*, was introduced by Harasewych (2002), which was earlier informally classified as *Perotrochus* Group B by Bayer (1965). Among the three extinct genera, *Chelotia* is restricted to the Cenozoic, whereas *Leptomaria* and *Conotomaria* crossed the K-Pg boundary. These are the seven genera that have been so far reported from the Cenozoic rocks (Fig. 1).

There are numerous reports of pleurotomariid gastropods from India, with ~40 species recorded from the Mesozoic of western India, especially from the Jurassic and the Cretaceous of Kutch (Jaitley et al., 2000; Das, 2002; Das et al., 2005). However, reports of Cenozoic pleurotomariid gastropods from the Indian sub-continent are very rare. *Entemnotrochus bianconii* (d'Archiac and Haime, 1854) from the Eocene of Kutch, Sindh, and Baluchistan (western India) was reported by d'Archiac and Haime (1854). *Pleurotomaria* sp. from the Miocene of Meghalaya (North-East India) was mentioned, but a systematic description was not provided by Lyngdoh et al. (1999). Apart from that, only one extant species, *Bayerotrochus indicus* (Anseeuw, 1999), was reported from the vicinity of the Bay of Bengal and Andaman Sea.

Although there is a plethora of work on fossil and extant pleurotomariids from different regions of the world (e.g., Kellum, 1926; Hickman, 1976; Szabo, 1980; Harasewych and Kiel, 2007), the taxonomic classification of this group, especially of the fossil pleurotomariids, remained ambiguous during the past two centuries. The existing classification schemes (Knight et al., 1960; Szabo, 1980) have numerous limitations and remain inadequate for classifying fossil pleurotomariids, and thus requires further detailing. The taxonomy and phylogenetic relationships of the extant genera, on the other hand, are very well known, based on molecular data and soft part morphology (which includes a highly specialized radula) (Hickman, 1976; Harasewych et al., 1997; Das, 2002; Harasewych, 2002). The major cause of conflicting classification schemes of fossil pleurotomariids lies in the fact that these classifications are mostly

based on a few simple morphological characters (e.g., shell shape; position and width of the selenizone; the presence or absence of an umbilicus). Several authors included both Mesozoic and Cenozoic species in the genus *Pleurotomaria* DeFrance, 1826, and thus regarded this genus as a 'living fossil' (see Hickman, 1976). However, significant morphological differences exist between Mesozoic and Cenozoic taxa initially placed in *Pleurotomaria*, and as a result, these taxa were assigned to several genera and subgenera (Fischer, 1885; Szabo, 1980; see Das, 2002). *Pleurotomaria* sensu stricto has noded ornamentation as a diagnostic character, which is altogether lacking in the Cenozoic taxa (see Hickman, 1976). Also, *Pleurotomaria* sensu stricto is regarded as a Mesozoic genus with a stratigraphic range from the Lower Jurassic to the Lower Cretaceous by Knight et al. (1960) (Fig. 1). Thus, Hickman (1976, 1984) assigned all the Cenozoic 'Pleurotomaria' under *Pleurotomaria* sensu lato in a provisional sense and considered *Pleurotomaria* as a living fossil. Later, Das (2002) re-evaluated *Pleurotomaria* as a Mesozoic genus and disqualified its status as a 'living fossil' as well as its existence as a Cenozoic genus. It is, therefore, essential to revise the taxonomic status of those taxa assigned to Cenozoic 'Pleurotomaria' s. l. and re-assign them to the seven strictly Cenozoic genera.

Herein, we report four species, of pleurotomariid gastropods from western India—three from the Oligocene of the Kutch Basin, and one from the Miocene of the Dwarka Basin. Two of these described species are new. We also provide a literature review of all the previously described Cenozoic pleurotomariids and propose a new classification scheme for this taxonomic group. We have used all conventional characters, mostly adopted from Knight et al. (1960), Szabo (1980), and Harasewych and Kiel (2007), as well as several new characters (supported by multivariate analyses). Applying this scheme, Mesozoic pleurotomariids can readily be distinguish from the Cenozoic forms.

Geological setting

Stratigraphic information.—The Cenozoic beds of western India are known for their rich and diverse heritage of marine faunas (Biswas, 1992; Harzhauser et al., 2009; Kulkarni et al., 2010; Jain, 2014). The specimens upon which this study is

based were collected from different localities in the Kutch and Devbhumi Dwarka districts of Gujarat, western India (Fig. 2).

The Cenozoic strata of the Kutch Basin are divided into the Matanomadh, Naredi, Harudi, Fulra, Maniyara Fort, Khari Nadi, Chhasra, and Sandhan formations, in stratigraphic order (Biswas, 1992) (Fig. 3.1). The Oligocene stage is represented by the Maniyara Fort Formation, which consists of well-bedded, yellow to ochre foraminiferal limestone, with a basal grayish green glauconitic siltstone overlying the middle Eocene Fulra Formation (Biswas, 1992; Catuneanu and Dave, 2017). The type section of this formation is well exposed along the Bermoti Stream and the Maniyara Fort (Biswas, 1992). The formation is subdivided into four members, the Basal Member, the Lumpy Clay Member, the Coral Limestone Member, and the Bermoti Member, in stratigraphic order. The lower three members were deposited during the early Oligocene (Rupelian), while the Bermoti Member is late Oligocene (Chattian) in age (Biswas, 1992; Catuneanu and Dave, 2017). Fossils for the present study were collected from the Coral Limestone Member and the Bermoti Member. The Coral Limestone Member comprises beds of white nodular limestone alternating with calcareous claystone in its lower part, while the upper part consists of white massive limestones with abundant corals. The upper Bermoti Member is composed of thinly bedded yellow foraminiferal limestone with interbeds of silty marlite. An overall marginal marine to shallow inner shelf environment has been suggested for the Maniyara Fort Formation. The sediments were deposited during a transgressive interval in the Oligocene, with a gradual shift from a restricted lagoonal to a high energy, open shelf environment, which facilitated the formation of coral bioherms (Catuneanu and Dave, 2017).

The Dwarka Basin, situated at the western fringe of the Kathiawar Peninsula, is a peri-cratonic shelf basin, and filled with an extensive succession of marine sediments. The succession is subdivided into three formations—the Gaj, Dwarka, and Miliolite Limestone formations, in stratigraphic order—ranging from the early Miocene to Holocene and overlying unconformably on the Deccan Traps and laterite (Jain, 2014). A single pleurotomariid specimen from the Kuranga Member of the Gaj Formation is reported in the present study. The Gaj Formation is early–middle Miocene in age and is subdivided into seven members (Fig. 3.2). The Kuranga Member is early Miocene (Burdigalian) in age. It is 15 m thick and comprises alternations of marly limestone, white calcareous clays, and ash gray clays. The main fossiliferous unit of the Kuranga Member that hosted the pleurotomariid specimen is a coralline limestone that was deposited in a shallow marine, inner shelf environment. The Kuranga Member is well exposed in and around the Kuranga village and Kuranga railway station (22° 03'35.7"N, 69°11'17"E) (Jain, 2014).

Materials and methods

Revision of Cenozoic Pleurotomaria sensu lato.—Several workers have attempted to compile lists of all the pleurotomariid species reported from the Cenozoic (e.g., Pritchard, 1903; Malaroda, 1950; Palmer and Brann, 1966; Hickman, 1976; Pacaud, 2004). For the present study, we have compiled and tabulated data encompassing all the previously

reported Cenozoic pleurotomariid species (see Appendix 1). The new species reported in the present paper have been added to the data.

All Cenozoic pleurotomariid genera have broad similarities, for example in overall shell shape (Character [Ch.] 1), which is conical, but they differ in several characters and each genus has its distinctive character combination. To show this, we have compiled a character data matrix for generic discrimination. Additional characters included in the character matrix and thereafter used for classification are (Table 1): shell profile (Ch. 2); Height/Diameter (H/D) ratio (Ch. 3); apical angle (Ch. 4); type of suture (Ch. 5); whorl angulation (Ch. 6); the presence of an umbilicus (Ch. 7); outer whorl face shape (Ch. 8); selenizone elevation (Ch. 9); selenizone position (Ch. 10); width of the selenizone (Ch. 11); shape of the base of the shell (Ch. 12); apertural outline (Ch. 13); number of whorls (Ch. 14); and dominant ornamentation (Ch. 15). The character matrix was constructed based on 81 different Cenozoic pleurotomariid species for which detailed descriptions were readily available from the literature (Supplementary Table 1). These characters have been tested individually to see whether they can be used to distinguish genera from each other. However, considering the large overlap in characters among different genera, the character data matrix (Supplementary Table 1) has been subjected to multivariate analysis using non-metric multi-dimensional scaling (nMDS) plotting using Euclidian distance ($k = 2$) to achieve optimal clustering of different genera. Even though the nMDS plot provides a better clustering of the data, it does not provide the loading of the characters essential for generic discrimination. Thus, Principal Component Analysis (PCA) is used to establish the loadings of different characters essential for the generic discrimination.

Based on the multivariate (nMDS and PCA) analyses, we propose a classification scheme for Cenozoic pleurotomariids that is based on those morphological characters that incorporate the maximum variation among the genera. The genera that show significant overlapping in the plots are distinguished based on several significant conventional morphological characters used by previous workers (mostly adopted from Knight et al., 1960 and Szabo, 1980). Based on the newly proposed classification scheme, Cenozoic species previously assigned to *Pleurotomaria* are revised and transferred to the following seven genera, which comprise all Cenozoic pleurotomariids: *Leptomaria*, *Conotomaria*, *Perotrochus*, *Entemnotrochus*, *Chelotia*, *Mikadotrochus*, and *Bayerotrochus*. The remaining '*Pleurotomaria*' species, whose generic status established by the proposed classification scheme because of the lack of data on character states, are classified as Genus uncertain.

Collection of the new pleurotomariid specimens.—The pleurotomariid specimens from the Kutch and Dwarka basins were collected by following the random sampling protocol (Kowalewski, 2002; Mallick et al., 2013). The specimens from the Maniyara Fort Formation are from two stratigraphic levels, the Coral Limestone Member and the Bermoti Member, from four different localities. The locality near Bermoti Village (23°27'45.1"N, 68°36'06.4"E) yielded eight specimens; a locality near Lakhdi Dam, 4.8 km NW of Vayor (23°27'02.2"N, 68°40'03"E) yielded two specimens; a locality

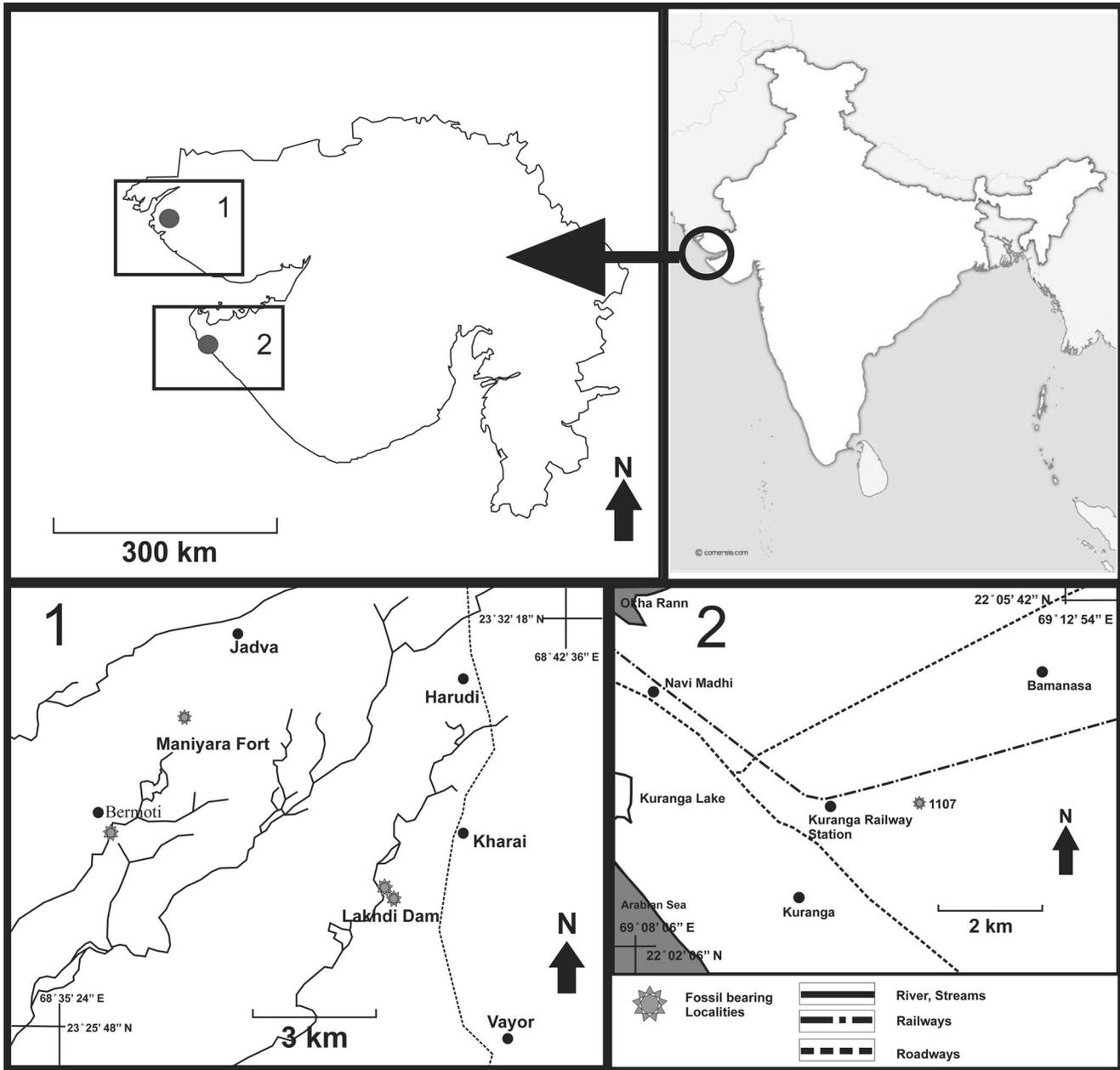


Figure 2. (1, 2) Geographic location of (1) Kutch, and (2) Devbhumi Dwarka districts of Gujarat, India, as shown in the upper panels; inset figure (1) shows fossil-bearing localities in the Kutch Basin; inset figure (2) shows fossil-bearing localities in the Dwarka Basin.

in the Kharoi Village near Lakhdi Dam, 4.5 km NW of Vayor ($23^{\circ}26'55.5''\text{N}$, $68^{\circ}40'09.4''\text{E}$) yielded one specimen; and a locality in the Maniyara Fort near Bermoti Village ($23^{\circ}29'15''\text{N}$, $68^{\circ}37'10''\text{E}$) yielded only one specimen (Fig. 2.1). Only one specimen was collected from 200 m east from Kuranga Railway Station ($22^{\circ}03'35.7''\text{N}$, $69^{\circ}11'17''\text{E}$), which belongs to the Kuranga Member of the Gaj Formation (Fig. 2.2). The specimens were coated with MgO before photography.

Repository and institutional abbreviations.—All specimens are archived in the museum of Geological Studies Unit, Indian Statistical Institute, Kolkata, India. Specimens are numbered

following the institutional abbreviation: ISI/dwk/Pleu/19 and Mani/17/Pleu. ISI = Indian Statistical Institute; dwk = Dwarka; Pleu = Pleurotomariidae; Mani = Maniyara Fort Formation.

Results

The Cenozoic pleurotomariid database.—The database comprises a total of 149 species of Cenozoic Pleurotomariidae assigned to the following eight genera in the literature: *Leptomaria*: 14 species; *Conotomaria*: 5 species; *Perotrochus*: 34 species; *Entemnotrochus*: 17 species; *Chelotia*: 4 species; *Mikadotrochus*: 9 species; *Bayerotrochus*: 14 species; and lastly *Pleurotomaria*: 52 species.

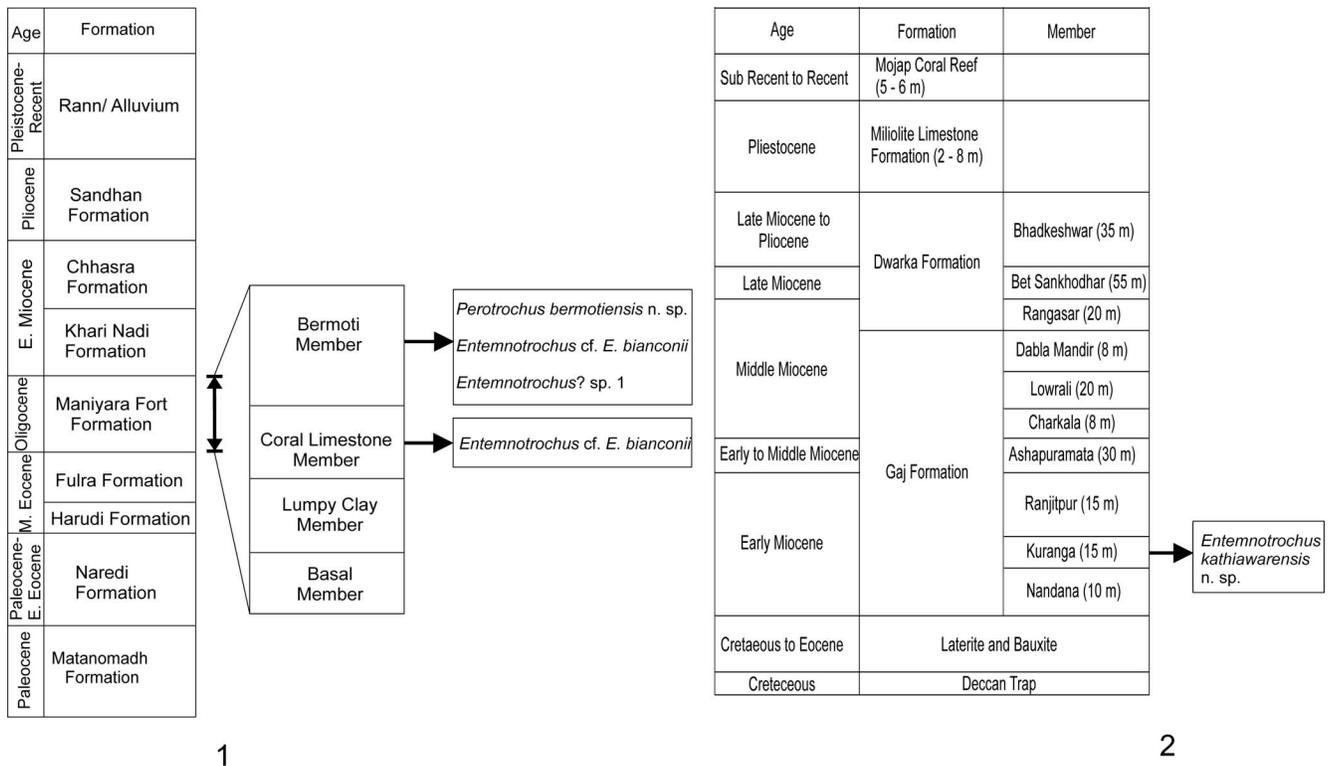


Figure 3. (1, 2) Lithostratigraphic tables of the Cenozoic succession of the Kutch Basin (1) (after Biswas, 1992) and the Dwarka Basin (2) (after Jain, 2014) showing the pleurotomariid-bearing horizons.

Revision of Cenozoic ‘Pleurotomaria’.—The nMDS 3D plot using Euclidean distance has a stress value of 0.26, which is very poor for getting separate clusters for different genera (Supplementary Fig. 1). Consequently, most of the ranges of the genera are overlapping, although the plot demarcates three poorly defined clusters, referring to *Entemnotrochus*, *Perotrochus*, and *Mikadotrochus*. Of the remaining genera, *Bayerotrochus* and *Leptomaria* show significant overlaps with *Perotrochus* and *Mikadotrochus*, whereas, *Chelotia* and *Conotomaria* occupy isolated areas in the plot. It should be noted that the latter two genera are represented by very few data points. Therefore, their positions in the morphospace are less reliable and may be subject to sampling bias.

The PCA plots show a similar picture. The first three PC axes account for 58.4% of the total variation. PC 1 (explaining ~27.5% of the variation) mostly represents selenizone position (Ch. 10) (loading: 59%), width of the selenizone (Ch. 11) (loading: 51%), type of suture (Ch. 5) (loading: 42%), and the presence/absence of an umbilicus (Ch. 7) (loading: 31%). PC 2 (explaining ~19% of the variation) represents dominant ornamentation (Ch. 15) (loading: 65%) and Ch. 5 (loading: 58%), whereas PC 3 (explaining ~11.49% of the variation) represents Ch. 15 (loading: 63%), Ch. 5 (loading: 61%), Ch. 11 (loading: 28%), and Ch. 3 (H/D ratio) (loading: 26%). In the PC1/PC2 morphospace (Fig. 4.1), the genus *Entemnotrochus* forms a cluster in the left half of the plot, with relatively

Table 1. Different morphological characters with character states used for constructing character matrix data set. Character state numbers are 0, 1, 2, and 3.

Character No.	Character	0	1	2	3
Ch 1	Shell Shape	Gradate	Conical		
Ch 2	Shell Profile	Cyrtconic	Coeloconic		
Ch 3	H/D	<0.5	0.5 to ≤0.75	>0.75–1.00	>1.00
Ch 4	Apical angle	Acute (0–90)	Obtuse (>90–180)		
Ch 5	Suture	Impressed	Flush	Adpressed	Grooved
Ch 6	Whorl Angulation	Present	Absent		
Ch 7	Umbilicus	Anomphalous	Phaneromphalous		
Ch 8	Outer face character	Convex	Concave		
Ch 9	Selenizone elevation	Convex	Concave		
Ch 10	Selenizone position	Above mid-whorl	At mid-whorl	Below mid-whorl	
Ch 11	Width of the selenizone	<1 mm	1 to ≤2 mm	>2–4 mm	>4 mm
Ch 12	Base of the shell	Flat	Curved		
Ch 13	Apertural outline	Pentagonal	Quadrangular	Ovate/Rounded	
Ch 14	Number of Whorls	≤5	>5		
Ch 15	Dominant ornamentation	Spiral	Collabral	Collabral and spiral with same strength	

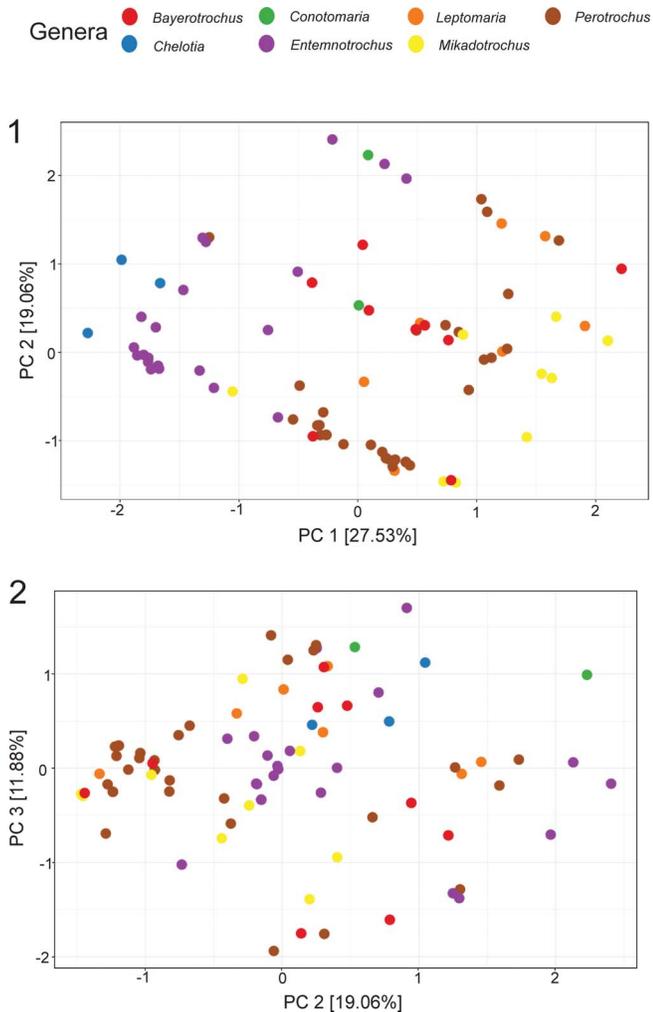


Figure 4. (1, 2) Discrimination of pleurotomariid genera applying Principal Component Analysis (PCA) to the character matrix dataset. The plots show a similar picture to the nMDS plot, with the genera showing poor clusters. (1) PC1-PC2 morphospace; (2) PC2-PC3 morphospace.

low PC 1 values, whereas the genus *Mikadotrochus* is clustered at the right side of the plot and has high PC1 values. This indicates that these two genera can be distinguished based on Ch. 10 and Ch. 11, followed by Ch. 7 and Ch. 5. The genus *Bayerotrochus* has a near-separate cluster in the upper half of the plot, while *Perotrochus* plots in the center, occupying a wide range, but generally below *Bayerotrochus*, implying that these two genera can be distinguished by Ch. 15 and Ch. 5. The genus *Leptomaria* has significant overlap with *Perotrochus* and *Mikadotrochus* in the PC morphospace. *Chelotia* is constrained to the extreme left of the PC morphospace, whereas *Conotomaria* overlaps with the area covered by *Entemnotrochus*. However, these two genera can be differentiated along the PC 1 axis. The PC2/PC3 plot (Fig. 4.2) does not show any significant clusters and thus is not useful for the generic discrimination.

Based on these plots, the genera *Chelotia*, *Entemnotrochus*, *Perotrochus*, *Mikadotrochus*, and *Bayerotrochus* can readily be distinguished by the characters Ch. 10, Ch. 11, Ch. 7, Ch. 5, and Ch. 15. However, the remaining two genera, *Leptomaria* and

Conotomaria, show consistent overlap and thus need to be distinguished based on conventional morphological characters.

For the Cenozoic pleurotomariids, the first division in the classification scheme (Fig. 5; Supplementary Table 2) is based on the width of the selenizone (Ch. 11). Two genera, *Conotomaria* and *Chelotia*, fall in the narrow selenizone group (<1 mm). *Entemnotrochus* has a broad selenizone (1–2 mm), *Leptomaria*, *Perotrochus*, and *Bayerotrochus* have a moderately broad selenizone (2–4 mm), and *Mikadotrochus* has a very broad selenizone (>4 mm).

Conotomaria and *Chelotia* both have a narrow selenizone, but can be readily distinguished on the basis of their shell profile (Ch. 2), which is coeloconic in the former, and cyrtconic in the latter.

With regard to the position of the selenizone (either above or below the mid-whorl) (Ch. 10), *Conotomaria*, *Chelotia*, *Entemnotrochus*, and *Bayerotrochus* have the selenizone at or above mid-whorl, whereas the remaining genera have their selenizone at or below mid-whorl.

Entemnotrochus can be distinguished from *Bayerotrochus* based on the presence/absence of the umbilicus (Ch. 7), as well as the width of the selenizone. As stated earlier, *Entemnotrochus* is strictly phanerocephalous, whereas *Bayerotrochus* is anomphalous.

Leptomaria is variable with regard to the umbilicus, ranging from anomphalous to broadly phanerocephalous. However, *Leptomaria* is mostly characterized by an adpressed suture (Ch. 5) along with the spiral and reticulate shell ornamentation (Ch. 15). *Perotrochus* is strictly anomphalous along with an impressed suture and predominantly spiral ornamentation.

In addition, the length of the slit can also be considered as a distinguishing morphological character for extant genera (described in Knight et al., 1960 and Harasewych, 2002). *Perotrochus* has a shallow slit (length of $\sim 30^\circ$ of the last whorl), followed by *Mikadotrochus* ($<40^\circ$) and *Bayerotrochus* ($<60^\circ$). *Entemnotrochus* has the longest slit, extending for $\sim 160\text{--}180^\circ$.

Based on the proposed classification scheme, 20 species out of the 54 species previously classified as *Pleurotomaria* are here reassigned. Two of them are transferred to *Leptomaria*, one to *Conotomaria*, two to *Chelotia*, seven to *Perotrochus*, and eight to *Entemnotrochus*.

Following revision, the 149 Cenozoic pleurotomariid species belong seven genera in the Family Pleurotomariidae, and are assigned as follows: *Leptomaria*: 14 species; *Conotomaria*: six species; *Chelotia*: six species; *Perotrochus*: 41 species; *Entemnotrochus*: 25 species; *Mikadotrochus*: nine species; *Bayerotrochus*: 16 species. Finally, 32 species are classified as Genus uncertain, which is due to the lack of data enabling their reassignment (Appendix 1). Examination of their type material or of additional specimens may resolve their generic allocation in the future.

Discussion

The Cenozoic pleurotomariids are less diverse compared to the Mesozoic ones and are represented by only seven genera. The overall diversity declined until the late Miocene, but a sudden increase followed toward the modern fauna. The bathymetric distribution of extant species is limited to deeper water on the

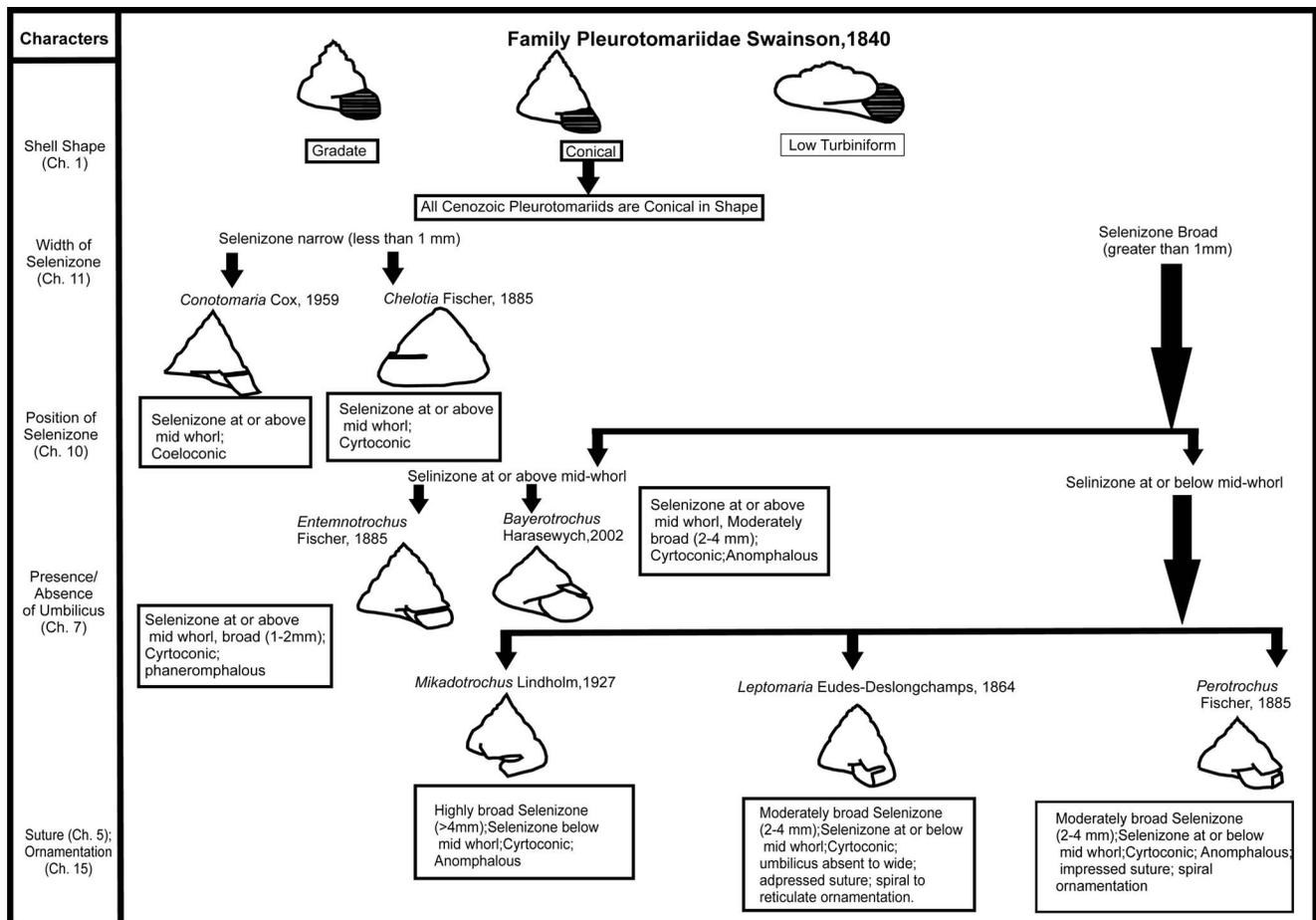


Figure 5. The newly proposed classification scheme for the Cenozoic pleurotomariid genera based on conventional characters (mostly adopted from Knight et al., [1960], Szabo [1980] and Harasewych and Kiel [2007]) and several new characters supported by the multivariate analyses. For details see text.

outermost shelf and upper continental slope. Most of the Cenozoic fossil pleurotomariids are also reported from strata representing deep marine environments (Hickman, 1976; Lin, 1976; Harasewych, 2002; Harasewych and Kiel, 2007). On the other hand, several fossil Cenozoic pleurotomariids (as described in Kase and Katayama, 1981 and Tomida and Sako, 2016), including our finds from the Oligocene and early Miocene of western India, have been found in shallow water (i.e., marginal marine to inner shelf settings). These observations indicate that Cenozoic pleurotomariids occurred over a greater range of water depth and contradicts the generalization that they only occur in deep water.

While successfully addressing the problems of taxonomic classifications of Cenozoic pleurotomariids, our character matrix and the multivariate analyses (nMDS and PCA plots) indicate that multiple characters are required for accurate classification. Conventional classification is preferable for a general morphology-based grouping of taxa, but not always adequate for generic distinction. In addition, there is very little morphological diversification within Cenozoic members of the family. As a consequence, previous authors assigned several Cenozoic pleurotomariid species to the genus *Pleurotomaria*. The classification scheme proposed in the present study reduces the chances of misidentification of Cenozoic pleurotomariids

because it considers conventional morphological characters along with newly recognized morphological characters supported by multivariate statistics.

The K-Pg mass extinction was a fatal blow for both the representatives of gradate and conical genera of the Family Pleurotomariidae. The gradate forms became extinct at the boundary, whereas two genera with conical form (*Leptomaria* and *Conotomaria*) were the sole survivors (Harasewych and Kiel, 2007). Even though the pleurotomariids survived the K-Pg mass extinction, recovery of the group throughout the entire Cenozoic was very slow (Hickman, 1976; Das, 2002; Harasewych and Kiel, 2007). It is important to know the migration patterns of the different pleurotomariid genera throughout the Cenozoic, so that the recovery, as well as the evolutionary change of this family, can be traced. To do so, the primary requirement is to determine the global paleobiogeographic distribution of species and genera during the Cenozoic. In addition, knowledge of the global distribution of pleurotomariids during the Late Cretaceous is important, so that the impact of the K-Pg mass extinction can be determined. The lack of a Cenozoic fossil record of pleurotomariids from the Indian sub-continent has limited past researchers to find a link between the distribution areas of Atlantic and Pacific pleurotomariids. The new finds from the Oligocene and early Miocene of western India shed light on the migration pathways of two

pleurotomariid genera between the Atlantic and Pacific oceans. The revision of Cenozoic *Pleurotomaria* results in the definition of several strictly Cenozoic genera, and the generic status of numerous pleurotomariid species is updated so that these issues can be addressed in future publications.

Systematic paleontology

Class Gastropoda Cuvier, 1797
 Subclass Vetigastropoda Salvini-Plawen, 1980
 Order Pleurotomariida Cox and Knight, 1960
 Superfamily Pleurotomarioidea Swainson, 1840
 Family Pleurotomariidae Swainson, 1840
 Genus *Entemnotrochus* Fischer, 1885

Type species.—*Entemnotrochus adansoniana* (Crosse and Fischer, 1861); (by original designation); Recent; Gulf of Mexico, Caribbean.

Entemnotrochus kathiawarensis new species

Figure 6

Holotype.—Holotype: specimen no. ISI/dwk/Pleu/19/110701/01. Kuranga Member, Gaj Formation, Dwarka Basin; early Miocene (Burdigalian).

Diagnosis.—Flat to slightly convex whorl profile, no shoulder present, smooth selenizone, weakly convex and smooth base, broad umbilicus.

Occurrence.—Early Miocene (Burdigalian); Kuranga Member, Gaj Formation, Dwarka, Gujarat, India.

Description.—Shell medium sized, with diameter slightly greater than height ($H = 30.89$ mm, $D = 38.42$ mm), trochiform, with flat to slightly convex whorl profile. Five whorls preserved; earlier whorls missing. H/D ratio is 0.80. Apical angle 84° , pleural angle 61° . Suture impressed. Base weakly convex, smooth, with broad and deep umbilicus ($UD = 13.33$ mm). Shell surface ornamentation is not clearly discernible; feebly developed spiral threads present below selenizone.

Width of selenizone (SW) is 1.29 mm; selenizone positioned between upper third of whorl height and mid-whorl. Selenizone feebly convex and smooth. Aperture slightly broken with sub-rectangular in shape ($AH = 10.30$ mm, $AW = 13.95$ mm); base of aperture more or less flat.

Etymology.—Named after Kathiawar Peninsula of Gujarat, India from where the present specimen was collected.

Material.—One moderately preserved specimen (specimen no. ISI/dwk/Pleu/19/110701/01), an internal mold with parts of the shell preserved. The specimen was collected 200 m east of Kuranga Railway Station, Devbhumi Dwarka District, Gujarat, India ($22^\circ 03' 35.7''$ N, $69^\circ 11' 17''$ E). For measurements of the specimen, see Table 2 and Supplementary Figure 2 (1).

Remarks.—The species is represented by only one moderately preserved specimen, but the overall shape of the shell, position of

the selenizone, surface ornamentation, smooth and weakly convex base, and broad umbilicus justify assignment of the present species to the genus *Entemnotrochus* Fischer, 1885. The specimen closely resembles the Recent species *Entemnotrochus rumphii* (Schepman, 1879) with regards to its overall shape, the flat to convex whorl profile, and the smooth selenizone. However, the entire shell of *Entemnotrochus rumphii* is ornamented with a cancellate ‘beaded’ sculpture, while *E. kathiawarensis* n. sp. only has feeble spirals threads below the selenizone.

The species can be distinguished from other Miocene species of *Entemnotrochus* based on overall shell shape, size, and surface ornamentation. In *Entemnotrochus panchangwui* Lin, 1975 and *Entemnotrochus siuyingae* Lin, 1975 from the Miocene of Taiwan, the H/D ratio is greater than one, while it is less than one in *E. kathiawarensis* n. sp. In addition, the umbilical diameter (UD) to shell diameter (D) ratio in *E. panchangwui* is 1:4, whereas *E. kathiawarensis* n. sp. has a UD/D ratio of 1:2.88. *Entemnotrochus kathiawarensis* n. sp. has a smooth selenizone while *E. siuyingae* has a beaded selenizone.

Entemnotrochus cf. *E. bianconii* (d’Archiac and Haime, 1854)

Figure 7

cf. 1854 *Pleurotomaria?* *bianconii* d’Archiac and Haime, p. 291, 369, pl. 26, fig. 19.

Occurrence.—Late Oligocene (Chattian), Bermoti Member, Maniyara Fort Formation, Kutch, India.

Description.—Shell medium to large sized, with diameter slightly greater than height ($H = 81.49$ mm, $D = 85.44$ mm), trochiform. Slightly convex whorl profile with a very narrow shoulder, gradually curving towards broad outer face of whorl. No more than five whorls preserved; earlier whorls missing in most specimens. Apical angle $\sim 100^\circ$. Pleural angle ranging from 70 – 89° . Suture weakly impressed. Base nearly flat to slightly convex. Umbilicus wide ($UD = 24.59$ mm). Ornamentation indiscernible, but a narrow, faint impression of the selenizone can be observed above mid-whorl on several whorls. Aperture nearly tetragonal with apertural width much greater than apertural height ($AW = 33.78$, $AH = 19.12$); base of aperture feebly convex.

Material.—Ten poorly preserved specimens, all internal molds. Specimens no. Mani/17/Pleu/10, 175, 176, Mani/19/Pleu/1, 2, 3 were collected from Bermoti Village ($23^\circ 27' 45.1''$ N, $68^\circ 36' 06.4''$ E); specimens no. Mani/18/Pleu/1, 2 were collected from Lakhdi Dam, 4.8 km NW of Vayor ($23^\circ 27' 02.2''$ N, $68^\circ 40' 03''$ E); specimen no. Mani/18/Pleu/3 was collected from Kharoi Village near Lakhdi Dam, 4.5 km NW of Vayor ($23^\circ 26' 55.5''$ N, $68^\circ 40' 09.4''$ E); specimen no. Mani/10/Pleu/322 was collected from Maniyara Fort near Bermoti Village ($23^\circ 29' 15''$ N, $68^\circ 37' 10''$ E). For measurements of the specimens see Table 2 and Supplementary Figure 2 (2). Specimens no. Mani/17/Pleu/175, Mani/19/Pleu/1, 3, Mani/17/Pleu/175, 176, 10 are the figured specimens.

Remarks.—The specimens are poorly preserved, all of them being internal molds. The trochiform, slightly broader than high with a convex whorl profile, wide umbilicus, and a narrow

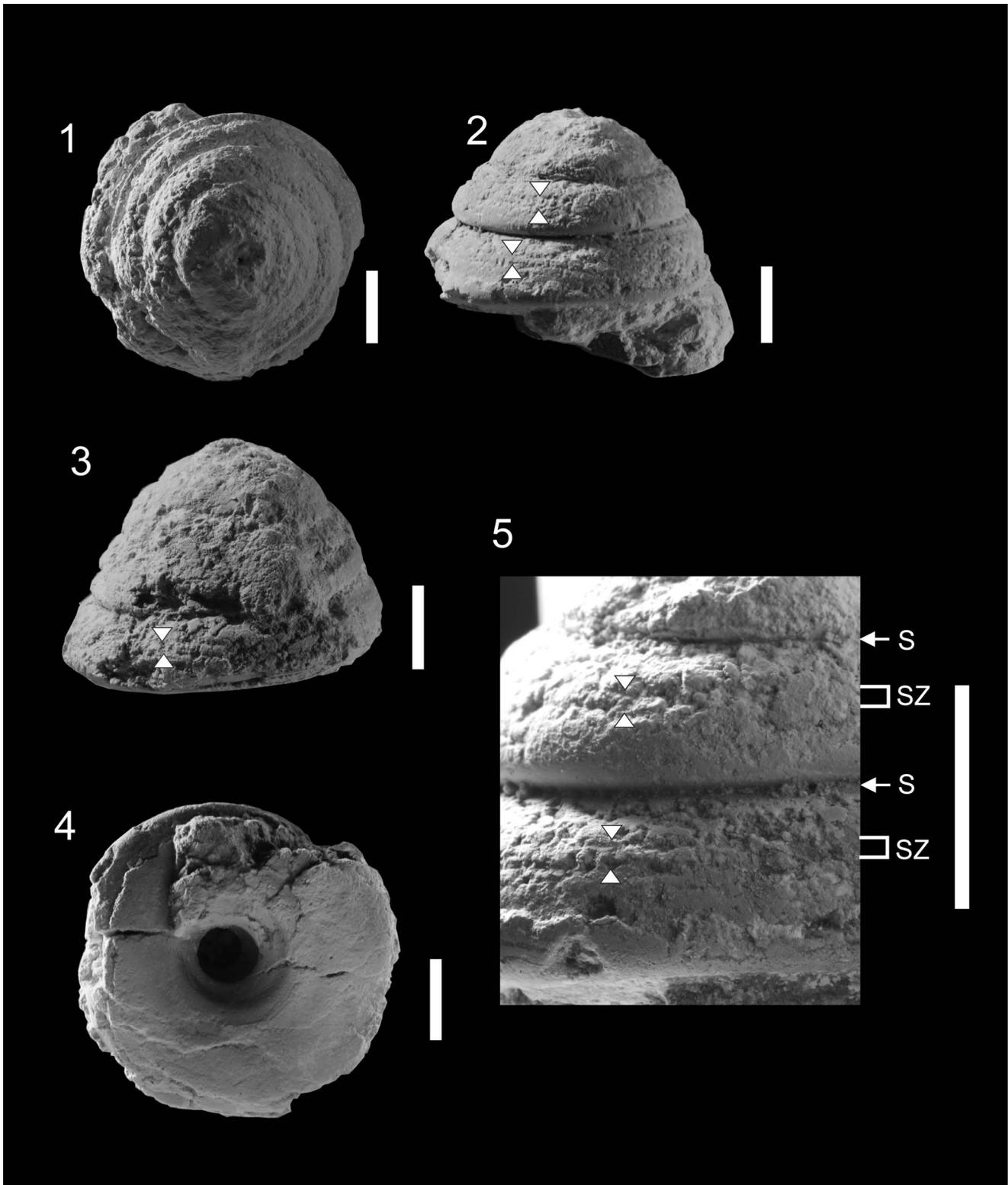


Figure 6. (1–5) *Entemnotrochus kathiawarensis* n. sp., specimen no. ISI/dwk/Pleu/19/110701/01 (holotype): (1) apical view; (2) apertural view; (3) abapertural view; (4) basal view; (5) close up view of selenizone and sculpture between suture and last two dorsal whorls; scale bars = 10.0 mm. The white arrows mark the selenizone. Abbreviations: SZ = selenizone; S = suture.

selenizone positioned above mid whorl justify assignment to *Entemnotrochus*. *Entemnotrochus bianconii* (d'Archiac and Haime, 1854), reported from the Eocene of Kutch, western

India, shows striking similarity with regard to overall shell outline and size when compared to our specimens. The species *E. bianconii* was not described in detail, but only illustrated by

Table 2. Measurement table for the newly described pleurotomariid specimens from the Oligocene and the early Miocene of Kutch and Dwarka basins of western India. Other abbreviations used in descriptions: D = Diameter; H = Height; H/D = Height by Diameter ratio; N = Number of Whorls; AA = Apical Angle; PA = Pleural Angle; SW = width of the Selenizone; AH = Apertural Height; AW = Apertural Width; UD = Umbilical Diameter; dwk = Dwarka; Pleu = Pleurotomariidae; Mani = Maniyara Fort Formation; ‘-’ represents data could not be measured.

Specimens	Present collection	Diameter (D)	Height (H)	H/D	No. of Whorls (N)	Apical angle (AA)	Pleural angle (PA)	Width of Selenizone (SW)	Apertural Height (AH)	Apertural Width (AW)	Umbilical Diameter (UD)
ISI/dwk/Pleu/19/110701/01	<i>Entemnotrochus kathiawarensis</i> n. sp.	38.42	30.89	0.80	(5)	84°	61°	1.29	10.30	13.95	13.33
Mani/17/Pleu/176	<i>Entemnotrochus</i> cf. <i>E. bianconii</i>	85.44	81.49	0.95	(5)	100°	70°	-	-	-	21.17
Mani/17/Pleu/175	<i>Entemnotrochus</i> cf. <i>E. bianconii</i>	72.26	54.28	0.75	(4)	104°	75°	-	-	-	-
Mani/19/Pleu/1	<i>Entemnotrochus</i> cf. <i>E. bianconii</i>	76.82	67.13	0.87	(5)	103°	76°	-	30.92	-	22.22
Mani/19/Pleu/2	<i>Entemnotrochus</i> cf. <i>E. bianconii</i>	68.57	46.67	0.68	(4)	99°	75°	-	18.65	-	22.23
Mani/19/Pleu/3	<i>Entemnotrochus</i> cf. <i>E. bianconii</i>	57.91	36.99	0.64	(3)	-	89°	-	-	-	23.45
Mani/17/Pleu/9	<i>Entemnotrochus</i> cf. <i>E. bianconii</i>	62.81	37.65	0.60	(2)	-	78°	-	18.69	30.65	22.97
Mani/17/Pleu/10	<i>Entemnotrochus</i> cf. <i>E. bianconii</i>	65.04	36.16	0.56	(2)	-	84°	-	21.38	25.67	24.59
Mani/18/Pleu/2	<i>Entemnotrochus</i> cf. <i>E. bianconii</i>	30.76	27.49	0.89	(4)	-	81°	-	11.08	12.80	11.13
Mani/10/Pleu/322	<i>Entemnotrochus</i> cf. <i>E. bianconii</i>	70.65	36.12	0.51	(2)	-	85°	-	19.12	33.78	22.85
Mani/18/Pleu/1	<i>Entemnotrochus</i> cf. <i>E. bianconii</i>	34.12	26.02	0.76	(3)	101°	88°	-	11.36	18.15	16.10
Mani/17/Pleu/322	<i>Entemnotrochus?</i> sp. 1	18.04	17.98	0.99	(3.5)	65°	43°	-	7.73	10.02	6.67
Mani/17/Pleu/314	<i>Perotrochus bermotiensis</i> n. sp.	36.25	23.56	0.649	(4)	-	71°	2.13	-	-	-

d’Archiac and Haime (1854) due to the very poor preservation of the specimens. Although the specimens described here are closely similar to *E. bianconii*, better-preserved specimens are needed for confident assignment.

Entemnotrochus? sp. 1
Figure 8

Occurrence.—Late Oligocene (Chattian), Bermoti Member, Maniyara Fort Formation, Kutch, India.

Description.—The specimen is a poorly preserved, small (D = 18.04 mm, H = 17.98 mm) internal mold. Shell trochiform, whorls nearly flat to slightly convex, suture impressed. Apical angle 65°, pleural angle 43°. Base convex; umbilicus indiscernible. Ornamentation cannot be discerned. Faint impression of very narrow selenizone visible above the mid-whorl (Fig. 8.5). Aperture rectangular with apertural width greater than height (AW = 10.02, AH = 7.73). Base of aperture convex.

Material.—One poorly preserved specimen, an internal mold, Mani/17/Pleu/322, collected from Bermoti Village (23°27’45.1”N, 68°36’06.4”E). For measurements of the specimen see Table 2 and Supplementary Figure 2 (3).

Remarks.—The specimen is poorly preserved and the umbilicus is indiscernible. The shell is characterized by an overall trochiform shape, and a nearly flat to slightly convex whorl profile, with a very faint impression of the narrow selenizone present above mid whorl, indicating its affinity with the genus *Entemnotrochus*. Thus, the specimen is placed tentatively in *Entemnotrochus*. For an exact determination of the generic position, better-preserved specimens are needed. Also, because the specimen is an internal mold and lacks external shell features, it cannot be assigned to any species. The small size and elongated shell profile (H/D = 0.99) of the present species clearly differentiated it from the coeval species, *Entemnotrochus* cf. *E. bianconii* (d’Archiac and Haime, 1854), which has large size and has slightly depressed shell profile (H/D = 0.95). Moreover, overall shape with flat whorl

profile and absence of shoulder clearly distinguishes it from *Entemnotrochus* cf. *E. bianconii* (d’Archiac and Haime, 1854).

Genus *Perotrochus* Fischer, 1885

Type species.—*Pleurotomaria quoyanus quoyanus* Fischer and Benardi, 1856 (by original designation); Recent; from the Caribbean.

Perotrochus bermotiensis new species
Figure 9

Holotype.—Specimen no. Mani/17/Pleu/314, the figured specimen. Oligocene (Rupelian), Coral Limestone Member, Maniyara Fort Formation, Kutch, India.

Diagnosis.—Shell trochiform, with flat whorl profile; no shoulder present; convex selenizone sculptured with two feebly visible narrow spiral threads.

Occurrence.—Oligocene (Rupelian), Coral Limestone Member, Maniyara Fort Formation, Kutch, India.

Description.—Shell medium-sized, trochiform, vaguely anomphalous; diameter greater than height (H = 23.56 mm, D = 36.25 mm), apex not preserved. Pleural angle is 71°, four whorls preserved. Whorls feebly convex; suture impressed. Shell ornamented with two spiral ribs between the suture and the selenizone. Faint spiral ornamentation also present near the base of the shell. Selenizone situated at the lower third of the body whorl. Width of selenizone 2.13 mm. The selenizone is feebly convex, with two narrow inconspicuous spiral threads on the selenizone. Base of the shell obscured by adhering sediment. Aperture poorly preserved.

Etymology.—Named after Bermoti village, Kutch, Gujarat, India from where the present specimen collected.

Material.—One moderately preserved specimen, an internal mold with parts of the shell preserved. Specimen no. Mani/17/

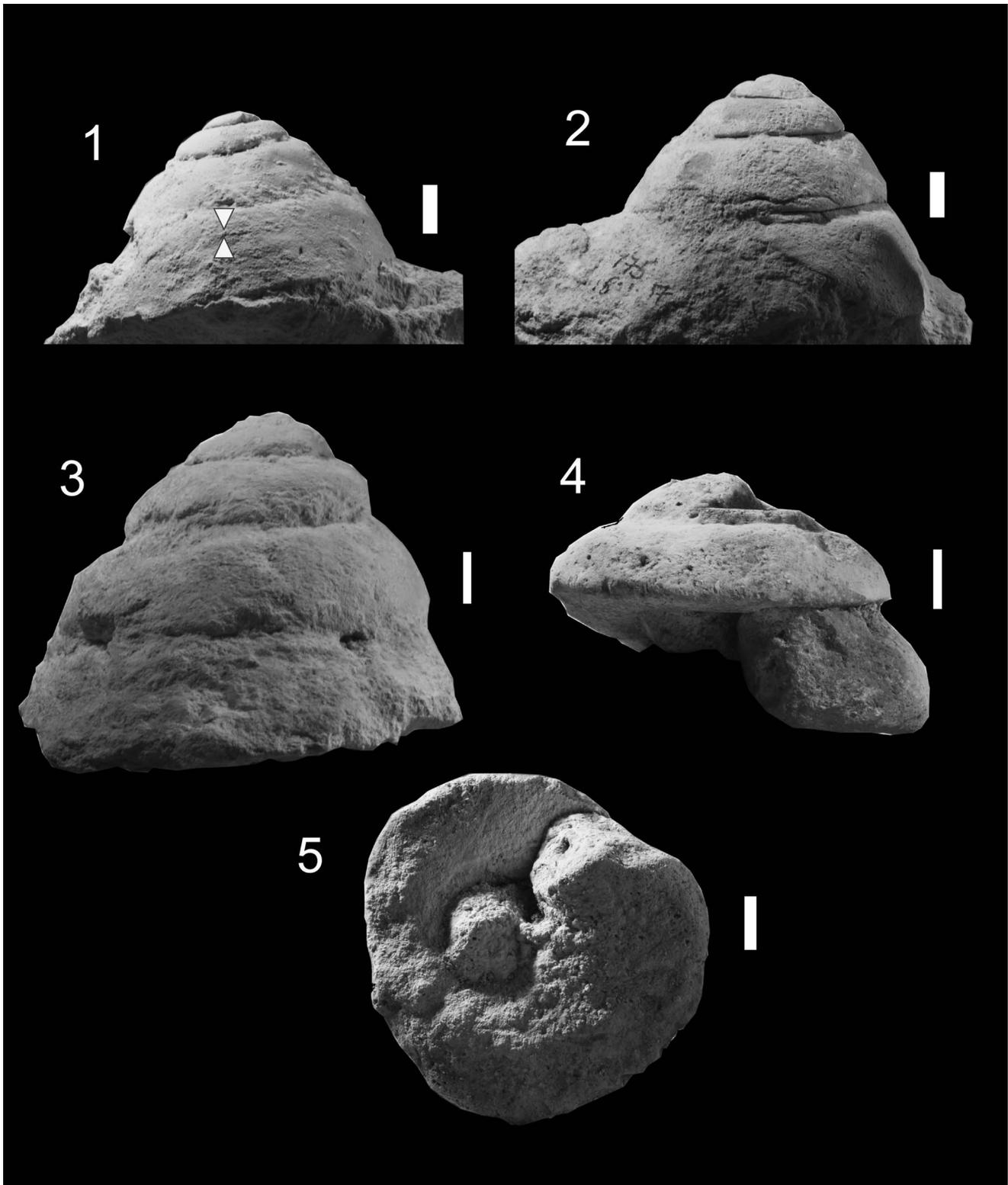


Figure 7. (1–5) *Entemmotrochus* cf. *E. bianconii* (d'Archiac and Haime, 1854), specimen no. Mani/17/Pleu/175: (1) abapertural view; (2) apertural view; Mani/17/Pleu/176: (3) abapertural view; Mani/17/Pleu/10: (4) apertural view; (5) basal view; scale bars = 10.0 mm. The white arrows mark the selenizone.

Pleu/314 collected at Bermoti River, near Bermoti village (23°27'45.1"N, 68°36'06.4"E). For measurements of the specimen see [Table 2](#) and Supplementary Fig. 2 (4).

Remarks.—*Perotrochus bermotiensis* n. sp. is represented by a single moderately preserved specimen, but the overall shape of the shell, position of the selenizone (below mid-whorl), width

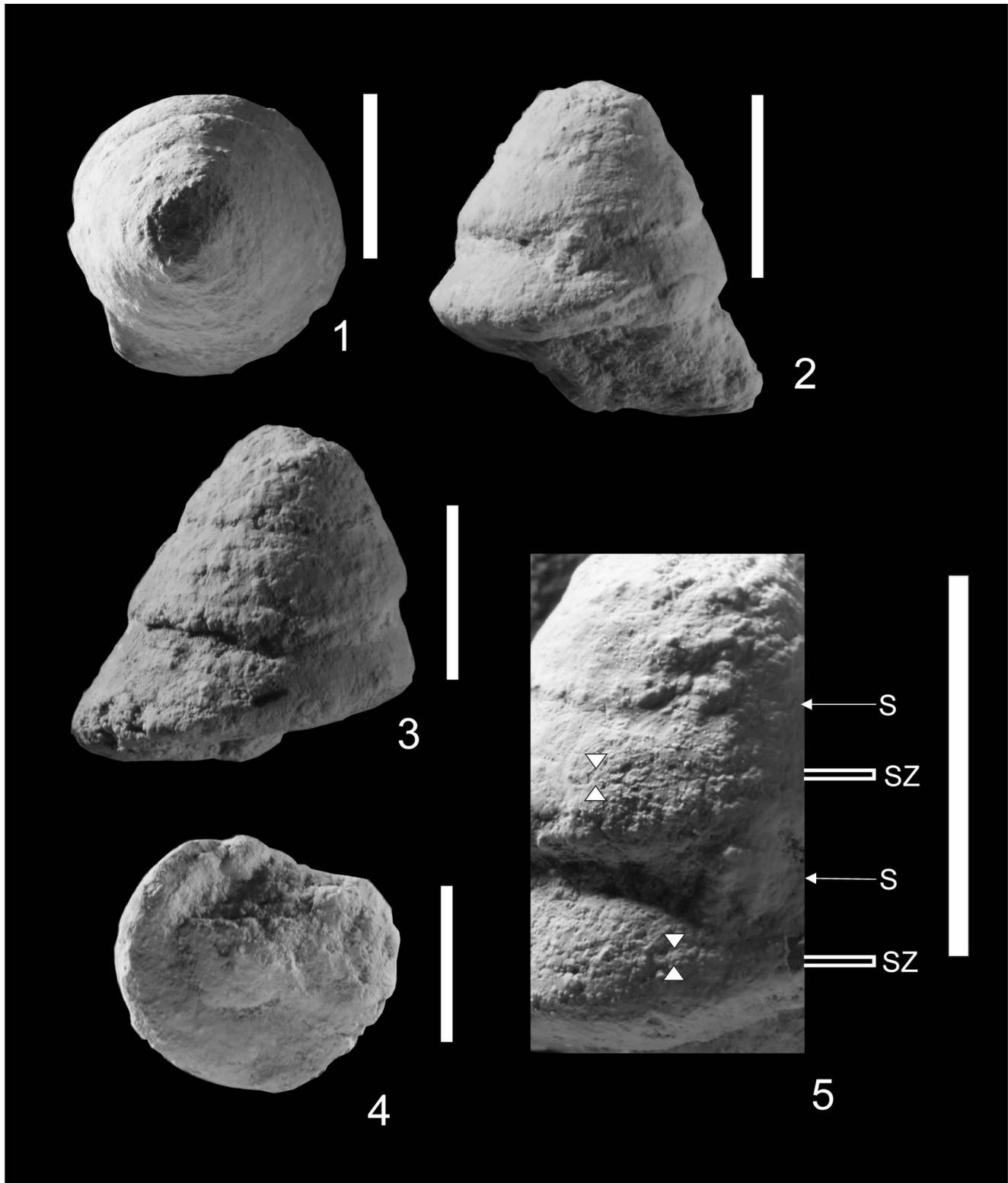


Figure 8. (1–5) *Entemnotrochus?* sp. 1, Specimen no. Mani/17/Pleu/322: (1) apical view; (2) apertural view; (3) abapertural view; (4) basal view; (5) close up view of selenizone and sculpture between suture and last two dorsal whorls; scale bars = 10.0 mm. The white arrows mark the selenizone. Abbreviations: SZ = selenizone; S = suture.

of the selenizone in the range of 2–4 mm, surface ornamentation, and the weakly convex anomphalous base place this in the genus *Perotrochus*. The specimen closely resembles *Perotrochus*

hsiehwanghoi Lin, 1976 in overall shell outline and position and width of the selenizone. However, the shell of *P. hsiehwanghoi* Lin, 1976 is much larger (max D = 130 mm),

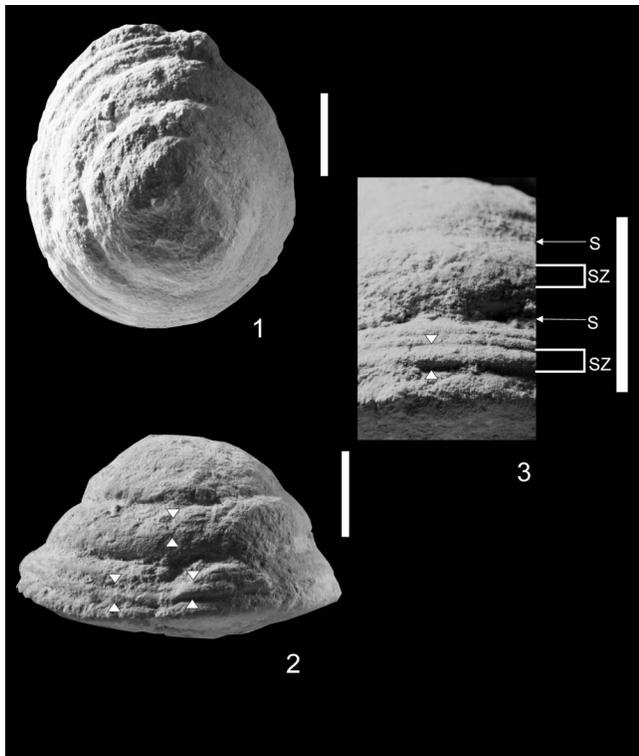


Figure 9. (1–3) *Perotrochus bermotiensis* n. sp., Mani/17/Pleu/314 (holotype): (1) apical view; (2) abapertural view; (3) close up view of selenizone and sculpture between suture and last two dorsal whorls; scale bars = 10.0 mm. The white arrows mark the selenizone. Abbreviations: SZ = selenizone; S = suture.

its whorls are much higher, and it has a narrow shoulder on the last whorl.

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Data Availability Statement

Data available in Dryad Digital Repository: <https://doi.org/10.5061/dryad.m905qfv0d>.

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