

Pleurotomarioidean Gastropods

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Pleurotomarioidean gastropods are continuously present in the fossil record since the Upper Cambrian and survive into the Recent fauna, thus providing rare insights into the evolutionary history of the class Gastropoda. Pleurotomarioidea achieved greatest numerical and morphological diversity during the Paleozoic, and dominated global shallow water marine gastropod faunas during the Paleozoic and Mesozoic. Only a single family, the Pleurotomariidae, survived the end-Cretaceous Extinction, but was restricted to deep water through most of the Cenozoic. The first living

pleurotomariid was discovered during the mid-nineteenth century, along the bathyal zone of the western Atlantic. Subsequently collected specimens of these "living fossils" revealed that these animals comprise a mosaic of primitive and highly derived characters that originally inspired a new model of gastropod evolution, but more recently defy the orderly inclusion of this group within a cladistic framework of gastropod phylogeny. Molecular studies have likewise shown that the 18S rDNA gene of pleurotomariids contains novel insertions, and evolves more rapidly than in related taxa. A number of studies confirm that the Pleurotomarioidea may be included in the clade Vetigastropoda together with the Trochoidea, Fissurelloidea, Haliotoidea, and Scissurelloidea. However, neither the position of the superfamily within Vetigastropoda, nor the position of Vetigastropoda within Gastropoda is yet robustly resolved. The anatomical and molecular data are reviewed; the latter used to produce a well-resolved phylogeny of the genera within the family, and to justify the naming of the long-used informal grouping "Perotrochus Group B" as the genus Bayerotrochus. A review of the geographic and bathymetric distributions of pleurotomariids reveals that the higher taxa segregate bathymetrically, while the species within each genus generally segregate geographically, so that most species exist in allopatry. The diet of pleurotomariids is reviewed, based on direct observations as well as analyses of gut contents, and is shown to consist primarily of sponges, but may include stalked crinoids, octocorals and, under aquarium conditions, fish and clam tissue. Despite their thin and relatively fragile shells, Pleurotomariidae survive an extraordinary number of attacks by predators, primarily crustaceans and fish. Their hypobranchial glands are capable of rapidly secreting a white fluid that probably serves as a chemical defense to repel predators. Circumstantial evidence suggests that this defensive mechanism may have originated during the Paleozoic. Despite the great antiquity of this lineage, pleurotomariids possess a substantial number of morphological, molecular and ecological novelties.

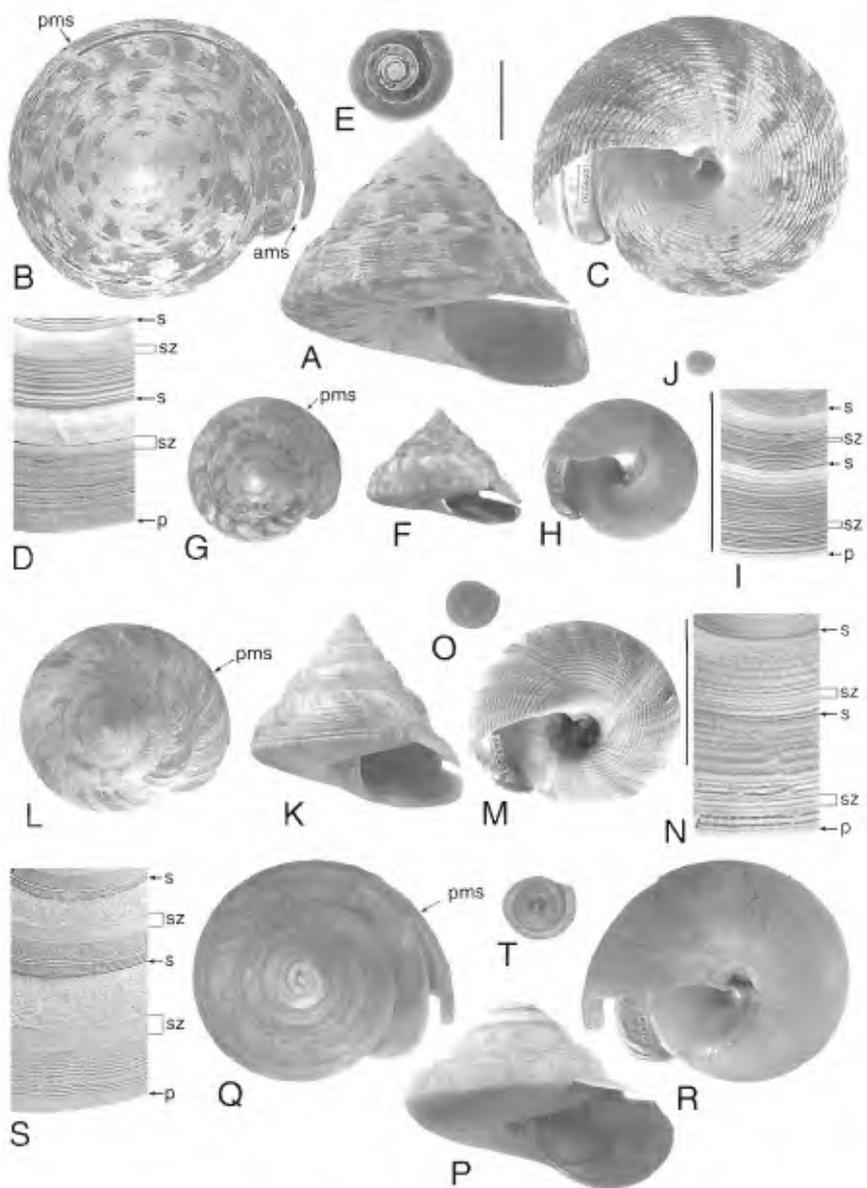
1. INTRODUCTION

Gastropods of the superfamily Pleurotomarioidea are readily distinguished by their dextral, conispirally coiled shell with an inner nacreous layer and a characteristic emargination along the outer lip that produces a selenizone, a spiral trace of the slit that is evident throughout the adult shell (Figure 1). At least two families of pleurotomarioideans, Sinuopeidae Wenz, 1938, and Raphistomatidae Koken, 1896, occur in Upper Cambrian fossil beds, making the Pleurotomarioidea not only the oldest undisputed gastropod lineage, but also the only gastropod superfamily to be continuously

represented in the fossil record from the Cambrian to the present (Woodward, 1885; Wenz, 1938; Cox, 1960b; Knight *et al.*, 1960; Tracey *et al.*, 1993).

Species and generic diversity were greatest during the Paleozoic (Figure 2A), while the number of families proliferated to 13 during the Triassic, contributing to the maximum family level diversity during this period (Knight *et al.*, 1960). The family Pleurotomariidae Swainson, 1840 (as refined by Knight *et al.*, 1960; Tracey *et al.*, 1993) has its origins in the Lower Triassic, and is the only family within the Pleurotomarioidea to survive beyond the Jurassic and into the Recent fauna. Of the more than 1500 described species and subspecies, 25 are living today (Anseeuw and Goto, 1996; Anseeuw, 1999). Pleurotomarioideans were abundant and diverse components of shallow water marine faunas throughout the Paleozoic (e.g., Thomas, 1940; Hayasaka and Hayasaka, 1953; Batten, 1958, 1966; Wolfenden, 1958; Ingles, 1963; Shikama and Nishida, 1968) and Mesozoic (e.g., Hudleston, 1895 in 1887–1896; Cox, 1960a; Kanie *et al.*, 1980; Benfrika, 1984; Ziegler, 1984). However, Cenozoic fossils are relatively rare, and tend to be limited to deep-water facies (e.g., Hirayama, 1955; Kanno, 1961; Jung, 1968, 1970; Hickman, 1976; Tomida *et al.*, 1999), while living species are usually restricted to depths ranging from 100m to nearly 1000 m (Anseeuw and Goto, 1996; Figure 12A).

Fossil pleurotomariids were known to pre-Linnean authors (e.g., Lister, 1678), and were allied with the Trochidae in early classifications (e.g., Swainson, 1840; Adams and Adams, 1858). Although records of living pleurotomariids appear in eighteenth century Japanese literature (Kenkado, 1755), it was not until the early stages of the era of deep-sea exploration that a living pleurotomariid became known to the western world with the discovery of *Perotrochus quoyanus* (Fischer and Bernardi, 1856). This was among the earliest of the “living fossils” to be discovered in the deep sea. For over a century, each collection of additional specimens of pleurotomariids prompted intense anatomical scrutiny and a series of publications (e.g., Crosse and Fischer, 1861; Crosse, 1882; Mitsukuri, 1897; Bouvier and Fischer, 1898, 1901, 1902; Kosuge and Suzuki, 1969; Oyama, 1980). This, in turn, led to the formulation of a new paradigm of gastropod evolution, one in which anatomical bilateral symmetry was considered to be the primitive gastropod condition. Pleurotomariids have since been regarded almost universally as the most primitive living gastropods. Their symmetrical, paired, pallial cavity organs and an asymmetrically coiled shell were thought to be transitional between extinct, planispirally coiled, bilaterally symmetrical ancestors and asymmetrical modern gastropods (e.g., Thiele, 1902, 1935; Wenz, 1938; Yonge, 1947; Knight 1952; Knight *et al.*, 1960; Fretter and Graham, 1962;



Morton and Yonge, 1964; Hickman, 1984a, b; Graham, 1985). This view persists in many modern textbooks (e.g., Brusca and Brusca, 1990; Rupert and Barnes, 1994), no doubt because of its heuristic value, despite the accumulation of evidence that docoglossan limpets (renamed Patellogastropoda and Eogastropoda) comprise the most basal clade within Gastropoda. More recent phylogenetic classifications generally place the Pleurotomariidae within the order Vetigastropoda (e.g., Golikov and Starobogatov, 1975; Salvini-Plawen, 1980; Haszprunar, 1988; Ponder and Lindberg, 1996, 1997; Harasewych *et al.*, 1997), frequently as a sister taxon to Trochidae. While the inclusion of the Pleurotomariidae within Vetigastropoda is well supported, its relationships to other vetigastropod taxa and the relationship of Vetigastropoda to other gastropod groups has yet to be robustly resolved, despite substantial research efforts.

The rarity of Recent pleurotomariids in museum collections (Hickman, 1984b: 228) had earlier led to suggestions of low population densities (Hickman, 1976). However, the expansion of commercial fisheries into deeper waters, the use of more sophisticated deep-sea sampling techniques for biological research, and especially the increasing use of research submersibles during the past two decades, have revealed pleurotomariids to be among the numerically dominant macroinvertebrates in rocky and steep-walled bathyal habitats, which are difficult to sample by conventional methods such as dredging and trawling. The increased sampling and opportunities for *in situ* observations, in turn, led to rapid increases in our understanding of the diversity and geographic distribution of this family in the Recent fauna (Figure 2B, e.g., Bayer, 1965; Endo, 1995; Anseeuw and Goto, 1996), its evolutionary relationships (e.g., Haszprunar, 1988; Harasewych *et al.*, 1997), and various aspects of its biology and ecology (e.g., Hickman, 1984a; Kanie *et al.*, 1986;

Figure 1 Representatives of living pleurotomariid clades. (A–E) *Entemnotrochus adansonianus* (Crosse and Fischer, 1861). Type species of *Entemnotrochus* Fischer, 1885. (A) Apertural, (B) dorsal, and (C) ventral views of shell. (D) Sculptural detail and selenizone. (E) Operculum. (F–J) *Perotrochus quoyanus* (Fischer and Bernardi, 1856). Type species of *Perotrochus* Fischer, 1885. (F) Apertural, (G) dorsal and (H) ventral views of shell. (I) Sculptural detail and selenizone. (J) Operculum. (K–O) *Mikadotrochus beyrichii* Hilgendorf, 1877. Type species of *Mikadotrochus* Lindholm, 1972. (K) Apertural, (L) dorsal and (M) ventral views of shell. (N) Sculptural detail and selenizone. (O) Operculum. (P–T) *Perotrochus midas* Bayer, 1965. Example of *Perotrochus* “Group B” (Bayer, 1965). (P) Apertural, (Q) dorsal and (R) ventral views of shell. (S) Sculptural detail and selenizone. (T) Operculum. All shells and opercula to same scale. All scale bars = 3 cm. ams, anterior margin of slit; p, periphery of whorl; pms, posterior margin of slit; s, suture; sz, selenizone.

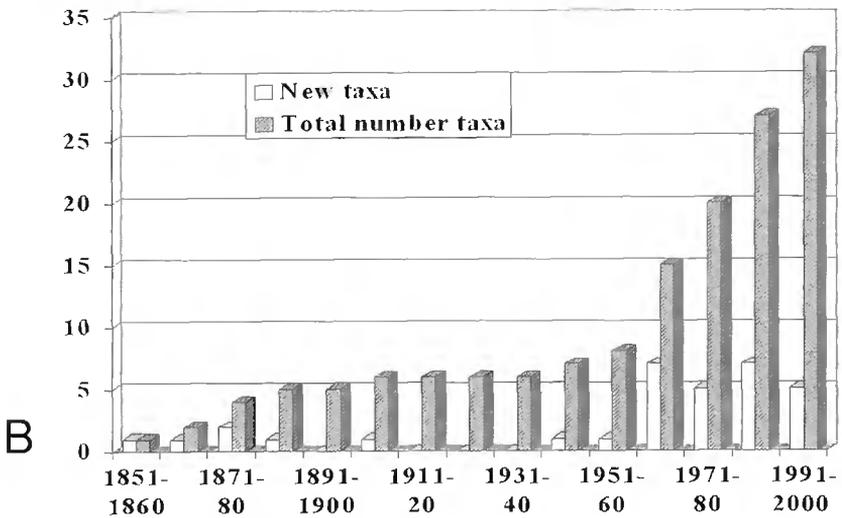
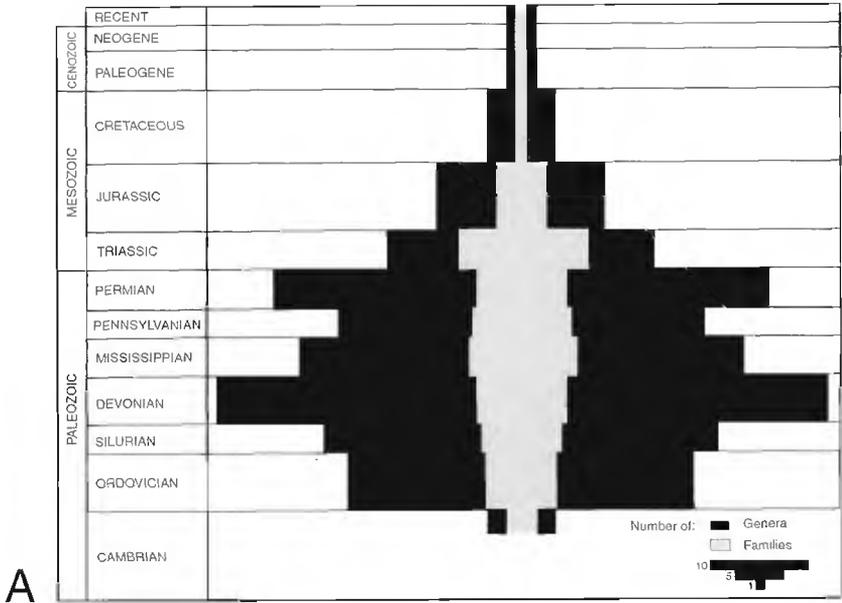


Figure 2 Diversity of Pleurotomarioidea. (A) Genus and family level diversity of the Pleurotomarioidea through Phanerozoic time. Data from Knight *et al.* (1960), *The Zoological Record* 1960–2000, and other sources. (B) Known species level diversity of Recent Pleurotomariidae (by decade) since the discovery of the first living specimen. Data from Anseeuw and Goto (1996) and Anseeuw (1999).

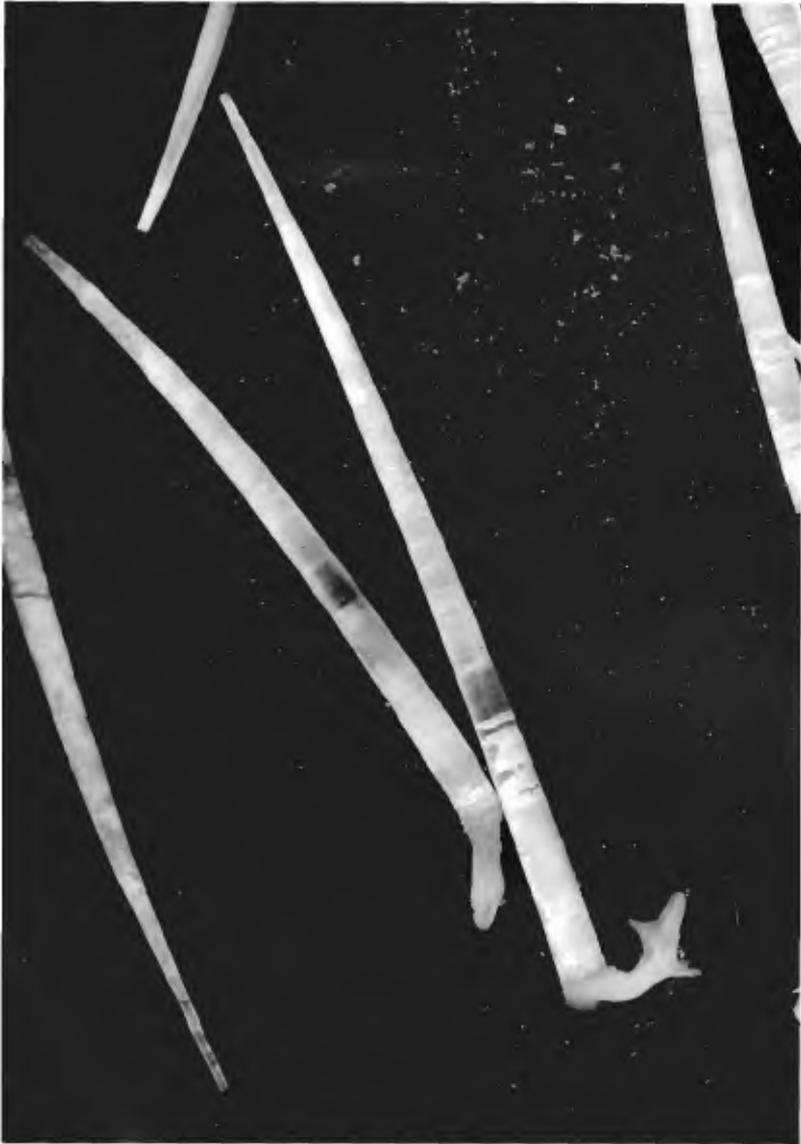


Plate 1 Adults of *Rhabdus rectius*, order Dentaliida, with protruding muscular foot. Note maximum diameter at anterior aperture, transparent secondary shell in upper left and lower apices, dark digestive gland in mid-region, beige kidney immediately anterior to it (center-left specimen), and protruding foot of the two center specimens. On the left the foot is being extended, on the right it is being retracted with flared epipodial lobes. Approximate shell length = 42 mm. © Patrick D. Reynolds.



Plate 2 Individual of *Gadila aberrans*, order Gadilida, family Gadilidae, subfamily Gadilinae. Note narrowing of anterior aperture and notched apex. Approximate shell length = 18 mm. ©Patrick D. Reynolds.



Plate 3 The scaphopod *Fissidentalium acinophorum* with attached anemone, *Anthosactis nomados*. Approximate shell length = 36 mm. © Ronald L. Shimek.



Plate 4 The hermit crab *Orthopagus minimus*, inhabiting the shell of *Dentalium pretiosum*. Approximate shell length = 35 mm. © Ronald L. Shimek.

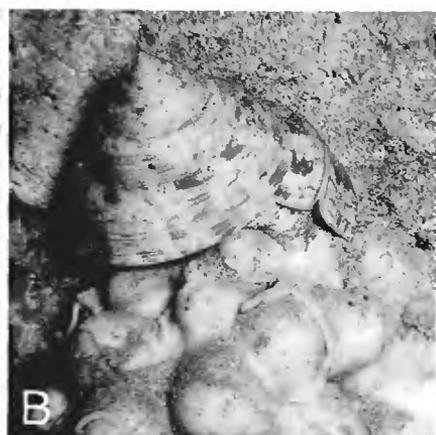
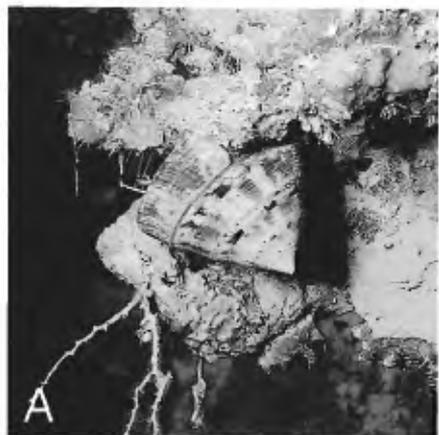
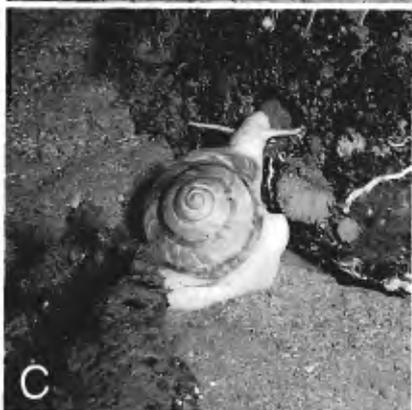
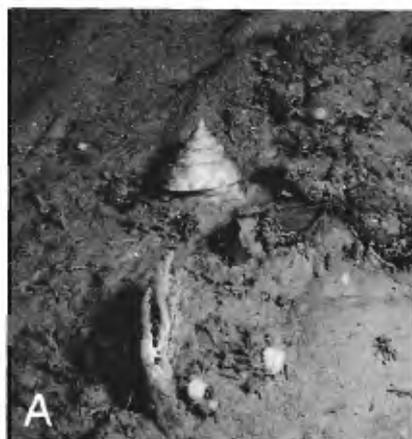


Plate 5 Photographs of living pleurotomariids. **(A-D)** *Entemnotrochus adansonianus* (Crosse and Fischer, 1861). **(A)** Off Riding Rock, San Salvador, Bahamas, 22°53'24"N, 74°54'49"W in 106 m, JOHNSON-SEA-LINK II Station JSL-II-3620, 12 September 1993. **(B)** Off Guadeloupe, Lesser Antilles, 16°16'30"N, 61°50'36"W, in 176 m, JOHNSON-SEA-LINK I Station JSL-I-1844, 10 July 1989. **(C)** *Entemnotrochus adansonianus* in aquarium, with foot and snout exposed. Specimens collected off Navassa Island, Greater Antilles, 18°24'43"N, 75°03'00"W, in 123-141 m, JOHNSON-SEA-LINK I Station JSL-I-2322, 14 October 1988. **(D)** The secretion produced by the hypobranchial glands of *Entemnotrochus adansonianus* when the animal was disturbed in an aquarium. Specimen collected off Chubb Key, Berry Islands, Bahamas, 25°23'06"N, 77°51'36"W, in 108 m, JOHNSON-SEA-LINK I Station JSL-I-4189, 20 October 1999. **(E-F)** *Perotrochus lucaya* Bayer, 1965. **(E)** *Perotrochus lucaya* feeding on a small sponge, off Middle Point, Great Inagua Island, Bahamas, 21°01'45"N, 73°43'48"W, in 380 m, JOHNSON-SEA-LINK II Station JSL-II-2323, 15 October 1988. **(F)** *Perotrochus lucaya* crawling in an aquarium. Specimen collected off West End, Grand Bahama Island, Bahamas, 26°37'36"N, 78°58'30"W, in 399 m, JOHNSON-SEA-LINK I Station JSL-I-4191, 20 October 1999.

Plate 6 Photographs of living pleurotomariids. **(A)** *Perotrochus quoyanus* off Îlets-à-Goyaves, Guadeloupe, Lesser Antilles, 16°10'00"N, 61°49'08"W, in 235 m, JOHNSON-SEA-LINK II Station JSL-II-1845, 10 July 1989. **(B-C)** *Bayerotrochus pyramus*. **(B)** *Bayerotrochus pyramus* feeding on octocoral, off Îlets-à-Goyaves, Guadeloupe, Lesser Antilles, 16°10'00"N, 61°49'08"W, in 306 m, JOHNSON-SEA-LINK II Station JSL-II-1845, 10 July 1989. **(C)** *Bayerotrochus pyramus* feeding on encrusting sponge, off Îlets-à-Goyaves, Guadeloupe, Lesser Antilles, 16°10'12"N, 61°49'00"W, in 312 m, JOHNSON-SEA-LINK II Station JSL-II-1848, 11 July 1989. **(D-F)** *Bayerotrochus midas*. **(D)** *Bayerotrochus midas* and starfish all feeding on sponge, off Egg Island, Bahamas, 25°27'51"N, 76°54'38"W, in 752 m, JOHNSON-SEA-LINK I Station JSL-I-3622, 13 September 1993. **(E)** *Bayerotrochus midas* feeding on sponge, off SW tip of Long Island, Bahamas, 22°50'30"N, 74°53'00"W, in 645 m, JOHNSON-SEA-LINK I Station JSL-I-2324, 16 October 1988. **(F)** *Bayerotrochus midas* feeding on sponge, off Sandy Point, San Salvador, Bahamas, 23°57'04"N, 74°34'54"W, in 695 m, JOHNSON-SEA-LINK I Station JSL-I-2329, 18 October 1988.



Harasewych *et al.*, 1988; Healy, 1988; Healy and Harasewych, 1992; Kanie and Oba, 1993; Goodfriend *et al.*, 1994; Kuramochi *et al.*, 1996).

This article reviews the natural history of living pleurotomariid gastropods by integrating the substantial number of detailed, published observations on various aspects of the anatomy and ecology of many of the living taxa. This information is corroborated and/or supplemented with data garnered from the author's *in situ* observations of most western Atlantic species, dissections of well preserved specimens, and various analyses of shells and tissues. The objective is to provide a cohesive and well-corroborated synthesis of the morphology, ecology and biology of these animals that may be of use in clarifying our still imperfect understanding of the relationships of pleurotomariids to other gastropods, the evolution and functional morphology of their organs systems and genes, and the patterns of their bathymetric and geographic distribution in the world's oceans.

2. STRUCTURE AND FUNCTIONAL MORPHOLOGY

2.1. Shell morphology and ultrastructure (Figures 1, 3, 4)

The shell of pleurotomarioideans is most readily identified by it being conispirally coiled and by it having both an inner nacreous layer and an emargination or slit along its outer lip that produces a selenizone, a band that marks the position of the slit from its posterior margin along all of the whorls of the shell to within a quarter whorl of the protoconch. All pleurotomarioideans have indeterminate growth, with the exception of the Devonian family Catantostomatidae Wenz, 1938, in which the last half whorl is sharply deflected beyond the point at which the slit terminates to form a foramen (Knight *et al.*, 1960; 213, figure 128). While the majority of taxa since the Cambrian have been dextral and conispiral, the subfamily Agnesiinae Knight, 1956 [Lower Devonian to Upper Triassic] was characterized by sinistrally coiled shells. A great variety of shell forms, encompassing planispiral, discoidal, turritiform and auriform lineages was evident during the Paleozoic (Knight *et al.*, 1960). Taxa with a disjunct last whorl were present during the Upper Cambrian to Lower Ordovician (Knight *et al.*, 1960), while uncoiled or open coiled taxa were reported from the Lower Devonian (Rohr and Smith, 1978). With the exception of the discoidal family Porcelliidae Broili, 1924, lineages surviving the Permian extinction had a more limited repertoire of morphology, consisting primarily of trochiform and turbiniform shells. All post-Jurassic pleurotomarioideans are members of the family

Pleurotomariidae, with 4 of 14 genera surviving into the Recent fauna. In dealing with Mesozoic taxa, paleontologists have devised a classification scheme based on the sequential discrimination of characters including: (1) the shape of the whorl section; (2) the position and width of the selenizone; (3) the form of the periphery and base; (4) the allometry of the spire; and (5) surface ornamentation and presence/features of the umbilicus (Szabó, 1980). According to these criteria, taxa with gradate and low turbiniform whorl profiles have become extinct, and only the subset of taxa with conical whorl profiles that have a broad selenizone at or near mid-whorl survive in the Recent fauna (Figure 9A, see page 266).

The pleurotomariid protoconch (Figure 3A–D) consists of 1–1¼ smooth, glassy, translucent whorls, and ranges from about 500 µm (*Perotrochus maureri*, Harasewych and Askew, 1993: figures 2–3) to 720 µm (*Mikadotrochus beyrichii*, Sasaki, 1998: figure 23) in diameter. It is slightly deflected from the coiling axis of the shell (12–19°), lacks a slit and terminates in a slightly flared lip. The transition to the teleoconch is

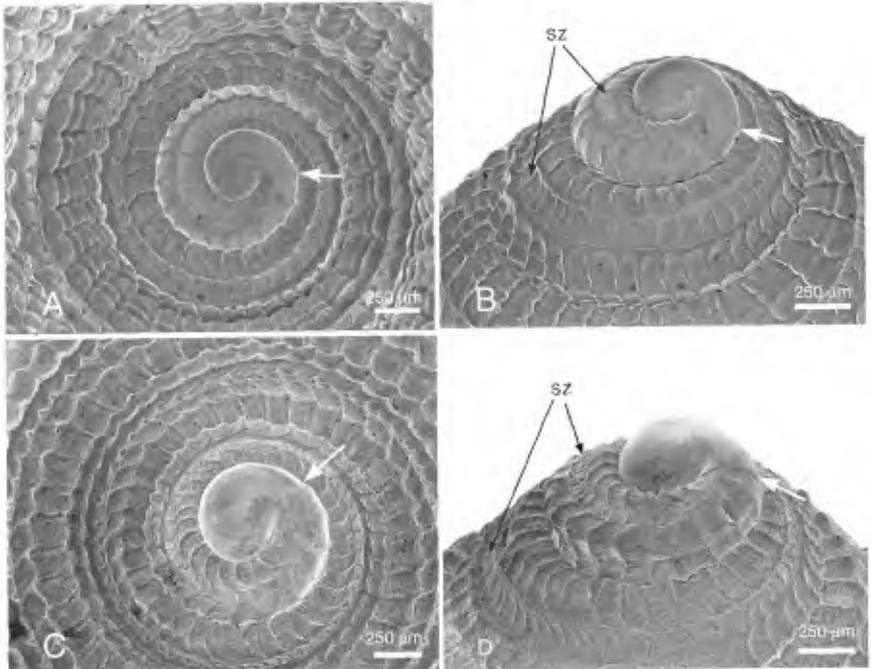


Figure 3 Morphology of the protoconch and early whorls. (A) Apical and (B) oblique views of *Entemnotrochus adansonianus* (Crosse and Fischer, 1861). (C) Apical and (D) oblique views of *Perotrochus deforgesii* Métivier, 1990. White arrows = protoconch/teleoconch boundary; sz, selenizone.

marked by an abrupt change in shell surface from glassy to chalky, and by the onset of weak spiral and pronounced axial sculpture (Figure 3A–D, arrows). Fine, irregular spiral threads extend onto strong, axial ribs (17–26 on the first whorl). The selenizone appears within the first quarter teleoconch whorl, with traces in evidence by the second axial rib. Initially, the selenizone nearly abuts the suture, but descends to a position that is near mid-whorl by the second teleoconch whorl, reaching its final relative position by the fifth or sixth teleoconch whorl, depending on the taxon.

Among the extant taxa, shells of the genus *Entemnotrochus* (Figure 1A–C) are strongly conical, generally with straight to convex profiles, have an aperture that is roughly rhomboidal, and a narrow slit that extends nearly 160° from the aperture (Figure 1B, pms) and produces a selenizone that is substantially above mid-whorl (Figure 1D, sz). The edges of the outer lip on either side of the selenizone are roughly aligned. *Entemnotrochus* have a broad, open umbilicus that extends from the base to the protoconch. Axial sculpture is prominent on the early whorls, but becomes diminished or reduced to axial growth lines in subsequent whorls. Spiral sculpture likewise is reduced to broad, weak bands or becomes entirely inconspicuous. Early whorls are bright yellow in color, while adult shells are white with irregular, dark red, axial markings. The operculum of *Entemnotrochus* (Figure 1E) is thick, dark brown, chitinous, multispiral and larger in diameter than the height of the shell aperture. Maximum shell diameter ranges from 17 to 28 cm, depending on species (Hutsell *et al.*, 1999).

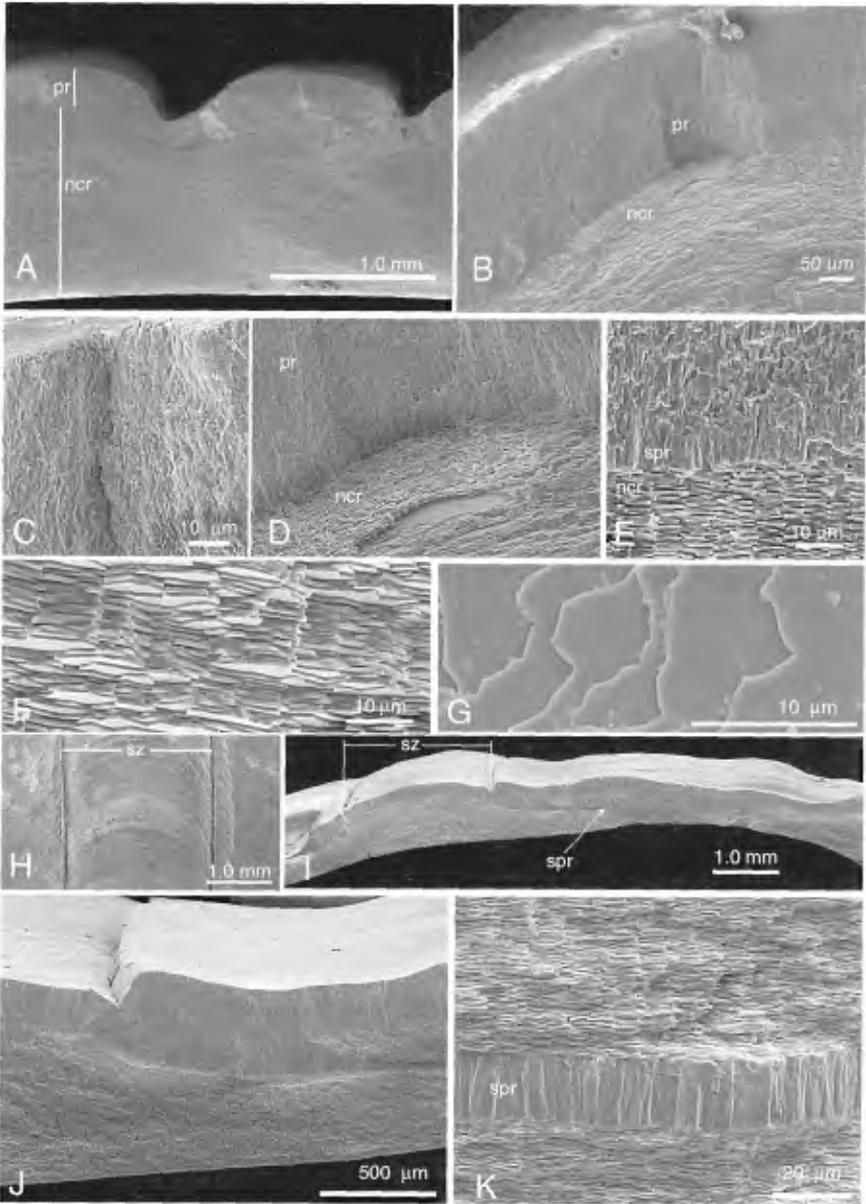
The genus *Perotrochus*, as exemplified by its type species, *P. quoyanus* (Figure 1F–H) has shells that are more broadly conical, with straight to weakly concave profiles, and broad, short slits that never extend more than 60° from the aperture (Figure 1G, pms). The slit produces a selenizone that is at or slightly below mid-whorl (Figure 1I, sz). The outer lip on the abapical side of the emargination is significantly offset posteriorly (by as much as 30°) from the outer lip along the adapical side of the slit (Figure 1H). Shells lack an umbilicus, and instead have a nacreous, twisted columellar callus. Spiral sculpture remains prominent on all whorls, while axial sculpture may become reduced to weak cancellations upon the spiral cords, or become entirely absent. Shells tend to be more heavily pigmented in shades of brown to reddish brown, marked with irregular, darker, collabral banding. Opercula (Figure 1J) tend to be thinner, lighter in color and significantly smaller than half the minimum aperture dimension. Maximum shell diameters for most species are in the range of 4.2–7 cm, although some species reach 9.5 cm (Hutsell *et al.*, 1999).

The genus *Mikadotrochus* encompasses species characterized by a thick, heavy, conical shell (Figure 1K–M), with a straight to very weakly concave

profile, and a very broad, short slit (Figure 1L, pms) that produces a wide selenizone below mid-whorl (Figure 1N, sz). The lip abapical to the selenizone is offset posteriorly (Figure 1M). No umbilicus is present, and the columella is thick and twisted. While spiral sculpture remains dominant on all whorls, axial ribs produce a strongly cancellated surface in many of the species. Shells tend to be strongly pigmented with browns and reds, although albino specimens are rarely encountered. Opercula (Figure 1O) are thicker and proportionally larger than in *Perotrochus*, spanning about 60% of the minimum apertural dimension. Woodward (1901: 217) reported that the operculum was absent in some specimens of *M. beyrichii*. He suggested that, due to its relatively small size, the operculum of *Mikadotrochus* (and probably also that of *Perotrochus*) is of little utility in closing the aperture for protection against predators. Rather, it is more likely used to support the shell and to protect the foot from abrasion by the shell. Maximum shell diameters for species of *Mikadotrochus* are in the range of 7–13 cm (Hutsell *et al.*, 1999).

A fourth group of pleurotomariids, nominally included in the genus *Perotrochus*, but informally segregated as “*Perotrochus* Group B” by Bayer (1965: 754), is distinguished on the basis of having large, thin, turbiniform shells (Figure 1P–R) with inflated whorls and weakly to strongly convex profiles. The slit is relatively broad and shallow ($<60^\circ$; Figure 1Q, pms), and the selenizone is at or slightly below mid-whorl (Figure 1S, sz). The outer lip is strongly offset on the abapical side of the slit. The columella is thin and twisted. No umbilicus is present. Sculpture tends to be limited to fine spiral cords or very fine spiral threads that may be weakly cancellated. Pigmentation tends to be lighter than in *Perotrochus sensu stricto*, or in *Mikadotrochus* due to the thinness of the pigment-containing shell layer. Opercula (Figure 1T) are thin and amber in color, their diameters roughly three-quarters of the minimum aperture dimension. Maximum shell diameters range from 6.3 to 14 cm, depending on species (Hutsell *et al.*, 1999).

Figure 4 Shell ultrastructure of *Entemnotrochus adansonianus* (Crosse and Fischer, 1861). (A) Fracture section through ventral surface of shell, about 1 cm behind and parallel to outer lip. (B) Enlarged view of the entire outer prismatic layer and outer surface of the nacre. (C) Prismatic layer at shell edge, showing intersected crossed platy substructure. (D–E) Interfaces between intersected crossed platy substructure, regular simple prismatic crystals, and columnar nacre. (F) Cross-sectional and (G) planar views of columnar nacre. (H) Outer and (I) cross-sectional views of region containing selenizone. (J) Detail of crystal structure along the adapical side of the selenizone. (K) Detail at three-quarters of the distance between selenizone and suture, showing progressively thinning band of simple prismatic crystals between layers of columnar nacre. ncr, columnar nacre; pr, prismatic layer; spr, simple prismatic crystals, sz, selenizone.



While the protoconch of pleurotomariids consists entirely of complex prismatic crystals (Erben and Krampitz, 1972), the teleoconch is composed of two primary layers. A thinner, outer prismatic layer (Figure 4A, B, D, pr) comprises most of the finer details of the surface sculpture and contains the shell pigments, while the thicker inner layer is nacreous (Figure 4A, B, D, ncr, F, G). Both layers are composed entirely of aragonite (Hedegaard, 1990: 144). Bøggild (1930: 299) identified these two layers in well-preserved Mesozoic taxa, while Batten (1972) confirmed their presence in five Paleozoic (Pennsylvanian) species, and reported the presence of two additional layers that he could only detect on the outer surface of a single specimen (possibly mineralized periostracum). Erben and Krampitz (1972) and Hedegaard (1990, 1997) further subdivided the outer prismatic layers of the extant genera into inner and outer regions with differing crystalline substructures. Erben and Krampitz (1972) documented ontogenetic changes in these layers in three living and one Oligocene species.

The outer prismatic shell layer of an adult specimen of *Entemnotrochus adansonianus* (Figure 4B, pr) is approximately 210 μm thick, and consists predominantly of intersected crossed platy substructure (Figure 4C), except for a thin ($\sim 15 \mu\text{m}$) layer of regular simple prismatic crystals (Figure 4E, spr) immediately adjacent to the columnar nacre (Figure 4E, ncr). In *Mikadotrochus* and *Perotrochus* "Group B" (the latter based on *P. westralis* (as *P. teramachii*) in Hedegaard, 1990, 1997), the outermost layers consist of regular spherulitic prismatic crystals, grading into intersected crossed platy crystals. In *Mikadotrochus*, as in *Entemnotrochus*, there is a thin layer of simple prismatic crystals adjacent to the columnar nacre. In *Perotrochus* "Group B", the intersected crossed platy crystals grade into blocky prismatic crystals adjacent to the columnar nacre. The thick, homogeneous layer of columnar nacre comprises the major portion of most pleurotomariid shells. Specimens of several species in *Perotrochus* "Group B" may have an exceptionally thin outer prismatic layer, which becomes translucent, revealing the nacre beneath. It should be noted, however, that the nacreous layer does not overlie the prismatic layer along the free margin of the outer lip, so that a band consisting only of the prismatic layer is present along the margin of the slit and outer lip. This band is exceptionally broad and most evident in *Perotrochus gotoi* (see ventral views of shells in Anseeuw and Goto, 1996: 94–96).

The pattern of shell layers along the outer lip of the shell beyond the posterior margin of the slit becomes more complex, due to the superposition of the selenizone over previously deposited shell (Figure 4H–K). The material comprising the selenizone (Figure 4H–I, sz) fills the space between the slit edges on the outer surface of the shell. Along the interior surface, the prismatic layer contiguous with the selenizone extends apically as far as the whorl suture, and abapically as far as the shell

periphery, rapidly becoming thinner with increasing distance from the slit (Figure 4I–J). At a distance of a few millimeters from the slit edge, the prismatic layer is limited to only a thin ($\sim 16\ \mu\text{m}$) layer of simple prismatic crystals (Figure 4K, spr) between layers of columnar nacre. Hedegaard (1990: 70, plate 3, figure 4) described and illustrated the columnar nacre of *Perotrochus westralis* (as *P. teramachii*) as being intercalated with bands of regular, simple prismatic layers. It appears likely that the portion of the shell upon which this observation was based was located near the selenizone.

2.2. External anatomy (Plates 5 and 6, Figure 5A)

Table 1 provides an annotated list of previously published anatomical studies of pleurotomariids. The pleurotomariid body (Figure 5A) is

Table 1 Published observations on the anatomy of pleurotomariids (studies of radular morphology are listed separately in Table 2).

Taxon	Reference	Notes
<i>Entemnotrochus adansonianus</i>	Dall (1889)	Gross anatomy of poorly preserved specimen
<i>Entemnotrochus rumphii</i>	Tan (1974)	Gross anatomy
<i>Perotrochus quoyanus</i>	Dall (1889)	External morphology only
	Bouvier and Fischer (1898)	Radula and nervous system
<i>Perotrochus anabilis</i>	Fretter (1964)	Detailed anatomy on specimen lacking upper whorls, but otherwise well preserved
<i>Perotrochus maureri</i>	Harasewych and Askew (1993)	Anatomical features compared with <i>P. anabilis</i>
<i>Perotrochus lucaya</i>	Fretter (1966)	Detailed anatomy of major organ systems
<i>Perotrochus atlanticus</i>	Leme and Penna (1969)	Gross anatomy (as <i>P. notialis</i>)
<i>Bayerotrochus midas</i>	Fretter (1966)	Detailed anatomy of major organ systems
<i>Mikadotrochus beyrichii</i>	Woodward (1901); Bouvier and Fischer (1901, 1902); Sasaki (1998)	Each work contains independent, comprehensive descriptions of all major organ systems

conspirally coiled, consisting of $4\frac{1}{2}$ (*Mikadotrochus*, *Perotrochus* "Groups A and B") to $6\frac{1}{2}$ (*Entemnotrochus*) whorls. The mantle cavity (Figure 5B) is deep ($< \frac{1}{2}$ whorl - *Mikadotrochus*) to very deep ($> \frac{3}{4}$ whorl - *Entemnotrochus*). The slit (Figure 5A, B, ms) is shallow ($< 60^\circ$) to deep ($\sim 160^\circ$) in living animals of corresponding taxa, but may appear constricted and significantly shorter in preserved specimens. The mantle edge has long, pigmented papillae, especially along the margins of the slit, where they are capable of interdigitating along the midline. In living animals (Plates 5, 6), some portion of the slit is often closed, except for a small opening at the posterior margin that serves as the exhalant aperture of the functionally tubular mantle cavity (Plate 5B, F; see also photographs in Anseeuw and Goto, 1996: 13, 161; Okutani and Hasegawa, 2000: 38–39). Observations of western Atlantic species in aquaria revealed that the size and position of these openings may vary over time, and that multiple openings may occasionally be produced (Plate 5F).

The head has a broadly cylindrical snout (Figure 5A, B, sn) and long, bluntly rounded tentacles (Figure 5A, B, ten) with black eyes (Figure 5A, B, e) at their bases (even species that live well below the photic zone have pigmented eyes). Bifid or trifid tentacles have been reported to occur sporadically in several species (e.g., *M. beyrichii*, Woodward, 1901: 221; *P. maureri*, Harasewych and Askew, 1993: 131), and probably are the result of injuries. The ventral surface of the snout is flattened, unpigmented and covered by numerous papillae, which, in turn, are covered by a cuticle. The foot (Figure 5A, f) is long and narrow, its posterior portion trapezoidal in cross section when examined in preserved specimens, but is capable of substantial turgid inflation of the epipodial lobes in living specimens, particularly in *Perotrochus* "Group B" (Plate 6B–F). The snout and lateral surfaces of the foot of most taxa are mottled to varying degrees with dark reddish brown (which appears black at depths in excess of 25 m), while the dorsal, epipodial region, the sole of the foot and distal surface of the snout are unpigmented and usually a very light tan (Plates 5, 6). The posterior limit of the foot is not normally extended beyond the edge of the shell in living *Entemnotrochus* (Plate 5A–C), and protrudes only slightly in *Perotrochus* (Plates 5E–F, 6A) or *Mikadotrochus*. In *Perotrochus* "group B" (Plate 6B–F), however, the foot is approximately $1\frac{1}{2}$ times as long as the shell diameter and is normally engorged. The posterior portion of the epipodium enfolds dorsally until it meets the posterior margin of the shell (see photographs in Anseeuw and Goto, 1996: 9, 16). The multispiral operculum, secreted by an opercular lobe on the dorsal surface of the foot, supports the shell at approximately mid-radius. Broad epipodial folds (Figure 5A, epf) have minute papillae, but lack lappets, tentacles, or macroscopic sense organs in all species that were studied (Woodward, 1901: 220; Fretter, 1966: 605; Sasaki, 1998: 42).

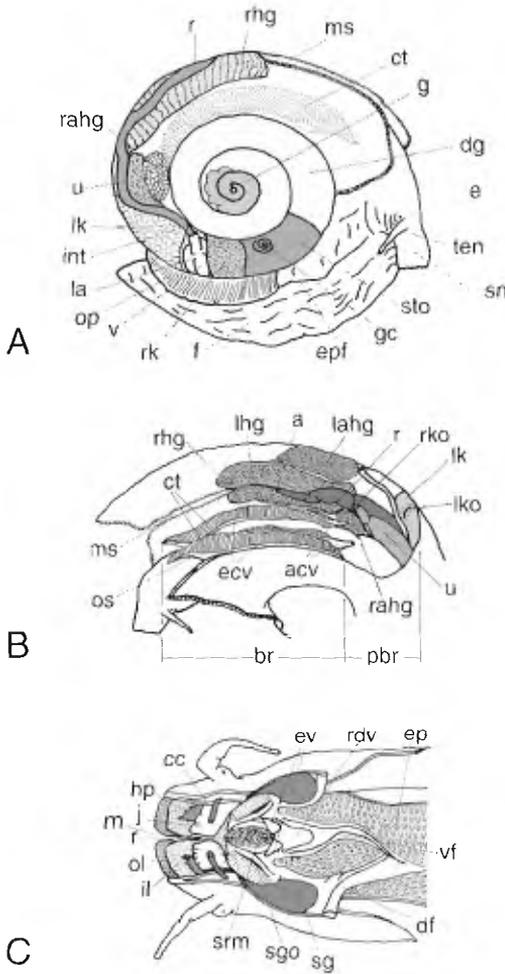


Figure 5 Gross anatomy of *Entemmotrochus adansonianus*. (A) Apical view of animal with shell removed. (B) Left lateral view of the pallial cavity, opened above left ctenidium. (C) Buccal cavity, opened along dorsal mid-line. a, anus; acv, afferent ctenidial vessel; br, branchial portion of mantle cavity; cm, columellar muscle; ct, ctenidium; df, dorsal fold; dg, digestive gland; e, eye; ecv, efferent ctenidial vessel; ep, esophageal pouch; epf, epipodial flap; ev, esophageal valve; f, foot; g, gonad; gc, coiled gastric caecum; i, intestine; la, left auricle; lahg, left accessory lobe of hypobranchial gland; lhg, left hypobranchial gland; lk, left kidney; lko, left kidney opening; ms, mantle slit; os, osthradium; pbr, post-branchial portion of mantle cavity; r, rectum; ra, right auricle; rd, radula; rdv, radular diverticulum; rahg, right accessory lobe of hypobranchial gland; rk, right kidney; rko, right kidney opening; rhg, right hypobranchial gland; sg, salivary gland; sgo, salivary gland opening; sn, snout; srm, subradular membrane; sto, stomach; ten, cephalic tentacle; v, ventricle; vf, ventral fold.

2.3. Mantle cavity organs (Figure 5A–B)

The mantle cavity of pleurotomariids (Figure 5B) is unusually deep (spanning about $\frac{1}{2}$ to $\frac{3}{4}$ whorl), and divided into the branchial (Figure 5B, br) and post-branchial (Figure 5B, pbr) regions. Unlike other gastropods, the gills of pleurotomariids do not extend to the rear of the mantle cavity. The branchial region spans the anterior $\frac{1}{2}$ (*Perotrochus* and *Mikadotrochus*) to $\frac{2}{3}$ (*Entemnotrochus*) of the mantle cavity, and contains the paired gills (ctenidia), osphradia and hypobranchial glands (each with an accessory lobe). While these organs maintain an approximately bilaterally symmetrical orientation on either side of the midline of the mantle cavity, defined by the slit and rectum, they are clearly asymmetrical in size. Organs on the left side of the body are larger and longer than their counterparts on the right. Ctenidia are bipectinate and suspended from the sides of the mantle cavity by long membranes containing efferent and afferent branchial vessels, nerves and retractor muscles. Each gill leaflet is broadly triangular in outline, and is stiffened by a skeletal support rod. Haszprunar (1987: 47) reported ctenidial bursicles in the gills of *Perotrochus caledonicus*, while Sasaki (1998: 211) noted their absence in *Mikadotrochus beyrichii*. The anterior end of each gill is not attached, but extends forward into the mantle cavity. The free ends of the ctenidia do not extend beyond the mantle edge in living animals, but may appear to do so in preserved specimens (see Fretter, 1964: figure 1; 1966: figure 1). Chemosensory osphradia are situated on the efferent membranes along the free ends of the ctenidia. The large, hypobranchial glands line the roof of the mantle cavity from just behind the posterior margin of the slit. A median furrow separates the smaller right from the larger left hypobranchial gland anteriorly, while the rectum separates them posteriorly. Each gland has an accessory lobe between its posterior margin and the base of each gill. Both the left hypobranchial gland and its accessory lobe are significantly larger than their counterparts on the right side of the body. These glands are bright white to ivory in color and are capable of rapidly secreting large volumes of a dense, opaque, white fluid that is heavier than sea water and not readily soluble in it (Plate 5D, see also Kanie *et al.*, 1986: figure 4). The post-branchial portion of the mantle cavity contains the rectum, and the openings of the left kidney and the urinogenital papilla of the right kidney.

2.4. Digestive system (Figures 5C, 6A–B, 7)

The mouth (Figures 5C, 6A, m) is situated at the center of the ventral, flattened face of the snout, and is surrounded by cuticle-covered papillae.

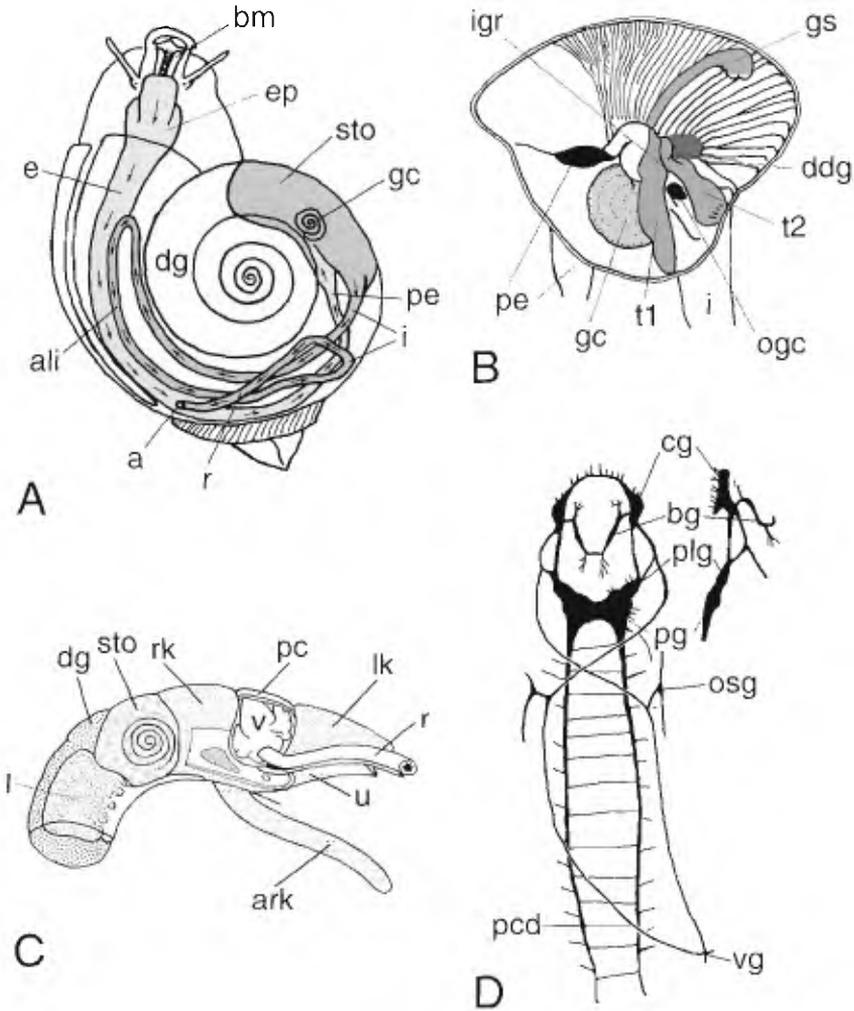


Figure 6 Gross anatomy of *Entemnotrochus adansonianus*. (A) Orientation of alimentary tract within animal, dorsal view. (B) Stomach, opened mid-dorsally. (C) Reproductive system and associated organs, viewed from right side. (D) Nervous system, viewed dorsally and laterally. a, anus; ali, anterior loop of intestine; ark, anterior lobe of right kidney; bg, buccal ganglion; bm, buccal mass; cg, cerebral ganglion; ddg, duct of digestive gland; dg, digestive gland; e, esophagus; ep, esophageal pouch; g, gonad; gc, coiled gastric caecum; i, intestine; igr, intestinal groove; lk, left kidney; m, mouth; osg, osphradial ganglion; pc, pericardium; pcd, pedal nerve cord; pe, posterior esophagus; pg, pedal ganglion; plg, pleural ganglion; r, rectum; rk, right kidney; sto, stomach; ty, typhlosole; u, urinogenital papilla; v, ventricle; vg, visceral ganglion.

It leads into a thick-walled buccal cavity (Figure 5C) within the snout that enfolds the buccal mass. The large, muscular buccal mass is surrounded by the ganglia of the nerve ring, and is attached to the body wall by numerous fine muscles. Sasaki (1998: 74, figure 25, a–d) provides detailed descriptions of the buccal musculature and cartilages of *Mikadotrochus beyrichii*. Paired jaws line the dorsal surface of the buccal cavity. Dall (1889) and Woodward (1901) believed that the jaws serve to protect the walls of the buccal cavity from abrasion by the radula and food particles, while Fretter (1966: 607) suggested that the jaws function to depress the anterior end of the odontophore as it is protruded in order to spread the radula into the feeding position. A lining of chitin protects the whole of the buccal cavity (Woodward, 1901: 232). In fact, the inner and outer lips, the jaws and the horny papillae (Fretter, 1966: figure 2) are all interconnected by chitin.

The highly specialized radula of pleurotomariids (Figure 7) has been described and illustrated by numerous authors (Table 2), and is the most complex gastropod radula, both in terms of the number of teeth per row and the number and types of highly specialized teeth. Hyman (1967: 236) coined the term “hystricoglossate” for the pleurotomariid radula because of the presence of bristle teeth that she believed to be unique to this family, but recognized that this was a variant of the rhipidoglossan radula. Hickman (1984a: 35) has since shown that *Seila*, an unrelated caenogastropod (Family Cerithiopsidae) that also feeds on sponges, has similar bristle teeth, and suggested that bristle tooth morphology is convergently derived as a specialized adaptation to feeding on sponge tissues.

The pleurotomariid radula is long (ranging from 88% of shell diameter in small *Perotrochus* to 68% of shell diameter in large specimens of *Entemnotrochus*), and consists of about 90–140 rows of teeth arranged in acutely angled, inverted V-shaped rows that produce a bifid posterior end. A transverse section through the radula (Figure 7A) will therefore intersect six or more rows of teeth. Each row of teeth is also conformationally asymmetrical (Hickman, 1981), being skewed either to the left (Figure 7D) or right (Figure 7B) side (Table 2), in order to accommodate the zipper-like alternation of the sickle teeth (Figure 7A) when the radula is retracted. Based on relatively few records, Harasewych and Askew (1993: 136) speculated that the direction of skew might prove to be constant within a species. However, additional data have shown that skew direction varies in at least some species (Table 2, *E. adansonianus* and *P. quoyanus*). The radula is contained in a straight radular sack that runs parallel to the esophagus. The radula has been divided into inner and outer (usually called marginal) tooth fields based on functional morphology (Table 2, A), and consists of six different, morphologically distinct, yet intergrading tooth types (Table 2, D). The inner field is composed of

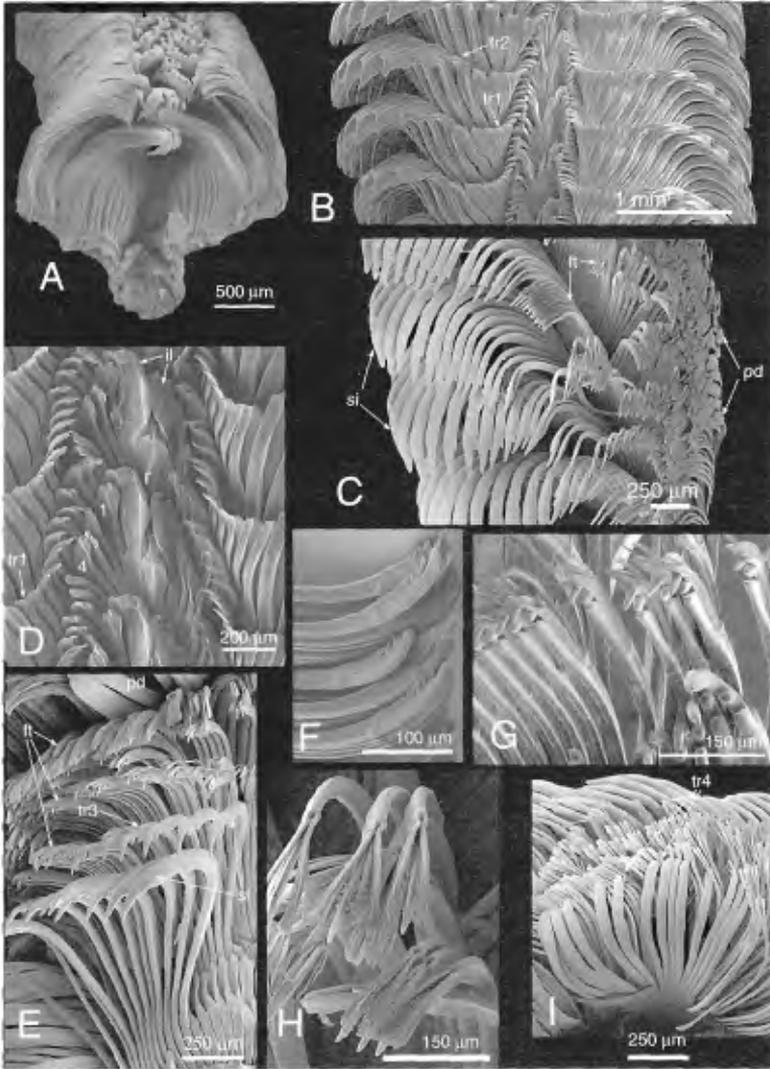


Figure 7 Radular morphology of *Entemnotrochus adansonianus*. (A) Cross-section of radular ribbon in retracted state, viewed from the posterior end. (B) Radula expanded to show rachidian, inner and outer lateral teeth, and sickle teeth. (C) Radula viewed laterally to show sickle, filament-tipped and paddle-shaped teeth. (D) Detail of rachidian, inner and outer lateral teeth. (E) Detail showing adjacent rows of, from bottom to top, outer sickle teeth, transition from sickle to filament teeth, three rows of filament-tipped teeth and paddle-shaped teeth. (F) Lateral, (G) frontal and (H) dorsal views of filament-tipped teeth. (I) Lateral view of radula showing transition from filament-tipped to paddle-shaped teeth. ft, filament-tipped teeth; pd, paddle-shaped teeth; r, rachidian tooth; si, sickle teeth; tr1, outer lateral teeth, shift of dominant cusp from inner to outer surface of tooth; tr2, transition from outer lateral to sickle teeth; tr3, transition from sickle teeth to filament-tipped teeth; tr4, transition from filament-tipped to paddle-shaped teeth. 1, 4, first and fourth outer lateral teeth.

Table 2 Comparison of radular formulae and asymmetries of pleurotomariid radulae.

Taxon	N	A: _____ Inner _____ Outer (marginal) _____		B: Rachidian _____ Lateral teeth _____ Marginal teeth _____		C: Rachidian _____ Central _____		D: Rachidian _____ Inner laterals _____ Outer laterals _____		Brush	Filament-tipped	Paddle-shaped	Skew* ^c
		Hooked	Sickle	Lamellate	Hooked	Outer laterals	Sickle	Inner laterals	Outer laterals				
<i>Entemnotrochus adansoniatus</i> ^a	7	1	1	21-23	17-19	25-33	14-16	4R/3L ^a					
<i>Entemnotrochus rumpffii</i> ^b	5	1	1	21-26	13-15	21-24	7-8	1R/1L ^b					
<i>Peroirochus quoyanus</i> ^c	1	1	3	24	13	63	6/7	1R/1L ^c					
<i>P. lucaya</i> ^d	1	1	3	25	13	61	6	?					
<i>P. amabilis</i> ^c	1	1	3	24	21	63	8	R'					
<i>P. maureri</i> ^f	5	1	2	24-26	21	61-63	8-9	5L'					
<i>P. atlanticus</i> ^g	1	1	2	29	13	63	10	L ^g					
<i>P. caledonicus</i> ^h	1	1	1	22	14	53	7	R ^h					
<i>Bayerotrochus midas</i> ⁱ	1	1	3	26	13	63	6	L'					
<i>B. africanus</i> ⁱ	2	1	3-4	23-25	12	50	6	?					
<i>B. ditluculum</i> ^g	2	1	3	18-26	12-14	32	?	R ^k					
<i>B. feramachi</i> ⁱ	1	1	3	18	12	33	8	R'					
<i>Mikadotrochus beyrichii</i> ^m	6	1	3	20-24	17-25	63-66	5-12	1R/1L'					
<i>M. hirasei</i> ⁿ	3	1	3	20-28	24-32	58-81	6-10	L''					
<i>M. sabiniatus</i> ⁿ	2	1	3	24	20-23	44-46	7-9	1R/1L''					

? indicates that the character could not be inferred from the cited text or figure.

A = functional tooth fields. B = standard terminology for gastropod radular tooth types, e.g., Fretter and Graham (1962: 169); Brusca and Brusca (1990: 730). C = terminology of Woodward (1901). D = terminology of Hickman (1984a). *L = left-skewed asymmetry. R = right-skewed asymmetry.

"Both left-skewed (Plate 6D) and right-skewed (Plate 6B) radulae are illustrated herein. An additional right-skewed radula is shown in Anseeuw and Goto (1996: 179).

^bTan (1974) reported the radular formula (R-27-14-∞). Anseeuw and Goto (1996: 179) illustrated a right-skewed radula with a single inner lateral tooth and 23 outer lateral teeth. Kuramochi *et al.* (1996: table 2) reported counts for three specimens, and illustrated a left-skewed radula (their figures 1 and 3). Based on their figures, only a single inner lateral tooth is present in a half row of teeth.

^cHickman (1981: 190, 1984a: 30) illustrated a right-skewed radula, while Anseeuw and Goto (1996: 180) illustrated a left-skewed radula with seven paddle-shaped teeth. Bouvier and Fischer (1898) and Fretter (1966: 608) reported identical radular formulae.

^dFretter (1966) reported the radular formula.

^eFretter (1964) reported the radular formula. Harasewych and Askew (1993: table 2) reported that two radulae were right-skewed.

^fHarasewych and Askew (1993) reported the radular formula and skew of five specimens.

^gLeme and Penna (1969) reported the radular formula in their description of *P. notialis* (a synonym of *P. atlanticus* Rios & Matthews, 1968). Their figure 6 indicates a left-skewed orientation.

^hBouchet and Meivier (1982: 310, figure 2) reported the radular formula. Skew is based on their illustration.

ⁱFretter (1966: 608) reported the radular formula. Hickman (1981: 190, 1984a: 30) reported skew.

^jBarnard (1963: 157) reported radular formula as approximate counts. Azuma (1964: 352) also provided approximate counts of an additional specimen.

^kPartial radular formula and skew derived from illustrations of radula in Anseeuw and Goto (1996: 180). Kuramochi *et al.* (1996: table 2) provided partial tooth counts and SEM photos of a single, right-skewed radula (their figure 11).

^lKuramochi *et al.* (1996: table 2) reported the radular formula for a single specimen, determined to be right-skewed based on their figures 7 and 10. "The radular formula for the three specimens examined by Woodward (1901: 252) is (R-3-21-17-63-7) as corrected by Harasewych and Askew (1993: table 2). Bouvier and Fischer (1902) reported a radular formula of (R-3-20-22-65-12), while Sasaki (1998: 47) reported the radular formula as being "roughly ca. 60-ca.40-1-ca.40-ca.60". Kuramochi *et al.* (1996: table 2) provided counts for two additional specimens. Their figures 20 and 22 show a left-skewed radula.

"Radular formula derived from figure in Matsumoto (1929). The radula is depicted as roughly symmetrical in his drawing. Kuramochi *et al.* (1996: table 2) provided counts for two additional specimens. Their figures 16 and 17 show a left-skewed radula.

"Kuramochi *et al.* (1996: table 2) reported tooth counts for two radulae, and illustrate one left-skewed and one right-skewed radula (their figures 13 and 14, respectively).

short, flat teeth, and includes the rachidian, and inner and outer lateral teeth, while the outer tooth field consists of the longer sickle, filament-tipped and paddle-shaped teeth (terminology of Hickman, 1984a). The inner and outer lateral teeth, as well as the sickle teeth, are homologous to the lateral teeth of other orthogastropods, while the filament-tipped and paddle-shaped teeth are homologous to marginal teeth.

The rachidian tooth (Figure 7D, r) is long and narrow, and has dorsally expanded lateral flanges, but lacks the dorsally reflected, cusp-bearing shaft present in other vetigastropods. Its main function appears to be to maintain the alignment between the lateral teeth. The rachidian tooth is generally asymmetrical and reflects the skew of the radula. The inner lateral teeth (Figure 7D, il), which range in number from 1 in *Entemnotrochus* to 3 in most *Perotrochus* and *Mikadotrochus*, are longer than the rachidian, have broad, outwardly directed, distally spatulate surfaces, and flank the rachidian on either side. Adjacent are 20–29 outer lateral teeth (Figure 7D 1,4), which begin nearest the inner lateral teeth as short, nearly flat, triangular teeth with a broad attachment area and a weak, dorsally recurved cusp at the anterior end. The outer lateral teeth become progressively longer and stouter, with the edge closest to the rachidian tooth becoming thicker with increasing distance from the rachidian. By the 15–16th tooth, the terminal cusp shifts from the anterior to the posterior edge of the tooth (Figure 7B, D, tr1). Subsequent teeth elongate and develop the sharp, recurved, multicuspate ends (Figure 7B, tr2) of the sickle teeth. The sickle teeth are the largest and most robust teeth in the radula. The more medially situated teeth are most strongly buttressed, becoming thinner, narrower, more blade-like and tricuspsate closer to the outer margins of the radula (Figure 7C, E, si). The transition from sickle teeth to filament-tipped teeth is marked by the development of bristles along the convex side of the tooth opposite the most proximal cusp (Figure 7E, tr3). The bristles increase in length and number in successive teeth, while the cusps decrease in prominence (Figure 7C, E, ft, F, G, H) and are lost near the outer edges of the radula. While filament-tipped teeth are the most numerous (Table 2), they occupy a relatively small area along the margins of the radula (Figure 7C, I). The outermost teeth of each radular row are termed paddle-shaped teeth, and are broad, smooth, rounded distally, and lack cusps or filaments. The transition from filament-tipped teeth to paddle-shaped teeth (Figure 7I, tr4) spans 2–5 teeth. Based on their morphology and topological arrangement, Hickman (1984a: 35) suggested that the elements of the inner tooth field (rachidian + inner lateral teeth) function primarily to separate and orient the outer tooth field (outer lateral + sickle + filament-tipped + paddle-shaped teeth), which actively gather and prepare food. Woodward (1901: 252) inferred that the sickle teeth function in shredding and rasping tissues

of the sponge prey of pleurotomariids, while filament-tipped teeth might "rasp some of the flesh from the spicules". The function of the paddle-shaped teeth is probably to provide a smoothly telescoping envelope to contain the filament-tipped teeth and to facilitate the unimpeded motion of the radula within its sheath during the rasping stroke (Harasewych and Askew, 1993: 132).

The anterior esophagus lies dorsally over the buccal mass, and is expanded to form buccal pouches that envelop the buccal mass laterally. Both the anterior and the mid-esophagus are lined with papillae. Paired salivary glands (Figure 5C, sg) flank the buccal cavity and empty into it via long, lateral openings. The mid-esophagus is elongated, while the posterior esophagus constricts to form a sphincter before joining the stomach. The stomach (Figure 6A, sto, 6B) is very large, U-shaped, with a large, spiral gastric caecum (Figures 5A, 6A, gc) composed of four whorls, and gastric shield. The large digestive glands, which comprise most of the apical 2–3 whorls of the visceral mass, open into the stomach by separate ducts. Two widely separated typhlosoles give rise to a broad intestinal groove that runs from the posterior digestive gland duct down to the intestine. The intestine (Figure 6A, int) descends into the cephalic hemocoel and runs anteriorly, parallel to the esophagus, before turning sharply on itself, and running posteriorly to the rear of the pallial cavity, where it again turns forward to pass through the pericardium and ventricle before entering the mantle cavity near its dorsal midline to form the rectum (Figures 5B, 6A, r). The rectum runs anteriorly and terminates in an anus, situated near the posterior midline of the hypobranchial glands. Arakawa *et al.* (1978) illustrated the feces of *Mikadotrochus hirasei*, reporting them to be round, 4–5 mm in diameter, and of the orthocylindric type (Arakawa, 1962).

2.5. Circulatory system (Figures 5A, 6C)

The elongated pericardium (Figures 5A, 6C, pc) is positioned transversely at the rear of the post-branchial portion of the mantle cavity, between the left and right kidneys. It contains the elongated, narrow ventricle, with the rectum passing through its long axis, two auricles, and a short, bifurcating bulbous aorta. The left auricle, fed by the efferent branchial vessel from the left ctenidium, opens into the anterior wall of the ventricle, while the right auricle, fed by the efferent branchial vessel from the right ctenidium, opens into the rear wall of the ventricle. The anterior aorta, which branches from the bulbous aorta, runs adjacent to the efferent branchial vessel before descending into the cephalic hemocoel, where it divides into the cephalic and pedal arteries below the buccal mass. The posterior aorta leads from the bulbous aorta to the visceral mass, where it branches to feed

the stomach, digestive glands and gonad. The venous sinuses drain into the basibranchial sinus, situated below the posterior end of the mantle cavity. The basibranchial sinus sends blood into the afferent branchial vessels, and, via the rectal sinus, to the hypobranchial vein. After passing through the ctenidia, blood returns to the heart via the efferent branchial vessels. Fretter (1964: figure 4) provided a schematic diagram of the vascular system of *Perotrochus amabilis*.

2.6. Excretory system (Figures 5A, B, 6C)

The kidneys are large and asymmetrical, flanking the pericardium within the post-branchial portion of the mantle cavity. The left kidney (Figures 5A, B, 6C, lk) is smaller, anterior to the pericardium, and opens into the mantle cavity by a simple slit near its tapered anterior end. Its large, sac-like lumen has papillated walls that are thickest along the dorsal and posterior regions. A long, reno-pericardial canal extends from the pericardium near the right margin of the left auricle, runs along the floor of the left kidney, and opens near the left kidney opening to the mantle cavity. The right kidney (Figures 5A, 6C, rk) is situated posterior to the pericardium, and lines the anterior surface of the digestive gland and stomach. Its pallial section gives rise to a long, narrow lobe that penetrates into the cephalic hemocoel, where it runs anteriorly along the loop of the intestine to its anterior margin. The right kidney opens into the post-branchial portion of the mantle cavity via a long, cylindrical, urinogenital papilla that parallels the rectum, but opens posterior to the anus.

2.7. Reproductive system (Figures 5A, 6C)

The gonad (Figures 5A, 6C, g) of pleurotomariids lines the dorsal and columellar sides of the digestive gland. Its septate lumen empties via a simple, tubular gonadal duct that runs anteriorly to open into the right kidney (Figure 6C, ga), at the base of the urinogenital papilla (Figures 5B, 6C, u), which is glandular in mature females, but not in males. Fretter (1964: 179) observed that the urinogenital papilla of an immature female of *P. amabilis* was not glandular, and suggested that glands may develop in the wall of the papilla only when the gonads become mature. Healy and Harasewych (1992) noted that Fretter (1964) based these observations on one of the largest known specimens of *P. amabilis*, and instead hypothesized that the urinogenital papilla only becomes glandular seasonally during spawning.

Sexes of mature specimens may be discerned most readily by the color and texture of the gonad. The ovary is whitish and granular, with individual ova ranging from about 500 μm to nearly 1 mm in diameter, depending on species. Testes range from yellow to mustard brown and are much finer in texture.

Fretter (1966: 610) reported that the ova of *P. midas* are covered by a gelatinous sheath as thick as the diameter of the ovum that is produced by the ovum while still in the ovary. She hypothesized that, as in certain trochoideans, pleurotomariid eggs are embedded in a secretion from the glandular urinogenital papilla to form a spawn mass that is fertilized externally. Neither the spawn mass nor the details of oogenesis have been studied for any pleurotomariid.

The spermatozoa of pleurotomariids were first studied by Healy (1988), who noted that the sperm of *Perotrochus westralis* Whitehead, 1987 (as *P. africana* Tomlin, 1948) was primitive and unmodified, consisting of a conical acrosomal vesicle, a short, cylindrical nucleus with numerous lacunae, a midpiece of four roughly spherical mitochondria, and a long flagellum. Healy and Harasewych (1992) subsequently described in greater detail the ultrastructure of the sperm and spermatogenesis in *P. quoyanus*, and concluded that the sperm of Pleurotomariidae is more similar to that of Trochidae than to those of Haliotidae, Scissurellidae or Fissurellidae.

Although larval development has not been studied for any pleurotomariid, Bouchet and Metivier (1982: 313) reported that "*Perotrochus* species certainly have non-planktonic larval development...". The pleurotomariid protoconch has a large initial diameter (approximating the egg diameter), few, smooth whorls, a pronounced protoconch/teleoconch boundary, and lacks a protoconch II, as is typical of vetigastropods. These features are all indicative of the absence of a long, feeding (planktotrophic) larval stage (Shuto, 1974; Lima and Lutz, 1990). However, protoconch morphology cannot be used to distinguish between non-feeding pelagic development (as occurs in many vetigastropods), benthic development, where the larva develops within the egg mass (as occurs in some trochids, e.g., *Margarites*), or brooding (as in the scissurellid *Larochaea*, and some trochids) (Sasaki, 1998: 189).

2.8. Nervous system (Figure 6D)

The nervous system has been described in considerable detail for *Perotrochus quoyanus* (Bouvier and Fischer, 1898) and *Mikadotrochus beyrichii* (Woodward, 1901: 240–247, figures 27–29; Sasaki, 1998: 48–49, figure 26d), while Fretter (1966: 610–611) provided comparative comments on the nervous systems of *Perotrochus midas* and *P. lucaya*. The nervous

system of *Entemnotrochus adansonianus* is described here, and agrees in most features with that of other pleurotomariids.

The circumesophageal nerve ring is hypoathroid, with the pleural ganglia fused to the pedal ganglia, while the large cerebral ganglia are located anteriorly, at the base of the snout, near the cephalic tentacles. The labial ganglia are fused to the cerebral ganglia. The cerebro-pedal connectives are longer than, and ventral to, the cerebro-pleural connectives (Figure 6D). The cerebral ganglia innervate the tentacles and eyes, and join the buccal ganglia, situated along the dorsal surface of the buccal mass, via connectives. The buccal ganglia innervate the buccal muscles, while the cerebral commissure gives rise to numerous nerves leading to the buccal cavity and anterior face of the snout. The visceral loop is very long, and originates from the cerebro-pleural connectives, rather than from the pleural ganglia. Pleurotomariids lack distinct visceral ganglia, but the visceral loop innervates the osphradia (which have ganglia). A pair of statocysts are situated anterior to the pedal ganglia and are innervated from the cerebro-pleural connectives. The pedal cords run roughly in parallel along the length of the foot and are joined by numerous (>10) ladder-like commissures.

3. SYSTEMATIC RELATIONSHIPS

3.1. Morphology-based classifications (Figure 8)

3.1.1. Relationships of Pleurotomarioidea to other Gastropoda

Because of their abundance in Paleozoic and Mesozoic deposits, pleurotomarioideans have been well known to paleontologists since at least the seventeenth century (e.g., Lister, 1678). Early workers included pleurotomarioidean species in the genera *Trochus*, *Turbo* and *Cirrus* (e.g., Pulteney, 1813; Sowerby, 1816 in 1812–1846; Mantell, 1822) based on the general shape of their fossilized shells. During the 1820s, several authors began to distinguish fossils with trochiform shells that also bore a spiral band and a deep notch on the outer lip by applying permutations of the generic name *Pleurotomaria* (Sowerby, 1821 in 1812–1846; Ferussac, 1822 in 1821–1822; Blainville, 1825 in 1825–1827; DeFrance, 1826). The International Commission on Zoological Nomenclature (1960: 276) subsequently ruled that the name *Pleurotomaria* should be attributed to DeFrance. Early researchers at first included the genus *Pleurotomaria* in the family Trochidae, while noting that the shell morphology of some of the included species appeared more similar to the related family

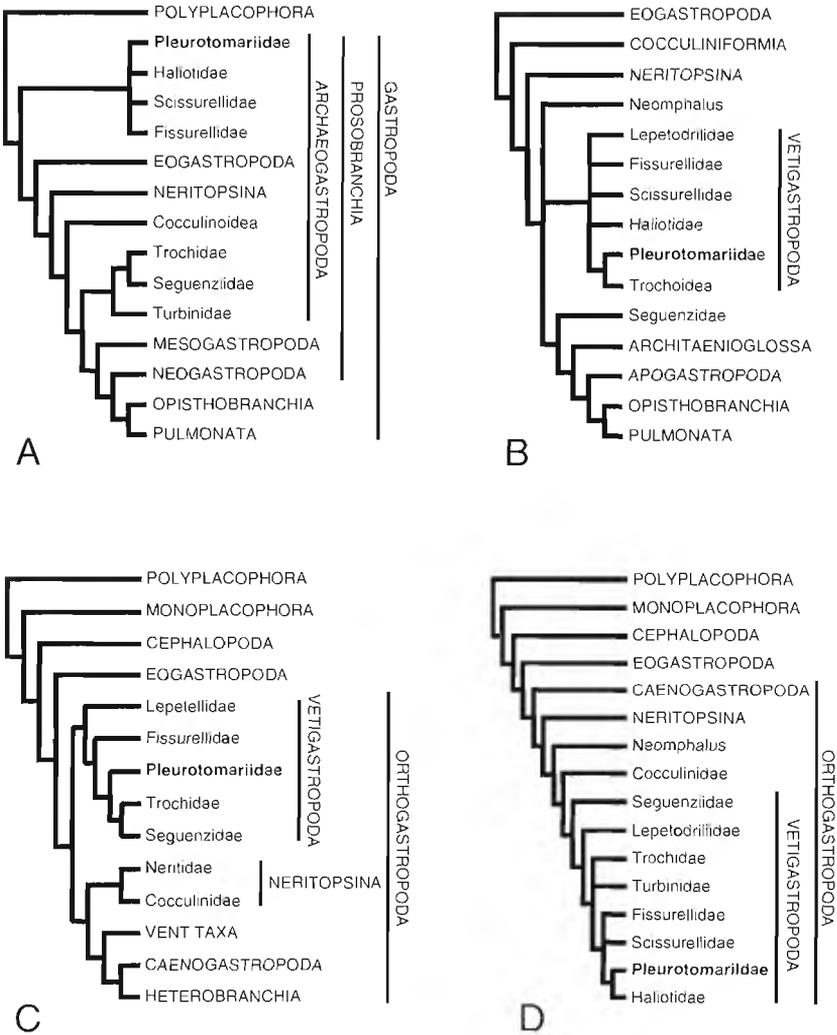


Figure 8 Relationships of Pleurotomarioidea to other Gastropoda based on morphological data. Trees constructed to represent major hypotheses of gastropod evolution, with taxon names and ranks modified to emphasize the position of the Pleurotomariidae in the respective classifications. (A) Classification of Thiele (1929) represented as a phylogenetic tree (modified from Ponder and Lindberg, 1996: figure 11.3.A). (B) Phylogenetic hypothesis of Haszprunar (1988: figure 5). (C) Phylogenetic hypothesis of Ponder and Lindberg (1996: figure 11.3.D). (D) Phylogenetic hypothesis of Sasaki (1998: figure 104).

Turbinidae (J. de C. Sowerby, 1832). In fact, Pleurotomariidae was originally proposed as a subfamily of Trochidae by Swainson (1840: 213), who proclaimed (1840: 223), "that it was impossible to arrange [fossil genera] with precision, from ignorance of the animal!"

The discovery and infrequent collection of living pleurotomariids during the second half of the nineteenth century (e.g., Fischer and Bernardi, 1856; Dall, 1889) gave rise to a series of publications documenting the novel anatomical organization and radular morphology of these animals (Tables 1 and 2). Systematists of the time varied in their views of the relationships of Pleurotomariidae, relying on the morphology of the shell or of one or a few organ systems in reaching their conclusions. Some continued to place it close to the family Trochidae (e.g., Adams and Adams, 1858), while others aligned it with the Scissurellidae, Haliotidae or Fissurellidae (e.g., Fischer, 1887: 845; Dall, 1889; Pilsbry, 1890: 69; Troschel, 1891). At the beginning of the twentieth century, a new view of gastropod evolution was advanced, based on the belief that gastropods had a bilaterally symmetrical ancestor (Thiele, 1902, 1935; Wenz, 1938, 1940). Under this hypothesis, pleurotomariids were considered to be the most primitive living gastropods. Their asymmetrically coiled shell and symmetrically paired pallial organs were regarded as transitional between extinct, planispirally coiled, bilaterally symmetrical ancestors, generally believed to be bellerophonids, and asymmetrical modern gastropods. This classification (Figure 8A) had subsequently gained almost universal acceptance (e.g., Yonge, 1947; Fretter and Graham, 1962, 1985; Taylor and Sohl, 1962; Morton and Yonge, 1964; Abbott, 1974; Boss, 1982; Hickman, 1984a, b; Vaught, 1989; Brusca and Brusca, 1990; Ruppert and Barnes, 1994; see Bieler, 1992 for a detailed review).

The rapid technological advances in deep-sea exploration during the past several decades have led to discoveries of a significant number of primitive, previously unknown gastropod groups, principally from hydrothermal vents. In addition, the unprecedented pace of development of molecular techniques and computational methods for reconstructing phylogeny has prompted a series of increasingly rigorous and quantitative reassessments of gastropod phylogeny (e.g., Golikov and Starobogatov, 1975; Salvini-Plawen, 1980; Haszprunar, 1988; Ponder and Lindberg, 1996, 1997; Sasaki, 1998). These studies all recognized that the patellogastropod limpets (in some cases together with extinct Paleozoic groups, = subclass Eogastropoda Ponder and Lindberg, 1996) were an early, monophyletic sister group to the remaining gastropods (subclass Orthogastropoda Ponder and Lindberg, 1996). So profound are the differences between Eogastropoda and the Orthogastropoda that some authors have questioned whether these limpets are gastropods (Termier and Termier, 1968; Shileyko, 1977; Tillier *et al.*, 1992).

The evolutionary relationships among the basal taxa included within Orthogastropoda, have not yet been reliably or robustly resolved, despite extensive, ongoing research. Using detailed anatomical data from many of the newly discovered deep-sea groups, Haszprunar (1988) published a hypothesis of gastropod phylogeny (Figure 8B) depicting the successive emergence of a series of higher taxa. In this classification, the Pleurotomariidae emerged as the sister taxon of Trochidae within the order Vetigastropoda (see Section 3.1.2), but far from the base of the gastropod tree. Using parsimony-based analyses and an expanded anatomical data set, Ponder and Lindberg (1996: figures 11.1.B, 11.3.D) published a phylogenetic hypothesis of gastropod evolution (Figure 8C), in which the Pleurotomariidae are also included within Vetigastropoda, which, however, emerges as the basal group within the Orthogastropoda. In order to achieve this tree topology, which avoided the “unacceptable reversals” in the number of gills, osphradia and auricles from paired to single then back to paired, the authors had to constrain several characters as irreversible. After further expanding their data set, these authors (Ponder and Lindberg, 1997: figures 2, 5) subsequently published a revised hypothesis, in which the Neritopsina (now including Cocculinidae) emerges at the base of the Orthogastropoda, and a series of hot vent families are placed at the base of a clade containing Vetigastropoda (including Pleurotomariidae).

Most recently, Sasaki (1998) re-analyzed the relationships among the lower gastropods, using newly generated anatomical data. The resulting consensus tree (Figure 8D) agreed with prior studies in separating the Eogastropoda and Orthogastropoda, and in segregating orthogastropods into the groups Vetigastropoda, Neritopsina and Caenogastropoda. However, resolution of the evolutionary relationships among these major groups, or of the families included within Vetigastropoda is not strongly supported, nor does it concur with prior trees. As in previous phylogenetic analyses, Sasaki’s tree topology predicts the evolutionary loss of paired gills, osphradia and auricles, followed by their re-appearance (possibly by atavistic re-expression) within some Vetigastropoda.

3.1.2. *Composition of superfamily Pleurotomarioidea*

The ongoing studies of gastropod phylogeny have resulted in substantial revisions and speculations with regard to the taxa composing the superfamily Pleurotomarioidea. The most comprehensive work to date (Knight *et al.*, 1960) defined Pleurotomarioidea as containing 20 extinct families as well as the living families Pleurotomariidae, Scissurellidae and Haliotidae. This arrangement is followed in the majority of contemporary

classifications (e.g., Hyman, 1967; Hickman, 1984b, 1998; Vaught, 1989). Based on the shared presence of several apomorphic anatomical features (including epipodial sense organs, ctenidial bursicles, an esophagus that is transversely sickle-shaped, with papillated lateral pouches, and an osphradium located along the efferent ctenidial membrane) the Pleurotomarioidea (defined to include the families Pleurotomariidae + Scissurellidae + Haliotidae) were united with the Fissurelloidea and Trochoidea, and questionably the Neomphalidae, in the order Vetigastropoda (Salvini-Plawen, 1980; Salvini-Plawen and Haszprunar, 1987). Boss (1982: 1092) added Neomphalidae to Pleurotomarioidea, but considered Fissurelloidea to be a separate superfamily. The inclusion of the Haliotidae and Scissurellidae within Pleurotomarioidea has been based primarily on the presence of a slit or series of tremata, and vestiges of bilateral symmetry in the mantle cavity. Both these groups appear in the fossil record in a recognizable form during the late Mesozoic (Hickman, 1984b: figure 2). Salvini-Plawen and Haszprunar (1987) recognized that no synapomorphies could be found to unite the living pleurotomarioidean families, and suspected that Pleurotomarioidea was polyphyletic. Haszprunar (1989) elevated each of the living families to superfamilies, and restricted Pleurotomarioidea to contain only Pleurotomariidae. Noting that the highly derived morphology of the pleurotomariid radula is not shared by Scissurellidae or Haliotidae, Haszprunar (1989: 15) hypothesized that the anatomy of the Paleozoic and Mesozoic families usually included in Pleurotomarioidea might have been more similar to that of living Scissurellidae than to Pleurotomariidae, and suggested that the fossil families previously included in Pleurotomarioidea might more appropriately be assigned to Scissurelloidea.

The most recent phylogenetic studies consider Pleurotomariidae to be the sister taxon of Trochidae + Seguenziidae (Ponder and Lindberg, 1996: figure 11.3.D), Trochidae (Haszprunar, 1988: figure 5), Haliotidae (Sasaki, 1998: figure 104) or Trochidae + Haliotidae (Ponder and Lindberg, 1997: figures 2, 5). However, many of the characters considered to be synapomorphic in the construction of these trees (e.g., fecal groove, epipodial sense organs, sensory papillae) are absent in Pleurotomariidae, and must be hypothesized to be secondarily lost within this family.

3.1.3. *Relationships of taxa within Pleurotomariidae*

The earliest records for the family Pleurotomariidae are from Upper Middle Triassic (Ladinian) strata (Tracey *et al.*, 1993). Of the 14 genera assigned to the family, more than half originated during the Jurassic and most were extinct by the end of the Cretaceous. All of the genera were

defined on the basis of relatively few, easily recognizable shell characters. Classification systems for the diverse Mesozoic species tend to be based on keys, using shell characters in a particular sequence, and are phenetic. Most modern authors concede that generic distinctions are not always clear and that many taxa are not readily assigned to available genera (Cox, 1960a; Hickman, 1976; Szabó, 1980). Studies of fossil pleurotomariids tend to be of a regional, faunistic nature, with few attempts to assess relationships among the genera. Notable exceptions include the work of Szabó (1980), who produced a phenogram based on a dichotomous key of shell characters (Figure 9A), and Benfrika's (1984) dendrogram of hypothesized relationships (Figure 9B) in an unpublished thesis. Kanie *et al.* (1995: figure 4) published an evolutionary tree of the Cenozoic genera occurring in Japan.

The genus *Pleurotomaria* Defrance, 1826, was proposed based on a Jurassic type species (*Trochus anglicus* Sowerby, 1818 in 1812–1846) and is generally considered to have lived during the Lower Jurassic to the Lower Cretaceous (Knight *et al.*, 1960). Living species serve as the basis for the generic names *Perotrochus* Fischer, 1885, *Entemnotrochus* Fischer, 1885 and *Mikadotrochus* Lindholm, 1927. A number of authors have treated the living supraspecific taxa as, at best, subgenera of *Pleurotomaria* (e.g., Dall, 1889; Hickman, 1976, 1984a, b, 1998; Abbott and Dance, 1982), while others (e.g., Knight *et al.*, 1960; Bayer, 1965; Benfrika, 1984; Vaught, 1989; Koizumi, 1993; Endo, 1995; Kanie *et al.*, 1995; Anseeuw and Goto, 1996; Okutani and Hasegawa, 2000) believe that at least some of them merit generic rank.

In a review of the Recent species, Bayer (1965) not only recognized *Entemnotrochus*, *Mikadotrochus* and *Perotrochus* as valid genera, but went on to subdivide *Perotrochus* into three separate groups. He considered *Perotrochus* "Group A" to be restricted to species with small, conical shells, including *P. quoyanus*, the type species of *Perotrochus*. Species of *Perotrochus* with large, turbiniform shells and inflated whorls were segregated as *Perotrochus* "Group B", while *Perotrochus* "Group C" contained only a single species, *Perotrochus hirasei*. A synopsis of available information on living Pleurotomariidae has recently been published (Anseeuw and Goto, 1996) in which the genus *Perotrochus* is considered to include all living species other than the two assigned to *Entemnotrochus*. Okutani and Hasegawa (2000) divided the Japanese species among the genera *Entemnotrochus*, *Perotrochus* and *Mikadotrochus*, but followed Bayer (1965) by including *P. hirasei* in the genus *Perotrochus*.

There have yet to be studies of phylogenetic relationships among the Recent species based on cladistic analyses of morphological/anatomical data.

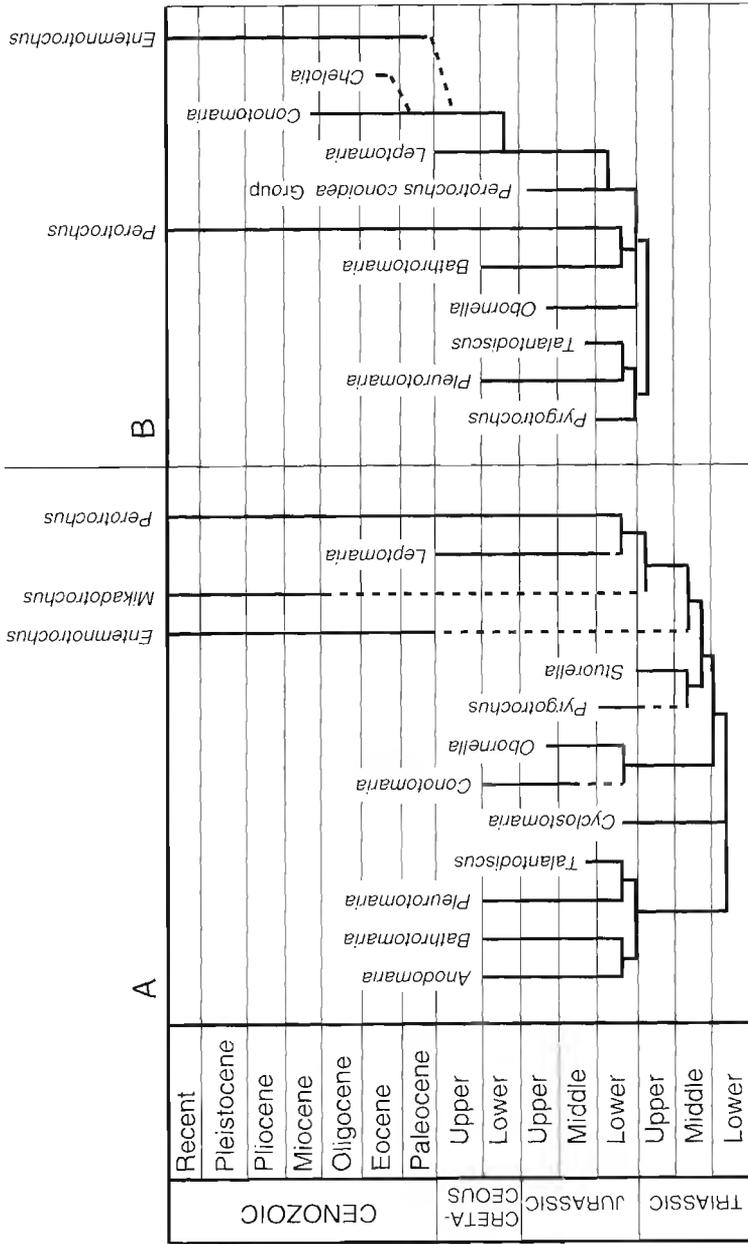


Figure 9 Relationships among living and fossil genera of Pleurotomariidae based on shell morphology and reflecting their representation in the fossil record. (A) Classification of Szabó (1980) represented as a tree, with taxon ages derived from Knight *et al.* (1960) and Benfrikia (1984). (B) Phylogenetic hypothesis and taxon ages from Benfrikia (1984; figure 21).

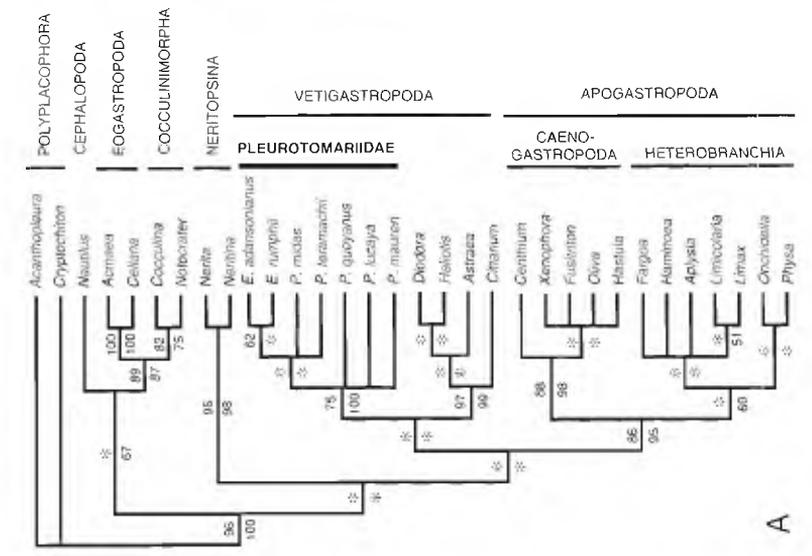
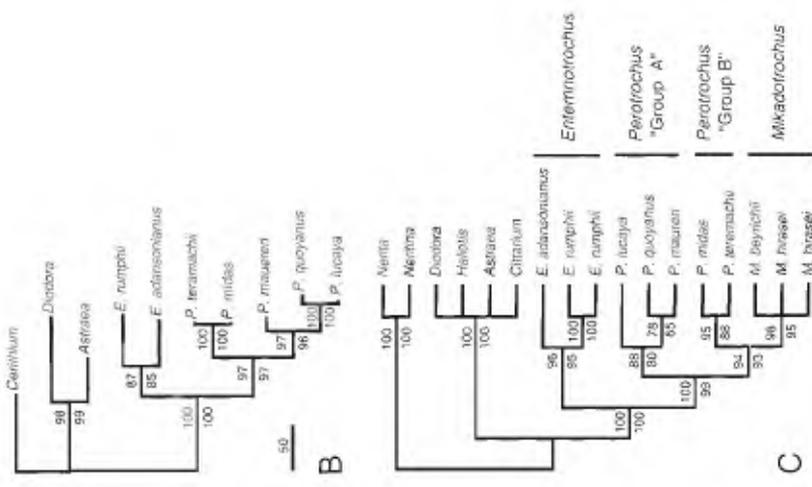
3.2. Classifications based on molecular data (Figure 10)

To date, there have been but a small number of phylogenetic studies to incorporate sequence data derived from any species of Pleurotomariidae, although some publications report on relationships of the Pleurotomarioidea based on sequences obtained from Haliotidae (e.g., Tillier *et al.*, 1992, 1994). Rosenberg *et al.* (1994) included *Perotrochus maureri* in a preliminary survey of gastropod and bivalve phylogeny based on a small and irregular sampling of taxa that were sequenced for a 150-nucleotide region from the D6 domain of the 28S RNA. Their results were anomalous in grouping the Pleurotomariidae in a clade with Neogastropoda, which together formed the sister group of the remaining caenogastropods in their study.

A more comprehensive investigation of the phylogenetic relationships of living pleurotomariids was conducted by Harasewych *et al.* (1997), who used data from both nuclear (~450 bp from the 18S rDNA gene) and mitochondrial (579 bp from the cytochrome *c* oxidase I (CO I) gene) genomes of seven species of Pleurotomariidae to determine the position of this family within the Gastropoda, as well as to delineate relationships among its genera and species. Their phylogeny of the Gastropoda based on partial 18S rDNA sequences (compare Figure 10A with Figure 8) most closely approximates the morphology-based hypothesis proposed by Haszprunar (1988). While the family Pleurotomariidae emerges within Vetigastropoda, it appears as the sister group of all remaining vetigastropod taxa, rather than of Trochidae or Haliotidae. All pleurotomariids sequenced were characterized by the presence of large insertions, especially in the regions coding for helices 10, E-10-1, and 11 of the 18S RNA, as well as by accelerated rates of sequence evolution in the 18S rDNA gene, when compared to other Vetigastropoda and Caenogastropoda in their study. These insertions were not only unique to, and diagnostic of Pleurotomariidae, but contained length variations that could themselves be used to differentiate between and infer relationships among pleurotomariid genera and species groups (Harasewych *et al.*, 1997: figures 7, 8).

Phylogenies based on partial 18S rDNA sequences (Harasewych *et al.*, 1997: figure 6), insert polymorphisms (Harasewych *et al.*, 1997: figure 7), and partial cytochrome *c* oxidase I sequences (Harasewych *et al.*, 1997: figure 10A), as well as on "total molecular evidence" (a combination of these three data sets), all reliably segregate *Perotrochus* "Group A" from *Perotrochus* "Group B", which together form a clade that comprises the sister taxon of *Entemnotrochus* (Figure 10B).

Since the publication of Harasewych *et al.* (1997), sequences for a comparable portion of the 18S rDNA were determined for one specimen of *Mikadotrochus beyrichii* (GenBank AF 417116) the type species of



POLYPLACOPHORA
 CEPHALOPODA
 EOGASTROPODA
 COCCULINIMORPHA
 MERITOPSINA
 PLEUROTOMARIIDAE
 VETIGASTROPODA
 CAENO-GASTROPODA
 HETEROBRANCHIA
 APOGASTROPODA

Mikadotrochus, and two specimens of *Mikadotrochus hirasei* (GenBank AF 417117 and GenBank AF 417118), as well as a second specimen of *Entemnotrochus rumphii* (GenBank AF 417119). The three specimens of *Mikadotrochus* contained the large insertions characteristic of Pleurotomariidae. They all shared the pattern of insert segments characteristic of *P. midas* (see Harasewych *et al.*, 1997: figure 8), but differed in having a gap in insert segment 10 (at positions 318–320, using the alignment shown in Harasewych *et al.*, 1997: figure 3). Figure 10C shows the strict consensus of four most parsimonious trees (CI=0.872, RI=0.943) resulting from a reanalysis of the 18S rDNA sequence data (PAUP 4.02, branch and bound search, gaps treated as a fifth base) after the four additional sequences were aligned to the previously published data.

The three specimens of *Mikadotrochus* form a strongly supported clade that is the sister group of *Perotrochus* "Group B". These two groups form a clade that is the sister taxon of *Perotrochus* "Group A", and these in turn comprise the sister group of *Entemnotrochus*. This sequence-based phylogeny strongly corroborates Bayer's (1965) division of *Perotrochus* into three distinct groups. His *Perotrochus* "Group A" contains the type species of *Perotrochus*, and therefore retains the name *Perotrochus*. *Perotrochus* "Group C" is shown here to contain the type species of *Mikadotrochus*, and retains that generic name. As inclusion of *Perotrochus* "Group B" within *Perotrochus* would make *Perotrochus* a paraphyletic taxon, the name *Bayerotrochus* (type species: *Perotrochus midas* Bayer, 1965) is proposed here for *Perotrochus* "Group B" of Bayer (1965) in recognition of Dr Bayer's pioneering work on the Pleurotomariidae of the western Atlantic and his early recognition of this most widespread and diverse pleurotomariid clade. *Bayerotrochus* is

Figure 10 Phylogenetic relationships of Pleurotomariidae, inferred from DNA sequence data. (A) Position of Pleurotomariidae within Gastropoda based on partial 18S rDNA sequence data (after Harasewych *et al.*, 1997: figure 5B). Strict consensus of 60 most parsimonious trees (CI=0.779, RI=0.845) based on a data matrix that was reweighted by the rescaled consistency index (base weight=1). (B) Relationships among living species based on "total molecular evidence", consisting of 559 bp of 18S rDNA + 579 bp of CO I + 19 indel characters (after Harasewych *et al.*, 1997: figure 10B). Single most parsimonious tree (CI=0.729; RI=0.685). (C) Relationships among living species based on partial 18S rDNA sequences. Newly produced sequences for *Mikadotrochus beyrichii* and *M. hirasei* aligned against previously published sequences (Harasewych *et al.*, 1997) using Clustal W. PAUP 4.02 [Branch and bound search; gap=5th base] was used to produce this strict consensus of 4 most parsimonious trees (CI=0.894, RI=0.944). Bootstrap proportions are shown above the nodes, jackknife proportions below the nodes. An asterisk denotes a value below 50.

defined as comprising all species sharing a more recent common ancestor with the type species, *B. midas*, than with *Mikadotrochus beyrichii*, the type species of its sister group. Morphologically, it may be identified by its large, thin, turbiniform shell with inflated, convex whorls, its broad, shallow slit, forming a selenizone slightly below mid-whorl, its lack of an umbilicus, its thin prismatic layer with weak sculpture generally limited to spiral threads, and its relatively large operculum. *Bayerotrochus* has a distinctive, large, tumescent foot that extends beyond the shell and enfolds its posterior edge. In *Bayerotrochus*, the gene coding for the 18S RNA contains a three-base insert (aligned positions 318–320, Harasewych *et al.*, 1997: figure 3) within helix E-10-1 that is not present in any other pleurotomariid. In addition to the type species, *Bayerotrochus* contains *B. africanus* (Tomlin, 1948), *B. charlestonensis* (Askew, 1988), *B. diluculum* (Okutani, 1979), *B. metivieri* (Anseeuw, 1999), *B. pyramus* (Bayer, 1967), *B. tangaroana* (Bouchet and Métivier, 1982), *B. teramachii* (Kuroda, 1955) and *B. westralis* (Whitehead, 1987).

4. ECOLOGY

4.1. Geographic distribution (Figure 11)

Although pleurotomariids had a global distribution during the Paleozoic and Mesozoic, ranging from Alaska (Rohr and Blodgett, 1985) and the islands of Arctic Canada (Rohr and Smith, 1978) to Antarctica (Oleinik, personal communication), Recent species are confined to tropical and temperate latitudes (about 35°N to 30°S). All living species are limited to continental margins and edges of tectonic plates along the western shores of the Atlantic and Pacific Oceans, and all but the southern margin of the Indian Ocean, including northwestern Australia, southeastern Asia and the intervening islands and archipelagos (Figure 11; see also Anseeuw and Goto, 1996 for review).

The greatest species diversity occurs in the Philippines and southern Japan, while the Caribbean Sea has the greatest number of species among the western Atlantic faunas (Figure 11). These areas also have the only known post-Miocene fossil records for pleurotomariids (Hickman, 1976: figure 2), although this may be an artifact of sampling. Zezina (1997: 401) noted that the bathyal faunas along the western margins of oceans are far more diverse than those along the corresponding eastern margins (by factors as high as 25 times in the Pacific), due in part to the deleterious effects of upwelling upon benthic taxa, especially over long intervals of geologic time. The distribution of living pleurotomariids is



Figure 11 Map showing geographic distribution of living Pleurotomariidae. The numbers indicate the number of species that have thus far been reported from the respective regions.

highly congruent with those bathyal regions that have been colonized by warm water species (Zezina, 1997: figure 8).

Examination of the distribution of individual pleurotomariid genera reveals finer scale patterns. The genus *Entemnotrochus* is represented in the Recent fauna by two wide-ranging species, one in the western Atlantic, and the other in the western Pacific. *Entemnotrochus adansonianus* occurs in the warmer waters of the western Atlantic, from Bermuda southward, throughout the Gulf of Mexico and the Caribbean, to near the mouth of the Amazon River, while *E. rumphii* is known from the southern islands of Japan to the central Philippines and Indonesia. Species of *Perotrochus sensu stricto* (i.e., *Perotrochus* "Group A"), however, have much smaller geographic ranges. Three species occur allopatrically within the range of *E. adansonianus* (*P. amabilis* – Gulf of Mexico and the Florida Keys, *P. lucaya* – Bahamas, *P. quoyanus* – Caribbean Sea and Bermuda), while two species live beyond the range of *E. adansonianus* (*P. maureri* – off South Carolina, *P. atlanticus* – off Southern Brazil). Of the three Pacific species included in *Perotrochus*, only *P. gotoi* lives within the range of *E. rumphii*, while *P. caledonicus* and *P. deforgesii* live beyond the southern limit of its known range. More intriguing are the distributions of species of *Mikadotrochus*. Three species (*M. beyrichii*, *M. hirasei*, *M. salmianus*) appear to have broad geographic distributions ranging from central Japan to the Philippines, while two (*M. anseeuwi*, *M. vicdani*) are restricted to the Philippines. Okutani (1963: figure 7) documented a pattern of longitudinal replacement and allopatry for the three species occurring

along the insular shelves and submarine banks off southern Japan, a pattern later confirmed by Kanie *et al.* (1995). More detailed studies over larger areas, particularly in the Philippines, may reveal fine scale allopatry among the species of *Mikadotrochus*. The genus *Bayerotrochus* (= *Perotrochus* "Group B") has the broadest geographic distribution both on a global scale and within the Indo-Pacific region. It is the only genus to be represented along the margins of the Indian Ocean. Within the western Pacific, it represents the northernmost and southernmost records for the family. Within the western Atlantic, the range of *B. charlestonensis* approximates the northern limits of *E. adansonianus*, but the southernmost records for *Bayerotrochus* are from the Caribbean Tectonic Plate, far short of the southern limits of *Entemnotrochus* or *Perotrochus*. The Caribbean species *B. midas* and *B. pyramus* are known to co-occur throughout the Antilles, and both species have been collected on the same submarine dives. Most Indian and Pacific Ocean species of *Bayerotrochus* have clearly allopatric geographic distributions, although both *B. teramachii* and *B. metivieri* have been reported from the South China Sea. Records for these species are too sparse and imprecise to determine the degree to which their ranges overlap.

The geographic distribution of pleurotomariids, once thought to be patchy and limited to islands of hard substrata, steep walls and tops of submarine banks, was attributed to the hypothesized incompatibility of the primitive mantle cavity and bipectinate gills with significant sediment load (Hickman, 1984b). However, both Thomas (1940) and Batten (1958) reported substantial dwarfing in Paleozoic pleurotomariids from depositional environments indicative of fine, suspended sediments, confirming that these animals could at least survive significant turbidity.

4.2. Bathymetric distribution and zonation (Figure 12)

Figure 12A summarizes the bathymetric ranges of the living species of Pleurotomariidae based on records from the literature and museum collections. Geographically co-occurring species often appear to have overlapping bathymetric ranges, suggesting that two or more species, usually from different genera, might be expected to live in sympatry. However, detailed observations from multiple submersible dives transecting the depth ranges of all pleurotomariid species at localities throughout the Bahamas and off Guadeloupe (Table 3, Figure 12B) clearly show that western Atlantic pleurotomariids inhabit sharply demarcated, non-overlapping bathymetric zones, each corresponding to a distinct bottom topology and habitat. *Entemnotrochus adansonianus* inhabits a relatively narrow zone of substratum that is encrusted with diverse large

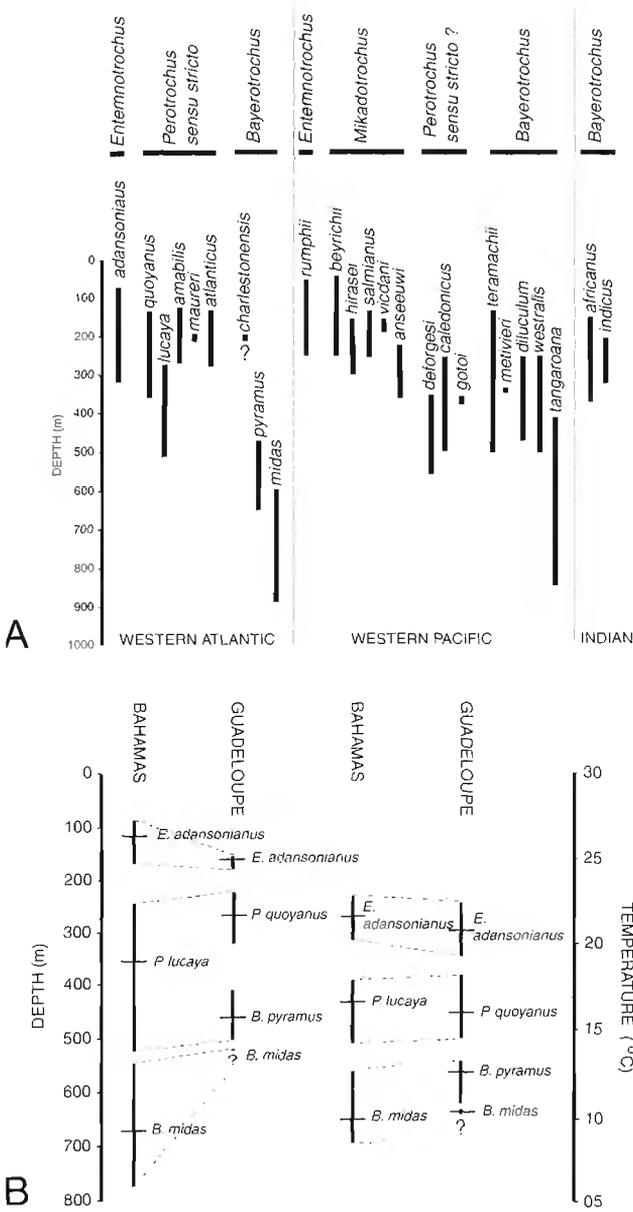


Figure 12 Distribution of living Pleurotomariidae by depth and temperature. (A) Depth ranges for living species of Pleurotomariidae based on museum and literature records. (B) Zonation of living Pleurotomariidae by depth and temperature based on *in situ* observations from the submersibles JOHNSON-SEA-LINK I and II, at two locations in the western Atlantic.

Table 3 Depth and temperature distribution of western Atlantic Pleurotomariidae (based on direct observation from submersibles).

Taxon/locality	Number of observations	Depth (meters)			Temperature (°C)		
		Mean	SD	range	Mean	SD	range
<i>Entemnotrochus adansonianus</i>							
Bahamas	35	114	21	87–169	21.8	1.7	20.7–23.0
Navassa	8	156	23	123–179	23.0	1.3	21.5–24.9
Guadeloupe	4	170	9	156–178	20.7	1.4	19.2–22.3
<i>Perotrochus maureri</i>							
Charleston Lumps	56	202	9	198–221	9.8	0.1	9.6–9.9
<i>Perotrochus lucaya</i>							
Bahamas	14	354	115	244–520	16.5	1.6	14.0–17.9
<i>Perotrochus quoyanus</i>							
Guadeloupe	11	263	30	223–322	16.0	1.4	14.1–18.0
<i>Bayerotrochus pyramus</i>							
Guadeloupe	5	361	31	306–399	12.5	0.9	11.4–13.7
<i>Bayerotrochus midas</i>							
Bahamas	26	664	83	542–774	9.9	1.4	8.5–12.9
Navassa	2	655	–	638–672	9.0	–	8.6–9.3
Guadeloupe	1	413	–	–	10.7	–	–

sponges and runs along the middle portion of a vertical to somewhat undercut wall (Plate 5A–B). This wall extends from the reef break downward to a talus slope that further descends at a pitch ranging from 15 to 45°, and is covered by rocks, rubble and fine sand. Dead shells and an occasional living *E. adansonianus* are rarely encountered at the base of the wall, while species of *Perotrochus* achieve their greatest density along the middle region of the talus slope, among small sponges and stalked crinoids (Plates 5E, 6A). At the base of the talus slope, the substrate again descends more steeply (45–85°) and consists of sharply faceted outcrops covered by a thin veneer of sediment, with infrequent outcrops of large sponges and stalked crinoids. *Bayerotrochus* inhabit the lowest levels of the talus slope (Plate 6B–D) and the upper regions of the sharply descending wall (Plate 6E–F). The depths at which the inflection points between these topographic regions occur vary widely throughout the western Atlantic and Caribbean, and no doubt account for a substantial portion of the variation in the reported bathymetric range for each species.

Transects conducted along the tropical western Atlantic might be expected to encounter the wall-dwelling *Entemnotrochus adansonianus*, a single species of *Perotrochus* along the talus slope, and one species of *Bayerotrochus* on the lower wall, the species of *Perotrochus* and *Bayerotrochus* being determined by the location of the transect. Only in the Antilles (Guadeloupe and Navassa) have four species of pleurotomariids been encountered along a single transect. The species

Bayerotrochus pyramus occurs along the lower portion of the talus slope, a habitat usually populated by *Perotrochus*. However, the temperature of the water in which *B. pyramus* was collected is more typical of the habitat of *B. midas* than of *Perotrochus* (see Figure 12B), possibly allowing for a finer partitioning of the habitat.

Despite more than a decade of observations in submersibles spanning dozens of transects, two species of western Atlantic pleurotomariids have never been found sympatrically.

Fewer data are available regarding the habitats of western Pacific species. Kanie *et al.* (1986) observed *Mikadotrochus beyrichii* on a sandy bottom around rocks, in an area of rapid current populated by stalked crinoids. Kanie *et al.* (1995) deduced that the genus *Mikadotrochus* adapted to rocky substrata after diverging from *Bayerotrochus* some time during the Miocene. Okutani and Hasegawa (2000) reported that species of *Mikadotrochus* inhabit rocky bottoms, while *Entemnotrochus rumphii* and species of *Bayerotrochus* occur on coarse, sandy bottoms. Given the greater density of species in close geographic proximity and their narrower bathymetric ranges, it is possible that Pacific pleurotomariids may partition their habitat more finely, based on factors other than temperature or depth. Rex (1977: 525) hypothesized that biological interactions rather than physical factors are responsible for different rates of zonation among groups occupying different trophic levels in the deep sea. He noted that, where interspecific competition is absent, species ranges may overlap along an environmental gradient. However, in areas where species compete for food, they will occupy mutually exclusive zones along an environmental gradient.

Despite the lack of detailed data, there are general similarities between the bathymetric patterns of the western Pacific and the western Atlantic. In both faunas, *Entemnotrochus* is the genus with the shallowest bathymetric range, *Bayerotrochus* inhabits the deepest waters, while *Perotrochus* occupies intermediate depths. *Mikadotrochus*, however, lives at the same depths as *Entemnotrochus*, but inhabits rocky rather than sandy substrata.

4.3. Biogeography

Attempts to infer the biogeographic history of the Pleurotomariidae in the context of the phylogenetic hypothesis shown in Figure 10C reveal that the most basal divergences segregate along bathymetric rather than geographic boundaries. The boundary between *Entemnotrochus* and the remaining genera corresponds to the shelf-slope transition, with *Entemnotrochus* inhabiting outer shelf depths, while the remaining genera segregate into zones along the upper continental slope.

Within the bathyal zone, *Bayerotrochus* has the broadest geographical range, spanning the Indo-Pacific, Caribbean and North Atlantic regions from which pleurotomariids have been reported. Its absence from the Atlantic coast of South America may either be an artifact of insufficient sampling at appropriate depths and on suitable substrata, or may reflect a faunal boundary between the Caribbean and South American tectonic plates. The lack of records from Bermuda and the Gulf of Mexico may likewise be a sampling artifact.

In the western Atlantic, the boundary between *Bayerotrochus* and *Perotrochus* is entirely bathymetric, as the two genera co-occur throughout the known range of *Bayerotrochus*. In this context, the single record of *B. charlestonensis* from 200 m must be considered anomalous, as this species has not been collected during two subsequent submersible cruises to the type locality. Based on available data, patterns of bathymetric zonation are less clear cut in the western Pacific, where the taxa assigned to *Perotrochus* (*P. caledonicus*, *P. deforgesii* and *P. gotoi*)¹ separate most clearly from *Mikadotrochus*, but appear to overlap in depth range with *Bayerotrochus* in the case of the *P. gotoi*, the only species presently known to overlap in geographic range with *Mikadotrochus* or *Bayerotrochus*. Similarly, the bathymetric ranges of all species of *Mikadotrochus* overlap to a large extent with both *Entemnotrochus rumphii* and *Bayerotrochus teramachii*, with which they share geographic ranges. It is unclear whether these species partition their habitats by substratum type, or whether they are truly sympatric.

Based on the fossil record, the divergence between *Entemnotrochus* and *Perotrochus* of authors (*Perotrochus* + *Mikadotrochus* + *Bayerotrochus*) dates to at least the Jurassic, when these taxa or their ancestors were members of shallow-water faunas. The bathymetric segregation of these lineages clearly predates the isolation of the Atlantic from the Pacific faunas. The time of divergence between *Bayerotrochus* and *Perotrochus*, and their bathymetric zonation along the upper continental slope is less clear. If the clade containing *Perotrochus caledonicus*, *P. deforgesii* and *P. gotoi* proves to be the sister taxon of the western Atlantic species of *Perotrochus*, this would indicate that the divergence of *Perotrochus* and *Bayerotrochus* predates the separation of the Atlantic and Pacific faunas, but that the bathymetric zonation of these genera occurred only in the

¹ These three species have been included in the genus *Perotrochus sensu lato* based on overall conchological similarity and their small size. However, they share some characteristics (e.g., shell and body pigmentation patterns) that are not present in *Perotrochus sensu stricto*. The relationship of this likely monophyletic group to *Perotrochus* and *Mikadotrochus* is not yet clear.

western Atlantic. The radiation of *Petrotrochus* to form geographically allopatric western Atlantic species occurred after the bathymetric limits of the lineage had been confined. Should the clade containing *Petrotrochus caledonicus*, *P. deforgesii* and *P. gotoi* prove to be more closely related to *Mikadotrochus*, it would suggest an independent and possibly more recent bathymetric zonation along the western Pacific. Although additional, more precise data will be required to reconstruct bathymetric patterns of pleurotomariid evolution in the western Pacific, it appears clear that, within genera, species tend to be geographically isolated.

4.4. Diet

With a single exception (Barnard, 1963), all published reports indicate that the gut contents and/or feces of pleurotomariids consist primarily of sponge spicules, but commonly contain foraminiferal tests and diatoms (Table 4). These findings have been variously interpreted as being

Table 4 Reports of gut contents/feces of pleurotomariid gastropods.

Species	Food	Reference
<i>Entemnotrochus adansonianus</i>	Sponge spicules	Herein
<i>Entemnotrochus runghii</i>	Sponge spicules	Tan (1974)
<i>Mikadotrochus beyrichii</i>	Sponge spicules, order Poecilosclerida	Woodward (1901: 252)
<i>Mikadotrochus hirasci</i>	Sponge spicules, orders Haplosclerida, Poecilosclerida and Hadromerida	Arakawa <i>et al.</i> (1978: table 1)
<i>Petrotrochus quoyanus</i>	Sponge spicules	Herein
<i>Petrotrochus amabilis</i>	Sponge spicules, foraminiferans, diatoms and algal fragments	Fretter (1964: 182)
<i>Petrotrochus maureri</i> ^a	Sponge spicules, foraminiferans and diatoms	Harasewych <i>et al.</i> (1988: 97)
<i>Bayerotrochus pyramus</i>	Sponge spicules, octocorals	Anseeuw and Goto (1996: 13)
<i>Bayerotrochus africanus</i>	Amorphous mass with a few tiny foraminiferans	Barnard (1963: 156)
<i>Bayerotrochus midas</i>	Sponge spicules, foraminiferans and diatoms	Harasewych <i>et al.</i> (1988: 97)
	Stalked crinoid	Anseeuw and Goto (1996: 123)

^a Originally reported as *Petrotrochus amabilis*.

indicative of a diet consisting of a single species of sponge (Woodward, 1901: 252), a larger diversity of sponge taxa (Arakawa *et al.*, 1978: 118), a diet consisting principally of sponges (Thiele, 1935: 1129; Hyman, 1967: 360; Yonge and Thompson, 1976: 52), a diet of encrusting invertebrates, primarily sponges (Hickman, 1984a: 29), or detrital feeding (Frøtter and Graham, 1976: 1). When kept in aquaria, pleurotomariids have been observed to consume a wide variety of organisms and tissue. Both *M. beyrichii* (Matsumoto *et al.*, 1972) and *P. teramachii* (Sekido *et al.*, 1976) were reported to feed on slices of raw fish (*Trachurus japonicus*), while *M. hirasei* fed on the meat of the bivalve mollusk *Tapes philippinarum* and the starfish *Asterina* sp. (Arakawa *et al.*, 1978).

Based on *in situ* observations of feeding corroborated by gut content analyses, Harasewych *et al.* (1988) documented that *Bayerotrochus midas* and *Petrotrochus maureri* (as *P. amabilis*) feed predominantly and selectively on sponge tissue, and suggested that the diatoms and foraminiferal tests present in the guts of pleurotomariids are derived from sediments that coat the surfaces of sponges. Subsequent observations, both *in situ* and in shipboard aquaria, confirmed that *E. adansonianus*, *P. quoyanus*, *P. lucaya*, *B. pyramus* and *B. midas* are all primarily spongivores. However, *B. midas* has been photographed eating a stalked crinoid (Anseeuw and Goto, 1996: 123) and *B. pyramus* was photographed feeding on an octocoral (Plate 6B). Both specimens were collected and esophageal contents confirmed that prey tissues were ingested.

Woodward (1901: 252) was the first to suggest that the pleurotomariid radula, with its multiple, distinctive tooth types, was specialized for feeding on sponges. The presence of morphologically similar, filament-tipped teeth in *Seila*, an unrelated ptenoglossan caenogastropod that also feeds on sponges, prompted Hickman (1984a: 35) to infer that this brush-like tooth morphology is a convergently evolved, functional adaptation to sponge predation. The voluminous, chitin-lined buccal cavity of pleurotomariids also appears to be an adaptation for ingesting large volumes of abrasive food.

Several authors (e.g., Yonge, 1973; Hickman, 1984a) have proposed that pleurotomariids were originally herbivorous. Yonge (1973) further suggested that the change to a carnivorous diet was associated with the ecological shift of this family from shallow water habitats, which it occupied during the Paleozoic and Mesozoic, to deeper waters by the end of the Eocene. However, the radulae of all living pleurotomariids have filament-tipped teeth, which are specialized for feeding on sponges. Thus, spongivory in pleurotomariids either predates the divergence of *Eutemnotrochus* from the *Petrotrochus* group during the Lower Jurassic (Benfrika, 1984: figure 21), or this highly derived tooth morphology evolved convergently in these two pleurotomariid lineages.

4.5. Predators and chemical defenses (Figures 13–15)

According to the “onshore-innovation, offshore-archaic” model for the evolution of Phanerozoic communities (Jablonski *et al.*, 1983), the disappearance of the diverse, shallow-water pleurotomariid communities of the Cretaceous, and the subsequent restriction of the family to outer slope and bathyal depths during the Cenozoic, is presumed to be a result of differential extinction of onshore as compared to offshore clades. The extreme diversification of predators, including fish and crustaceans, that was part of the major reorganization of benthic marine faunas termed the “Mesozoic Marine Revolution” by Vermeij (1977), probably contributed to the extinction of pleurotomariids in tropical, shallow water, hard bottom communities, where crushing predators are most diversified (Vermeij, 1982). While some related gastropods (e.g., Trochidae, Turbinidae) modified their shells to a more spherical shape, with tighter coils, a smaller aperture reinforced by a thicker outer lip and reinforcing sculptural elements, in order to resist predation, pleurotomariids did not incorporate such changes and, for the most part, remained thin-shelled and, in some cases, umbilicate.

The incidence of unsuccessful predation (measured as frequency of shell repair) is usually considered to be a measure of both predation pressure and the prey’s resistance to crushing predation. Thus, species with a high incidence of shell repair have a high exposure to crushing predators, as well as the ability to survive their attacks. Vermeij (1989) reported that among shallow water gastropods, the incidence of unsuccessful shell breakage is greatest in the Indo-West Pacific and lowest in the Atlantic. Rarely did his reported frequency of shell repair exceed 0.5 breaks per individual, and never averaged more than 1 break per individual, even in the most prey-resistant taxa. In a survey to determine the importance of predation in structuring deep-sea communities, Vale and Rex (1989) analyzed patterns of repaired shell damage in bathyal rissoid snails, and concluded that levels averaging 0.27 breaks per individual constituted a comparatively high level of potentially lethal predation.

Therefore, it was surprising that even a cursory examination of pleurotomariid shells reveals a multitude of repaired breaks (Figure 13). In fact, a specimen without multiple repaired breaks is a rarity, and 6–9 repaired breaks are not uncommon in individual specimens of *Bayerotrochus midas*. These initial observations prompted a survey of repaired shell breakage, western Atlantic specimens collected alive, and museum specimens with opercula (to ensure that the specimens were collected living, and that breaks were not lethal) for the western Pacific species (Figure 14A–F). The results indicated an extraordinarily high level of unsuccessful predation for all species examined (all species averaged

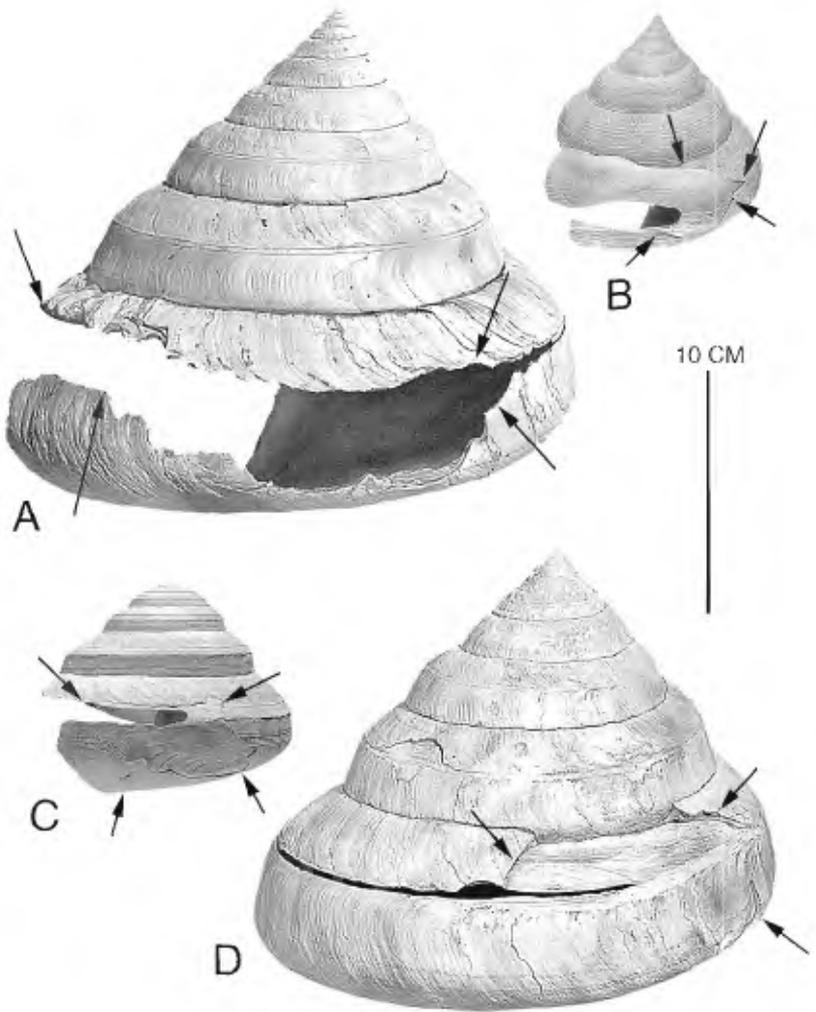
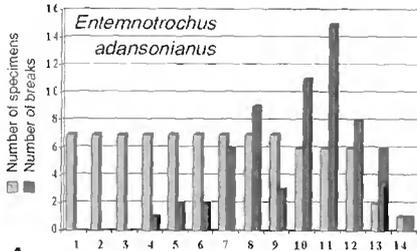


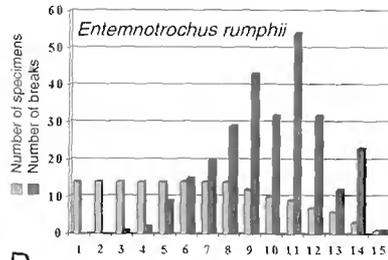
Figure 13 Repaired breaks in the shells of pleurotomariids, indicating unsuccessful attacks by predators. Peeling of the shell along the slit, indicative of attack by a crustacean, in (A) *Entemnotrochus rumphii*, (B) *Mikadotrochus hirasei* and (C) *Perotrochus midas*. Breakage due to biting attack by a fish in (D) *Entemnotrochus rumphii*. Arrows indicate limits of break from a single attack. All specimens were coated with NH_4Cl .

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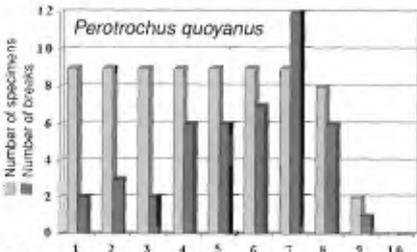
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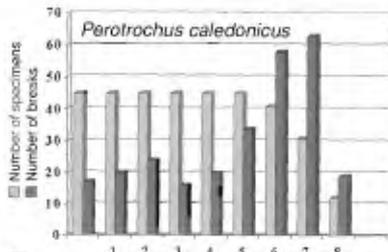
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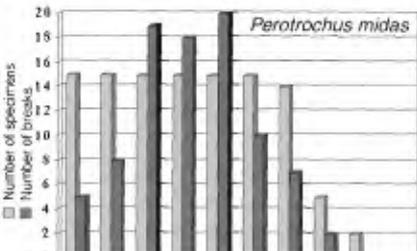
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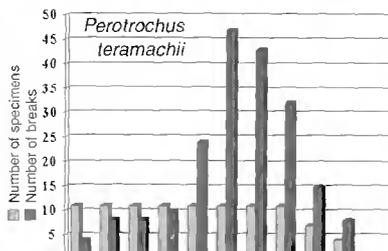
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E



C



F

WHORL NUMBER

WHORL NUMBER

Figure 14 Frequency and distribution of repaired breaks in western Atlantic and western Pacific pleuromariids. (A) *Entemnotrochus adansonianus*, (B) *Perotrochus quoyanus*, (C) *Perotrochus midas*, (D) *Entemnotrochus rumphii*, (E) *Perotrochus caledonicus* and (F) *Perotrochus teramachii*.

more than 1 repaired break per whorl at some stage of growth). Levels of predation for the western Pacific species were substantially higher, reaching 4–5 repaired breaks per whorl (Figure 14D, F). Nor was size a refuge from predation, as *Entemnotrochus rumphii*, which reaches 28 cm in diameter, had one of the highest frequencies of repaired breaks, especially in the later whorls. In some cases (e.g., *Perotrochus caledonicus*, Figures 14E, 15H), the frequency distribution of breaks

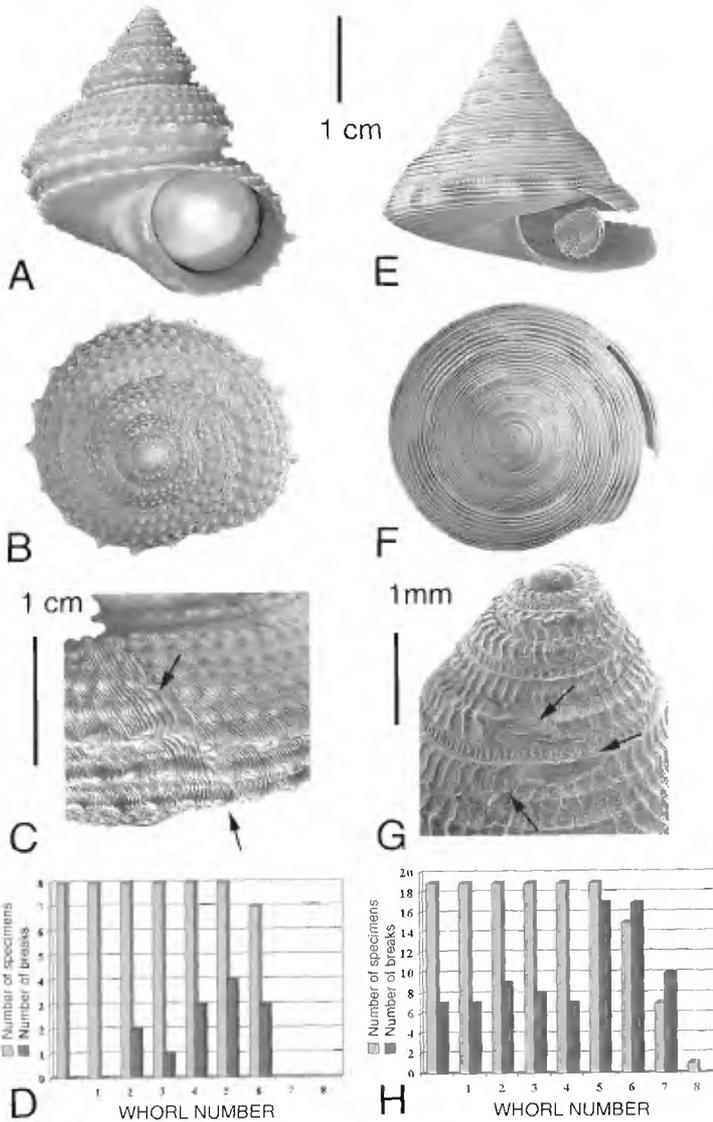


Figure 15 Repaired breaks in sympatrically occurring (A–B) *Bolma guttata* (A. Adams, 1863) and (E–F) *Perotrochus caledonicus* Bouchet and Metivier, 1982, both from N. O. “Vauban” MUSORSTOM 4, Station DW222, 30 September 1985. Off Southern New Caledonia, 22°58’S 167°33’E, in 410–440 m. (C) Example of shallow penetration of typical repaired break (arrows) in shell of *B. guttata* at 6 2/3 whorls. (G) Example of deep penetration of typical repaired break (arrows) in shell of *P. caledonicus* at 3 1/2 whorls. Relative frequency and distribution of repaired breaks in (D) *B. guttata* and (H) *P. caledonicus*.

appears bimodal, suggesting there may be two size classes of predators. Figure 15 illustrates the shell morphologies as well as the types and frequencies of repaired breaks in the trochid *Bolma guttata* A. Adams, 1863 (Figure 15A–D) and the pleurotomariid *Perotrochus caledonicus* Bouchet and Metivier, 1982 (Figure 15E–H) that were collected in the same dredge haul off southern New Caledonia. Although *Bolma* had a larger and thicker shell with stronger spiral and axial sculpture, as well as a calcified operculum that completely sealed the aperture (Figure 15A, B), repaired breaks were shallower (Figure 15C), less numerous, and confined to later whorls (Figure 15D). Despite having a thinner, less structurally reinforced shell, and a thinner, smaller, uncalcified operculum, the co-occurring *Perotrochus caledonicus* was able to survive more deeply penetrating shell breakage (Figure 15G) more frequently, and from a smaller size (Figure 15H).

Preston *et al.* (1993) observed the attacks of three species of crabs (*Carcinus maenus*, *C. pagurus* and *Liocarcinus puber*) on *Calliostoma ziziphynum*, a shallow-water trochid, and found that only 13–50% of attacks caused considerable damage to the shell aperture and, of these, only half resulted in the *Calliostoma* being eaten. The frequency of unsuccessful attacks by predators could therefore be substantially higher than indicated by the number of repaired breaks.

Observations of living animals, both in their habitat and in aquaria, revealed that when the animal is disturbed and especially when the shell is damaged, the hypobranchial glands of all species of Pleurotomariidae produce voluminous amounts (15–30 ml within 2 min by a specimen of *E. adansonianus* 10 cm in diameter) of a bluish white fluid that emanates from the rear of the slit and coats the shell (Plate 5D; see also Kanie *et al.*, 1986: figure 4). Preliminary experiments in aquaria suggest that this fluid is irritating to crustaceans, and possibly fish, while analyses of purified extracts of this secretion reveal the principal component to be structurally related to the alarm pheromone Navanone, produced by the nudibranch *Navanax inermis* (A. White, pers. comm.).

It would appear that all pleurotomariids are capable of deterring predators by secreting a repellent that causes them to release their prey. Given the steep-walled environment in which many of these animals live, the act of dropping a pleurotomariid will often cause it to roll 5–20 m down slope (distances based on observations of pleurotomariids dislodged and subsequently recovered after coming to rest), clearly out of the reach of the predator. As all pleurotomariids have two pairs of large hypobranchial glands that are capable of secreting large quantities of fluid in response to shell damage, this mechanism must have evolved prior to the divergence of *Entemnotrochus* and the remaining genera prior to the late Jurassic.

In a study of crushing predation among Pennsylvanian gastropods from north Central Texas, Schindel *et al.* (1982) observed that the frequency of shell repair was highest for trochiform shells, and concluded that this shell form was most resistant to crushing predation.

A perusal of the list of studied taxa (Schindel *et al.*, 1982: table 2) revealed that all specimens with trochiform shells were pleurotomarioideans spanning the families Raphistomatidae, Eotomariidae Wenz, 1938, Phymatopleuridae Batten, 1956, and Lophospiridae Wenz, 1938. While there was a strong correlation between spire height and frequency of repaired breaks among the pleurotomarioidean taxa, it is possible that this mode of chemical defense against predators might date from the Paleozoic and may have been more widespread among the pleurotomarioidean families.

ACKNOWLEDGEMENTS

Much of this work would not have been possible without the support and participation of Jack Lightbourne, Walter Paine, Yoshihiro Goto, Marilee McNielus and the late Connie Boone, in a number of the research cruises to study living pleurotomariids. I especially thank Craig Young and Shirley Pomponi for their gracious hospitality during a number of their research cruises. I am also grateful to Robert Costello, Steven Pappas, Glen Goodfriend, Paul Calomon, Patrick Anseeuw, Stephen Cairns, John Wise, Andrew McArthur and Guido Pastorino for their assistance during the research cruises, and for many insightful discussions over the past decade.

Special thanks are due to Tim Askew, Director of Marine Operations and to the Captains and crews of the *R/V Edwin Link*, the *R/V Seward Johnson*, and *R/V Sea Diver*, and to the pilots and crews of the research submersibles *Johnson-Sea-Link I, II, Clelia* and *Nekton Delta* for their assistance, and especially for sharing their years of personal observations on pleurotomariids. The assistance of Yolanda Villacampa, Susann Braden and Julie Whitis with many aspects of data collection, including literature searches, scanning electron microscopy, measurements and counts of repaired breaks, is recognized with thanks.

I would also like to acknowledge my gratitude to Dr Frederick M. Bayer for his pioneering works on the pleurotomariid fauna of the tropical western Atlantic and for generously sharing his notes and observations.

This is Smithsonian Marine Station at Fort Pierce Contribution Number 251.

REFERENCES

- Abbott, R. T. (1974). "American Seashells, Second Edition". Van Nostrand Reinhold Co., New York.
- Abbott, R. T. and Dance, S. P. (1982). "Compendium of Seashells". American Malacologists, Melbourne.
- Adams, H. and Adams, A. (1858). "The Genera of Recent Mollusca; Arranged According to their Organization, Volume 2". John Van Voorst, London.
- Anseeuw, P. (1999). *Petrotrochus indicus*: A new species of pleurotomariid from India. *Gloria Maris* **37**, 88–95.
- Anseeuw, P. and Goto, Y. (1996). "The Living Pleurotomariidae". Elle Scientific Publications, Osaka, Japan.
- Arakawa, K. Y. (1962). A coprological study on the molluscan faeces (a preliminary note). *Venus* **22**, 151–172, plates 9–11.
- Arakawa, Y., Nakano, D., Tsukuda, O. and Hoshino, T. (1978). On faecal pellets and food habits of emperor's slit shell, *Mikadotrochus hirasei* (Pilsbry). *Venus* **37**, 116–120.
- Azuma, M. (1964). Notes on the radula of *Petrotrochus africanus* (Tomlin, 1948). *Venus* **22**, 350–355.
- Barnard, K. H. (1963). Notes on the animals of *Gyrina gigantea* (Lam.) and *Pleurotomaria africana* Tomlin. *Proceedings of the Malacological Society of London* **35**, 155–158.
- Batten, R. L. (1958). Permian Gastropoda of the southwestern United States. 2. Pleurotomariacea: Portlockiellidae, Phymatopleuridae and Eotomariidae. *American Museum of Natural History Bulletin* **114**, 153–246.
- Batten, R. L. (1966). "The Lower Carboniferous Gastropod Fauna from the Hotwells Limestone of Compton Martin, Somerset". Palaeontographical Society, Monograph, London.
- Batten, R. L. (1972). The ultrastructure of five common Pennsylvanian pleurotomarian gastropod species of eastern United States. *American Museum Novitates* **2501**, 1–34.
- Bayer, F. M. (1965). New pleurotomariid gastropods from the western Atlantic, with a summary of Recent species. *Bulletin of Marine Science* **15**, 737–796.
- Benfrika el Mostafa (1984). "Systematique, Biogéographie et Écologie des Pleurotomariidés Post-paléozoïques". Thèse, Université de Paris, Centre d'Orsay.
- Bieler, R. (1992). Gastropod phylogeny and systematics. *Annual Review of Ecology and Systematics* **23**, 311–338.
- Blainville, H. M. de (1825–1827). "Manuel de Malacologie et de Conchyliologie, etc., Volumes 1 and 2". Paris and Strasbourg.
- Bøggild, O. B. (1930). The shell structure of the mollusks. *Det Kongelige Danske Videnskabernes Selskabs Skrifter, Naturvidenskabelige og Mathematisk Afdeling*, 9. Række, **2**, 231–326. plates 1–15.
- Boss, K. J. (1982). Mollusca. In "Synopsis and Classification of Living Organisms, Volume 2" (S. P. Parker, ed.), pp. 1092–1096. McGraw-Hill, New York.
- Bouchet, P. and Metivier, B. (1982). Living Pleurotomariidae (Mollusca: Gastropoda) from the South Pacific. *New Zealand Journal of Zoology* **9**, 309–318.
- Bouvier, E. L. and Fischer, H. (1898). Étude Monographique des Pleurotomaires Actuels. *Archives de Zoologie Expérimentale et Générale Series 3*, **6**, 115–180, plates 10–13; reprinted in (1899) *Bulletin of the Museum of Comparative Zoology*

- at Harvard College **32**, 193–246, plates 2–4, and (1899) *Journal de Conchyliologie* **47**, 77–151, plates 4–7.
- Bouvier, E. L. and Fischer, H. (1901). Sur l'organisation interne du *Pleurotomaria beyrichii* Hilg. *Comptes Rendus Academie des Sciences (Paris)* **132**, 845–847.
- Bouvier, E. L. and Fischer, H. (1902). L'organisation et les affinités des Gastéropodes primitifs d'après l'Étude anatomique du *Pleurotomaria beyrichii*. *Journal de Conchyliologie* **50**, 117–272, plates 2–6.
- Brusca, R. C. and Brusca, G. J. (1990). "Invertebrates". Sinauer Associates, Inc., Sunderland, Massachusetts.
- Cox, L. R. (1960a). The British Cretaceous Pleurotomariidae. *British Museum (Natural History) Geological Bulletin* **4**, 385–423.
- Cox, L. R. (1960b). Thoughts on the classification of the Gastropoda. *Proceedings of the Malacological Society of London* **33**, 239–261.
- Crosse, H. (1882). Les Pleurotomaires de l'Époque actuelle. *Journal de Conchyliologie* **30**, 5–22.
- Crosse, H. and Fischer, P. (1861). Observations sur le genre Pleurotomaire, et description d'une deuxième espèce vivante appartenant au même genre. *Journal de Conchyliologie* **9**, 155–167, plate 5, figs 1, 2.
- Dall, W. H. (1889). Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–1878) and in the Caribbean Sea (1879–1880), by the U.S. Coast Survey Steamer "Blake", Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., Commanding 29 – Report on the Mollusca. Part 2 – Gastropoda and Scaphopoda. *Bulletin of the Museum of Comparative Zoology at Harvard College* **18**, 1–492, plates 10–50.
- Defrance, M. J. L. (1826). Genus *Pleurotomaria*. In "Dictionnaire des Sciences Naturelles, dans Lequel on Traite Méthodiquement des Différens Êtres de la Nature, Considérés Soit en Eux-mêmes d'Après l'État Actuel de nos Connoissances, soit Relativement à l'Utilité qu'en Peuvent Retirer la Médecine, l'Agriculture, le Commerce et les Artes: Suivi d'une Biographie des plus Célèbres Naturalists, par Plusieurs Professeurs du Muséum National d'Histoire Naturelle et des Autres Principales de Écoles de Paris, Volume 41". (F. Cuvier, ed.) p. 381. Paris and Strasbourg.
- Endo, H. (1995). "Slit Shells: Pleurotomariidae". Endo Shell Museum, Manazuru.
- Erben, H. K. and Krampitz, G. (1972). Ultrastruktur und Aminosäuren-Verhältnisse in den Schalen der rezenten Pleurotomariidae (Gastropoda). *Biomínéralisation* **6**, 12–31.
- Férussac, A. É. J. P. F. d'A. de (1821–1822). "Tableaux Systématiques des Animaux Mollusques Classés en Familles Naturelles: Dans Lesquels on a Établi la Concordance de tous les Systèmes: Suivis d'un Prodrôme Général pour tous les Mollusques Terrestres ou Fluviatiles Vivants ou Fossiles". A. Bertrand, Paris.
- Fischer, P. (1887). "Manuel de Conchyliologie et de Paléontologie Conchyliologique ou Histoire Naturelle des Mollusques Vivants et Fossiles". Savy, Paris.
- Fischer, P. and Bernardi, A. C. (1856). Description d'un Pleurotomaire vivante. *Journal de Conchyliologie* **5**, 160–166, plate 5.
- Fretter, V. (1964). Observations on the anatomy of *Mikadotrochus amabilis* Bayer. *Bulletin of Marine Science* **14**, 172–184.
- Fretter, V. (1966). Biological investigations of the deep sea. 16. Observations on the anatomy of *Perotrochus*. *Bulletin of Marine Science* **16**, 603–614.
- Fretter, V. and Graham, A. (1962). "British Prosobranch Molluscs, their Functional Anatomy and Ecology". The Ray Society, London.

- Fretter, V. and Graham, A. (1976). The prosobranch molluscs of Britain and Denmark. Part 1 – Pleurotomariacea, Fissurellacea and Patellacea. *Journal of Molluscan Studies*, Supplement 1, iv + 37.
- Golikov, A. N. and Starobogatov, Y. I. (1975). Systematics of Prosobranch Gastropods. *Malacologia* 15, 185–232.
- Goodfriend, G., Kashgarian, M. and Harasewych, M. G. (1994). Use of aspartic acid racemisation and post-bomb ^{14}C to reconstruct growth rate and longevity of the deep-water slit shell *Entemnotrochus adansonianus*. *Geochimica et Cosmochimica Acta* 59, 1125–1129.
- Graham, A. (1985). Evolution within the Gastropoda: Prosobranchia. In “The Mollusca. Volume 10 – Evolution” (E. R. Trueman and M. R. Clarke, eds), pp. 151–186. Academic Press, Orlando.
- Harasewych, M. G. and Askew, T. M. (1993). *Petrotrochus maureri*, a new species of pleurotomariid from the western Atlantic (Gastropoda: Pleurotomariidae). *Nautilus* 106, 130–136.
- Harasewych, M. G., Pomponi, S. A. and Askew, T. M. (1988). Spongivory in pleurotomariid gastropods. *Nautilus* 102, 92–98.
- Harasewych, M. G., Adamkewicz, S. L., Blake, J. A., Saudek, D., Spriggs, T. and Bult, C. J. (1997). Phylogeny and relationships of pleurotomariid gastropods (Mollusca: Gastropoda): an assessment based on partial 18S rDNA and cytochrome *c* oxidase I sequences. *Molecular Marine Biology and Biotechnology* 6, 1–20.
- Haszprunar, G. (1987). The fine structure of the ctenidial sense organs (bursicles) of Vetigastropoda (Zeugobranchia, Trochoidea) and their phylogenetic significance. *Journal of Molluscan Studies* 53, 46–51.
- Haszprunar, G. (1988). On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. *Journal of Molluscan Studies* 54, 367–441.
- Haszprunar, G. (1989). New slit limpets (Scissurellacea and Fissurellacea) from hydrothermal vents. Part 2. Anatomy and relationships. *Los Angeles County Museum, Contributions to Science* 408, 1–17.
- Hayasaka, I. and Hayasaka, S. (1953). Fossil assemblages of molluscs and brachiopods of unusually large sizes from the Permian of Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, 10, 34–44.
- Healy, J. M. (1988). Ultrastructural observations on the spermatozoa of *Pleurotomaria africana* Tomlin (Gastropoda). *Journal of Molluscan Studies* 54, 309–316.
- Healy, J. M. and Harasewych, M. G. (1992). Spermatogenesis in *Petrotrochus quoyanus* ((Fischer and Bernardi) Gastropoda, Pleurotomariidae). *Nautilus* 106, 1–14.
- Hedegaard, C. (1990). “Shell Structures of the Recent Archaeogastropoda, Volumes 1 and 2”. Thesis for the Cand. Scient. Degree at the Department of Ecology and Genetics, University of Aarhus, Denmark.
- Hedegaard, C. (1997). Shell Structures of the Recent Vetigastropoda. *Journal of Molluscan Studies* 63, 369–377.
- Hickman, C. S. (1976). *Pleurotomaria* (Archeogastropoda) in the Eocene of the northeastern Pacific: a review of Cenozoic biogeography and ecology of the genus. *Journal of Paleontology* 50, 1090–1102.
- Hickman, C. S. (1981). Evolution and function of asymmetry in the archeogastropod radula. *The Veliger* 23, 189–194.
- Hickman, C. S. (1984a). Form and function of the radulae of pleurotomariid gastropods. *The Veliger* 27, 29–36.

- Hickman, C. S. (1984b). *Pleurotomaria*: Pedigreed Perseverance? In "Living Fossils" (N. Eldredge and S. M. Stanley, eds), pp. 225–231. Springer-Verlag, New York.
- Hickman, C. S. (1998). Superfamily Pleurotomarioidea. In "Mollusca: The Southern Synthesis. Fauna of Australia. Volume 5. Part B" (P. L. Beesley, G. J. B. Ross and A. Wells, eds), pp. 664–669. CSIRO Publishing, Melbourne.
- Hirayama, K. (1955). Discovery of *Perotrochus* in the Miocene deposits of Tochigi Prefecture, Japan. *Venus* **18**, 266–272.
- Hudleston, W. H. (1887–1896). "The British Jurassic Gasteropoda, Part 1. A Monograph of the Inferior Oolite Gasteropoda". Palaeontographical Society, Monograph, London.
- Hutsell, K. C., Hutsell, L. L. and Pisor, D. L. (1999). "Registry of World Record Size Shells". Snail's Pace Publications, San Diego.
- Hyman, L. H. (1967). "Mollusca I. Aplacophora, Polyplacophora, Monoplacophora, Gastropoda, The Coelomate Bilateria. The Invertebrates, Volume 6". McGraw-Hill Book Company, New York.
- Ingles, J. C. (1963). Geometry, paleontology and petrography of the Thornton reef complex, Silurian of northeastern Illinois. *American Association of Petroleum Geologists Bulletin* **47**, 405–440.
- International Commission on Zoological Nomenclature. (1960). Opinion 582. Validation of the generic name *Pleurotomaria* as from DeFrance 1826 (Class Gastropoda). *Bulletin of Zoological Nomenclature* **17**, 276–280.
- Jablonski, D., Sepkowski, J. J., Botjer, D. J. and Sheehan, P. M. (1983). Onshore-offshore patterns in the evolution of Phanerozoic shelf communities. *Science* **222**, 1123–1125.
- Jung, P. (1968). Fossil *Pleurotomaria* and *Haliotis* from Barbados and Carriacou, West Indies. *Ecologiae Geologicae Helveticae* **61**, 593–605.
- Jung, P. (1970). Fossil *Pleurotomaria* from Jamaica. *Caribbean Journal of Science* **10**, 83–86.
- Kanie, Y. and Oba, T. (1993). Oxygen and carbon isotopic measurements on the shell of *Mikadotrochus beyrichii* (Pleurotomariidae: Mollusca) from Sagami Bay, central Japan. *Proceedings of the Jamstec Symposium on Deep Sea Research* **9**, 233–236.
- Kanie, Y., Takahashi, T. and Mizuno, Y. (1980). Color patterns of Cretaceous pleurotomariid gastropods from Hokkaido. *Science Reports, Yokosuka City Museum* **27**, 37–42.
- Kanie, Y., Sugiura, A. and Egawa, K. (1986). Submarine observations on *Mikadotrochus beyrichii* (Archeogastropoda) in Sagami-Nada, Central Honshu, Japan. *Venus* **45**, 203–209.
- Kanie, Y., Hattori, M., Kuramochi, T. and Ikeda, H. (1995). Ecology and phylogenetic classification of the Pleurotomariidae (Gastropoda: Mollusca). *Jamstec Journal of Deep Sea Research* **11**, 279–284.
- Kanno, S. (1961). Miocene "*Pleurotomaria*" and its associated fauna from Tochigi Prefecture, Japan. *Japanese Journal of Geology and Geography* **32**, 111–118, plate 6.
- Kenkado, K. (1755). "Kikai Zufu". Rice paper scroll.
- Knight, J. B. (1952). Primitive fossil gastropods and their bearing on gastropod classification. *Smithsonian Miscellaneous Collections* **117**, 1–56.
- Knight, J. B., Cox, L. R., Keen, A. M., Batten, R. L., Yochelson, E. L. and Robertson, R. (1960). Gastropoda. Systematic Descriptions. In "Treatise of

- Invertebrate Paleontology. J – Mollusca 1:1169–1331” (R. C. Moore, ed.). University of Kansas Press, Lawrence.
- Koizumi, H. (1993). Generic comparison with *Perotrochus* and *Mikadotrochus* (Pleurotomariidae). *Chiribotan* **24**, 9–11.
- Kosuge, S. and Suzuki, M. (1969). *Entemnotrochus rumphii* (Schepman, 1879), newly collected from the South China Sea. *Venus* **28**, 155–158, plate 12.
- Kuramochi, T., Kanje, Y., Hattori, M. and Uematsu, K. (1996). Radula morphologies of the Pleurotomariidae Gastropoda from Japanese waters. *JAMSTEC Journal of Deep Sea Research* **12**, 197–215.
- Leme, J. L. M. and Penna, L. (1969). Ocorrência de *Mikadotrochus* no Brasil, com descrição de uma nova espécie (Gastropoda, Pleurotomariidae). *Papéis Avulsos de Zoologia, Sao Paulo* **22**, 225–230.
- Lima, G. M. and Lutz, R. A. (1990). The relationship of larval shell morphology to mode of development in marine prosobranch snails. *Journal of the Marine Biological Association of the United Kingdom* **70**, 611–639.
- Lister, M. (1678). “Historiæ animalium Angliæ tres tractus. Unus de Araneis. Alter de Cochleis tum terrestribus tum fluviatilibus. Tertius de cochlies marinis”. Royal Society, London.
- Mantell, G. (1822). “The fossils of the South Downs, or Illustrations of the Geology of Sussex”. H. G. Bohn, London.
- Matsumoto, Y. (1929). Radula description of *Pleurotomaria hirasei*. *Venus* **1**, 138–139.
- Matsumoto, Y., Kataoka, T. and Sekido, M. (1972). On the behavior of Beyrich’s slit shell, *Mikadotrochus beyrichii* (Hilgendorf) kept in the aquarium. *Venus* **30**, 147–152.
- Mitsukuri, K. (1897). A living specimen of *Pleurotomaria beyrichii*. *Annotationes Zoologicae Japonenses* **1**, 67–68.
- Morton, J. E. and Yonge, C. M. (1964). Classification and Structure of the Mollusca. In “Physiology of Mollusca, Volume 1” (K. M. Wilbur and C. M. Yonge, eds), pp. 1–58. Academic Press, New York.
- Okutani, T. (1963). Preliminary notes on molluscan assemblages of the submarine banks around the Izu Islands. *Pacific Science* **17**, 73–89.
- Okutani, T. and Hasegawa, K. (2000). Superfamily Pleurotomarioidea. In “Marine Mollusks in Japan” (T. Okutani, ed.), pp. 37–44. Tokai University Press, Tokyo.
- Oyama, K. (1980). A collection of the third *Entemnotrochus rumphii* Schepman from Taiwan. *Bulletin of Malacology, Republic of China* **7**, 131–133.
- Pilsbry, H. A. (1890). Family Pleurotomariidae. *Manual of Conchology* **12**, 69–72, plates 56–57.
- Ponder, W. F. and Lindberg, D. R. (1996). Gastropod phylogeny – challenges for the 90s. In “Origin and Evolutionary Radiation of the Mollusca” (J. Taylor, ed.), pp. 135–154. Oxford University Press, Oxford.
- Ponder, W. F. and Lindberg, D. R. (1997). Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society* **119**, 83–265.
- Preston, S. J., Roberts, D. and Montgomery, W. I. (1993). Shell scarring in *Calliostoma ziziphynum* (Prosobranchia: Trochidae) from Stangford Lough, Northern Ireland. *Journal of Molluscan Studies* **59**, 211–222.
- Pulteney, R. (1813). Catalogues of the birds, shells and some of the more rare plants of Dorsetshire. In “History and Antiquities of the County of Dorset, Volume 3” (J. Hutchins, ed.), pp. 1–110, plates 1–24. Nichols, Son, and Bentley, London.

- Rex, M. A. (1977). Zonation in deep-sea gastropods: the importance of biological interactions to rates of zonation. In "Biology of Benthic Organisms" (B. F. Keegan, P. O. Ceidigh and P. J. S. Boaden, eds), pp. 521–530. Pergamon Press, New York.
- Rohr, D. M. and Blodgett, R. B. (1985). Upper Ordovician Gastropoda from west-central Alaska. *Journal of Paleontology* **59**, 667–673.
- Rohr, D. M. and Smith, R. E. (1978). Lower Devonian Gastropoda from the Canadian Arctic Islands. *Canadian Journal of Earth Sciences* **15**, 1228–1241.
- Rosenberg, G., Kuncio, R. S., Davis, G. M. and Harasewych, M. G. (1994). Preliminary ribosomal RNA phylogeny of gastropod and unionoid bivalve mollusks. *Nautilus, Supplement* **2**, 111–121.
- Rupert, E. E. and Barnes, R. D. (1994). "Invertebrate Zoology, 6th edition". Saunders College Publishing, New York.
- Sasaki, T. (1998). Comparative anatomy and phylogeny of the Recent Archaeogastropoda (Mollusca: Gastropoda). *Bulletin of the University Museum, University of Tokyo* **38**, 1–224.
- Salvini-Plawen, L. v. (1980). A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia* **19**, 249–278.
- Salvini-Plawen, L. v. and Haszprunar, G. (1987). The Vetigastropoda and the systematics of streptoneurous Gastropoda (Mollusca). *Journal of Zoology, London* **211**, 747–770.
- Schindel, D. E., Vermeij, G. J. and Zipser, E. (1982). Frequencies of repaired shell fractures among the Pennsylvanian gastropods of north-central Texas. *Journal of Paleontology* **56**, 729–740.
- Sekido, M., Tsukada, O., Matsumoto, Y. and Kataoka, T. (1976). On the keeping of Teramachi's Slit Shell, *Perotrochus teramachii*. *Journal of the Japanese Association of Zoological Gardens and Aquariums* **18**, 49–52.
- Shikama, T. and Nishida, T. (1968). On some species of Carboniferous pleurotomariaceans from Akioshi (Molluscan paleontology of the Akiyoshi limestone group, III). *Transactions and Proceedings of the Paleontological Society of Japan (New Series)* **69**, 211–217.
- Shileyko, A. A. (1977). The symmetry of the Docoglossa and the problem of the origin of the order. *Bulletin of the Moscow Naturalists Society, Biology Series* **81**, 60–65.
- Shuto, T. (1974). Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. *Lethaia* **7**, 239–256.
- Sowerby, J. (1812–1846). "The Mineral Conchology of Great Britain". Sowerby, London.
- Sowerby, J. de C. (1832). *Pleurotomaria*. In Sowerby, G. B. (1822–1840). "The Genera of Recent and Fossil Shells, for the Use of Students of Conchology and Geology" (G. B. Sowerby, ed.). Sowerby, London.
- Swainson, W. (1840). "A Treatise on Malacology: or the Natural Classification of Shells and Shell Fish". John Taylor, London.
- Szabó, J. (1980). Lower and Middle Jurassic gastropods from the Bakony Mountains (Hungary). Part 2. Pleurotomariacea and Fissurellacea. *Annales Historico-Naturales Musei Nationalis Hungarici* **72**, 49–71.
- Tan, T. H. (1974). A preliminary study on the anatomy of *Pleurotomaria (Entemnotrochus) rumphii* Schepman. *Bulletin of the Malacological Society of China* **1**, 15–20.
- Taylor, D. W. and Sohl, N. F. (1962). An outline of gastropod classification. *Malacologia* **1**, 7–32.

- Termier, H. and Termier, G. (1968). "Évolution et Biocinèse. Les Invertébrés dans l'histoire du Monde vivant". Masson and Cie, Paris.
- Thiele, J. (1902). Die systematische Stellung der Solenogastren und die Phylogenie der Mollusken. *Zeitschrift für wissenschaftliche Zoologie* **72**, 249–266, plates 18–27.
- Thiele, J. (1929–1935). "Handbuch der Systematischen Weichtierkunde". Gustav Fischer, Jena.
- Thomas, E. G. (1940). Revision of the Scottish Carboniferous Pleurotomariidae. *Transactions of the Geological Society of Glasgow* **20**, 30–72.
- Tillier, S., Masselot, M., Philippe, H. and Tillier, A. (1992). Phylogénie moléculaire des Gastropoda (Mollusca) fondée sur le séquençage partiel de l'ARN ribosomique 28 S. *Comptes Rendus de l'Académie des Sciences (Paris)* **314** (Ser. 3), 79–85.
- Tillier, S., Masselot, M., Guerdoux, J. and Tillier, A. (1994). Monophyly of major gastropod taxa tested from partial 28S rRNA sequences, with emphasis on Euthyneura and hot-vent limpets Peltospiroidea. *Nautilus, Supplement* **2**, 122–140.
- Tomida, S., Teraoka, A., Okumura, Y. and Karazawa, H. (1999). A fossil pleurotomariid gastropod from the Miocene Bihoku Group in southwestern Japan and its paleontological significance. *Bulletin of the Mizunami Fossil Museum* **26**, 115–119.
- Tracey, S., Todd, J. A. and Erwin, D. H. (1993). Mollusca: Gastropoda. In "The Fossil Record 2". (M. J. Benton, ed.), pp. 137–167. Chapman and Hall, London.
- Troschel, F. H. (1891). "Das Gebiss der Schnecken zur Begründung einer Natürlichen Classification. Volume 2, Part 7", pp. 251–334, plates 25–28. Nicolaische Verlags, Berlin.
- Vale, F. K. and Rex, M. A. (1989). Repaired shell damage in a complex of rissoid gastropods from the upper continental slope south of New England. *Nautilus* **103**, 105–108.
- Vaught, K. C. (1989). "A Classification of Living Mollusca". American Malacologists, Melbourne.
- Vermeij, G. J. (1977). The Mesozoic marine revolution: evidence from snails, predation and grazers. *Paleobiology* **3**, 245–258.
- Vermeij, G. J. (1982). Gastropod shell form, breakage, and repair in relation to predation by the crab *Calappa*. *Malacologia* **23**, 1–12.
- Vermeij, G. J. (1989). Interoceanic differences in adaptation: effects of history and productivity. *Marine Ecology Progress Series* **57**, 293–305.
- Wenz, W. (1938). Gastropoda. Allgemeiner Teil und Prosobranchia. In "Handbuch der Paläozoologie" (O. H. Schindewolf, ed.), pp. 1–948. Gebrüder Borntraeger, Berlin.
- Wenz, W. (1940). Ursprung und frühe Stamm Geschichte der Gastropoden. *Archiv für Molluskenkunde* **72**, 1–10.
- Wolfenden, E. B. (1958). Paleoecology of the Carboniferous reef complex and shelf limestones in northwestern Derbyshire, England. *Bulletin of the Geological Society of America* **69**, 871–898.
- Woodward, H. (1885). On Recent and fossil Pleurotomariae. *Geological Magazine*, Decade 3 **2**, 433–439, plate 11.
- Woodward, M. F. (1901). The anatomy of *Pleurotomaria beyrichii*, Hilg. *The Quarterly Journal of the Microscopical Society* **44**, 215–268, plates 13–16.
- Yonge, C. M. (1947). The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Philosophical Transactions of the Royal Society, London. B* **232**, 443–518.

- Yonge, C. M. (1973). Observation of the pleurotomariid *Entemnotrochus adansoniana* in its natural habitat. *Nature* **241**, 66–68.
- Yonge, C. M. and Thompson, T. E. (1976). "Living Marine Mollusks". William Collins Sons and Co., Ltd, London.
- Zežina, O. N. (1997). Biogeography of the Bathyal Zone. *Advances in Marine Biology* **32**, 389–420.
- Ziegler, V. (1984). Family Pleurotomariidae Swainson 1840 (Gastropoda, Archeogastropoda) from the Bohemian Cretaceous Basin. *Sbornik Narodního Muzea v Praze Rada b Přírodní Vedy* **39**, 255–291.