

# The genera and biogeography of Fasciolariinae (Gastropoda, Neogastropoda, Fasciolariidae)

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The classification of Fasciolariinae, a group of large predatory fascioliid neogastropods, is revised at the generic level. Type selections for all genera are made, and all types are illustrated. On the basis of shell characters of most fossil and all living species, we recognize fourteen genera: *Africolaria* gen. nov. (type species: *Fasciolaria rutila* Watson, 1882), Recent, Agulhas Bank, South Africa; *Aurantilaria* gen. nov. (type species: *Fasciolaria aurantiaca* Lamarck, 1816), Early Miocene to Recent, western Atlantic and Europe; *Australaria* gen. nov. (type species: *Pyrula australasia* Perry, 1811), Middle Miocene to Recent, southern and eastern Australia; *Cinctura* Hollister, 1957 (type species: *Pyrula hunteria* Perry, 1811), Pliocene to Recent, eastern North America; *Fasciolaria* Lamarck, 1799 (type species: *Murex tulipa* Linnaeus, 1758), Early Pliocene to Recent, western Atlantic; *Filifusus* gen. nov. (type species: *Fusus filamentosus* Röding, 1798), Recent, Indo-West Pacific; *Granolaria* gen. nov. (type species: *Murex salmo* Wood, 1828), Early Miocene to Recent, tropical America; *Kilburnia* gen. nov. (type species: *Fasciolaria heynemanni* Dunker,

1870), Recent, South Africa; *Liochlamys* Dall, 1889 (type species: *Mazzalina bulbosa* Heilprin, 1886), Early Pleistocene, Florida; *Lugubrilaria* gen. nov. (type species: *Fasciolaria lugubris* A. Adams & Reeve in Reeve, 1847), Pleistocene and Recent, South Africa and Namibia; *Pleuropoca* Fischer, 1884 (type species: *Murex trapezium* Linnaeus, 1758), Late Miocene to Recent, Indo-West Pacific; *Pliculofusus* gen. nov. (type species: *Fasciolaria scalarina* Heilprin, 1886), Early Miocene to Pleistocene, southern and eastern United States (containing species formerly included in *Terebraspira*); *Terebraspira* Conrad, 1862 (type and only species: *Fasciolaria elegans* Emmons, 1858), Early Pliocene, eastern North America; and *Triplofus* Olsson & Harbison, 1953 (type species: *Fasciolaria gigantea* Kiener, 1840), Pliocene to Recent, western Atlantic and eastern Pacific. We also describe *Australaria tenuitesta* spec. nov.

Unusual features that have evolved in the Fasciolariinae include an enveloped shell (*Liochlamys*), small folds on the inner side of the siphonal canal (*Pleuropoca*, *Pliculofusus*,

*Terebraspira*), beaded or discontinuous ridges on the inner side of the outer lip (some *Aurantilaria*, *Filifusus*, *Pliculofusus*, *Terebraspira*), and a corrugated operculum (*Aurantilaria*, some *Triplofusus*).

Several taxa associated in the past with *Fasciolaria* or Fascioliariinae are reassigned to other major groups. Besides *Pleia* Finlay, 1930, which Beu (2011) reassigned to Peristerniinae in Fascioliariidae, these taxa include: *Fusus buxeus* Reeve, 1847 (type species of *Viridifusus* gen. nov. Recent, Cape Verde Archipelago); *Neolatirus* Bellardi, 1884 (type species: *Fasciolaria recticauda* Fuchs, 1877), Middle to Late

Miocene, Europe; *Tarantinaea* Monterosato, 1917 (type species: *Murex lignarius* Linnaeus, 1758), Miocene to Recent, Europe; and *Saginafusus* Wenz, 1943 (type species: *Fusus pricei* E. A. Smith, 1887), northern Australia and Indonesia. *Viridifusus* is assigned to Fusiniinae (Fascioliariidae); *Tarantinaea* and *Neolatirus* are assigned to Peristerniinae; and *Saginafusus* is assigned to Melongenidae.

Key words: Fascioliariidae, Fascioliariinae, Gastropoda, Miocene, Pliocene, Recent, shell morphology, classification, biogeography.

## INTRODUCTION

The fascioliariid gastropod subfamily Fascioliariinae is a small, morphologically compact group of large to gigantic buccinoidean neogastropods. Despite their large, showy shells, many of which were well known to early European naturalists, the group remains taxonomically and ecologically poorly known. This surprising ignorance is common among large-bodied molluscs generally, including many genera within Turbinidae, Turbinellidae, and Melongenidae, among others.

Our purpose in this paper is to outline genus-level classification and biogeographic relationships of the Fascioliariinae based on our examination of shell characters of the living species and of many fossil taxa. Eight new generic names are introduced (*Africolaria*, *Aurantilaria*, *Australaria*, *Filifusus*, *Granolaria*, *Kilburnia*, *Lugubrilaria*, *Pliculofusus*) and a new species is described (*Australaria tenuitesta*). We have chosen to name these groups at the genus level rather than at the level of species group as a taxonomic hypothesis to be tested later with molecular data. The genera are distinguished from each other by combinations of characters rather than by single traits.

Nearly every character used in combination to discriminate among genera varies in expression among species and even among populations. For example, although *Pleuroploca*, *Aurantilaria*, and *Australaria* may all have multiple rows of nodes on the last whorl, there are species and populations in each genus in which nodes are either entirely absent or

confined to a single row at the shoulder angulation. In *Australaria*, sculptural simplification and the tendency to lose lirae (internal ridges) particularly characterize species that occur in cool-temperate waters, such as Victorian and South Australian populations of *A. australasia*. A keel-like entrance fold to the siphonal canal characterizes many (but not all) species of *Australaria* as well as species of *Filifusus*. The entrance fold never develops into a keel-like feature in *Pleuroploca* and *Aurantilaria*, even in species with a full complement of spiral rows of nodes. Our diagnoses therefore reflect maximal expressions of characters.

Type species are identified for all genera and type-specimens are located or designated for each type species; all are illustrated. We also exclude several genera and species usually assigned to Fascioliariinae and suggest placement in other groups. An additional new generic name (*Viridifusus*) is introduced to accommodate some of those species. We do not comment on the taxonomic status of many of the species names at this time. We are aware that some names listed in our “included species” lists have been synonymized by others, but feel that the status of these taxa should be re-examined in light of our generic conclusions. We note that modern genetic work has tended to support the work of “splitters” as opposed to “lumpers” with respect to various other examined genera.

Abbreviations: AMS, Australian Museum, Sydney South, NSW, Australia; ANSP, Academy of Natural Sciences, Philadelphia, PA, USA; BMSM, Bailey-Matthews Shell Museum, Sanibel, FL, USA; CAS, Cali-

ifornia Academy of Sciences, San Francisco, CA, USA; ICZN, International Commission of Zoological Nomenclature; IWP, Indo-west Pacific; MHNG, Muséum d'Histoire Naturelle Genève, Geneva, Switzerland; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHMUK, The Natural History Museum of the United Kingdom, London, England; NSMT, National Museum of Nature and Science, Tokyo, Japan; PRI, Paleontological Research Institute, Ithaca, New York; SBMNH, Santa Barbara Museum of Natural History, Santa Barbara, CA, USA; SL, Shell length; USNM, National Museum of Natural History, Smithsonian Institution, WashingtonDC, USA; TU, Tulane University (prefix for paleontological localities and associated collections; specimens now at UF); UF, Florida Museum of Natural History, Gainesville, FL, USA; WFIS, Wagner Free Institute of Science, Philadelphia, PA, USA; WGL, Collection of William G. Lyons, St. Petersburg, FL, USA.

#### SYSTEMATIC PART

Subfamily Fasciolarinae Gray, 1853

Description. — Shell fusiform, medium-sized to extremely large; outer lip usually medially convex, without adapical sinus; outer-lip edge usually with paired crenulations; inner lip adherent, abapically bearing two columellar folds and a more prominent fold at entrance of siphonal canal; adaxial margin of siphonal canal often erect; siphonal process parallel to axis of coiling.

Remarks. — The Fasciolarinae are morphologically similar to the fasciolariid subfamily Peristerniinae Tryon, 1880. Both groups are characterized by the presence of abapical columellar folds, an entrance fold to the siphonal canal situated immediately anterior to the columellar folds, and a (usually) crenulated, simple outer lip that is usually lirate on its inner (adaxial) side. These lirae are present in fully formed shells. However, mature individuals in *Triplofus* Olsson & Harbison, 1953, are often smooth on the inner side of the outer lip, and all *Africolaria* lack such lirae. Internal lirae are created late in the shell depositional process, and a shell with an apparently complete lip (as evidenced by a relatively thick edge) may not yet have deposited its full complement of lirae. Nevertheless, the Fasciolarinae are relatively homogeneous in shell features. All Fasciolarinae have an adherent inner lip that merges imperceptibly into

the shell exterior. The outer lip lacks an adapical sinus in all genera except some members of *Australaria*, a feature present in all Peristerniinae except some species of *Hemipolygona* Rovereto, 1899 (see Vermeij & Snyder, 2006). No fasciolarine has developed denticles on the inner side of the outer lip, features that are well-developed in several peristerniine genera including *Peristernia* Mörch 1852, *Turrilatirus* Vermeij & Snyder, 2006, and *Latirus* Montfort, 1810, among others. The siphonal process of Fasciolarinae is always parallel to the axis of coiling, not deviated either dorsally or to the side as in some Peristerniinae. Although the Fasciolarinae and most Peristerniinae are characterized by the presence of abapical columellar folds, there are important differences in the magnitude and orientation of the folds. The folds in Fasciolarinae are elongate and very oblique and this character unites the species of the subfamily.

Besides the extremely large size of several fasciolarines, especially in *Triplofus*, but also in *Fasciolaria* Lamarck, 1799, *Pleuroploca* P. Fischer, 1884 and the extinct new genus *Pliculofusus* (*Terebraspira* auctt., non Conrad, 1862), the Fasciolarinae have evolved three character states that are otherwise unknown in the Fasciolaridae. These are (1) an externally glazed shell (in the extinct genus *Liochlamys* Dall, 1889), indicating envelopment by the mantle or foot; (2) the extreme development of the entrance fold to the siphonal canal into a keel-like feature, as seen in the genera *Australaria* and *Filifusus*; and (3) the presence of distinct folds along the adaxial margin of the siphonal canal abapical to the entrance fold, as seen in adults of *Pleuroploca*, *Pliculofusus* and *Terebraspira*.

For genera that typically contain species with nodular axial ribs, our descriptions may only mention that condition. However, most species that typically have shells with nodular axial ribs also occur, not uncommonly, in anodose forms. Individuals or even local populations with anodose shells occur among species of *Triplofus*, *Pleuroploca*, *Filifusus*, *Granolaria*, *Aurantilaria*, and *Australaria*, and several of these anodose forms have received separate names. Smooth forms of species with normally nodose shells may result from ecophenotypy (*Aurantilaria aurantiaca*), local geographic isolation (*Filifusus filamentosus altimastus*), regional variation (*Pleuroploca trapezium audouini*; *P. t. lischkeana*) or for reasons

not yet understood (*Triplofusus giganteus reevei*; *Granolaria valenciennesii*; *Pleuroploca t. trapezium*; *Australaria australasia coronata*; *Lugubrilaria lugubris*). And of course some genera have species with typically nodose shells and others with typically smooth (anodose) shells. If the type species has nodose shells, the other conditions may not be mentioned.

Taxonomically, most members of the Fasciolarinae have been assigned to two genera: *Fasciolaria* and *Pleuroploca*, though some American species have been placed in *Triplofusus* and the extinct *Terebraspira* and *Liochlamys*. These genera have not been critically compared or carefully defined, and in the case of *Fasciolaria* and *Pleuroploca* as conventionally used, they are heterogeneous, comprising several distinct clusters that we prefer to treat as separate genera. We believe the proposal of formal generic names for these clusters will facilitate future molecular and phylogenetic studies of this surprisingly overlooked group of gastropods.

*Fasciolaria* Lamarck, 1799

Type species: *Murex tulipa* Linnaeus, 1758, by monotypy.

Lectotype: specimen figured by d'Argenville, 1842: pl. 13 fig. K, selected herein (Fig. 1).

Description. — Shell large (2 largest living species to 275 and 278 mm SL), broadly fusiform, usually rather thin; protoconch with distinct or faint axial riblets on final whorl; teleoconch sculpture usually predominantly of low to obsolete spiral cords which are strongest on the basal constriction and sutural ramp and may be absent on the central sector of the body whorl (however, some shells with rugose cords over entire teleoconch); axial sculpture, when present, consisting of weak rounded ribs on early teleoconch whorls; shell surface ornamented with many intact or interrupted spiral bands; outer lip medially convex, its edge often with strong, sometimes paired crenulations representing termini of spiral bands, its inner side with fine smooth lirae; shallow notch or simple flexure, caused by flexure in sutural ramp, present near junction of outer lip and penultimate whorl; parietal ridge at adapical end of aperture absent; entrance fold more prominent than columellar folds, rounded; no folds abapical to entrance fold. Radula of type species described and figured by Troschel (1868: 62, pl. 5 fig. 12), Wells

(1970: 99, 100, text fig. 5) and Bandel (1984: 144, text fig. 260, pl. 17 figs 9, 10).

Included species:

- Fasciolaria bullisi* Lyons, 1972: Recent, off western Florida and Yucatán Platform, Mexico;  
*Fasciolaria calusa* Petuch, 1994: Early Pleistocene (Caloosahatchee Formation), Florida;  
*Fasciolaria hollisteri* Weisbord, 1962: Pleistocene to Recent, western Venezuela, Caribbean Colombia, and Aruba;  
*Fasciolaria (distantis var.) monocingulata* Dall, 1890: Early Pleistocene (Caloosahatchee Formation), Florida;  
*Fasciolaria okeechobeensis* Tucker & Wilson, 1932: Middle Pleistocene (Bermont Formation), Florida;  
*Fasciolaria seminole* Petuch, 1994: Early Pleistocene (Caloosahatchee Formation), Florida;  
*Fasciolaria semistriata* G. B. Sowerby I, 1850: Early Pliocene (Gurabo Formation), Dominican Republic;  
*Fasciolaria semistriata leura* Woodring, 1928: Plio-Pleistocene (Bowden Formation), Jamaica;  
*Fasciolaria semistriata mareana* Weisbord, 1962: Plio-Pleistocene (Lower Mare Formation), Venezuela;  
*Fasciolaria tephрина* de Souza, 2002: Recent, off Honduras, Nicaragua and northern Colombian islands, western Caribbean;  
*Murex tulipa* Linnaeus, 1758: Late Pleistocene to Recent, North Carolina to Florida, the Gulf of Mexico and Caribbean Sea to Suriname and Maranhão, and Amapá, Brazil.

Remarks. — Of three specimens of *Murex tulipa* in the collection of the Linnean Society, Burlington House, London, one is marked “489” (the number given the species by Linnaeus in his 10<sup>th</sup> edition), a specimen probably in Linnaeus’ hands when he described the species, but, as S.P. Dance indicated in a note that accompanies the material “that shell is in a ‘shocking state’; the spire is broken, the siphon is chipped, and the body whorl is riddled with worm holes”. Another is marked “562” (the corresponding species number in the 12<sup>th</sup> edition) and one is unmarked. The unnumbered specimen is immature and also shows considerable wear, perhaps from use by hermit crabs. Preference as a lectotype might go to the shell marked “489”. Linnaeus (1758) cited for *Murex tulipa* figures by Buonanni (1684: fig. 187), Rumphius (1705:

pl. 49 fig. H), Gualtieri (1742: pl. 46 fig. A), Dezallier d'Argenville (1742: pl. 13 fig. K) and Regenfuss (1758: pl. 9 fig. 35). Of these, the figure by d'Argenville is least stylized and truest to the form of the adult shell, and we select it, rather than the decrepit specimen "489", as lectotype of *Murex tulipa*. In the 1757 second edition figure K appears on plate 10.

As restricted here, *Fasciolaria* is a western Atlantic genus with rather thin shells in which the sculpture is reduced relative to that of most other Fascioliinae. An exception involves the *scheepmakeri* (Kobelt, 1875) form of *F. tulipa*, a Recent shell that is heavier than the typical form and whose entire surface is covered with strong cords; similar heavily sculpted shells sometimes occur among specimens of *F. okeechobeensis*. There is variation in the extent and strength of spiral sculpture, with *F. tulipa* and *F. hollisteri* having subsutural cords that are lacking in other living species. *Fasciolaria bullisi* and *F. tephрина* are retained in *Fasciolaria* rather than *Cinctura* because: 1) their shells lack any indication of a parietal ridge; 2) they exhibit flexure in their sutural ramps, albeit slight, that creates a slight angle and interrupts the curvature of the outer lip; 3) their spiral bands are numerous and often interrupted, and 4) their shells are thinner and lighter in weight than those of *Cinctura* of comparable size.

Placement of the Early Pleistocene *Fasciolaria monocingulata* is problematic. Dall (1890) introduced the taxon as a subspecies of *F. distans* (now = *Cinctura lilium*) and placement in *Cinctura* is supported by its possession of an emergent parietal ridge. However, the shell also has a channeled sutural ramp, which creates a distinct inflection in the sutural ramp and outer lip, a feature characteristic of *Fasciolaria*. We have examined two specimens of *Fasciolaria tulipa* with well-developed parietal ridges, among more than 600 specimens that lack that feature, suggesting that the ridge may be related to a gene usually recessive in the *Fasciolaria* lineage but which may have been overtly expressed in *F. monocingulata*.

We have not attempted to evaluate each of the species-level taxa assigned to *Fasciolaria*. This applies in particular to the several taxa of Pliocene and Early to Middle Pleistocene fossils. Given the paucispiral protoconchs (and implicitly nonplanktonic dispersal) of the living species, it is possible

that many of the fossil taxa are valid, and that additional Recent species may be recognized with molecular sequencing.

The earliest species of *Fasciolaria* that we are able to verify is *F. semistriata*, which according to B. M. Landau (personal communication to GJV, 16 November, 2009) is from the basal Gurabo Formation (early Pliocene) of the Dominican Republic. This late origin of the genus likely accounts for the absence of *Fasciolaria* in the eastern Pacific, because the Central American seaway connecting the Atlantic with the Pacific was already substantially constricted by that time. Very similar to but much younger than *F. semistriata* is *F. semistriata leura*, from the Plio-Pleistocene Bowden Beds of Jamaica. Concurrent with *leura*, *F. semistriata mareana* and *F. hollisteri* appeared in the Plio-Pleistocene Lower Mare Formation of Venezuela, followed by *F. calusa*, *F. okeechobeensis*, *F. seminole*, and *F. tulipa* in the Early to Late Pleistocene of Florida. Although *F. tulipa* now ranges northward to North Carolina, all fossil records of *Fasciolaria* from the Carolinas and Virginia are of species now classified in *Cinctura*, *Pliculofusus*, *Triplofusus* or *Terebraspira*. Likewise, a species reported as *Fasciolaria semistriata* from Miocene beds of Mexico (Perrilliat Montoya, 1960: 22, 23, pl. 3 figs 12-15) and later assigned to the middle Miocene Agueguexquite Formation (Perrilliat, 1981: 64) is not *F. semistriata* and appears to be a species of *Cinctura*. See more on this record in Remarks for *Cinctura*. Although several of the Recent species (e.g., *F. bullisi*, *F. hollisteri* and *F. tephрина*) have rather limited distributions, the range of *F. tulipa* (Amapá, Brazil to North Carolina) is among the greatest of any western Atlantic fascioliid, being exceeded only by that of the peristerniine *Leucozonia nassa* (Gmelin, 1791), which ranges from North Carolina to oceanic islands off central Brazil and formerly extended to Bermuda (Lyons & Snyder, 2008). *Fasciolaria tulipa* has also been recorded at virtually every Caribbean island, regardless of the depths of surrounding waters, altogether a remarkable feat of dispersal for a species with demersal development.

#### *Cinctura* Hollister, 1957

Type species: *Pyrgula hunteria* Perry, 1811, by original designation.

Neotype: USNM 615769, 86.5 mm SL, Recent, Charleston, South Carolina, selected herein (Fig. 3).

Description. — Shell of small to moderate size (2 largest living species to 131 and 140 mm SL), broadly fusiform, slender to relatively globose, solid; protoconch with or without axial riblets on final whorl; teleoconch surface generally smooth except for occasional faint spiral incisions and very low axial ribs on first 1-3 whorls and transverse spiral cords on base and siphonal process; distinct, uninterrupted spiral bands, usually black, on all whorls, bands on body whorl varying in number from 4 to as many as 14, depending on species; outer lip medially convex, its edge sometimes bearing thickened nodes representing termini of spiral bands, its inner side with fine smooth lirae; adapical flexure absent in outer lip; parietal ridge at adapical end of aperture absent in earliest (early to mid-Pliocene) material, present and often prominent in all late-Pliocene to Recent species; entrance fold more prominent than columellar folds, rounded; no folds abapical to entrance fold. Radula of type species described and figured by Hackney (1945: 46, 48, pl. 1 figs 5, 6, as *F. distans* auctt., non Lamarck, 1822) and Wells (1970: 99, 100, text fig. 5).

Included species:

- Fasciolaria apicina* Dall, 1890: Early Pleistocene (Caloosahatchee Formation), Florida;
- Fasciolaria beaufortensis* Ward & Blackwelder, 1987: Early Pleistocene (James City Formation), North Carolina and Virginia;
- Fasciolaria distans branhamae* Rehder & Abbott, 1951: Recent, southern Texas and Bay of Campeche, Mexico;
- Fasciolaria (Cinctura) capeletti* Petuch, 1994: Middle Pleistocene (Bermont Formation), Florida;
- Fasciolaria (Cinctura) evergladesensis* Petuch, 1991: Middle Pleistocene (Bermont Formation), Florida;
- Fasciolaria (Cinctura) holeylandica* Petuch, 1994: Middle Pleistocene (lower Bermont Formation), Florida;
- Pyrula hunteria* Perry, 1811: Late Pleistocene (Ft. Thompson Formation) to Recent, North Carolina to Florida, Alabama, Mississippi and eastern Louisiana
- Fasciolaria liliium* Fischer von Waldheim, 1807: Recent, Cancun, Mexico to southeastern Texas;
- Fasciolaria (Cinctura) lindae* Petuch, 1994: Early Pleistocene (Caloosahatchee Formation), Florida;
- Fasciolaria rhomboidea* W. B. Rogers & H. D. Rogers, 1839: Early and Mid-

dle Pliocene (Yorktown, Jackson Bluff and Tamiami Formations), Virginia, North Carolina, South Carolina and Florida;

*Fasciolaria (Cinctura) rucksorum* Petuch, 1994: Early Pleistocene (Nashua Formation), Florida;

*Fasciolaria (Cinctura) sarasotaensis* Petuch, 1994: Late Pliocene (Upper Pinecrest beds, Tamiami Formation), Florida;

*Fasciolaria (Cinctura) liliium tortugana* Hollister, 1957: Recent, North Carolina to Florida, Alabama, Mississippi and eastern Louisiana.

Remarks. — Hollister (1957) differentiated *Cinctura* as a subgenus of *Fasciolaria*, principally on the basis of a prominent parietal ridge that emerges from within the aperture of the shell. Species he assigned to *Cinctura* also lack the inflected sutural ramp, sometimes with subsutural spiral cords, the resultant flexure on the outer lip, and often-interrupted spiral bands of *Fasciolaria* species and have spiral sculpture confined to the concave base of the body whorl and the siphonal process. We here elevate *Cinctura* to genus-level rank as a clade distinguished from *Fasciolaria* by a suite of characters equivalent to those of many similar taxa recognized at genus level in other families (e.g., Cypraeidae, Muricidae, Conidae).

The blue-gray color and relatively globose form of the shell depicted by Perry (1811) for *Pyrula hunteria* (Fig. 2) are features most often found in estuarine *Cinctura* populations of the southeastern United States east of the Mississippi River, but shells of similar color and shape also occur uncommonly in some Mexican populations. Features that distinguish the Atlantic and eastern Gulf *Cinctura hunteria* from the western Gulf *C. liliium* are numbers of primary spiral bands on the body whorl (4-7 on *C. hunteria*, 7-11 on *C. liliium*) and absence (*C. hunteria*) or presence (*C. liliium*) of distinct riblets on the protoconch. Perry's figured shell has 7 primary bands, its protoconch is too small for inspection, and its type is not known to be extant (Petit, 2003: 17), so its status as an "eastern" or "western" shell is ambiguous. Because of this ambiguity we have elected not to designate a lectotype based upon this illustration.

In what was then a controversial action (see Burch, 1957: 9; Petit, 2003: 15), Hollister (1957) invoked the law of priority to replace the universally recognized *Fasciolaria distans* Lamarck, 1822, with *F. liliium* Fischer von Waldheim, 1807

(called the Campeche form by Hollister) for western Gulf banded tulips and *Pyrula hunteria* Perry, 1811 (called the Florida form) for eastern populations. Hollister also designated the latter as type species of his new genus-level taxon *Cinctura*. Presuming that Perry's type of *hunteria* was lost and recognizing the need for nomenclatural stability, Hollister (1957: 75, 83) tried to clarify and fix the identity of his type species by designating two specimens collected by Edmund Ravenel near Charleston, South Carolina (USNM 615769) as neosyntypes of *Pyrula hunteria* thereby fixing Perry's name to the eastern form. A reasonable reading of Hollister's rationale and the information he considered reveals that his action was justified and he satisfied each of the several requirements set forth by the International Code of Zoological Nomenclature for designation of a neotype. Regrettably, though, the Code makes no provision for neosyntypes, so Hollister's designation cannot stand. In accord with Hollister's intent, we select the 86.5-mm specimen from this USNM "neosytype lot" as neotype.

*Cinctura rhomboidea*, an Early and Middle Pliocene species known from Virginia to Florida, is the oldest known representative of the genus. Its smooth shell and lack of an inflected sutural ramp are similar to features of its later congeners, but earliest examples of the species lack a parietal ridge. The parietal ridge appears in the upper Pinecrest beds of the Tamiami Formation in Florida, where shells with and without the ridge, all still called *C. rhomboidea*, occur within the same strata. Shells of the Late Pliocene *C. sarasotaensis*, Early Pleistocene *C. apicina*, *C. beaufortensis*, *C. lindae* and *C. rucksorum*, Middle Pleistocene *C. capelettii*, *C. evergladesensis* and *C. holeylandica*, and the Recent *C. hunteria*, *C. lilium*, and *C. branhamae* all display the parietal ridge that characterizes members of *Cinctura*.

As noted above, shells figured as *Fasciolaria semistriata* by Perrilliat-Montoya (1960; 1981) from the Miocene Agueguexquite Formation near Coatzacoalcos, Veracruz, Mexico seem to represent a species of *Cinctura*. Several immature *Cinctura* specimens examined by one of us (WGL) from the Agueguexquite Formation at loc. TU 638 near Coatzacoalcos, Veracruz, Mexico (E. H. Vokes, 1993: 149) may be conspecific, although they are too immature to be certain. These seem to be the only records of fossil *Cinctura* in Mexico, but

they are not Miocene. A note appended to the Tulane material by Dr. Emily Vokes adds: "up. Miocene [really L. Pliocene] correlates with Brighton Beds = uppermost Pinecrest," i.e. Late Pliocene or Early Pleistocene.

Fossil and Recent *Cinctura* are confined to waters contiguous to the southeastern United States and the Gulf of Mexico, and there is no evidence that the genus has ever occurred in the Caribbean region or elsewhere. We have traced and disproved several Caribbean listings of Recent species now assigned to *Cinctura*, and we regard those remaining as erroneous. The *Cinctura* species group is a continental lineage much like the melongenid *Busycon* clade (e.g., *Busycon*, *Busycotypus*, *Pyruella*) that evolved in eastern North America and has not extended its range beyond the Yucatan Platform of Mexico and into the Caribbean Basin.

#### *Liochlamys* Dall, 1889

Type species: *Mazzalina bulbosa* Heilprin, 1886, by original designation.

Holotype: WFIS 909, 59.2 mm SL, by subsequent designation, Spamer & Forster (1988: 48) (Fig. 4).

Description. — Shell rather small for subfamily (largest species to 120 mm SL), broadly fusiform, polished, externally enameled, devoid of sculpture except for weak threads on adapical half of siphonal process; outer lip strongly convex, crenulated, its inner side with strong smooth lirae; junction of outer lip with penultimate whorl marked by deep adapical notch; two columellar folds, the abapical one of approximately equal prominence as the rounded entrance fold to the siphonal canal; folds abapical to entrance fold on inner side of siphonal canal absent; parietal ridge absent.

Included species:

*Mazzalina bulbosa* Heilprin, 1886: Early Pleistocene (Caloosahatchee Formation), Florida;

*Liochlamys griffini* Petuch, 1994: Early Pleistocene (Caloosahatchee Formation), Florida.

Remarks. — The fossil genus *Liochlamys* is unique within Fascioliariidae in having a polished, enameled exterior, indicating envelopment by the mantle or foot during life (Vermeij, 2005). We cannot accept Petuch's (1994) suggestion that

*Liochlamys* is derived from a species such as *Fasciolaria calusa* Petuch, 1994, also from the Caloosahatchee Formation of Florida. Shells of *Liochlamys* are more globose with relatively shorter spires, lack any substantial sutural constriction between whorls, and have a siphonal process relatively shorter than that of any other Fascioliariinae. The shell shape of *F. calusa* is very much like that of *F. tulipa*, with well-rounded whorls, distinct sutures, a well-developed siphonal process, and a prominent protoconch, but its shell surface is generally smoother, sculpture on its sutural ramp is fainter, and protoconchs of the two species are quite different.

*Terebraspira* Conrad, 1862

Type species: *Fasciolaria elegans* Emmons, 1858, by monotypy.

Lectotype: specimen figured by Emmons, 1858: fig. 114, designated herein (Fig. 5).

Description. — Shell of medium size for subfamily, length of one specimen examined 149.8 mm, with very high spire and very short siphonal process; teleoconch with nine weakly shouldered whorls separated by deeply channeled suture; last whorl with conspicuous subsutural ramp, separated from main part of whorl by deep groove; axial sculpture present only on first two teleoconch whorls; other whorls with high, wide, flat-topped spiral cords separated by deep interspaces; aperture broad, outer lip somewhat broken but probably planar, its edge with paired crenulations, its inner side with thick spiral ribs representing interspaces between external cords; internal lirae absent; adapical end of aperture extended as channel; entrance fold to siphonal canal rounded, more prominent than two columellar folds; four very weak folds abapical to entrance fold along adaxial side of siphonal canal; parietal ridge thin but distinct, extending out of aperture as a thickened, polished rib not coincident with spiral sculpture; inner lip polished, extending as glaze over part of ventral side of last whorl; siphonal fasciole prominent, rounded, with five spiral threads.

Included species:

*Fasciolaria elegans* Emmons, 1858: Early Pliocene (Raysor Formation), North Carolina.

Remarks. — The generic name *Terebraspira* has been widely used for Oligocene to Pleistocene fascioliariines from the southeastern United States, but our examination of the type species, *Fasciolaria elegans* Emmons, 1858, reveals the species to be so distinctive that it cannot be grouped with any taxa that others have assigned to *Terebraspira*. As discussed below, those other species are here assigned to the new genus *Pliculofusus*.

The now-restricted monotypic genus *Terebraspira* has a distinctive combination of characters. The absence of axial sculpture on all but the first two teleoconch whorls recalls *Fasciolaria*, *Cinctura*, and morphotypes of several other genera, but the spiral sculpture of high, wide, flat-topped cords is unique. In *T. elegans*, there are 21 such cords on the last whorl, becoming smaller and more closely spaced abapically, and 7 on the penultimate whorl. The subsutural ramp of later whorls resembles the spirally corded ramp in *Fasciolaria* but is much broader. The protruding parietal ridge of *Terebraspira* is seen also in *Cinctura*, whose shell is, however, mostly smooth. The spire of *Terebraspira* is exceptionally high, being only slightly less than half the height of the aperture plus canal. A comparably high spire is seen only in some species of the new genera *Africolaria* and *Australaria* (see below). The high, rounded siphonal fasciole is unusual for the subfamily; it is shared only with *Pliculofusus*. The adapically extended aperture into a channel-like feature is exceptionally well marked in *Terebraspira* and differs from the condition seen in other members of the subfamily. Explicit comparisons between *Terebraspira* and the genera *Pliculofusus* and *Triplofus* are given under *Pliculofusus*.

Emmons' original illustration serves to identify *T. elegans* and we select the specimen depicted in that figure as lectotype. L. D. Campbell informs us (e-mail to GJV, 3 May, 2011) that Emmons' specimen is lost. One of the few known specimens of *T. elegans* is in the USNM collection, no. 429895 (Fig. 6). According to Campbell, L. W. Ward collected that specimen in the Lumber River section at Lumberton, North Carolina, in a deposit that Campbell considers a stratigraphic equivalent of the Raysor Formation of Early Pliocene age (3.8 Ma). We have examined and illustrate this specimen, and our description of *Terebraspira* is based upon it.



*Pliculofusus* gen. nov.

Type species: *Fasciolaria scalarina* Heilprin, 1886, designated herein.

Holotype: WFIS 904, 158.6 mm SL, by subsequent designation, Spamer & Forster (1988: 56) (Fig. 7).

Description. — Shell medium-sized to large, to 190 mm SL (*P. scalarinus*), high-spired; suture deeply impressed but not channeled; teleoconch sculpture of broad, low axial ribs with rounded cross-section; spiral sculpture of high, rounded or  $\Lambda$ -shaped cords over entire shell; aperture narrow to broad, outer lip medially convex, its edge with paired crenulations, its inner side with beaded or discontinuous lirae, especially on anterior (abapical) sector; adapical end of outer lip not forming apertural extension; entrance fold to siphonal canal rounded, more prominent than columellar folds; four distinct folds abapical to entrance fold on adaxial side of siphonal canal; parietal ridge thin, distinct, not extending beyond edge of aperture; inner lip callus spreading onto ventral side of last whorl, recessed where it borders external sculpture of last whorl; siphonal process short to moderately long, bearing distinct rounded siphonal fasciole.

Included species:

*Fasciolaria acuta* Emmons, 1858: Pliocene (Duplin and Tamiami Formations), Virginia to Florida;

*Terebraspira calusa* Petuch, 1994: Pliocene, Florida;

*Terebraspira diegelae* Petuch, 1994: Pliocene, Florida;

*Terebraspira kissimmeensis* Petuch, 1994: Pliocene, Florida;

*Terebraspira labelleensis* Petuch, 1994: Pleistocene, Florida;

*Terebraspira lindae* Petuch, 1994: Pliocene, Florida;

*Terebraspira maryae*, Petuch, 1994: Pliocene, Florida;

*Fasciolaria nodulosa* Emmons, 1858: Pliocene (Duplin, Raysor and Tamiami Formations), North Carolina to Florida;

*Terebraspira okeechobeensis* Petuch, 1994: Pliocene, Florida;

*Terebraspira osceolai* Petuch, 1994: Pliocene, Florida;

*Fasciolaria petrosa* Dall, 1915: Late Oligocene or Early Miocene (Tampa Formation), Florida;

*Fasciolaria ramondi* Maury, 1902: Early Miocene (Chipola Formation), Florida;

*Fasciolaria scalarina* Heilprin, 1886: Early Pleistocene (Caloosahatchee Formation), Florida;

*Fasciolaria scalarina macgintyi* M. Smith, 1936: Pleistocene, Florida;

*Terebraspira seminole* Petuch, 1994: Pliocene, Florida;

*Fasciolaria sparrowi* Emmons, 1858: Early Pliocene, North Carolina.

Etymology. — The name is Latin, formed of *plicula* (small fold) and *fusus* (spindle), referring to the presence of small folds on the adaxial side of the siphonal canal; the gender is masculine.

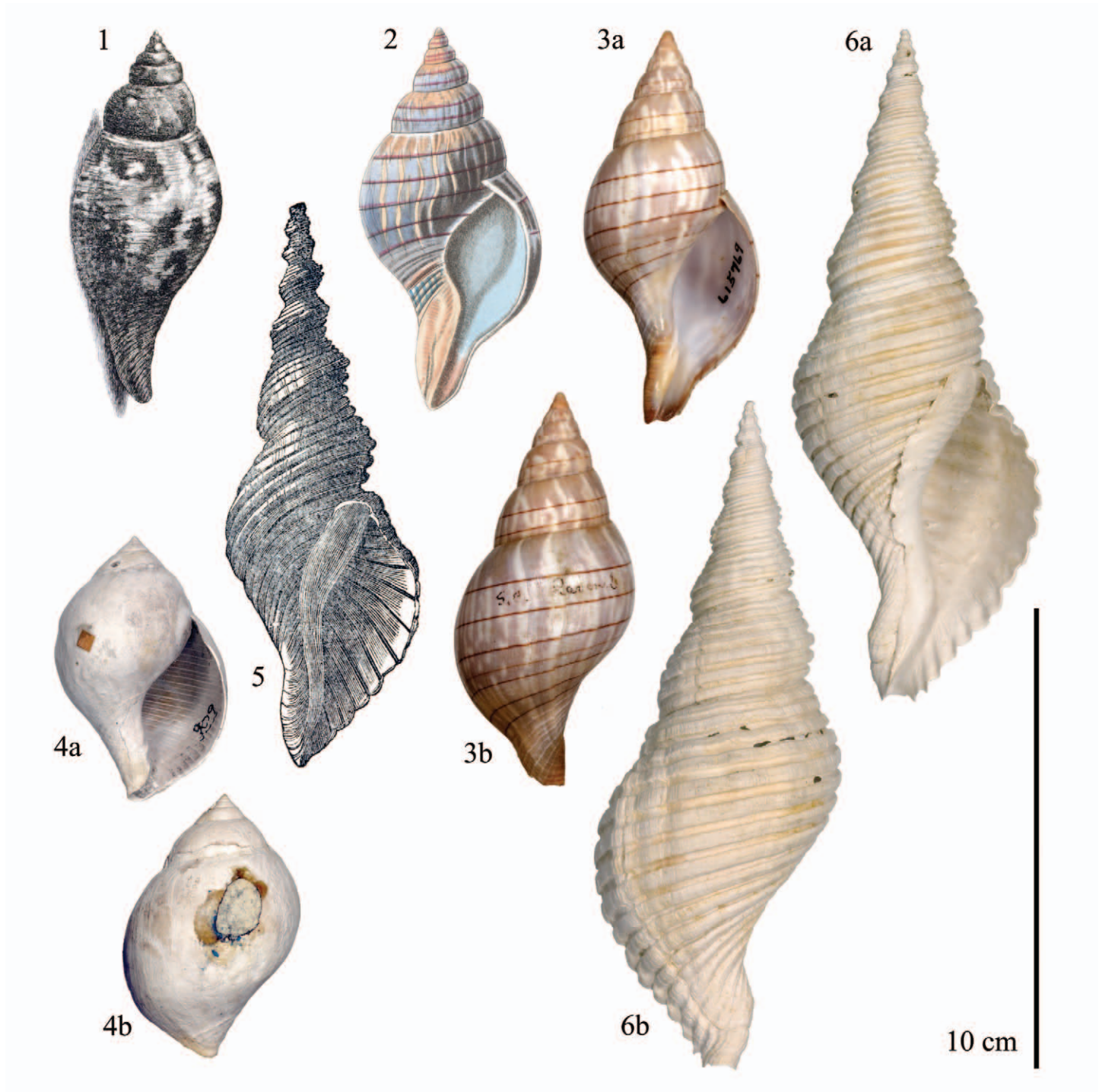
Remarks. — Most species in *Pliculofusus* gen. nov. were assigned by late twentieth-century authors to *Terebraspira* (see e.g. Campbell, 1993; Petuch, 1994). As noted under *Terebraspira*, however, all these species differ in significant ways from the type and only described species of *Terebraspira*, *T. elegans* (Emmons, 1858). This circumstance necessitates the proposal of the new genus *Pliculofusus*.

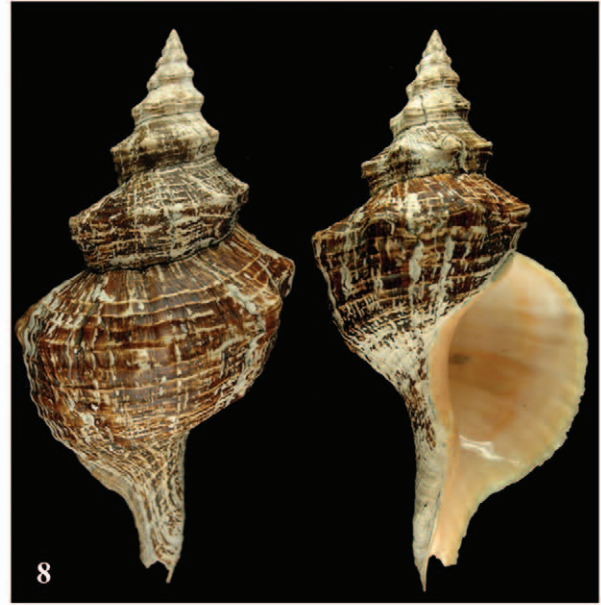
Species of *Pliculofusus* gen. nov. are most similar to species of *Terebraspira* and *Triplofusus*, but at least eight features distinguish the genera: (1) *Pliculofusus* has a glazed inner lip that extends onto the ventral side of the last whorl, as in *Triplofusus* and *Terebraspira*, but in contrast to those genera its edge is recessed with respect to the external sculpture, implying resorption; (2) there is a thin but distinct parietal ridge in *Pliculofusus*, as in *Terebraspira*, but this ridge is not extended beyond the aperture as it is in *Terebraspira*; *Triplofusus* lacks the ridge; (3) as in *Terebraspira*, *Pliculofusus* has small folds on the adaxial side of the siphonal canal, although they are stronger than in *Terebraspira*; these folds are absent in *Triplofusus*; (4) there is a prominent, rounded siphonal fasciole in *Pliculofusus* and *Terebraspira*, but this

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(next page) Figs 1-6. Fasciolarinae species. 1, Lectotype of *Murex tulipa* Linnaeus, 1758, type species of *Fasciolaria*; figure after d'Argenville, 1742: pl. 13 fig. K; 2, Original illustration of *Pyrula hunteria* Perry, 1811, type species of *Cinctura*; figure after Perry, 1811: pl. 50 fig. 4; 3, Neotype of *Pyrula hunteria* Perry, 1811, type species of *Cinctura*; USNM 615769, 86.5 mm SL; 4, Holotype of *Mazzalina bulbosa* Heilprin, 1886, type species of *Liochlamys*; WFIS 909, 59.2 mm SL; 5, Lectotype of *Fasciolaria elegans* Emmons, 1858, type species of *Terebraspira*; figure after Emmons, 1858: fig. 114; 6, *Terebraspira elegans* (Emmons, 1858), USNM 429895, 149.8 mm SL.

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10 cm

feature is absent in *Triplofusus*; (5) axial sculpture is present on all whorls in *Pliculofusus* and *Triplofusus* but absent on all but the first two whorls in *Terebraspira*; (6) *Pliculofusus* has prominent, sharp, beaded or discontinuous internal lirae, whereas lirae are smooth or absent in *Triplofusus* and replaced by the spiral impressions of external interspaces in *Terebraspira*; (7) the outer lip of *Pliculofusus* joins the last whorl adapically without either an extension or notch, whereas in *Terebraspira* there is a long, narrow adapical extension coincident with the prominent subsutural ramp in that genus; and (8) the outer lip of adult *Pliculofusus* is medially convex, whereas it is planar in *Triplofusus* and probably also in *Terebraspira*.

By the presence of folds on the adaxial side of the siphonal canal, *Pliculofusus* resembles the Indo-West Pacific genus *Pleuroploca*, but the latter genus differs widely in having lower, broader cords, very prominent crenulations at the edge of the outer lip, and usually at least one row of prominent nodes or spines.

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(previous page) Figs 7-15, Fascioliinae species. 7, Holotype of *Fasciolaria scalarina* Heilprin, 1886, type species of *Pliculofusus*; WFIS 904, 158.6 mm SL; 8, Syntype of *Fasciolaria gigantea* Kiener, 1840, type species of *Triplofusus*; MNHN, 335 mm SL (photo courtesy of MNHN); 9, Lectotype of *Murex salmo* Wood, 1828, type species of *Granolaria*; figure after Wood, 1828: pl. 5 fig. 14e; 10, Lectotype of *Fasciolaria aurantiaca* Lamarck, 1816, type species of *Aurantilaria*; MHNG INVE 51699 (ex MHNG 1098/1), 99.5 mm SL (photo courtesy of Yves Finet, MHNG); 11, Lectotype of *Fusus filamentosus* Röding, 1798, type species of *Filifusus*; figure after Chemnitz, 1780: pl. 140 fig. 1310; 12, Lectotype of *Murex trapezium* Linnaeus, 1758, type species of *Pleuroploca*; specimen marked "trapezium A" in lot of three syntypes in Linnean Society collection, 127.2 mm SL; 13, Holotype of *Fasciolaria rutila* Watson, 1882, type species of *Africolaria*; NHMUK 1887.2.9.839; 102.0 mm SL  
Fig. 14 Holotype of *Fasciolaria purpurea* Jonas var. Dunker, 1867, = *Fasciolaria heynemanni* Dunker, 1870, type species of *Kilburnia*; figure after Dunker, 1867: pl. 32 figs 1, 2; 15, Lectotype of *Fasciolaria lugubris* A. Adams & Reeve in Reeve, 1847, type species of *Lugubrilaria*; figure after Reeve, 1847b: pl. 1 fig. 2a, b.

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The genus *Pliculofusus* is the oldest fascioliinae group in the Americas, but it has been confined to the Atlantic sector in the southeastern United States throughout its history. The earliest species that we confidently assign to *Pliculofusus* is *Fasciolaria petrosa* from the Tampa Formation (earliest Miocene) of Florida. Our examination of the holotype (USNM 165073) reveals several characters overlooked by earlier authors. The anterior lirae on the inner side of the outer lip are distinctly beaded. There is a thin but distinct parietal ridge. Finally, there are at least two distinct folds along the inner edge of the siphonal canal abapical to the entrance fold. These abapical folds cannot be seen when looking at the ventral side of the siphonal canal, because they have been worn away on the exposed part of the inner edge of the canal. They are, however, discernible by inserting a pin or needle into the siphonal canal and running its side against the inner edge. The three traits in question are similar to those of undoubted later species of *Pliculofusus*. A likely descendant of *P. petrosus* is the Early Miocene (Burdigalian) *P. ramondi* from the Chipola Formation of Florida. The geologically youngest species of the genus is *P. labelleensis* from the Pleistocene of Florida.

*Triplofusus* Olsson & Harbison, 1953

Type species: *Fasciolaria gigantea* Kiener, 1840, by original designation.  
Syntype: MNHN, 335 mm SL (see below under remarks), selected herein (Fig. 8).

Description. — Shell large to very large (two living species to 400 and 600 mm SL), high-spired; teleoconch sculpture of broad axial ribs, sometimes forming nodes at shoulder angulation, and spiral cords, which are sharp and prominent in subadults but often broad and rounded in adults; outer lip almost planar, its inner side smooth or with smooth lirae which may be rather prominent in subadult shells, its junction with penultimate whorl lacking adapical notch; two columellar folds less prominent than the rounded entrance fold to the siphonal canal; abapical folds on adaxial side of siphonal canal absent. Radula of type species discussed by Hollister (1954: 44-46).

Included species:

- Fasciolaria acutispira* Strebel, 1911 (= *Fasciolaria princeps* G.B. Sowerby I, 1825): Recent, locality unknown;
- Fasciolaria cronlyensis* Gardner, 1948: Pliocene, North and South Carolina;
- Fasciolaria gigantea* Kiener, 1840 (= *Fasciolaria papillosa* auctt., non G. B. Sowerby I, 1825): Early Pleistocene to Recent, southeastern United States and northeastern Mexico;
- Fasciolaria papillosa acmensis* B. Smith, 1940: Pliocene, North Carolina to Florida;
- Fasciolaria papillosa duplinensis* B. Smith, 1940: Pliocene, southeastern United States;
- Fasciolaria princeps* G. B. Sowerby I, 1825: Plio-Pleistocene to Recent, tropical eastern Pacific.

Remarks. — There is no material for *Fasciolaria gigantea* in the MNHN type collection. However, a search of the general collection produced a probable syntype with an old metallic label reading “Ocean Pacifique.” The specimen measures 335 mm SL; using the conversion ratio 1 pouce = 27.07 mm, this length converts to 12.37 pouce. Kiener (1840: 5) stated the habitat of this species to be “l’océan Pacifique?” and stated its length to be 13 pouce. This may well be the shell upon which Kiener based his description, and it is here recognized as syntype.

A comparison with the similar genus *Pliculofusus* is given under that genus. Although most characters of the two living species of *Triplofusus* are similar, the eastern Pacific *Triplofusus princeps* is distinctive in having a plicate operculum. The only other fasciolarine with a somewhat plicate operculum is *Aurantilaria aurantiaca* (see below), but in that species the ridges and grooves are much less expressed. The protoconch of *T. princeps* also indicates a planktotrophic veliger stage whereas that of *T. giganteus* is in accord with its complete lecithotrophic development. The only other fasciolarine with a planktotrophic protoconch is *Fasciolaria acutispira* Strebel, 1911, a name introduced without locality for a juvenile shell that looks very much like a *Triplofusus* (Strebel, 1911: 27, fig. 26); we regard it as a junior synonym of *Triplofusus princeps*.

Fossils of *T. giganteus* and its precursors are common and widespread in Pliocene and Pleistocene deposits of Florida

and the Atlantic coastal plain, and their records are too numerous to mention here. Plio-Pleistocene records for *T. princeps* in Mexico and southern California are to be found in Hanna (1926), Hanna & Hertlein (1927), Emerson (1960), Emerson & Hertlein (1964), Dowlen & Minch (1973), and Schneider (2004). Specimens from Neogene deposits at Punta Gavilan, northern Venezuela, reported and figured as “*Fasciolaria (Pleuroploca)* aff. *papillosa* Sowerby” by Rutsch (1934: 73, 74, pl. 5 fig. 2, pl. 6 fig. 4) are so similar as to be nearly indistinguishable from modern shells of *T. princeps*; this constitutes the only evidence of *Triplofusus* in the Caribbean region.

***Granolaria* gen. nov.**

Type species: *Murex salmo* Wood, 1828, selected herein.

Lectotype: specimen figured by Wood, 1828: pl. 5 fig. 14e, selected by Rosenberg et al., submitted (Fig. 9).

Description. — Shell medium-sized for subfamily (two living species to 150 and 203 mm SL), relatively low-spired, with a long, weakly notched siphonal process; teleoconch whorls with fewer than ten short axial ribs, forming nodes at shoulder angulation that point adapically; spiral sculpture of fine, axially roughened cords; outer lip almost planar, its edge with well expressed, paired crenulations, its inner side with smooth lirae; junction of outer lip with penultimate whorl lacking adapical notch; parietal ridge prominent, rounded; two columellar folds more weakly expressed than the rounded entrance fold to the siphonal canal; abapical folds on inner side of siphonal canal absent. Radula of type species described by Gray (1856: 42, 43) and Troschel (1868: 62, 63).

Included species:

- Fasciolaria (Pleuroploca?) crassinoda* Weisbord, 1962: Early Pleistocene, Venezuela;
- Fasciolaria gorgasiana* Brown & Pilsbry, 1913: Late Miocene (Gatun Formation) of Panama, Early Pliocene of Colombia and Venezuela;
- Fasciolaria kindlei* Maury, 1902: Early Miocene (Chipola Formation), Florida;
- Fasciolaria macdonaldi* Olsson, 1922: Early Pliocene (Banano Formation), Costa Rica;

*Fasciolaria olssoni* Anderson, 1929: Early Pliocene, Colombia;  
*Murex salmo* Wood, 1828 (= *Fasciolaria granosa* Broderip, 1832): Recent,  
eastern Pacific;  
*Fasciolaria (Pleuroploca) turamensis* Jung, 1969: Early Pliocene, Trinidad;  
*Fasciolaria valenciennesii* Kiener, 1840 (= *Pleuroploca salmo auctt., non*  
Wood, 1828): Recent, tropical eastern Pacific.

**Etymology.** — This name references the granular perios-  
tracum of the type species; the gender is feminine.

**Remarks.** — *Granolaria* gen. nov. comprises tropical Ameri-  
can fasciolarines of moderate size (maximum SL slightly  
greater than 200 mm) characterized by a long siphonal  
process, a well-expressed, rounded parietal ridge, generally  
smooth and prominent lirae on the inner side of the outer  
lip, a round entrance fold to the siphonal canal, and the ab-  
sence of folds on the inner edge of the siphonal canal abapi-  
cal to the entrance fold. In shell characters it most closely  
resembles the IWP genus *Pleuroploca*, which differs from  
*Granolaria* gen. nov. by the presence of folds on the inner  
edge of the siphonal canal. Moreover, in most species of *Gra-*  
*nolaria*, the lip shows little or no convexity. *Granolaria* gen.  
nov. differs from *Triplofusus* by the presence of a distinct  
parietal ridge and by having a lower spire, and from *Pliculo-*  
*fus* by a much lower spire, finer spiral sculpture, and the  
absence of folds on the inner edge of the siphonal canal.

Both living species of *Granolaria* have fossil counterparts:  
*G. salmo* and *G. valenciennesii* are most closely related to *G.*  
*crassinoda* from the Early Pleistocene of Venezuela and *G.*  
*turamensis* from the Early Pliocene of Trinidad, respectively.  
This species group therefore joins a long list of taxa referred  
to by Woodring (1966) as Paciphiles, those with living repre-  
sentatives in the eastern Pacific but known fossil representa-  
tives also in the western Atlantic. For a discussion of  
confusion surrounding the names *Murex salmo*, *Fasciolaria*  
*granosa* and *F. valenciennesii* see Rosenberg et al., (submitted).

There is considerable variation in sculpture among and  
within species of *Granolaria* gen. nov. The eastern Pacific  
*G. salmo* has a single row of tubercles at the shoulder angula-  
tion. These may be reduced or absent, especially in *G. valen-*  
*ciennesii*, whose spiral cords are also less expressed. Varying  
degrees of sculptural reduction are also seen in the fossil

species *G. gorgasiana*. In that species from the Gatun Forma-  
tion (Late Miocene) of Panama, a species we here assign to  
*Granolaria* on the basis of a well preserved specimen (USNM  
643661) collected by Woodring (1964), the body whorl abapi-  
cal of the sharp shoulder spines is smooth except for weak  
spiral threads in the concave constriction. Although the  
aperture of this specimen is filled with matrix, a parietal  
ridge is discernible. A parietal ridge is also evident on a  
specimen figured by Landau & Silva (2010: pl. 16, fig. 1a)  
from the Lower Pliocene Araya Formation of Venezuela.  
Other fragmentary specimens discussed by Woodring (1964)  
(USNM 643672 and 643673) display distinct smooth lirae.  
Our examination of the holotype and paratype of *G. olssoni*  
(CAS 4617 and 4618 respectively) indicates that this species  
resembles a smooth *G. salmo* with seven heavy shoulder  
nodes, a thin parietal ridge, and smooth lirae.

#### *Aurantilaria* gen. nov.

Type species: *Fasciolaria aurantiaca* Lamarck, 1816, selected herein.

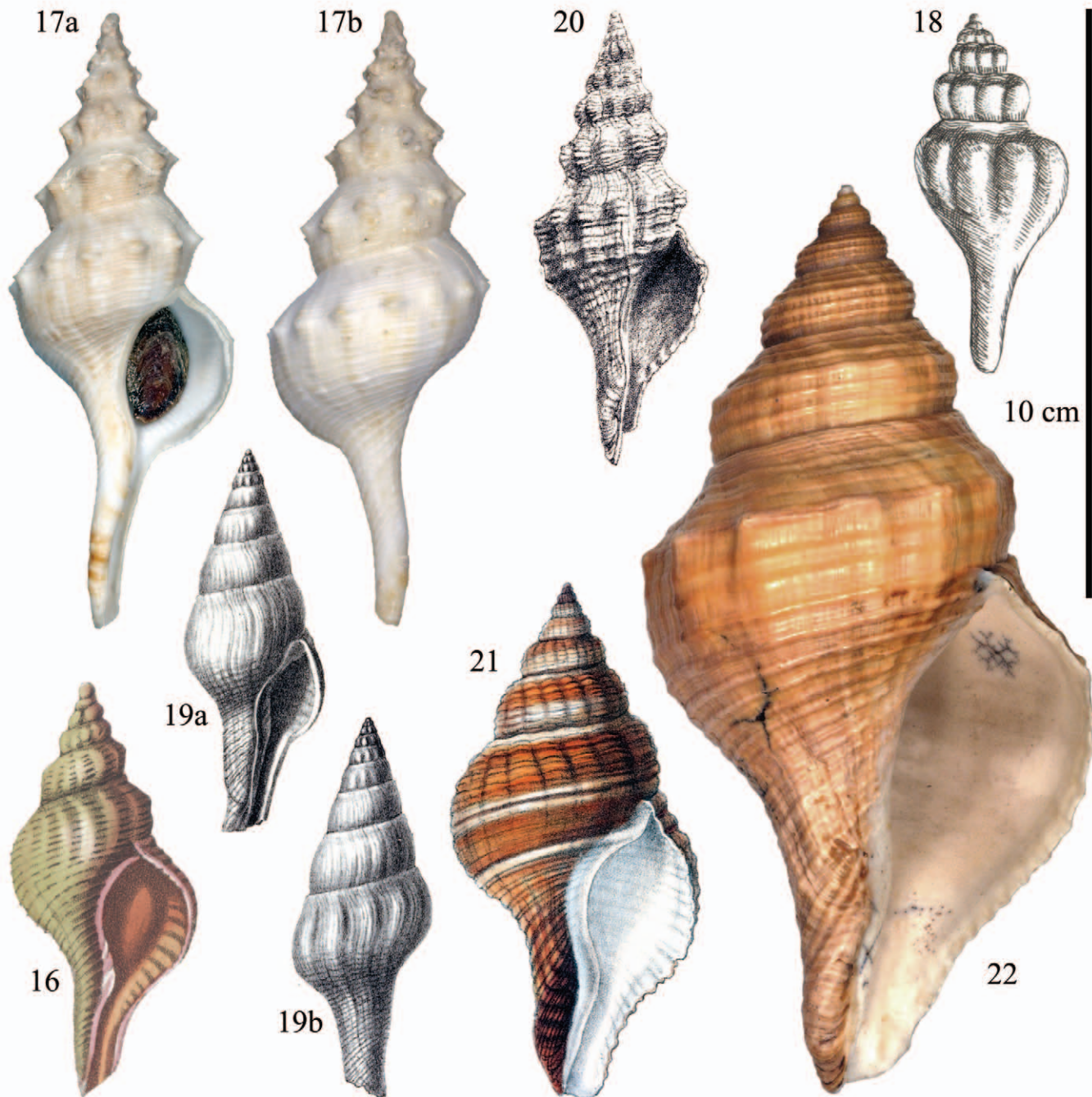
Lectotype: Three probable syntypes MHNG INVE 51699 (ex MHNG  
1098/1); 99.5 mm, 62.7 mm, 42.0 mm SL; 99.5 mm specimen selected  
herein as lectotype (Fig. 10).

**Description.** — Shell medium-sized to large for subfamily,  
maximum length of type and largest species 211 mm; shell  
broadly fusiform, with relatively high spire; when fully

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Figs 16-22, Fasciolarinae species. 16, Lectotype of *Pyrula australasia*  
Perry, 1811, type species of *Australaria*; figure after Perry, 1811: pl. 54 fig.  
4; 17, Holotype of *Australaria tenuitesta* Snyder, Vermeij & Lyons spec.  
nov., ANSP 425075, 105.4 mm SL; 18, Lectotype of *Tarantinaea lignaria*  
[sic] Linnaeus, = *Murex lignarius* Linnaeus, 1758, type species of *Taranti-*  
*naea*; figure after Buonanni, 1684: fig. 32; 19, Lectotype of *Fasciolaria rec-*  
*ticauda* Fuchs, 1877, type species of *Neolatirus*; figure after Fuchs, 1877:  
pl. 16 fig. 3; 20, Lectotype of *Fasciolaria decipiens* Tate, 1888, type species  
of *Pleia*; figure after Tate, 1888: pl. 8 fig. 1; 21, Lectotype of *Fusus buxeus*  
Reeve, 1847, type species of *Viridifusus*; figure after Reeve, 1847: pl. 5 fig.  
18; 22, Lectotype of *Fusus pricei* E.A. Smith, 1887, type species of *Sagina-*  
*fus*; NHMUK 82.3.25.1, 156.6 mm SL.

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expressed, sculpture of up to five rows of ten or more abaxially pointing nodes; other spiral sculpture of prominent cords; outer lip edge weakly convex and angled at periphery, with paired black crenulations, the termini of paired black lines on the spire and body whorl; internal lirae on adaxial side of outer lip mostly smooth, but some discontinuous toward anterior; junction of outer lip with penultimate whorl often without notch; parietal ridge prominent, rounded; entrance fold to siphonal canal prominent, rounded, more strongly expressed than the two columellar folds; folds abapical to entrance fold absent. Radula of type species described and figured by Calvo (1987: 149-151, fig. 123) and Matthews-Cascon et al. (1989: 359, figs 1, 2).

Included species:

*Fasciolaria (Pleuroploca) antwerpiensis* Glibert, 1952: Middle Miocene, Belgium;

*Fasciolaria aurantiaca* Lamarck, 1816: Recent, northeastern Brazil to Grenadines, Lesser Antilles;

*Fasciolaria carminamaris* Maury, 1917: Late Miocene (Baitoa Formation), Dominican Republic;

*Siphonalia kempi* Maury, 1910: Early Miocene (Chipola Formation, Florida?, Cantaure Formation, Venezuela?), Dominican Republic;

*Pleuroploca lindae* Petuch, 2004: Late Pliocene, Florida;

*Fasciolaria michelottiana* Grateloup, 1847: Early Miocene, France;

*Fasciolaria nodifera* Dujardin, 1837: Middle Miocene, Europe;

*Fasciolaria pyrulaeformis* Hoernes & Auinger, 1890: Late Miocene, Romania;

*Fasciolaria tarbelliana* Grateloup, 1847: Late Miocene to Early Pliocene, Europe.

**Etymology.** — The genus name incorporates *aurantiaca*, the name of the type species, and *Fasciolaria*; the gender is feminine.

**Remarks.** — We propose the new genus *Aurantilaria* for the Recent southeastern Caribbean and Brazilian species *Fasciolaria aurantiaca* Lamarck, 1816, several new world fossils and two groups of European fossils. The genus is characterized by one to five rows of abaxially pointing nodes, a modestly convex outer lip whose inner side possesses strong lirae that are often discontinuous (especially anteriorly), a strong

rounded parietal ridge, paired crenulations that are black in the type species, a rounded entrance fold to the siphonal canal, and the absence of folds abapical to the entrance fold. In its multiple rows of nodes and black paired crenulations, *Aurantilaria* resembles the IWP genus *Pleuroploca*, but it differs from that genus by lacking folds abapical to the entrance fold and by having a consistently higher spire. The paired black lines and associated crenulations are restricted to *Aurantilaria*, *Filifusus* and *Pleuroploca* and could indicate a close phylogenetic relationship between these genera. Lamarck's fasciolariid and related types are illustrated and discussed in a forthcoming paper by Finet & Snyder, to appear in *Zootaxa*. We herein select the 99.5-mm SL syntype as lectotype

*Aurantilaria* gen. nov. differs from the new American genus *Granolaria* by having a higher spire, abaxially rather than adapically pointing nodes, and by usually having discontinuous internal lirae. Shells of living *Aurantilaria* have paired black spiral lines and terminal crenulations, which are lacking in *Granolaria*, and may have more than one spiral row of nodes, a state not seen in any species of *Granolaria*. The holotype of *A. kempi*, PRI 28697, has a single peripheral row of rather broad, low nodes on whorls of the spire and body whorl. This species will be discussed in detail in a forthcoming paper by Landau and Vermeij. Species of *Triplofus* resemble *Aurantilaria* in having a high spire, but lack the parietal ridge of *Aurantilaria* and have a planar rather than convex outer lip. The outer lip of *Triplofus* lacks the terminal crenulations of *Aurantilaria* and is either smooth on its inner side or has smooth internal lirae. In the Late Miocene *Aurantilaria carminamaris*, lirae are smooth rather than discontinuous, and the parietal ridge is reduced to a thin cord-like feature. This tropical American species may be ancestral to *Triplofus*. *Aurantilaria aurantiaca* is the only living species other than *Triplofus princeps* to have grooves and ridges on the outer surface of the operculum, although they are more subdued in *A. aurantiaca* than in *T. princeps*. There is also a close resemblance between *Aurantilaria* and the new IWP genus *Filifusus*. *Aurantilaria* differs from *Filifusus* by having fewer, coarsely beaded lirae, a rounded instead of keel-like parietal ridge, and a rounded rather than keel-like entrance fold to the siphonal canal.



Besides the typical American group, we include in *Aurantilaria* all European Miocene and Pliocene species that belong to the group of *Fasciolaria michelottiana* and *F. tarbelliana*. The species-level taxonomy of these European fossils is in need of revision. Lozouet et al. (2001) assigned Early Miocene (Aquitanian and Burdigalian) populations from France to *F. michelottiana*. Late Miocene (Tortonian) and Pliocene populations from southern Europe and the Paratethys are assigned to *F. tarbelliana*. Northern populations from the Middle Miocene of France and Belgium have been named *F. nodifera* and *F. antwerpiensis* (see Hoernes & Auinger, 1890; Glibert, 1963; and Muñiz Solis, 1988). Through the kindness of B. M. Landau, we (GJV) have examined well preserved specimens of *Aurantilaria tarbelliana* from the Late Miocene (Tortonian) of Cacela Velha, Portugal, and the Early Pliocene Huelva Formation at Lucena, southern Spain. At the Naturhistorisches Museum (Wien) we have also examined material of Tortonian age assigned to various forms of *A. tarbelliana*, as well as the endemic Romanian *A. pyrulaeformis*.

Matthews-Cascon et al. (1989) noted considerable variation in the expression of sculpture in Brazilian populations of *A. aurantiaca*. Sand-dwelling individuals have almost smooth shells, whereas more typical specimens from rockier environments have up to five rows of nodules on the last whorl. Similar variation exists among the fossil taxa. Axial sculpture is absent in the Middle Miocene *A. antwerpiensis* and obsolete in the *inermis* Hoernes & Auinger (1890) variety of *A. tarbelliana* (non *Fasciolaria inermis* Jonas, 1846a) from the Vienna Basin of Austria. By contrast, Late Miocene specimens of *A. tarbelliana* from Portugal have sharp, slightly abaperturally pointing nodes at the shoulder angulation, together with very short axial ribs that hardly extend below these nodes. Pliocene specimens from Spain have low rounded nodules. Two rows of nodes characterize the specimens of *A. pyrulaeformis* that we have examined. The original figures of this species depict six rows of nodes, diminished in size after the first three. This is the only European species with more than one row of nodes on the last whorl.

As in the American fossil *A. kempi* and the living *A. aurantiaca*, the European *A. michelottiana* and *A. tarbelliana* possess prominent, coarse, discontinuous lirae on the inner side

of the outer lip. The resemblance between Early Miocene European and American species of *Aurantilaria* is particularly close in that these species have a high spire, coarsely beaded internal lirae, a rounded parietal ridge, and a rounded entrance fold. Later species can be more divergent: Portuguese *A. tarbelliana* have stronger nodes than any American species, and the American Late Miocene *A. carminamaris* has a weaker parietal ridge than other species.

If our assignments are correct, *Aurantilaria* presents several striking cases of geographic restriction since the Pliocene. During the Early Miocene the genus was present in Florida and the Dominican Republic (*A. kempi*) and Venezuela (*Fasciolaria* cf. *carminamaris* of Gibson-Smith & Gibson-Smith, 1979, to be described by Landau & Vermeij), and Europe. *Aurantilaria* occurred in the Caribbean and in Europe during the Late Miocene, and in Florida and Spain during the Pliocene. Today, the genus is restricted to the southeasternmost Antilles, Guyane, and northeastern Brazil.

#### *Filifusus* gen. nov.

Type species: *Fusus filamentosus* Röding, 1798, selected herein.

Lectotype: specimen figured by Chemnitz, 1780: pl. 140 fig. 1310, selected herein (Fig. 11).

Description. — Shell medium-sized for subfamily (largest species to about 193 mm SL), elongate, fusiform, with high spire and long siphonal process; teleoconch sculpture of broad, short, rounded axial ribs forming nodes (sometimes absent) at shoulder angulation, and many relatively sharp spiral cords, often black and paired; outer lip with sharp, closely spaced, paired crenulations, sharpest on the sinus just abapical to the convex sector; inner side of outer lip with numerous fine slender lirae, usually straight but occasionally interrupted near abapical end; junction of outer lip with penultimate whorl without adapical notch; parietal ridge present; two columellar folds weak; entrance fold to siphonal canal sharp, keel-like; inner side of siphonal canal smooth, without abapical folds. Radula of type species described by Troschel (1868: 62, 63) and figured by Thiele (1929: 328, fig. 377), Maes (1967: 48-54, figs 1-3), Cernohorsky (1972: 153, text figs 1-3) and Bandel (1984: 138, text fig. 264).

Included species:

*Pleuroploca altimasta* Iredale, 1930: Recent, eastern Australia;

*Fusus filamentosus* Röding, 1798: Recent, Indian and western Pacific Oceans;

*Fasciolaria glabra* Dunker, 1882: Recent, southern Japan;

*Fasciolaria inermis* Jonas, 1846a: Recent, Red Sea and Indian Ocean;

*Pleuroploca manuelae* Bozzetti, 2008a: Recent, southern Madagascar.

**Etymology.** — This Latin name is a combination of *filus* (thread) and *fusus* (spindle), referring to the fine spiral sculpture of most species and the spindle shape of the shell; the gender is masculine.

**Remarks.** — We propose *Filifusus* as a new genus for moderate-sized (largest species to 193 mm SL) fusiform fasciolarines confined to the Indo-West Pacific region. The most distinctive features of the genus are the very numerous lirae on the inner side of the outer lip (up to 50 in *F. filamentosus*), and the sharp, keel-like entrance fold to the siphonal canal. *Filifusus* gen. nov. differs from *Pleuroploca*, another Indo-West Pacific genus, in having a more slender, fusiform shell with more numerous, sharper spiral cords, more numerous lirae, a much more prominent entrance fold, and by lacking abapical folds along the inner side of the siphonal canal. Röding (1798: 118) referred to figures in Chemnitz (1780: pl. 140 figs 1310, 1311), which clearly depict shells of this species. We select the specimen depicted in fig. 1310 as the lectotype.

*Pleuroploca* P. Fischer, 1884

Type species: *Fasciolaria trapezium* (Linnaeus, 1758), by monotypy.

Types: Three syntypes in Linnean Society collection, London, of which 127.2 mm SL specimen marked “*trapezium A*” is herein designated lectotype (Fig. 12).

**Description.** — Shell small to large (largest species to 287 mm SL), heavy, broadly fusiform, with relatively low spire; teleoconch sculpture of short, rounded axial ribs, sometimes forming large tubercles at shoulder angulation, with sometimes a second row at the abapical termination of the axial ribs, and low, broad, rounded spiral cords; outer lip nearly planar, with widely separated, paired crenulations; inner

side of outer lip with or without weak, smooth lirae; junction of outer lip with penultimate whorl not forming adapical notch; parietal ridge prominent, rounded, sometimes a few inner-lip ridges immediately abapical to it; two columellar folds weaker than the rounded entrance fold to the siphonal canal; abapical to the entrance fold in adults are four small, distinctive folds along adaxial side of siphonal canal. Radula of type species described and figured by Troschel (1868: 62, pl. 5, fig. 12), Maes (1967, 48-54, figs 4-7) and Bandel (1984: 138, text fig. 258).

Included species:

*Fasciolaria audouini* Jonas, 1846a: Recent, Indian Ocean;

*Fasciolaria clava* Jonas, 1846b: Recent, eastern Indian Ocean;

*Fasciolaria lischkeana* Dunker, 1863 in [1858-1870]: Recent, Japan;

*Pleuroploca lyonsi* Bozzetti, 2008b: Recent, southern Madagascar;

*Fasciolaria ponderosa* Jonas in Philippi, 1850 in [1847-1850]: Recent, northern Indian Ocean to Indonesia;

*Fasciolaria purpurea* Jonas in Philippi 1849 in [1847-1850]: Recent, eastern Africa;

*Fasciolaria (Fasciolaria) suryai* Beets, 1941: Late Miocene, Borneo;

*Murex trapezium* Linnaeus, 1758: Recent, western Pacific.

**Remarks.** — Linnaeus (1758: 755) cited figures in four works in his original description of *Murex trapezium*: Buonanni (1684: fig. 287); Rumphius (1705: pl. 29 fig. E & pl. 49 fig. K); Gualtieri (1742: pl. 46 fig. B); and DeZallier d’Argenville (1742: pl. 13 fig. F) and, apparently following Rumphius, gave its locality as Amboina, i.e., Ambon, an island in the Moluccas, Indonesia. Except for Rumphius’ pl. 29 fig. E, all figures that Linnaeus cited represent the strongly noded morph of *Pleuroploca trapezium* common in Indonesia and the Philippines, with perhaps the best figure being Rumphius’ pl. 49 fig. K. Of three *Murex trapezium* syntypes in the Linnean Society collection, a shell marked “*trapezium B*” has much-reduced nodes, but the others, a juvenile shell and an adult marked “*trapezium A*” conform to the figures cited by Linnaeus. The less worn immature shell bears the number “567,” the species number for *trapezium* in Linnaeus’ (1767) twelfth edition and thus may not have been among his original material, so we here select the adult shell marked “*trapezium A*” as lectotype.

Comparative remarks with other genera are given under *Pliculofusus*, *Granolaria*, *Aurantilaria* and *Filifusus*. Species of *Pleuroploca* have notably heavy shells, often with large tubercles but sometimes with no tubercles at all. *Pleuroploca trapezium* has traditionally been regarded as a single, widespread species in the Indian and western Pacific Ocean, with *P. audouini*, *P. lischkeana* and *P. ponderosa* representing regional variants and thus synonyms. We were tempted to recognize at least three living species: typical *P. trapezium* from the western Pacific has two rows of tubercles, whereas the Indian-Ocean *P. audouini* and the Japanese *P. lischkeana* usually have the lower row of nodes weak to obsolete. However, we have seen Red Sea *P. audouini* with two rows of large tubercles, and Philippine *P. trapezium* without nodes are not uncommon. *Fasciolaria ponderosa*, usually considered a variety of *P. trapezium* from the northern Indian Ocean, has a single row of massive, spine-like tubercles at the shoulder. Further study will be needed to analyze the *P. trapezium* species complex. Other species are more distinctive: *Pleuroploca clava* from the northern Indian Ocean and northwestern Indonesia has prominent tubercles on the shoulder angulation and resembles a very colorful, low spired *P. trapezium*. *P. lyonsi*, endemic to southern Madagascar, has a smooth, more slender shell usually devoid of nodes or tubercles.

The earliest and only known fossil species of *Pleuroploca* is *Fasciolaria suryai* from the Late Miocene of East Borneo. Although Beets compared his species to *Fasciolaria filamentosa* and *Fasciolaria coronata* Lamarck 1822, (a synonym of *Australaria australasia* (Perry, 1811)), the species is actually closest to *P. trapezium*. At a length of 72 mm, *P. suryai* is small for the genus, but Beets clearly describes small folds abapical to the entrance fold on the inner side of the siphonal canal, which are characteristic of *Pleuroploca* but not *Filifusus* or *Australaria*. Spiral sculpture of *P. suryai* is sharper and more prominent than that of living *Pleuroploca* species. Axial ribs of *P. suryai* are also relatively more narrow and rounded, and extend in convex arcs from suture to suture across all teleoconch whorls, unlike those of its living congeners.

### *Africolaria* gen. nov.

Type species: *Fasciolaria rutila* Watson, 1882, selected herein.

Holotype: NHMUK 1887.2.9.839; 102.0 mm SL, by subsequent designation, Kaicher (1986: card 4632) (Fig. 13).

Description. — Shell of medium size for subfamily (3 species to 118, 140 and 196 mm SL), narrowly fusiform, lightweight, with large cylindrical to bulbous protoconchs, convex whorls and high spires; teleoconch sculpture of very fine spiral threads and short axial ribs, the latter absent in some specimens and highly developed in others; outer lip convex, without crenulations on edge, inner side smooth, lacking lirae; junction of outer lip with penultimate whorl lacking adapical notch; parietal ridge rounded to keel-like; columellar folds weak, entrance fold to siphonal canal developed to prominent and keel-like; inner side of siphonal canal without abapical folds. Radula of type species figured by G.B. Sowerby III (1903: pl. 3 fig. 2) and Barnard (1959: fig. 19c).

Included species:

*Fasciolaria rutila* Watson, 1882: Recent, Agulhas Bank to waters off Cape Town, South Africa, and northward to southern Namibia;

*Turbinella thersites* Reeve, 1847a: Recent, off Agulhas Bank; Cape St. Francis to Algoa Bay, South Africa;

*Fasciolaria (Pleuroploca) wattersae* Kilburn, 1974: Recent, off Agulhas Bank; Tsitsikama coast to Port Alfred, South Africa.

Etymology. — The name is a combination formed from Africa, the continent to which the genus is confined, and *Fasciolaria*, the genus in which the type species was introduced; like its stem name *Fasciolaria*, the gender is feminine.

Remarks. — In a review of what he called the *Fasciolaria lugubris* group, Kilburn (1993: 25) suggested that the temperate-water South African fasciolarine species agree in teleoconch and radular characters with the genus *Fasciolaria* in its broadest sense, but the species are distinguished from all others by their extremely large and bulbous protoconchs with basal diameters as great as 3-5 mm. Kilburn proposed that “recognition of the South African species-complex [in which he included *F. lugubris*, *F. rutila*, *F. scholvi*, *F. ther-*

sites and *F. wattersae*] at the subgenus level may ultimately prove warranted on grounds of protoconch size and perhaps [egg] capsule form." Here we divide this group into three endemic South African species groups representing the new genera *Africolaria* gen. nov., *Lugubrilaria* gen. nov. and *Kilburnia* gen. nov.

*Africolaria* gen. nov. differs from other fasciolarine genera in that the outer lip is not crenulated and the inner side of the outer lip is smooth, lacking lirae. Lighter shell weight, surface sculpture of fine spiral threads of uniform size, lack of paired surface spiral bands, relatively long siphonal processes and very thin periostracum also distinguish *Africolaria*, in various combinations, from all other fasciolarine genera. Reduced spiral sculpture also occurs in *Fasciolaria*, but spiral threads in *Africolaria* persist over the entire exterior shell surface, whereas in the American *Fasciolaria* parts of the body whorl may be devoid of spiral sculpture; axial ribs, usually present and sometimes prominent in *Africolaria*, are also absent in *Fasciolaria*.

There is considerable variation among species of *Africolaria* in the form and prominence of axial sculpture, in the morphology and prominence of the parietal ridge, and in the prominence of the entrance fold. In *A. thersites* the axial ribs are often raised into peculiar, strongly prosocline, ear-like structures with a steeply concave abapertural and a convex adapertural face. In other species, axial ribs are either absent or simple unelaborated axial swellings. The parietal ridges of *A. rutila* and *A. wattersae* are low and rounded, whereas the ridge of *A. thersites* may be keel-like, more sharply defined, and thus more prominent. The entrance fold of *A. thersites* is also extremely prominent and keel-like.

The periostracum of *Africolaria* species is greenish to pale yellow, very thin, and rather fragile. Of 90 live-collected specimens we examined (52 *A. rutila*, 18 *A. thersites*, 20 *A. wattersae*), only about 20% had a periostracum, which was more often retained on younger than on older specimens. The periostracum is darker, thicker, and more persistent on shells of *Lugubrilaria* and *Kilburnia*.

Radulae of *Africolaria* species have broad, multicuspid, typically fasciolarine lateral teeth. Numbers of cusps on laterals of fasciolarines increase with increasing size (age), but also differ among genera and species (Hollister, 1954; Maes,

1967). Lateral cusps of adult *Africolaria* are fewer (about 13 on *A. rutila* (Barnard, 1959: fig. 19c); about 10 on *A. wattersae* (Kilburn, 1974: fig. 16)) than are those of most other fasciolarine genera: *Fasciolaria* (about 30 on *F. tulipa* (Hollister, 1954: 45; Wells, 1970: 100)), *Cinctura* (about 16 on *C. hunteria* (Wells, 1970: 100)), *Pleuroploca* (18-28 on *P. trapezium* (Maes, 1967: 52)), *Filifusus* (17-21 on *F. filamentosus* (Maes, 1967: 52)), and *Triplofusus* (about 25-35 on *T. giganteus* (Hollister, 1954: 45)). In addition, lateral cusps among *Africolaria* species are broader, relatively shorter, and more recurved than the straighter, more slender, dagger-like cusps of *Fasciolaria*, *Cinctura*, *Pleuroploca*, *Triplofusus*, and *Filifusus*. Radular laterals of *Kilburnia* have recurved cusps that are relatively shorter and more numerous (about 18 on *K. heynemanni* (Barnard, 1959: fig. 19d)), whereas lateral cusps of *Lugubrilaria* are similar in shape and number (about 12 on *L. lugubris* (Barnard, 1959: figs 19a, b)) to those of *Africolaria*.

#### *Kilburnia* gen. nov.

Type species: *Fasciolaria heynemanni* Dunker, 1870, selected herein.

Lectotype: specimen figured as *Fasciolaria purpurea* Jonas var. Dunker, 1867 in [1858-1870]: pl. 32 figs 1, 2, selected herein (Fig. 14).

Description. — Shell moderately large for subfamily (largest species to 237 mm SL), with large protoconch and high spire; axial sculpture of short ribs on upper part of body whorl, forming two rows of nodes on each of the last three whorls; spiral cords low, rounded; outer lip convex, its edge with paired crenulations, its inner side bearing very short smooth lirae; adapical notch absent; parietal ridge prominent; rounded; entrance fold to siphonal canal prominent, keel-like, much more strongly expressed than the two columellar folds; folds on inner edge of siphonal canal absent. Radula of type species described and figured by Barnard (1959: 79, fig. 19d).

Included species:

*Fasciolaria agulhasensis* Tomlin, 1932: Recent, eastern South Africa;

*Fasciolaria alfredensis* Bartsch, 1915: Recent, eastern South Africa;

*Fasciolaria dunkeri* Strebel, 1911: Recent, eastern South Africa;

*Fasciolaria heynemanni* Dunker, 1870: Recent, eastern South Africa;

*Fasciolaria scholvieni* Strebel, 1911: Recent, Agulhas Bank, South Africa;

*Fasciolaria strebeli* Fulton, 1930: Recent, eastern South Africa.

**Etymology.** — This name honors Richard N. Kilburn who has contributed enormously to our knowledge of the malacology of South Africa; the gender is feminine.

**Remarks.** — See Snyder et al. (2010) for the date of description of the type species. Species here assigned to the genus *Kilburnia* gen. nov. were included by Kilburn (1993) in his *Fasciolaria lugubris* species group, the other members of which are referred to our new genera *Africolaria* and *Lugubrilaria*. In fact, Kilburn considered *Fasciolaria heyne-manni*, the type species of *Kilburnia*, as an eastern subspecies of *F. lugubris*, but we consider them not only to be separate species but representatives of separate genera; for more on this see remarks for *Lugubrilaria*. *Kilburnia* gen. nov. resembles *Africolaria* gen. nov. in often having a keel-like entrance fold to the siphonal canal, but it differs in having a convex, crenulated outer lip, a lirate inner side of the outer lip, and a more nodose axial sculpture. Comparisons with the new genus *Australaria* are given under that genus (below). *Kilburnia* gen. nov. is known thus far only from the Recent of South Africa.

#### ***Lugubrilaria* gen. nov.**

Type species: *Fasciolaria lugubris* A. Adams & Reeve, in Reeve, 1847b, selected herein.

Lectotype: specimen figured by Reeve, 1847b: pl. 1 fig. 2a, selected herein (Fig. 15).

**Description.** — Shell of medium size for subfamily (3 species to 101, 110 and 179 mm SL), broadly to narrowly fusiform, with cylindrical protoconchs, convex whorls and moderate to high spires; teleoconch sculpture of coarse to fine spiral cords and threads and low axial ribs, latter being absent in one species; outer lip convex; (usually) paired lirae on inside of outer lip correspond to paired spiral threads and grooves on outer surface of body whorl, inner lirae and outer threads and grooves intersecting to form (usually) bifid denticles on crenulated edge of outer lip; parietal ridge elevated, keel-like, prominent, sometimes accompanied by 1-3 smaller parallel ridges; columellar folds weak, entrance fold to siphonal

canal weakly to rather strongly developed, keel-like; inner side of siphonal canal without abapical folds. Radula of type species described and figured by Troschel (1868: 63, pl. 5 fig. 16; as *Fasciolaria badia* Krauss, 1848, a synonym) and Barnard (1959: 76, fig. 19a, b).

Included species:

*Fasciolaria lugubris* A. Adams & Reeve, in Reeve, 1847b: Recent, Cape Agulhas, southern Indian Ocean to St. Helena Bay, Atlantic coast of South Africa and northward to Namibian border; problematic records along Namibian coast;

*Fasciolaria badia* Krauss, 1848 (= *Fasciolaria lugubris* Adams & Reeve, 1847); Recent, southern South Africa;

*Fasciolaria dinglei* Kensley & Pether, 1986: Pliocene, western Cape Province, South Africa.

**Etymology.** — This name is Latin, a combination of the type species *lugubris*, meaning mournful, i. e., draped in a funeral garment, with reference to the persistent dark periostracum, and *Fasciolaria*, the genus in which the type species was introduced; the gender is feminine.

**Remarks.** — Reeve (1847b) indicated that his figured specimen of *Fasciolaria lugubris* was in the Hanley collection, but we were unable to find any extant type material. However, illustrations by Reeve and by Krauss serve to identify the species and we select the specimen depicted in Reeve's figure as the lectotype.

Shells of the type species, *L. lugubris*, occur with or without slightly angled or shouldered whorls, produced by the presence or absence of a larger cord at the whorl periphery. Shells of each condition are shown in figures by Marais & Kilburn (2011: 110). Both Reeve's figured specimen and the specimen originally figured as *Fasciolaria badia* Krauss (1848: pl. 6 fig. 12), a synonym, have the shouldered condition, which may thus be considered typical.

Marais & Kilburn (2011: 110) labeled their shouldered shell as showing characters intermediate between "*Fasciolaria lugubris lugubris* and *Fasciolaria lugubris heyne-manni*," but we reject the implied relationship and classify the two species in separate genera. Among other characters, *Lugubrilaria* shells lack the row of well-developed nodes on the

shoulder that characterize all species of *Kilburnia*; the entire surface of *Lugubrilaria* shells is covered with densely packed coarse to fine spiral cords and threads, whereas the surface of *Kilburnia* shells has relatively few low, broad spiral ridges which may be virtually obsolete in some populations. The outer lip of *Kilburnia* has a marked angle at the periphery, a consequence of the peripheral nodes, but the outer lip of *Lugubrilaria* is only slightly inflected by the corresponding peripheral cord, and even that cord is often absent.

Species of *Lugubrilaria* are distinguished from those of *Africolaria* by the lirate sculpture on the inner side of the outer lip, the paired series of cords and threads on the shell outer surface, and the resultant crenulations where cords and grooves meet on the outer lip. *Lugubrilaria* shells also have tough, relatively thick and dark periostracum which commonly persists on adult shells.

The Recent species of *Lugubrilaria* have limited ranges along the southwestern coast of Africa. *Lugubrilaria lugubris* is known with confidence from Cape Agulhas in the southern Indian Ocean around the Cape of Good Hope and northward to the vicinity of St. Helena Bay, South Africa. More northern records of *L. lugubris* from along the western coast of South Africa and Oranjemund at the southern Namibian border (Richards, 1988: 35; Steyn & Lussi, 1998: 124) need confirmation.

The identity of *L. dinglei* (Kensley & Pether, 1986) is problematic. Carrington & Kensley (1969) reported two shells from Pleistocene deposits near Hondeklip Bay on the Namaqualand coast as *Fasciolaria* sp. and in their figure caption identified those shells as *F. lugubris*; this was perhaps the source of the Namaqualand range limit that Kilburn & Rippey (1982) cited for *F. lugubris*. Kensley & Pether (1986: 189, 190, figs 27, 28) then described *F. dinglei* from supposed Pliocene beds along the west coast. All of the features they described for *F. dinglei* fit *F. lugubris*, and their photographs of the intact holotype and partial paratype depict shells very similar to those of *F. lugubris*. Based on available information we suspect the names to be synonyms, but verification using side-by-side comparison of specimens is recommended.

Kensley & Pether (1986) may have described *L. dinglei* because they did not understand the identity of *L. lugubris*, as

indicated by their statement “The most distinctive feature of [*dinglei*] is the presence of three pleats [folds] on the columella (*F. lugubris* is unpleated).” This indicates that they confused *F. lugubris* with *Fusinus cinnamomeus* (Reeve, 1848), a species that lives sympatrically with *L. lugubris*. Shells of *Fusinus cinnamomeus* are very similar in sculpture, color and periostracum to those of *L. lugubris* and they are often misidentified in collections. The feature that distinguishes them best is a subfamilial character – shells of *F. cinnamomeus* lack abapical columellar folds that characterize all fasciolarini. These are the “pleats on the columella” that Kensley & Pether said were lacking in *F. lugubris*.

Given the aforementioned confusion between taxa, it seems that specimens that prompted Carrington & Kensley’s Namaqualand record may have been *F. cinnamomeus*, not *L. lugubris*. The range of *F. cinnamomeus* does not seem to extend around the Cape of Good Hope to False Bay, but it does extend northward to southern Namibia (live-collected specimens at SBMNH and WGL), so Namaqualand is well within the range of that species. Specimens we examined from Saldanha Bay, Paternoster, and Jacob’s Bay along the western coast, together with Barnard’s (1959) report of Recent records from Saldanha Bay and St. Helena Bay, establish the northernmost confirmed range of *L. lugubris*, but occurrence farther north seems feasible. The Pliocene record of *L. dinglei*, the immediate predecessor to or more likely a synonym of *L. lugubris*, supports such occurrence. An additional new species of *Lugubrilaria* will be described by W.G. Lyons in a separate paper.

#### *Australaria* gen. nov.

Type species: *Pyruia australasia* Perry, 1811, selected herein.

Lectotype: specimen figured by Perry, 1811: pl. 54 fig. 4, selected herein (Fig. 16).

Description. — Shell small to medium-sized for subfamily (largest species to 190 mm SL), high-spired, fusiform; axial sculpture of short, narrow, sharply rounded ribs, forming one or more rows of nodes at intersections with spiral cords; shoulder angulation often sharp, keel-like in some species; outer lip weakly convex, with paired crenulations at its edge, its inner side with short smooth lirae; adapical notch

absent; entrance fold to siphonal canal prominent, often keel-like, much more strongly expressed than the very weak columellar folds; abapical folds on inner edge of siphonal canal absent; parietal ridge prominent, rounded. Radula of type species described and figured by Verco (1895: pl. 3, fig. 8) as *Fasciolaria coronata* Lamarck, 1822, a junior synonym.

Included species:

- Pyrula australasia* Perry, 1811: Recent, southeastern Australia;  
*Fasciolaria bakeri* Gatliff & Gabriel, 1912: Recent, eastern Australia;  
*Fasciolaria coronata* Lamarck, 1822: Recent, southeastern Australia;  
*Fasciolaria cristata* Tate, 1888: Middle Miocene, southern Australia;  
*Fasciolaria cryptoploca* Tate, 1888: Middle Miocene, southern Australia;  
*Pleuroploca eucla* Cotton, 1953: Recent, Western Australia;  
*Fasciolaria fusiformis* 'Valenciennes' Kiener, 1840: Recent, southeastern Australia;  
*Fasciolaria fusilla* Tate, 1889: Middle Miocene, southern Australia;  
*Siphonalia lamellifera* Tate, 1888: Middle Miocene, southern Australia;  
*Fasciolaria rugata* Tate, 1888: Middle Miocene, southern Australia;  
*Australaria tenuitesta* Snyder, Vermeij & Lyons, new species (herein): Recent, central Queensland to New South Wales; Papua New Guinea?

Etymology. — This name is a combination of *austral* (southern) or Australia and *Fasciolaria*; the gender is feminine.

Remarks. — Morphologically, shells assigned to *Australaria* cover a range of variation similar to those of *Lugubrilaria* gen. nov. and *Kilburnia* gen. nov.. Recent specimens, which Wilson (1994) treated as the single highly variable and widespread temperate Australian taxon *Pleuroploca australasia*, vary in the strength and number of spiral cords, but all have at most a single row of nodes at the shoulder angulation. In some specimens of the typical form of *A. australasia* from South Australia and Victoria, nodes are entirely absent, and the shoulder angulation is rounded. Cotton (1953) divided the Australian material into several species, collectively ranging from southern Queensland to Western Australia. We tentatively prefer this approach in view of the nonplanktonic mode of development in *Australaria* and the demonstrated genetic divergences among populations in other temperate Australian gastropod taxa with this type of development. However, molecular sequence data are needed to

clarify the specific composition of Recent members of the genus. Perry's figure serves to illustrate the common smooth form of *A. australasia*, later named *fusiformis* Kiener, 1840 (see Hedley, 1902: 27, 28 and Pritchard & Gatliff, 1905: 43) and we select the specimen depicted in that figure as the lectotype.

Two fossil species were examined, Tate's *Fasciolaria cristata* and *F. cryptoploca*, both from the Middle Miocene of Victoria. They differ from the Recent taxa in their much smaller size (maximum SL 72 mm) and their much stronger sculpture. In *F. cristata* there are eight to nine high axial ribs per whorl, forming four rows of nodes whose prominence decreases abapically on the body whorl. The shoulder angulation is a high keel. The siphonal process is exceptionally long, comprising about 40% of total shell length. *F. cryptoploca* has about ten axial ribs, five rows of nodes on the body whorl, a more cylindrical profile of the upper part of the body whorl, and a shorter siphonal canal. Other fossil taxa are likely to belong to *Australaria* and we have listed them as *included species* but have been unable to examine specimens of these species. Ponder (1973: 402) concluded that *Siphonalia lamellifera* was wrongly assigned by Tate (1888) and Darragh (1970) (to *Penion*, as now interpreted). Ponder tentatively placed it in *Pleuroploca* because it has two folds on the columella. Other species likely to belong to *Australaria* are *Fasciolaria fusilla* and *F. rugata*, both also from the Middle Miocene of Victoria.

Several fasciolarini elsewhere in the world share with *A. cristata* and *A. cryptoploca* the character of multiple rows of nodes. In *Aurantilaria aurantiaca* from Brazil, there can be up to five such spiral rows, but these are distributed over the whole of the body whorl rather than in the upper sector only. Species of *Pleuroploca* in the Indo-West Pacific and of the South African genus *Kilburnia* can have two widely separated spiral rows of nodes, again unlike the four to five rows concentrated on the upper sector of the body whorl in fossil species of *Australaria*.

Although we cannot unambiguously separate the South African *Kilburnia* from the Australian *Australaria* on shell characters, we provisionally maintain them as distinct genera because of their likely long separate histories. Broad indirect support for this action comes from molecular data

and phylogenetic relationships in other largely tropical clades that have endemic, separate South African and Australian temperate representatives, including Turbinidae (Williams, 2007), Cypraeidae (Meyer, 2003), and Littorinidae (Reid & Williams, 2004). Again, molecular work is needed to settle this matter.

There is an additional deep-water species of *Australaria* from eastern Australia which we take this opportunity to describe.

*Australaria tenuitesta* spec. nov. (Fig. 17)

*Pleuroploca* sp.: Hinton, 1978: 32, fig. 7;

*Pleuroploca australasia* "bakeri" form: Wilson, 1994: 254, pl. 12 fig. 2c.

Description. — Shell elongate, fusiform, with high spire and long siphonal process, of moderate size for genus (to 141.1 mm SL); protoconch elongate, large, maximum diameter 3.5 mm; teleoconch of seven sharply angulate whorls separated by adpressed sutures; spire whorls marked by central peripheral keel; abapical and adapical sectors of spire whorls strongly sloping; spiral keel bearing ten to twelve sharp, spirally elongate, axially compressed nodules; adapical sector of spire whorls initially with five fine sharp spiral threads, increasing to twelve on penultimate and body whorls; abapical sector of spire whorls initially with three spirals, increasing to eight on penultimate whorl; body whorl with keel bearing twelve to fifteen nodules; below the keel a much weaker angulation coincides with the continuation of the suture line; spiral sculpture abapical to the spiral keel consists of about twenty fine but sharp threads on convex part of whorl, and another twenty on constriction and siphonal process, weakening abapically; outer lip thin, sharp, crenulations reduced or absent; inner side of outer lip with twenty very fine continuous lirae; parietal ridge rounded and very weak; entrance fold to siphonal canal rounded to almost keel-like; immediately adapical to it are one or two very weak columellar folds. Shell color white or straw to pale orange or pale lilac, sometimes with patches of brown near peripheral nodes, less commonly with faint brown and white bands encircling spire and body whorl. Operculum brown, obliquely tapered anteriorly, with fine concentric growth increments on outer surface.

Type material. — Holotype: 105.4 mm, in Capricorn Channel, depth 240 m (ANSP 425075). Paratypes: Queensland: 89.9 mm, Hydrographers Passage, depth 120-140 m (ANSP 425068); 91.2 mm, off Swain Reefs, depth 180-210 m (WGL); 85.5 mm, off Lady Musgrave Island, depth 220 m (BMSM 17950); 93.3 mm, east of Lady Musgrave Island, depth 220 m (WGL); 141.1, 119.9 & 95.7 mm, off Mooloolabar, depth 80-120 m (WGL/3); 92.6 mm, Capricorn Channel, depth 80-100 m (WGL); 94.3 mm, Capricorn Channel, depth 80-100 m (UF 447275); 120.0 mm, off Cape Moreton, no depth recorded (WGL); 82.2 mm, off southern end of Swain Reefs, depth 200 m (MNHN); 88.9 mm, off southern end of Swain Reefs, depth 200 m (NHMUK); 87.0 mm, east of Lady Musgrave Island, depth 300-400 m (AMS); 85.4 mm, east of Lady Musgrave Island, depth 300-400 m (NSMT). New South Wales: 126.3, 99.1 & 89.3 mm, Brunswick Heads, no depth recorded, (WGL/2); 85.9 & 81.0 mm, Broken Bay, no depth recorded (ANSP 425074/2).

Type locality. — Capricorn Channel, Queensland, depth 240 m.

Range. — Central Queensland southward to central New South Wales; Papua New Guinea?; depth range 80-400 m.

Other material examined. — Queensland. In WGL: 83.4mm, off Swain Reefs, depth 80-100 m; 90.2, 84.9, 83.6 & 76.1 mm, off Swain Reefs, depth 100 m; 92.6 & 92.2 mm, off Swain Reefs, depth 100 m; 96.2 & 92.9 mm, off Swain Reefs, depth 100 m; 69.6 mm, off Swain Reefs, depth 100-120 m; 87.0 mm, off Swain Reefs, depth 180-210 m; 77.1 mm, off Swain Reefs, depth 180-210 m; 80.7mm, off Swain Reefs, depth 180-202 m; 76.9 mm (siphon broken and regenerated), off Swain Reefs, depth 240 m; 79.9 mm, off Swain Reefs, depth 250 m; 79.0 mm, off Swain Reefs, "deep water"; 88.7 & 87.1 mm, off Swain Reefs, depth not recorded; 82.8 & 75.3 mm, off Swain Reefs, depth not recorded; 82.9, 82.6 & 80.6 mm, off Swain Reefs, depth not recorded; 82.2 & 81.6 mm, southeast of Swain Reefs, depth 220-227 m; 83.9 mm, off Hixson Cay, depth 210-240 m; 75.8 & 60.1 mm, off Hixson Cay, depth 160-175 m; 85.5 & 66.6 mm, off Hixson Cay, depth 160-175 m; 93.3 mm, off Bundaberg, depth 200 m; 116.5 mm, off Cape Moreton, depth not recorded; 105.9 & 79.5 mm, off Moreton Bay, depth not recorded; 70.4 mm, off Surfer's Paradise, depth 90-100 m; 87.4 & 87.3 mm, "Queensland," depth ~ 128 m. In ANSP: 83.6 & 81.4 mm, off Swain Reefs, depth 160 m (ANSP 425073/2); 89.8 & 70.1 mm, off Swain Reefs, depth not recorded (ANSP 425070/2); 67.6 & 66.0 mm, east of Swain Reefs, depth 240 m (ANSP



425076/2); 73.4 mm, southern end of Swain Reefs, depth 200 m (ANSP 425072); 99.6, 98.4 & 84.5 mm, Lady Musgrave Island, depth 200 m (ANSP 425067/3); 93.2 mm, Fitzroy Reef, Bunker Group, depth 260 m (ANSP 425066); 83.4 & 74.1 mm, Capricorn Channel, depth 140 m (ANSP 425071/2); 89 mm, off Cape Moreton, no depth recorded (ANSP 425069).

**Etymology.** — The species name is Latin and derives from *tenuis*, thin, and *testa*, shell, referring to the thin shell; it is a feminine noun.

**Remarks.** — This distinctive northern offshore species of *Australaria* differs from congeners by its sharply angled whorls, peripheral keel bearing ten to fifteen spirally elongate nodules, and the fine but sharp spiral sculpture. Apertural folds are very weakly developed. The shell is notably thin, elongate, and high-spired.

*Australaria tenuitesta* spec. nov. occurs off northern New South Wales and Queensland in lower latitudes and greater depths than those occupied by its congeners; most specimens we examined were taken in the trawl fishery conducted near the Swain Reefs off central Queensland, usually in depths between 100 and 240 m, but occasionally from as shallow as 80 m or as deep as 400 m. Shells from off Swain Reefs tended to be smaller than those from most localities and were usually entirely white or straw (e.g., see Wilson, 1994: pl. 12 fig. 2c), unlike more colorful shells from several other localities (e.g., see Hinton, 1978: 32, fig. 7). Hinton figured his specimen as *Pleuroploca* sp., which he cited as rather scarce in trawls off Yule Island, Gulf of Papua; if confirmed, this would be the northernmost occurrence of the species.

#### GENERA EXCLUDED FROM FASCIOLARIINAE

Subfamily Peristerniinae

##### *Tarantinaea* Monterosato, 1917

Type species: *Tarantinaea lignaria* [sic] Linnaeus, Recent, Mediterranean Sea, = *Murex lignarius* Linnaeus, 1758, by monotypy.

Lectotype: specimen figured by Buonanni, 1684: fig. 32, by subsequent designation, Pallary (1900: 267) (Fig. 18).

Included species:

*Turbinella crassicostata* Michelotti, 1847: Late Miocene, Italy and France;  
*Fusus danconae* Pecchioli, 1864: Pliocene, Italy;

*Murex fimbriatus* Brocchi, 1814: Miocene and Pliocene, Europe (including many forms);

*Fasciolaria lawleyana* d'Ancona, 1872: Pliocene, Italy;

*Murex lignarius* Linnaeus, 1758: Pleistocene (?) and Recent, Mediterranean Sea;

*Fasciolaria pecchiolii* Semper, 1861: Pliocene, France and Italy.

**Remarks.** — The inclusion of *Fusus danconae* in *Tarantinaea* was first suggested by Glibert (1963: 136) with the use of the combination *Fasciolaria* (*Tarantinaea*?) *d'anconae* [sic]. This species is one of the five originally assigned to the genus *Plesiolatirus* when it was introduced by Bellardi (1884: 32). We remark on this in some detail since Malatesta (1974: 344) selected *Fusus danconae* as the type of *Plesiolatirus*. He was apparently unaware that Cossmann (1901: 42) had already made a type designation for this genus: *Latirus* (*Plesiolatirus*) *nodosus* Bellardi, 1884, derived from a Michelotti manuscript name (as *Fasciolaria*). The holotype of *L. nodosus*, illustrated by Tampieri (1981: pl. 38 fig. 3), is a very poor badly broken specimen from the Oligocene of Italy. Were *L. nodosus* to be placed in *Tarantinaea* the genus would become a junior synonym of *Plesiolatirus* but the type of material of the latter genus is sufficiently poor that we cannot make such a judgement.

The five species Bellardi originally included in *Plesiolatirus* form a disparate group and seem unlikely to be congeneric. These species are as follows:  
Series 1. *Latirus nodosus* Bellardi, 1884: Oligocene, Italy.  
Series 2. *Fusus danconae* Pecchioli, 1864: Pliocene, Italy.  
Series 3. *Fasciolaria fusoidea* Michelotti, 1847: Miocene, Italy;  
*Latirus* (*Plesiolatirus*) *aratus* Bellardi, 1884: Pliocene, Italy.  
Series 4. *Latirus* (*Plesiolatirus*) *proximus* Bellardi, 1884: Pliocene, Italy.

This group requires careful study, which is beyond the scope of this paper.

*Murex lignarius* was reclassified in *Fasciolaria* by Lamarck (1822) and retained there in all subsequent monographic treatments of the genus (e.g., Reeve, 1847b; Kobelt, in Küster & Kobelt, 1844-1876; Tryon, 1881; G.B. Sowerby II, 1882;

Strebel, 1911); the only exceptions were by Melvill (1891), who classified the species in *Latirus*, and Coen (1914) who placed it in *Pleuroploca* (as a subgenus of *Fasciolaria*). Pallary (1900: 267) remarked that the type of *Murex lignarius* was figured by Buonanni (1684: fig. 32), and this remark constitutes subsequent designation of a lectotype. Although nearly universally treated as feminine, Rosenberg & Petit (2003: 115) pointed out that the species name *lignarius* is a masculine noun whose ending does not change to modify the gender of its genus.

Perhaps uncomfortable with previous classifications, Monterosato (1917) introduced *Tarantinaea* as a genus-level taxon to contain a single living Mediterranean species, *T. lignarius* (Linnaeus, 1758). Thiele (1929) and Wenz (1943) treated *Tarantinaea* as a section and subgenus, respectively, of *Fasciolaria*. Wenz' classification of *Tarantinaea* as a subgenus was adopted by a few workers (e.g., Glibert, 1963; Nordsieck, 1968; Settepassi, 1985), but a great majority of reports have continued to maintain *lignarius* in *Fasciolaria*, with no mention of *Tarantinaea*.

Pending molecular confirmation we consider this genus to represent a clade of Peristerniinae. The most distinctively peristerniine feature is the adapical sinus on the outer lip. This sinus is typical of most Peristerniinae, but it is not present in Fascioliinae except in *Kilburnia*, especially the Transkei population of *K. heynemanni* where it is prominent. The radula of *T. lignarius*, described and figured by Gray (1857: 28, fig. 14); Troschel (1868: 63, 64, pl. 5 fig. 17), Kobelt, in Küster & Kobelt (1876: pl. 32 fig. 8), Orr (2000: 137, fig.) and Kosyan et al. (2009: 102, fig. 36), has fewer, shorter and more curved cusps on laterals, thereby resembling radulae of Peristerniinae more than those of Fascioliinae.

Philippi (1844) and Glibert (1963) mentioned Pleistocene records for *P. lignarius*, but these need verification. We also include in this group of peristerniines five Miocene and Pliocene species, all with taxonomic histories much too extensive to present but which we summarize here. Four of them are well illustrated by Chirli (2000). Most of these species have been moved back and forth between the genus *Fasciolaria* (sometimes in the subgenus *Pleuroploca* or rarely in *Tarantinaea*) (see e.g., Cossmann, 1901; Glibert, 1963) and the peristerniine genus *Latirus* Montfort, 1810 in the broad

sense (see e.g. Bellardi, 1884; Sacco, 1890; Montanaro, 1934; Muñiz Solis, 1988). *Latirus*, however, is a different genus restricted to the Indo-West Pacific region, and the European fossils lack features that characterize *Latirus s.s.* as redefined by Vermeij & Snyder (2006). Instead, we interpret features of shell morphology (columellar folds, external shell sculpture, etc.) of the fossil taxa to most resemble those of the Recent species *T. lignarius*, prompting our placement of them here.

#### *Neolatirus* Bellardi, 1884

Type species: *Fasciolaria recticauda* Fuchs, 1877, Miocene, southern Europe, by subsequent designation, Cossmann (1901: 45).

Lectotype: specimen figured by Fuchs, 1877: pl. 16 fig. 3, designated herein (Fig. 19).

Included species:

*Fasciolaria bellardii* M. Hörnes, 1854, in [1851-1856]: Miocene, Central Europe [renamed *Latirus (Neolatirus) danubicus*];

*Latirus (Neolatirus) danubicus* Strausz, 1960: Miocene, Europe;

*Latirus (Neolatirus) obliquicauda* Bellardi, 1884: Miocene, Italy;

*Fasciolaria recticauda* Fuchs, 1877: Miocene, southern Europe.

Remarks. — Several species, including the type species of *Neolatirus*, have been referred to *Fasciolaria*, although most recent authors attribute these species to *Latirus* Montfort, 1810, with *Neolatirus* as subgenus (see e.g. Strausz, 1960, 1966). Species of *Neolatirus* are characterized by the disappearance of axial sculpture on later teleoconch whorls, by a lirate or smooth inner side of the outer lip, by the presence of a parietal ridge, and by having one columellar fold in addition to the entrance fold to the siphonal canal. On the basis of the columellar characters, we assign *Neolatirus* as a distinct genus to the Peristerniinae. Species belonging to *Neolatirus* range from the Middle to Late Miocene in age and are confined to southern Europe and the Paratethys region.

Although we have not seen specimens of this species, photographs of actual specimens by Csepregy-Meznerics (1956: pl. 8, figs 1,2) agree closely with Fuch's original figure, and in consequence we select the specimen depicted in Fuch's original figure as the lectotype.

#### *Pleia* Finlay, 1930

Type species: *Fasciolaria decipiens* Tate, 1888, = *Fasciolaria tenisoni* Teni-

son- Woods, 1879, fide Beu (2011: 67); by original designation. Lectotype: specimen figured by Tate, 1888: pl. 8 fig. 1, designated herein (Fig. 20).

Included species:

*Fasciolaria tenisoni* Tenison-Woods, 1879: Middle Miocene (Muddy Creek Formation), Victoria, Australia;

*Fasciolaria concinna* Tate, 1888: Middle Miocene, Schnapper Point, Victoria, Australia;

*Fasciolaria decipiens* Tate, 1888: Middle Miocene (Muddy Creek Formation), Victoria, Australia.

Remarks. — Finlay (1930) designated *Fasciolaria decipiens* Tate, 1888, from the Middle Miocene Muddy Creek Formation of Victoria, Australia, as type species of *Pleia*, a genus he introduced to accommodate *Pleia otaioensis* Finlay, 1930, Miocene, New Zealand. Tate's excellent figure clearly illustrates the type species, and we select the specimen depicted in that figure as the lectotype. Cotton (1957) added *Fasciolaria concinna* to *Pleia*, and Darragh (1970) later added *Fasciolaria tensioni*; both of these species are also from the Middle Miocene of Victoria. Dell (1956) and Powell (1979) tentatively added *P. cryptocarinata* Dell, 1956, a Recent bathyal species from the Chatham Rise.

Beu (2011: 67-71) re-evaluated *Pleia* and made the following revisions: 1) the Early Miocene *P. otaioensis* and Recent *P. cryptocarinata* were transferred to a new genus, *Cryptofusus* Beu, 2011, which was assigned to Turbinellidae; 2) per a personal communication from T. A. Darragh, Beu accepted *F. decipiens* as a junior synonym of *F. tenisoni*, making that the first available name for the type species of *Pleia*; and 3) *Pleia* was removed from Fasciolarinae and reclassified in the subfamily Peristerniinae.

*Pleia tensioni* has two rows of nodules, one at the shoulder angulation and one on the central cord on the last whorl demarcating the base. There is one deeply recessed columellar fold.

Subfamily Fusininae, Wrigley, 1927

***Viridifusus* gen. nov.**

Type species: *Fusus buxeus* Reeve, 1847, designated herein.

Lectotype: specimen figured by Reeve, 1847 in [1847-1848]: pl. 5 fig. 18, designated herein (Fig. 21).

Description of shell. Shell small to medium-sized for Fusininae (largest species to 112 mm SL), broadly fusiform, with relatively short siphonal process; teleoconch with rounded whorls, sculptured with narrow rounded axial ribs crossed by numerous rugose cords which do not form nodules on axial ribs; outer lip almost planar, its edge with closely set pairs of crenulations, its adaxial side with distinct lirae that are coarsely beaded; inner lip smooth, erect for most of its length; parietal ridge and columellar folds absent. Radula of type species described and figured by Rolán & Schoenherr (1997: 48-51, fig. 22; as *Fusinus buxeus*).

Included species:

*Fusus buxeus* Reeve, 1847: Recent, Cape Verde Archipelago;

*Latirus maximus* G.B. Sowerby III, 1893: Recent, Cape Verde Archipelago.

Etymology. — This name is derived from the Latin *viridis*, green, and refers to the type locality, the Cape Verde Islands; the gender is masculine.

Remarks. — We designate *Fusus buxeus* Reeve, 1847, Recent, Cape Verde Archipelago, eastern Atlantic Ocean, as the type species of *Viridifusus*. A thorough search of the NHMUK collection has failed to turn up Reeve's original material. However, his 1847 illustration serves to identify this species and we select the specimen depicted in that figure as the lectotype. We recognize *Viridifusus* as a distinct genus of West African fusinines for a group of broadly fusiform species with a nearly planar outer lip and a relatively short siphonal process. Although species in this genus have been variously assigned to *Fusus* (Reeve, 1847), *Neptunea* (H. & A. Adams, 1853), *Fasciolaria* (Petit de la Saussaye, 1856), *Turbinella* (Kobelt in Küster & Kobelt, 1876), *Siphonalia* (Tryon, 1881), *Austrofusus* (Tryon, 1881), *Latirus* (G.B. Sowerby III, 1893), *Fusinus* (Kaicher, 1978) and *Pleuroploca* (Abbott & Dance, 1982), an inspection of the radula of the type species demonstrates *Viridifusus* to belong to the Fusininae (Rolán & Schoenherr, 1997). The absence of columellar folds is consistent with this assignment.

*Saginafus* Wenz, 1943

Type species: *Saginafus princei* [sic] = *Fusus pricei* E. A. Smith, 1887, by original designation.

Lectotype: Two syntypes NHMUK 82.3.25.1, 156.6 mm and 87.2.2.2, 38.8 mm SL, the larger mature specimen designated herein as lectotype (Fig. 22).

Remarks. — The enigmatic genus *Saginafus*, with shells measuring up to 240 mm SL, has typically been assigned to the Fascioliidae (Wilson, 1994). Wilson described it as *Pleuroploca*-like but lacking columellar folds. Based on our examination of shell characters, we assign this genus to the Melongenidae, although even in this family its shell features are unusual. Two characteristics in particular stand out as atypical for either family: a reflected, determinate, polished outer lip bearing paired crenulations that are strongest on the lower part of the convex central sector; and axial sculpture of narrow short ribs that are absent on early whorls and commence only on later teleoconch whorls. The early whorls bear only spiral cords. There is a thick periostracum.

Within Melongenidae, *Saginafus* is closest to *Hemifusus* Swainson, 1840, a group of large gastropods known from Japan to Indonesia. *Saginafus* differs from *Hemifusus* by having a determinate outer lip and in having axial ribs that commence late in ontogeny. It is notable that the geographic range of *S. pricei* (Kimberley, Western Australia, to northern New South Wales (Wilson, 1994), Gulf of Papua (Hinton, 1972: 32, pl. 16 fig. 4), and recently in southern Indonesia) lies outside the distributional limits of *Hemifusus*. There is no known fossil record of *Saginafus*. We suspect that examination of a radula of *Saginafus pricei* will confirm our familial assignment.

This genus is usually attributed to Iredale, 1931. However, he gave no description of the genus so his introduction of the name was invalid under ICZN Art.13.1.1, as was its subsequent use by Thiele (1934: 1000), and the name must be attributed to Wenz, 1943 (private communication, P. Bouchet, 2012).

*Pleuroploca granulilabris* Vermeij & Snyder (2004):

This species from Brazil was named as a member of what the authors termed the *Pleuroploca filamentosa* species group. Although the species superficially resembles *Filifusus* in having a simple convex outer lip and generally similar shell sculpture, we here reassign it to the Amphiatlantic peristerniine genus *Leucozonia* Gray, 1847. This reassignment was previously made by Rosenberg (2009) electronically. The Brazilian species belongs to that section of *Leucozonia* in which a labral tooth is absent (see Vermeij & Snyder, 2002). The species differs from *Filifusus* in having weak outer-lip crenulations, in lacking the sharp entrance fold, and in having a marked adapical sinus on the outer lip. The last character state is typical of Peristerniinae but absent in Fascioliinae.

*Fasciolaria insularis* Fernández, 1977:

We cannot accept Rosenberg's (2009) suggestion that this recent species, collected off Isla de los Estados, southernmost Argentina, appears to be a buccinid (*Prosipho* or *Cavineptunea*) or a turbinellid (*Ptychatractus*). Absence of columellar folds excludes the species from *Fasciolaria* and Fascioliinae, but its radular morphology (small, narrow, tricuspid central tooth flanked by single, broad laterals bearing about 15 short, recurved cusps) dictates that the species be retained in Fascioliidae. We suspect that the species represents an unnamed, cold-water clade in Fascioliidae similar to the endemic New Zealand taxa *Taron* Hutton, 1883 and *Glaphyrina* Finlay, 1927, whose radulae (see Ponder, 1968: pls 2 figs 17-19; Powell, 1929: fig. 132) seem to be typically peristerniine and fusinine respectively. The *Ptychatractus* radula is illustrated by Harasewych (1987, fig. 19). The radula of "*F.*" *insularis* is different than those of these genera and in fact any other fascioliid genus; its laterals are extraordinarily high at their inner margins but taper quickly as they proceed to their slender distal tips. The radula of the monotypic peristerniine genus *Opeatostoma* Berry, 1958 also has laterals with unusually high inner margins (Kosyan et al., 2009: 102, fig. 37), but those margins are associated with a greatly enlarged inner cusp, not a general enlargement of the lateral

structure as in "*F.* *insularis*, and its laterals are not tapered distally.

*Fasciolaria agatha* Simone & Abbate, 2005:

This Recent species, collected at 260 m on the Canopus Bank, 120 miles off Fortaleza, Ceará, northeastern Brazil, was transferred to the genus *Fusinus* by Rosenberg (2009), and we concur.

#### BIOGEOGRAPHY

Fascioliariinae in the New World are confined to tropical and warm-temperate zones, but in the Old World they also extend into much colder environments. Of the zoogeographic provinces with fasciolarines, most support only a few species, but there are notable exceptions. The Tropical Eastern Pacific supports three species (two *Granolaria*, one *Triplofusus*), the Brazilian two (one *Aurantilaria* plus one *Fasciolaria* slightly overlapping from the north), and the Caribbean Sea three (two *Fasciolaria* plus one *Aurantilaria* slightly intruding from the south), but the southeastern United States and Gulf of Mexico support six species (two *Fasciolaria*, three *Cinctura*, one *Triplofusus*). Fossil evidence indicates greater richness in the Caribbean Sea when *Granolaria* and *Triplofusus* also occurred there during the Neogene, and the southeastern United States lost three genera (*Terebraspira*, *Pliculofusus*, *Liochlamys*) during the extinctions of the late Neogene. In the Old World, the Indo-West Pacific (IWP) province supports six species (three *Filifusus*, three *Pleuroploca*, each genus with one wide-ranging species and two species confined to small enclaves).

Southern Africa encompasses four biogeographic provinces: the northeastern subtropical Natal Province, the southeastern warm temperate Agulhas Province, and the western cold temperate Namaqua and Namib provinces (Branch et al., 1994). These Provinces support separate generic components, with very little overlap. The single *Pleuroploca* and one (possibly two) *Filifusus* species that occur in the subtropical Natal Province are among those that also occur in the tropical IWP Province, but the other provinces contain only genera endemic to southern Africa. For the warm temperate (northern Transkei to Cape Point) Agulhas

Province, these include three species of *Africolaria* and three, possibly five species of *Kilburnia*. The cold temperate Namaqua Province (Cape Point north to Lüderitz, southern Namibia) and the southern part of the Namib Province support two species of *Lugubrilaria*, and a single species of *Africolaria* (overlapping from the Agulhas Province) may also occur in deeper offshore waters.

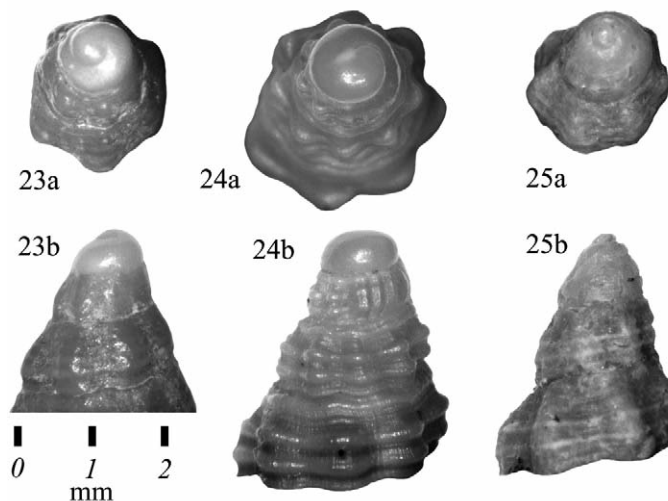
Fascioliariinae generally live along the coasts of continents and high islands, but both *Filifusus filamentosus* and *Pleuroploca trapezium* have managed to reach most remote islands in the Indian Ocean, including the Mascarenes, Chagos Atoll, the Cocos-Keeling Islands, and Diego Garcia. In the western Pacific, *F. filamentosus* ranges eastward to the Marshall Islands, the Caroline Islands (Palau and Yap), Fiji, Tonga, Samoa, and the Cook Islands (Niue); there is a record from Jarvis in the Line Islands (Kay, 1971), and the species occasionally reaches northernmost New Zealand (Marshall & Crosby, 1998), although apparently it does not maintain permanent populations there. *Pleuroploca trapezium* ranges eastward in the Pacific to the Marianas (Guam), the Carolines (Palau), Fiji, and Tonga.

In the New World, *Fasciolaria tulipa* ranges from Amapá, Brazil (Rios, 1970), north of the Amazon River, to North Carolina and includes virtually every Caribbean island, regardless of the depth of surrounding waters. *Aurantilaria aurantiaca*, which lives principally along central and northeastern Brazil, has an outlier population in the southern Lesser Antilles (Khomasurya, 1980) and was recently recorded off Guyane (Massemin et al., 2009). *Triplofusus princeps* ranges along continental western Central and South America from Mexico to Peru but also occurs offshore at Clipperton Island (Hertlein & Allison, 1966), Isla del Coco, Costa Rica and Isla de Malpelo, Colombia (both Kaiser & Bryce, 2001), and the Galápagos Islands (Stearns, 1893).

No living Fascioliariinae is known from the Hawaiian Islands, French Polynesia, tropical West Africa, the Mediterranean Sea, or the oceanic islands of the Atlantic, nor is any species known from the Chilean or Argentine coasts of South America. Instead, living Fascioliariinae except those mentioned above have relatively restricted ranges, probably due in great part to mode of reproduction. Among wide-ranging species, *Fasciolaria audouini* (a probable Red Sea geo-

graphic variant of *Pleuroploca trapezium*) spends 6 to 8 days in the plankton as a free-swimming veliger before metamorphosing to a benthic crawling stage (Gohar & Eisawy, 1967). Egg capsules of *Filifusus filamentosus* are more similar in shape and size to those of *Pleuroploca trapezium* than to capsules of other fascioliariines (D'Asaro, 2000), allowing speculation that they too may have a planktotrophic larval stage. The protoconch morphology of *Triplofusus princeps* (Fig. 25) clearly indicates a swimming veliger, and the protoconchs of *P. trapezium* and *F. filamentosus* (Figs 23 & 24) are smaller than those of other fascioliariines, another possible indicator of a brief free-swimming stage. A free-swimming veliger stage, albeit brief, may allow settling snails access to floating objects, enabling transport to areas inaccessible to crawlers. The presence or absence of swimming veligers may explain why some Fascioliariinae have crossed large distances over deep waters, whereas most have smaller ranges and are restricted to continental margins.

Most Fascioliariinae inhabit rather shallow environments on the inner halves of continental shelves. Three New World species with large numbers of depth records (*Fasciolaria tulipa*, *Cinctura hunteria* and *Triplofusus giganteus*) occur in the intertidal zone and each has a greatest known depth of about 73 m. Among other New World species, *Aurantilaria aurantiaca*, *Cinctura liliium*, *Granolaria salmo* and *G. valenciennesii* all occur in intertidal or shallow coastal waters and range offshore to mid-shelf depths ( $\leq 100$  m). Most specimens of *Triplofusus princeps* are from shallow water but the species also occurs in the intertidal zone and specimens have been collected from 40-50 m. In deeper water, *Cinctura branhamae* occurs in the Gulf of Campeche and adjacent waters off eastern Mexico in mid-shelf depths of 80 to 140 m. However, a few species live principally on deeper parts of continental shelves and even on the upper slopes. *Fasciolaria bullisi* has a disjunct distribution in the Gulf of Mexico, occurring off western Florida in 73 to 201 m, and along the eastern edge of the Yucatan Platform in 120 to 190 m but not elsewhere in the western Gulf. Shells of *Fasciolaria tephрина* have been trawled from 480 m depth north of Quitasueño Bank, Colombia (off northern Nicaragua) and from 420 m off Roatan, Honduras (de Souza, 2002); live-collected specimens later trawled from the same region were said to be



Figs 23-25. Protoconchs of Fascioliariinae species. 23, Protoconch of *Pleuroploca trapezium* (Linnaeus, 1758); Bohol, Philippines. ANSP 448537; 24, Protoconch of *Filifusus filamentosus* (Röding, 1798); Palawan, Philippines. ANSP 448539; 25, Protoconch of *Triplofusus princeps* (G.B. Sowerby I, 1825); Montijo Bay, Panama. ANSP 448538.

from 350 m, still deeper than any other New World Fascioliariinae.

Some Old World species are also restricted to relatively shallow depths. In southwestern Africa, *Lugubrilalaria lugubris* occurs from the intertidal zone to depths of 15-20 m. Published depth records for the widespread Indo-west Pacific species *Filifusus filamentosus* and *Pleuroploca trapezium* are relatively scarce, but their presence in intertidal and shallow subtidal depths is well known. Of 76 lots of *F. filamentosus* with depth data that we examined, most were from intertidal or shallow collections but a few were from  $\geq 25$  m and two were from 60 m. Likewise, of 90 lots of *P. trapezium* with depth data, the majority were from intertidal or very shallow collections but some were from 30 to 40 m and a few were from as deep as 80 m, particularly off Kyushu, Shikoku and southern Honshu, Japan, perhaps indicating northern submergence there of a more typically warm-water faunal element. Both *F. filamentosus* and *P. trapezium* are common in shallow waters of Madagascar, but they are replaced in 50

to 100 m depths in southeastern Madagascar by their congeners *F. manuelae* and *P. lyonsi*. Of other congeners, *F. glaber* seems restricted to southern Japan; two of eleven depth records we examined were from shallow waters (~5 m) and the rest were from 35 to 80 m. Seven of eight records for *P. clava* we saw are from 15 to 60 m but the other is from 7 to 8 m, and specimens in the Maldives are known from even shallower water. Thus, no *Filifusus* or *Pleuroploca* is known from depths greater than 100 m.

Like *Fasciolaria*, several other fascioliine genera have evolved to accommodate a greater range of depth. Along southeastern South Africa, *Kilburnia heynemanni* ranges from the intertidal to about 30 m and is replaced offshore by *K. strebeli*, principally in depths of 60-200 m although there are a few shallower records; a third species, *K. scholvienei*, occurs from 50 to 250 m (Marais & Kilburn, 2010). Marais and Kilburn reported *Africolaria wattersae* from 50 to 120 m, *A. theristes* from 100 to 200 m, and *A. rutila* from 150 to 500 m.

The Australian continent has single species of *Filifusus* and *Pleuroploca* in the north, west, and northeast as part of the tropical IWP fauna, whereas colder waters of south and southeastern Australia are the realm of the genus *Australaria*. We tentatively consider this genus to be represented by four living species-level taxa: *A. australasia*, *A. bakeri*, *A. eucla* and *A. tenuitesta*. Of these, *A. australasia* lives along coastal South Australia, Victoria, Tasmania, and southern New South Wales, principally in intertidal and shallow subtidal zones although we have seen a few lots from as deep as 30 to 50 m. *Australaria bakeri* lives off Victoria and New South Wales; published depth records, though scarce, indicate a habitat of from 55-128 m. Along the Great Australian Bight, *A. eucla* occurs offshore in 102 m and we have seen other material from 30 and 50 m depths. Probably an example of tropical submergence of a cold-temperate lineage, *A. tenuitesta* lives in depths of 80 to 250 m off northern New South Wales, Queensland, and perhaps Papua New Guinea.

The young of *Aurantilaria aurantiaca*, *Australaria australasia*, *Cinctura hunteria*, *Fasciolaria tulipa*, *Granolaria salmo*, *Lugubrilaria lugubris* and *Triplofusus giganteus* develop within capsules attached to the bottom, from which they emerge and crawl directly onto surrounding substrate (D'Asaro,

2000; Meirelles & Matthews-Cascon, 2005) and protoconch morphologies indicate similar modes of development for most of their congeners. Species from deeper waters tend to have larger protoconchs than their congeners, and species that range deepest (e.g., *Fasciolaria tephрина*, *Africolaria rutila*, *Kilburnia scholvienei*, and *Australaria tenuitesta*) have large, bulbous, paucispiral protoconchs clearly indicative of demersal development.

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