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Type specimens of  
Fusinae  
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## Proposed genus-level classification of large species of Fusininae (Gastropoda, Fasciolaridae)

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The fasciolarid gastropod genus *Fusinus* Rafinesque, 1815, is a highly heterogeneous taxon. We present a genus-level revision for large-shelled living members and some fossil species in this group based on shell characters. *Fusinus* is restricted to a group of Indo-West Pacific (IWP) species around *F. colus* (Linnaeus, 1758). We expand *Cyrtulus* Hinds, 1843 (type: *C. serotinus* Hinds, 1943) to include members of the *Murex undatus* Gmelin, 1791, group from the IWP. Several temperate Japanese species are added to the IWP genus *Marmorofusus* Snyder & Lyons, 2014. We resurrect *Gracilipurpura* Jousseame, 1880, for a group of fossil and extant species from Europe centered on *Murex rostratus* Olivi, 1792. We establish ten new genera, which with their type species are: *Enigmofusus* (*Fusinus nicki* Snyder, 2002) from the Indian Ocean; *Goniofusinus* (*Fusus dupetitthouarsi* Kiener, 1840) from tropical America; *Lyonsifusus* (*Murex ansatus* Gmelin, 1791) from the western Atlantic (WA); *Aristofusus* (*Fusus excavatus* G.B. Sowerby II, 1880) from the western Atlantic; *Callifusus* (*Fusinus irregularis* Grabau, 1904) from the eastern Pacific; *Apertifusus* (*Fusus meyeri* Dunker, 1869) from the tropical Atlantic; *Ariefusus* (*Fusinus rutilus* Nicolay & Berthelot, 1996) from West Africa; *Africofusus* (*Fusus ocellifer* Lamarck, 1816) from

southern Africa; and the extinct *Anguistofusus* (*Fusus vindobonensis* Hoernes & Auinger, 1890) and *Eofusus* (*Murex porrectus* Solander in Brander, 1766). The new extinct subfamily Clavilithinae is introduced for Paleocene to Pleistocene large fasciolarids with a barrel-shaped last whorl. We remove from Fusininae the West African species *Fusus filiosus* Schubert & Wagner, 1829, and assign it to the fasciolarine genus *Polygona* Schumacher, 1817. The extinct genus *Falsifusus* Grabau, 1904, is transferred to Turbinellidae. A review of the biogeography and functional shell morphology of large Fusininae reveals that size increased substantially in most lineages worldwide beginning in the Early Miocene. Traits interpreted as antipredatory are best expressed in tropical shallow-water species, especially in the IWP and WA. Geographical restriction is documented for *Apertifusus*, *Ariefusus* and the non-fusinine fasciolarid *Polygona*, all represented by fossil taxa in Europe but today restricted in the eastern Atlantic to West Africa; and *Goniofusinus*, which no longer occurs in the Caribbean region.

Key words: Neogastropoda, Fasciolaridae, Fusininae, new genus, biogeography, shell morphology.

## INTRODUCTION

It is commonly assumed that large, showy shells of marine molluscs are taxonomically well understood. Although this is indeed the case for groups like Muricidae, Cassidae, Conidae, Strombidae and Turbinidae, many other groups are still housed in large catch-all genera whose members encompass a very wide range both morphologically and geographically. Notable in this respect are large members (shell length 80 mm or more) of *Fusinus* Rafinesque, 1815, which despite substantial taxonomic re-evaluation in recent years still remains unacceptably heterogeneous. A list of genus-level taxa that have been recognized as full fusinine genera in the last twenty years and that were previously allocated to *Fusinus* includes *Aegeofusinus* Russo, 2017; *Amiantofusus* Fraussen et al., 2007; *Angulofusus* Fedosov & Kantor, 2012; *Araiofusus* Callomon & Snyder, 2017; *Carinofusus* Ceulemans et al., 2014; *Chryseofusus* Hadorn & Fraussen 2003; *Hesperaptyxis* Snyder & Vermeij, 2016; *Lamarckofusus* Vermeij & Lozouet, 2012; *Marmorofusus* Snyder & Lyons, 2014; *Okutanius* Kantor et al., 2018; *Parvofusus* Tabanelli, 2014; *Vermeijius* Kantor et al., 2018; and *Viridifusus* Snyder et al., 2012. Now that a molecular framework for the phylogeny of the Fascioliariidae has been established (Couto et al., 2016; Kantor et al., 2018), we believe the time has come to attempt a comprehensive genus-level review of large-bodied members of the Fusininae.

We approach this review in part from what could be called a palaeontological perspective, in which shell traits are emphasized. In addition, however, we have also relied on published molecular sequence data when these are available, as well as on biogeographical considerations. In cases where comprehensive phylogenies have been carried out for tropical clades of gastropods, deep divergences have been detected between Indo-West Pacific (IWP) and Atlantic-east Pacific (AEP) clades in nearly all shallow-water groups (Vermeij, 2012). Well-established examples are seen in Turbinidae (Williams & Ozawa, 2006), Cypraeidae (Meyer, 2003, 2004), Conidae (Puillandre et al., 2014), Rapaninae (Claremont et al., 2013a), Ergalataxinae (Claremont et al., 2013b), *Nerita* (Frey & Vermeij, 2008), *Patellogastropoda* (Nakano et al., 2004, 2007), Costellariidae (Fedosov et al., 2017), Mitridae (Fedosov et al., 2018), Nassariidae (Galindo et al., 2016), Rissoidae and related families (Criscione et al., 2017), Terebridae (Castelin et al., 2012), Littorinidae (Reid et al., 2010, 2013), Potamididae (Reid et al., 2008), and Siphonariidae (Dayrat et al., 2014). Similar deep phylogenetic divisions were inferred on the basis of anatomical and shell characters in Modulidae (Landau et al., 2014), Columbelloidae (de Maintenon, 1999), Fascioliariinae and Peristerniinae (Vermeij & Snyder, 2006;

Snyder et al., 2012), Melongenidae (Landau & Vermeij, 2013), and Strombidae (Kronenberg & Vermeij, 2002). Given the early (Late Oligocene to Early Miocene) separation of the IWP and AEP realms by closure of the Tethyan seaway in what is today the Middle East (Harzhauser et al., 2002, 2007), a phylogenetic separation of shallow-water lineages between these two tropical realms would appear to be a more defensible biogeographical classification (Vermeij, 2012) than one based on the proportion of endemic species in provinces as defined by living species (Briggs, 1974; Costello et al., 2017). Accordingly, we take geographical distributions into account for members of the Fusininae living above bathyal depths. Bathyal genera such as *Amiantofusus* and *Chryseofusus* are like many other bathyal clades in that they occupy more than one major ocean basin; their biogeography therefore contrasts markedly with that of clades in shallower water.

## MATERIALS AND METHODS

We have examined nearly all the living species of large-shelled Fusininae. Our review is based on material amassed by one of us (MAS), now located in the Academy of Natural Sciences of Philadelphia, Drexel University (ANSP). In addition, we examined material at the Natural History Museum in London (NHMUK) and from the Naturhistorisches Museum, Wien (MHMW).

## SYSTEMATIC PART

Family Fascioliariidae Gray, 1853  
Subfamily Fusininae Wrigley, 1927

Remarks. — Molecular sequence data indicate that the Fascioliariidae is a clade of buccinoidean neogastropods that comprises four subclades (Couto et al., 2016; Kantor et al., 2018). Two of these (Fascioliariinae and Peristerniinae) are characterized by the presence of columellar folds situated immediately adapical to the siphonal canal on the inner lip. These two sister clades are themselves sister to the clade Fusininae. At the base of the Fascioliariidae is a fourth clade, comprising two species with a close affinity to *Granulifusus* Kuroda & Habe, 1954 (see Kantor et al., 2018).

In their molecular phylogeny, Couto et al. (2016) showed that the Fusininae is a clade that includes, besides a broadly conceived genus *Fusinus*, also the aberrant *Cyrtulus* Hinds, 1843. Members of Fusininae are characterized by elongate fusiform shells with a smooth columella, a planar to gently convex adult outer shell lip, external spiral sculpture of primary, secondary, and often tertiary elements, and axial shell

sculpture consisting of rounded or rarely angular ribs, tubercles or nodes at least in early stages of post-larval growth. The teleoconch whorls are rounded to angulate in profile and are not flat-sided. The protoconch of most living species comprises one smooth whorl and a half whorl ornamented with axial riblets, but some living species of the new genus *Goniofusus* have a multispiral one. The aperture in fusininae is ovate to almost round; the variably elongate siphonal canal is typically straight except for a weakly dorsally deflected distal sector. Fusinines with a long siphonal canal are unusual among gastropods in having the parietal (or adaxial) edge of the canal free-standing and not fully adherent. This feature distinguishes fusinines with a long canal from members of the new subfamily Clavilithinae (see below).

Despite their ornate shells, large Fusininae show variations within a narrow range of morphologies, and much of the variation that does exist is expressed within species and often within individual ontogenies. Among these variations are the expression and extent of axial and spiral sculpture, the presence or absence of a raised parietal lip, the length of the straight or sometimes slightly wavy siphonal process, and the presence or absence of a tooth or ridge at the adapical end of the inner lip (hereafter the parietal ridge). The suture between whorls is appressed, incised, or almost channeled depending on the position of the suture relative to the profile of the whorl it borders. Characters that are potentially more diagnostic of groups of species are the shape of spiral cords, the nature and presence of spiral lirae on the inner side of the outer lip, the presence or absence of an adapical channel where the outer lip joins the penultimate whorl, and the relative width of the opening of the siphonal canal. Characters of the spiral sculpture on the siphonal process can also distinguish among species groups. The profile of the last whorl - rounded, adapically angulate, or biangulate - can sometimes be helpful in characterizing taxa above the species level.

The genus-level classification we propose here constitutes a hypothesis that should be tested with independent evidence, especially from DNA sequences. We argue that a proposal of this kind is important for setting the stage for tests of the reliability of shell characters in the taxonomy and phylogeny of fossil gastropods, for which molecular data are unavailable. We note that our earlier similar approach with fasciolaridiids bearing columellar folds (Vermeij & Snyder, 2006; Snyder et al., 2012) was largely vindicated by molecular evidence, albeit it with inevitable realignments that in hindsight make morphological sense.

Below we present a key to the large-bodied, shallow-water genera of Fusininae. The key does not

cover all variations in each genus but does provide the most substantial differences among the taxa. Most of the genera are discussed in the systematics section, except for *Araiofusus*. That genus, which is included in the key, is fully discussed along with *Harfordia* by Callomon & Snyder (2017). Although we briefly consider the genus *Chryseofusus* below, we have not included it in the key, because its species are predominantly found in deep water.

#### KEY TO LARGE-BODIED FUSININE GENERA

1. a. Outer lip lirate on inner side - 2  
b. Outer lip smooth on inner side, or lirae only near lip edge - 13
2. a. Siphonal process with conspicuous spiral bulge - *Cyrtulus*  
b. Siphonal process without spiral bulge - 3
3. a. Siphonal process with highly differentiated spiral cords, some very conspicuous - *Marmorofusus*  
b. Siphonal process with relatively evenly expressed spiral sculpture - 4
4. a. Siphonal canal elongate, very narrowly open (width 2 mm or less) - 5  
b. Siphonal canal relatively broadly open (width more than 3 mm) - 9
5. a. Growth lines prominent, tending to roughen spiral sculpture - 6  
b. Spiral sculpture smooth - 7
6. a. Parietal lip erect in adult - *Fusinus*  
b. Parietal lip adherent; shoulder angulation a high keel with or without open spines - *Gracilipurpura*
7. a. Protoconch whorls ribbed throughout - *Heilprinia*  
b. First whorl of protoconch smooth; last half of protoconch ribbed - 8
8. a. Whorl profile rounded, without angulations or nodes - *Aristofusus*  
b. Whorls strongly noded at shoulder angulation; nodes axially elongate - *Ariefusus*
9. a. Lirae on inner side of outer lip, when fully expressed, beaded - *Viridifusus*  
b. Lirae smooth - 10
10. a. Whorls rounded in profile, without angulations or nodes; axial ribs often becoming obsolete in later growth stages - *Apertifusus*  
b. Whorls angulate, with high spirally elongate nodes at least on spire whorls - 11
11. a. Lirae short; siphonal canal flexuous, not flaring at tip - *Callifusus*  
b. Lirae long and well expressed; tip of siphonal canal flaring - 12
12. a. Aperture with distinct adapical channel; cords roughened by growth lines - *Goniofusus*  
b. Aperture without adapical channel; cords smooth - *Lyonisifusus*
13. a. Siphonal canal narrowly open (3 mm or less) - 14



- b. Siphonal canal broadly open - 17
- 14. a. Parietal ridge present - 15
  - b. Parietal ridge absent - 16
- 15. a. Two distinct spiral rows of nodes on last whorl - *Enigmo-fusus*
  - b. Numerous axial ribs adorned with more than two rows of low rounded nodules - *Propefus*
- 16. a. Aperture round - *Eofusus*
  - b. Aperture ovate - *Angustifusus*
- 17. a. Shell gradually constricted toward base; nodes or tubercles present - *Africofusus*
  - b. Shell with sharp constriction toward base; whorls with rounded profile, lacking angulation or nodes - *Araiofusus*

*Fusinus* Rafinesque, 1815

Type species. — *Murex colus* Linnaeus, 1758 (Fig. 1)

Remarks. — The genus name *Fusinus* has been applied to a wide variety of large and small fusinines distributed around the world. We here restrict the use of the name *Fusinus* to large-shelled species from the IWP, characterized by the following shell traits: form elongate-fusifiform (shell length to diameter 2.9 : 6.1) with a very long siphonal process (canal length to shell ratio 0.38 : 0.50) and high spire; spiral sculpture consisting of strong angular close-set cords between which there can be occasional spiral elements in the narrow interspaces; axial sculpture consisting of prominent rounded ribs that on many species carry spirally elongated, anteroposteriorly compressed tubercles where they are crossed by an enlarged peripheral cord or keel; spiral cords on siphonal process and sometimes elsewhere on the shell roughened by growth lines; inner lip typically spirally sculptured, with an erect edge; aperture usually small, adapically rounded and not channeled; outer lip strongly lirated on its inner side; siphonal process with spiral sculpture that gradually diminishes in prominence toward tip, and with enlarged cords or spiral bulge; siphonal canal opening extremely narrow (less than 2 mm).

We include the following extant and fossil species in *Fusinus*: *F. amadeus* Callomon & Snyder, 2008b; *F. arabicus* (Melvill, 1898); *F. aurinodatus* Stahlschmidt & Lyons, 2009; *F. chuni* (von Martens in von Martens & Thiele, 1904); *F. colus* (Linnaeus, 1758); *F. crassiplicatus* Kira, 1959; *F. cratis* Kilburn, 1973; *F. diandraensis* Goodwin & Kosuge, 2008; *F. ferrugineus* Kuroda & Habe in Habe, 1960; *F. forceps* (Perry, 1811); *F. gracillimus* (Adams & Reeve, 1848); *F. jasmineae* Hadorn, 1996; *F. lavinae* Snyder & Hadorn, 2006; *F. longissimus* (Gmelin, 1791); *F. marisinicus* Callomon & Snyder, 2009b; *F. menengtenganus* (Martin, 1895); *F. midwayensis* Kosuge, 1979; *F. nobilis* (Reeve, 1847); *F. nodosoplicatus* (Dunker, 1867); ? *F. penioniformis* Habe, 1970; *F.*

*percyanus* Sowerby II, 1880; *F. perplexus* (A. Adams, 1864); *F. salisburyi* Fulton, 1930; *F. sandwichensis* (G. B. Sowerby II), 1880; *F. stannum* Callomon & Snyder, 2008a; *F. teretron* Callomon & Snyder, 2008b; *F. townsendi* (Melvill, 1899). Several species of *Fusinus* have been critically reviewed, based on type specimens, by Callomon & Snyder (2004, 2007, 2008b, 2009a, b).

Species of *Fusinus* vary considerably in form, size and sculpture. *Fusinus colus* (the type species), *F. crassiplicatus*, *F. gracillimus* and *F. marisinicus* may have rounded whorls without tubercles or a prominent keel. Two species from the northwestern Indian Ocean (*F. arabicus* and *F. townsendi*) have relatively small shells (82 mm and 66 mm respectively) with an elongate aperture and a somewhat more widely open siphonal canal than is typical. At the other extreme, *F. longissimus* reaches a length of 337 mm (Callomon & Snyder, 2008b). *Fusinus stannum* is highly unusual in that the early teleoconch whorls and the last whorl bear axial ribs but the middle whorls lack them entirely, being sculptured only with spiral cords (Callomon & Snyder, 2008b). *Fusinus gracillimus*, with a length: diameter ratio of 6.1, is the most slender fusinine known. The aperture is very small in such species as *F. colus*, *F. crassiplicatus*, *F. cratis*, *F. chuni*, *F. gracillimus* and the very heavily corded *F. salisburyi*; whereas in others it is comparatively larger, as in *F. marisinicus*, *F. longissimus*, *F. nobilis*, *F. perplexus*, and *F. teretron*.

The deep-water Indian Ocean species *F. malhaensis* Hadorn, Fraussen and Bondarev, 2001, could be a highly divergent member of *Fusinus*. In common with more typical members of *Fusinus*, *F. malhaensis* has a strongly erect inner lip and a central keel with raised, spirally elongate protrusions in the middle of the last whorl. The siphonal canal is very narrowly open. The species differs from typical *Fusinus* by having very fine spiral threads and above all by lacking lirae on the inner side of the outer lip. The shell is thin, typical of many deep-water fusinines.

Several Japanese fusinines could also be aberrant members of *Fusinus*. These include *F. amadeus* Callomon & Snyder, 2008b, and perhaps *F. penioniformis* Habe, 1970. *Fusinus amadeus* has a slightly raised peripheral cord without nodes, growth lines that roughen the spiral sculpture, and low rounded axial ribs. *Fusinus penioniformis* has a nodose peripheral cord as well as a second more basal enlarged cord; lirae on the inner side of the outer lip are obsolete. Both species differ from typical *Fusinus* by having an adherent inner lip and by having relatively broad shells (length to diameter ratio 2.7 : 2.8) and a shorter canal (canal length to shell length ratio 0.33 : 0.37). Although Callomon & Snyder (2008b) compared *F.*

*amadeus* to the Australian genus *Propefusus*, it lacks the spiral rows of small nodes typical of that genus. *Fusinus penioniformis* was compared to *F. akitai*, Kuroda & Habe in Habe, 1961, but that species, which we tentatively assign to *Marmorofusus* (see below), has some enlarged cords on the siphonal process. It is possible that the Japanese species form a distinct group related to more typical *Fusinus*.

As circumscribed here, the genus *Fusinus* is confined to the tropical IWP region including temperate Japan. Although most species have ranges close to the continents, *F. sandwichensis* is found in the Hawaiian Islands. To our knowledge, the fossil record of *Fusinus* extends back only to the Pliocene of Indonesia and Sarawak (*F. menengtenganus*) (see Cox, 1948) and Okinawa (*F. nodoplicatus* and *F. perplexus*) (Noda, 1988) and mainland Japan in the Kawae Formation of Niigata Prefecture (Amano et al., 2000).

### *Cyrtulus* Hinds, 1843

Type species. — *Cyrtulus serotinus* Hinds, 1843 (Fig. 2)

Here we propose to expand the concept of the genus *Cyrtulus* by including, in addition to the type species, members of what Callomon & Snyder (2006) called the *undatus* group of *Fusinus*. These species are: *C. bountyi* (Rehder & Wilson, 1975); *C. galathea* (Powell, 1967); *C. genticus* (Iredale, 1936); ? *C. kilburni* (Hadorn, 1999); *C. mauiensis* (Callomon & Snyder, 2006); *C. similis* (Baird, 1873); *C. undatus* (Gmelin, 1791).

Remarks. — The genus *Cyrtulus* was erected to accommodate a bizarre species endemic to the Marquesas Archipelago in eastern Polynesia. *Cyrtulus serotinus* is remarkable for its convergence to the shell form in members of the fossil Clavilithinae, new subfamily (see below).

Grabau (1904) noted on the basis of the different protoconch characters of *Cyrtulus* in comparison with Clavilithinae that *Cyrtulus* does not belong to that group but is instead an aberrant fusinine. His hypothesis received support from molecular data (Couto et al., 2016).

Morphologically, the most distinctive difference between *Cyrtulus* and members of the Clavilithinae is a thick external spiral bulge on the siphonal process in *Cyrtulus*. This bulge is absent in Clavilithinae, whose shells have a long, uniformly narrow siphonal process. Moreover, the adaxial edge of the siphonal canal in *C. serotinus* is erect and free-standing as in *Fusinus*, a condition that is rare or unknown in the Clavilithinae.

Here we propose to expand the concept of the genus *Cyrtulus* to include, in addition to the type

species *C. serotinus*, members of what Callomon & Snyder (2006) called the *undatus* group of *Fusinus*. Features uniting species of *Cyrtulus* include a very narrowly open siphonal canal (opening less than 2 mm wide), a distinct, broad spiral bulge on the siphonal process, a moderately high spire with shallow appressed sutures, relatively reduced development of spiral external sculpture, especially on the siphonal process, the presence of an adapical channel in the aperture, an erect inner lip, fine lirae on the inner side of the outer lip, abapically convex profile of outer lip, and axial sculpture, when fully expressed, consisting of high, rounded ribs that end abapically and adapically in rounded tubercles on the last whorl. *C. serotinus* represents one extreme variation, in which tubercles and spiral sculpture are absent on the adult whorl, and the adapical channel is highly exaggerated. In its early growth stages, however, *C. serotinus* resembles the early stages of growth of other members of the genus *Cyrtulus*.

Shell proportions vary within the genus. The shell can be relatively broad, as in *C. serotinus* (length to diameter ratio about 2.1), or more slender, as in *C. undatus* (ratio 3:8); but the siphonal canal is typically of moderate length (canal length to shell length ratio 0.31:0.37). Most species are heavy for their size.

In a genus of extremes, another possible member with highly divergent morphology is the subtropical southeast African *Fusinus kilburni* Hadorn, 1999. Characters consistent with assignment to *Cyrtulus* include the presence of a spiral bulge on the siphonal process, a shallow appressed suture, a very narrowly open siphonal canal, fine and weak spiral threads, and a small but distinct adapical channel in the aperture. The most divergent aspect of the shell is the absence of tubercles or nodes; instead, axial sculpture consists of about eighteen low, rounded ribs. If the species does belong to *Cyrtulus*, it would be by far the smallest species, with a length of about 68 mm.

The alternative to our proposal for an expanded *Cyrtulus* is to retain *Cyrtulus* as a monospecific genus and to establish a new genus for members of the *undatus* group. Given the geographically remote distribution of *C. serotinus*, we believe that this species represents an extreme, phylogenetically derived condition within *Cyrtulus*. A two-genus interpretation would therefore likely entail a paraphyletic status for the *undatus* group. We note that no other endemic cases of marine genera are known in Polynesia or the insular Pacific generally in groups that have been taxonomically and phylogenetically well studied. All Polynesian and other Pacific Plate endemics belong to genera with representatives elsewhere in the IWP.

*Cyrtulus* differs from *Fusinus* by having much weaker to obsolete spiral sculpture, by the presence

of an adapical channel at the adapical end of the aperture, and by the presence of a spiral bulge on the siphonal process. Moreover, there are often two rows of tubercles when axial sculpture is well developed, in contrast to the single row in *Fusinus*. *Cyrtulus* differs from *Marmorofusus* in its reduced spiral sculpture, especially on the siphonal process, and by the presence of the spiral bulge on the siphonal process. It shares with that genus the presence of an adapical channel. All three IWP genera have a very narrowly open siphonal canal.

Among fusinine genera, *Cyrtulus* has the most oceanic distribution, extending east in the Pacific to the Marquesas (*C. serotinus*), the Hawaiian Islands (*C. mauiensis*), Pitcairn Island (*C. bountyi*), the Kermadec Islands (*C. galathea*) and northern New Zealand (*C. genticus*). *Cyrtulus* is not, however, confined to remote Pacific islands and is not known from all such islands. It is apparently absent from the Mariana Islands and the Marshall Islands, as well as from the Society and Tuamotu islands. *Cyrtulus* co-occurs with *Fusinus* and *Marmorofusus* as well as with many small-bodied fusinine genera in Japan, the Philippines and the Indian Ocean. We are unaware of any fossil representatives of *Cyrtulus*.

#### *Marmorofusus* Snyder & Lyons, 2014

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Type species. — *Syrinx nicobaricus* Röding, 1798 (Fig. 3)

Remarks. — This genus is characterized by angular whorls, strong spiral and axial sculpture, a relatively short and very narrowly open siphonal canal (canal length to shell length ratio 0.22:0.32, width 2 mm or less), a relatively broad shell (shell length to diameter ratio 2.1:2.4), a distinct adapical channel where the outer lip joins the preceding whorl, and above all by the presence of several very prominent cords on the siphonal process in addition to smaller spirals.

Almost all species have tubercles in one or two spiral rows where spiral cords cross high, prominent axial ribs. As in *Fusinus*, the inner side of the outer lip bears lirae, and the parietal edge of the inner lip is erect or free. Snyder & Lyons (2014) recognize some 16 species in *Marmorofusus*, all with a tropical Indo-West Pacific distribution collectively extending from southwestern Australia and New South Wales to Japan and from East Africa and the Red Sea east to Papua New Guinea, New Caledonia, and Hawaii (Callomon & Snyder, 2018). For comparative remarks see under *Fusinus* and *Cyrtulus*.

In addition to the tropical species of *Marmorofusus*, we assign with confidence one Japanese species, *M. tuberosus* (Reeve, 1847), and more hesitantly two further Japanese species, *M. akitai* (Kuroda & Habe in

Habe, 1961) and *M. nigrirostratus* (E. A. Smith, 1879). Although the distinctive sculpture of tropical members of *Marmorofusus* is reduced in these temperate species, especially in the latter two, the enlarged cord on the siphonal process is present in all. The most divergent species we assign to *Marmorofusus* is *M. akitai*, in which tubercles are hardly evident. All three Japanese species have stronger sculpture on the upper whorls than on the last whorl, and this sculpture conforms to that of other members of *Marmorofusus*.

The fossil record of the genus extends back to the Pliocene, with *M. tuberosus* (Dainichi Formation and Umegata Formation of Shimane and Chiba Prefecture respectively; Ozawa et al., 1998) and the extinct *M. idjowensis* (Oostingh, 1939) from Java (Oostingh, 1939).

The unusual prominence of several of the spiral cords on the siphonal process in *Marmorofusus* recalls a similar but convergent condition in *Nodolattirus* Bouchet & Snyder, 2013, a genus of large-shelled Indo-West Pacific fasciolarids with high, node-like axial ribs. In most other fasciolarids, siphonal cords on the siphonal processes diminish in strength abapically toward the distal end.

#### *Goniofus* gen. nov.

Type species. — *Fusus dupetitthouarsi* Kiener, 1840 (Fig. 5)

Diagnosis. — Large fusinines with broad to relatively elongate shell (shell length to diameter ratio 2.4:3.3), relatively widely open siphonal canal (width 3 to 4 mm), distal opening of canal slightly flaring; moderately long siphonal process (canal length to shell length ratio 0.31:0.35); sculpture consisting of angular spiral cords on entire shell and short axial ribs usually forming spirally elongate tubercles on well-marked peripheral cord; other cords high, sometimes alternating with secondary cords; aperture large, with short but distinct narrow adapical channel marked by one or two prominent parietal ridges; inner side of outer lip with ten paired well-marked lirae; inner lip adherent; growth lines prominent, slightly roughening spiral sculpture.

Etymology. — Prefix gonio-, Greek for angular; and fusus.

Included species. — *Goniofus dupetitthouarsi* (Kiener, 1840); *G. brasiliensis* (Grabau, 1904); *G. spectrum* (Adams & Reeve, 1848); "*G. strigatus*" (Philippi, 1846); *G. turris* (Valenciennes, 1832).

Remarks. — The new genus *Goniofus* is proposed for a group of tropical American fusinines characterized by a distally flaring, relatively widely open siphonal canal, strongly angular whorls, paired lirae, an adapically slightly channeled aperture, and very short axial ribs that, when expressed, form spirally



elongate peripheral tubercles. The genus differs from *Lyonsifusus* gen. nov. (described next) from the western Atlantic in having shorter ribs, a larger aperture, the presence of an adapical channel or notch, well-marked growth lines, and a distally flaring siphonal canal. For differences with the eastern Pacific genus *Callifusus* gen. nov. see under that genus.

The five species assigned here to *Goniofus* gen. nov. differ in size as well as in the expression of tubercles and spiral cords. At a length of 258 mm, *G. turris* is one of the largest fusinines in tropical America. *Goniofus brasiliensis*, at a length of 82.5 mm, is the smallest species of the genus. The high peripheral tubercles characteristic of adult "*G. strigatus*", *G. dupetitthouarsi* and *G. spectrum* are suppressed on the last whorl of *G. brasiliensis* and *G. turris*, although all species are tuberculate on spire whorls. The spiral cords and apertural lirae of *G. spectrum* are less well expressed than in the other species of the genus.

Poorman (1981) assigned *G. dupetitthouarsi* to *Falsifusus*, apparently because of its multispiral protoconch in which the first very small whorl is smooth and the remaining three whorls are finely ribbed with a basal keel. *F. turris*, with a paucispiral protoconch, belongs to *Fusinus* according to Poorman (1981). We disagree with these assignments and consider both species to belong to *Goniofus*. As shown below, *Falsifusus* belongs to Turbinellidae and is therefore unrelated to Fusininae. *Goniofus brasiliensis* is only one of two large-shelled fusinines taxon outside the IWP that Couto et al. (2016) included in their molecular phylogeny of Fusininae. We note that this species falls outside the IWP clade comprising *Fusinus*, *Marmorofusus* and *Cyrtulus*. This result therefore lends support to our shell-based hypothesis that *Goniofus* gen. nov. can be considered a distinct genus.

As presently understood, *Goniofus* gen. nov. has a disjunct distribution in the living fauna, with two species in Brazil (*G. brasiliensis* and "*G. strigatus*") and three in the tropical eastern Pacific (*G. dupetitthouarsi*, *G. spectrum* and *G. turris*). Brazil has long been recognized as one of several geographical refuges for clades that at one time had a broader western Atlantic distribution and that are still found in the eastern Pacific.

Filling in the geographical gap is the Early Pliocene species *G. haitensis* (Sowerby I, 1850) from the Gurabo Formation of the Dominican Republic. Examination of the type indicates that this species has all the characters of *Goniofus* gen. nov. except that the siphonal canal does not appear to flare distally. The only other fossil occurrences of *Goniofus* gen. nov. are *G. baumanni* (Maury, 1925) from the Pirabas Formation (Early Middle Miocene) of Brazil, and *G. dupetitthouarsi*, which is reported from the Latrania

Formation in the Imperial Group (Late Miocene) of southern California (Demere & Rugh, 2006) and from the Pleistocene of the Gulf of California (Emerson & Hertlein, 1964).

The three species here assigned to *Goniofus* gen. nov. differ in the expression of tubercles and spiral cords as well as in size. At a length of 258 mm, *F. turris* is one of the largest fusinines in tropical America. The high peripheral tubercles characteristic of the adults of the other two species are suppressed on later whorls of *G. turris*. *Goniofus spectrum* is the smallest species, and its spiral cords and apertural lirae are notably less well expressed than in *G. dupetitthouarsi* and *G. turris*. The protoconch of *G. turris* is a standard one and one-half whorls with riblets on the last half whorl; the protoconch of *G. spectrum* is not known. *Goniofus dupetitthouarsi* has a four-whorl protoconch, a character that caused Poorman (1981: 346-347) to place this species in *Falsifusus*.

#### *Lyonsifusus* gen. nov.

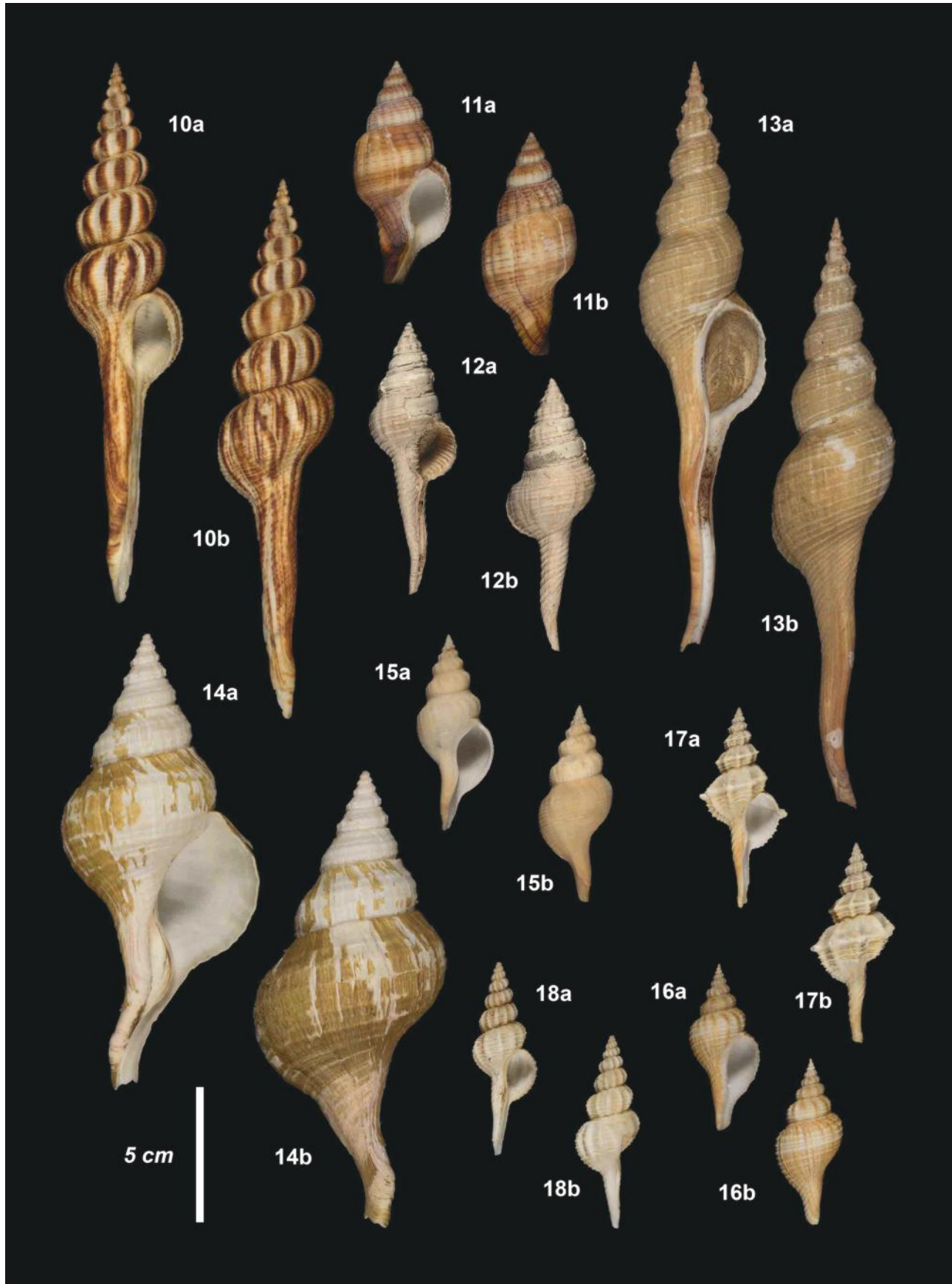
Type species. — *Murex ansatus* Gmelin, 1791 (Figs 6-7)

Diagnosis. — Fusinines with relatively elongate shell (length to diameter ratio approximately 3.0); relatively long, widely open siphonal canal (canal length to shell length ratio approximately 0.4, opening about 3 mm); sculpture consisting of high smooth angular spiral cords on entire shell and broad rounded axial ribs extending on last whorl to basal constriction;

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**Figs 1-7.** Type species of Fusininae. **1**, *Murex colus* Linnaeus, 1758, type species of *Fusinus* Rafinesque, 1815, off Cebu, Philippine Islands, 143.3 mm (ANSP 423653). **2**, *Cyrtulus serotinus* Hinds, 1843, type species of *Cyrtulus* Hinds, 1843, at 15 m, crabbed on rubble, Marquesas, 88.6 mm (ANSP 476302). **3**, *Syrinx nicobaricus* Röding, 1798, type species of *Marmorofusus* Lyons & Snyder, 2014, Sulu Sea, Philippine Islands, 104 mm (ANSP 476301). **4**, *Fusinus nicki* Snyder, 2002, type species of *Enigmofusus* gen. nov., in fish traps at 70 m, off south Mozambique, 156 mm (ANSP 476307). **5**, *Fusus dupetitthouarsi* Kiener, 1840, type species of *Goniofus* gen. nov., by shrimpers at 30 m, off Baja California, Mexico, 219.5 mm (ANSP 476304). **6-7**, *Murex ansatus* Gmelin, 1791, type species of *Lyonsifusus* gen. nov. **6**, by shrimpers at 50 m in sand, Gulf of Venezuela, 170 mm (ANSP 476305). **7**, El Pico, Peninsula de Paraguana, Venezuela, 195 mm (ANSP 476306). **8**, *Fusus excavatus* G.B. Sowerby II, 1880, type species of *Aristofusus* gen. nov., dredged at 100 m, Florida Straits, 79.5 mm (ANSP 476310). **9**, *Fusus meyeri* Dunker, 1869, type species of *Apertifusus* gen. nov., trawled at 50-60 m off Guinea, West Africa, 253 mm (ANSP 476309).







whorl profile rounded to angulate; aperture adapically rounded; outer lip with long smooth lirae on inner side; inner lip adherent.

Included species. — *Lyonsifusus ansatus* (Gmelin, 1791); *L. carvalhariosi* (Macsotay & Campos Villarroel, 2001).

Etymology. — Named in honor of William G. Lyons, who has contributed extensively to the taxonomy of Fasciolaridae and other molluscs.

Remarks. — We propose *Lyonsifusus* gen. nov. for a small group of southern Caribbean fusinines characterized by high, smooth, angular spiral cords, long axial ribs, an adherent inner lip, strong lirae, an adapically rounded aperture, and a relatively widely open siphonal canal. There is a single enlarged central cord that can form tubercles where it crosses the broad ribs.

*Lyonsifusus* gen. nov. differs from *Fusinus* in having smooth spiral cords, an adherent inner lip, and a more widely open siphonal canal. It differs from *Heilprinia* and the new genus *Aristofusus*, both from the western Atlantic, in having a more widely open siphonal canal and an adherent inner lip, and from *Heilprinia* by having the first protoconch whorl smooth rather than finely ribbed. For differences with the new genus *Goniofusus* see under that genus.

The living species have been discussed by Hadorn & Rogers (2000) and Lyons & Snyder (2018a, in review). The early life history of *L. ansatus* (as *Fusinus*

*closter* (Philippi, 1850)), including intracapsular veliger and hatching as crawling juveniles, was documented by Miloslavich & Panchaszadeh (1997). Although we have not undertaken a critical review of fossil species, a likely early member of *Lyonsifusus* gen. nov. is *Fusinus mithras* Jung, 1965, from the Cantaure Formation (Early Miocene) of Venezuela. This species, which has an angular whorl profile, was recently discussed by Landau et al. (2016). It occurred in the same region of northern South America as do the living species.

#### *Aristofusus* gen. nov.

Type species. — *Fusus excavatus* G. B. Sowerby II, 1880 (Fig. 8)

Diagnosis. — Shell very slender (length to diameter ratio 3.4 : 4.1), with very long, very narrowly open siphonal canal (canal length to shell length ratio 0.39 : 0.48, opening 2 mm or less wide); sutures very deeply impressed to almost channeled; spiral sculpture consisting of smooth high angular cords overriding broad rounded ribs without forming nodes or tubercles; aperture ovate, adapically rounded; outer lip with strongly developed lirae; adult inner lip erect; parietal ridge present; protoconch of the typical fusinine form with a smooth first whorl and a terminal portion with fine riblets.

Included species. — *Aristofusus benjamini* (Hadorn, 1997); *A. couei* (Petit de la Saussaye, 1853); *A. excavates* (G. B. Sowerby II, 1880); *A. helenae* (Bartsch, 1939); *A. stegeri* (Lyons, 1978).

Etymology. — Aristos, Greek for beautiful, striking.

Remarks. — We establish the new genus *Aristofusus* gen. nov. for a group of fusinines from the tropical western Atlantic with elegant, slender shells having a high spire, very long, very narrowly open siphonal canal, and smooth high spiral cords. The genus is morphologically very similar to *Heilprinia* (see below) but differs by having a typical fusinine protoconch with a smooth first whorl instead of a protoconch in which all whorls are finely ribbed. In addition, species of *Aristofusus* gen. nov. have more slender shells with even smoother cords and a more deeply impressed suture. *Aristofusus* gen. nov. differs from *Lyonsifusus* gen. nov. by having a much longer, much more narrowly open siphonal canal, no tendency to form nodes or tubercles where spiral cords cross the broad axial ribs, and even smoother spiral cords.

In most species of *Aristofusus* gen. nov., axial ribs are confined to the early teleoconch whorls. The exception is *A. stegeri*, in which the closely spaced, unusually narrow ribs continue to the last whorl.

In their phylogenetic study of Fasciolaridae,

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**Figs 10-18.** Type species of Fusininae. **10**, *Fusinus rutilus* Nicolay & Bertholet, 1996, type species of *Ariefusus* gen. nov., off Mayumba, Gabon, west Africa, 200.3 mm (collection of W.G. Lyons). **11**, *Fusus buxeus* Reeve, 1847, type species of *Viridifusus* Snyder et al., 2012, trawled by shrimpers at 45 m, Sao Vicente, Cape Verde Archipelago, 83.2 mm (ANSP 476300). **12**, *Fusus caloosaensis* Heilprin, 1886 [Plio-Pleistocene], type species of *Heilprinia* Grabau, 1904, Caloosahatchie River, Florida, 101.4 mm (ANSP-IP13811). **13**, *Fusus irregularis* Grabau, 1904, type species of *Callifusus* gen. nov., Gurro Negro Lagoon, outer coast of Baja California, 219.9 mm (ANSP 466135). **14**, *Fusus ocellifer* Lamarck, 1816, type species of *Africofusus* gen. nov., trawled at 250 m off Alguhas Bank, South Africa, 170.0 mm (ANSP 476308). **15**, *Fusinus chryso-domoides* Schepman, 1911, type species of *Chryseofusus* Hadorn & Fraussen, 2003, at 150 m off Aliguay Island, northeast Dipolog, Zamboanga del Norte, Mindanao, Philippine Islands, 73.2 mm (ANSP422739). **16**, *Fusus pyrulatus* Reeve, 1847, type species of *Propefusus* Iredale, 1924: trawled at 20-30 m in Coffin Bay, South Australia, 62.0 mm (ANSP 476303). **17-18**, *Murex rosstratus* Olivi, 1792, type species of *Gracilipurpura* Jousseaume, 1880. **17**, dredged at 50 m on sandy rock off Isole Egadi, Sicily, 74.5 mm (ANSP 476311). **18**, by Scuba off Savona, Italy, 72 mm. (ANSP 476312)



Couto et al. (2016) included *A. excavatus*, one of only two large-shelled fusinines from tropical America. This species falls outside the IWP clade and is also phylogenetically separated from the only other tropical American species Couto et al. (2016) included, *Goniofusinus brasiliensis*.

Several fossil species appear to belong to *Aristofusus* gen. nov., all from the tropical western Atlantic. We confirm this placement for *A. henekeni* (Sowerby I, 1850) from the Gurabo Formation (Pliocene) of the Dominican Republic, a species that Hadorn & Rogers (2000) suspected to be ancestral to *A. excavatus*. Other species that are likely members of the genus include *A. isthmicus* (Böse, 1910) from the Agueguexquite Formation (Early Pliocene) of southern Mexico; *A. miocosmos* (Olsson, 1922) from the Late Miocene or Early Pliocene of Bocas del Toro, Panama; *A. vonderschmidti* (Rutsch, 1934) from the Early Pliocene of Venezuela (see also Landau & da Silva, 2010); and *A. waltonensis* (Gardner, 1944) from the Oak Grove Sand (Middle Miocene) of northern Florida.

#### *Apertifusus* gen. nov.

Type species. — *Fusus meyeri* Dunker, 1869 (Fig. 9)

Diagnosis. — Shell moderately to very elongate (length to diameter ratio 2.9 : 4.0) with moderately to very long, broadly open siphonal canal (canal length to shell length ratio 0.28 : 0.40, opening 4 mm wide); canal tip flaring; whorls rounded in profile; spiral sculpture consisting of high angular widely separated cords, often with a strong secondary cord in interspaces, roughened by growth lines; axial sculpture consisting of low broad rounded ribs, often obsolete on last whorl, not forming nodes or tubercles; aperture relatively large, adapically rounded; outer lip with weak, often short smooth lirae on inner side; inner lip adherent or very weakly erect, its adapical end with weak parietal ridge.

Included extant species. — *Apertifusus meyeri* (Dunker, 1869); *A. caparti* (Adam & Knudsen, 1955); *A. "frenguelli"* (Carcelles, 1953); ? *A. josei* (Hadorn & Rogers, 2000).

Etymology. — *Aperta*, Latin, open, referring to the widely open siphonal canal.

Remarks. — We propose the new genus *Apertifusus* to accommodate three or four tropical Atlantic fusinines, characterized by relatively thin-walled, large, very elongate shells, a very long, widely open and distally flaring siphonal canal, high angular cords, rounded ribs roughened by growth lines, and weakly expressed lirae. Ribs continue onto the last whorl in *A. caparti* whereas they become obsolete on shells of *A. "frenguelli"* and *A. meyeri*. The inner lip is

generally adherent except in *A. "frenguelli"*, in which it is slightly erect.

*Apertifusus* gen. nov. differs from most other tropical genera except *Aristofusus* gen. nov. in having rounded whorls without nodes or tubercles. It differs from *Aristofusus* gen. nov., *Lyonsifusus* gen. nov. and *Fusinus* by having relatively poorly expressed, short lirae. The axial ribs of *Aristofusus* gen. nov. and *Lyonsifusus* gen. nov. are much broader and smoother, and the siphonal canal in those genera is more narrowly open.

The name *Fusinus "frenguelli"* Carcelles, 1953, has been applied to what we believe are two distinct species, a small form from Uruguay and Argentina, to which the name *F. frenguelli* explicitly applies; and a larger, apparently undescribed species from Brazil. It is the latter Brazilian species that we include in *Apertifusus* gen. nov. Hadorn & Rogers (2000) described *Fusinus josei* from a depth of 400 m in the Florida Strait. They noted that this species, in which the axial ribs fade out on the last whorl, resembles *A. meyeri*. We have not examined this species, but it is possible that *F. josei* belongs to *Apertifusus* gen. nov.

At a reported maximum length of 370 mm (Nicolay & Berthelot, 1996, as *Fusinus caparti*), *A. meyeri* is the largest living fusinine. This species is part of an offshore fauna in West Africa that includes several other exceptionally large gastropods.

A likely fossil member of *Apertifusus* gen. nov. is *A. clavatus* (Brocchi, 1814) from the Early Pliocene of Italy. Examination of specimens from Asti indicates that this large species (length 143 mm) has all the characteristics of *Apertifusus*. *Apertifusus clavatus* is also recorded from the Middle Miocene ("Helvetian") of France (Peyrot, 1928). Based on Chirli's (2000) description, we also tentatively include in *Apertifusus* gen. nov. the very large (175 mm) *A. etruscus* (Pecchioli, 1862) from the Early Pliocene of Italy. *Apertifusus* gen. nov. is therefore one of numerous molluscan genera that occurs as a fossil in Europe and that has subsequently become restricted in the eastern Atlantic to the coast of tropical West Africa.

#### *Ariefusus* gen. nov.

Type species. — *Fusinus rutilus* Nicolay & Berthelot, 1996 (Fig. 10)

Diagnosis. — Shell elongate fusiform (length to diameter ratio 2.4 : 3.1) with a long straight tapering siphonal canal (canal length to shell length ratio 0.30 : 0.41) that is very narrowly open (less than 2 mm); axial sculpture consisting of very high, sharply rounded ribs forming axially elongate nodes at periphery; spiral sculpture consisting of fine cords not expanded into nodules where crossing ribs below pe-

riphery and not roughened by growth lines; aperture small, ovate, adapically rounded; outer lip edge abapically slightly convex; inner side of outer lip with smooth lirae; inner lip adherent, its adapical end with obsolete parietal ridge.

Included extant species. — *Ariefusus rutilus* (Nicolay & Berthelot, 1996).

Etymology. — From the senior author: we take exceptional pleasure in naming this genus of beautiful shells in honor of my brother Arie Pieter Vermeij, who has done so much for me throughout his life. Mijn eeuwige dank.

Remarks. — According to Nicolay & Berthelot (1996), *A. rutilus* has a protoconch consisting of two smooth whorls and reaches an adult length of 191 mm. Specimens of *A. rutilus* from West Africa we have examined are unusual in having very fine spiral sculpture and axially elongate tubercles at the periphery, which are situated at a relatively adapical position on the whorl. *Ariefusus* gen. nov. bears some resemblance to the IWP fasciolarine genus *Nodolaturus* Bouchet & Snyder, 2013 (type species: *N. nodatus* (Gmelin, 1791)). Similarities include the elongate fusiform shape, high round axial ribs, weak rounded spiral cords and the tendency to form high peripheral nodes. *Nodolaturus* differs, however, by having a much shorter, broader siphonal process adorned with several very prominent spiral cords and by the presence of four or five weak columellar folds. The spiral cords in *Nodolaturus* are fewer and more differentiated in size than in *Ariefusus* gen. nov., and there is a pseudoumbilicus in *Nodolaturus* but not in *Ariefusus* gen. nov.

In addition to the type species, we include *Fusus prevosti* Hörnes, 1853, from the Late Middle Miocene (Badenian) of Austria and Romania. Thanks to the kindness of Matias Harzhauser, we have examined several specimens of this striking fossil species. It bears a very strong resemblance to *A. rutilus*, and differs only by being smaller (130 mm). A possible third member of *Ariefusus* gen. nov. is *Fusus prevosti* var. *szobiensis* Strausz, 1960, from the Badenian of Hungary. This taxon is said to differ from typical *A. prevosti* by having a much more slender shell and higher spire, by having fewer ribs (seven to eight per whorl) that extend to the adapical suture, and reduced axial sculpture on adult whorls. We have not examined this taxon and therefore include it in *Ariefusus* gen. nov. provisionally.

#### *Viridifusus* Snyder, Vermeij & Lyons, 2012

Type species. — *Fusus buxeus* Reeve, 1847 (Fig. 11)

Remarks. — Following the observation by Rolan &

Schoenherr (1997) that *Fusus buxeus* has a fusinine rather than a fasciolarine radula, Snyder et al. (2012) transferred this species to Fusininae and established the genus *Viridifusus* for it. They also included *Fusus maximus* Sowerby II, 1880, a species that, like *V. buxeus*, is endemic to the Cape Verde archipelago. Here we add two species from southern Angola, *Fusus albinus* A. Adams, 1856, and the much smaller *F. mollis* Sowerby III, 1913.

The genus *Viridifusus* is characterized by a broadly fusiform shell (length to diameter ratio 2.2 : 2.7), a relatively widely open siphonal canal (opening 3 mm) with flaring tip, a very weakly erect inner lip on the main part of the last whorl but strongly erect along the siphonal canal, a slight channel and parietal ridge at the adapical end of the aperture, beaded lirae on the inner side of the outer lip (the beads very weakly expressed in *V. albinus* and absent in *V. mollis*), a shallow suture, and a sculpture consisting of fine spiral threads and very low, numerous (11 to 22 on last whorl) rounded ribs that extend on the last whorl to the basal constriction. The whorls are rounded and without angulations or nodes. The beaded lirae set *Viridifusus* apart from all other fusinine genera. The relatively widely open siphonal canal is reminiscent of a similar condition in *Africofusus* gen. nov., but that genus lacks lirae, has a relatively much larger aperture, and usually has angulated, nodose whorls. Species of *Ariefusus* gen. nov. have a strongly angulated shell with axially elongated nodes and smooth lirae and a very narrowly open siphonal canal.

#### *Heilprinia* Grabau, 1904

Type species. — *Fusus caloosaensis* Heilprin, 1886 (Fig. 12)

Included fossil species. — *Heilprinia burnsii* (Dall, 1890); *H. caloosaensis* (Heilprin, 1886); *H. carolinensis* (Dall, 1892); *H. dianae* (Petuch, 1994); *H. diegelae* Petuch, 1994; *H. exilis* (Conrad, 1832); *H. hasta* Petuch, 1994; *H. miamiensis* Petuch, 1994; *H. portelli* Petuch, 1994.

Included extant species. — *Heilprinia coltrorum* (Hadorn & Rogers, 2000); *H. dowiana* (Olsson, 1954); *H. timessa* (Dall, 1889).

Remarks. — The genus *Heilprinia* was originally proposed for a number of species from the Pleistocene and present of the Americas, in which the protoconch is sculptured with fine riblets throughout. In other fusinines, the protoconch is smooth except for the last half whorl, which is sculptured with fine riblets. In addition to the protoconch, several adult shell traits set *Heilprinia* apart from other fusinine taxa. These include a very narrowly open siphonal canal (opening less than 2mm), very small rounded to ovate aperture,

strong lirae on the inner side of the outer lip, rounded adapical end of the aperture, a small but distinct parietal ridge, conspicuously smooth spiral cords overriding broad, rounded and generally short axial ribs, and an erect adult inner lip.

*Heilprinia* is a predominantly Pliocene to Early Pleistocene genus from the Atlantic and Gulf Coastal Plains of the United States. Following Hadorn & Rogers (2000), we recognize three extant species as well (see above), again from the same geographical region. The extant species are slender (length to diameter ratio 3.1 : 3.4) with a relatively long siphonal canal (canal length to shell length ratio 0.32 : 0.41). *Heilprinia dowiana* is unusual among fusinines in that its adult outer lip is both externally and internally thickened.

As currently understood, *Heilprinia* is biogeographically confined to what Petuch (1982) called the Caloosahatchian Province, encompassing the coasts of the southeastern United States and Gulf of Mexico to Honduras, like dozens of other Pliocene to living genera. Fascioliid examples include *Pliculofusus* Snyder et al., 2012, and *Terebraspira* Conrad, 1862 (both fossil only) and *Cinctura* Hollister, 1957. It is highly likely that *Heilprinia* arose from an ancestor that would be placed in *Aristofusus* gen. nov. (see below).

#### *Callifusus* gen. nov.

Type species. — *Fusus irregularis* Grabau, 1904 (Fig. 13)

Diagnosis. — Fusinines with angular whorls; shell relatively elongate (length to diameter ratio about 3.4) with elongate, relatively widely open siphonal canal (canal length to shell length ratio about 0.38, opening 3 mm wide); spiral sculpture consisting of low rounded alternating cords, including a peripheral cord; axial sculpture present on early whorls or throughout; aperture adapically rounded with prominent parietal ridge; inner side of outer lip with short, poorly developed, often paired lirae; growth lines roughen spiral sculpture.

Included species. — *Callifusus irregularis* (Grabau, 1904); *C. edjanssi* (Callomon & Snyder, 2017).

Etymology. — Calli, Greek, meaning beautiful.

Remarks. — We propose *Callifusus* gen. nov. for a small group of subtropical eastern Pacific fusinines characterized by a broadly open siphonal canal, a notably flexuous siphonal process, poorly developed and often paired lirae that do not extend far into the aperture, and a central peripheral cord. Although the whorls have an angular profile, they are much more weakly sculptured than those of *Goniofusus* gen. nov., and the lirae are much weaker and shorter. The tem-

perate northeastern Pacific genus *Araiofusus* has rounded whorls and lacks lirae altogether. In its indistinct lirae and its widely spaced rounded cords, *Callifusus* gen. nov. resembles the Australian genus *Propefusus* and the new South African *Africofusus*. *Callifusus* gen. nov. differs from *Propefusus* by having fewer axial ribs or nodes and by having only one row of nodes or tubercles if these are developed at all. It differs from *Africofusus* gen. nov. by having a longer siphonal process, a narrower siphonal canal opening, and having the aperture adapically rounded instead of angulate.

#### *Africofusus* gen. nov.

Type species: *Fusus ocellifer* Lamarck, 1816 (Fig. 14)

Diagnosis. — Shell broadly fusiform (length to diameter ratio 1.8 : 2.4); siphonal canal widely open (5 mm or more), often dorsally curving; spiral sculpture consisting of widely spaced rounded cords; axial sculpture variable, can form nodes or tubercles at single enlarged shoulder cord or keel when well expressed; basal constriction of last whorl gradual; siphonal process usually short (canal length to shell length ratio 0.32 : 0.37); aperture large; outer lip smooth or with very short lirae on inner side.

Etymology. — Referring to South Africa, the region where the component species are found.

Included species. — *Africofusus adamsii* (Kobelt, 1880); *A. africanus* (Sowerby III, 1897); *A. cinnamomeus* (Reeve, 1847); *A. ocellifer* Lamarck, 1816; *A. robustior* (G. B. Sowerby II, 1880).

Remarks. — When they discussed the South African *Fusus ocellifer* complex, Kilburn & Rippey (1982) recognized that these taxa (which they considered subspecies of *F. ocellifer* rather than as full species as we do here) are atypical fusinines in having a large aperture, inflated last whorl, a relatively low spire, and widely separated, low, rounded spiral cords. Furthermore, their siphonal canals are relatively widely open. Species in this group closely resemble the South African fascioliine genera *Kilburnia* Snyder et al., 2012, and *Lugubrilaria* Snyder et al., 2012. *Africofusus* gen. nov. differs from these taxa primarily in lacking the columellar folds that characterize members of the Fascioliinae. D'Asaro (2000) observed that egg capsules of *A. ocellifer* have a rounded apex without ridges, in this way resembling the capsules of *Lugubrilaria* and of the small eastern Pacific species *Hesperaptyxis cinereus* (Reeve, 1847). For these reasons, we propose the new genus *Africofusus* gen. nov. As noted by Kilburn & Rippey (1982), the expression of axial sculpture, including shoulder tubercles, varies widely among populations (here



considered species) of *Africofusus* gen. nov. In this respect, the genus recalls *Kilburnia*, whose species also cover a very wide range of sculpture (see Snyder et al., 2012).

In addition to the *A. ocellifer* group of species, we provisionally include *Fulgur africanus*. This species diverges from other members of *Africofusus* gen. nov. by its long, more narrowly open siphonal canal, abapically slightly free-standing inner-lip edge, and a distinct channel at the adapical end of the aperture; but it shares with the *A. ocellifer* group the very low, widely spaced spiral cords, smooth surface on the inner side of the outer lip, and angular whorl profile. Most of its unusual features are exaggerations of the traits that characterize the *A. ocellifer* group.

*Africofusus* gen. nov. is represented in the fossil record by a species identified by Kensley & Pether (1986) as *Fasciolaria lugubris* (Reeve, 1847) from the Pliocene of Hondeklip, South Africa. The absence of columellar folds in the fossil led us (Snyder et al., 2012) to suggest that this taxon is actually *Fusinus cinnamomeus*, a species we here transfer to our new genus *Africofusus*.

#### *Enigmofusus* gen. nov.

Type species. — *Fusinus nicki* Snyder, 2002 (Fig. 4)

Diagnosis. — Shell narrowly elongate fusiform with very long, narrowly open siphonal canal; distal end of siphonal canal not flaring; spiral sculpture consisting of widely separated low angular cords, of which two (the peripheral and central cord) are enlarged and bear spirally elongate projections; cords on siphonal process well expressed, none enlarged; axial sculpture consisting of low, short, rounded ribs roughened by growth lines; aperture relatively large, ovate, its adapical end rounded and without channel; outer lip smooth-edged or crenulated, its inner side with or without fine lirae; inner lip adherent, with distinct parietal ridge at adapical end.

Included species: *Enigmofusus nicki* Snyder, 2002; *E. beckii* (Reeve, 1848).

Etymology. — Enigma, referring to the peculiarities of this genus.

Remarks. — The two species we assign to the new genus *Enigmofusus* exhibit a peculiar combination of characters, distinguishing them from other Indo-West Pacific genera. The two enlarged spiral cords on the last whorl bear spirally elongate nodes, as in *Marmorofusus*; but the absence of enlarged and differentiated cords on the siphonal process distinguishes *Enigmofusus* gen. nov. from *Marmorofusus*. Lirae are absent in *E. nicki* but present and fine in *E. beckii*.

The genus *Enigmofusus* gen. nov. is perhaps most

similar to our new genus *Africofusus*. It differs from that temperate genus by having a longer siphonal protuberance that is more abruptly set off from the main part of the last whorl. The cords of *Enigmofusus* gen. nov. are more sharply rounded and the shell is more elongate. Nevertheless, it is possible that *Africofusus* gen. nov. is derived from a tropical lineage whose members would be assigned to *Enigmofusus* gen. nov.

Both species of *Enigmofusus* gen. nov. are from the Indian Ocean. *Enigmofusus nicki* is found in southwestern Madagascar, whereas *E. beckii* is recorded from the Andaman Islands.

#### *Chryseofusus* Hadorn & Fraussen, 2003

Type species. — *Fusinus chrysodomoides* Schepman, 1911 (Fig. 15)

Remarks. — As currently understood, the genus *Chryseofusus* comprises mostly deep-water, light-shelled fusinines with a markedly beaded or scaly spiral sculpture, a large aperture, relatively widely open siphonal canal, and few or no lirae on the inner side of the outer lip. Axial ribs are mostly confined to the upper teleoconch whorls. All but one of the 21 species placed in *Chryseofusus* by Hadorn & Fraussen (2003) and Hadorn et al. (2008) are from the IWP realm, but *C. kazdailisi* (Fraussen & Hadorn, 2000) occurs off Valparaiso, Chile.

Here we add *Fusinus bonaespei* (Barnard, 1959), from the Agulhas Bank off South Africa to the list of species of *Chryseofusus*. This species bears a striking resemblance to such species as *C. jurgeni* (Hadorn and Fraussen, 2002) from off southwestern Madagascar in its strongly granulate cords. *Chryseofusus bonaespei* shares with *C. jurgeni* the unusual character of a slightly internally thickened adult outer lip. Some mature specimens of *C. bonaespei* have a longer siphonal process than other members of this genus. If our assignment of this South African species is correct, *C. bonaespei* would be the second species of the genus to occur outside of (but adjacent to) the IWP realm. Such a wide geographical distribution would not be unusual for a deep-water genus such as *Chryseofusus*.

#### *Propefus* Iredale, 1924

Type species. — *Fusus pyrulatus* Reeve, 1847 (= *Pyrula undulata* Perry, 1811) (Fig. 16)

Remarks. — Iredale's (1924) genus *Propefus* was originally proposed to accommodate *Fusus pyrulatus*, a broadly fusiform, thin-shelled species with a relatively low spire and short siphonal process. Here we expand the concept of *Propefus* to include two additional species from the living fauna of temperate Aus-



tralia, *P. australis* (Quoy & Gaimard, 1833) and *P. novaehollandiae* (Reeve, 1848).

Despite their great differences in shape - *P. pyrulatus* is broadly fusiform (shell length to diameter ratio 2.2) with a short siphonal canal (canal length to shell length ratio 0.29), *P. novaehollandiae* is elongate fusiform with a very long canal, and *P. australis* is intermediate (ratios 2.5 and 0.31 respectively) - the species of *Propefusus* share the following characters: narrowly open siphonal canal (2 to 3 mm), outer lip without lirae or with very poorly expressed lirae at the edge; aperture adapically rounded with one or more parietal ridges; inner lip adherent; spiral sculpture consisting of low rounded or almost angular cords axially roughened by growth lines, the intervals between them wide and sculptured by a secondary cords and several flanking tertiary threads; axial sculpture consisting of very low ribs on upper whorls, 13 to 15 per whorl, represented on later whorls by low rounded tubercles on one or more primary cords. The combination of numerous low axial elements, widely separated primary cords, and very narrowly open canal makes this genus highly distinctive. At a length of almost 30 cm, *P. novaehollandiae* is one of the largest living fusinines, in keeping with the large body sizes of several other temperate Australian gastropods with tropical affinities.

#### *Gracilipurpura* Jousseume, 1880

Type species. — *Fusus strigosus* Lamarck, 1822 (= *Murex rostratus* Olivi, 1792) (Figs 17-18)

Remarks. — We take this opportunity to resurrect the genus name *Gracilipurpura* to full generic rank. Bouchet & Waren (1985) considered *Gracilipurpura* as a synonym of a broadly defined *Fusinus*, but with the division of *Fusinus* proposed here, we consider *Gracilipurpura* to be a distinct Mediterranean and temperate northeastern Atlantic group of small fusinines characterized by a strongly carinate periphery that is often adorned with open spines; long axial ribs; a weakly crenulated outer lip with lirae on its inner side; and a narrowly open siphonal canal. There is a parietal tooth at the adapical end of the inner lip, which is adherent throughout most of its length. Shells of this genus are relatively broad (length to diameter ratio 2.3 : 2.9) with a relatively long siphonal canal (canal length to shell length ratio about 0.40 in the type species).

We restrict *Gracilipurpura* to a group of mainly fossil species close to the Pliocene to extant type species *G. rostrata*. These species tentatively include *G. affinis* (Bronn, 1831) from the Pliocene of Italy; *G. austriaca* (Hoernes & Auinger, 1890) from the Late Miocene

(Tortonian) of Austria; *G. cincta* (Bellardi & Michelotti, 1840) from the Late Miocene to Pliocene of Italy; *G. raouli* (Lozouet, 2015) from the Late Oligocene (Chattian) of the Aquitaine Basin in southwestern France. Following Gründel & Tembrock (1992), it is possible that the genus extends back to the Early Oligocene (Rupelian) of Germany, with *G. acuticostata* (Speyer, 1860). The Pliocene representatives from Italy have been well described and illustrated under the genus name *Fusinus* by Chirli (20000) and Tabanelli (2014).

The aptly named genus *Carinofusus* Ceulemans et al., 2015 (type species: *Clavella neogenica* Cossmann, 1901) from the Pliocene of Atlantic France differs from typical *Gracilipurpura* in being nearly twice the shell length (101.5 mm) of *G. rostrata* (56 mm), in having an even more exaggerated peripheral keel, and in lacking axial sculpture on the last two teleoconch whorls. We suspect that *Carinofusus* represents an extreme variation of *Gracilipurpura* from near the northern limit of the latter genus, and tentatively consider it a subjective synonym of *Gracilipurpura*.

#### *Angustifusus* gen. nov.

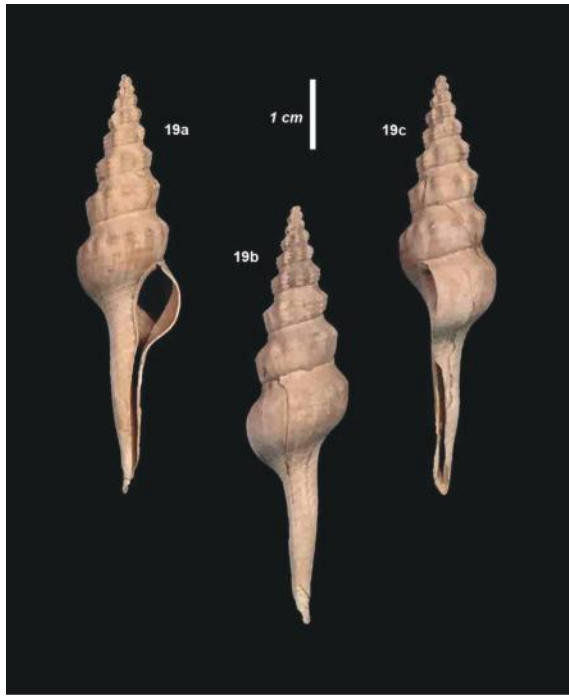
Type species. — *Fusus vindobonensis* Hoernes & Auinger, 1890 (Fig. 19)

Diagnosis. — Shell elongate to very elongate (shell length to diameter ratio 2.7 : 4.0) with small aperture and elongate, very narrowly open siphonal canal (canal length to shell length ratio 0.32 : 0.42, opening less than 2 mm wide); sutures shallow and closely appressed; axial sculpture consisting of low ribs forming spirally elongate nodes at shoulder angulation, usually expressed only on spire whorls and obsolete or absent on last one or two whorls; spiral sculpture consisting of very low threads and cords, usually reduced on adult whorls; aperture adapically rounded; outer lip edge planar to abapically convex; inner side of outer lip smooth; inner lip adherent or weakly erect, usually with parietal ridge at its adapical end.

Included species. — *Angustifusus vindobonensis* (Hoernes & Auinger, 1890) (Tortonian, Vienna and Romanian Basins); *A. aturensis* (Grateloup, 1845) (Late Miocene, France); *A. hoessii* (Hoernes & Auinger, 1890) (Late Miocene, Austria); *A. longiroster* (Brocchi, 1814) (Tortonian to Pliocene, widespread in Europe); *G. raulini* (Peyrot, 1928) (Late Oligocene, France); *A. semirugosus* (Bellardi & Michelotti, 1840) (Late Miocene, Italy and Austria).

Etymology. — *Angustus*, Latin narrow, slender.

Remarks. — Although this paper is chiefly concerned with large living fusinines, we take this opportunity to formalize as a genus a group of fossil



**Figs 19-20.** Type species of Fusininae. **19**, *Fusus vindobonensis* Hörnes & Auinger, 1890 [= *F. semirugosus* Bellardi & Michellotti, 1840, sensu Hörnes, 1853], type species of *Angustifusus* gen. nov., Baden-Sooss, Vienna Basin, Austria, Middle Miocene, 60.7 mm (NHMW 0300). **20**, *Fusus porrectus* Solander in Brander, 1766, type species of *Eofusus* gen. nov., Barton Clay Formation ('Middle Barton Beds'), Bartonian, Middle Eocene, 78.3 mm (NHMUK PI TG 26971).

European species that Glibert (1963) referred to as the *Fusinus vindobonensis* group. Although Glibert (1963) appears to have linked this group to the *F. rostratus* group in his (subgenus) taxon *Gracilipurpura*, *Angustifusus* gen. nov. differs markedly from *Gracilipurpura* by having very slender shells, a very long and very narrowly open siphonal canal, and reduced spiral and axial sculpture on adult whorls. The inner side of the outer lip is smooth in *Angustifusus* gen. nov., whereas it is lirate in *Gracilipurpura*. The characteristic keel of *Gracilipurpura* is absent in *Angustifusus* gen. nov. In its very slender form, tiny round aperture, long and very slender siphonal process, very narrowly open siphonal canal, absence of lirae, and low external sculpture, *Angustifusus* gen. nov. closely resembles Eocene species that have been assigned to *Fusinus*, to which we assign the new genus name *Eofusus*. For comparisons with this genus see *Eofusus* below.

A possible additional species assigned to *Angustifusus* gen. nov. is *Fusinus clavilithoides* Landau et al., 2016, from the Serrvallian (Middle Miocene) of the Caraman Basin in Turkey. This species differs from other members of the genus by having a barrel-shaped, *Clavilithes*-like last whorl, but its characters

are otherwise consistent with placement in *Angustifusus* gen. nov.

At its widest geographical extent during the Pliocene, *Angustifusus* gen. nov. spread as far north as the North Sea Basin (*A. longiroster* in the Oorderen Sands of Belgium; Marquet, 1997) and even the Isle of Man. This makes *Angustifusus* gen. nov. the northernmost large fusinine in the northeastern Atlantic. The earliest member of the genus is the small *A. raouli* from the Chattian of southwestern France. To our knowledge, *Angustifusus* gen. nov. is the only genus of large fusinines besides the mostly smaller Eocene genus *Eofusus* without living representatives.

#### *Eofusus* gen. nov.

Type species. — *Murex porrectus* Solander, 1766 (Fig. 20)

Diagnosis. — Shell relatively small (maximum length 83 mm), elongate to extremely elongate (length to diameter ratio 3.4 : 5.9), with a very small rounded aperture and very long, very narrowly open siphonal canal (canal length to shell length ratio 0.29 : 0.50, opening less than 2 mm wide); sculpture generally weak, consisting of low, sharply rounded axial ribs that form one or more closely spaced rows of nodules at the shoulder angulation in some species including the type species, but nodes absent in others; aperture adapically rounded, without parietal ridge; outer lip smooth on inner side; inner lip adherent.

Included species. — *Eofusus porrectus* (Solander, 1766); *E. aciculatus* (Lamarck, 1803); *E. acuminatus* (J. Sowerby, 1821); *E. anglorum* (Wrigley, 1927); *E. asper* (J. Sowerby, 1821); *E. insectoides* (Harris, 1897).

Etymology. — Eos, Greek dawn, referring to the early appearance of fusinines.

Remarks. — We propose *Eofusus* gen. nov. for a compact group of Middle to Late Eocene slender fusinines of generally small size with a tiny aperture, very long and very narrowly open siphonal canal, simple aperture and low sculpture. The earliest species are from the Middle Eocene (Lutetian) of France. The genus extends into the Late Eocene of southern England and the latest Eocene of the Gulf Coastal Plain of the United States (*E. insectoides*).

*Eofusus* gen. nov. is very similar to *Angustifusus* gen. nov., from which it differs by having a rounder, less ovate aperture. For a comparison with *Falsifusus* see below under family Turbinellidae.

The species *E. acuminatus*, with a shell length to diameter ratio of 5.9 and a siphonal canal about half the length of the shell, is one of the most slender fusinines known, being rivaled only by *Fusinus gracillimus*. This species is also one of the least strongly sculptured members of the genus, the axial ribs being obsolete or absent.

## TAXA EXCLUDED FROM FUSININAE

Subfamily Fascioliariinae Gray, 1853

*Polygona* Schumacher, 1817

Type species. — *Murex infundibulum* Gmelin, 1791

*Polygona filosa* (Schubert & Wagner, 1829)

Remarks. — Rolan & Schoenherr (1997) examined the radula of the species that had been commonly known as *Latirus filiosus* from Angola and concluded that this species belongs to the genus *Fusinus* in the broad sense rather than to *Latirus* in the broad sense. The lateral cusps are shorter than in members of the latter group and are therefore more like those in the radula of *Fusinus* (Rolan & Schoenherr, 1997). We have examined lots from Senegal, Ivory Coast and Angola at ANSP and the Natural History Museum, London and the Naturalis Biodiversity Center, Leiden. Shell characters unambiguously place this species in the genus *Polygona*, which in the phylogenetic scheme proposed by Couto et al. (2016) belongs to the Fascioliariinae. These characters include the presence of a distinct siphonal fasciole, a very broad, short siphonal process, a sudden step-like basal constriction, high rounded axial ribs that continue in diminished form onto the siphonal process, and above all by the presence of three low but distinct abapically placed columellar folds close to the siphonal canal. *Polygona filiosus* has smooth lirae, high sharp spiral cords on the main part of the whorl as well as on the spiral process, and two strong cords on the subsutural slope. These characters are strikingly similar to those of such well-known southern European fossil species as *P. crassa* (Michelotti, 1847) from the Early Miocene, *P. lynchi* (Basterot, 1825) from the Early Miocene, and *P. zahlbruckneri* (Glibert, 1963) from the Late Miocene, among other species. As the only known living West African member of *Polygona*, *P. filosa* is likely the lone survivor of a more diverse Neogene lineage in the Eastern Atlantic, Mediterranean and Paratethys.

**Clavilithinae subfam. nov.**

Type genus. — *Clavilithes* Swainson, 1840

Diagnosis. — Fascioliariids marked by a profound ontogenetic shift from a high-spined, spirally and axially sculptured early teleoconch to a late stage in which the whorls become more inflated, more cylindrical in profile, and strongly overlapping earlier whorls; siphonal process long, straight; adaxial margin of siphonal canal not separated from columellar side of shell by a groove; outer lip simple, usually smooth on

inner side (but lirate in some Miocene to Pleistocene species from southeast Asia); inner lip often free-standing; adapical end of aperture often forming short channel.

Remarks. — We take this opportunity to formalize the subfamilial status of a group of fossil gastropods around the genus *Clavilithes* Swainson, 1840, which has long been recognized as distinct from other fascioliariids (see Grabau, 1904; Wrigley, 1927). The subfamily differs from Fusininae most consistently in that the inner (adaxial) edge of the siphonal canal is not separated by a groove from the columellar side of the shell as it is in Fusininae. Most clavilithines lack lirae on the inner side of the outer lip, whereas most Fusininae are lirate. Clavilithines sometimes have a columellar fold or entrance fold to the siphonal canal, whereas in Fusininae these folds are usually absent. As noted in the discussion under *Cyrtulus*, that genus is not a clavilithine despite its striking ontogenetic shift in the type species *C. serotinus* from a typical *Fusinus*-like early stage to a smooth, cylindrical last whorl.

The taxonomy of Clavilithinae is in considerable disarray and requires revision at both the species and genus level. The list of genera we include in Clavilithinae follows that of Snyder (1999): *Africolithes* Eames, 1957; *Austrolithes* Finlay, 1931; *Chiralithes* Olsson, 1930; *Clavellofus* Grabau, 1904; *Clavilithes* Swainson, 1840 (= *Rhopalithes* Grabau, 1904); *Cosmolithes* Grabau, 1904; *Mancorus* Olsson, 1931; *Papillina* Conrad, 1855; *Perulithes* Olsson, 1930. As Eames (1950) has pointed out, several Oligocene to Early Pleistocene species from southeast Asia and East Africa will likely require a separate genus name, but we refrain from taking formal action pending further study of the species involved.

As circumscribed here, the Clavilithinae extend from the Early Palaeocene to the Early Pleistocene. Although the subfamily occurred throughout the tropics during the Eocene, it became extinct in South America at the end of the Eocene, in North America after the Early Oligocene, in Australia after the Middle Miocene, in Europe after the Late Miocene, and in southeast Asia in the Early Pleistocene. West African species are confined to the Late Palaeocene and Eocene; and a single species is known from the Early Eocene of New Zealand. The subfamily was also found on the west coast of North America only during the Eocene.

It is possible that the Clavilithinae represents a heterogeneous group. As noted under the genera *Cyrtulus* and *Angustifusus* gen. nov. above, the *Clavilithes* form appeared independently in at least two fusinine lineages, and therefore could have evolved more than once in other fascioliariids as well. In par-



ticular, the presence of one or two columellar folds in some clavilithine clades, and of a lirated outer lip in the Neogene Indo-West Pacific lineage in this subfamily, could indicate convergence rather than common ancestry with other clavilithines. Further paleontological research will have to resolve this issue, but for now we believe it is useful to attach a name to this distinctive and iconic group of large fossil gastropod.

Family Turbinellidae Swainson, 1835

*Falsifusus* Grabau, 1904

Type species. — *Fusus ottonis* Aldrich, 1897

Remarks. — The Eocene genus *Falsifusus* has until now always been assigned to Fusininae (Grabau, 1904; Palmer, 1937). The type species, however, bears a very close resemblance to *Fusus unicarinatus* Deshayes, 1834 and other related species from the Early Eocene to the latest Eocene of Europe, which have been assigned to the columbariine turbinellid genus *Coluzea* Finlay in Allan, 1926 (Pacaud & Le Renard, 1995; Belliard et al., 2017). The genus name *Falsifusus* therefore seems an appropriate name for the American and European taxa with keeled, spinose or nodulose whorls and a multispiral protoconch. The question whether *Falsifusus* should be distinguished from *Coluzea* is beyond the scope of this paper, but it is clear that *Falsifusus* must be considered a turbinellid and not a fascioliid genus.

As originally noted by Grabau (1904), *Falsifusus* differs from most Fusininae by having a multispiral rather than a paucispiral protoconch. Although its shell resembles that of *Eofusus*, it differs from that fusinine genus by having carinated whorls in which the peripheral keel (and often a basal keel as well) bears small nodes or spines. The spire of *Falsifusus* tends to be lower, but the long, straight siphonal process is extremely similar to that of *Eofusus*, characterized by being almost smooth on its distal half. Palmer (1937) noted that the Gulf Coastal Plain fauna of the United States contains several species of *Falsifusus*, but with the exception of the latest Eocene *Eofusus insectoides* (see Harris & Palmer, 1947), this fauna lacks what she called "true *Fusinus*" (i.e. *Eofusus*). *Falsifusus* seems to have become extinct in North America after the Middle Eocene, whereas in Europe it persisted until the latest Eocene or earliest Oligocene.

BIOGEOGRAPHICAL AND MORPHOLOGICAL PATTERNS

The group comprising large fusinines is an essentially tropical assemblage of about 130 carnivorous gastropods about whose ecology we know next to nothing.

As with most other tropical clades, the large-shelled Fusininae reach their maximum diversity in the IWP realm, with at least 80 species (including those extending to warm-temperate Japan). Tropical American diversity is much lower, with 19 western Atlantic species and nine eastern Pacific species; there are seven large fusinines in West Africa. The group has penetrated most warm-temperate regions including the northeastern Pacific (eight species, one extending to British Columbia and perhaps to southeastern Alaska), the southeastern Pacific (one deep-water species), southern Africa (seven species) and southern Australia and New Zealand (five species). Only small-shelled species occur in the northeastern Atlantic and Mediterranean region, and no fusinine occurs in the temperate northwestern Atlantic.

It is far from clear how and when large size and the broad distribution of fusinines were achieved. In contrast to Paleogene clavilithines, which often exceeded a length of 100 mm, early fusinines were generally small. The largest Eocene species we have seen is *Eofusus porrectus* from the Middle Barton beds (Late Eocene) of southern England. At a length of 83.0 mm, this species was not exceeded in size by fusinines until the Early Miocene. Size increase occurred independently in nearly all fusinine genera during the Neogene. European Late Oligocene species of *Gracilipurpura* and *Angustifusus* gen. nov. are small (less than 35 mm), with larger species appearing during the Miocene, especially the Late Miocene. The earliest fusinine so far known to exceed 100 mm is *Lyonsifusus mithras* from the Cantaure Formation (Early Miocene) of Venezuela. Species exceeding a length of 200 mm, as seen in *Apertifusus* gen. nov., *Cyrtulus*, *Fusinus*, *Goniofusinus* gen. nov. and *Lyonsifusus* gen. nov., and approaching this size as in *Ariefusus* gen. nov., *Marmorofusus* and *Propefusinus*, are known only in the living fauna.

The first cool-temperate fusinines were small species (less than 30 mm) of *Priscofusinus* Conrad, 1865, from the Early Oligocene of Japan (*P. ishijimai* Hirayama, 1955) and Oregon (*P. stewarti* Tegland, 1933). No member of this genus, ranging from the Early Oligocene to the latest Miocene, exceeded a shell length of 50 mm. Species of the Late Miocene to present northeastern Pacific genus *Harfordia*, Dall, 1921, reach a length of 70 mm. Cool-temperate species of *Araiofusinus*, a genus not known fossil, reach 118.6 mm in the living northeastern Pacific fauna.

Several morphological patterns of distribution are noteworthy. Among shallow-water fusinines, a very narrowly open siphonal canal characterizes the IWP genera *Cyrtulus*, *Enigmofusus* gen. nov., *Fusinus* and *Marmorofusus*, as well as the western Atlantic genera *Aristofusus* gen. nov. and *Heilprinia*, the eastern At-



lantic *Ariefusus* gen. nov. and fossil *Eofusus* gen. nov. and *Angustifusus* gen. nov., and to a lesser extent the temperate Australian genus *Propefusus*. More broadly open canals, often with a distal flare, characterize the other temperate-zone genera including *Africofusus* gen. nov. in southern Africa, three northeastern Pacific genera (*Araiofusus*, *Barbarofusus* Grabau & Shimer, 1909, and *Harfordia* Dall, 1921), and *Gracilipurpura* in the Mediterranean. They also occur in some tropical taxa (*Apertifusus* gen. nov. and *Viridifusus* gen. nov. in West Africa, and *Callifusus* gen. nov. in the eastern Pacific) and in most deep-water genera (*Amiantofusus*, *Angulofusus*, *Chryseofusus*, and *Harasewychia* Petuch, 1987). We speculate that an extremely narrowly open siphonal canal offers protection against attack by predators on the proboscis, an otherwise highly vulnerable organ.

Lirae on the inner side of the outer lip also appear to be more or less confined to species living in warm, shallow waters. The function of lirae has been little studied, but rapid or precise retraction and extension of the head and foot into and out of the shell are plausible benefits. The erect inner lip and small aperture of many tropical fusinines (especially in *Aristofusus* gen. nov. *Heilprinia*, *Cyrtulus*, *Fusinus* and *Marmorofusus*) indicate a relatively small foot that, together with the long straight siphonal process, deeply impressed suture, inflated whorls, and often prominent axial and spiral sculpture imply very slow locomotion on the surfaces of rock, sand or silt. No fusinine exhibits morphological features indicating an ability to burrow actively in soft sediments.

It is curious that, whereas outer-lip lirae are widespread among fusinines, columellar folds that might also aid in effectively extending and withdrawing the soft parts are absent in Fusininae. The two types of features - lirae and columellar folds - co-occur in the same shell in cancellariids and many fasciolarini and peristerniines. The absence of lirae and columellar folds in cool-water and deep-water fusinines, as well as in the Eocene *Eofusus* and the Neogene *Angustifusus* gen. nov., could indicate a diminished premium on effective withdrawal or rapid extension of the body of fusinines in these habitats.

This discussion is offered to stimulate interest not only in the taxonomy and phylogeny of Fusininae, but also in the biology and functional aspects of the shells of these striking and often beautiful animals. We especially wish to encourage divers and other collectors to observe and to publish on these animals in life.

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