

SHELL CHARACTERS AND TAXONOMY OF *LATIRUS* AND RELATED FASCIOLARIID GROUPS

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ABSTRACT

The neogastropod family Fasciolaridae contains a complex of genera related to *Latirus* Montfort, 1810, many of which have traits unusual for the family. In a taxonomic revision of some of these genera, based on shell characters, we restrict *Latirus* to a mainly Indo-West Pacific group of Pliocene to Recent species, which closely resemble the middle Miocene to Recent pantropical genus *Hemipolygona* Rovereto, 1899. *Hemipolygona stenomphalus* (Habe & Kosuge, 1966) is synonymized with *H. recurvirostris* (Schubert & Wagner, 1829). *Lathyropsis* Oostingh, 1939, based on a small Pliocene species from Indonesia, is here tentatively subsumed under *Polygona* Schumacher, 1817. The latter genus, ranging from the late Oligocene to Recent, occurs mainly in the New World and eastern Atlantic, and contains at least two species groups centered on *P. infundibulum* Schumacher, 1817 (type of genus) and *P. angulatus* (Röding, 1798). Taxa assigned by many authors to *Latirulus* Cossmann, 1889, are here reassigned to the new genus *Turrilatirus* (type species: *Voluta turrita* Gmelin, 1791), from the Pliocene to Recent of the Indo-West Pacific. *Latirulus* is restricted to Eocene species. We assign various early Miocene to Recent species from the western Atlantic and eastern Pacific to the new genus *Pustulatirus* (type species: *Latirus mediamericus*, Hertlein & Strong, 1951a). Taxa formerly assigned to *Latirus* but here removed from Fasciolaridae include *Latirus ewekoroensis* Adegoke, 1977; the Eocene *Ruscula* Casey, 1904; *Lathyrus granifer* and *L. compactilis*, both of Martin, 1931; *Latirus kirbyi* Clark, 1938; *Latirus tortilis* var. *nanafaluis* Harris, 1899; and *Latirus quercotillaensis* Olsson, 1931.

INTRODUCTION

One of the many gastropod groups that diversified extensively during the Neogene (23.8 Ma to the present) is the gastropod family Fasciolaridae, especially the Fasciolarinae and Peristerniinae, including *Latirus* and related genera. These predatory gastropods are found on hard bottoms throughout the tropics, and have a fossil record extending back to at least the middle Eocene. The genus-level taxonomy and phylogenetic relationships of this group have long been problematic. Many genus-level names have been applied indiscriminately, and there have been few comparative studies that have taken both living and fossil species into account. Several members of the group have shell features that are unusual either within the family or within the Neogastropoda as a whole. These include a labral tooth, beaded spiral ridges in the aperture, deeply recessed denticles on the outer lip, a secondarily smooth columella and an enveloped shell. In order to understand how these shell features evolved and to gain insight into the deployment of the Neogastropoda as a whole over the course of their middle Cretaceous to Recent history, it is important to describe these features and to provide a shell-based taxonomy that is useful to palaeontologists.

Our purposes in this paper are (1) to describe the unusual shell traits and their taxonomic distribution in Fasciolaridae; (2) to undertake a partial, shell-based, genus-level revision of *Latirus* and related genera; (3) to explore the fossil record of Peristerniinae and to a lesser extent Fasciolarinae; and (4) to evaluate and reassign some taxa that have been wrongly attributed to *Latirus* or related peristerniine genera.

SHELL CHARACTERS

We first introduce the descriptive framework in which the teleoconch of all members of the Fasciolaridae can be described. The last whorl of the teleoconch is divisible into three sectors, which are delineated by distinctive spiral sculptural elements. These are the subsutural sector, the central sector and the base. The shoulder angulation separates the subsutural from the central sector; a central cord, often not strongly expressed, demarcates the generally convex central sector from the typically concave base. On the shell's outer lip, the three sectors are expressed respectively as the subsutural edge (typically a concave sinus), the central sector (typically convex) and the abapical sector (typically a concave sinus merging into the right margin of the siphonal canal). In the spire whorls, the subsutural sector of the whorl is always exposed, but the base never is. During ontogeny, the suture typically migrates across the central sector, usually in an abapical direction but sometimes adapically. In most species, the central cord lies just below the suture.

Besides the spiral elements demarcating sectors of the whorl, external sculpture typically consists of rounded axial ribs and weaker spiral cords and threads. In the aperture, the inner (adaxial) side of the outer lip is often marked by spiral ridges (lirae) or by denticles. The inner lip is often characterized by an adapical (or parietal) tubercle or rib, and by one or more columellar folds at and just adapical to the entrance of the siphonal canal.

We use the following abbreviations:

BGM, Bandung Geological Museum, Indonesia
MNRJ, Museu Nacional, Rio de Janeiro, Brazil
MCZ, Museum of Comparative Zoology, Cambridge, MA, USA
SC, Snyder Collection, Villanova, PA, USA
SL, Shell length
ZMA, Zoologisch Museum, Amsterdam, The Netherlands

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SYSTEMATICS

Family Fasciolariidae
Subfamily Peristerniinae

Revised diagnosis (based on shell characters): teleoconch from about 12 mm to more than 120 mm in length, fusiform, solid; aperture relatively narrow, its length: breadth typically between 2.0 and 3.0; inner lip usually with adapical parietal denticle and with two to four abapical folds, including large fold at entrance to siphonal canal; inner side of outer lip of adults usually lirated; central cord well expressed; edge of central sector of outer lip usually convex.

Remarks: On shell characters alone, it is difficult to distinguish unambiguously between Peristerniinae and Fasciolariinae. The latter group (including *Fasciolaria* Lamarck, 1799; *Pleuroploca* Fischer, 1884; *Terebraspira* Conrad, 1862; *Triplofusus* Olsson & Harbison, 1953; and related genera) appears to be characterized mainly by a larger adult size and a thinner shell, and the siphonal protuberance rarely bears a distal fasciole. We strongly suspect that fasciolariines are phylogenetically derived from early peristerniines, and that the two groups are part of a single clade Fasciolariinae.

D'Asaro's (2000) analysis of egg capsule morphology in fasciolariids offers support to the recognition of the Peristerniinae, the group containing *Latirus* and related genera. Peristerniines have funnel-shaped capsules that vary little among species. D'Asaro (2000) noted that *Pleuroploca filamentosa* (Röding, 1798) and '*P. lignarius* (Linnaeus, 1758) (type of *Tarantinaea* Monterosato, 1917) have capsules similar to those of peristerniines and different from other fasciolariines. This fact may point to the inclusion of these taxa in Peristerniinae. D'Asaro (2000) also noted that species of *Dolicholaturus* Bellardi, 1884 and the South African '*Latirus rousi* Sowerby, 1886, which he referred to Peristerniinae, differ from other members of that subfamily by having bullate instead of funnel-shaped capsules. As noted in our discussion of the new genus *Turrilatirus* below, *Dolicholaturus* likely belongs to the Turbinellidae and is not a fasciolariid.

Within Peristerniinae, the genus name *Latirus* Montfort, 1810, has been applied broadly to any medium-sized to large, relatively thick-shelled, fusiform species with a lirated aperture, well-developed axial and spiral external sculpture, abapical columellar folds, and a more or less long siphonal protuberance. Woodring (1928) recognized that *Latirus* in this broad sense is a heterogeneous assemblage. The taxa in which the living and fossil species can be grouped have often not, however, been carefully defined. In previous papers, we have dealt with the genera *Benimakia* Habe, 1958; *Dentifusus* Vermeij & Rosenberg, 2003; *Fusolatirus* Kuroda & Habe, 1971; *Leucozonia* Gray, 1847; and *Psammotoma* Vermeij & Snyder, 2002 (Vermeij & Snyder, 2002, 2003; Vermeij & Rosenberg, 2003; Snyder & Bouchet, 2006). Here we treat *Latirus* in the strict sense, as well as *Hemipolygona*, *Polygona* and the new genera *Turrilatirus* and *Pustulatirus*.

Genus *Latirus* Montfort, 1810

(Fig. 1)

Type species, by monotypy: *Latirus aurantiacus* Montfort, 1810 (= *Murex gibbulus* Gmelin, 1791) (Fig. 1E).

We note that Bullock (1974: 71) erroneously 'selected' *Latirus cariniferus* [sic] (Lamarck, 1816) as the type species of *Latirus s.s.* Vermeij & Snyder (2002) restricted *Latirus* to an essentially Indo-West Pacific group of species in which the shoulder angulation and central cord typically form nodes where they cross the axial ribs. We provide a revised diagnosis here in order to

compare this group of species with other similar taxa, especially *Hemipolygona*.

Revised diagnosis: Shell medium to large in size, maximum height 50 mm to 113 mm, fusiform, basally constricted; whorls of teleoconch shouldered; last teleoconch whorl typically with two spiral rows of nodes, one at shoulder angulation, the other at central cord, the two rows connected by rounded axial ribs; outer lip of adult minutely reflected, its edge with paired crenations on central sector; adapical and abapical sectors of outer lip concave; inner side of outer lip with beaded lirae or rarely smooth, none of the lirae enlarged to form denticles; inner lip with three or four oblique abapical folds, and in the adult a parietal nodule at adapical end; pseudoumbilicus usually present.

Species included in Latirus:

- L. abnormis* G.B. Sowerby III, 1894, Recent, southeastern Africa (Fig. 1A)
- L. amplustris* (Dillwyn, 1817), Recent, Indo-West Pacific (Fig. 1B)
- L. barclayi* (Reeve, 1847), late Tertiary? to Recent, western Pacific (Fig. 1C)
- L. belcheri* (Reeve, 1847), Recent, western Pacific and Isla Clarión (Fig. 1D)
- L. gibbulus* (Gmelin, 1791), Recent, western Pacific (Fig. 1E)
- L. pictus* (Reeve, 1847), Recent, western Pacific (Fig. 1F)
- L. polygonus* (Gmelin, 1791), late Tertiary? to Recent, tropical Indo-West Pacific (Fig. 1H)
- L. tigroides* Kilburn, 1975, Recent, southeastern Africa (Fig. 1G)

Remarks: Bullock (1974: 69) pointed out that the radula of *Latirus gibbulus* closely resembles that of *Latirolagena* and *Leucozonia*, and he suggested that the latter two genera are closely related to *Latirus* in our restricted sense. We agree with this assessment. *Latirus* resembles *Hemipolygona* in having nodes on at least two spiral cords on the last whorl, and beaded lirae on the inner side of the outer lip. It differs consistently from *Hemipolygona* in having a distinct abapical and adapical sinus on the outer lip. In *Hemipolygona*, the lip is almost planar and the sinuses are either absent or extremely poorly developed. *Latirus* differs from *Dentifusus* by the absence of a labral tooth, by usually having columellar folds, and consistently by having axial ribs on all whorls. As here restricted, *Latirus* is an essentially Indo-West Pacific genus. The only record of the genus outside this region is that of Shasky (1995), who records *L. belcheri* from Clarión Island in the eastern Pacific. The oldest fossil record of which we are aware is Ladd's (1977) report of *L. barclayi* from the Alifan Limestone of the Mariana Islands. The age of this limestone is uncertain, but Ladd (1977) gives it as late Tertiary.

Several species of *Latirus* have phenotypes that are rare among nonfusuline Fasciolariidae. As noted above, thick callus obscures the columellar folds in adult *L. gibbulus*. The aberrant South African *L. abnormis* has an exceptionally deep, almost turrid-like adapical sinus, as well as an essentially smooth columella, greatly reduced spiral sculpture and an outer lip that is smooth on its inner side. In this species, the suture of later teleoconch whorls is accentuated by a prominent subsutural cord. Though less well expressed, a similar cord is present in some specimens of *L. barclayi* and *L. polygonus*.

Genus *Hemipolygona* Rovereto, 1899

(Figs. 2, 3A)

Type species, by monotypy: *Chasacx maderensis* Watson, 1873 (= *Latirus armatus* A. Adams, 1855) (Fig. 2C).

The name *Hemipolygona* was proposed by Rovereto (1899) to replace *Chasacx* Watson, 1873, a junior homonym (not Ritgen,

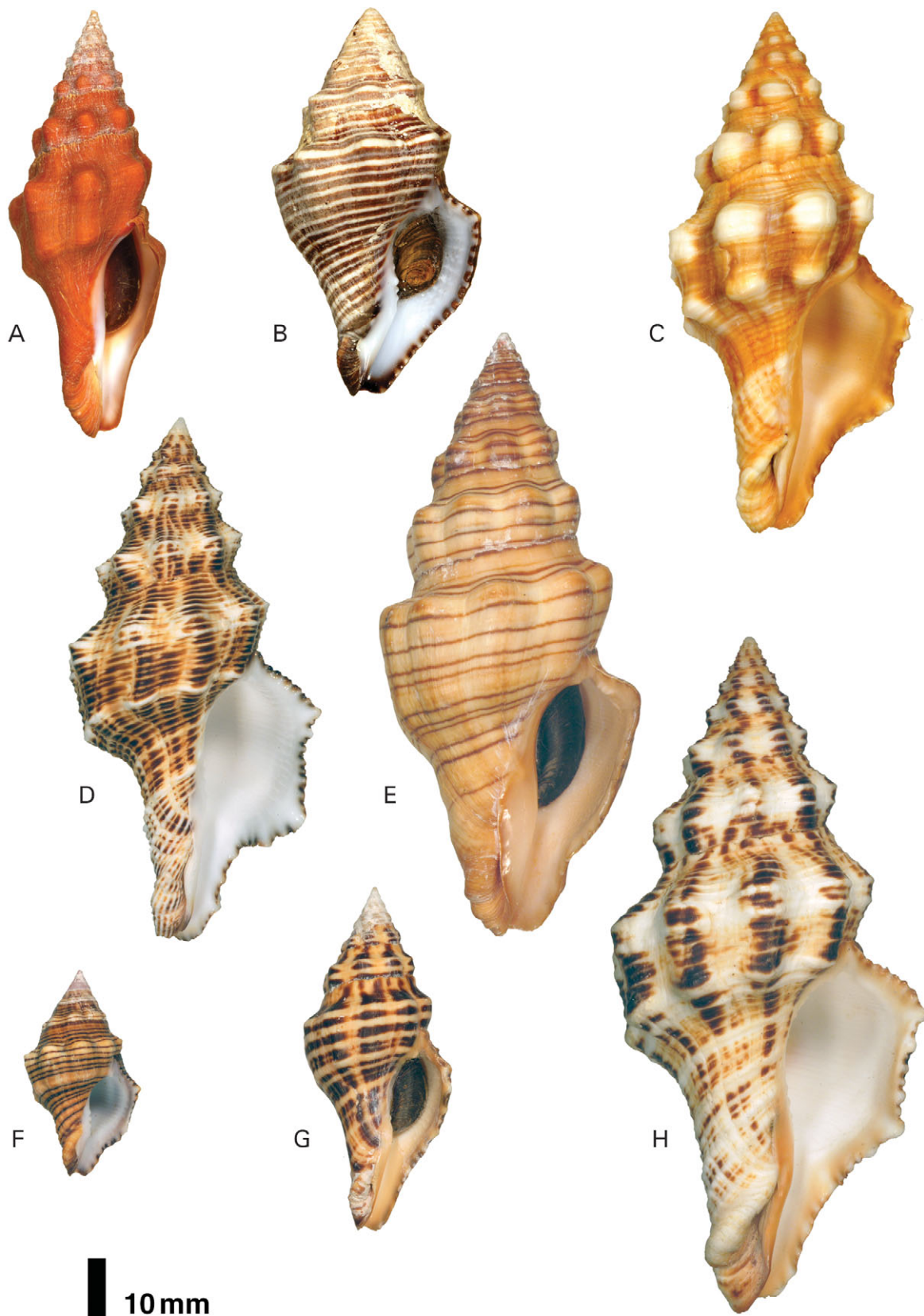
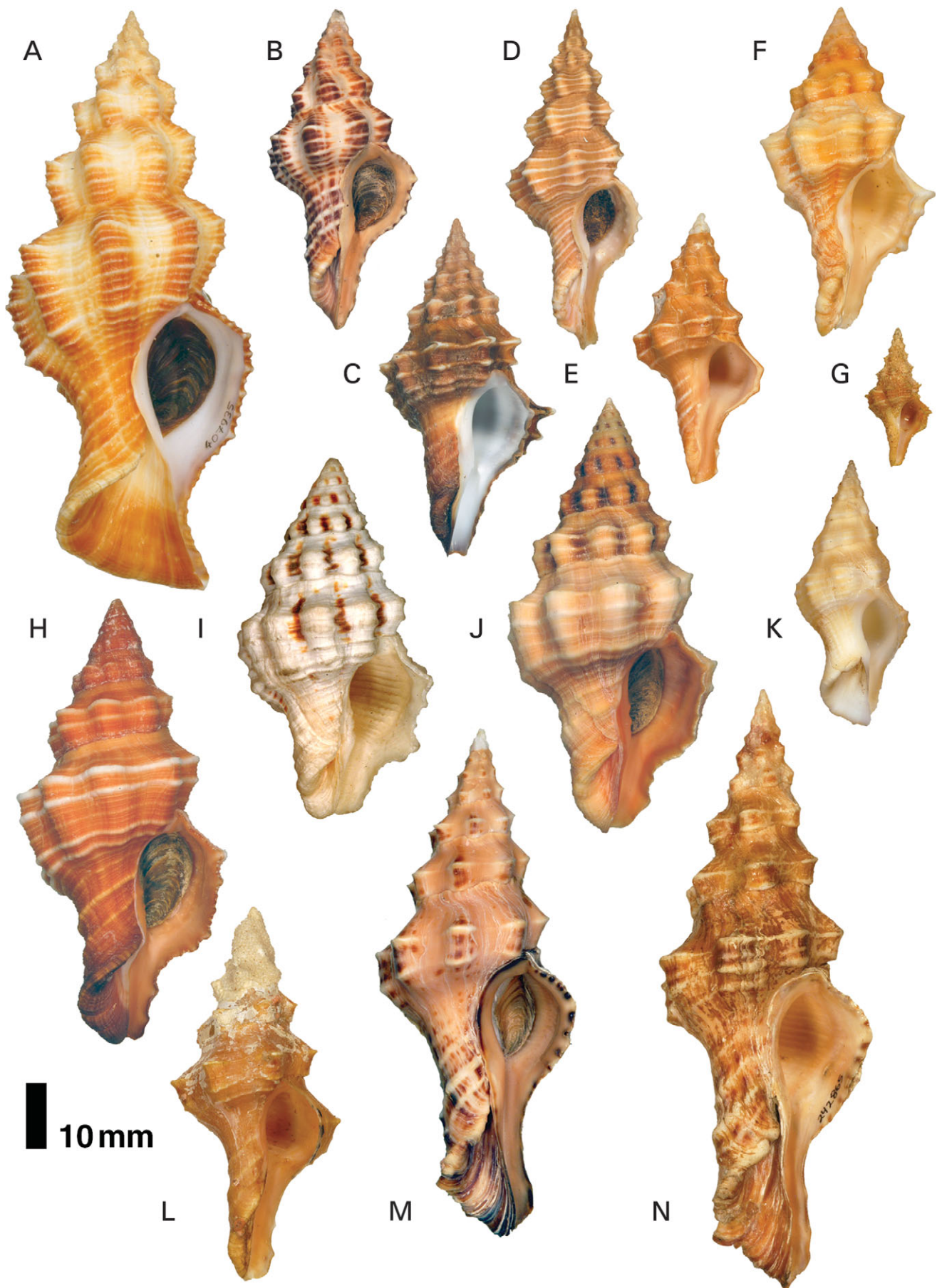


Figure 1. *Latirus* s.s. **A.** *Latirus abnormis* G.B. Sowerby III, 1894. 74.1 mm SL. Natal, South Africa, 56 m (SC). **B.** *Latirus amplustris* (Dillwyn, 1817). 67.6 mm SL. Tuamotos, *Latirus* S.S. intertidal (SC). **C.** *Latirus barclayi* (Reeve, 1847). 90.5 mm SL. Nha Trang, Vietnam (SC). **D.** *Latirus belcheri* (Reeve, 1847). 91.8 mm SL. Olango, Philippines (SC). **E.** *Latirus gibbulus* (Gmelin, 1791). 107.6 mm SL. On reef rubble at 20–25 m, Mactan, Cebu, Philippines (SC). **F.** *Latirus pictus* (Reeve, 1847). 36.1 mm SL. Mactan, Philippines. Intertidal (SC). **G.** *Latirus tigroides* Kilburn, 1975. 54.9 mm SL. Ummikaba, Pondoland, South Africa (SC). **H.** *Latirus polygonus* (Gmelin, 1791). 110.7 mm SL. Panglao, Philippines, 160 m (SC).



1828, Reptilia). Watson (1873) assigned *Chascax* to the Muricidae, probably because of its exceptionally scaly texture, but later authors have recognized it as a fasciolariid. Bullock (1974) synonymized *Hemipolygona* with *Latirus*, but Lyons (1991) considered it to be a probable subgenus of *Latirus*. In our view, the group differs sufficiently from typical *Latirus* to warrant generic rank.

Revised diagnosis: Shell medium to large, maximum length 30 to 109 mm, fusiform, with strongly constricted base; siphonal protuberance straight, moderately long; spire whorls stepped; last whorl with deeply concave subsutural sector, crossed by subdued axial ribs; central sector of last whorl with twelve or fewer prominent, high, rounded axial ribs, and high spiral cords that usually form nodes at prominent shoulder angulation, central cord, and sometimes other points of intersection with axial ribs; outer lip of adult usually sharp, strongly to weakly ornamented with paired crenations on central sector; lip planar to weakly convex, with abapical and adapical sinuses absent or very poorly developed; inner side of outer lip with beaded lirae, not forming denticles; inner lip with several abapical folds and, in adults, a very weakly developed parietal nodule; pseudumbilicus usually present.

Species included in Hemipolygona:

- H. aldeynzeri* (Garcia, 2001), Recent, Philippine Islands (Fig. 2A)
- H. amaliae* (Küster & Kobelt, 1874), Recent, southeastern India (Fig. 2B)
- H. armata* (A. Adams, 1855), Recent, West Africa from Canaries and Madeira to Senegal (Fig. 2C)
- H. beckyaе* (Snyder, 2000b), Recent, Brazil (Fig. 2D)
- H. bonniae* (Smythe, 1985), Recent, eastern Arabia (Fig. 2E)
- H. carinifera* (Lamarck, 1816), Recent, Greater Antilles (Fig. 2F)
- H. centrifuga* (Dall, 1915), Recent, Gulf of California and Galapagos (Fig. 2G)
- H. cuna* (Petuch, 1990), Recent, Atlantic Panama (Fig. 2H)
- H. distincta* (A. Adams, 1855), Recent and early Pleistocene, southeastern Florida, Gulf of Mexico and western Caribbean (Fig. 2I)
- H. erinaceus* (Peyrot, 1928), middle Miocene, France
- H. mcgintyi* (Pilsbry, 1939), early Pleistocene, Recent, northwest Florida to West Indies (Fig. 2J)
- H. mcmurrayi* (Clench & Aguayo, 1941), Recent, Cuba and Bahamas (Fig. 2K)
- H. mosseleensis* (Tomlin, 1932), Recent, southeastern Africa (Fig. 2L)
- H. nosali* (Lyons, 1991), middle Pliocene (Pinecrest Member, Tamiami Formation), Florida
- H. recurvirostris* (Schubert & Wagner, 1829), Recent, western Pacific and Indian Ocean (Fig. 2M, N)
- H. stephensae* (Lyons, 1991), late Pliocene, Caloosahatchee Formation, Florida
- H. taurus* (Olsson, 1922), Pliocene, Atlantic Panama
- H. varai* (Bullock, 1970), Recent, Caribbean (Fig. 3A)

Remarks: *Hemipolygona* comprises strongly sculptured species with a pronounced shoulder angulation, nodes where the shoulder angulation, central cord, and sometimes other cords cross axial ribs, a relatively long siphonal protuberance and beaded lirae. Comparisons with *Latirus* are given under that genus. In some species, such

as *H. beckyaе* (Fig. 2D) from Brazil and a closely similar but undescribed Pliocene species from the Dominican Republic, only the shoulder angulation is noded. These species resemble more typical *Hemipolygona* in having a small number (four or five) of high, sharp spiral cords on the central sector of the last whorl and a more or less planar outer lip. *Hemipolygona stephensae* from the Pliocene of Florida is also similar, but its cords are less sharp and the shoulder angulation is less distinct. Bullock (1974: 71–74) makes a rather broad interpretation of the taxon *Hemipolygona carinifera*, including in synonymy *Latirus distinctus* A. Adams, 1855 and *Latirus mcgintyi* Pilsbry, 1939 (Fig. 2F, I, J). We prefer to follow the suggestions of Lyons (1991: 175) and separate these three species. We tentatively include *Latirus mcmurrayi* in *Hemipolygona* because this deep-water species shares with *H. distincta*, *H. carinifera* and *H. stephensae* the trait that the shoulder angulation is closely followed abapically by a second strong cord. *Hemipolygona mcmurrayi* differs from other species of the genus in having smooth rather than beaded lirae.

Among members of the *Latirus* group, *Hemipolygona* is the only genus living in all four major tropical biogeographic regions (Indo-West Pacific, eastern Atlantic, western Atlantic and eastern Pacific). The earliest species we can assign with confidence to this group is *H. erinaceus* from the middle Miocene of France. The genus likely arose no later than the early Miocene, when marine connections between the Mediterranean and the Indo-West Pacific were still open. *Hemipolygona* did not reach the western hemisphere until the late Miocene (*H. taurus*). Its first occurrence in the abundant fossil record of Florida was as *H. nosali* in the Pinecrest Member (middle Pliocene) of the Tamiami Formation. This record indicates that *Hemipolygona* had extended its range from the Caribbean region to Florida by middle Pliocene times. In the Indo-West Pacific, the genus is more or less confined to the margins of the western Pacific and Indian Oceans. The easternmost occurrence in this province is *H. recurvirostris*, which is recorded from Guam (SC). All species of *Hemipolygona* appear to have a subtidal distribution.

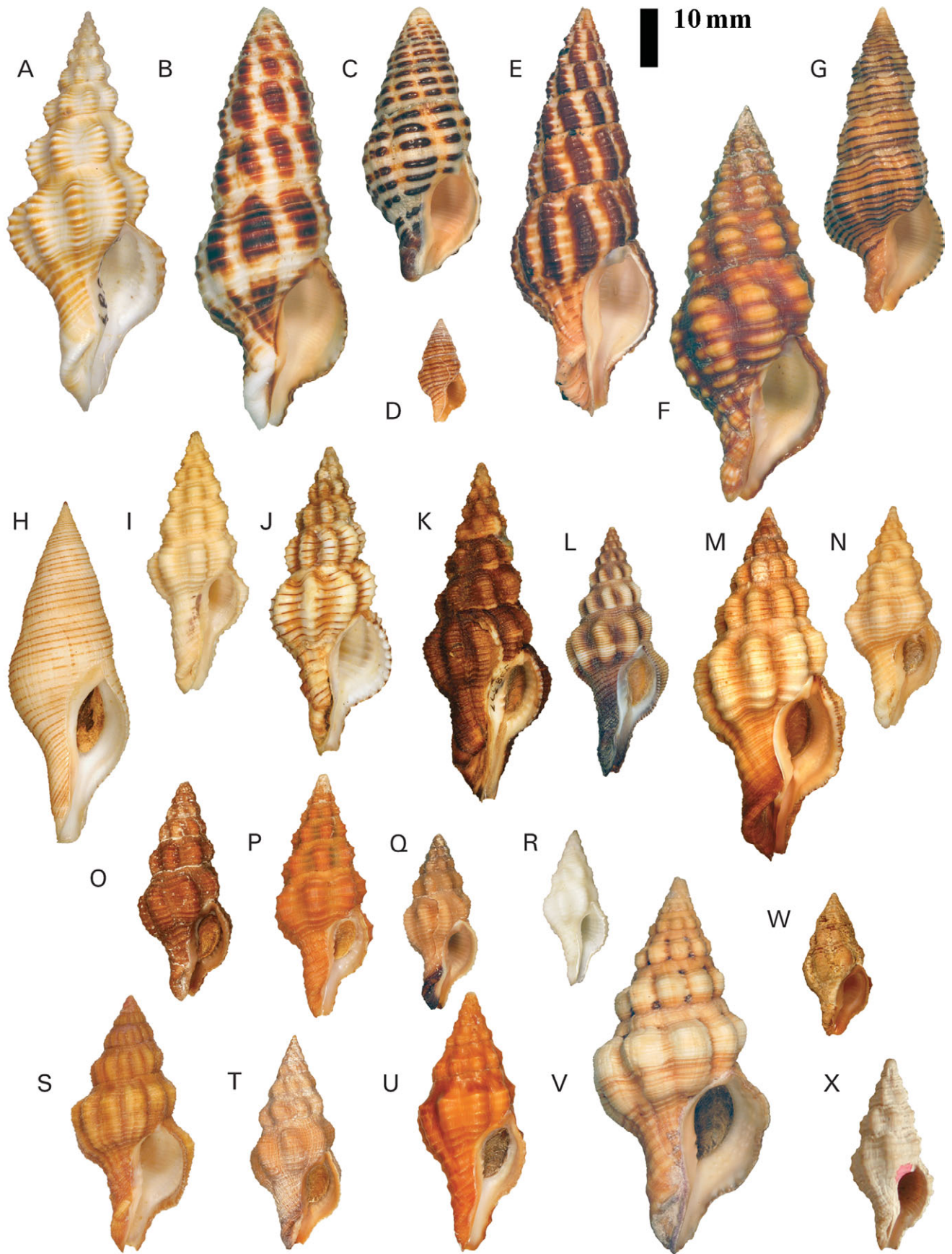
With one possible but unlikely exception discussed below, the species of *Hemipolygona* are strictly allopatric and allochronic; that is, only one species of the genus exists in any region and time interval. *Hemipolygona varai* regionally coexists with *H. carinifera* but is found at greater depths (Bullock, 1970). The only possible exceptions to this generalization are *H. recurvirostris* and *H. stenomphalus*, which evidently coexist in parts of the Indo-West Pacific. However, inspection of shell characters persuades us that these two taxa belong to a single species. *Hemipolygona stenomphalus* differs from *H. recurvirostris* only in having a narrower pseudumbilicus, but the width of the pseudumbilicus varies greatly among individuals and ontogenetically in the same individual. We consider *H. stenomphalus* a junior synonym of *H. recurvirostris* (Fig. 2M, N).

Genus *Turrilatirus* n. gen.
(Fig. 3B–G)

Type species: *Voluta turrita* Gmelin, 1791 (Fig. 3G)

Characterization: Shell small to medium-sized, maximum adult length 18 to 74 mm, high-spined, fusiform, basally constricted,

Figure 2. *Hemipolygona*. **A.** *Hemipolygona aldeynzeri* (Garcia, 2001). 90.5 mm SL. Talikud, Philippines. Holotype, ANSP 407935. **B.** *Hemipolygona amaliae* (Küster & Kobelt, 1874). 50.1 mm SL. Madras, India (SC). **C.** *Hemipolygona armata* (Adams, 1855). 52.4 mm SL. Casamanca, Senegal (SC). **D.** *Hemipolygona beckyaе* (Snyder, 2000). 53.0 mm SL. Vittoria, Brazil (SC). **E.** *Hemipolygona bonniae* (Smythe, 1985). Muscat, Oman (SC). **F.** *Hemipolygona carinifera* (Lamarck, 1816). 51.0 mm SL. Puerto Rico (SC). **G.** *Hemipolygona centrifuga* (Dall, 1915). 21.7 mm SL. Galapagos Islands. Holotype, USNM 96370. **H.** *Hemipolygona cuna* (Petuch, 1990). 65.4 mm SL. Utila Island, Honduras (SC). **I.** *Hemipolygona distincta* (A. Adams, 1855). 44.2 mm SL. (no collecting data). Syntype, BMNH 196738/1. **J.** *Hemipolygona mcgintyi* (Pilsbry, 1939). 67.7 mm SL. Palm Beach, Florida, USA, 20 m (SC). **K.** *Hemipolygona mcmurrayi* Clench & Aguayo, 1941. 41.5 mm SL. West end, Grand Bahama Island, 420 m (SC). **L.** *Hemipolygona mosseleensis* (Tomlin, 1932). 50.8 mm SL. Dog Point, Kwazulu Natal, South Africa (SC). **M.** *Hemipolygona stenomphalus* (Habe & Kosuge, 1966). 77.0 mm, SL. Mikawa, Japan, 160–200 m (SC). **N.** *Hemipolygona recurvirostris* (Schubert & Wagner, 1829). 93.0 mm SL. Wakayama, Japan. ANSP 242865.



with a short siphonal protuberance; spire usually longer than aperture plus canal; spire flat-sided, with appressed sutures; last whorl evenly rounded, without shoulder angulation; axial sculpture of last whorl consisting of six to ten low, broad, rounded ribs, mainly confined to central sector; spiral sculpture consisting of two or three strong subsutural cords, six or seven smooth rounded cords on central sector, often with a thread between adjacent cords, and three to five low cords on base; intersections between cords and axial ribs without nodes; aperture relatively small, elongate-oval; outer lip of adult convex, adapical sinus shallow or absent, abapical sinus absent; edge of adult outer lip very slightly reflected, with paired crenations on central sector; inner side of outer lip with smooth lirae, which in adults of large species form two or three enlarged, deeply recessed denticles on abapical part. These denticles do not occur in *Pustulaturus*. Inner lip usually slightly erect, with four abapical folds and in adults a parietal nodule; pseudoumbilicus usually absent.

Etymology: Latin *turris* (tower, referring to the high spire) and genus *Latirus*.

Species included in Turrilatirus:

- T. craticulatus* (Linnaeus, 1758), Pliocene to Recent, tropical Indo-West Pacific (Fig. 3B)
- T. iris* (Lightfoot, 1786), Recent, tropical Pacific (Fig. 3C)
- T. melvilli* (Schepman, 1911), Recent, Indonesia (Fig. 3D)
- T. nagasakiensis* (Smith, 1880), Recent, Japan (Fig. 3E)
- T. quadruplicatus* (Abrard, 1946), Pleistocene, Vanuatu
- T. sanguifluus* (Reeve, 1847), Recent, Polynesia (Fig. 3F)
- T. turritus* (Gmelin, 1791), Pliocene to Recent, Indo-West Pacific (Fig. 3G)

Remarks: Several of these species have been previously assigned to *Latirulus* Cossmann, 1889. Cossmann (1889: 169) proposed *Latirulus* as a section of *Latirus* for the type species, *Fusus subaffinis* D'Orbigny, 1850. In addition to this type species, Cossmann included *Turrilatirus turritus* and related Recent species. Wilson (1994) followed this same assignment for the Recent species. Our examination of material of *F. subaffinis* from the early Eocene (Cuisian) of the Paris Basin in France reveals that this species lacks a parietal nodule and is smooth on the inner side of the outer lip. The protoconch of this species and of related early Eocene species is paucispiral (Cossmann, 1889, 1897, 1923). We prefer to restrict the name *Latirulus* to Eocene species, which include besides *F. subaffinis* both *L. clavelloides* (Cossmann, 1923), early Eocene, southern France and *L. gouetensis* (Cossmann, 1897) from the middle Eocene of Normandy.

Other taxa assigned to '*Latirulus*' probably belong elsewhere, and certainly not in *Turrilatirus*. We doubt that ?*Latirulus fraudator* Maxwell, 1992, from the late Eocene of New Zealand, belongs to the Eocene genus *Latirulus*, because it is said to have one or

two very weak abapical and one central columellar fold (Maxwell, 1992). The latter feature could imply a relationship with *Dolicholatirus*. *Turbinella coarctata* Michelotti, 1847, from the early to middle Miocene of southern Europe, was assigned to *Lathyrus* (*Lathyrulus*) (= *Latirulus*) by Cossmann (1901: 44), and to *Latirus* (*Latirulus*) by Glibert (1963). Bellardi (1884), who allocated this species to his second series of *Latirus* (*Polygona*), noted similarities to his genus *Dolicholatirus*, because *T. coarctata* is very slender and bears two strong columellar folds. We take Bellardi's comments a step further and provisionally assign *T. coarctata* to *Dolicholatirus*. We also exclude *Latirus* (*Latirulus*) *thoenesi* Beets, 1942 (originally as *thoenesi*) not only from *Turrilatirus* but also from Fasciolaridae. This species from the Pliocene of Buton, Indonesia, has a strong external varix, and therefore likely belongs to the Buccinidae.

Latirulus fasciatus Habe & Okutani, 1968 (Fig. 3H), from deep water in Japan and the Hawaiian Islands, is also clearly not a species of *Turrilatirus*. It differs from *Turrilatirus* by lacking a parietal knob, lacking folds on the inner lip, and lacking axial ribs. Spiral sculpture in *L. fasciatus* consists of minutely roughened fine spiral cords, about 17 on the penultimate whorl and about 50 on the body whorl, including the siphonal protrusion. In *Turrilatirus*, spiral sculpture is much coarser. In form and spiral sculpture, *L. fasciatus* somewhat resembles *Euthria solifer* Fraussen & Hadorn, 2003 from New Caledonia, but it differs by lacking axial ribs, by having almost imperceptible instead of slightly impressed sutures, in having the inside of the outer lip lirate instead of smooth, and in lacking a fold at the entrance of the siphonal canal. The siphonal fasciole of *L. fasciatus* is barely perceptible, whereas that of *E. solifer* is prominent and rounded. The protoconch is caramel brown, of about 3½ whorls, smooth for the first three whorls then with reticulated sculpture continuing without transitional break onto the teleconch. All we can conclude at present is that *L. fasciatus* is not a *Turrilatirus*; it may not even be a fasciolariid, although its indeterminate, lirate outer lip would be consistent with assignment to the fasciolariid subfamily Fusininae.

The Indo-West Pacific genus *Turrilatirus* resembles *Polygona* in having broad axial ribs lacking nodes, abapical denticles deeply recessed on the outer lip and lirae that are smooth as in the type species of *Polygona*, but it differs from *Polygona* in having a high spire and consistently short siphonal protuberance, and in usually lacking a pseudoumbilicus.

Genus *Polygona* Schumacher, 1817

(Fig. 3I–W)

Type species, by monotypy: *Polygona fusiformis* Schumacher, 1817 (= *Murex infundibulum* Gmelin, 1791) (Fig. 3K).

Revised diagnosis: Adult shell small to large, maximum length of adults 30 to 100 mm, fusiform, basally constricted, spire high

Figure 3. *Turrilatirus*, *Polygona* and others. **A.** *Hemipolygona varai* (Bullock, 1970). 69.9 mm SL. Off Gibara, Cuba. Holotype, MCZ 262589. **B.** *Turrilatirus craticulatus* (Linnaeus, 1758). 73.2 mm SL. Mactan, Philippines, 40 m (SC). **C.** *Turrilatirus iris* (Lightfoot, 1786). 47.7 mm SL. Marshall Islands (SC). **D.** *Turrilatirus melvilli* (Schepman, 1911). 18.0 mm SL. Siboga st. 213, Indonesia. Figured syntype, ZMA. **E.** *Turrilatirus nagasakiensis* (E.A. Smith, 1880). 71.0 mm SL. Punta Engano, Philippines (SC). **F.** *Turrilatirus sanguifluus* (Reeve, 1847). 60.9 mm SL, Ua-Pou Island, Marquesas, 3–4 m (SC). **G.** *Turrilatirus turritus* (Gmelin, 1791). 53.4 mm SL. Olango, Philippines (SC). **H.** *Latirulus fasciatus* Habe & Okutani, 1968. Off Haleiwa, Oahu, Hawaii (SC). **I.** *Polygona bernadensis* Bullock, 1974. 45.4 mm SL. Off Barbados (SC). **J.** *Polygona filosa* (Schubert & Wagner, 1829). 53.6 mm SL. Carimba Bay, Luanda, Angola (SC). **K.** *Polygona infundibulum* (Gmelin, 1791). 71.3 mm SL. Off Freeport, Texas. ANSP 338377. **L.** *Polygona abbotti* (Snyder, 2003). 43.1 mm SL. Roatan Island, Honduras (SC). **M.** *Polygona angulata* (Röding, 1798). 77.5 mm SL. On coral reef, Santa Martha Bay, Curacao, 20–22 m (SC). **N.** *Polygona bayeri* (Petuch, 2001). 38.5 mm SL. Off Recife, Brazil, 10–20 m (SC). **O.** *Polygona brevicaudata* (Reeve, 1847). 37.9 mm SL. Salvador, Bahia State, Brazil, 6 m (SC). **P.** *Polygona concentrica* (Reeve, 1847). 42.3 mm SL. Isla de Plata, Manabi, Ecuador, 10–15 m (SC). **Q.** *Polygona jucunda* (McGinty, 1940). 30.5 mm SL. Rosalind Banks, Honduras, 25 m (SC). **R.** *Polygona lactea* (Matthews-Cascon *et al.*, 1991). 27.0 mm SL. Off Para, Brazil. Holotype, MNRJ 6201. **S.** *Polygona martini* (Snyder, 1988). 44.5 mm SL. Roatan Island, Honduras (SC). **T.** *Polygona nemata* Woodring, 1928. 37.1 mm SL. Off Pompano Beach, Florida, USA, 20 m (SC). **U.** *Polygona socorroensis* (Hertlein & Strong, 1951). 44.9 mm SL. Clarion Island, off western Mexico, 20–25 m (SC). **V.** *Polygona tumens* (Carpenter, 1856). 65.7 mm SL. Off western Mexico (SC). **W.** *Polygona vermetiji* (Petuch, 1986). 24.7 mm SL. Fernando de Noronha Island, Brazil (SC). **X.** *Lathyropsis mamillifer* Oostingh, 1939. 30.0 mm SL. Cijjow Ganten, Java, Pliocene. Holotype, BGM J. 5619.

but usually equal to or shorter than aperture plus canal, siphonal protuberance long; axial sculpture of last whorl consisting of low, broad, rounded ribs; spiral sculpture varying from obsolete to strong, high cords, forming nodes only when intersecting axial ribs at shoulder angulation (if present); outer lip planar to medially convex, with weak adapical sinus and weak or absent abapical sinus; edge of adult outer lip minutely reflected, with paired crenations on central sector; adaxial side of outer lip with smooth or beaded lirae, which in some species (including the type) form a slightly enlarged abapical denticle deeply recessed in aperture; inner lip with two or three folds, and in the adult an adapical parietal nodule; pseudoumbilicus usually present. *Polygona* differs from *Latirus* and *Hemipolygona* in lacking nodes where axial ribs intersect spiral cords except at the shoulder angulation. The genus as restricted here is confined to the tropical Atlantic and eastern Pacific.

We employ the genus name *Polygona* in the same sense as Lyons (1991). Previous authors have recognized but not formally named groups within *Polygona*. Bellardi (1884) identified seven series and Glibert (1963) identified two groups, based respectively on *Latirus concentricus* (Reeve, 1847) and *L. castaneus* (Reeve, 1847) (= *Latirus mediamericus* Hertlein & Strong, 1951a). Lyons (1991) likewise recognized that *Polygona* consists of two distinct lineages. We briefly characterize two groups of species, but we elect not to introduce them formally in view of the absence of more definitive molecular evidence.

Typical group, group of *Polygona infundibulum*

Characterization: Last whorl cylindrical to very weakly inflated, with or without low shoulder angulation; axial ribs extending onto long, straight siphonal protuberance; outer lip planar, with six to nine usually smooth lirae on inner side; pseudoumbilicus usually present.

Species included in Polygona infundibulum group:

- P. bernadensis* (Bullock, 1974), Recent, Caribbean (Fig. 3I)
- P. crassa* (Michelotti, 1847), early Miocene, southern Europe
- P. crassa vindobonensis* (Csepregy-Meznerics, 1956), middle Miocene, Austria and Romania
- P. filosa* (Schubert & Wagner, 1829), Recent, West Africa (Fig. 3J)
- P. gurabensis* (Maury, 1917), early Pliocene, Dominican Republic
- P. infundibulum* (Gmelin, 1791), Recent, Caribbean (Fig. 3K)
- P. lynchi* (Basterot, 1825), early to middle Miocene, southern Europe
- P. polius* (Woodring, 1928), late Pliocene, Caribbean

Remarks: It is possible that *P. lynchi* is better placed in the group of *P. angulata*, described below.

Group of *Polygona angulata*

Characterization: Stepped spire; shoulder angulation distinct, nodose where crossing axial ribs; adapical sinus present on outer lip; central sector of outer lip convex; lirae on inner side of outer lip usually beaded, but smooth in some small species.

Species included in Polygona angulata group:

- P. abbotti* (Snyder, 2003), Recent, Honduras (Fig. 3L)
- P. anapetes* (Woodring, 1964), Late Miocene, Atlantic Panama; Recent?, southern Caribbean?
- P. angulata* (Röding, 1798), Recent, southern Caribbean (Fig. 3M)
- P. bayeri* (Petuch, 2001), Recent, Brazil (Fig. 3N)
- P. brevicaudata* (Reeve, 1847), Recent, Caribbean (Fig. 3O)
- P. concentrica* (Reeve, 1847), Recent, eastern Pacific (Fig. 3P)

- P. duerri* (Petuch, 2004), late Pliocene, Florida
- P. floridana* (Heilprin, 1886), late Oligocene, Florida (= *P. callimorpha* and *P. multilineata* (Dall, 1890))
- P. hypsipettus* (Dall, 1890), late Pliocene, Florida
- P. irazu* (Olsson, 1922), late Pliocene or early Pleistocene, Atlantic Costa Rica
- P. jucunda* (McGinty, 1940), early Pleistocene to Recent, Florida (Fig. 3Q)
- P. lactea* (Matthews-Cascon, Matthews & Rocha, 1991), Recent, Brazil (Fig. 3R)
- P. martini* (Snyder, 1988), Recent, Honduras (Fig. 3S)
- P. maxwelli* (Pilsbry, 1939), early Pleistocene, Florida
- P. nemata* (Woodring, 1928), late Pliocene to Recent, Caribbean (Fig. 3T)
- P. socorroensis* (Hertlein & Strong, 1951b), Recent, eastern Pacific (Fig. 3U)
- P. tumens* (Carpenter, 1856), Recent, eastern Pacific (Fig. 3V)
- P. vermeiji* (Petuch, 1986a), Recent, Fernando de Noronha, Brazil (Fig. 3W)

Remarks: Bullock (1974: 74–76) interpreted *P. angulata* (Röding, 1798) very broadly to include forms distributed from Florida to Brazil. Given the nonplanktotrophic dispersal of these forms, and the fact that geographic differences exist among these forms, we suspect that several distinct species may be involved although satisfactory names have not been proposed for them. Typical *P. angulata* is a large species restricted to the southern Caribbean, where it is common on reefs immediately below the tidal zone. *Polygona brevicaudata*, (Fig. 3O), is from the Greater Antilles and *P. vermeiji*, (Fig. 3W), is endemic to Fernando de Noronha. *Polygona abbotti* and *P. martini* are species from off Honduras. The eastern Pacific *P. tumens* is extremely similar to *P. angulata*, but larger. Bullock (1974: 72) noted that ‘radular studies reveal that *L. cariniferus* [sic] is probably more closely related to *L. tumens* Carpenter from the Panamic Province than to *armatus*.’

Typical species of the *P. angulata* group have beaded lirae, but smooth, continuous lirae occur in *P. anapetes*, *P. brevicaudata*, *P. floridana*, *P. hypsipettus*, *P. irazu*, *P. jucunda*, *P. maxwelli*, *P. nemata* and *P. vermeiji*.

Although the species group of *P. angulata* was present in Florida as early as the late Oligocene—in fact, *P. floridana* is the oldest species we assign to *Polygona*—we consider the occurrence of *Polygona* in Florida during and after the late Pliocene to represent at least two cases of invasion from the Caribbean. No species of *Polygona* is recorded from the extraordinarily rich early Miocene fauna of the Chipola Formation of Florida, suggesting that *Polygona* became locally extinct after the Oligocene. In the Caribbean, by contrast, *Polygona* has a continuous record from early Miocene times onward. The *P. angulata* group arrived in Florida during the late Pliocene, as *P. duerri* in the Fruitville Member (=Golden Gate Member equivalent) of the Tamiami Formation. The *P. mediamericana* group existed in Florida during the late Pliocene as two stratigraphically separated species, *P. miamiensis* in the Golden Gate Member and *P. caloosahatchiensis* in the overlying Caloosahatchee Formation.

The genus *Lathyropsis* Oostingh, 1939 was proposed for the small (17.75 mm) Pliocene species *Latirus (Lathyropsis) mamillifer* Oostingh, 1939 (Fig. 3X), from South Bantam, Java, Indonesia. He compared this monotypic section to the section he referred to as *Latirus* by which he meant ‘*Latirus turritus* and its allies (here placed in *Turritulus*). He distinguished *Lathyropsis* from this group of ‘*Latirus*’ by its having a paucispiral instead of a multispiral protoconch. Given the observation that transitions from multispiral to paucispiral protoconchs are frequent in neogastropods, Oostingh’s observation may not be definitive. We feel *Lathyropsis* is very close to *Polygona*, with its small size being a possibly notable difference, and for the moment subsume this genus under *Polygona*.

Genus *Pustulaturus* n. gen.

(Fig. 4)

Type species: *Latirus mediamericanus* Hertlein & Strong, 1951a (Fig. 4E).

Characterization: Shell slender, with or without very low shoulder angulation; spiral sculpture on later whorls reduced to absent on central sector and distal end of siphonal protuberance; axial sculpture of low, short, axially elongated nodes; outer lip strongly convex at point just above basal constriction; inner side of outer lip with strongly beaded lirae; adapical and abapical sinuses distinct.

Etymology: Latin *pustula* (pustule, referring to beaded lirae) and genus *Latirus*.

Species included in *Pustulaturus*:

P. annulata (Röding, 1798), Recent, Cuba, Lesser Antilles, Jamaica (Fig. 4A)

P. attenuata (Reeve, 1847), Recent, western Atlantic (Fig. 4B)

P. caloosahatchiensis (Lyons, 1991), late Pliocene, Florida

P. elongata (Gabb, 1881), early Miocene, Dominican Republic

P. eppi (Melvill 1891), Recent, southern Caribbean (Fig. 4C)

P. hemphilli (Hertlein & Strong, 1951a), Recent, eastern Pacific (Fig. 4D)

P. mediamericana (Hertlein & Strong, 1951a), Recent, eastern Pacific (Fig. 4E)

P. miamiensis (Petuch, 1986b), late Pliocene, Florida

P. penita (Olsson, 1942), early Pliocene, Pacific Panama

P. praestantior (Melvill, 1892), Recent, eastern Pacific (Fig. 4F)

P. sanguinea (Wood, 1828), Recent, Galapagos Islands (Fig. 4G)

P. tumbeziensis (Olsson, 1932), early Miocene, Peru and Venezuela

P. virginensis (Abbott, 1958), Recent, Caribbean (Fig. 4H)

Questionable taxa and taxa excluded from the *Latirus* group: Many species assigned to *Latirus* from the Paleocene and Eocene are either of indeterminate affinity or do not belong to the Fasciolaridae. We briefly discuss some of these taxa below.

Latirus (?*Polygona*) *ewekoroensis* Adegoke, 1977. This small species from the Ewekoro Formation (late Paleocene) of Nigeria is difficult to place, because columellar characters are concealed by matrix in the aperture. We hesitate to base the potentially earliest record of the *Latirus* group on this poorly preserved material, and regard its placement in *Latirus* as questionable.

Genus *Ruscula* Casey, 1904. Type species, *Turbinella plicata* Lea, 1833. The taxon *Ruscula* has traditionally been considered to be either a subgenus or synonym of *Latirus*, and therefore to be a member of the Fasciolaridae (Casey, 1904; Palmer, 1937; Harris & Palmer, 1947). Palmer (1937: 341) observed that the Gulf Coast Eocene species of *Latirus* (that is, *Ruscula*) are characterized by a very thin columellar callus, so that external spiral cords appear as columellar plications. In the type species, *R. plicata*, from the Gosport Sand (middle Eocene) of Alabama, there are only two columellar folds, including the entrance fold. Moreover, as Palmer (1937) notes, this species and other related Eocene species sometimes have denticles on the inner side of the outer lip. Together with a short recurved siphonal protuberance, these characters indicate to us that *Ruscula* might be a buccinid rather than a fasciolariid. Cossmann (1893: 35) suggested that *Turbinella plicata* belongs to *Latirus* (*Peristernia*) because of shape, ornament and columellar characters. Dall probably had Cossmann's (1889) concept of *Peristernia* in mind, which was based on the type species *Turbinella crenulata* (Reeve, 1847) (= *Turbinella wagneri* Anton, 1838) rather than on the more generally recognized and now fixed type species, *Turbinella nassatula* (Lamarck, 1816) (see Snyder, 2000a, 2001). *Turbinella wagneri* is a pisanine buccinid belonging to the genus *Clivipollia* Iredale, 1929 (see Cernohorsky, 1971, 1975; Vermeij, 2001), whereas *Peristernia nassatula* is an undoubted fasciolariid. *Ruscula* differs from *Clivipollia* and other members of the Pisaninae of the *Engina* group (to which *Clivipollia* belongs) by having an indeterminate outer lip.

Lathyrus granifer Martin, 1931. Based on Martin's (1931) original description this species from the Nanggulan beds (middle Eocene) of Java, Indonesia, is a buccinid. Martin (1931) describes it as having an externally thickened outer lip, a strong tooth-like fold at the entrance of the siphonal canal and one additional columellar fold. There are strong lirae on the inner side of the outer lip. Despite its long siphonal protuberance, this species has characters more like those of buccinids than of fasciolariiids. The thickened lip and the presence of only two columellar folds (including the entrance fold) are especially diagnostic of pisanine buccinids. In the same publication, Martin (1931) named *Lathyrus compactilis*, also from the Nanggulan beds. This species is said to have three folds and to

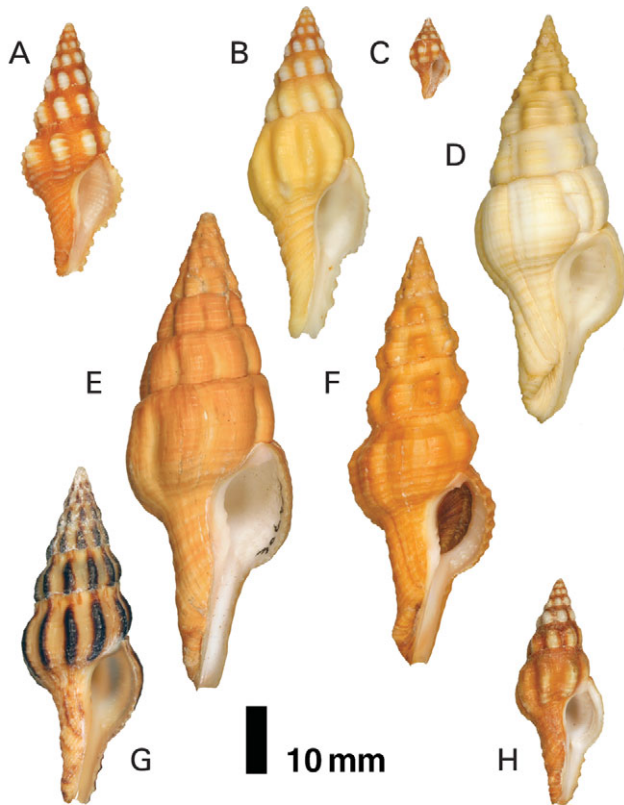


Figure 4. *Pustulaturus*. **A.** *Pustulaturus annulata* (Röding, 1798). 38.4 mm SL. St Johns, Virgin Islands (SC). **B.** *Pustulaturus attenuata* (Reeve, 1847). 50.3 mm SL. Dredged off St Thomas, Virgin Islands (SC). **C.** *Pustulaturus eppi* (Melvill, 1891). 12.5 mm SL. Off Natal, Rio Grande do Norte, Brazil, 10–15 m (SC). **D.** *Pustulaturus hemphilli* (Hertlein & Strong, 1951). 61.7 mm SL. Western Mexico (SC). **E.** *Pustulaturus mediamericanus* (Hertlein & Strong, 1951). 71.9 mm SL. Venado Island, Panama Bay. ANSP 306950. **F.** *Pustulaturus praestantior* (Melvill, 1892). 64.6 mm SL. Punta San Antonio, Bahia San Carlos, western Mexico, 20 m (SC). **G.** *Pustulaturus sanguinea* (Wood, 1828). 51.1 mm SL. Bahia Isabel, Ferdinanda Island, Galapagos, 10–15 m (SC). **H.** *Pustulaturus virginensis* (Abbott, 1958). 34.2 mm SL. St Thomas, Virgin Islands. Holotype, ANSP 196459.

have a shorter canal than *L. granifer*. Its outer lip is unknown. The description is insufficient to allow confident familial and generic placement.

Latirus kirbyi Clark, 1938. This species from the Markley Formation (middle Eocene) of northern California lacks columellar folds and is therefore unlikely to be a member of the *Latirus* group. The relatively high spire, axial ribs not extending abapically to the base, and the lirae inside the outer lip may have led Clark to place this species in a broadly conceived genus *Latirus*. Species of this morphology may indeed lie at the phylogenetic base of the *Latirus* group. *Latirus kirbyi* is either a buccinid or a fusinine fascioliariid with a short canal.

Latirus tortilis var. *nanafalius* Harris, 1899. This species from the Nanafalia Formation (late Paleocene) of Alabama and the Pendleton Ferry Formation of Arkansas (Palmer & Brann, 1966) does not appear to be a fascioliariid. Inspection of the holotype at the Paleontological Research Institute, Ithaca (number 251) reveals the presence of seven adaxially oriented spines per whorl, a weak fold at the entrance of the siphonal canal and an adaxially smooth outer lip. Together with the absence of a parietal nodule or rib, the features of this taxon suggest an assignment to Melongenidae. This assignment may also apply to *Latirus tortilis* Whitfield, 1865, from the Matthews Landing Member of the Tuscahoma Formation (early Paleocene) of Mississippi, but we have not seen the type.

Latirus quercotillaensis Olsson, 1931. Olsson (1931) was unsure about the generic placement of this latest Eocene or earliest Oligocene species from the Chira Formation of northern Peru. The holotype (Paleontological Research Institute 2141) has a broken siphonal protuberance and an aperture concealed by matrix. The last whorl appears to lack axial sculpture and is highly inflated. We doubt that this taxon is a fascioliariid, but there are too few characters discernible to allow confident placement.

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