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The Genus *Pustulatirus* Vermeij and Snyder, 2006 (Gastropoda: Fasciolariidae: Peristerniinae) in the Western Atlantic, with Descriptions of Three New Species

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Abstract

Western Atlantic species of the New World genus *Pustulatirus* Vermeij and Snyder, 2006 are revised. Types of previously named taxa are figured. Species recognized as valid include *P. attenuata* (Reeve, 1847), range uncertain; *P. eppi* (Melvill, 1891), Curaçao; *P. ogum* (Petuch, 1979), northeastern Brazil; and *P. virginensis* (Abbott, 1958), Bahama Islands and eastern Caribbean Sea to Aruba. *Latirus karinae* Nowell-Usticke, 1969 is confirmed as a junior subjective synonym of *P. virginensis*. *Syrinx annulata* Röding, 1798, treated as a Caribbean *Pustulatirus* by Vermeij and Snyder (2006), and *Latirus annulatus* Melvill, 1891 are regarded as *species inquirenda*. Three new species are described: *P. biocellatus*, northeastern Brazil; *P. utilaensis*, Bay Islands, Honduras and northwestern Panamá; and *P. watermanorum*, Honduras continental shelf and offshore Colombian banks. Most western Atlantic *Pustulatirus* shells exhibit little intraspecific variability in morphology or color and occur within rather precise, well-defined ranges; an exception is *P. virginensis*, whose shells exhibit much variability in size, morphology and color.

Key words: Fasciolariidae; *Pustulatirus*; systematic; western Atlantic; Caribbean; Brazil; Recent; Neogene

Introduction

Species of *Pustulatirus* were previously classified in the genus *Latirus* Montfort, 1810, an obviously polyphyletic taxon. Vermeij and Snyder (2006) proposed a more satisfactory classification of that taxon by elevating to generic rank *Polygona* Schumacher, 1817 and *Hemipolygona* Rovereto, 1899, taxa previously treated as subgenera of *Latirus*, and erecting the new genera *Pustulatirus* and *Turrilatirus* for other species-groups formerly placed in *Latirus*. Species of *Turrilatirus* and all species of *Latirus* live in the tropical Indo-West Pacific whereas species of *Polygona* and *Pustulatirus* live in the New World tropics. In addition to the type species and several others endemic to the tropical eastern Pacific, Vermeij and Snyder placed four Recent western Atlantic species in *Pustulatirus*: *P. annulatus* (Röding, 1798), *P. attenuatus* (Reeve, 1847), *P. eppi* (Melvill, 1891), and *P. virginensis* (Abbott, 1958); several Neogene New World taxa were also included.

We report results of a more extensive study of the western Atlantic component of *Pustulatirus* in which we examine all known type material of six named taxa and more than 600 other specimens. We combine three previously named taxa as a single species, clarify the identity of one oft-misidentified species, provide evidence to support the reclassification in *Pustulatirus* of another previously named species, and describe three new species. We also reject the recent reclassification in *Pustulatirus* of a Neogene species from South America.

Materials and Text Conventions

Most specimens were acquired from commercial shell dealers or amateur collectors. Animals had been removed and discarded but opercula still accompanied many shells. Most shells had passed through several hands before we obtained them, and collection data for such material may be inaccurate and/or imprecise; however, most species

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were represented by numerous lots obtained from several sources, and data are in sufficient agreement to instill confidence in their general accuracy.

Individual lots are identified by acronyms and catalogue numbers of institutions where deposited or, if in private collections, by abbreviations of owner names. Institutional acronyms are: AMNH: American Museum of Natural History, New York; ANSP: Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania; ANSP-IP: Invertebrate Paleo Collection, ANSP; BMSM: Bailey-Matthews Shell Museum, Sanibel, Florida; MNHN, Muséum national d'Histoire naturelle, Paris; MZUSP: Museu de Zoologia, Universidade de São Paulo, Brazil; NHMUK: The Natural History Museum, London; NMWC: National Museum of Wales, Cardiff; RMNHL: Rijksmuseum van Natuurlijke Historie, Leiden; UF: Florida Museum of Natural History, Gainesville, Florida; USNM: National Museum of Natural History, Smithsonian Institution, Washington, D.C.; and ZMA, Zoologische Museum, Amsterdam. Specimens were examined in personal collections of Kevan and Linda Sunderland (SC), Plantation, Florida; Dominique Lamy (DLC), Guadeloupe, French West Indies; and William G. Lyons (LC), St. Petersburg, Florida.

Measurements are reported in metric units. Depths of collection, sometimes initially recorded in feet (ft) or fathoms (fm), are converted to meters (m), and distances initially recorded in miles (mi) are converted to kilometers (km). Shell sizes are reported in millimeters (mm), measured to nearest 0.1 mm with electronic digital calipers; single measures are of shell length (sl = height) whereas two measures signify shell length and width (sl x w) or a range of shell lengths (sl—sl); lv denotes live-taken specimens, dd empty shells.

Robert C. Bullock's Master of Science thesis on western Atlantic *Latirus* and genera then presumed to be close relatives (Bullock 1968) was helpful to our study. Although parts of the thesis were later published (Bullock 1970, 1974), the portion that addressed species we report was not. Still, his reproductions of original illustrations and his figures of type specimens and radulae were invaluable, and we cite them here as we did in an earlier report (Lyons and Snyder 2008). In his thesis, Bullock proposed new genus- and species-level names which, because the work was unpublished, were not made available for formal taxonomic use. Some names that Bullock proposed in thesis were intended for taxa described later by authors who chose other names for them. To mention Bullock's unpublished names could cause nomenclatural confusion and risk the introduction of *nomina nuda*. Consequently, we cite Bullock's text and figures, as appropriate in individual species accounts, but not his manuscript names.

Systematics

Family Fasciolariidae J. E. Gray, 1847

Subfamily Peristerniinae Tryon, 1881.

Genus *Pustulatirus* Vermeij and Snyder, 2006

Type Species: *Latirus mediamericanus* Hertlein and Strong, 1951 (Figures 1–4), Recent, tropical eastern Pacific, by original designation (Vermeij and Snyder 2006).

Revised Diagnosis: Shells of small to moderate size, largest to about 100 mm sl, generally slender, with tall spire and well-developed siphonal process. Shells ornamented with narrow to broad axial ribs and low spiral cords, latter often most developed near outer lip; whorl surface sometimes nearly smooth, waxy on central sectors and on abapical end of siphonal process; outer lip markedly convex just above basal constriction, edge rendered serrate by extensions of interspaces between spiral cords of body whorl; inner side of outer lip with beaded lirae resembling pustules; 3 or 4 plicae aligned obliquely to axis of columella, sometimes with a smaller plica adapically; adapical and abapical sinuses distinct.

Radula formula 1-1-1, median tooth quadrate, with 3 cusps; lateral teeth broad, somewhat curved; species for which radula known with 6 slender, well-developed, subequal cusps, sometimes with single smaller cusps at inner and/or outer corners.

Remarks: Vermeij and Snyder (2006) treated *Pustulatirus* as feminine. However, Article 30.1.1 of the International Code of Zoological Nomenclature (ICZN 1999) states, in part, "a genus-group name that is or ends in a Latin word takes the gender given for that word …," in this case that word being the masculine *Latirus*.

To the original description of *Pustulatirus* (Vermeij and Snyder, 2006) we add a diagnosis of the radula, figured for a Caribbean species by Abbott (1958) and Bullock (1968), and we note the serrate edge of the outer lip, which we found to occur consistently on all western Atlantic and all but one eastern Pacific species. We caution that pustulose lirae and serrate outer lips are features of mature shells and may be poorly developed or absent on immature specimens. We did not find serrate edges on outer lips of *Hemipolygona*, *Polygona*, *Leucozonia* Gray, 1847, *Opeatostoma* Berry, 1958, or *Bullockus*, *Lamellilatirus*, and *Lightbournus* Lyons and Snyder, 2008, the other New World peristerniine genera. Outer lips of some *Fusolatirus* Kuroda and Habe, 1971, an Indo-west Pacific genus, also have serrate edges, but their internal lirae are uninterrupted, not beaded or pustulose.

Pustulose lirae are not diagnostic solely for *Pustulatirus*. Lyons and Snyder (2008) also described pustulose lirae in *Lamellilatirus* and *Bullockus*. Pustules varied from few and faint to numerous and distinct among seemingly mature specimens of single species.

We did not consistently find pustulose lirae or labral serrata on shells of *Latirus hemphilli* Hertlein and Strong, 1951, a Panamic species placed in *Pustulatirus* by Vermeij and Snyder (2006). Both features were uncommon among 44 specimens in 21 lots from México and Panamá. When present, the features tended to occur on immature shells or, in the case of labral serrata, on repaired lips of adult shells.

The type species and other eastern Pacific *Pustulatirus* species have small, tapered protoconchs that suggest a planktotrophic veliger whereas protoconchs of western Atlantic species are lecithotrophic, suggesting demersal development.

The eastern Pacific *P. mediamericanus* and *P. praestantior* (Melvill, 1891c) are larger than any Atlantic congener, attaining sizes of about 91 and 100 mm respectively (Pisor & Poppe 2008) whereas the largest Atlantic species, *P. ogum* and *P. virginensis*, attain only 53.2 and 52.8 mm (both herein).

Species Accounts

Pustulatirus attenuatus (Reeve, 1847)

(Figures 5–7)

Turbinella attenuata Reeve, 1847: pl. 13, fig. 69. Reeve, 1860: 121; Krebs,1864: 16; Kobelt in Küster and Kobelt, 1876: 101, 102, pl. 24, fig. 5; Dall, 1885: 314; Clench *et al*., 1947: 35; Bullock, 1968: 67; Snyder, 2003: 45.

Lathyrus attenuata [*sic*] (Reeve)—Mørch, 1852: 99.

Latirus attenuatus (Reeve)—H. and A. Adams, 1853: 152. Kobelt, 1877: 58; Tryon, 1881: 90, 234, 299, pl. 67, fig. 122, pl. 68, fig. 144; Paetel, 1887: 162; Abbott, 1958: 77; Bullock, 1968: 26; Santos Galindo, 1977: 221; Sutty, 1986: 62.

Turbinella (Plicatella) attenuata Reeve—Kobelt, 1876: 20.

Turbinella attenuata? Reeve—Arango y Molina, 1880: 221.

Plicatella attenuata (Reeve)—Dall, 1885: 240.

Latirus alternatus [*sic*] (Reeve)—Melvill, 1891b: 403.

Latirus [unnamed subgenus] *attenuatus* (Reeve)—Bullock, 1968: 67 (*pars*). *Non Latirus attenuatus* Bullock (1968: 67–69, pl. 4, figs. 3–5, 10, pl. 5, figs. 11, 12, 14), = *Pustulatirus virginensis* (Abbott, 1958), Recent, eastern Caribbean.

Turbinella attenuale [*sic*] Coomans, 1974: 185.

[?] *Latirus attenuata* [*sic*] (Reeve, 1847)—Mallard and Robin, 2005: 16, pl. 40.

Pustulatirus attenuata [*sic*] (Reeve)—Vermeij and Snyder, 2006: 421 (*pars*). *Non Pustulatirus attenuata* [*sic*] Vermeij and Snyder (2006: fig. 4B), = *Pustulatirus virginensis* (Abbott, 1958), Recent, eastern Caribbean.

Description: Shell small for genus (holotype 31.1 mm sl), narrowly fusiform, with rounded whorls, broad axial ribs, well-developed spiral cords, shallow suture, and narrow post-sutural ramp bearing closely-packed axial lamellae. Teleoconch of about 7 regularly expanding convex whorls separated by shallow suture; suture undulant in accord with adjacent whorls and interspaces; each whorl with about 8 broad axial ribs; 4 subequal spiral cords on first whorl, enlarging in size but not increasing in number on succeeding whorls of spire, 10–11 cords on body whorl; cords on sutural ramp low, parallel to and undulating in concert with suture, crossed by numerous well-developed subsutural lamellae; cords crossing ribs larger than those of ramp, sometimes with single spiral threads between; 6 or more oblique cords of unequal size on siphonal process, occasionally with single smaller thread between. Aperture ovate, constricted adapically by thick parietal node and abapically by small tooth-like node opposite fold at base of columella; outer lip broadly arcuate, rendered serrate by extensions of interspaces between spiral cords, inner surface with about 8 beaded lirae; columella with 4 oblique plicae, another smaller plica

adapically; siphonal canal typical of genus, outer lip thin, crenulated by termini of interspaces between larger dorsal cords, inner lip simple, straight. Shell outer surface yellow with white axial ribs on first 3 or 4 teleoconch whorls, interior white. Operculum and radula unknown.

Type Material:Holotype (Figures 5–7), 31.1 mm, dd, locality unknown, NHMUK 196735.

Type Locality:Unknown; probably tropical western Atlantic.

Remarks: The holotype of *Turbinella attenuata* Reeve, 1847 resembles shells in the *Pustulatirus virginensis* species-complex of the eastern Caribbean and also resembles shells of a new species from Honduras and Panamá that is described herein, yet it differs from both.

Described without locality, *T. attenuata* was soon recognized as a western Atlantic species by nineteenth century authors (Mørch 1852, Krebs 1864, Kobelt in Küster & Kobelt 1876, Kobelt 1876, 1877, Arango y Molina 1880). However, Kobelt in Küster and Kobelt (1876) suggested that the name might represent a variety of *Turbinella infundibulum* (Gmelin, 1791), now the type species of *Polygona* Schumacher, 1817, prompting Tryon (1881) to relegate the name to synonymy with that species. Tryon's action effectively shelved the name until Abbott (1958) mentioned specimens at ANSP, previously labeled *Latirus attenuatus*, among those he was naming *L. virginensis*. Bullock (1968, in thesis) also addressed the name but distinguished it as a species separate from *L. virginensis* and others in a related species-complex (see below). The name (as *Turbinella attenuale* [*sic*]) also appeared on an early list of shells from St. Martin prepared by H. E. Rijgersma, but Coomans (1974) dismissed it as a supposed synonym of *Latirus* [= *Polygona*] *brevicaudatus* (Reeve, 1847). Then Sutty (1986: 62, 64, 65, fig. 70) reported and figured as "*Latirus* species (cf. *attenuatus* (Reeve, 1847))" a shell from Guadeloupe that in her opinion "bears a distinct resemblance to *Latirus virginensis* Abbott, 1958 and, better still, [to] *L. attenuatus* (Reeve, 1847)." Thereafter, Snyder (2003) cited *L. attenuatus* as a valid Caribbean species that ranged from Cuba to the Lesser Antilles, apparently sympatrically with *L. virginensis*. Mallard and Robin (2005) cited *L. attenuata* [*sic*], range Cuba to Lesser Antilles, and *L. virginensis*, range "Caribbean," again suggesting sympatry. Those authors speculated that *attenuata* may be the species they figured as *L. bernadensis* Bullock, 1974, on their plate 41, but that shell was correctly identified and is a species of *Polygona*. Vermeij and Snyder (2006) reclassified both *attenuatus* and *virginensis* in *Pustulatirus* and treated them as distinct. In this we concur. However, we include other shells figured as *attenuatus* by Bullock (1968), Sutty (1986) and Vermeij and Snyder (2006) in *Pustulatirus virginensis*.

***Pustulatirus virginensis* (Abbott, 1958)**

(Figures 8–30)

[?] *Lathyrus annulata* [*sic*] (Bolt. Link)—Mørch, 1852: 99. *Non Syrinx annulata* Röding, 1798.

[?] *Turbinella annulata* (Bolt.)—Krebs, 1864: 16. Poulsen, 1878: 11; Dall, 1885: 314; Clench *et al*., 1947: 35. *Non Syrinx annulata* Röding, 1798.

[?] *Peristernia annulata* (Bolten)—Melvill, 1891b: 407. *Non Syrinx annulata* Röding, 1798.

[?] *Peristernia annulata* (A. Ad.)—Melvill, 1891b: 411, pl. 2, fig. 1. *Non Syrinx annulata* Röding, 1798.

Latirus (Polygona) virginensis Abbott, 1958: 76, 77, text-figs. 4.7, 4.8, pl. 2, fig. 6. Rios, 1970: 96 (*pars*); Abbott, 1974: 227; Rios, 1975: 104 (*pars*); Ortiz-Corps, 1983: 121; Rios, 1985: 107, pl. 36, fig. 471 (*pars*); Rios, 1994: 133 (*pars*); Espinosa *et al*., 1995: 36; Harasewych, 1997: 62; Snyder, 2003: 218; Rios, 2009: 253 (*pars*). *Non Latirus (Polygona) virginensis* 'Abbott' *auctt.* northeastern Brazil, = *Pustulatirus* n. sp.

Latirus virginensis—Abbott, 1958: 77. Warmke and Abbott, 1961: 120, 272, pl. 22, fig. n; Arnow *et al*., 1963: 169; Wagner and Abbott, 1964: 167; Holeman, 1966: 29, 30; Wagner and Abbott, 1967: 247; Nowell-Usticke, 1971: pl. 6, fig.; Morris and Clench, 1973: 218, pl. 60, figs. 4; Abbott, 1974: color pl. 11, fig. 2493; Ekdale, 1974: 648; Lipka, 1974: 155; Riggs, 1975: 14; Kaicher, 1978: card 1763; Wagner and Abbott, 1978: 80–231; Woodlock, 1980: 189; Pointier *et al*., 1982: 9; Sarasúa and Espinosa, 1984: 8, 9, 18, fig. 6c; Sutty, 1986: 62; Pointier *et al*., 1987: 12; Faber, 1988: 82; Lyons, 1991: 177, 178, figs. 36-41; Espinosa *et al*., 1994: 113; Goto and Poppe, 1996: 393; K. and L. Sunderland, 1996: 17, 2 figs.; Pointier and Lamy, 1998: 131, 2 figs.; Snyder, 2000: 162; Redfern, 2001: 103, pl. 46, fig. 432; Snyder, 2003: 121; Henkel and Kurtz, 2004: 14, 15, fig.; Mallard and Robin, 2005: 19, pl. 52; Rios, 2009: 253 (*pars*); Landau and Vermeij, 2012: 88. *Non Latirus virginensis* 'Abbott' *auctt*., northeastern Brazil, = *Pustulatirus* n. sp.

Latirus [new subgenus] *annulatus* (Melvill)—Bullock, 1968: 65-67, pl. 4, figs. 2, 14, pl. 5, fig. 10.

Latirus [new subgenus] *attenuatus* (Reeve)—Bullock, 1968: 67-69, pl. 4, figs. 3–5, 10, pl. 5, figs. 11, 12, 14 (*pars*). *Non Pustulatirus attenuatus* (Reeve, 1847), ?Caribbean region, *nec Latirus eppi* Melvill, 1891, treated by Bullock as junior synonym of *attenuatus*.

Latirus [new subgenus] *virginensis* Abbott—Bullock, 1968: 71-73, pl. 4, figs. 1, 19.

Latirus karinae Nowell-Usticke, 1969: 18, pl. 4, fig. 821. Faber, 1988: 82; Lyons, 1991: 178; Boyko and Cordeiro, 2001: 76; Redfern, 2001: 103; Snyder, 2003: 121; Rios, 2009: 253.

Latirus virgineus [*sic*] (Abbott)—Santos Galindo, 1977: 222.

Latirus elegans (Gray)—Kaicher, 1986: card no. 4671 (*pars*; larger [right] shell only). *Non Fusus elegans* J. E. Gray, 1838 = *Fusinus filosus* (Schubert and Wagner, 1829), West Africa, new synonymy.

Latirus species (cf. *attenuatus*) (Reeve, 1847)—Sutty, 1986: 62, 64, 65, color fig. 70. *Non Turbinella attenuata* Reeve, 1847.

[?] [no genus] *annulatus* (Bolten) Röding—Trew, 1990: 13.

Latirus eppi Melvill y Schapman [*sic*], 1891—Espinosa *et al*., 1994: 113. *Non Latirus eppi*, = *Pustulatirus eppi* (Melvill, 1891), Curaçao.

Latirus (Latirus) eppi Melvill y Schapman [*sic*], 1891—Espinosa *et al*., 1995: 36. *Non Latirus eppi* Melvill, 1891.

Latirus annulata [*sic*] (Röding, 1798)—Mallard and Robin, 2005: 16. *Non Syrinx annulata* Röding, 1798.

Latirus abbotti Snyder, 2003—Mallard and Robin, 2005: pl. 39. Robin, 2008: 219, figs. 9. *Non Latirus abbotti*, = *Polygona abbotti* (Snyder, 2003), Caribbean Sea.

Latirus eppi Melvill, 1891—Mallard and Robin, 2005: pl. 43 (*pars*; right figs. only, shell from Puerto Rico); Robin, 2008: 221, figs. *Non Latirus eppi* Melvill, 1891.

Pustulatirus annulata [*sic*] (Röding, 1798)—Vermeij and Snyder, 2006: 421. *Non Syrinx annulata* Röding, 1798.

Pustulatirus attenuata [*sic*] (Reeve, 1847)—Vermeij and Snyder, 2006: 421, fig. 4B. *Non Pustulatirus attenuatus* (Reeve, 1847), ?Caribbean region.

Pustulatirus virginensis (Abbott, 1958)—Vermeij and Snyder, 2006: 421, fig. 4H. Rosenberg *et al*., 2009: 654; Zhang, 2011: 129, figs. 445(1–3); Landau and Vermeij, 2012: 88.

Pustulatirus sp. Zhang, 2011: 129, figs. 446(1–3).

Description: Shell of medium size for genus (largest 52.7 x 18.7 mm), elongate, fusiform, slender, with rounded whorls, broad axial ribs, and low spiral cords; outer lip serrate and internal lirae beaded as in generic diagnosis. Variability in shell morphology, size, and color is so extensive that we choose simply to illustrate types and several other specimens (Figures 8–30) to demonstrate the range of variation. Variation is also exemplified by three shells figured as *Latirus virginensis* by Mallard and Robin (2005) and four shells figured as *Pustulatirus* sp. and *P. virginensis* by Zhang (2011). Further comments on variation appear in remarks for the species.

Type Material:*Latirus virginensis*: holotype 34.2 mm (Figures 8–9), St. Thomas, Virgin Islands, ANSP 196459; 2 paratypes, 32.0 and 29.4 mm, St. Thomas, ANSP 34975; 2 paratypes, 36.6 mm, lv, 29.5 mm, dd?, St. Thomas, ANSP 34968; 4 paratypes, 29.8, 29.3, 26.6 (Figures 10–11) and 25.4 mm, dd, "West Indies," ANSP 34969; *Latirus karinae*: lectotype, 32.7 mm (Figures 12–13), "Puerto Rico," AMNH 198490.

Type Localities: *Latirus virginensis*: St. Thomas, Virgin Islands; *Latirus karinae*: "Puerto Rico."

Other Material: **Bahama Islands**—2, 27.1 (Figure 24) and 25.5 mm, lv, reef north of Sandy Cay, West End, Grand Bahama, 15–17 m, 1999, ANSP 449716; 2, 20.0 and 10.3 mm, dd, Sandy Cay, West End, 40 ft [12.2 m], coral rubble, LC; 1, 25.5 mm, lv, Sandy Cay, West End, LC; 2 fragments (1 shell?), dd, Gold Rock, Grand Bahama, 80 ft [24.4 m], ANSP 369654; 2, 27.9 and 25.8 mm, lv, Bimini, reef, 35 ft [10.7 m], LC; 1, 24.5 mm, lv, Bimini, reef, 45 ft [13.7 m], LC; 1, 20.7 mm (Figures 27-28), dd, Bimini, 7/1985, ANSP 499719; 1, 24.2 mm, lv, Turtle Rocks, South Bimini, 30 ft [9.1 m], LC; 2, 24.6 and 18.9 mm, lv, 3.2 km south of Northwest Channel Light, 19.2 km southwest of Chub Cay, Bahamas, 70-90 ft [21.4-27.6 m], LC; 1, 26.4 mm, dd, Silver Cay Beach, Nassau, New Providence, LC; 2, 33.7 and 24.6 mm, dd, beach 1.6 km south of Fresh Creek, Andros, LC; 1, 19.0 mm, dd, off Fresh Creek, Andros, LC; 4, 31.4, 29.7, 20.5 and 20.5 mm, dd, AUTEC Base, Andros, beached by storm, LC; 1, 28.0 mm, dd, off Windimere, Eleuthera, 3 m, 6/1988, ANSP 449778. **Turks and Caicos Islands**—1, 23.8 mm, lv, "Turks and Caicos," LC. **Dominican Republic**—1, 30.0 mm (Figure 25), lv, 1, 11.7 mm, dd, northern coast at Castillo, Duarte, rubble, 4 ft [1.2 m], 8/1994, ANSP 449715; 15, 43.3, 42.2, 40.3, 39.2, 39.0, 38.6, 35.2, 33.6, 20.8, 20.0, 19.4, 19.2, 16.3 and 14.0 mm, lv, 14, 40.3, 39.0, 37.2, 32.4, 32.2, 29.4, 27.3, 23.6, 23.1, 23.0, 21.7, 21.0, 19.8 and 19.2 mm, dd, Las Galeras, Samaná, 3 to 10 ft [0.9-3.1 m], *ex* Glenn Duffy, LC; 1, 41.4 mm (Figure 14), lv, same data, ANSP 449754; 2, 25.1 and 23.6 mm, lv, Las Galeras, Samaná, 1-2 m, 1994, ANSP 449791; 1, 20.0 mm, lv, Meces, on dead coral at low water, LC. **Puerto Rico**—1, 21.3 mm, dd, Bahía Salinas, Cabo Rojo, 15 ft [4.6 m], on *Thalassia*, 3/2000, LC; 1, 16.2 mm, dd, same locality and date, 18 ft [5.5 m], LC; 1, 34.8 mm, dd, San Juan Harbor, 1980, ANSP 449771; 1, 24.2 mm, dd, "Puerto Rico," "paratype," ANSP 219064; 1, 27.4 mm, dd, "Puerto Rico," *ex* Warmke, UF 162196; 1, 25.7 mm, dd, "Puerto Rico," *ex* Warmke, UF 162197; 12, 33.1, 32.9, 29.7, 27.9, 27.8, 27.5, 26.7, 26.4, 26.2, 26.0, 21.2 and 20.8 mm, dd, "Puerto Rico," Usticke Coll. [identified as *Latirus karinae* by Usticke, = paralectotypes?], AMNH 191472. **U. S. Virgin Islands**—2, 27.4 and 19.6 mm, dd, Krause's Reef, St. Croix, *ex* Usticke via McGinty, UF 135674; 39, 30.2 to 5.0 mm, dd, St. Croix at Long Reef, 2/1964 and Krause's

Reef, 3/1965, Usticke Coll., AMNH 191463; 2, 24.2 and 21.9 mm, dd, off St. Croix, 1992, ANSP 449788; 20, 29.0, 26.2, 24.6, 22.3, 22.3, 22.3, 22.2, 22.2, 22.1, 21.7, 21.2, 21.0, 21.0, 20.9, 20.8, 20.6, 20.2, 18.6, 17.4 and 16.3 mm, Cowpet Bay, St. Thomas, *ex* J. E. Holeman, AMNH 170501; 2, 21.6 and 9.7 mm, dd, Cowpet Bay, St. Thomas, AMNH 191476; 3, 33.7, 24.8 and 23.7 mm, dd, Cowpet Bay, St. Thomas, ANSP 449795; 1, 34.3 mm, dd, Cowpet Bay, St. Thomas, 1990, ANSP 449784; 3, 30.8, 16.9 and 16.4 mm, dd, Cowpet Bay, St. Thomas, *ex* J. Holeman via McGinty, UF 156255; 1, 38.6 mm, dd, Crown Bay, St. Thomas, *ex* Usticke via McGinty, UF 135675; 17, 40.9, 37.5, 36.6, 34.9, 33.3, 31.7, 31.1, 29.3, 27.3, 25.1, 22.9, 20.3, 19.0, 16.7, 14.0, 13.8 and 13.0, dd, Yacht Club, Jessup Bay, St. Thomas, 1969, AMNH 191470; 1, 38.4 mm, dd, Jessup Bay, St. Thomas, *ex* Usticke via McGinty, UF 156254; 1, 36.2 mm, dd, St. Thomas Harbor, *ex* J. Holeman via McGinty, UF 135673; 2, 28.0 and 26.9 mm, dd, St. Thomas Harbor, St. Thomas, *ex* McGinty, UF 135677; 4, 30.6, 17.5, 16.9 and 8.9 mm, dd, Water Island, St. Thomas, *ex* J. Holeman via McGinty, UF 363808; 1, 16.9 mm, dd, West Gregorie Channel between Water Isle and St. Thomas, ANSP 255163; 1, 35.3 mm, dd, dredged off St. Thomas, 1980, ANSP 449774; 2, 52.7 (Figure 15) and 50.3 mm, dd, off St. Thomas, dredged, 1987, ANSP 449714; 1, 36.9 mm, dd, off St. Thomas, 1988, ANSP 449779; 1, 45.4 mm, dd, off St. Thomas, 1990, ANSP 449786; 3, 30.9, 24.4 and 23.2 mm, dd, off St. Thomas, 1992, ANSP 449790; 9, 40.0, 33.0, 20.8, 20.2, 16.7, 14.5, 10.8, 9.9 and 8.8 mm, dd, St. Thomas, *ex* Joan Brindley, 1965, AMNH 182520; 3, 47.7 (Figure 16), 25.5 and 25.1 mm, dd, St. Thomas, 1976, ANSP 449713; 3, 18.0, 15.3 and 13.4 mm, dd, St. Thomas, Usticke Coll., AMNH 191490; 4, 30.1, 29.1, 25.7 and 16.2 mm, dd, St. Thomas, AMNH 114569; 1, 24.4 mm, dd, St. Thomas, 1983, ANSP 449776; 2, 23.2 and 19.0 mm, dd, St. Thomas, ANSP 449796; 4, 29.9, 29.7, 28.4 and 24.2 mm, dd, St. Thomas, LC; 1, 31.9 mm, lv, St. Thomas, LC; 1, 30.6 mm (Figure 26), dd, Little St. James Island, 24 ft [7.3 m], 6/1996, ANSP 449720; 8, 24.2, 22.3, 20.9, 20.6, 20.4, 19.9, 19.9 and 16.8 mm, lv, Little St. James Island, 27 ft [8.2 m], 7/9/2000, LC; 1, 26.7 mm (Figures 29-30), same data, ANSP 449718; 1, 24.3 mm, lv, same data, SC; 6, 24.7, 22.6, 22.6, 22.3, 21.7 and 21.5 mm, lv, Little St. James Island, 27 ft [8.2 m], 7/2002, LC; 5, 38.4, 37.7, 31.2, 28.4 and 27.9 mm, dd, St. John, 1978, ANSP 449748; 2, 47.0 and 45.3 mm, dd, St. John, 1980, ANSP 449775; 1, dd, 20.5 mm, "Virgin Islands," scuba at night in rubble, 9-10 m, 1997, ANSP 449793; 2, 31.7 and 26.9 mm, dd, "Virgin Islands," LC. **British Virgin Islands**—1, 29.4 mm (Figure 22), dd, 1.6 km NE of East Point, Anegada Island, ANSP 249155; 1, 27.7 mm, Anegada, dd, deep-water fish trap, LC; 1, 29.9 mm, dd, 0.8-1.6 km SSW, SSE and E of the Bluff, Sir Francis Drake Channel, Beef Island, 12 to 14 fm [22.0-25.6 m], ANSP 331162; 2, 10.6 and 7.5 mm, dd, Beef Island, LC; 1, 34.0 mm, dd, Beef Island, shallow reef, LC; 1, 29.1 mm, lv, Buck Island, 3 ft [0.9 m], eel grass (*Thalassia*), LC; 11, 26.7, 26.6, 24.0, 20.7, 17.7, 17.5, 17.4, 17.0, 15.5, 12.5 and 11.4 mm, dd, Fat Hog Bay, Tortola, 1–5 m, in fire coral (*Millepora*) and eel grass (*Thalassia*), 2/1985, ANSP 449777; 2, 21.9 and 19.3 mm, dd, Fat Hog Bay, Tortola, 8 ft [2.4 m], LC; 3 rolled fragments, dd, Virgin Gorda, Usticke Coll., AMNH 181489. **Anguilla—**2, 48.5 and 40.6 mm, dd?, Anguilla, 1988, DLC. **St. Martin**—4, 40.6, 37.7, 29.9 and 22.5 mm, dd, St. Rose, DLC. **St. Barthelemy**—6, 31.7, 24.4, 24.3, 22.0, 20.3 and 19.1 mm, off St. Barts, Leeward Islands, 1970, *ex* Usticke, ANSP 421134; 1, 32.8 mm, dd, off St. Barthelemy, ANSP 449794; 3, 35.8, 31.0 and 27.9 mm, lv, 3, 28.3, 26.3 and 24.5 mm, dd, St. Barthelemy, DLC; 1, 34.2 mm, lv, "St. Barthelemy, Guadeloupe," Gaudiat, 1977, DLC; 1, 31.9 mm, lv?, St. Barthelemy, Pointier, 1986, DLC; 1, 33.6 mm, lv, off St. Barthelemy, trap, 100 m, ANSP 449797; 1, 32.6 mm (Figures 19–21), lv, St. Barthelemy, Guadeloupe, 100 m, ANSP 449717. **Barbuda**—3, 25.2, 23.2 and 22.2 mm, lv, Cocoa Point, 2-5 m, LC; 2, 24.8 and 20.9 mm, lv, Barbuda, 5 ft [1.5 m], LC. **Antigua**—34, 40.4, 38.1, 37.2, 34.6, 34.6, 33.3, 32.2, 32.2, 31.5, 31.5, 31.5, 31.2, 30.8, 30.1, 29.9, 29.7, 29.4, 29.2, 28.3, 28.3, 26.5, 25.8, 25.6, 25.1, 24.4, 21.9, 21.1, 20.1, 19.0, 18.4, 16.5, 14.5, 12.0 and 11.9 mm, dd, Maid Island, 6/1961, Usticke Coll., AMNH 191465; 4, 34.0, 27.8, 20.6 and 14.1 mm, dd, Maid Island, *ex* Usticke, McGinty Coll., UF 135671; 16, 50.5 (Figure 17), 47.9, 43.8, 38.0, 36.2, 35.6, 33.5, 32.7, 25.8, 25.7, 25.3, 22.4, 22.3, 19.9, 18.9 and 17.3 mm, dd, St. Johns, Usticke Coll., AMNH 191464; 10, 41.6, 33.3, 29.4, 28.5, 28.2, 25.8, 25.5, 25.3, 21.8 and 20.1, dd, St. Johns, 11/1967, Usticke Coll., AMNH 191466; 6, 51.4, 44.8, 43.9, 38.3, 35.3 and 30.3 mm, dd, St. Johns, Usticke Coll., AMNH 191467; 1, 26.3 mm, dd, Antigua, Lesser Antilles, "paratype [of *virginensis*]," ANSP 210740; 5, 42.3, 38.3, 35.1, 33.2 and 22.9 mm, dd, Antigua Island, 1979, ANSP 449768; 1, 21.2 mm, dd, Antigua Island, *ex* Usticke, Warmke Coll., UF 162195; 1, 27.3 mm, dd, Antigua Island, *ex* Usticke, UF 162198; 4, 39.2, 39.1, 35.8 and 30.4 mm, dd, off Antigua, 1993, ANSP 449792. **Guadeloupe**—4, 31.8, 27,2, 26.7 and 19.8 mm, dd, 2, 17.0 and 11.1 mm, lv, Deshaies, Pointier, 1983, DLC; 2, 33.7 and 24.5 mm, lv, Deshaies, 18 m, DLC; 2, 38.3 and 31.8 mm, Pointe Plate, Pointier, 1982, DLC; 1, 32.8 mm, lv, Port Louis, 10 m, DLC; 2, 34.7 (Figure 18) and 30.3 mm, dd, Guadeloupe, 30-50 m, ANSP 449712. **Martinique**—1, 31.8 mm, Anse Mitan, *ex* J. Holeman via McGinty, UF 135676. **St. Lucia**—2, 37.2 and 37.1 mm, dd, St. Lucia

Island, *ex* C. W. Sheafer via McGinty, UF 135672. **Netherlands Antilles—**1, 23.4 mm, dd, Malmok, Aruba, *ex* Fr. Fredricus, AMNH 245863; 1, 23.9 mm, dd, Malmok, Aruba, *ex* M. Koolman, AMNH 245864; 2, 28.2 and 25.3 mm, dd, Malmok, Aruba, "de Jong & Bijur," *ex* Jerome M. Bijur Coll., AMNH 245865. **No locality** – 1, 38.5 mm (Figure 23), dd, *ex* J. S. Phillips, ANSP 35033 (figured as *Latirus elegans* (Gray) by Kaicher, 1986a, card 4671, right fig.); 1, 24.8 mm, dd, *ex* Warmke, incorrectly marked as paratype, UF 162199; 1, 30.6 mm, lv, DLC; 1, 39.1 mm, dd, LC.

Distribution: This species, the best known of western Atlantic *Pustulatirus*, ranges throughout the eastern Caribbean region from the northernmost Bahama Islands to the Greater Antilles, the Virgin Islands, and southward to Antigua, Guadeloupe, Martinique, St. Lucia, and Aruba in the southern Netherlands Antilles; there is also an unverified record from Quintana Roo, México, in the northwestern Caribbean (Ekdale 1974). Most records with stated depths are from beaches or the shallow subtidal zone (1–30 m) but one lot from off Guadeloupe is from 30–50 m and two from off St. Barthelemy are from 100 m.

Remarks: Morphology of individual shells may vary greatly, even among specimens from a single location. Some forms are so different morphologically that it is difficult to believe they represent the same species, but the forms invariably blend into others, rendering it difficult to determine where one ends and another begins. With the large number of specimens we examined from throughout the range, we conclude that the various forms represent a single variable species. We hope this conclusion may be tested in the future using genetic information.

The name *Latirus virginensis* Abbott, 1958, has been used most often for these shells, but several other names have been associated with the group, including *Syrinx annulata* Röding, 1798, *Turbinella attenuata* Reeve, 1847, *Peristernia annulata* "(A. Adams)" Melvill, 1891, and *Latirus karinae* Nowell-Usticke, 1969. Most pieces of this taxonomic puzzle were examined by Bullock (1968), who recognized a species-group that included *Latirus attenuatus* (Reeve, 1847), *L. annulatus* (Melvill, 1891), and *L. virginensis* Abbott, 1958, all occurring sympatrically in the West Indies. Bullock (1968) noted a "tremendous amount" of morphological variation among shells in these groups and also noted many intergrades that left relationships among the species unclear. Bullock proposed (in thesis) but did not formally introduce a new subgeneric name for the group, with *Turbinella attenuata*, a species we already discussed, as its type species. Bullock cited the range of what he called *L. attenuatus* as Cuba to the Lesser Antilles, reported records from Cuba, the Dominican Republic, Puerto Rico, and St. Thomas, U. S. Virgin Islands, and figured specimens from the Dominican Republic, Puerto Rico, and St. Thomas, but we have seen no material from any of those locations that conforms to the type of *P. attenuatus*. Bullock (1968: 69) also cited *Latirus eppi* "Melvill and Schepman" as a junior synonym of *L. attenuatus*, characterizing the holotype of *L. eppi* as a squat specimen quite unlike the holotype of *L. attenuatus* but noting that "a series of intergrades appear to exist between the two forms." He concluded that further study may distinguish them as separate species. We provide an account for *Pustulatirus eppi* as a separate species-level taxon, but we consider shells assigned by Bullock to *L. attenuatus* (except its holotype and the holotype of *L. eppi*) to be more appropriately assigned to *Pustulatirus virginensis*.

The name *Latirus annulatus* (Melvill) traces to a shell figured by Chemnitz (1780: pl. 141, fig. 1316). Chemnitz (1780) grouped the figure with several others (pl. 140, figs. 1306–1309; pl. 141, 1314–1316), all of which he associated with a (non-binominal) species-group. Gmelin (1791) later assigned all of the Chemnitz figures (and some by other authors) to his new species *Murex polygonus*. [For several decades thereafter, some authors (e.g., Bosc 1802, Dillwyn 1817, Wood 1818, Lamarck 1822, Anton 1838) indiscriminately repeated all of the Chemnitz figures that Gmelin had cited for *polygonus*, but those citations are not germane here.] Röding (1798) reallocated the Chemnitz figures cited by Gmelin as follows: (1) *M. polygonus* Gmelin was restricted to figures 1306 and 1307 and reclassified as *Fusus polygonus*—now known as *Latirus polygonus* of the Indo-West Pacific; (2) figures 1308 and 1309 were reassigned to *Fusus tapetepersicum* Röding, 1798—now a junior synonym of *Latirus gibbulus* (Gmelin, 1791), another Indo-West Pacific species and the type species of *Latirus*; (3) figures 1314 and 1315 were reassigned to *Fusus angulatus* Röding, 1798—now *Polygona angulata* (Röding, 1798) of the southern Caribbean region; and (4) Chemnitz figure 1316 was reassigned both to *Syrinx annulata* Röding, 1798, and to *Syrinx clathrata* Röding, 1798. Link (1807) reclassified *S. annulata* as *Cymatium annulatum* but did not mention *S. clathrata*. Lacking other criteria by which to differentiate them, the two Röding names are primary subjective synonyms. Regardless of which name is preferred (one may argue that Link, 1807 preferred *annulata*), we believe that Chemnitz figure 1316 is too poor to allow confident identification to species level, and both names should be considered *nomina dubia*.

Mørch (1852) first listed *Lathyrus annulatus* "Bolt." (i.e., Röding) among the West Indian fauna; H. and A.

Adams (1853) listed the name as *Latirus annulatus* (Bolten); and Krebs (1864) listed *Turbinella annulata* (Bolten) among West Indian shells. Finally, *Peristernia annulata* (Bolten) was listed by Melvill (1891b: 407) but refigured as *Peristernia annulata* (A. Ad.) by Melvill (1891b: 411, fig. 1). Bullock (1968: 65) contended that Chemnitz pl. 141, fig. 1316, the only figure cited by Röding for *Syrinx annulata*, "could certainly be a *Latirus*, [but] it is impossible to determine the species as the illustration is poor and the aperture is not shown. Therefore, Röding's name should be considered a *nomen dubium* and the [name] *annulatus* credited to Melvill."

Melvill (1891b) referred authorship for the name with his figured shell not to Bolten (Röding) but to Arthur Adams. According to Trew (1992), the only species that Adams named *annulatus*, *-a*, *-um* were in Fissurellidae and Pyramidellidae, families unlikely to be confused with Fasciolariidae. However, if Melvill's reference to Adams as author was in error, publication by Melvill of the unused combination *Peristernia annulata* and the accompanying new figure constituted valid introduction of a name. Thus, the binomen *Peristernia annulata* "(A. Ad.)" Melvill (1891b) seems to be available for taxonomic purposes; it only remains to prove what that name represents. The type specimen must be the shell that Melvill figured, but the location of that specimen is unknown and its identity could not be confirmed. Trew (1990) reported a specimen of *annulatus* in the Melvill-Tomlin Collection at the National Museum of Wales. At our request, museum staff photographed that specimen, which proves to be a young *Hemipolygona carinifera* (Lamarck, 1816) (Figure 31) quite unlike Melvill's figure. We hesitate to replace the well-known *Latirus virginensis*_Abbott with the Melvill name. Absence of an original description and lack of access to a type render the status of *Peristernia annulata* uncertain. Until the figured type is found and its identity confirmed, we recommend that Melvill's name be considered a *species inquirenda*.

Bullock (1968: 65-67) reported as *Latirus annulatus* (Melvill) specimens from Cuba, Jamaica, St. Thomas and Antigua, figured by that name shells from Jamaica, St. Thomas and Antigua, and cited the species' range as Cuba to the Virgin Islands and southward in the Lesser Antilles. Bullock characterized *L. annulatus* as "the most commonly found and least variable of the [species group]." He distinguished *L. annulatus* from *L. attenuatus* by its "more angular shoulder on the body whorl and by having white axial ribs on every whorl," stating that *L. virginensis* differs from *L. annulatus* "by having a more rounded body whorl lacking the white color of the axial ribs." Shells that Bullock figured as *L. annulatus* generally resemble Melvill's figure, which in turn resembles shells that Nowell-Usticke (1969) named *Latirus karinae* from Puerto Rico, the Virgin Islands, and Antigua. Nowell-Usticke (1971) tacitly acknowledged synonymy of *L. karinae* with *L. virginensis* by captioning as *virginensis* in 1971 the figure he had used for *karinae* in 1969; his figured shell is now the lectotype of *karinae* (see Boyko and Cordiero, 2001). *Latirus karinae* was formally relegated to synonymy with *L. virginensis* by Faber (1988).

Bullock (1968: 71, 72) characterized *Latirus virginensis* as a very variable species whose status "will not be known until large series of specimens have been studied. The relationship between this species, *attenuatus*, and *annulatus* is very unclear. The type of *virginensis* is a mature specimen and seems different from the largest *annulatus* seen." Bullock defined the range of *L. virginensis* as Puerto Rico and the Virgin Islands to Brazil, citing specimens examined from Puerto Rico (four lots) and St. Thomas (one lot). Bullock also cited his pl. 4, fig. 19 for *L. virginensis*, but its caption identifies that shell as *L. attenuatus* from St. Thomas.

Abbott (1958) defined the type series of *Latirus virginensis* as: holotype ANSP 196459; two paratypes ANSP 34975; two paratypes ANSP 34968; and four paratypes ANSP 34969, and we examined all of these specimens at ANSP. We also examined three other specimens (ANSP 210740; ANSP 219064; UF 162199) labeled as paratypes of *Latirus virginensis*, but Abbott did not mention those specimens and they cannot be type material. Abbott (1958) only figured the holotype of *L. virginensis*, and Bullock's thesis does not indicate that he examined the type series at ANSP, but Lyons (1991) illustrated the holotype and three paratypes from the series; those figures suggest that, had he seen them, Bullock would have classified the holotype and two paratypes (Lyons figs. 36–40) as *L. attenuatus* and one paratype (Lyons fig. 41) as *L. annulatus*, further exemplifying the confusing variability of shells in this species-group.

Simplistically, there are two dissimilar morphotypes in the group. The first type, a "*virginensis*" form, is typified by a mostly smooth shell with broad axial ribs, low to absent spiral cords, and a rather waxy shell surface. The shell color is usually olivaceous brown with lighter-colored ribs, but completely orange or yellow specimens are known, and some shells are mostly orange or yellow but with brown patches between ribs on posterior whorls. A population from Little St. James Island in the U. S. Virgin Islands is uniformly olivaceous.

The other morphotype, a "*karinae*" form, is typified by robust, swollen ribs and well-defined spiral cords. The shell

color is usually orange-brown but may be yellow, dark brown, or even black, with white axial ribs in stark contrast to the background color. Axial ribs are usually more developed on the *karinae* form than on the *virginensis* form and may occur on all whorls, but more often become subdued on the penultimate and body whorls of large specimens.

Shell sizes vary considerably among and between populations. Large shells (≥ 35 mm sl) were examined from the Dominican Republic, St. Thomas and St. John in the U. S. Virgin Islands, Anguilla, St. Martin, St. Barthelemy, Antigua, Guadeloupe, and St. Lucia. We saw no shells larger than 28 mm from Aruba, and only two shells larger than 30 mm from the Bahama Islands.

Finally, having examined nearly 400 specimens, we could not distinguish one phenotype that could not be linked by intergrades to other quite different phenotypes. We conclude that all of the specimens represent a single, morphologically variable species for which *Pustulatirus virginensis* (Abbott, 1958) is the first available name.

The shell that Kaicher (1986: card 4671) figured as *Latirus elegans* (Gray) is in the ANSP collection (ANSP 35033; Figure 23), where it was catalogued as "*L. elegans* A. Ad. (?)" without stated locality. That specimen, actually *P. virginensis*, is much darker brown than indicated by Kaicher's figure but is identifiable by a chip in the abapical portion of the outer lip that is visible on the specimen and in the figure. It differs from the shell Kaicher figured on the same card as the holotype of *Fusus elegans* Gray, 1838, which has a shorter, more canted siphonal process, relatively shorter and broader axial ribs, and distinct threads between spiral cords. We doubt that the shell Kaicher figured as holotype of *Fusus elegans* Gray (NHMUK 1968453) is the shell that Gray described from Sierra Leone; his description includes the phrase "with … rather distant, acute, raised, narrow, brown topped spiral ridges," a condition that fits perfectly shells of *Fusinus filosus* (Schubert and Wagner, 1829) from West Africa but not evident on the NHMUK shell, and we are inclined to treat *F. elegans* Gray as a junior subjective synonym of *Fusus filosus* Schubert and Wagner.

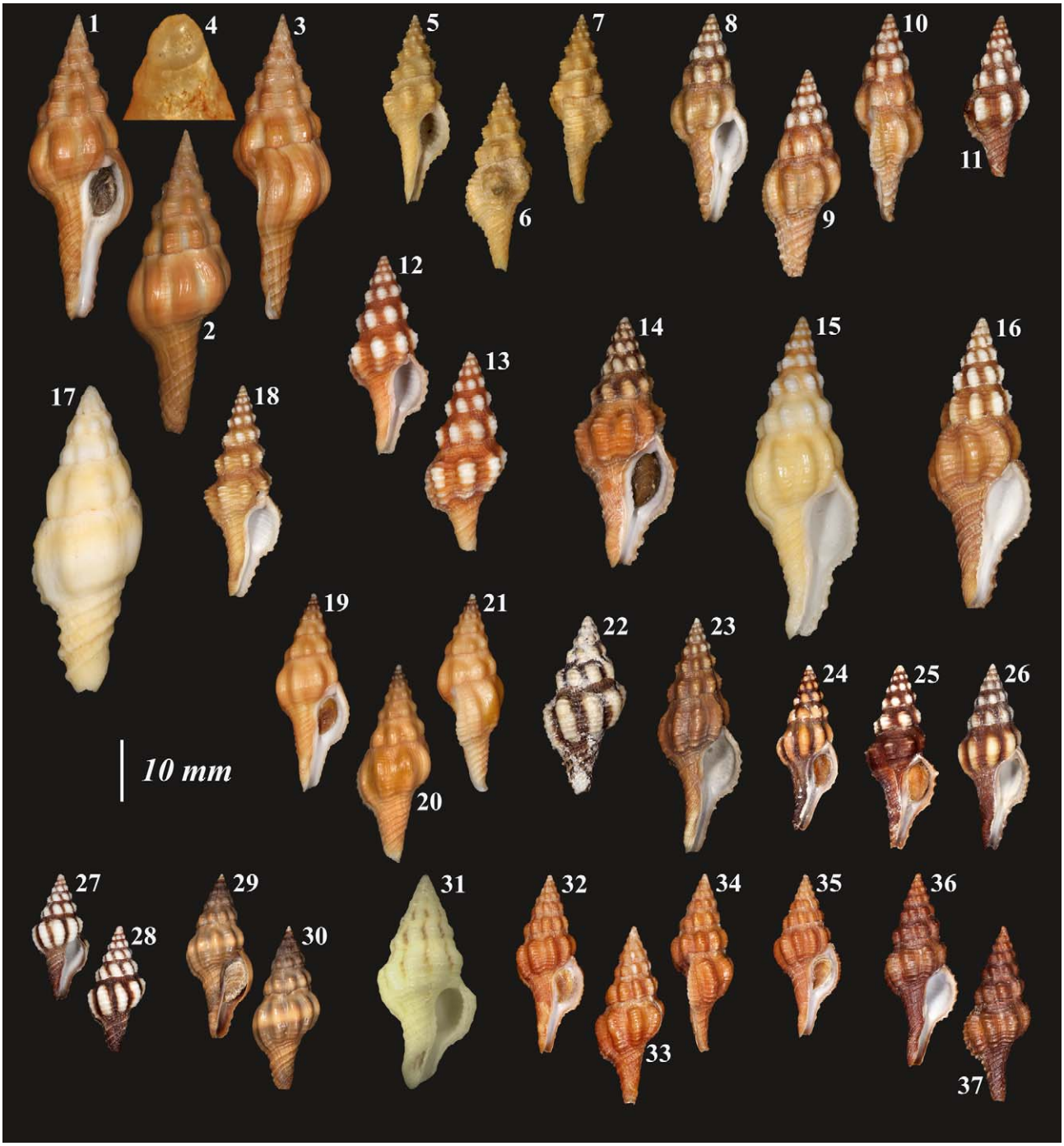
A shell from off Fortaleza, Ceará, Brazil that Bullock (1968) reported and figured as *Latirus virginensis* is instead a new Brazilian endemic which we describe as *Pustulatirus biocellatus* n. sp. in an account that follows. The shell figured as *Latirus virginensis* from the Bay Islands of Honduras by K. and L. Sunderland (1996) is *Pustulatirus utilaensis* n. sp., described next.

Pustulatirus utilaensis **new species**

(Figures 32–37)

Latirus virginensis Abbott, 1958—K. and L. Sunderland, 1996: 17, 2 figs. *Non Latirus virginensis* Abbott, 1958, Recent, eastern Caribbean.

Description: Shell small for genus (largest 31.6 x 11.5 mm), moderately fusiform, with rounded whorls, broad, somewhat adapically shouldered axial ribs, low spiral cords, shallow suture, and narrow sutural ramp bearing closely-packed axial lamellae. Protoconch of about 2 whorls; first whorl smooth, broadly globose, with rounded sides; second whorl no wider than first, with straight sides, about 4 broad axial riblets near terminus. Teleoconch of 6 to 7 rapidly expanding convex whorls, each with 8 or 9 broad axial ribs, whorls separated by well-developed suture; suture undulant in accord with adjacent ribs and interspaces; 5 subequal spiral cords on first whorl, becoming more numerous on each succeeding whorl, 10-11 cords on penultimate whorl and 14–16 on body whorl; cords on sutural ramp low, parallel to and undulant in concert with suture, and crossed by numerous well-developed subsutural lamellae; cords crossing ribs larger than those of ramp, sometimes with single spiral threads between; 6 or more oblique cords of unequal size on siphonal process, occasionally with single smaller threads between, larger oblique cords raised at intersections with subaxial growth lines, forming lamella-like scales, similar scales sometimes on anterior-most cord of body whorl. Aperture ovate, constricted adapically by thick parietal node and abapically by tooth-like node opposite fold at base of columella; outer lip broadly arcuate, crenulated by extensions of interspaces between spiral cords, inner surface with 10–12 beaded lirae; columella with 2 or 3 oblique plicae, sometimes with smaller plicae adapically; siphonal canal typical of genus, outer lip thin, crenulated by termini of interspaces between larger dorsal cords, inner lip simple, straight, slightly raised, sometimes forming shallow pseudoumbilicus near tip. Outer shell surface uniformly reddish brown or dark brown, interior white. Operculum thin, corneous, yellow or light brown, ovate, with anterior terminal nucleus, outer surface with many arcuate growth increments. Radula unknown.



FIGURES 1–37. New World *Pustulatirus* species. **1–4**. *Pustulatirus mediamericanus* (Hertlein and Strong, 1951). **1–3**. ANSP 449744, 50.0 mm, off Cebaco Island, Panamá, 36.6 m. **4**. Same specimen, protoconch. **5–7**. *Turbinella attenuata* Reeve, 1847. Holotype, NHMUK 196735, 31.1 mm, locality unknown. **8–11**. *Latirus virginensis* Abbott, 1958. **8-9**. Holotype, ANSP 196459, 34.2 mm, St. Thomas, U.S. Virgin Islands. **10–11**. Paratype, ANSP 34969, 26.6 mm West Indies. **12–13**. *Latirus karinae* Nowell-Usticke, 1969. Lectotype, AMNH 198490, 32.7 mm, Puerto Rico. **14–30**. *Pustulatirus virginensis*. **14**. ANSP 449754, 41.4 mm, Las Galeras, Samana, Dominican Republic. **15**. ANSP 449714, 52.7 mm, off St. Thomas, U. S. Virgin Islands. **16**. ANSP 449713, 47.7 mm, St. Thomas. **17**. AMNH 191464, 50.5 mm, St. Johns, Antigua. **18**. ANSP 449712, 34.7 mm, off Guadeloupe, 30-50 m. **19–21**. ANSP 449717, 32.6 mm, off St. Barthelemy, 100 m. **22**. ANSP 249155, 29.4 mm, off East Point, Anegada Island. **23**. ANSP 35033, 38.5 mm, shell figured as *Latirus elegans* (Gray) by Kaicher (1986), locality unknown. **24**. ANSP 449716, 27.1 mm, north of Sandy Cay, West End, Grand Bahama Island, 15-17 m. **25**. ANSP 449715, 30.0 mm, Castillo, Duarte, Dominican Republic, 1.2 m. **26**. ANSP 449720, 30.6 mm, Little St. James Island, U. S. Virgin Islands, 7.3 m. **27–28**. ANSP 449719, 20.7 mm, Bimini, Bahamas. **29–30**. ANSP 449718, 26.7 mm, Little St. James Island, 8.3 m. **31**. *Hemipolygona carinifera* (Lamarck, 1816). Shell erroneously labeled "*Latirus annulatus*" in Melvill-Tomlin Collection; NMWC photo. **32–37**. *Pustulatirus utilaensis* new species. **32–34**. Holotype, ANSP 449739, 29.2 mm, off Sandy Key Reef, Utila, Honduras. **35**. Paratype, ANSP 449664, 26.6 mm, southwest coast of Utila. **36–37**. Paratype, ANSP 449659, 31.6 mm, Roatán.

Type Material: Holotype 29.2 x 11.2 mm (Figures 32–34), lv, off Sandy Key Reef, Utila, Bay Islands, Honduras, depth 70 ft [21.4 m], ANSP 449739. Paratypes: **Honduras**—5, 28.6, 25.8 and 24.0 mm, lv, 2, 13.4 and 13.2 mm, dd, with same data as holotype, SC; 4, 26.6 (Figure 35), 22.6, 18.9 and 18.9 mm, lv, from live reef off southwestern coast of Utila, 40–60 ft [12.2–18.3m], ANSP 449664; 2, 27.1 and 16.7 mm, lv, high-profile reef at Utila, 65 ft [19.8 m], LC; 1, 26.5 mm, lv, same data, USNM 1192971; 1, 30.4 mm, lv, southern coast of Utila, outcrop of rock wall, 40 ft [12.2 m], MNHN 25670; 5, 27.2, 25.9, 25.4, 20.9 and 18.4 mm, lv, same data, LC; 1, 28.4 mm, lv, same data, BMSM 17940; 1, 22.3 mm, lv, off Oyster Bed Lagoon, Utila, coral reef at night, 10-15 m, ANSP 449741; 1, 14.0 mm, lv, Ragged Cay, Utila, reef at night, 12 m, ANSP 449740; 1, 15.5 mm, dd, Ragged Cay, Utila, reef at night, 13 m, ANSP 449742; 2, 21.7 and 16.7 mm, dd, Utila, high profile reef at night, 65 ft (19.8 m), LC; 2, 28.3 and 26.0 mm, lv, Utila, UF 455468; 1, 26.5 mm, lv, Utila, NHMUK 20120249; 1, 22.1 mm, lv, Utila, 20–30 ft [6.1–9.1 m], diver, 5/2008, ANSP 449743; 1, 17.5 mm, lv, Utila, 20 ft [6.1 m], night dive, LC; 2, 16.0 and 14.1 mm, dd, Utila, 60 ft [18.3 m], ANSP 449662; 1, 17.0 mm, dd, Utila, reef, ANSP 449660; 1, 25.4 mm, lv, pillar coral reef, Roatán, Honduras, 30 ft [9.1 m], UF 455471; 1, 25.4 mm, lv, reef at Roatán, 40 ft [12.2 m], LC; 1, 31.6 mm (Figures 36–37), lv, Roatán, living reef, 10-12 m, ANSP 449659. **Panamá**—1, 21.6 mm, dd, Isla Escudo de Veraguas, eastern Panamá, depth 12-15 m, under rocks, ANSP 449661; 1, 22.3 mm, dd, same data, LC; 1, 22.1 mm, dd, Isla Escudo de Veraguas, Panamá, 20-25 m, ANSP 449663.

Other Material: **Honduras**—1 worn shell, 27.2 mm, dd, Utila, live reef off southwestern coast, 12.2–18.3 m, LC; 1 shell with broken apex, 21.6 mm, dd, Utila, reef, LC; 3 broken or encrusted shells, 25.5 and 23.3 mm, dd and 21.1 mm, lv, same data as holotype, SC.

Type Locality: Off Sandy Cay Reef, Utila, Bay Islands, Honduras, depth 21.4 m.

Etymology: The species is named for the island of Utila, Bay Islands, Honduras, Caribbean Sea, where it seems to be most abundant.

Distribution: Known principally from vicinity of Utila, Bay Islands, Honduras, depth range: 6.1–21.4 m; three specimen examined were from nearby Roatán, Honduras, and three more were from Isla Escudo de Veraguas, east-southeast of Bocas del Toro, Panamá.

Remarks:All Honduran shells of *P. utilaensis* are identical morphologically, differing only in color related to their localities of capture. Specimens from Utila are consistently reddish brown, but all six shells from Roatán, Honduras and Isla Escudo de Veraguas, Panamá are dark brown. The Panamá shells are more worn and smooth, but their patterns of ribs and cords as well as their size and general outlines are consistent with those of Honduran specimens and we believe them to be conspecific.

Morphological features of *P. utilaensis* are consistent within parameters defined in the description, and unworn shells never have smooth surfaces or lighter colored axial ribs like those that often occur on *P. virginensis*, whose shells are often larger than the maximum length known for *P. utilaensis*. Shells of *P. utilaensis* also resemble the type of *P. attenuatus*, but the latter is a relatively more slender shell with axial ribs that are less shouldered adapically; *P. utilaensis* shells are consistently reddish brown or dark brown whereas the type of *P. attenuatus* is yellow with white ribs on early adapical whorls.

Pustulatirus watermanorum new species

(Figures 38–42)

Description: Shell small for genus (largest 32.2 x 10.5 mm), fusiform, with rounded whorls, prominent axial ribs and obscure spiral cords, surface generally appearing smooth, waxy. Protoconch of 2 whorls, first whorl broadly globose, nearly flat on top, with rounded sides; second whorl no wider than first, with straight sides and two or three faint axial riblets just before terminus. Teleoconch of 6 to 7 rapidly expanding whorls, each with 8 or 9 broad, evenly rounded axial ribs that extend from suture to suture; about 7 spiral cords on first whorl, including 3 faint ones on sutural ramp; cords increasing in number abapically, penultimate whorl with 4 cords on ramp and 8 more crossing axial ribs, sometimes with single lesser threads between cords crossing ribs; central area of body whorl nearly smooth, but with about 13 very low cords, followed by 2 stronger cords adjacent to junction with base; dorsal surface of siphonal process with 9 or 10 oblique cords of varying strength, sometimes with single faint threads between. Aperture ovate, constricted adapically by parietal node at anal sinus and abapically by tooth-like node opposite entrance fold at junction of columella and siphonal canal; outer lip arcuate, edge crenulated by

extensions of interspaces between spiral cords on body whorl, inner surface with about 10 beaded lirae, some incomplete; inner lip adherent, columella with 3 or 4 oblique plicae near base, sometimes with smaller plica adapically; siphonal canal typical for genus, straight, outer edge crenulated, inner edge simple, straight, slightly raised, sometimes forming shallow pseudoumbilicus near tip. Outer surface of shell uniformly orange, interior white.

Operculum corneous, brown, drop-shaped, with terminal nucleus at pointed anterior end, outer surface with many concentric, arcuate growth increments; prominent posterior muscle scar occupying about 70% of inner surface, bounded by thick, raised ridge. Radula unknown.

Type Material: Holotype 27.4 x 10.5 mm (Figures 38–40), lv, off Roatán, Honduras, depth 80 m, in baited shell trap, ANSP 449721. Paratypes: **Honduras**—1, 27.7 mm, dd, same data as holotype, LC; 2, 26.4 and 23.6 mm, dd, off Roatán, 30–40 m, in lobster traps, 1996, ANSP 449722; 3, 26.6 and 24.8 mm, lv and 26.7 mm, dd, off Roatán, 200–300 ft (60.7–91.5 m), ANSP 449723; 20, 29.1, 27.0, 25.1, 20.6, 15.6 and 9.5 mm, lv and 27.6, 27.4, 25.6, 25.5, 24.4, 24.2, 22.1, 19.2, 17.9, 17.6, 15.4, 15.2, 13.5 and 12.1 mm, dd, off Roatán, 200–300 ft (60.7–91.5 m), shell traps, SC; 2, 25.4 and 25.3 mm, lv, off Roatán, 80 m, traps, 1999, ANSP 449724; 2, 25.7 mm, lv and 25.0 mm, dd, off Roatán, 100 m, UF 455469; 1, 25.1 mm, lv, off Roatán, 480 ft (146.4 m), BMSM 17942; 2, 26.1 (Figures 41–42) and 24.6 mm, lv, off Roatán, 160 m, traps set on undersea slope, 1995, ANSP 449725; 2, 28.2 and 25.9 mm, dd, Cabo Faisa, Mosquitia, diver, 10-15 m, 1996; ANSP 449726; 1, 29.2 mm, lv, Gorda Bank, 30-35 m, coral reef, on sand, MNHN 25669; 1, 27.7 mm, dd, Gorda Bank, 30-45 m, near coral reef, USNM 1192972; 2, 32.2 and 30.0 mm, lv, Rosalind Bank, 90 ft (27.4 m), from lobster boat, SC. **Colombian Islands**—4, 27.9, 27.4, 27.1 and 24.5 mm (last with chipped apex), dd, Banco Quitasueño, 15–18 m, under coral slabs, diver, 2004, ANSP 449727; 1, 27.3 mm, dd, Banco Quitasueño, 15–18 m, under coral slab, NHMUK 20120250; 3, 25.9, 25.1 and 20.9 mm, dd, Banco Quitasueño, 15–18 m, LC; 1, 26.2 mm, dd, Banco Quitasueño, 15-18 mm, LC; 1, 16.6 mm, San Andres Island, rubble, 15 m, diver, 2007, ANSP 422779.

Other Material:**Honduras**—11 specimens, 21.1 to 16.6 mm, all immature with thin lips, dd, off Roatán, 300 ft (91.2 m), in baited shell traps, LC; 4 specimens, 27.6 to 12.0 mm, all with severe break repairs, etc., dd, off Roatán, 200–300 ft (60.7–91.2 m), shell traps, SC.

Type Locality:Off Roatán, Honduras, depth 80 m.

Etymology: The species name honors the James Waterman family, whose interest and acts of kindness encouraged the Sunderlands in assembling their important collection of western Atlantic gastropods.

Distribution:Continental shelf of Honduras, including Gorda Bank and Rosalind Bank, and at Banco Quitasueno and Cayos San Andres, Colombia, western Caribbean Sea; depth range: 10–160 m.

Remarks: The uniformly bright orange color is helpful in distinguishing *P. watermanorum* from the partially sympatric *P. utilaensis*. *Pustulatirus watermanorum* also differs from *P. utilaensis* by its proportionally shorter spire and longer body whorl and siphon. Axial ribs of *P. watermanorum* extend from suture to suture whereas those of *P. utilaensis* (and *P. attenuatus*) are separated from the suture adapically by a narrow ramp. Sutures of *P. utilaensis* are more impressed, whorls are more convex, and spiral cords are stronger.

The two largest specimens (32.2 and 30.0 mm sl) constitute a single paratype lot (SC) from Rosalind Bank. Features of the smaller shell are consistent with those of other *P. watermanorum*, but the larger shell is attenuated, with a relatively taller and more slender spire than its conspecifics.

The range of depths we report for this species (10–160 m) is the greatest known for any species of *Pustulatirus*. We offer no explanation for this but note that all specimens were obtained from commercial dealers, who in turn obtained some of them from fishermen. More reliable locational and bathymetric data may reveal a narrower depth range.

***Pustulatirus eppi* (Melvill, 1891)**

(Figures 43–45)

Latirus eppi Melvill, 1891a: 158. Melvill, 1891b: 394, 411, pl. 2, fig. 11; Horst and Schepman, 1894: 92; Schepman, 1916: 477; van Bentham Jutting, 1927: 6, 32; Coomans, 1958: 49, 93; Warmke and Abbott, 1961: 14; de Jong and Kristensen, 1965: 39; Bullock, 1968: 69, 99, 101, pl. 4, fig. 10; Tello, 1975: 125; Princz, 1982: 123; Trew, 1987: 38; de Jong and Coomans, 1988: 88, pl. 25, fig. 479; Trew, 1990: 2; Lyons, 1991: 177, 178, fig. 42, 43; Díaz, 1995: 118; Snyder, 2003: 91; Mallard and Robin, 2005: 17 (*pars*); Rios, 2009: 253 (*pars*) ; Faber, 2010: 8, fig. 1; van der Bijl *et al*., 2010: 54, 4 figs. *Non Latirus*

eppi Espinosa *et al*. (1994: 113; 1995: 36; both Cuba), Mallard and Robin (2005: pl. 43, right figs. only, 'Porto Rico'), and Robin (2008: 221, figs. 2, = same figs. of shell from 'Porto Rico'), all = *P. virginensis* (Abbott, 1958); *nec Latirus eppi auctt*. = *P. biocellatus* Lyons and Snyder, herein.

Pustulatirus eppi (Melvill, 1891)—Vermeij and Snyder, 2006: 421 (*pars*; *non* fig.4C, = *Pustulatirus biocellatus* n. sp.).

Description: Shell small for genus (largest 24.1 x 10.8 mm), solid, broadly fusiform, axially compressed and compact, with rapidly expanding whorls, broad axial ribs, and low spiral cords. Protoconch too worn for description. Teleoconch with about 6 whorls, suture slightly undulant in accord with ribs and interspaces, sutural ramp lacking; whorls shorter than wide, with 8 or 9 axial ribs extending from suture to suture; spiral sculpture of low cords, 3 or 4 cords on whorls 2 and 3, 4 or 5 cords on whorl 4, cords on later whorls becoming nearly obsolete except for about 3 cords near adapical suture and 1 or 2 on body whorl near junction with siphonal process; about 5 stronger, oblique cords on dorsal surface of broad, abapically tapering siphonal process. Aperture ovo-elongate, constricted adapically by parietal node at posterior sinus and abapically by node opposite entrance fold at base of columella; outer lip lowly arcuate, with flexure near junction with siphonal process; outer lip smooth, worn on specimens examined, but with remnants between termini of cords suggesting extensions of interspaces; inside of outer lip with about 6 pustulose lirae emerging from aperture; inner lip smooth, adherent, with 3 or 4 oblique plicae on abapical half. Shell surface chestnut brown, apparently fading to yellow in older dead shells, interior white. Operculum and radula unknown.

Type Material: Holotype 24.1 x 10.8 mm (Figures 43–45), dd, RMNHL.

Type Locality:Curaçao, Netherlands Antilles.

Other Material: 1, 20.0 mm, dd, beach at Boca Santa Maria, Curaçao, ZMA.

Etymology: Named for Dr. Epp, its discoverer (Melvill, 1891a); Carolus T. Epp was a pharmacist with the Netherlands West Indian army on Curaçao from 1876 until 1886 (van der Bijl *et al*. 2010).

Distribution: The species is known only from Curaçao, Netherlands Antilles, where it seems to be both endemic and rare.

Remarks: The authorship of *Latirus eppi* has been a subject of debate. The name was attributed solely to Melvill by van Benthem Jutting (1927), Coomans (1958), de Jong and Coomans (1965), Princz (1982), Trew (1987, 1990), Snyder (2003) and Mallard and Robin (2005). Others (Horst & Schepman 1894, Schepman 1916) attributed the name to Schepman and Melvill; and still others (Bullock 1968, de Jong & Coomans 1988, Lyons 1991, Díaz 1995, Rios 2009) attributed authorship to Melvill and Schepman, 'Melvill y Schapman [*sic*]' (Espinosa *et al*. 1994, 1995) or, most recently to Melvill and Schepman in Melvill 1891 (van der Bijl *et al*. 2010, Faber 2010).

Melvill (1891), in *Notes from the Leyden Museum* described but did not figure *Latirus eppi*, taking credit for the name which he stated that Schepman had asked him to describe. Melvill's note bears the date "March, 1891," but that may be when he wrote it; the paper was published in August 1891 (Dickinson, 2005). In another description (with figure) published the same year in *Memoirs and Proceedings of the Manchester Literary and Philosophical Society*, Melvill (1891: 394) stated that "Mr. Schepmann [*sic*] unites with me in joint authorship" of *Latirus eppi*. Melvill cited himself as sole author in the caption for the figure of the type (p. 411, pl. 2, fig. 11), while on the same page *Peristernia retiaria* Melvill (pl. 2, fig. 13) was attributed to Melvill and Schepmann [*sic*]. Nothing in the text associates Schepman with *Peristernia retiaria*, so we surmise that 'Melvill and Schepmann' was intended for *Latirus eppi*, and 'Melvill' was intended for *Peristernia retiaria*. As indicated on its title page, the manuscript for Melvill's second paper was received on 24 March 1891, but Rosenberg (2009) cites its publication date as "post-July" of that year, so it too could have been published in August. Article 21.3.1 of the International Code of Zoological Nomenclature, Fourth Edition (ICZN, 1999) specifies that when the year and month but not the day of publication is known with certainty, the date to be adopted is the last day of the month, and Article 21.3.2 specifies that when neither the day nor the month of publication is known with certainty, the date to be adopted is the last day of the year. In the case at hand, the Code dictates that publication of *Notes from the Leyden Museum* be assigned a date of 31 August 1891 (i.e., 1891a), and *Memoirs and Proceedings of the Manchester Literary and Philosophical Society* be assigned a date of 31 December 1891 (i.e., 1891b).

The International Code of Zoological Nomenclature, Fourth Edition (ICZN 1999), Article 50.1 also states in part: "The author of a name … is the person who first publishes it ... in a way that satisfies the criteria of availability." As Melvill is the only author identified in the first publication (1891a), *Latirus eppi* must be attributed solely to Melvill, and efforts to add Schepman's name as an author are contrary to provisions of the Code.

Bullock (1968: 69, pl. 4, fig. 10) figured the holotype of *Latirus eppi*, which he treated tentatively as a "squat

specimen, quite unlike the type specimen of [*L.*] *attenuatus*." Bullock maintained that "a series of intergrades appear to exist between the two forms," but he conceded that further study could result in their separation. Bullock may have been confused by the figure that Melvill (1891b) provided for *L. eppi*; the shell in that figure looks more like a specimen of *P. virginensis* than it does the holotype and other material of *P. eppi* as figured by Bullock (1968), Lyons (1991), van der Bijl *et al.* (2010), Faber (2010) and herein. Those shells certainly are not conspecific with *P. virginensis*. Melvill's figure also may have influenced Mallard and Robin (2005) to misidentify a shell of *P. virginensis* from Puerto Rico as *L. eppi*. Shells of *P. virginensis* are larger, relatively more slender, seldom occur in a single color, and usually have more elevated ribs crossed by more prominent spiral cords than do shells of *P. eppi*. Dr. José Espinosa kindly provided a photograph of a specimen that had been reported as *Latirus eppi* from Cuban waters (Espinosa *et al*. 1994, Espinosa *et al*. 1995); that specimen proved to be *P. virginensis* of a small, dark form with white ribs that is rather common in the Bahama Islands; we illustrate a similar shell (ANSP 449719) in our Figures 27–28.

Pustulatirus eppi seems limited to waters around Curaçao. Most applications of its name (see synonymy) either have been reiterations of a few early records or misidentifications, including a new species described in the next account but also including a previously named species (see remarks for *P. virginensis*). Of the many Brazilian shells that we have seen offered for sale as *Latirus eppi* during the past decade, all have proved to be the new species.

Pustulatirus biocellatus **new species**
(Figures 46–51)

Latirus virginensis Abbott, 1958—Bullock, 1968: 72, 73, 99, 101, pl. 4, fig. 1. Matthews, 1968: 248. *Non Latirus virginensis* Abbott, 1958, Recent, eastern Caribbean.

Latirus (Polygona) virginensis Abbott, 1958—Rios, 1970: 96 (*pars*). Rios, 1975: 104 (*pars*), pl. 29, fig. 440; Rios, 1985: 107 (*pars*), pl. 36, fig. 471; Rios, 1994: 133 (*pars*), pl. 42, fig. 575; Rios, 2009: 253 (*pars*), figs. *Non Latirus (Polygona) virginensis* Abbott, 1958, Recent, eastern Caribbean.

Latirus eppi Melvill, 1891—Mallard and Robin, 2005: pl. 43, figs. (*pars*; 17-mm shell from Brazil only). *Non Latirus eppi* Melvill, 1891, Recent, Curaçao.

Pustulatirus eppi (Melvill, 1891)—Vermeij and Snyder, 2006: 421, fig. 4C, *pars*. *Non Pustulatirus eppi* (Melvill, 1891), Recent, Curaçao.

Description: Shell small for genus (largest 30.0 x 13.8 mm), solid, broadly fusiform. Protoconch of about 2 rounded whorls; first whorl smooth, second with 2 or 3 broad axial riblets on last quarter whorl; riblets increasing in strength toward junction with teleoconch. Teleoconch of as many as 7 whorls bearing prominent broad, well-rounded axial ribs crossed by low, smooth spiral cords; cords diminishing in strength abapically, causing shell surface to appear smooth; whorls 1 and 2 each with 7 or 8 ribs, subsequent whorls each with 6 or 7 ribs; about 3 evenly spaced cords on whorls 1 and 2, joined by 2 or 3 more broad, low cords on sutural ramp of whorl 3, number of cords increasing to about 14 on body whorl of largest shell; most body whorl cords very low and indistinct, presence of some indicated only by color changes atop ribs; 3 to 5 stronger, oblique cords atop siphonal process, sometimes with 1 to 3 faint spiral threads between. Aperture ovo-elongate, constricted adapically by callosity on parietal shield and abapically by prominent node at junction with siphonal canal; outer lip arcuate, serrate on mature shells, particularly on abapical edge in response to termini of extensions between spiral cords of body whorl and outer edge of siphon, inner side with 7 to 11 (usually 8 or 9) well-spaced, strongly beaded lirae, most evident on fully developed lip; inner lip and parietal shield adherent; columella straight, with 4 distinct plicae adapical to entrance fold of short, straight siphonal canal. Shell exterior reddish brown, with creamy white node-like ribs, light-colored ribs of body whorl crossed by narrow brown band, producing two distinctive spots on each rib; some mature shells uncommonly with ribs of body whorl tan, not white, rendering "biocellate" effect less evident; interior of shell white except for brown band at edge of outer lip. Operculum corneous, narrow, with anterior terminal nucleus, outer surface covered with many indistinct, concentric, arcuate growth increments. Radula unknown.

Type Material: Northeastern Brazil—Holotype 30.0 x 13.8 mm (Figures 46–48), dd, off Natal, Estado Rio Grande do Norte, Brazil, depth 10–15 m, MZUSP 108767. Paratypes: 1, 24.0 mm (Figure 51), dd, off Camocim, Estado Ceará, 15–25 m, diver, 2007, ANSP 422778; 1, 26.4 mm, dd, off Camocim, 20-25 m, in octopus pot, LC; 1,

22.1mm, dd, same data, LC; 1, 27.2 mm, dd, off Camocim, 20-25 m, SC; 1, 25.3 mm, dd in octopus pot, off Camocim, 20–35 m, BMSM 17941; 1, 21.2 mm, dd in octopus pot, off Camocim, 20–35 m, NHMUK 20120248; 1, 22.9 mm, dd, off Camocim, 25-30 m, USNM 1192973; 1, 28.3 mm , crabbed in octopus pot, dd, off Camocim, 25-35 m, LC; 1, 27.7 mm, dd *ex pisce*, off Fortaleza, Estado Ceará, 16 m, 7/1968, ANSP 449751; 1, 25.8 mm, dd *ex pisce*, off Fortaleza, 12 fm (22 m), AMNH 140147; 1, 23.5 mm, dd, off Rio do Fogo, north of Natal, Rio Grande do Norte, 15–25 m, sand under rock, 2008, ANSP 422777; 2, 16.0 and 20.6 mm, dd, off Rio do Fogo, north of Natal, 15-25 m, UF 455470; 1, 23.7 mm, dd, north of Natal, Rio Grande do Norte, 10–15 m, MNHN 25671; 1, 15.6 mm, dd, north of Natal, 10-15 m, sand under rock, diver, 1999, ANSP 449750; 1, 11.1 mm, dd, north of Natal, 10-15 m, sand under rock, 2000, ANSP 449749; 7, 18.1, 17.1, 17.0, 16.8, 15.7, 12.2 and 10.4 mm, lv, north of Natal, 10–15 m, sand under rock, 2007, ANSP 421133; 1, 22.1 mm, dd, north of Natal, 10–15 m, SC; 1, 18.0 mm, lv, north of Natal, 25 m, 11/2003, ANSP 449746; 1, 15.8 mm, lv, Rio Grande do Norte, reef, 10-20 m, UF 455467; 1, 17.0 mm, lv, Rio Grande do Norte, 10-20 m, ANSP 449747**;** 1, 26.7 mm, dd, off Alcobaça, Estado Bahía, 20-25 m, LC; 2, 26.5 (Figures 49–50) and 21.7 mm, dd, off Alcobaça, Bahía, Brazil, 40-45 m, ANSP 449745.

Other Material: **Northeastern Brazil**—23, 15.4, 15.3, 14.3, 14.8, 14.3, 13.8, 13.7, 13.6, 13.5, 13.2, 13.2, 13.0, 12.8, 12.6, 12.5, 12.5, 12.3, 12.0, 11.9, 11.7, 11.1, 10.0 and 8.6 mm, dd, north of Natal, 10-15 m, sand under rock, 2004, ANSP 449753; 2, dd, 17.3 and 17.0 mm, north of Natal, Rio Grande do Norte, 10–15 m, LC; 1 lv, 16.8 mm, 13 dd, 10.2-21.1 mm, north of Natal, 10–15 m; 7 lv, 13.3-15.6 mm, Rio Grande do Norte, 10-20 m, LC; 2, 13.6 and 15.5 mm, lv, Rio Grande do Norte, 25 m LC. **Venezuela?** (records considered spurious)—1, 16.1 mm, lv, Los Roques Islands, Venezuela, 6 m, LC; 1, 10.2 mm, dd, off Los Roques Islands, dredged, 200 m, 2006, ANSP 449752.

Type Locality: Off Natal, Estado Rio Grande do Norte, Brazil, 10–15 m.

Etymology: The species name, an adjective, is composed of the prefix *bi-*, meaning two, the Latin noun *ocellus*, meaning little eye, and the suffix *-atus*, *-a*, *-um*, meaning "provided with," referring to the pattern of paired spots on the body whorl.

Distribution: Off Camocim, Ceará southward to Alcobaça, Bahía, Brazil; depth range 10–45 m.

Remarks: *Pustulatirus biocellatus* seems relatively common in moderate depths (10–45 m) on the inner continental shelf off of the states of Ceará, Rio Grande do Norte, and Bahía in northeastern Brazil. We examined two shells labeled "off Los Roques, Venezuela," depths 6 m and 200 m, but we consider those data suspect and requiring confirmation.

This species was reported and figured as *P. eppi* (Melvill, 1891) by Vermeij and Snyder (2006), and Brazilian shells have been offered for sale as "*Latirus*" *eppi*, or sometimes as *L.* cf. *L. eppi*, for more than a decade. Between 1968 and 1994, records of the species were mistakenly reported as *L. virginensis* Abbott, 1958 (see synonymy). Recently, Rios (2009) reported and figured Brazilian specimens as *L. (Polygona) virginensis*, and then cited *L. eppi* as a junior synonym. However, we have found no valid record of the occurrence of either of those Caribbean species in Brazil, and we reject that synonymy.

The pattern of spots on the body whorl immediately distinguishes *P. biocellatus* from *P. eppi* and *P. virginensis*. Although their shells are similar in size, *P. biocellatus* has more rounded whorls, deeper sutures, and more conspicuous spiral cords than *P. eppi*. Shells of *P. virginensis* are larger and more attenuate than *P. biocellatus*, with longer, narrower ribs and a relatively longer and more slender siphonal process.

***Pustulatirus ogum* (Petuch, 1979)**

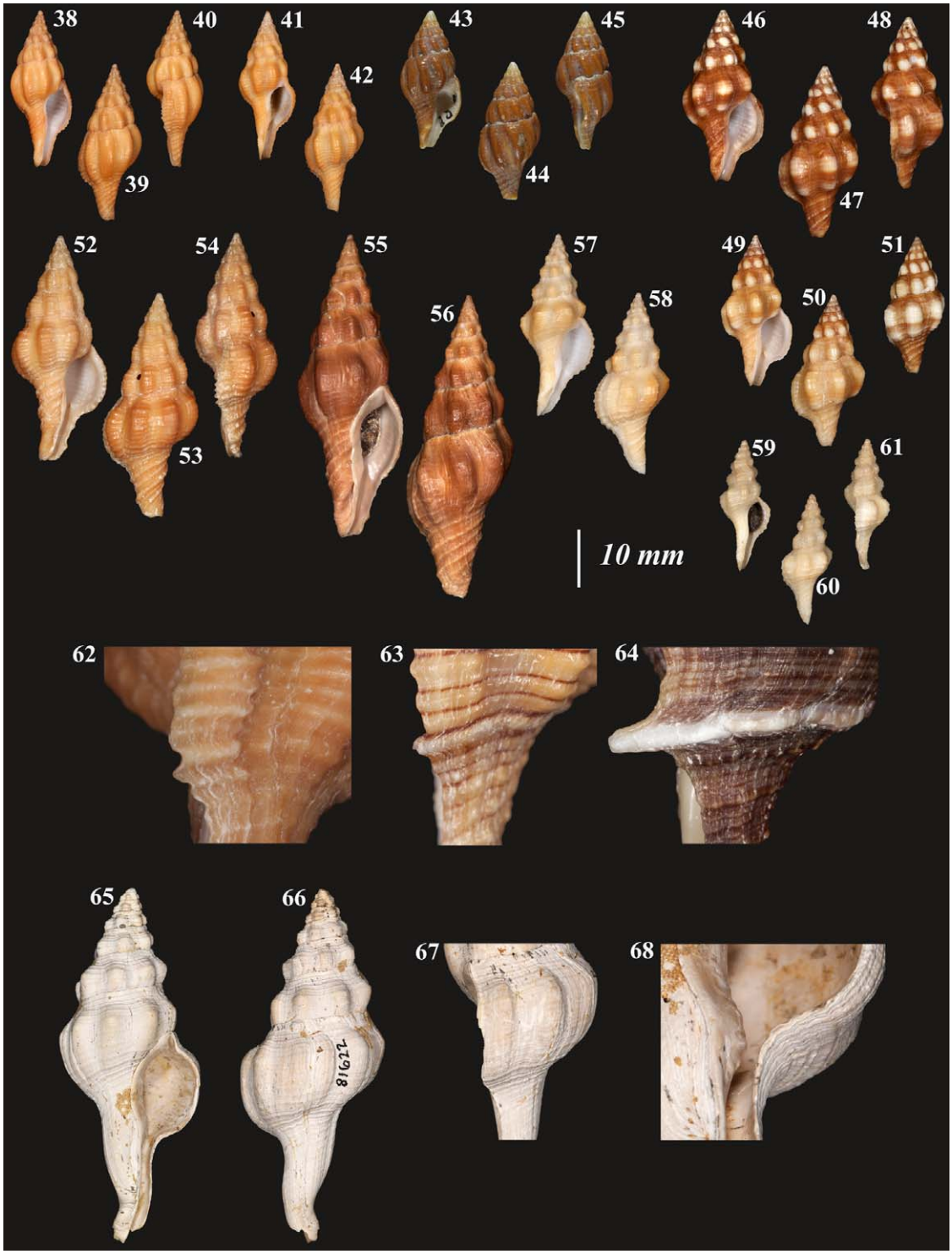
(Figures 52–62)

Latirus (Polygona) ogum Petuch, 1979: 519, 520, figs. 3A, B. Rios, 1985: 107, pl. 36, fig. 470; Costa and Moretzsohn, 1991: 59–60, figs. 4, 5; Rios, 1994: 133, pl. 42, fig. 574; Vermeij and Snyder, 2003: 18.

Latirus ogum—Petuch, 1979: 519, 520. Kaicher, 1986: card 4667; Petuch, 1986a: 9; Petuch, 1987: 140, 144, pl. 27, figs. 1, 2; Petuch, 1988: 163, pl. 39, fig. 13; Costa, 1991: 76; Lyons, 1991: 201; Matthews-Cascon *et al*., 1991: 1; Rios *et al*., 1994: 34; Goto and Poppe, 1996: 392; K. and L. Sunderland, 1996: 17, 2 figs; Snyder, 2000: 162; Petuch, 2001: 339; Vermeij and Snyder, 2003: 18, 20; Mallard and Robin, 2005: 18, pl. 47; Robin, 2008: 222, figs. 9; Landau and Vermeij, 2012: 88.

Benimakia ogum (Petuch, 1979)—Vermeij and Snyder, 2003: 15, 18-20, figs. 6a, b. Pisor and Poppe, 2008: 83; Snyder and Vermeij, 2008: 49, 50.

Pustulatirus ogum (Petuch, 1979)—Snyder, Landau and Vermeij *in* Landau and Vermeij, 2012: 88.



FIGURES 38–68. Western Atlantic *Pustulatirus* and *Pseudolatirus* species. **38–42**. *Pustulatirus watermanorum* new species. **38–40**. Holotype, ANSP 449721, 27.4 mm, off Roatán, Honduras. **41–42**. Paratype, ANSP 449725, 26.1 mm, off Roatán. **43–45**. *Pustulatirus eppi* (Melvill, 1891) Holotype, RMNHL, 24.1 mm, Curaçao. **46–51**. *Pustulatirus biocellatus* new species, Brazil. **46–48**. Holotype, MZUSP 108767, 30.0 mm, north of Natal. **49–50**. Paratype, ANSP 449745, 26.5 mm, off Alcobaça. **51**. Paratype, ANSP 422778, 24.0 mm, off Camocim. **52–62**. *Pustulatirus ogum* (Petuch, 1979), Brazil. **52–54**. Holotype, USNM 780654, 39.3 mm, Abrolhos reef complex. **55–56**. ANSP 449735, 53.1 mm, off Arraial do Cabo. **57–58**. ANSP 449733, 31.8 mm, off Barra, Salvador. **59–61**. ANSP 449799, 22.9 mm, off Cabo Frio. **62–64**. Labral "dentition." **62**. *Pustulatirus ogum*, ANSP 449736, enlarged serratum of 35.2 mm shell, off Alcobaça, Brazil. **63**. *Benimakia* species, ANSP 449800, labral tooth of 23.7 mm shell, Zanzibar. **64**. *Leucozonia nassa* (Gmelin, 1791), ANSP 195297, labral tooth of 41.2 mm shell, New Providence, Bahamas. **65–68**. *Pseudolatirus tumbeziensis* Olsson, 1932. **65–66**. ANSP-IP 81622, 61.8 mm, Paraguana Peninsula Venezuela, Cantaure Formation, Miocene. **67**. Same specimen, showing exterior cords and threads and edge of lip. **68**. Same specimen, showing plicae in siphonal canal.

Description: Shell of medium size for genus (largest 53.1 x 17.4 mm), elongate, fusiform, with rounded, rapidly expanding whorls, broad axial ribs, and low spiral cords; spire surface of large shells (≥ 40 mm sl) nearly smooth except for fine spiral cords on early whorls and stronger cords on body whorl and siphonal process. Protoconch brown, of about 2 equal-sized swollen whorls; first whorl smooth with rounded sides, remaining half whorl with straight sides, smooth except for few faint axial striae and one or two axial riblets near abrupt terminus. Teleoconch of 7 to 8 whorls; spire whorls each with about 7 broad axial ribs, 6 to 9 on body whorl; suture shallow, slightly impressed, somewhat undulant in concert with axial ribs and interspaces; sutural ramp hatched with fine spiral cords crossed by low, thin axial growth increments, hatching nearly obsolete in large shells; whorls 1 and 2 with 2 smooth spiral cords crossing ribs on abapical half of whorl, several finer spiral threads on adapical half (sutural ramp); cords increasing to 3 but diminishing in strength abapically, hardly perceptible on whorls 4 to 7; posterior half of body whorl initially smooth but then showing weak re-emergance of spiral cords, cords becoming increasingly evident on final (abapical) half whorl, about 13 to 15 smooth cords at lip; cords generally increasing in strength toward anterior end of whorl, occasionally with single spiral threads between; siphonal process with 4 or 5 strong, oblique cords, usually with single lesser cords between, sometimes with 7 or 8 small, oblique cords near tip; smaller shells (~30–39 mm sl) with prominent large and small cords over entire surface of spire, as many as 14 smilar cords on body whorl. Aperture ovo-elongate, constricted adapically by thick parietal callus and abapically by ridge-like, sometimes bifid node opposite entrance fold at base of columella; outer lip broadly arcuate to semicircular, crenulated by extensions of interspaces between termini of spiral cords of body whorl and siphonal process, conferring serrate or saw-toothed effect, less evident on large shells; serration created by interspace adjacent to large anterior cord near anterior flexure of body whorl larger than neighboring serrata; inner surface of outer lip (of mature shells) with 9 to 13 lirae of various strengths, all (or sometimes only those on abapical side) interrupted as though composed of dashes and dots; lirae separated from lip margin by smooth band-like strip; inner lip adherent, columella arcuate posteriorly, straight anteriorly, with 3 or 4 broad plicae, occasionally with 1 or 2 lesser plicae adapically; siphonal canal typical of genus, rather short, slender, broader adapically, smooth within; outer edge crenulated in accord with termini of interspaces between exterior cords, inner edge raised, smooth, forming narrow pseudoumbilicus near tip. Shell surface uniformly dark reddish brown to light yellowish brown, usually darker on ribs; interior light orange, tan or white. Operculum corneous, dark brown, sometimes nearly black, drop-shaped, longer than wide, with terminal nucleus at pointed, inwardly curved abapical end; outer surface with many fine, arcuate, concentric growth increments. Radula unknown.

Type Material: Holotype USNM 780654 (39.3 x 17.5 mm) (Figures 52–54), dd.

Type Locality: Tide pool at fringing reef around Coroa, Vermelha, Abrolhos Reef Complex, Estado Bahía, Brazil (17°57'S, 39°13'W) (Petuch, 1979: 519).

Other Material: **Brazil**—1, 21.1 mm, dd, north of Natal, Estado Rio Grande do Norte, depth 10–15 m, 8/2004, LC; 2, 33.6 and 33.3 mm, dd, off Barra, Estado Bahía, bryozoan/sand bottom, 10–15 m, diver, 1996, ANSP 449734; 1, 31.7 mm (Figures 57–58), dd, off Barra, Salvador, Bahia, bryozoan/sand bottom, 10–15 m, diver, 1997, ANSP 449733; 1, 23.6 mm, lv, 170 km northeast of Alcobaça, Bahía, depth 15–20 m, diver, 1/2005, LC; 1, 30.9 mm, dd, off Alcobaça, 20–25 m, 1/2003, LC; 1, 47.7 mm, dd, off Alcobaça, 20–25 m, 1/2003, LC; 1, 32.1 mm, lv, off Alcobaça, 20-25 m, 1/2004, LC; 2, 33.8 and 32.8 mm, lv, off Alcobaça, depth 20–25 m, diver, 1/2004, LC; 1, 35.2 mm, lv, 70 km off Alcobaça, 20–25 m, ANSP 449736 (Figure 62; shell figured by Vermeij and Snyder, 2003: figs. 6a, b); 1, 35.7 mm, lv, 70 km off Alcobaça, 20–25 m, diver, 1/2003, LC; 1, 21.6 mm, dd, 70 km off Alcobaça, 20–25 m, diver, 1/2004, LC; 2, 37.5 and 33.6 mm, dd, 70 km off Alcobaça, 20–25 m, diver, 7/2008, LC; 1, 28.2 mm, lv, off Conceição da Barra, Estado Espirito Santo, 60–80 m, net, 8/2006, LC; 3, 31.0, 27.8 and 22.1 mm, dd, off Conceição da Barra, trawled, 60–80 m, 8/2006, LC; 2, 28.8 and 28.1 mm, lv, off Conceição da Barra, lobster nets, 70–90 m, 2008, ANSP 449798; 4, 41.2, 34.0, 30.8 and 26.9 mm, lv, 1, 27.5 mm, dd, off Guarapari, Espirito Santo, under rocks, 15–20 m, diver, 8/1992, ANSP 449728; 3, 23.6 and 18.9 mm, dd, off Guarapari, 17–18 m, dredged, 8/2003, LC; 1, 35.8 mm, lv, off Guarapari, 17–21 m, diver, LC; 1, 42.5 mm, lv, off Guarapari, 17–21 m, diver, LC; 1, 41.0, lv, off Guarapari, under rocks, 17–21 m, diver, LC; 2, 30.9 and 29.1 mm, lv, off Guarapari, bryozoan/sand bottom, 20–25 m, diver, 12/1993; ANSP 449737; 1, 33.3 mm, lv, off Guarapari, 20–25 m, 12/1993, SC; 2, 22.0 and 18.1 mm, lv, off Guarapari, 20–25 m, diver, 12/1993, ANSP 449730; 1, 27.6 mm, dd, off Guarapari, 20–25 m, diver, 11/2003, LC; 1, 23.7 mm, lv, 3, 19.2, 18.3 and 17.2 mm, dd, off Guarapari, 20–25 m, 11/2003, LC; 1, 32.9 mm, dd, off Guarapari, 20–25 m, 12/2003, LC; 1, 17.2 mm, dd, off Guarapari, 50–60 m, net, 11/2006, LC; 1, 39.0 mm, lv, Ilha Escalvada, off Guarapari, 14–15 m, diver, LC; 1, 30.1 mm, lv, Ilha Escalvada, 15

m, diver, LC; 1, 47.5 mm, lv, Ilha Escalvada, 17 m, diver, LC; 1, 38.8 mm, lv, Ilha Escalvada, 17–21 m, diver, LC; 1, 27.4 mm, dd, Ilha Escalvada, 17–21 m, LC; 2, 37.4 and 32.4 mm, lv, Ilha Escalvada, 17–21 m, diver, LC; 1, 48.9 mm, lv, Ilha Escalvada, 25 m, diver, LC; 2, 34.0 and 30.7 mm, lv, Ilha Escalvada, 25 m, diver, LC; 1, 16.2 mm, dd, "off Ilhas," Guarapari, 18 m; SC; 3, 13.3, 13.2 and 12.1 mm, dd, Boldro Beach, Fernando de Noronha, under rocks, 20–25 m, diver, 2000, ANSP 449731; 1, 17.3 mm, lv, Boldro Beach, Fernando de Noronha, under rocks, 20–25 m, diver, 7/2000, LC; 2, 40.3 and 38.1 mm, lv, off Arrial do Cabo, Estado Rio de Janeiro, 20–25 m, diver, 2002, ANSP 449732; 1, 50.1 mm, lv, off Arrial do Cabo, 30–35 m, diver, 1/2003, LC; 1, 53.1 mm (Figures 55–56), lv, off Arraial do Cabo, under rocks, 30–35 m, ANSP 449735; 1, 51.5 mm, dd, off Arraial do Cabo, 30-35 m, diver, 1/2005, LC; 2, 52.8 and 49.4 mm, dd, off Arraial do Cabo, 30–35 m, diver, 1/2007, LC; 2, 31.3 and 30.4 mm, lv, off Arraial do Cabo, 30–35 m, diver, 3/2007, LC; 1, 27.8 mm, lv, off Arraial do Cabo, under rocks, 30–35 m, diver, 3/2007, LC; 1, 49.7 mm, dd, off Arraial do Cabo, 30–35 m, diver, 5/2011, LC; 1, 32.3 mm, dd, off Cabo Frio, Estado Rio de Janeiro, Brazil, 60–90 m, trawled, LC; 1, 22.9 mm (Figures 59–61), lv, off Cabo Frio, Estado Rio de Janeiro, Brazil, depth 80–100 m, "dredged by local fishermen," ANSP 449799.

Etymology: The species was named for "Ogum, a Macumba god often associated with the sea" (Petuch, 1979).

Distribution: Brazil, off Natal, Estado Rio Grande do Norte (rare, herein); off Salvador, Itapoã and Arquipélago dos Abrolhos, Estado Bahía; Guarapari, Estado Espirito Santo; and Estado Rio de Janeiro (Petuch, 1979; Rios, 1985; Costa, 1991; Costa and Moretzsohn, 1991; Rios, 1994; Vermeij and Snyder, 2003). Most material we examined was from off Alcobaça, Bahía, Guarapari, Espirito Santo, and Arraial do Cabo, Rio de Janeiro. Depth range: intertidal to 20–25 m (Petuch 1979, Sunderland & Sunderland 1994); 14–80 m (herein).

Remarks:We suspected initially that shells identified here as *Pustulatirus ogum* (Petuch, 1979) comprised more than one species. Larger shells (≥ 40 mm sl) agree with the original description and illustration of *Latirus ogum*; they are consistently brown, most have relatively smooth spires and body whorls, and their outer lips are only slightly serrate. Intermediate-sized shells (~30-39 mm sl, most with thin lips indicating immaturity) range from dark reddish brown to yellowish brown; spiral cords are well developed on all whorls and their interspaces extend prominently over the edge of the outer lip, conferring to the edge a distinctly serrate appearance. The cord that marks the abapical edge of the central area of the body whorl is larger than those around it, and an interspace adjacent to that cord usually is larger and more prominent than its neighbors. Small shells (< 30 mm sl) are yellow or light brown, in contrast to the generally darker color of intermediate-sized shells, but spiral cords and serrata are similar to those of the intermediate group. However, all features of individual groups tend to blend with those of other groups, and all groups show similar geographic and bathymetric distributions. Consequently, we found no objective criterion by which to distinguish groups, and we conclude that all shells represent growth stages within a single species.

Vermeij and Snyder (2003: 19, 20) reclassified *Latirus ogum* in *Benimakia* Habe, 1958, because "adult specimens with an intact outer lip usually have a distinct, low labral tooth at the end of an enlarged spiral cord separating the central sector of the last whorl from the concave base," and they figured as *B. ogum* a 35.2 mm immature specimen from 70 km off Alcobaça (ANSP 449736, above). Landau and Vermeij (2012: 88) reconsidered the classification of *Latirus ogum* in *Benimakia*, stating: "M. A. Snyder and we now assign *L. ogum* to the genus *Pustulatirus*" but they provided little explanation for that action. Our rationale for reclassification involves the form of the "distinct, low labral tooth" that prompted Vermeij and Snyder (2003: 20) to place the species in *Benimakia*; that "tooth" is the large serration formed by the interspace between spiral cords (described above; Figure 62). Similar serrata occur on shells of other *Pustulatirus*, but this tooth-like structure is unlike that of *Benimakia* (Figure 63), whose tooth, as in *Leucozonia* (Figure 64), is formed by direct extension of a prominent cord, not by an interspace between cords.

Of ten species classified in *Benimakia* by Vermeij and Snyder (2003) and Snyder and Vermeij (2008), all except '*Benimakia' ogum* are Indo-West Pacific taxa. Habe (1958) described and figured the radula of *B. rhodostoma* (Dunker, 1860), the type species of *Benimakia*, and noted its morphology to resemble that of *Peristernia* Mørch, 1852, in having large and small cusps scattered across the width of lateral teeth whereas lateral cusps of *Latirus* Montfort, 1810, are more equal in size or taper gradually from the inner to the outer cusp edge. Abbott (1958) described and figured a radula of *L. virginensis*, and Bullock (1968) figured radulae that he assigned to *L. virginensis* and *L. attenuatus* (i.e., the *P. virginensis* species complex); those radulae more resemble those of *Latirus* than they do the radulae of *Peristernia* or *Benimakia*. Radulae of the *Peristernia* and *Benimakia* type have

not been reported for any western Atlantic or eastern Pacific species, and it seems unlikely that such radulae will be found among species we assign to *Pustulatirus*.

Vermeij and Snyder (2006) reassigned four living western Atlantic species and several fossils to *Pustulatirus*. The living species were *P. annulatus* (Röding), *P. attenuatus* and *P. virginensis* [collectively the *P. virginensis* species-complex] and *P. eppi* ('Melvill'; = *Latirus eppi auctt., non* Melvill, 1891, = *P. biocellatus*, herein). The larger size and often smooth surface of adult shells suggest *P. ogum* to be more closely related to *P. virginensis* than to other western Atlantic species, but *P. ogum* also much resembles the Panamic *P. mediamericanus*, the type species of *Pustulatirus* (compare Figures 1–3 and 55–56). These two species are among the largest congeners in their respective regions; *P. mediamericanus* attains a size of 91.0 mm sl (Pisor & Poppe 2008) and is exceeded in the tropical eastern Pacific only by *P. praestantior* at 99.9 mm sl (Pisor & Poppe 2008). In the tropical western Atlantic *P. ogum*, at 53.1 mm sl (ANSP 449735) seems to be the largest species of its genus, the next largest being *P. virginensis* at 52.7 mm sl (ANSP 449714). As with shells of *P. mediamericanus*, the broad axial ribs of *P. ogum* assume a relatively lower profile as specimens approach maturity; the smooth surfaces of intermediate spire whorls and the initial portion of the body whorl are supplanted by spiral cords that become prominent near the terminal edge of the shell in each species.

Petuch (1979) speculated that "*Latirus* sp." of Rios (1975) from "Couves Is.," Estado São Paulo, depth 50 m, might be a juvenile shell of *Latirus ogum*, but Rios *et al*. (1994) assigned that specimen to their new species *Latirus devyanae*. The immature shell that Rios (1975) figured as *Latirus* sp. is the same shell that Rios *et al*. (1994) figured as the holotype of *L*. (*Polygona*) *devyanae* in their fig. 3, but that specimen is not the same shell they identified as the holotype in figs. 1 and 2. We believe the latter shell, larger and mature, is the true 36.3-mm holotype of *L. devyanae*. The shell in fig. 3 seems to be their paratype 3, the only shell that Rios *et al*. (1994) cited as from Isole di Couves, São Paulo, depth 50 m. However, Rios (1975) reported dimensions of his Couves Is. shell as 33 x 15 mm whereas Rios *et al*. (1994) cited paratype 3 as 26.8 x 12.0 mm. Given the evident immaturity of the shell, it seems probable that the smaller reported value is correct, but the specimen should be remeasured to confirm its size.

Discussion

We recognize six species of *Pustulatirus* in the tropical western Atlantic (seven including *P. attenuatus*). The species comprise a compact assemblage of taxa that are discretely distributed for the most part, although ranges of *P. utilaensis* and *P. watermanorum* overlap off Honduras and those of *P. biocellatus* and *P. ogum* overlap slightly off northeastern Brazil. Most of the species occur from shallow subtidal depths (≥ 1 m) offshore to about 50 m, which places them among fauna of the inner continental shelf. We examined a few lots of *P. ogum* from 70 to 100 m depths, three lots of *P. virginensis* from 50 to 100 m, and several lots of *P. watermanorum* from between 80 and 160 m, but most records of these species were shallower.

Problems remaining with classification of western Atlantic *Pustulatirus* involve the identity of *P. attenuatus* and the unraveling of the confusing morphological variability of *P. virginensis*. We have seen nothing quite like *P. attenuatus* among specimens we examined, yet the type resembles other western Atlantic species much more than any from the tropical eastern Pacific; its provenance will remain uncertain until similar specimens are discovered. Conversely, the several hundred specimens of *P. virginensis* we examined exhibit many variations, but every form connects to another through a multitude of intermediates.

In addition to Recent taxa, Vermeij and Snyder (2006) reclassified four western Atlantic Neogene species in *Pustulatirus*: *Latirus caloosahatchiensis* Lyons, 1991, late Pliocene, Florida; *Latirus elongatus* Gabb, 1881, early Miocene, Dominican Republic; *Latirus miamiensis* Petuch, 1986b, late Pliocene, Florida; and *Pseudolatirus tumbeziensis* Olsson, 1932, early Miocene, Peru and Venezuela. Landau and Vermeij (2012: 88) reiterated placement of the last species in *Pustulatirus*, reported additional material from the early Miocene Cantaure Formation of Venezuela, illustrated several specimens, and declared the species "the geologically oldest tropical American member of [*Pustulatirus*] as presently understood." Those authors defined *Pustulatirus* as having "a high-spired shell with a long straight siphonal protuberance and low, rounded spiral cords overriding but not nodulating the broad axial ribs ... Most living species have distinctly beaded lirae on the inner side of the outer lip (hence the name)." They afforded no significance to their observation that *P. tumbeziensis* has weakly developed

smooth lirae that lack pustules, but it prompted us to examine six specimens of *P. tumbeziensis* from the Cantaure Formation in the Lyons Collection, one of which we deposited as ANSP-IP 81622 (Figures 65–68).

Except for the relatively high spire (Figures 65–66), it is difficult to find a feature on the Cantaure shells that suggests a relationship to *Pustulatirus*. The siphonal process is unusually long and very slender, unlike the relatively shorter, more broadly tapered processes of *Pustulatirus* species. Lirae on the inside of the inner lip are smooth and uninterrupted on all six shells but are well developed, not weak as stated by previous authors. Many more spiral cords cover each whorl of *P. tumbeziensis*; the cords are distinct but relatively finer than those of *Pustulatirus*, and there are many finer threads between them (Figure 67). This sculpture of many fine cords and finer threads does not occur on any species of *Pustulatirus*. The edge of the outer lip of *P. tumbeziensis* (Figure 67) bears no evidence of serrata that characterize living *Pustulatirus*. Finally, the number and arrangement of columellar plicae on *P. tumbeziensis* is noteworthy: the three smaller specimens have five plicae and the three larger shells have seven (1) or eight (2), the orientation of plicae ranging from oblique to perpendicular to the long axis of the shell. Four of the shells have two plicae abapical to the entrance fold, *i.e.*, situated along the inner wall of the siphonal process (Figure 68), and the other two have one such plica. In contrast, Recent *Pustulatirus* species have three to five oblique columellar plicae but none within the siphonal process. Plicae within the siphon was previously known only among species of the fasciolariine genus *Pleuroploca* Fischer, 1884 (Snyder *et al*. 2012), but plicae of *P. tumbeziensis* do not resemble those of Fasciolariinae. Together, the differences suggest some genus other than *Pustulatirus* for *P. tumbeziensis*, perhaps one as yet un-named.

The other Miocene species, *Latirus elongatus* Gabb, 1881, is undoubtedly a *Pustulatirus* and thus the oldest known species of the genus. The holotype (ANSP-IP 2955) is a 49.4 mm fragment consisting of the final 2 ½ anterior whorls and a long, slender siphonal process. Sculpture is of narrow, rounded ribs that extend from suture to suture and are crossed by many low, equal-sized cords without threads between. There are 13 emergent lirae on the inner side of the outer lip, the adapical 4 lirae being unornamented, the remainder bearing distinct pustules. The columella has 4 oblique plicae and a hint of a fifth adapically, and there are no plicae on the wall of the siphonal canal. Size of the holotype fragment indicates that *P. elongatus* was larger than any of its Recent western Atlantic congeners. Only the relative length and slenderness of its siphonal process differ from those of Recent species.

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