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**Research Note**

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# Paleocene pareorine turritellid gastropods from the Pacific slope of North America

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## ABSTRACT

This paper presents the first detailed study of *Mesalia martinezensis* (Gabb, 1869) and *Mesalia clarki* (Dickerson, 1914a), the only two known pareorine (spout-bearing) turritellid gastropods from the Pacific slope of North America. Both species are redescribed, in light of new morphologic information that also confirms their assignment to genus *Mesalia* Gray, 1847, which we believe to be congeneric with *Sigmesalia* Finlay and Marwick, 1937. New stratigraphic information allows for refinement of the chronologic range of each species. *Mesalia martinezensis* is of early late Paleocene (late Danian) to early late Paleocene (early Thanetian) age and ranges from northern California to northern Baja California. *Mesalia clarki* is of late middle to early late Paleocene age (late Selandian to early Thanetian) age and is known only from California; in southern California it is restricted to a coralline-algal facies. Both species have considerable variability in their spiral sculpture.

*Mesalia* originated during either the Late Cretaceous (Maastrichtian) in northern Africa or the early Paleocene (Danian) in northern Africa and western Iran. It became widespread during the warm (greenhouse) conditions of the Paleocene and Eocene but became geographically restricted during subsequent cooler global conditions. *Mesalia* is an extant genus with possibly six species, and whose total geographic range is in coastal waters in southern Portugal, southern Spain, Mediterranean Sea (primarily the western part), Canary Islands, and the west coast of northern Africa.

## INTRODUCTION

The object of this study was to rectify the identification uncertainities concerning the only two known pareorine (spout-bearing) turritellid gastropod species from shallow-marine rocks on the Pacific slope of North America. They are *Mesalia martinezensis* (Gabb, 1869) and *Mesalia clarki* (Dickerson, 1914a). Most modern workers (e.g., Zinsmeister, 1983) have generally placed both species in *Mesalia* Gray, 1847, but some workers (e.g., Saul, 1983a: fig. 2; Squires, 2003: table 2.4) have been hesitant to unequivocally use the genus name because of inadequate morphologic information about these species. The shape of the aperture of the latter one was unknown until now, and apertural information is critical in distinguishing parerorine gastropods from similar looking turritellids (see "Systematic Paleontology" for morphological comparisons). There has also been the possibility that *Mesalia macreadyi* Waring, 1914, which has commonly been put into synonymy with *M. martinezensis*, could be a distinct species.

We conclude that there are only two species, both belonging to *Mesalia*, which we believe to be congeneric with *Sigmesalia* Finlay and Marwick, 1937. In addition to providing new morphologic information about the study area *Mesalia*, we refine their geographical (Figure 1) and chronologic ranges (Figure 2). Both *M. martinezensis* and *M. clarki* have considerable variability in their spiral sculpture.

*Mesalia* has long been reported (e.g., Cossmann, 1912) as originating during the Late Cretaceous in the region between northern Africa and western Iran. Our review of the literature shows that the genus most likely originated during either the Late Cretaceous (Maastrichtian) or the early Paleocene (Danian) in this Old World region.

Modern systematic studies of *Mesalia* are sorely lacking as are detailed ecologic studies of the few extant species. The classification scheme used here follows that of Bouchet et al. (2005: 249), and morphological terms are taken from Cox (1960). Pacific slope of North America *Turritella* zones are taken from Saul (1983b).

Institutional abbreviations used in the text are: ANSP: Academy of Natural Sciences of Philadelphia; LACM: Natural History Museum of Los Angeles County, Malacology Section; LACMIP: Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; UCMP: University of California, Berkeley, Museum of Paleontology.

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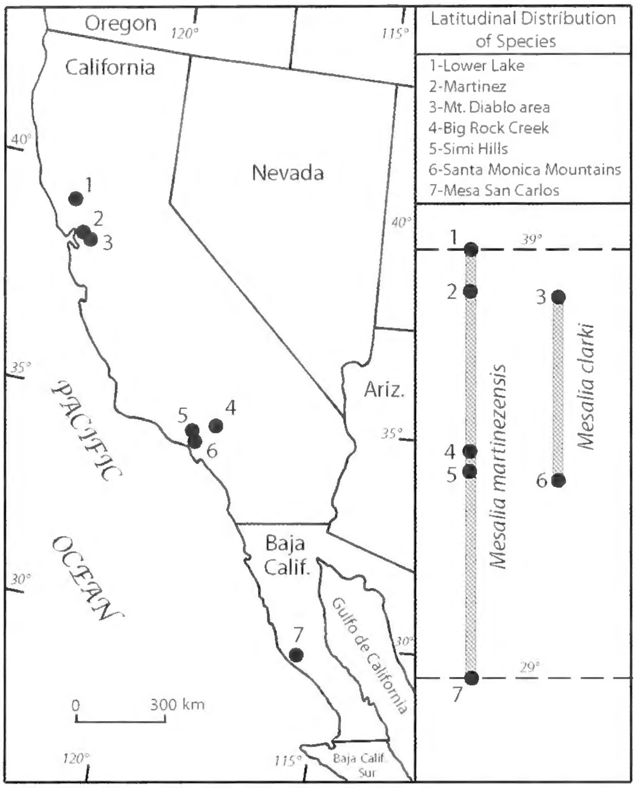


**Figure 1.** Locales and latitudinal distribution of the study area gastropods.

## STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENTS

The geologic ages of the formations and most of the depositional environments of the formations containing the two studied species are mentioned in Squires (1997).

*Mesalia martinezensis* is widespread in the study area (Figure 1) and always found in siltstone or sandstone beds that formed either as storm accumulations of mollusk-rich assemblages in shelfal-marine depths or as localized displaced shallow-marine mollusks in deeper depths. These mollusks commonly include shallow-marine mollusks such as naticid and buccinid gastropods, as well as glycymerid and crassatellid bivalves. All are indicative of normal marine salinities.

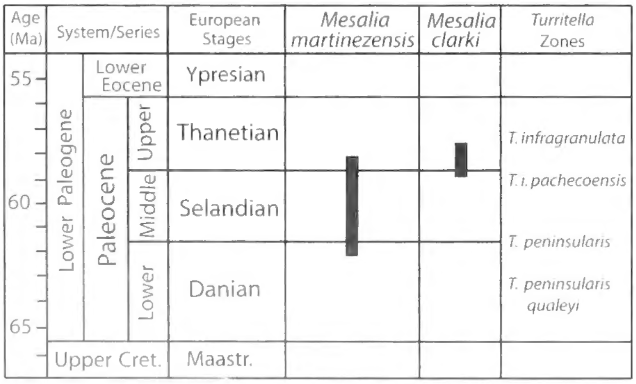


**Figure 2.** Chronostratigraphic position of the study area taxa. Ages of stage boundaries from Gradstein et al. (2004). *Turritella* zones from Saul (1983b).

The type locality of *Mesalia martinezensis* has been generally assigned (e.g., Keen and Bentson, 1944) to the "Martinez Formation" in the vicinity of the city of Martinez, Contra Costa County, northern California (Figure 1). The history of how early workers referred to this originally poorly defined "formation" has been summarized by Mallory (1959). In this present study, we follow the work of Weaver (1953), who refined the stratigraphy of the Paleocene and Eocene formations in the vicinity of the area where the "Martinez group" was first established. He established new stratigraphic names, and the rocks that pertain to the type locality of *M. martinezensis* belong in his Paleocene Vine Hill Sandstone.

*Mesalia clarki* is only known from two locales: 1) its type locality (UCMP loc. 1540, see "Appendix") on the north flank of Mount Diablo, Contra Costa County, northern California, and 2) from the Santa Monica Mountains, Los Angeles County, southern California (Figure 1). Its type locality is near the site of Stewartville, and approximately 24 km east-southeast of the city of Martinez, and, according to Dickerson (1914a: 74), this locality is "300 to 400 ft. above the base of the Martinez in hard, gray-green glauconitic sandstone." Numerous mollusks have been found at this locality (Dickerson, 1914a: 75). They consist of turritellid and buccinid gastropods, crassatellid bivalves, and other shallow-marine species, all indicative of normal marine salinities. *Turritella infragranulata pacheocensis* Stanton, 1896, which is found at this locality, is indicative of the upper middle Paleocene (upper Selandian) (Figure 2). On the geologic map of Brabb et al. (1971), the locality plots within the glauconitic sandstone lower member of the "Martinez" Formation. Megafossils are generally scarce in the "Martinez" Formation in the vicinity of this type locality (E. Brabb, personal commun.), thus, it seems plausible that the fossils probably occur in storm-derived, isolated lenses.

*Mesalia clarki* in the Santa Susana Formation in the Palisades Highlands area of the Santa Monica Mountains, southern California, is always found near outcrops of coralline-algal limestone. Hoots (1931: 91–92, 133–134, pl. 19B) reported that these limestones are resistant, can be cliff forming, weather white, are nodular and irregularly bedded, up to 35 m thick, up to 1200 m in lateral extent, and commonly terminate in an abrupt wall. Additional geologic and/or paleontologic details concerning these limestones are mentioned in Strathearn et al. (1988), Colburn (1996), Squires and Saul (1998), Squires and Kennedy (1998), and Squires and Saul (2001).

At LACMIP loc. 10508, in the Palisades Highlands area, abundant specimens of *M. clarki* are found in a thin coralline-algal-rich micaceous muddy siltstone bed about 1 m stratigraphically below a blocky, coralline-algal-limestone interval approximately 24 m thick. Also found in this bed is the large neritid gastropod *Corsania* (*Januncia*) *rhoga* Saul and Squires, 1997, as well as the bivalves *Plicatula lapidicina* Squires and Saul, 1998, and *Plicatula trailerensis* Squires and Saul, 1998. Occurring in nearby beds in close association with the coralline-algal deposits are the gastropods *Terebralia susana* Squires and Kennedy, 1998, and *Campanile greenellum* Hanna and Hertlein, 1939. All of these aforementioned mollusks indicate very nearshore, tropical to subtropical conditions (Squires and Saul, 1997; Squires and Kennedy, 1998). The latter workers concluded that the coralline-algal limestones, like those at locality 10508, were deposited in a protected bay (no deeper than 40 to 70 m) with warm-algal-limestone buildups associated with shoals on the bay floor. These limestone buildups are very similar in lithology and sedimentologic/tectonic setting to limestones in the Paleocene Sepultura and Bahia Ballenas formations in northern Baja California (Abbott et al., 1995), as well as similar to limestones in the upper Paleocene to lower middle Eocene Sierra Blanca Limestone in Santa Barbara County, southern California. These limestones were deposited when tectonic plate-edge strain in the fore-arc basin caused local basement highs to form within the otherwise deeper marine environment (Whidden et al., 1995; Abbott et al., 1995). It is likely that the Santa Susana Formation coralline-algal limestones formed under similar conditions.

Although *Mesalia clarki* and *Mesalia martinezensis* both occur in the Santa Susana Formation in the Santa Monica Mountains, southern California, they never occur together in the same beds. *Mesalia martinezensis* is not associated with the coralline-algal facies there or anywhere else in the study area.

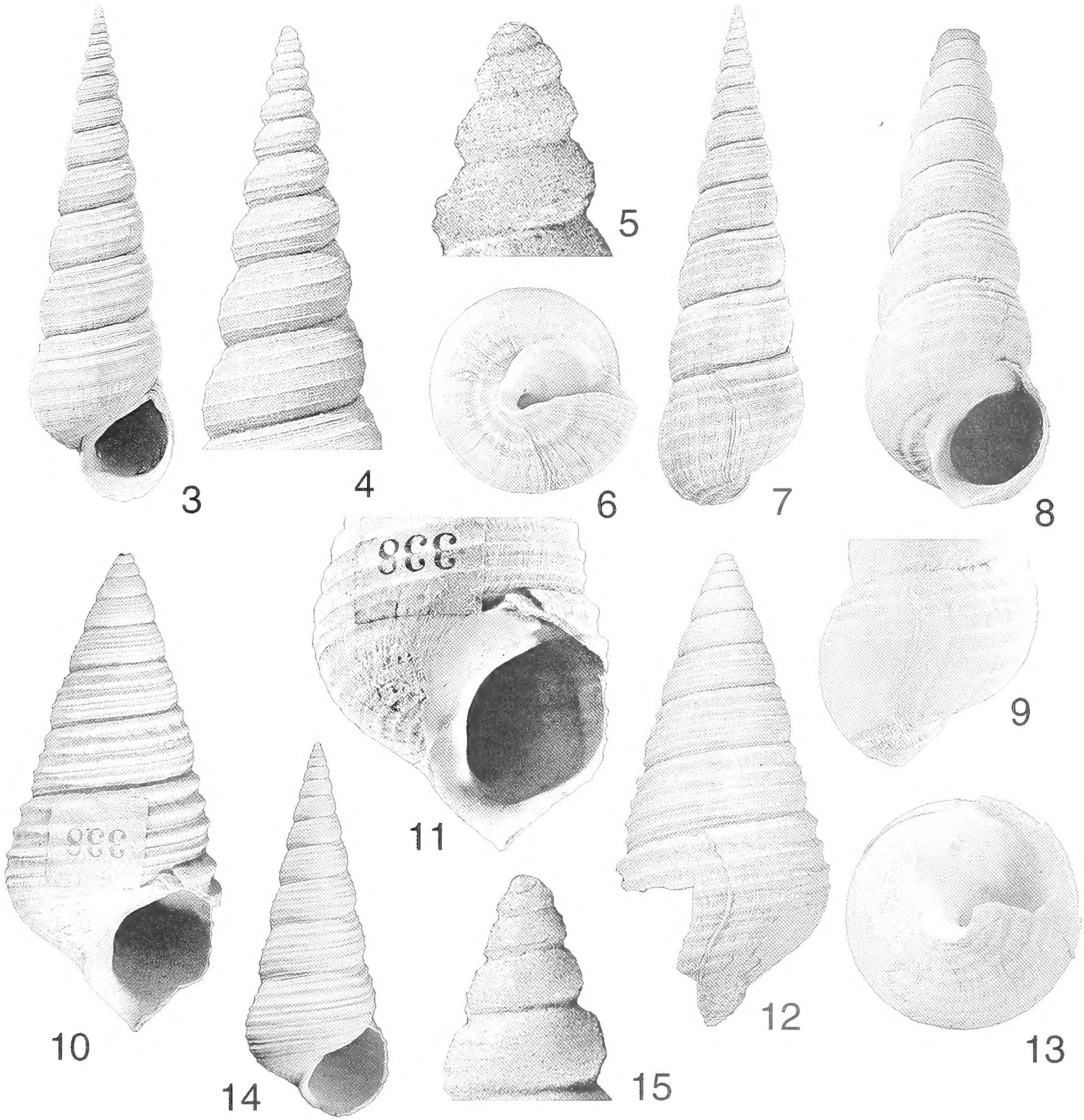
## PALEOBIOGEOGRAPHIC IMPLICATIONS

Kiel and Bandel (2004: 120, fig. 7I) reported two specimens of *Mesalia* cf. *multilineata* (J. Müller, 1851) from Cenomanian strata at the Kasssenberg quarry in Germany. If these specimens actually belong to *Mesalia*, they would be the geologically oldest. The conical-turriculate shell with convex whorls bearing strong spiral ribs does resemble *Mesalia*, but there are no specimens with an intact aperture nor with a protoconch. *Turritella multilineata* J. Müller (1851: 29, pl. 4, figs. 4, 6) was originally reported from the lower Campanian Aachen strata of Germany, thus, it is considerably younger than the Kassenberg quarry material. *Turritella multilineata* was also figured by G. Müller (1898: 97, pl. 13, figs. 4, 5), who reported it from middle Santonian to lower Campanian strata at Braunschweig/Ilsede, Germany. There is also a mention of *T. multilineata* in Kollmann and Odin (2001: 441), and they also consider this Campanian species to belong to genus *Turritella*. The pleural angle of J. Müller's figure is much narrower than that of Kiel and Bandel (2004), and in our opinion, Kiel and Bandel's *M.* cf. *M. multilineata* (J. Müller) does not look like J. Müller's species. Kiel and Bandel (2004) tentatively synonymized J. Müller's specimens and G. Müller's specimens with their Kassenberg quarry specimens. We believe, however, that Kiel and Bandel's Cenomanian specimens have nothing to do with *T. multilineata* and represent, at best, a very questionable *Mesalia*. More specimens of this possible *Mesalia* from the Cenomanian of Germany are needed in order to determine its generic assignment.

Cossmann (1912: 126) reported the chronologic range of *Mesalia* to be Late Cretaceous (Turonian) to Recent, as did Wenz (1939), who apparently simply reiterated Cossmann's findings. We were unable, however, to corroborate any of Cossmann's Cretaceous occurrences. He reported *Mesalia gazellensis* Whitfield (1891: 424, pl. 9, fig. 10) as being from the Turonian of Syria, but the aperture of this species is unknown. In addition, the sculpture is obsolete, which is unlike *Mesalia*.

Cossmann (1912: 126) listed five *Mesalia* species of Late Cretaceous (Senonian) age, and these are discussed in the following sentences. *Arcotia indica* Stoliczka (1868: 215, 469, pl. 16, figs. 12, 12a; pl. 19, fig 6) from southern India is not a *Mesalia*. This species is also discussed later under "Systematic Paleontology." Specimens of *Turritella ventricosa* Forbes (1846: 123, pl. 13, fig. 3; Stoliczka, 1868: 227, pl. 17, fig. 15) from southern India are missing the aperture. *Turritella martinezensis* Gabb (1869: 159, pl. 28, fig. 51) from California is not of Cretaceous age. *Mesalia nettoana* White (1887: 164–165, p. 18, figs. 3, 4) from the Maria Farinha beds in Brazil is Paleocene age. *Mesalia hebe* White (1887: 165, pl. 18, fig. 5), also from Brazil, looks like a juvenile specimen of *M. nettoana*.

Cossmann (1912: 126) also listed two Late Cretaceous (Maastrichtian) species. The first one is *Mesalia jovisammonis* (Quaas, 1902: 256, pl. 26, figs. 18–20), which Quaas reported, in a very generalized way, to be associated with the *Exogyra overwegi* biozone at Ammonite Hill in the Great Sand Sea in western Egypt. This biozone can also be recognized in the Maastrichtian (but not latest Maastrichtian) part of the Ammonite Hill Member of the Campanian to Paleocene Dakhla Formation in western Egypt (Barthel and Herrmann-Degen, 1981). Tantawy et al. (2001) assigned this member an early to early late Maastrichtian age, based on planktic foraminifera, calcareous nannofossils, and macrofossils. They also determined, however, that the entire formation ranges in age from early Maastrichtian to early Danian. Immediately above the widespread K/T disconformity in the region, a sedimentologically complex sequence marks the lower Danian Bir Abu Minquar horizon, which contains a mixture of Maastrichtian (reworked) and Danian fossils, including both microfossil and macrofossil species (e.g., including some ammonites.). Unfortunately, Quaas did not provide any information as to where exactly in the stratigraphic section he collected the specimens of *M. jovisammonis*. His specimens were lost, so it is not possible to match their rock matrix to actual outcrops. Recollecting of this gastropod is necessary to decipher its exact geologic age.



**Figures 3–15.** Type species of *Mesalia* and *Sigmesalia*, plus comparative pictures of *Mesalia solida* (Deshayes, 1861). Specimens coated with ammonium chloride. **3–9. Mesalia mesal** (Adanson, 1757), Baie de Hann, Senegal, West Africa (Recent). **3–7.** Hypotype LACM 173163. **3.** Apertural view, height 45 mm, diameter 15 mm. **4.** Tip of specimen shown in previous figure, height 14 mm, diameter 5.5 mm. **5.** Protoconch and earliest spire whorls, apertural/ right-lateral view, height 1 mm, diameter 0.7 mm. **6.** Base, diameter 15.6 mm. **7.** Abapertural view, height 45 mm, diameter 15 mm. **8–9.** Hypotype LACM 173164. **8.** Oblique apertural view, height 51 mm, diameter 16.3 mm. **9.** Close-up of abapertural view of last whorl, diameter 17.2 mm. **10–13. Mesalia koeneni** (Le Renard, 1994), LACMIP hypotype 13397, Grignon, Paris Basin, France (middle Eocene, Lutetian Stage), height 45.8 mm, diameter 20.3 mm. **10.** Apertural view. **11.** Close-up of aperture. **12.** Right-lateral view (outer lip broken). **13.** Base. **14–15. Mesalia solida** (Deshayes, 1861), hypotype LACMIP 13398, Le Guépelle, Paris Basin, France (late Eocene). **14.** Apertural view, height 21.6 mm, diameter 8.1 mm. **15.** Protoconch and earliest spire whorls, apertural to slightly right-lateral view, height 1 mm, diameter 0.7 mm.

Abbass (1963: 39–40, pl. 2, figs. 20–22) illustrated *M. jovisammonis* from eastern Egypt and referred to it as *Mesalia* (*Woodsalia*) *jovisammonis* of Maastrichtian age. He did not provide, however, any discussion as to how this age was determined.

*Mesalia* cf. *M. multisulcata* (Lamarck 1804), reported by Serra (1937: 313–315, pl. 16, figs. 12, 12a, 13) from near Tripoli, Libya, looks like it might be conspecific with *Mesalia jovisammonis*. Serra provided no detailed stratigraphic or geologic age information.

The second species that Cossmann (1912) listed from the Maastrichtian is *Mesalia fasciata* (Lamarck, 1804) from Iran. Cossmann based this occurrence on work by Douvillé (1904: 329–330, pl. 47, figs. 23–27), who reported *M. fasciata* from the "Couches à Cérithes" beds in the Luristan region in west-central Iran. Douvillé (1904) believed that these Iranian specimens of *M. fasciata*, whose type locality is in middle Eocene (Lutetian Stage) strata at Grignon in Paris Basin, France (Eames, 1952: 34), are of Maastrichtian age, but the "Couches a Cérithes" beds contain the bivalve "*Cardita*" *beaumonti* d'Archiac and Haime, 1854, which is diagnostic of earliest Danian age in Iran and Pakistan (Douvillé, 1928; Eames, 1952; Davies, 1975). *Mesalia fasciata* is long-ranged geologically (early Paleocene to late Eocene) and widespread geographically (western Europe to Pakistan) (Eames, 1952).

Another *Mesalia* that needs investigation as to its precise stratigraphic position and geologic age is *Mesalia foucheri* Pervinquière (1912: 44, pl. 3, figs. 6–15), from the Ghadames (Garat Temblili) region in Tunisia, northern Africa. Pervinquière (1912: 336) reported the species as being of Maastricthian age, but no critical geologic details are provided. He did differentiate between Maastrichtian and Danian fossils; thus, like in nearby Egypt and Libya, the stratigraphic section containing *M. foucheri* and other macrofossils in Tunisia, also spans the K/T boundary.

Two species of so-called *Woodsalia* Olsson, 1929, from Upper Cretaceous (Campanian?) strata in northwestern Peru (Olsson, 1944) might eventually be placed in *Mesalia*, once their apertures become known. They are: *Woodsalia paitana* Olsson (1944: 69–70, pl. 11, fig. 5) and *Woodsalia paitana robusta* Olsson (1944: 70, pl. 11, figs. 3, 9).

The so-called *Mesalia* (*Mesalia*) *mauryae* Allison (1955: 414–415, pl. 41, fig. 3; Perrilliat, 1989: 149, fig. 51h) from the upper Aptian upper member of the Alisitos Formation, Punta China region, Baja California, Mexico, is, according to Squires and Saul (2006), *Turritella seriatimgranulata* Roemer, 1849.

In addition to the above-mentioned Old World Danian species of *Mesalia*, three New World Danian species are known from the Gulf Coast of the southeastern United States. They are from the Clayton Formation (Palmer and Brann, 1966), which is of earliest Danian age (Dockery, 1986). The three species are: *Mesalia allentonensis* (Aldrich, 1894: 246–247, pl. 13, figs. 4a, 4b, 6; Stenzel and Turner, 1942: card 110); *Mesalia hardemanensis* (Gabb, 1860: 392, pl. 68, fig. 15; Stenzel and Turner, 1942: card 116); and *Mesalia pumila* (Gabb, 1860: 392, pl. 68, fig. 14; Stenzel and Turner, 1942: card 118).

In summary, our search of the literature revealed that *Mesalia* most likely originated during either the Maastrichtian in northern Africa or the early Paleocene (Danian) in northern Africa and western Iran. During the Danian it spread quickly to the Gulf Coast of the United States by means of westward-flowing ocean currents emanating from the western Tethyan region. These currents, which existed during the Late Cretaceous (Gordon, 1973; Johnson, 1999) and continued into the Paleocene and Eocene (Saul, 1986; Squires, 1987), were part of a circumglobal-tropical current that contributed to a widespread dispersal of marine biota (Haq, 1981). By the late Danian, it reached California and northern Baja California, Mexico, as well as Belgium (Cox, 1930; Glibert, 1973). By middle Paleocene, it reached Greenland (Kollmann and Peel, 1983), and by the late Paleocene, it reached Nigeria (Adegoke, 1977). During the Paleocene and Eocene, *Mesalia* reached its peak diversity and became most widespread, with occurrences mainly in the Old World western Tethys Sea region. We did not detect, however, any reported occurrences in Australia, New Zealand, Japan, or Antarctica. The Paris Basin of France (see Cossmann and Pissarro, 1910–1913), southwestern Nigeria (Adegoke, 1977), and the Gulf Coast of the United States (Stenzel and Turner, 1940, 1942; Palmer and Brann, 1966) are the principal areas in which numerous species of *Mesalia* have been recognized. Some species became very widespread. For example, as mentioned earlier, *Mesalia fasciata* ranged from the Paris Basin, France to Pakistan (Eames, 1952). After the warm greenhouse conditions that existed during the Eocene, *Mesalia* was much reduced in its distribution and mainly occurred in what is now the Mediterranean Sea region (Cossmann, 1912).

## MODERN *MESALIA*

*Mesalia* is extant and review of the scant literature, as well as use of the internet (note: <http://www.alboranshells.com/turritellidae> was particularly helpful), revealed as many as possibly six species. The they are the following: *M. mesal* (Adanson, 1757), *M. brevialis* Lamarck, 1822; *M. varia* Kiener, 1843; *M. opalina* Adams and Reeve, 1850; *M. freytagi* von Maltzan, 1884; and *M. flammifera* Locard, 1897, which includes the subspecies *M. flammifera flammifera* Locard, 1897 and *M. flammifera simplex* Locard, 1897. There is much confusion as to exactly how many species there are, and potential synonyms need to be resolved. For example, some workers (e.g., Smith, 1915; Bowles, 1939) equated *M. mesal* with *M. brevialis*, but other workers (e.g., Advovini and Cossignani, 2004) separated them. Bowles (1939) gave a thorough review of the nomenclatural history of *Mesalia brevialis*.

A comprehensive malacological study of the modern species of *Mesalia* is greatly needed. Because of the uncertainties stemming from the poorly known systematics, it is confusing to try to determine which species is found where. We were able to establish with certainty (see references below), however, that modern *Mesalia* is only found in the Atlantic coastal areas of southern Portugal, southwestern Spain, Morocco, Canary Islands, Western Sahara, Mauritania, Senegal, and Guinea, as well as in the westernmost Mediterranean Sea, particularly in the Alboran Sea (i.e., Strait of Gibraltar to southern Spain on the north and Morocco on the south) and the Aegean Sea region of western Turkey.

*Mesalia mesal* and *M. brevialis* have the widest distribution. *Mesalia mesal* has been reported from the Algarve region of southern Portugal, the Algeciras region of southwestern Spain, and the Alboran Sea (Poppe and Goto, 1991), the Canary Islands (Macedo and Borges, 1999), Senegal (Bouchet, 1977; Ardovini and Cossignani, 2004), and western Turkey (Demir, 2003). *Mesalia brevialis* has been reported from the Algarve region of southern Portugal (Afonso et al., 2000; Alves et al., 2003), southwestern Spain and the Alboran Sea (Hidalgo, 1917), Senegal (Ardovini and Cossignani, 2004), and Guinea (Pasteur-Humbert, 1962). *Mesalia opalina* has been reported from the Canary Islands and Morocco (Poppe and Goto, 1991), as well as from Mauritania (Ardovini and Cossignani, 2004). The other modern species/subspecies of *Mesalia* are apparently restricted to the northwestern coast of Africa (Ardovini and Cossignani, 2004).

*Mesalia melanioides* Reeve, 1849, was reported (Smith, 1915) to be from West Australia, but this species is now the type species of *Neodiastoma* Cotton, 1932, which differs from *Mesalia* by having axial sculpture on the early spire. Marwick (1957) summarized the systematics of *Neodiastoma* and classified it as a pareorine.

*Mesalia* is found today on both muddy and sandy bottoms in coastal waters ranging in depth from lower intertidal to 20 m (Hidalgo, 1917; Pasteur-Humbert, 1962; Poppe and Goto, 1991; Afonso et al., 2000; Demir, 2003; Alves et al., 2003). Bouchet (1977) reported that *M. mesal*, although not common there, can be found in the seaward part of mangrove-swamp systems along the coast of Senegal. Specimen LACM 17316 (Figures 3–7) of *M. mesal* was collected in approximately 5 m depth, on sand and rubble in Senegal.

Large numbers of *M. mesal* have been reported (Afonso et al., 2000) as almost always being partially infaunal (with their apices pointed upward) when found on exposed low-tide mud flats on the inner lagoon sides of islands within the Rio Formosa coastal-lagoon system of southern Portugal.

The modern ecological parameters mentioned above are not totally reliable for fossil *Mesalia* because preferences for substrate and depth of water might have possibly changed over time. In addition, the fossil occurrences of *Mesalia* had a pan-Tethyan distribution, whereas the modern occurrences have contracted primarily to the Iberian Peninsula, Alboran Sea, and northwestern Africa.

## SYSTEMATIC PALEONTOLOGY

Superfamily Cerithioidea Fleming, 1822
Family Turritellidae Lovén, 1847

**Discussion:** Allmon (1996: 9–12, table 1) thoroughly reviewed the history of the classification of turritellid gastropods and listed the five subfamilies and all the genera/subgenera within each subfamily. These subfamilies are: Turritellinae Lóven, 1847; Protominae Marwick, 1957; Pareorinae Finlay and Marwick, 1937; Vermiculariinae Lamarck, 1799; and Turritellopsinae Marwick, 1957. Bouchet et al. (2005) included the first four of these subfamilies, but removed Turritellopsinae. Instead, they included subfamily Orectospirinae Habe, 1955.

Subfamily Pareorinae Finlay and Marwick, 1937

**Discussion:** Pareorine turritellids are characterized from the other subfamilies of family Turritellidae by having an aperture obliquely effuse over the anterior end of the columella and forming a sinus (short spout), with the adapical margin of the sinus usually making a spiral ridge on the columella (Marwick, 1957).

*Mesalia* can be readily identified if its aperture is intact, but when it is missing, workers have commonly misassigned it to the similar looking genus "*Turritella*" Lamarck, 1799, sensu lato, a group comprising at least 35 genera and subgenera names (Allmon, 1996), all of which are turritellines whose apertures do not have a sinus (short spout) at the anterior end of the aperture nor have a spiral ridge on the columella. In addition, according to Smith (1915), the corneous operculum of *Mesalia* is paucispiral and not multispiral, as in "*Turritella*," but this later distinction is not useful when studying fossil species.

Ten pareorine genera were listed by Marwick (1957), who also provided illustrations of the growth-line traces of some of these genera. Comparative information about the stratigraphic range, growth-line details, whorl profile, and protoconch shape of most of these genera was given by Allmon (1996: table 1).

Genus *Mesalia* Gray (*nomen nudum*, 1840), 1847

**Type Species:** *Cerithium mesal* Adanson, 1757 [=*Turritella mesal* Deshayes, 1843], by original designation; Recent, southern Portugal, southwestern Spain, Alboran Sea, Canary Islands, Senegal, and western Turkey.

**Description:** Small to large (up to approximately 95 mm shell height), turritelliform, slender to conical rotund. Pleural angle ranges from 15° to 41°. Protoconch conical, small, smooth, and approximately two whorls. Protoconch to teleoconch transition gradual. Teleoconch whorls up to 16, whorl sides convex to flattish/concave. Sculpture on early juvenile teleoconch whorls variable, ranging from nearly smooth or with very fine, unicostate, bicostate, or tricostate spiral lirae; sculpture on adult whorls highly variable, ranging from smooth to numerous, weak to moderately strong closely spaced spiral ribs, but less commonly with fewer and more prominent spiral ribs. Growth lines parasigmoidal on last whorl (including base); lateral sinus variable in amount of concavity (flexure). Aperture with shallow effuse spout, ranging from somewhat constrained to broad. Adapical edge of spout usually forms weak spiral ridge that continues onto columella.

**Discussion:** *Mesaliopsis* Thiele, 1929 [type species: *Mesalia opalina* (Adams and Reeve, 1850)], Recent, was reported by Wenz (1939) to be a subgenus of *Mesalia*, but future work might show it to be synonymous with *Mesalia*.

*Mesalia* somewhat resembles *Lithotrochus* Conrad, 1855, of Jurassic age from Chile, South America. Cossmann (1912: 125) reported *Lithotrochus* to be a junior synonym of *Mesalia*, but Wenz (1938: 280, fig. 596) and Cox (1960: I248–I249, fig. 159,11) believed *Lithotrochus* to be a trochid. It is an extraordinarly large gastropod (height 125 mm) with a wide pleural angle, domed upper spire, turritelliform shape, anteriorly carinate whorls, and relatively few spiral ribs. Details of its aperture are unknown.

Cossmann (1912: 125) also reported *Lithotrochus* to be a junior synonym of *Arcotia* Stoliczka, 1868, whose type species, *Arcotia indica* Stoliczka (1868: 215, 469, pl. 16, figs. 12, 12a; pl. 19, fig. 6) is from Upper Cretaceous (Trichinopoly Group) strata near the town of Alundanapooram, southern India. According to Sundaram et al. (2001: fig. 3), this town's name is also referred to as Alundalippur and, from information in their map, this town is underlain by the Kulakkalnattam Formation of Turonian age. Wenz (1939) synonymized *Arcotia* with *Mesalia*. Finlay and Marwick (1937) reviewed the morphology of *Arcotia* and reported that, based on its straight growth lines and open umbilicus, this genus is not a synonym of *Mesalia*. They reported, furthermore, that *Aroctia* appears to be a mathildid. Bandel (2000) came to the same conclusion.

*Mesalia* is similar to the pareorine *Woodsalia* Olsson 1929, whose type species, *Woodsalia negritosensis* Olsson (1929: 13–15, pl. 4, figs. 5, 6) is from lower Eocene rocks in northwestern Peru. Woods (1922: 78–79, pl. 7, figs. 5–7; pl. 8, figs. 1–3) and Wenz (1939: 651, fig. 1852, two views) also illustrated this species. The full shape of the aperture of this Peruvian gastropod, however, is not known.

Genus *Sigmesalia* Finlay and Marwick, 1937, was originally erected to accommodate a group of Eocene gastropods from the Paris Basin, France that were previously identified as *Mesalia*. There has been no consensus as to whether or not *Sigmesalia* is a distinct genus. Marwick (1957) reported it to be a separate genus, as did Le Renard (1994). Eames (1952) reported it to be a subgenus of *Mesalia*, and Palmer and Brann (1966) reported *Sigmesalia* to be synonymous with *Mesalia*.

Various views of representative specimens of the type species of *Mesalia* are illustrated in Figures 3–9, and various views of a representative specimen of the type species of *Sigmesalia* are illustrated in Figures 10–13. Its type species, *Sigmesalia koeneni* Le Renard, 1994 [new name for *Turritella sulcata* Lamarck, 1804 (original designation), *non* Bosc, 1801], is of middle Eocene (Lutetian) age and from Paris Basin, France. Finlay and Marwick (1937) stated that the aperture and growth lines of the type species of *Mesalia* seem to be generically different than those of the Paris Basin shells, but they did not provide any details. Davies (1971: 312, figs. 677a, 677b) mentioned that the growth lines of *Sigmesalia* have a more flexed outer lip sinus than does *Mesalia*. According to Marwick (1957: 163), *Sigmesalia* differs from *Mesalia* by usually having a wider pleural angle. The following paragraphs deal with our observations concerning these proposed diagnostic features of *Sigmesalia*.

Inspection of representative specimens of several of the Eocene Paris Basin species, including the type species of *Sigmesalia*, stored in the LACMIP collection, as well as inspection of photographs of 17 Paris Basin species (see Cossmann and Pissarro, 1910–1913: pl. 21, figs. 126–1 to 126–15), revealed variability in the shape of the aperture of *Sigmesalia*. For example, the aperture of *Sigmesalia incerta* (Deshayes, 1832; Cossmann and Pissarro, 1910–1913: pl. 21: fig. 126–4, two views) is similar to that of *M. mesal*, in that the spout is broad and not well constrained. The aperture of *Sigmesalia koeneni* however, is better developed (Cossmann and Pissarro, 1910–1913: pl. 21, fig. 126–15).

The amount of flexure of the outer lip sinus is basically similar in all the Eocene Paris Basin species, although *Mesalia solida* (Deshayes, 1861) does show some variability. The amount of flexure of this feature is variable in *M. mesal* and can be similar to the amount seen on Eocene Paris Basin species. Variability in the amount of flexure for both the Eocene and modern *Mesalia* shells can also occur in proximity of growth checks and breakages of the outer lip incurred during the life of the gastropod.

The pleural angle of the Eocene Paris Basin shells is quite variable, ranging from 21° to 41°, but the low end of this range [e.g., *Mesalia ecki* (Laubrière, 1881; Cossmann and Pissarro, 1910–1913: pl. 21, fig. 126–2)] is very close to the value (16° to 18°) on *M. mesal*. *Sigmesalia koeneni* has one of widest pleural angles (41°; see Figures 10 and 12). For comparative purposes, an illustration (Figure 14) is provided for *Sigmesalia solida*. It has a relatively narrow pleural angle of 25°, more like that found on *M. mesal* (Figures 3, 4, and 7).

Other morphologic features that are variable on the Eocene Paris Basin shells are strength and number of spiral ribs, pattern of development of sculpture on the early juvenile teleoconch whorls, and degree of indentation of the suture. Even the strength of the spiral ridge (Figure 10) on the columella is variable. *Mesalia mesal* possesses a spiral ridge on the columella, as do most specimens of *Sigmesalia koeneni* (compare Figures 8 and 11)

A few species of *Sigmesalia* are similar to *Mesalia* in having a relatively narrow pleural angle and bicostate sculpture on the early juvenile whorls but not on the adult whorls. They are the following: *Sigmesalia instabilis* (Briart and Cornet, 1873: 86, pl. 12, figs. 9a–9b) of early Paleocene (Danian) age from Belgium; *Sigmesalia salvani* (Adegoke, 1977: 86–88, pl. 14, figs. 10–16) of Paleocene age from Nigeria; and *Sigmesalia fasciata* (Lamarck, 1804: 217) from Eocene strata in France, Belgium, and Pakistan (Cossmann and Pisarro, 1910–1913; Cox, 1930; Eames, 1952); *Sigmesalia pagoda* (Cox, 1930: 160–161, pl. 18, figs. 6a–b, 7a–b) from Eocene strata in Pakistan; *Sigmesalia biplicata* (Bowles, 1939: 328, pl. 34, figs. 6, 8) from Paleocene strata in Alabama; and *Sigmesalia gomin* (Bowles, 1939: 326–327, pl. 33, fig. 9) from Paleocene strata in South Carolina.

The protoconchs of *Mesalia mesal* and *Sigmesalia solida* are very similar (compare Figures 5 and 15); both are small, smooth, have essentially the same shape, and the transition to the teleoconch is gradual.

In summary, we found that the morphologic features of the Eocene Paris Basin shells are variable. We could find no reliable, constant morphologic characters to distinguish *Mesalia* from *Sigmesalia*; hence, we regard them as congeneric.

### *Mesalia martinezensis* (Gabb, 1869)
(Figures 16–23)

*Turritella martinezensis* Gabb, 1869: 169–170, 228, pl. 28, fig. 51; Dickerson, 1914a: pl. 13, fig. 10; Waring, 1917: 100, pl. 14, fig. 5.

*Turritella maccreadyi* Waring, 1914: 783; Waring, 1915: fig. 15 [not fig. 14]; Waring 1917: 87–88, pl. 12, fig. 10.

*Mesalia maccreadyi* (Waring).—Paredes-Mejia, 1989: 176–177, pl. 3, figs. 3–6.

*Mesalia martinezensis* (Gabb).—Cossmann, 1912: 126; Stewart, 1927: 353–354, pl. 25, fig. 1; Schenck and Keen, 1940: pl. 20, fig. 5; Merriam, 1941: 127–128, pl. 39, figs. 1–5, 7; Zinsmeister, 1974: 118–119, pl. 12, figs. 5, 9; Zinsmeister, 1983: pl. 2, fig. 14; Paredes-Mejia, 1989: 173–176, pl. 3, figs. 7–10; Saul, 1983a: text-fig. 2, pl. 1, fig. 2.

*Mesalia clarki* (Dickerson).—Zinsmeister, 1983: pl. 2, fig. 13.

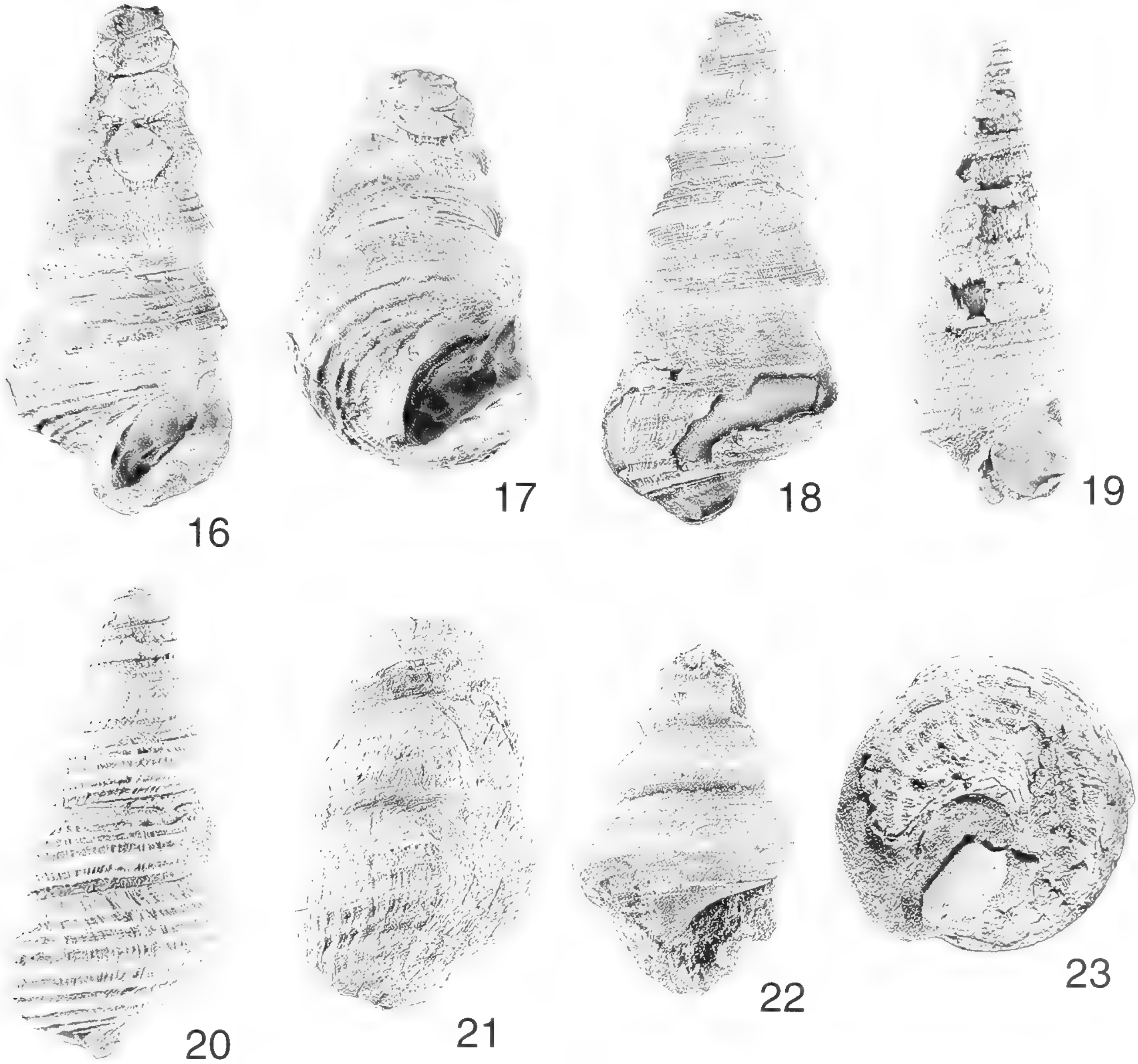
**Description:** Large (up to approximately 95 mm height). Turritelliform. Pleural angle approximately 20°. Protoconch unknown. Teleoconch up to 12 whorls, increasing rapidly in size from the apex. Suture slightly impressed. Sculpture consisting only of spiral ribs of differing strength but dominated by carina located anteriorly; ribs generally becoming stronger with growth; spiral threads on interspaces and on carina surface. Carina usually strongly angulate but can be rounded or even subdued. Posterior to carina, several widely spaced spiral ribs of variable strength occur, ranging from tertiaries to primaries: two ribs on uppermost spire, three to four on upper spire, and one to three on lower spire. Anterior to carina, several spiral ribs of variable strength occur, ranging from tertiaries to primaries: approximately five ribs on upper spire and one to two ribs (both occasionally quite prominent) on lower spire. Last whorl with three primaries, both posterior and anterior to carina. Base with three secondaries, anteriormost one weak; ribs obsolete on short neck. Aperture relatively small, D-shaped; columella relatively broad, smooth; spout effuse and short with anterior end projecting slightly; growth-line trace of last whorl (including base) parasigmoidal, with lateral sinus flexure strongest in vicinity of carina.

**Holotype:** ANSP 4344, height 57 mm, diameter 23 mm.

**Type Locality:** Martinez, northern California (details not given).

**Geologic Range:** Late early Paleocene to early late Paleocene (near the Danian-Selandian boundary to early Thanetian).

**Distribution:** DANIAN = *Turritella peninsularis qualeyi* Zone: lower San Francisquito Formation, Warm Springs Mountain, Los Angeles County, southern California (new stratigraphic occurrence, LACMIP loc. 21581). NEAR THE DANIAN-SELANDIAN BOUNDARY = *Turritella peninsularis qualeyi* Zone transitional with *Turritella peninsularis* Zone: Martinez Formation, Herndon Creek east of Lower Lake, Lake County, northern California (Stanton, 1896 [faunal list]; Dickerson, 1914a; Merriam, 1941); upper Las Virgenes Sandstone, Simi Hills, Ventura County, southern California (Waring, 1917; Nelson, 1925 [faunal list]; Merriam, 1941; Zinsmeister, 1983; Saul, 1983a). PROBABLY NEAR THE DANIAN-SELANDIAN BOUNDARY: Reworked specimens in Santa Susana Formation, Poison Oak Canyon, north side Simi Valley, Los Angeles County, southern California (new stratigraphic occurrence, LACMIP loc. 21554); Reworked specimens in Stokes Canyon Breccia Member of the middle Miocene Calabasas Formation, Stokes Canyon, Santa Monica Mountains, Ventura County (new stratigraphic occurrence, LACMIP loc. 25281). SELANDIAN = *Turritella peninsularis* Zone: Lower Vine Hill Sandstone, Martinez area, Contra Costa County, northern California (Weaver, 1953 [faunal list]); lower San Francisquito Formation, Pinyon Ridge east of Big Rock Creek, Valymero area, Antelope Valley, Los Angeles County, southern California (Dickerson, 1914b [faunal list]; Merriam, 1941; Kooser, 1980 [faunal list]); lower Santa Susana Formation (= "Martinez marine member" of Nelson, 1925 [faunal list]), Simi Hills, Ventura County, southern California (Kew, 1923 [faunal list]; Nelson, 1925 [faunal list]; Zinsmeister, 1983; Saul, 1983a). LOWER THANETIAN = *Turritella infragranulata* Zone: Upper Vine Hill Sandstone, Martinez area, Contra Costa County, northern California (Weaver, 1953 [faunal list]); upper Santa Susana Formation, Palisades Highlands, Santa Monica Mountains, Los Angeles County, southern California (new stratigraphic occurrence, LACMIP locs. 7060 and 11717); Sepultura Formation, Mesa San Carlos, northern Baja California, Mexico (Paredes-Mejia, 1989).



**Figures 16–23.** *Mesalia martinezensis* (Gabb, 1869). Specimens coated with ammonium chloride. **16–18.** Hypotype LACMIP 13399, height 58 mm, diameter 25.4 mm. **16.** Apertural view. **17.** Oblique apertural view. **18.** Abapertural view. **19.** Hypotype LACMIP 13400, LACMIP loc. 22557, apertural view, height 36.3 mm, diameter 14.1 mm **20.** Hypotype LACMIP 13401, LACMIP loc. 21607, abapertural view, height 38.3 mm, diameter 19.3 mm. **21.** Hypotype LACMIP 13402, LACMIP loc. 22698, abapertural view, height 33.9 mm, diameter 21.6 mm. **22.** Hypotype LACMIP 13403, LACMIP loc. 26897, apertural view, height 10.6 mm, diameter 6.5 mm. **23.** Hypotype LACMIP 13404, LACMIP loc. 22330, base, diameter 17.2 mm.

**Discussion:** The largest specimens of this species occur in the lower San Francisquito Formation, Pinyon Ridge east of Big Rock Creek, Valymero area, Antelope Valley, Los Angeles County, southern California.

There is considerable variability in the strength of the spiral ribs on *M. martinezensis*. Most specimens are carinate on all whorls, including the last whorl. On some specimens, however, the carina becomes weaker on the later whorls as the other spiral ribs become stronger, giving these whorls a convex shape (Figures 19–21), like shells misidentified by some workers as *Turritella macreadyi* Waring, 1914.

The overall teleoconch morphology of the 10 mm-high tip of *Mesalia martinezensis* superficially resembles that of the 15-mm high mathildid *Carinathilda diminuata* (Perrilliat, Vega, and Corona, 2004) illustrated by Kiel et al. (2002: 329–330, fig. 2.4) from the lower Maastrichtian of the Mexcala Formation, Guerrero, southern Mexico. *Carinathilda diminuata* is definitely a mathildid because it has a heterostrophic protoconch. The resemblance between these two gastropods, nevertheless, provides evidence that the Late Cretaceous mathildids and lower Paleogene turritellids can have similar looking adult shells.

*Mesalia martinezensis* resembles "*Mesalia*" *virginiae* Stilwell et al. (2004: 29–30, pl. 5, figs. 6–10) from lower Paleocene (Danian) rocks on Seymour Island, Antarctic Peninsula, but *M. martinezensis* has a subtle effuse spout rather than the longer and more distinct, twisted narrow anterior canal that "*M.*" *virginiae* possesses. In addition, *M. martinezensis* has stronger ribs and a parasigmoidal growth line, rather than an opisthocyrt one on the last whorl. In our opinion, the aperture of "*M.*" *virginiae* is unlike that of *Mesalia*.

Gabb (1869) mentioned that the broadly expanding whorl of *martinezensis* approaches that seen on *Turritella robusta* Gabb (1864: 135, pl. 21, fig. 74; not = *T.* (*Haustator*) *robusta* Grzybowski, 1899), but Merriam (1941: 128) reported that the Late Cretaceous *T. robusta*, which is represented by a single poorly preserved type specimen, is probably not a *Mesalia*. This type specimen has an umbilicus, therefore it is not a turritellid. It is from the Redding area, northern California, and not from Tuscan Springs, as erroneously reported by Merriam (1941). Jones et al. (1978: pl. 1, fig. 19) identified this specimen, which is of Turonian age, to be *Glauconia*? *robusta* (Gabb, 1864).

Merriam (1941: 10, 116) stated that mainly in profile the Pacific slope Miocene *Turritella temblorenesis* Wiedey, 1928, might readily be confused with *Mesalia martinezensis*. The latter also resembles the Pacific slope Miocene *Turritella temblorensis tritschi* Hertlein, 1928, and *Turritella ocoyana* Conrad, 1857. The latter, however, has a different growth line. In addition, *T. martinezensis* strongly resembles *Turritella fredeai* Hodson, 1926, of Miocene age from northern Colombia and northern Venezuela. None of these above-mentioned Miocene species, however, has the effuse spout of *Mesalia*.

### *Mesalia clarki* (Dickerson, 1914a)

(Figures 24–32)

*Turitella* [sic] *clarki* Dickerson, 1914a: 142–143, pl. 13, fig. 8.
*Mesalia clarki* (Dickerson).—Merriam, 1941: 128, pl. 39, fig. 6; Zinsmeister, 1983: table 1, pl. 2, fig. 14

**Description:** Medium small (up to approximately 31 mm height). Turritelliform. Pleural angle approximately 21 to 22°. Protoconch unknown. Teleoconch up to 12 whorls, consisting of two whorl shapes: flatish rounded and anteriorly angulate. Sutural area indented. Sculpture consisting only of spiral ribs, variable in number, strength, and spacing. Flattish to rounded whorl shape: upper spire with one or two secondaries on posterior part and two (bicostate) primaries on anterior part; lower spire and last whorl with seven to eight nearly equal strength primaries (anteriorly located ribs can be somewhat angulate); spiral threads on all interspaces; posteriormost rib part of broad band; ribs on anterior part of whorl tend to be slightly stronger than posteriorly located ribs; base of last whorl with three ribs. Angulate whorl shape: upper spire with one secondary on posterior part and two (bicostate), well developed, flat-topped primaries on anterior part; lower spire and last whorl with three primaries on posterior part and two stronger primaries, with one secondary in between each, on anterior part; spiral threads on all interspaces. Base (including short neck) of last whorl with approximately seven, evenly spaced ribs; interspaces and ribs covered by spiral threads. Aperture small; columella narrow with thin callus, occasionally with single, weak fold, slight twist on anterior end of columella. Spout effuse, short, and narrow. Growth-line trace on last whorl (including base) parasigmoidal, with lateral sinus flexure strongest medially.

**Holotype:** UCMP 11936, height 25 mm, diameter 16.5 mm.

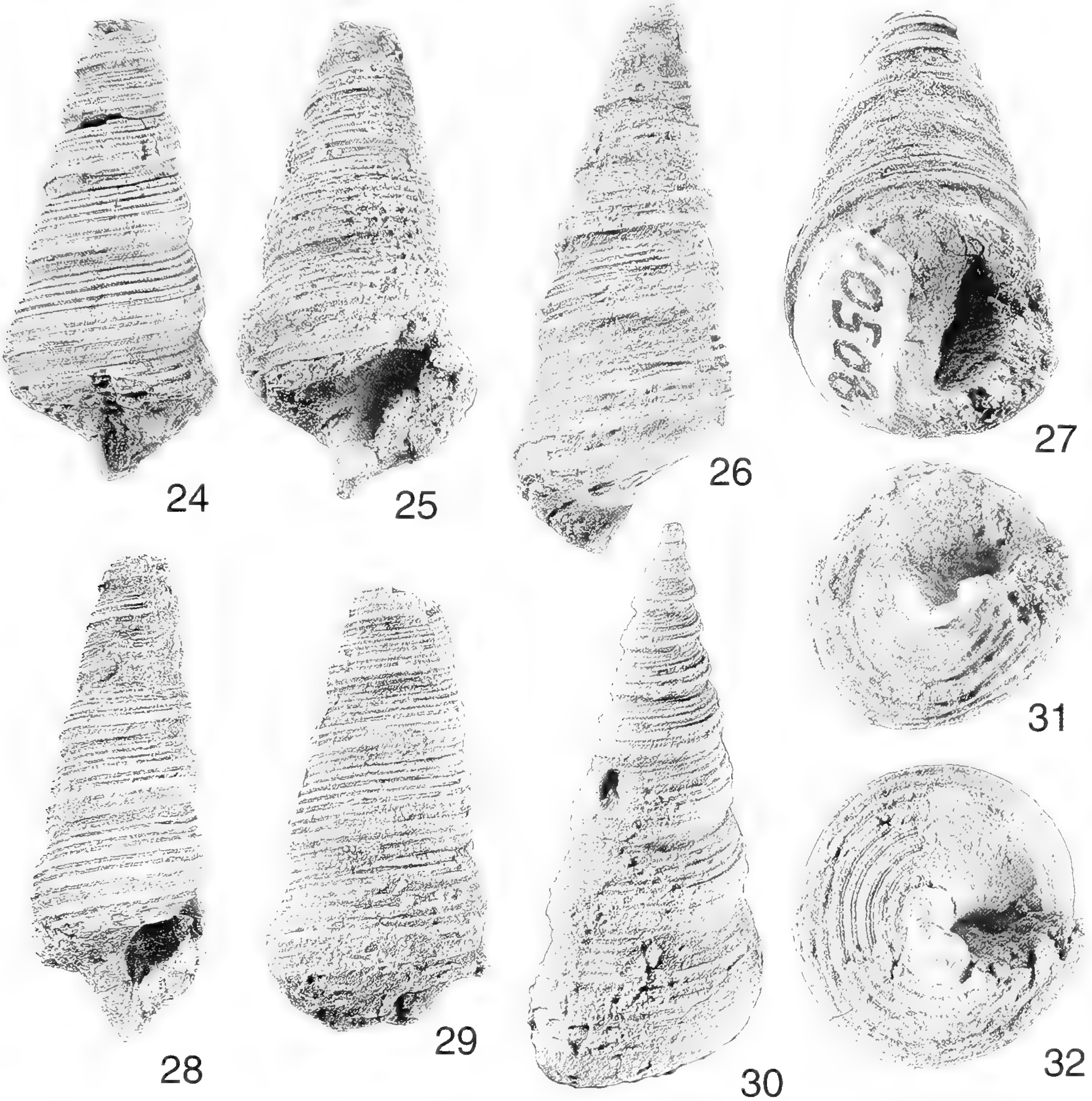
**Type Locality:** UCMP loc. 1540.

**Geologic Range:** Late Paleocene = *Turritella infragranulata* Zone.

**Distribution:** "Martinez" Formation, northeast side of Mount Diablo, Contra Costa County, northern California (Dickerson, 1914a; Merriam, 1941; Zinsmeister and Paredes-Mejia, 1988 [faunal list]; upper Santa Susana Formation, Trailer and Quarry canyons, Los Angeles County, Santa Monica Mountains, southern California (Strathearn et al., 1988 [faunal list]; Squires and Saul, 1998: 1025).

**Discussion:** *Mesalia clarki* is abundant in the upper Santa Susana Formation at LACMIP loc. 10508, in the Santa Monica Mountains, Los Angeles County, southern California. The anterior ends of the shells are very fragile, and nearly all the specimens have incomplete apertures. None of the specimens has retained their protoconch, and most specimens are missing their upper spire. Growth lines are hard to discern, usually visible only on a single whorl (typically the penultimate whorl), and were rarely preserved on the base of the last whorl. Some of the specimens appear to have a wider pleural angle (23°) than normal, but these particular specimens have been crushed. A few of the specimens (five percent) have naticid boreholes, and a few other specimens are encrusted, in part, by bryozoans. Rare specimens are coated by calcareous algae.

All previous workers assigned *Mesalia clarki* to various genera without knowledge of the shape of the aperture. Our cleaning of representative specimens of Dickerson's species revealed it to have a short, shallow effuse spout (Figures 24–25) and bicostate sculpture on the juvenile whorls (Figure 30). There is considerable variation in the sculpture and the shape of the whorls on *M. clarki*. Some



**Figures 24–32.** *Mesalia clarki* (Dickerson, 1914). Specimens coated with ammonium chloride. All from LACMIP loc. 10508. **24.** Hypotype LACMIP 13405, apertural view, height 21.5 mm, diameter, 19.6 mm. **25.** Hypotype LACMIP 13406, slightly oblique apertural view, height 23.1 mm, diameter 10.8 mm. **26–27.** Hypotype LACMIP 13407, height 22.6 mm, diameter 9.4 mm. **26.** Abapertural view. **27.** Oblique apertural view. **28.** Hypotype LACMIP 13408, apertural view, height 23.2 mm, diameter 9.2 mm. **29.** Hypotype LACMIP 13409, abapertural view, height 21.5 mm, diameter 11 mm. **30.** Hypotype LACMIP 13410, abapertural view, height 23.6 mm, diameter 9.7 mm. **31.** Hypotype LACMIP 13411, base, diameter 9.5 mm. **32.** Hypotype LACMIP 13408, base of same specimen shown in Figure 28, diameter 8.9 mm.

specimens have nearly uniform sculpture and flattish whorls (Figure 24), others have carinate whorls (Figure 26), whereas others have uniform sculpture with convex whorls (Figure 29).

Zinsmeister (1983: pl. 2, fig. 14), Zinsmeister and Paredes-Mejia (1988: table 1), and Paredes-Mejia (1989: table 3) reported *M. clarki* from the Santa Susana Formation in the Simi Hills, southern California. These reports, however, were based on the misidentification of a specimen of *Mesalia martinezensis* that happens to lack a strong anterior carina on the otherwise convex whorls.

*Mesalia clarki* resembles *Motyris aralica* (Michailovski, 1912; Wenz, 1939: 652, fig. 1856) from upper Eocene rocks in the Aral Sea region. *Motyris* Eames, 1952, was formerly known as *Tomyris* Michailovski, 1912. See Marwick (1957: 162–163) for more taxonomic information about *Motyris*. *Mesalia clarki* differs from *M. aralica* by not having tabulate whorls with strongly indented sutures. The full aperture of *M. aralica* is unknown, and details about its apical whorl development are wanting. The only other species of *Motyris* that we are aware of is *Motyris pseudoaralica* Eames (1952: 30–31, pl. 1, fig. 15; pl. 2, figs. 58a, b) from Pakistan, but its aperture is unknown. We believe that when the great variability of *Mesalia* is taken into account, *Motyris* will prove to be congeneric.

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Earl Brabb (U. S. Geological Survey, Menlo Park) provided very useful information regarding the stratigraphy of the beds in the vicinity of the type locality of *Mesalia clarki*. Lindsey T. Groves (LACM, Malacology Section) kindly provided key literature dealing with the ecology of modern *Mesalia*. The manuscript benefited from the reviews by Warren D. Allmon (Paleontological Research Institute, Ithaca, New York) and Steffen Kiel (University of Leeds, England and Department of Paleobiology, Smithsonian Institution's National Museum of Natural History). Steffen Kiel also provided us with an important hard-to-find reference and very useful stratigraphic information.

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## APPENDIX

### LOCALITIES CITED

Localities are LACMIP, unless otherwise noted. All quadrangle maps are U. S. Geological Survey maps.

7060. Elevation 1427 ft., on ridge between Temesal and Santa Ynez canyons at edge of fire road on top of ridge, Topanga Canyon Quadrangle (7.5 minute, 1952, photorevised 1981), Los Angeles County, southern California. Paleocene. Santa Susana Formation. Coll.: H. D. B. Wilson, June 1, 1941.

10508. North slope of Trailer Canyon near top of ridge between Quarry and Trailer canyons at approximately 1325 ft. elevation and just west of saddle, just below coralline-algal beds in limy siltstone west of small fault, road cut north side of unpaved road 5600 ft. north of San Vicente y Santa Monica Grant boundary, 10,400 ft. east of Los Angeles City boundary, Topanga Quadrangle (7.5 minute, 1952, photorevised 1981), east of Santa Ynez Canyon, Palisades Highlands, Santa Monica Mountains, Los Angeles County, southern California. Lower upper Paleocene (lower Thanetian). Santa Susana Formation. Coll.: G. Strathearn and others, fall, 1982.

11717. Float at about 1600 ft. elevation in bottom of south-flowing gully joining Quarry Canyon at about 1410 ft. elevation; 1500 ft. SW of hill 2036, Topanga Quadrangle (7.5 minute, 1952, photorevised 1981), Los Angeles County, southern California. Paleocene. Santa Susana Formation. Coll.: J. M. Alderson, November 11, 1980.

21581. Black nodular shale and conglomerate on road 1.1 mi. east from Cienaga Camp at Fish Canyon forks toward Warm Springs summit; on northwest side of ravine; north side East Fork Fish Canyon, T. 6 N, R. 16 W, approximately 2050 ft. north, 750 ft. east of bench mark 2205, Warm Springs Mountain Quadrangle (7.5 minute, 1958, photorevised 1974), Los Angeles County, southern California. Paleocene (upper Danian). San Francisquito Formation. Coll.: R. W. Webb and E. H. Quayle, June 23–24, 1941.

21607. South 1/2, SE 1/4, section 25, T. 2 N, R. 18 W, Calabasas Quadrangle (7.5 minute, 1952, photorevised 1967), Ventura County, southern California. Lower upper Paleocene (lower Thanetian). Santa Susana Formation. Coll.: Kinney and Sherman, date unknown.

21554. Reworked fossil boulders in conglomerate, in second spur canyon off Poison Oak Canyon east of Las Llajas Canyon, 2800 ft. up canyon (north) from Poison Oak Canyon; on west slope 25 ft. above bottom of canyon, Santa Susana Quadrangle (7.5 minute, 1951, photorevised 1969), north side Simi Valley, Ventura County, southern California. Paleocene. Santa Susana Formation. Coll.: P. L. Goldman, date unknown.

22330. Beds cropping out on nose of spur on west side of Meier Canyon, approximately 600 ft. north of second "n" in "Meier Canyon," Santa Susana Quadrangle (7.5 minute, 1951, photorevised 1969), south side of Simi Valley, Simi Hills, Ventura County, southern California. Lower middle Paleocene (Selandian) = *Turritella peninsularis* Zone. Santa Susana Formation, "Martinez marine member." Coll.: W. P. Popenoe, April 3, 1946.

22557. Sandstone bed below small waterfall [dry] west of road going south through Barclay Ranch, 10,162 ft. south and 5660 ft. wet of junction of Southern Pacific railroad and Los Angeles Ave. about 0.25 mi. east of Santa Susana, Santa Susana Quadrangle (7.5 minute, 1951, photorevised 1969), Simi Hills, Ventura County, southern California. Paleocene. Santa Susana Formation. Coll.: M. Murphy, spring, 1950.

22698. On first large ridge; trending southwest to west of ridge trending south of hill 2150. Bearing from the northwest corner of the Calabasas Quadrangle is S14°E; distance 12,210 ft., Calabasas Quadrangle (7.5 minute, 1952, photorevised 1967), Simi Hills, Ventura County, southern California. Paleocene. Santa Susana Formation. Coll.: J. H. Fantozzi, June 1, 1951.

25281. Sandstone at elevation of 1000 ft., about 400 ft. south and 1000 ft. west of northeast corner of section 5, T. 1 S, R. 17 W, Malibu Beach Quadrangle (7.5 minute, 1950, photorevised 1967), on west side of northern tributary to Stokes Canyon, western Santa Monica Mountains, Los Angeles County, southern California. Reworked Paleocene (Selandian) fossils in middle Miocene Calabasas Formation, Stokes Canyon Breccia Member. Coll.: J. Stark and T. Susuki family, May 5, 1965.

26897. Gully west side of Temesal Canyon opposite 2nd 'e' of Temesal at about 1475 ft. elevation; approximately 1082 m (3550 ft.) south; 533m (1750 ft.) east of hill 22036; San Vincente and Santa Monica Grant, Topanga Quadrangle (7.5 minute, 1952, photorevised 1967), Santa Monica Mountains, Los Angeles County, southern California. Middle upper Paleocene (middle Thanetian). Santa Susana Formation. Coll.: J. M. Alderson, March 9, 1980.

UCMP 1540. Elevation 1000 ft., 1 mi. south of Stewartville (site), northeast corner of NW 1/4, section 15, T. 1 N, R. 1 E, Antioch South Quadrangle (7.5 minute, 1973, photorevised), 300 ft. south of basal Tejon conglomerate and 600 ft. north of Chico-Martinez contact, northeast side of Mount Diablo, Contra Costa County, northern California. Upper middle Paleocene (Selandian) = *Turritella infragranulata pachecoensis* Zone. "Martinez" Formation, lower member. Coll.: R. E. Dickerson, circa 1912.

# *Vertigo malleata*, a new extreme calcifuge land snail (Gastropoda: Vertiginidae) from the Atlantic and Gulf coastal plains of the USA

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## ABSTRACT

*Vertigo malleata* new species is an extreme calcifuge land snail widely distributed in the Atlantic and Gulf costal plains of the eastern USA. This species appears to have gone undetected because of its small size and restriction to low pH sites—*Sphagnum* bogs, Atlantic white cedar (*Chamaecyparis thyoides* (L.) BSP) swamps, pocosins, and pine woodlands—which, it has been assumed, harbor little or no molluscan diversity. *Vertigo malleata* is distinguished from other members of the genus by the strongly pustulose surface of the body whorl, which gives the shell a malleated appearance at low to moderate magnification. While the major apertural lamellae/folds (parietal, columellar, and palatal) of this species are typical for *Vertigo*, the strongly pustulose shell sculpture, occurrence of an infraparietal lamella, and frequent development of subcolumellar and basal lamellae in the absence of an angular lamella appear unique. Although *V. malleata* is an abundant snail within its range, the common use of short-return fire regimens to manage forests of the eastern USA appears to be artificially limiting its distribution to wet, less frequently burned sites.

*Additional key words: Bothriopupa, Nesopupa,* biogeography, fire ecology, community ecology, eastern North America

## INTRODUCTION

Acidic and lime-poor habitats have long been thought to support depauperate molluscan community abundance and richness (Boycott, 1934; Baker, 1939; Kerney and Cameron, 1979; Burch and Pearce, 1990). Consequently, little molluscan survey work has been attempted in acidic sites even though they can represent a substantial fraction of the landscape. However, such areas should not be ignored for terrestrial gastropod biodiversity because base-poor habitats can be as speciose as base-rich habitats on a per-individual basis (Schilthuizen et al., 2003; Pokryszko and Cameron, 2005), and because some species like the European *Vertigo ronnebyensis* (Westerlund, 1871) and *Zonitoides excavatus* (Alder, 1830) are restricted to or more frequent in base-poor sites (Kerney and Cameron, 1979).

During land snail studies in eastern North America (Nekola, 2002a; Nekola and Coles, 2004; Coles and Nekola, unpublished data) we found that acidic habitats often supported substantial populations of land snail taxa that have been little reported since their original descriptions; e.g., *Vertigo cristata* (Sterki, 1919), *Vertigo nylanderi* Sterki, 1909, *Vertigo alabamensis* Clapp, 1915, and *Vertigo perryi* Sterki, 1905. In fact, *V. alabamensis* and *V. perryi* were each previously known from only two sites worldwide (Pilsbry, 1948; Hubricht, 1985). In the course of these acid-habitat surveys, we examined Saco Heath, an undisturbed domed ombotrophic *Sphagnum* bog in the Atlantic coastal plain of York County, Maine. At this site we located a species of the genus *Vertigo* that was strikingly different from all previously known taxa. This form was subsequently found to represent the most common land snail of highly acid, mesic to wet habitats of the Atlantic and Gulf coastal plains of the eastern USA. Here, we describe this taxon as *Vertigo malleata*, new species, document its biogeography and ecology, and briefly discuss its relevant conservation issues.

## MATERIALS AND METHODS

**Site Selection:** Approximately 130 sites were surveyed along the Atlantic and Gulf coastal plains of the eastern USA from Maine to western Alabama, including peninsular Florida south to Gainesville. These sites encompassed the entire soil base-status and moisture gradient of the region and covered a total geographic extent of 2400 km. Thirty sites represented base-neutral to base-rich habitats (i.e., calcareous wetlands, marl banks, rich forests, and limestone outcrops), while the remaining were base-poor (i.e., pine barrens, pine-wiregrass sa-

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vanna, heaths, Atlantic white cedar swamps, bay forest, *Sphagnum* bogs, and pocosins).

**Field Methods:** Latitude and longitude of each site was determined using a hand-held GPS. Terrestrial gastropod faunas were documented from a representative 100–1000 $m^2$ area within each site by hand collection of larger taxa and litter sampling for smaller taxa. Litter sampling was used as the primary method of collection because it provides the most complete assessment of site faunas (Oggier et al., 1998; Cameron and Pokryszko, 2005). As suggested by Emberton et al. (1996), collections were made at places of high micro-mollusk density such as loosely compacted leaf litter lying on top of highly compacted damp soil or humus. This loose litter was removed by hand and aggressively sieved in the field using a shallow sieve of 2 mm mesh nesting loosely inside a sieve of 0.6 mm mesh. The procedure consisted of throwing handfuls of litter onto the coarser mesh accompanied by vigorous shaking, tapping, or other agitation. The process was continued for 15–60 minutes, a time interval that yielded 50–500 ml of fine material (0.6–2.0 mm). In general, sites were sampled in parallel (but independently) by each of the authors, although several sites were sampled by only one worker (see Table 1).

**Laboratory Procedures:** Samples were slowly and completely dried at room temperature and then passed through an ASTME #30 sieve (0.6 mm mesh) with fractions being hand-picked against a neutral background. All shells, shell fragments, and slug plates were removed, and all identifiable shells from each site were assigned to species using the authors' reference collections and various museum collections (see below). The total numbers of shells per species per site were recorded, as were the number of unidentified immature individuals.

**Comparisons:** The new species was compared with specimens of all eastern North American and western Eurasian species of *Vertigo*, and to representative taxa in the related genera *Nearctula* of western North America, *Nesopupa* of the Old-World tropics, and *Bothriopupa* of the neotropics. Comparative material consisted of the authors' extensive reference collections, the collections of the Florida Museum of Natural History, Gainsville, FL (UF); the Field Museum of Natural History, Chicago, IL (FMNH), the Carnegie Museum of Natural History, Pittsburgh, PA (CM); the National Museum of Wales–Zoology, Cardiff, UK (NMW.Z); the Natural History Museum, London, UK, and the Queensland Museum, Brisbane, Australia. Additional comparisons were made with material presented by Pilsbry (1920; 1948).

**Imaging:** Shells were imaged at 40× magnification using a digital camera attached to a stereomicroscope. Approximately 12 separate 1388 × 1040 pixel images were made of each specimen with the image focal lengths positioned at 120μm increments from the front to back of the shell. CombineZ5 freeware (http://www.hadleyweb.pwp.blueyonder.co.uk/CZ5/ combinez5.htm) was used to assemble a final image from the well-focused parts of each separate image. The body whorl surface of the new taxon was also imaged at 150× with 60 images positioned at 5 μm focal length increments and assembled into a single image using CombineZ5. These separate images were imported into Adobe Photoshop, where brightness and contrast were optimized and the background made uniformly black. These images were then compiled into a single plate.

**Community Ecology:** Analysis of co-occurring terrestrial gastropod species and abundance was determined using data for sites sampled by the second author (i.e., all sites with accession numbers prefixed by JCN in Table 1). These analyses were performed for the whole dataset of 49 discrete sites and also by geographic sub-region—New England (Maine, Massachusetts), New Jersey, the North and South Carolina coastal plain, and the Gulf coastal plain—to allow for documentation of compositional gradients across the range of the new species. The physical habitat and plant community from each site was also noted.

**Nomenclature:** Taxonomic nomenclature follows that of Turgeon et al. (1998) with updates from Nekola (2004). Apertural lamellae and fold nomenclature follows that of Pilsbry (1948: 869, fig. 469), i.e., parietal "teeth" are referred to as "folds" and all other "teeth" are termed "lamellae", whatever their form.

## SYSTEMATICS

Class Gastropoda
Subclass Pulmonata
Order Stylommatophora
Family Vertiginidae
Genus *Vertigo* Müller, 1773
*Vertigo malleata* new species
(Figures 1–15, 20, Tables 1–2)

**Diagnosis:** Minute; shell ovoid, similar in size and shape to *Vertigo ventricosa* (Morse, 1865) but distinguished by malleated appearance of the body whorl at low to moderate (10–40×) magnification; upper whorls finely rib-striate, minutely decussated by spiral lines; aperture with parietal and columellar lamellae, a small infraparietal lamella (occasionally absent), and two palatal folds; one or more subcolumellar-basal lamellae usually present; angular lamella absent.

**Description:** Shell 1.8–2.1 mm tall × 1.25–1.4 mm wide (holotype 1.98 × 1.36 mm), ovoid to ovoid-conical, inflated, approximately 4–4.5 whorls, with deep suture; translucent, olive-yellow to brown in color; body whorl approximately 66% of total height. Protoconch and neanic whorls minutely papillose with fine spiral striation; subsequent whorls finely rib-striate; striae most distinct on penultimate whorl where they are minutely decussated by fine spiral lines; on body whorl the sculpture degenerates into an irregularly pustulose surface (Figure

4) which at low to moderate (10–40×) magnification takes on a malleated appearance as it appears hammered with small depressions; behind the aperture the sculpture takes the form of coarse, irregular rib-striae (Figures 2, 11). Aperture rounded, approximately 40% of shell height; lip reflexed but not thickened, peristome usually dark blackish-olive; sinulus moderate-weak; basally the aperture abruptly inflates to form a rounded swelling, but not a distinct crest (Figures 2, 8). Umbilicus closed (Figure 3). Aperture typically with six lamellae and folds (Figures 1, 5, 7, 9, 12–15): a strong, slightly sinuous parietal lamella (Figures 1, 5, 9, 15); a shelf-like columellar lamella that spirals internally around the columella for approximately one whorl; two palatal folds of approximately equal length that extend approximately 0.2 whorls into body whorl, the lower slightly more immersed than the upper (Figures 1, 5–7, 10, 15), both highest at mid-length (Figures 1, 5, 6, 15); a nodular infraparietal lamella usually present (Figures 1, 5, 9, 12–15), occasionally vestigial or absent (Figures 6, 10); angular lamella absent; presence of a nodular subcolumellar lamella and nodular subcolumellar-basal lamella variable (Figures 1, 6, 7, 9, 10). Apertural ends of the palatal folds coincide with abrupt inflation of basal aperture (Figures 7–8), in consequence appearing to be raised on a weak crest when viewed within the aperture but not associated with any internal shell thickening; externally shell only slightly impressed over palatal folds. Body of animal grey with several organs of a brown or cream color visible through the upper whorls of shell. All dissected individuals have proven to be aphallic (Beata Pokryszko, personal communication), hence the genitalic anatomy is unknown.

**Holotype (Figures 1–4):** NMW.Z.2005.011.03830, USA North Carolina, Pender County, Holly Shelter Game Land, Brian Coles, 1 April 2003.

**Paratypes (Figures 5–15):** NMW.Z.2005.011.03831-03839, figured material, see Figure legends for details; NMW.Z.2005.011.02118-02120, approximately 5100 individuals (split into three approximately equal lots) from type locality; UF 348143, approximately 700 individuals from type locality; CM 73971, 143 individuals from type locality; NMW.Z.2005.011.02597, 90 specimens, Wells Heath, York County, Maine (43°20′2″ N, 70°38′24″ W), Brian Coles; NMW.Z.2005.011.02591, 26 specimens, Skunknett Audubon Preserve, Barnstable County, Massachusetts (41°38′59″ N, 70°22′31″ W); NMW.Z.2005.011.02585, 170 specimens, Peterson Swamp Wildlife Management Area, Plymouth County, Massachusetts (42°0′37″ N, 70°49′4″ W), Brian Coles; NMW.Z.2005.011.02514, 122 specimens, Stafford Forge Wildlife Management Area, Ocean County, New Jersey (39°42′44″ N, 74°22′10″ W), Brian Coles; NMW.Z.2005.011.02197, 250 specimens, Lewis Ocean Bay Preserve, Horry County, South Carolina (33°47′16″ N., 78°50′56″ W.), Brian Coles; NMW.Z.2005.011.03035, 42 specimens, Collins Bay, Ware County, Georgia (31°5′12″ N., 82°36′56″ W.). Brian Coles: NMW.Z.2005.011.03065, 107 specimens, Wilma Station, Liberty County, Florida (30°9′34″ N., 84°57′39″ W.), Brian Coles; NMW.Z.2005.011.03079, 162 specimens, Pond Creek, Conecuh National Forest, Covington County, Alabama (31°6′12″ N., 86°32′3″ W.), Brian Coles.

**Type Locality:** Holly Shelter Game Land (34°31′57″ N, 77°44′41″ W), Pender County, North Carolina, USA; under dense scrub of mesic bay/pine forest at pocosin margin, individuals sieved from deep bracken fern and pine needle litter, collected by Brian Coles, 1 April 2003.

**Other Material (Table 1):** Sixty additional lots collected by Brian Coles are deposited in the Coles Collection of the National Museum of Wales. Fifty three lots representing 3133 individuals collected by Jeff Nekola are deposited in the Nekola collection (JCN).

**Etymology:** The specific name *malleata* refers to the hammered appearance of the body whorl at low to moderate magnification.

**Variation:** *Vertigo malleata* was rather constant in general appearance along its 2400 km range, although some variation in shape, size, color, sculpture, and development of the apertural lamellae was observed. Variation in size and shape has been noted above. In addition, the most southern populations (Georgia, Alabama, and Florida) tended to be darker in color and showed the most strongly developed shell sculpture (Figures 9–12). While the parietal lamella, columellar lamella, and the palatal folds varied little, the infraparietal lamella varied from strong (Figures 1, 5, 19) to weak (Figure 9) to occasionally absent (Figures 6,10). The subcolumellar and nodular basal lamella although usually distinct (Figures 1, 5, 7, 13) were also occasionally absent (Figure 5). Multiple subcolumellar-basal lamellae of variable placement were also noted most frequently in Gulf Coast populations (Figures 9, 10). However, such trends were not distinct enough to support the designation of geographical races, with most of this observed morphological variation occurring within local regions or populations.

**Comparison with Other Species of *Vertigo* and of Related Genera:** *Vertigo malleata* differs from all other *Vertigo* species by its strongly pustulose body whorl sculpture and possession of an infraparietal and subcolumellar-basal lamellae while lacking an angular lamella. Because of these unusual characteristics, we do not feel assignment of this taxon to a particular subgenus to be prudent at this time. Additional data, possibly based on DNA sequence information, will be required to accurately determine its closest relatives.

On casual inspection, *Vertigo malleata* could be taken for a member of the *V. gouldii* group (e.g. *Vertigo cristata*; see Pilsbry, 1948: 958, figs. 4, 5, 8; 967, figs. 1–16) because of its shell color, striated upper whorls, and silky luster. Like *V. malleata*, *V. cristata* has four prominent lamellae and strong striation on the penultimate whorl (Pilsbry, 1948: 967, figs. 4–5, 973, fig. 520; Nekola, 2001)

**Table 1.** *Vertigo malleata*: sites, brief habitat descriptions, collection dates, accession numbers, and total number of specimens taken.

| State/County | Site # | Site; Habitat[1] | Coordinates | Date | Accession Number | Specimens |
|---|---|---|---|---|---|---|
| Alabama | | | | | | |
| Covington | 1 | Pond Creek seep (Conecuh NF); *Ilex-Smilax*-bay scrub on seep margin | 31°06′12″ N, 86°32′03″ W | May 5 2005 | NMW.Z.2005.011.03079 | 162 |
| | | | | | JCN 12365 | 117 |
| | 2 | Moccasin Branch (Conecuh NF); old pine-bay-heath forest | 31°06′42″ N, 86°35′53″ W | May 5 2005 | JCN 12371 | 3 |
| | 3 | Bear Bay (Conecuh NF); heath-dominated scrub on wetland margin | 31°6′29″ N, 86°38′54″ W | May 5 2005 | NMW.Z.2005.011.03068 | 1 |
| Mobile | 4 | Grand Bay Forever Wild Preserve; wet bay and mixed forest | 30°25′07″ N, 88°19′35″ W | May 1 2005 | NMW.Z.2005.011.03019 | 3 |
| Florida | | | | | | |
| Columbia | 5 | Impassable bay (Osceola NF WMA); wet holly-bay scrub | 30°23′31″ N, 82°30′05″ W | Jan 8 2005 | NMW.Z.2005.011.02849 | 740 |
| | | | | May 2 2005 | JCN 12280 | 71 |
| | 6 | Osceola National Forest WMA; wet *Pinus-Lyonia-Vaccinium* savanna | 30°22′30″ N, 82°32′04″ W | May 2 2005 | NMW.Z.2005.011.03026 | 213 |
| | | | | | JCN 12285 | 75 |
| | 7 | Osceola National Forest WMA; wet *Acer-Taxodium-Lyonia* forest | 30°22′39″ N, 82°31′42″ W | Jan 8 2005 | NMW.Z.2005.011.02845 | 38 |
| | | | | May 2 2005 | NMW.Z.2005.011.03024 | 23 |
| | | | | May 2 2005 | JCN 12283 | 6 |
| Leon | 8 | Wolf Trap Bay (Apalachicola NF); tall pine-holly-bay forest | 30°22′04″ N, 84°34′11″ W | Jan 7 2005 | NMW.Z.2005.011.02813 | ~100 |
| | | | | May 4 2005 | NMW.Z.2005.011.03054 | 132 |
| | | | | May 4 2005 | JCN 12324 | 137 |
| | 9 | Wolf Trap Bay (Apalachicola NF); wet-mesic pine-holly-heath forest | 30°21′46″ N, 84°34′23″ W | Jan 7 2005 | NMW.Z.2005.011.02816 | 44 |
| | | | | May 4 2005 | NMW.Z.2005.011.03050 | 7 |
| | | | | May 4 2005 | JCN 12321 | 11 |
| | 10 | Otter camp (Apalachicola NF); regenerating mesic pine-holly heath | 30°20′20″ N, 84°36′41″ W | Jan 7 2005 | NMW.Z.2005.011.02820 | ~50 |
| | | | | May 4 2005 | NMW.Z.2005.011.03056 | 4 |
| Liberty | 11 | Wilma Station; mesic, old pine-magnolia-bay forest | 30°09′34″ N, 84°57′39″ W | May 4 2005 | NMW.Z.2005.011.03065 | 127 |
| | | | | | JCN 12344 | 30 |
| | 12 | Juniper Creek Islands (Apalachicola NF); old growth pine-holly-bay forest | 30°03′15″ N, 84°45′40″ W | May 4 2005 | NMW.Z.2005.011.03062 | 65 |
| | | | | | JCN 12337 | 41 |
| | 13 | Juniper Creek Islands (Apalachicola NF); white cedar-pine-holly forest | 30°04′46″ N, 84°45′41″ W | May 4 2005 | NMW.Z.2005.011.03059 | 5 |
| | | | | | JCN 12333 | 75 |
| | 14 | Juniper Creek Islands (Apalachicola NF); pine-red maple-white cedar forest | 30°02′07″ N, 84°49′38″ W | May 4 2005 | NMW.Z.2005.011.03064 | ~40 |
| | | | | | JCN 12339 | 48 |
| | 15 | Carr Bridge (Apalachicola NF); wet-mesic *Ilex* forest | 30°07′26″ N, 84°53′31″ W | May 4 2005 | JCN 12340 | 12 |
| Wakulla | 16 | South of Otter Camp (Apalachicola NF); wet-mesic pine-holly forest | 30°16′55″ N, 84°36′54″ W | May 4 2005 | NMW.Z.2005.011.03057 | 69 |
| | | | | May 4 2005 | JCN 12327 | 53 |
| | 17 | W Branch Sopchoppy R. (Apalachicola NF); pine-cypress-bay-holly forest | 30°15′05″ N, 84°37′30″ W | May 4 2005 | NMW.Z.2005.011.03058 | 5 |
| | | | | | JCN 12328 | 36 |

**Table 1.** *Continued*

| State/County | Site # | Site; Habitat[1] | Coordinates | Date | Accession Number | Specimens |
|---|---|---|---|---|---|---|
| Georgia | | | | | | |
| Ware | 18 | Collins Bay; wet holly-wax myrtle-bay forest | 31°05′12″ N, 82°36′56″ W | May 2 2005 | NMW.Z.2005.011.03035<br>JCN 12300 | 42<br>58 |
| | 19 | Dixon State Forest; wet *Pinus-Gordonia* forest | 31°05′36″ N, 82°16′13″ W | May 3 2005 | JCN 12301 | 4 |
| | 20 | Dixon State Forest; wet-mesic *Quercus-Ilex-Gordonia* forest | 31°06′49″ N, 82°16′16″ W | May 3 2005 | NMW.Z.2005.011.03038<br>JCN 12302 | 1<br>2 |
| Maine | | | | | | |
| York | 21 | Saco Heath 1 (TNC); sedge and heath litter on *Sphagnum* bog | 43°32′42″ N, 70°28′33″ W | Oct 14 2002 | NMW.Z.2005.011.01550 | 13 |
| | | | | Aug 8 2004 | NMW.Z.2005.011.02567<br>NMW.Z.2005.011.02577<br>JCN 12092<br>JCN 12099<br>JCN 12101 | 14<br>52<br>10<br>88<br>3 |
| | | | | Oct 01 2004 | NMW.Z.2005.011.02614<br>NMW.Z.2005.011.02616 | 55<br>40 |
| | 22 | Saco Heath 2 (TNC); low forest with *Carex* groundcover | 43°32′50″ N, 70°27′32″ W | Aug 08 2004 | NMW.Z.2005.011.02571<br>JCN 12095 | 45<br>59 |
| | 23 | Wells Heath (TNC); under heath scrub on *Sphagnum* bog | 43°20′02″ N, 70°38′24″ W | Oct 01 2004 | NMW.Z.2005.011.02597 | 90 |
| Massachusetts | | | | | | |
| Barnstable | 24 | Skunknett Audubon Preserve 2; *Myrica-Chamaecyparis* bog margin | 41°38′59″ N, 70°22′31″ W | Aug 13 2004 | NMW.Z.2005.011.02591<br>JCN 12180 | 26<br>22 |
| Bristol | 25 | Noquochoke WMA; *Chamaecyparis-Cryilla* swamp forest | 41°39′35″ N, 71°01′07″ W | Aug 12 2004 | NMW.Z.2005.011.02592<br>JCN 12168 | 21<br>17 |
| | 26 | Noquochoke WMA; leatherleaf island in acid sedge fen | 41°39′39″ N, 71°01′12″ W | Aug 12 2004 | NMW.Z.2005.011.02590<br>JCN 12164 | 4<br>12 |
| | 27 | Pine Swamp Brook; leatherleaf fringe of open acid bog | 41°55′57″ N, 71°03′49″ W | Aug 10 2004 | NMW.Z.2005.011.02586<br>JCN 12149 | 9<br>5 |
| Plymouth | 28 | Peterson Swamp WMA; *Chamaecyparis-Acer rubrum* forest | 42°00′37″ N, 70°49′04″ W | Aug 10 2004 | NMW.Z.2005.011.02585<br>JCN 12145 | ~170<br>137 |
| Worcester | 29 | Tom Bog; *Sphagnum* bog with scrub | 42°30′46″ N, 72°12′43″ W | Oct 05 2004 | NMW.Z.2005.011.02760<br>NMW.Z.2005.011.02761 | <br>~170 |
| New Jersey | | | | | | |
| Atlantic | 30 | Park Road (Wharton SF); moist *Ilex-Gaylussacia-Kalmia* scrub | 39°42′58″ N, 74°44′10″ W | May 22 2004 | NMW.Z.2005.011.02516<br>JCN 12050 | 18<br>54 |
| Burlington | 31 | Swan Bay WMA; low *Nyssa-Ilex-Acer rubrum* forest | 39°35′13″ N, 74°30′50″ W | May 20 2004 | NMW.Z.2005.011.02479<br>JCN 11983 | 107<br>103 |
| | 32 | Lebanon State Forest; open heath-*Smilax* scrub | 39°52′28″ N, 74°30′57″ W | May 19 2004<br>May 21 2004 | NMW.Z.2005.011.02469<br>JCN 12026 | 21<br>14 |
| | 33 | Roberts Brook; low *Nyssa-Chamaecyparis*-heath forest | 39°47′07″ N, 74°39′26″ W | May 19 2004<br>May 21 2004 | NMW.Z.2005.011.02466<br>JCN 11989 | 20<br>5 |
| | 34 | Brendan T Byrne State Forest; dry *Chamaecyparis*-bog | 39°53′07″ N, 74°30′22″ W | May 22 2004 | NMW.Z.2005.011.02499 | 1 |
| Camden | 35 | 2 miles WSW of Delette; moist bank with pine, oak, wax myrtle | 39°46′32″ N, 74°48′21″ W | May 19 2004<br>May 21 2004 | NMW.Z.2005.011.02461<br>NMW.Z.2005.011.02484<br>JCN 11995 | 6<br>28<br>8 |

**Table 1.** *Continued*

| State/County | Site # | Site; Habitat[1] | Coordinates | Date | Accession Number | Specimens |
|---|---|---|---|---|---|---|
| Gloucester | 36 | Winslow WMA; heath scrub in abandoned blueberry field | 39°37′08″ N,<br>74°53′43″ W | May 23 2004 | NMW.Z.2005.011.02518<br>JCN 12054 | 12<br>14 |
| Ocean | 37 | Colliers Mill WMA; acid bog with *Ilex*, *Chamaedaphne*, *Aronia* | 40°05′35″ N,<br>74°25′58″ W | May 22 2004 | NMW.Z.2005.011.02508<br>JCN 12036 | ~150<br>73 |
| | 38 | Stafford Forge WMA; moist *Kalmia-Pinus* forest | 39°42′44″ N,<br>74°22′10″ W | May 22 2004 | NMW.Z.2005.011.02514<br>JCN 12045 | 122<br>54 |
| | | | 39°53′34″ N,<br>74°19′58″ W | May 22 2004 | NMW.Z.2005.011.02511<br>JCN 12039 | 13<br>15 |
| North Carolina | | | | | | |
| Bladen | 39 | Johnson Mill Bay (Bladen Lakes SF); pocosin with *Chamaecyparis* | 34°42′44″ N,<br>78°31′33″ W | Jun 02 2003 | NMW.Z.2005.011.02204<br>JCN10613 | ~100<br>142 |
| Brunswick | 40 | Green Swamp (TNC); *Chamaecyparis*-bay forest | 34°06′14″ N,<br>78°18′35″ W | Jun 01 2003 | NMW.Z.2005.011.02193<br>JCN 10615 | 50<br>94 |
| | 41 | Green Swamp (TNC); medium pocosin | 34°05′42″ N,<br>78°17′48″ W | Jun 01 2003 | NMW.Z.2005.011.02194<br>JCN 10617 | 20<br>19 |
| | 42 | Prospect Ridge; mature pine-bay forest | 34°03′48″ N,<br>78°20′52″ W | Jun 01 2003 | NMW.Z.2005.011.02196<br>JCN 10622 | 25<br>2 |
| Carteret | 43 | Millis Road (Croatan NF); wet pocosin with leatherleaf | 34°46′16″ N,<br>76°58′39″ W | Feb 24 2003 | NMW.Z.2005.011.02128<br>JCN 10624 | 82 |
| Craven | 44 | Sheep Ridge (Croatan NF); medium pocosin | 34°56′07″ N,<br>77°04′14″ W | Feb 24 2003 | NMW.Z.2005.011.02132<br>NMW.Z.2005.011.02130<br>JCN10693<br>JCN 10708 | ~600<br>30<br>481<br>10 |
| | 45 | Catfish Lake South (Croatan NF); low, wet pocosin | 34°55′39″ N,<br>77°05′05″ W | Feb 24 2003 | NMW.Z.2005.011.02126<br>JCN 10678 | ~400<br>257 |
| | 46 | Catfish Lake South (Croatan NF); roadside ditch in medium pocosin | 34°55′10″ N,<br>77°05′24″ W | Feb 24 2003 | JCN 10668 | 1 |
| | 47 | Neusiok Trail North (Croatan NF); wet-mesic pine-bay forest | 34°54′03″ N,<br>76°49′06″ W | Jun 01 2003 | NMW.Z.2005.011.02190<br>JCN 10686 | 20 |
| Jones | 48 | Catfish Lake Wilderness (Croatan NF); mature bay-pine forest | 34°55′07″ N,<br>77°10′43″ W | Feb 24 2003 | NMW.Z.2005.011.02125<br>JCN 10713 | 40<br>64 |
| Moore | 49 | Pinebluff; bay forest in gulley along US 1 | 35°06′14″ N,<br>79°28′28″ W | Jun 03 2003 | JCN 10746 | 18 |
| Pamlico | 50 | Goose Creek Game Land; pine straw under scrub | 35°15′14″ N,<br>76°35′52″ W | May 31 2003 | NMW.Z.2005.011.02188 | 10 |
| Pender | 51 | Holly Shelter game land; edge of mature mesic bay/pine forest | 34°31′57″ N,<br>76°44′41″ W | Apr 01 2003 | NMW.Z.2005.011.03830<br>NMW.Z.2005.011.02119<br>NMW.Z.2005.011.02118<br>NMW.Z.2005.011.02120<br>CM73971<br>UF348143 | Holotype<br>~1700°<br>~1700°<br>~1700°<br>143°<br>~700° |
| | 52 | Holly Shelter game land; dense pocosin scrub | 34°32′57″ N,<br>77°46′54″ W | Apr 01 2003 | NMW.Z.2005.011.02428 | ~600 |
| | 53 | Holly Shelter game land; dense bay scrub | 34°33′06″ N,<br>77°47′37″ W | Apr 01 2003 | NMW.Z.2005.011.02117 | 115 |
| | 54 | Lanier Quarry (TNC); Shrubs bordering pine-wiregrass savanna | 34°37′49″ N,<br>77°40′27″ W | Jun 01 2003 | NMW.Z.2005.011.02192<br>JCN 10783 | ~80<br>64 |
| rrell | 55 | Pocosin Lakes NWR; low pocosin | 35°42′30″ N,<br>76′11′11″ W | Apr 03 2003 | NMW.Z.2005.011.02122<br>NMW.Z.2005.011.02123 | ~900<br>~900 |
| | | | | May 31 2003 | JCN 10824 | 92 |

**Table 1.** *Continued*

| State/County | Site # | Site; Habitat[1] | Coordinates | Date | Accession Number | Specimens |
|---|---|---|---|---|---|---|
| | 56 | Pocosin Lakes NWR; maple-oak-pine woodland | 35°40′19″ N, 76°12′16″ W | Apr 03 2003 | NMW.Z.2005.011.02121 | 50 |
| | 57 | Frying Pan Landing (Pocosin Lake NWR); pine pocosin | 35°48′03″ N, 76°06′00″ W | Apr 03 2003<br>May 31 2003 | NMW.Z.2005.011.02174<br>JCN 10823 | 1<br>1 |
| South Carolina | | | | | | |
| Horry | 58 | Lewis Ocean Bay Preserve; medium pocosin on roadside | 33°47′14″ N, 78°50′36″ W | Jun 02 2003 | NMW.Z.2005.011.02201<br>JCN 10955 | ~200<br>300 |
| | 59 | Lewis Ocean Bay Preserve; mesic pine-bay forest | 33°47′16″ N, 78°50′56″ W | Jun 02 2003 | NMW.Z.2005.011.02197<br>JCN 10960 | ~250<br>123 |
| | 60 | Lewis Ocean Bay Preserve; mesic longleaf pine forest | 33°47′33″ N, 78°51′02″ W | Jun 02 2003 | NMW.Z.2005.011.02200<br>JCN 10964 | 25<br>26 |

[1] Abbreviations used are: NF National Forest, NWR National Wildlife Refuge, SF State Forest, TNC The Nature Conservancy, WMA wildlife management area.

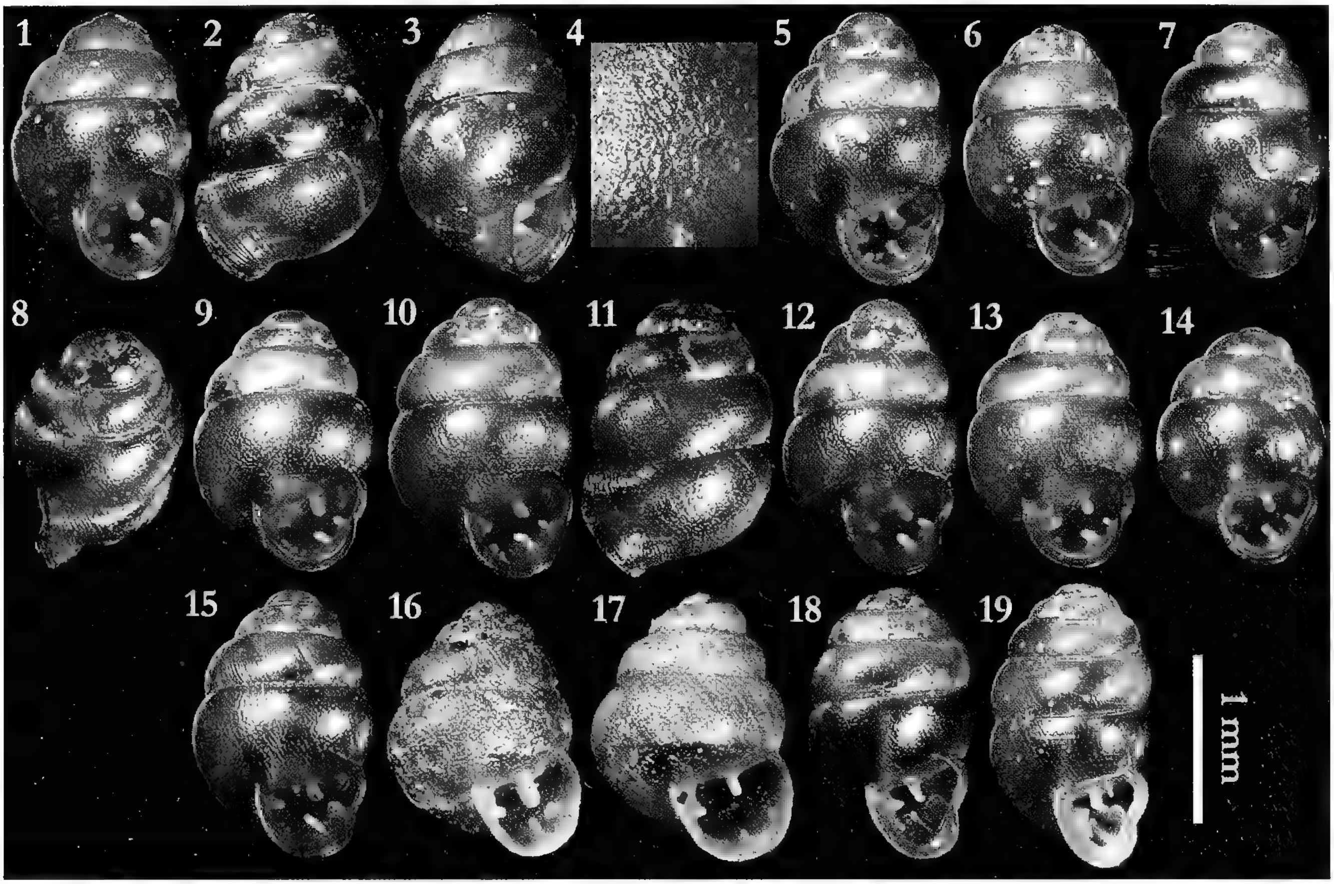
However, *V. cristata* has striate (not pustulose) sculpture on the body whorl, has a weak crest (rather than a basal inflation), lacks an infraparietal lamellae, and has a nodular (not shelf-like) columellar lamella. These two species were found co-occurring in several New England locations (Table 1, sites 21, 22, 23, and 29), where they could readily be distinguished under low magnification.

*Vertigo malleata* also resembles *Vertigo ventricosa* (Morse, 1865) and *Vertigo perryi* Sterki, 1905 with respect to the ovoid shape, large aperture vs. shell height ratio, reflected lip (Pilsbry, 1948: 958, figs. 1–3, 7), and basal apertural inflation (Coles and Nekola, *unpublished data*); *V. perryi* also has a dark colored peristome (Pilsbry, 1948: 968). However, these species cannot easily be confused because *V. ventricosa* and *V. perryi* have glossy shells with only weakly developed striae, lack an infraparietal lamella, and have a peg-like columellar lamella.

Although not previously reported in the genus *Vertigo*, the pustulose sculpture of the body whorl in *Vertigo malleata* is not unique to this species; *Vertigo alabamensis* and *Vertigo conecuhensis* (Pilsbry, 1948: 949, fig. 510, 9, 12–14; 950, fig. 511) of southeastern North America also weakly exhibit this trait (Figures 18, 19). At low magnification, the sculpture of *V. malleata* also somewhat resembles the pitted or granular surface of members of the Nesopupinae. However, members of the Nesopupinae commonly have an angular lamella (i.e., *Nesopupa*, *Sterkia*), while none are known to have an infraparietal lamella. Superficially, *V. malleata* also appears similar to the neotropical genus *Bothriopupa* (Pilsbry, 1948: 1011, fig. 539). However, with respect to shape, color, nature of the surface sculpture and configuration of the major apertural lamellae and folds, *V. malleata* much more closely resembles other members of the genus *Vertigo* (Figures 16, 17).

**Geographic Distribution:** *Vertigo malleata* occurs from southern Maine to southeastern Georgia along the Atlantic coastal plain to the west side of Mobile Bay along the Gulf coastal plain, apparently excluding peninsular Florida (Table 1, Figure 20). This distribution includes a number of regions of particular ecological interest and conservation concern, e.g., the Pine Barrens of New Jersey (sites 30, 32–35, 37–38), the sandhills and pocosins of the North Carolina and South Carolina coastal plain (sites 39–48, 51–60), the Okefenokee Swamp of southeastern Georgia (sites 19, 20), and the Appalachicola sand plain of western Florida (sites 8–17). It seems likely that its distribution extends into the Gulf coastal plain of Mississippi and eastern Louisiana. Although it is not yet known whether the species range extends beyond the eastern USA, given the known ranges of Atlantic coastal plain plant species (Sorrie and Weakley, 2001) the sand plains of southern Nova Scotia would appear to be an appropriate location for future surveys.

**Preferred Habitats:** *Vertigo malleata* occurred in approximately two-thirds of all surveyed acid habitats. In southern Maine and Massachusetts it was found in damp and lightly compacted leaf litter on *Sphagnum* bogs under a dense cover of ericaceous and other acidophile shrubs (e.g., *Gaylussacia*, *Vaccinium*, *Kalmia*, and *Myrica*). In this region it was also present in Atlantic white cedar bogs, where it occurred in leaf litter accumulations on mossy hummocks. In the New Jersey Pine Barrens *V. malleata* was found in dense leaf litter under tall heath (*Vaccinium*, *Gaylussacia*, *Kalmia*), *Myrica*, and *Ilex* scrub at the edges of bogs, Atlantic white cedar swamp forest, and mesic microsites in upland pine-oak forest. Populations in North and South Carolina were primarily located under dense heath, bay, holly, and wax myrtle scrub in pocosins, bay forest, wet-mesic pine woodland, and pine-wiregrass savanna. At Pocosin Lakes National Wildlife Refuge, for example, *V. malleata* was abundant in leaf litter on scrub vegetation islands within flooded pond pine woodland (Table 1, site 55), absent in adjacent broadleaf woodland, and present only in relatively low numbers at the transition zone (site 56). Popu



**Figures 1–19.** *Vertigo malleata* and related taxa. **1–4.** *Vertigo malleata.* Holotype, NMW.Z.2005.011.03830, Holly Shelter Game Lands, Pender County, North Carolina, 34°31′57″ N, 77°44′41″ W; **1.** Apertural view. **2.** Abapertural view. **3.** View showing parietal and upper palatal lamellae. **4.** Sculpture on body whorl surface, width of detail is 0.25 mm. **5.** *Vertigo malleata*, second specimen from the type locality, NMW.Z.2005.011.03831, showing more conical shell shape. **6.** *Vertigo malleata*, NMW.Z.2005.011.03832, Stafford Forge WMA, Ocean County, New Jersey, 39°42′44″ N., 74°22′10″ W, showing small size and lack of infraparietal and subcolumellar-basal lamellae. **7–8.** *Vertigo malleata*, NMW.Z.2005.011.03833, Wells Heath, York County, Maine, 43°20′2″ N, 70°38′24″ W. **7.** Apertural view. **8.** View from apex showing apical whorls and the basal apertural dilation. **9.** *Vertigo malleata*, NMW.Z.2005.011.03834, Wilma Station, Liberty County, Florida, 30°9′34″ N, 84°57′39″ W, showing strong shell sculpture, a series of subcolumellar-basal lamellae, and a weak infraparietal lamella. **10, 11.** *Vertigo malleata*, NMW.Z.2005.011.03835, Pond Creek seep, Covington County, Alabama, 31°6′12″ N, 86°32′3″ W. **10.** Apertural view showing subcolumellar and basal lamellae, an indistinct nodule below the columellar lamella, and lack of an infraparietal lamella. **11.** Abapertural view. **12.** *Vertigo malleata*, NMW.Z.2005.011.03836, Collins Bay, Ware County, Georgia, 31°05′12″ N, 82°36′56″ W, showing elongate shape, fused subcolumellar and basal lamellae, and distinct sinulus. **13.** *Vertigo malleata*, NMW.Z.2005.011.03837, Skunknett Audubon Preserve 2, Barnstable County, Massachusetts, 41°38′59″ N, 70°22′31″ W, showing light shell color and basal lamella only. **14.** *Vertigo malleata*, NMW.Z.2005.011.03838, Peterson Swamp WMA, Plymouth County, Massachusetts, 42°00′37″ N, 70°49′4″ W, showing small size, vestigal infraparietal, and reduced basal lamellae. **15.** *Vertigo malleata*, NMW.Z.2005.011.03839, Lewis Ocean Bay Preserve, Horry County, South Carolina, 33°47′16″ N, 78°50′56″ W, showing bi-lobed basal lamella. **16.** *Bothriopupa tenuidens* (C.B. Adams, 1845), FMNH 106420, Louis Brand Collection, Columbia University. **17.** *Bothriopupa conoidea* (Pfeiffer, 1853), FMNH 119055, Kyk-Over-All Island, Kartabo, British Guiana. **18.** *Vertigo conecuhensis*, JCN 12364, Pond Creek seep, Covington County, Alabama, 31°6′12″ N, 86°32′3″ W. **19.** *Vertigo alabamensis*, JCN 10781, Lanier Quarry, Pender County, North Carolina, 34°37′49″ N, 77°40′27″ W.

lations in Georgia, Florida, and Alabama were found primarily in bay scrub along swamp margins, small water courses, and seepage zones within pinelands. Populations were also rarely encountered in mesic pine forest fragments that had escaped frequent fire management (see below); again, individuals were restricted to humid litter accumulations. Throughout its range, *Vertigo malleata* appeared to avoid even moderately less acidic habitats such as sedge meadows (Maine, Massachusetts), cattail swamps and marshes (Maine, Massachusetts, New Jersey), and bottomland bald cypress/water tupelo/sweetgum forests (North and South Carolina, Georgia, Florida, and Alabama).

**Associated Land Snails and Community Composition:** Across all 49 analyzed sites (Table 2), *Vertigo malleata* constituted 35% of total individuals. This fraction appeared to be inversely correlated with latitude,

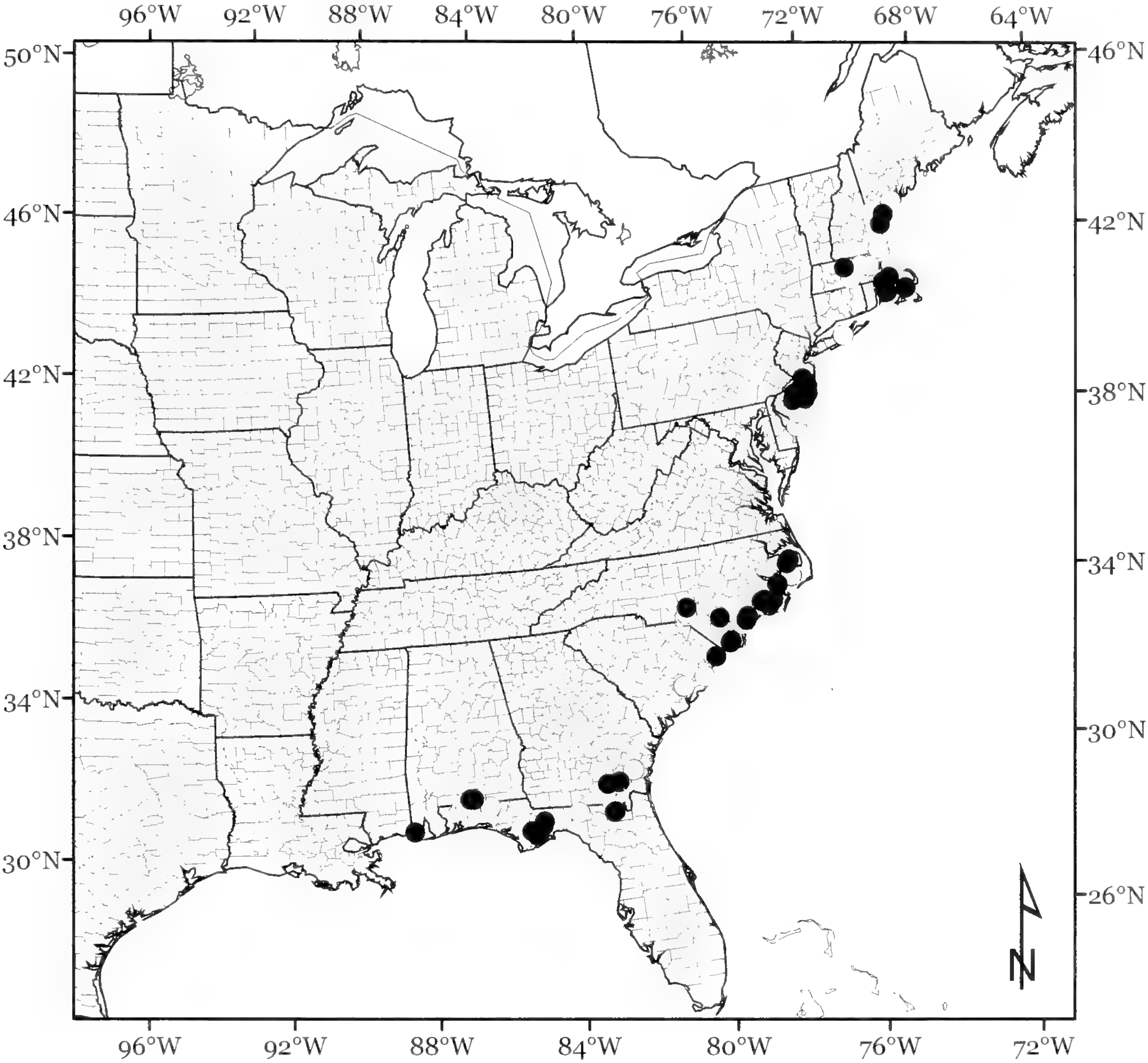


**Figure 20.** Distribution of *Vertigo malleata* in eastern North America. Black circles represent sites supporting populations and open circles represent inventoried sites that do not harbor this species.

ranging from 17% in the New Jersey Pine Barrens to 32% in New England, 35% in the Carolina coastal plains, and 76% in the Gulf coastal plain. Population densities of *V. malleata* were frequently observed to exceed 500 per m$^2$, with an estimated density of the order of 2000 per m$^2$ at the type locality (Table 1, site 51). These densities range among the highest reported for any land snail species (Frest and Johannes 1995, Cameron 2003).

A total of 34 terrestrial mollusk taxa and 5886 individuals were observed from these sites (Table 2). The average number of co-occurring taxa was 3.69 ± 0.37, and ranged from 0–9. Throughout its range, the ten most frequently co-occurring taxa were: *Striatura milium* (17% of all other individuals), *Strobilops texasiana* (15%), *Vertigo milium* (13%), *Punctum minutissimum* (11%), *Vertigo alabamensis* (9%), *Striatura meridionalis* (8%), *Gastrocopta pentodon* (8%), *Euconulus trochulus* (4%), *Euconulus chersinus* (2%), and *Gastrocopta contracta* (2%). The most frequent co-occurring taxa varied by region: *Striatura milium* and *Punctum minutissimum* in New England; *Striatura meridionalis*, *Striatura milium*, *Punctum minutissimum*, and *Gastrocopta pentodon* in the New Jersey Pine Barrens; *Strobilops texasiana*, *Vertigo milium*, and *Vertigo alabamensis* along the Carolina coastal plain; and *Vertigo alabamensis*, *Striatura meridionalis*, and *Gastrocopta pentodon* along the Gulf coastal plain. Co-occurring *Vertigo* taxa also varied by region: *Vertigo cristata*, *Vertigo perryi*, and *Vertigo*

**Table 2.** Frequency of co-occurring species across the range of *Vertigo malleata*[1]

| Taxon | Number of co-occurring individuals (%) | | | | |
|---|---|---|---|---|---|
| | New England | New Jersey | Carolina coastal plain | Gulf coastal plain | Total |
| *Vertigo malleata* sp. nov. | 308 | 340 | 1807 | 779 | 3234 |
| *Striatura milium* (Morse, 1859) | 480 | 407 | 119 | | 1006 |
| *Strobilops texasiana* Pilsbry & Ferris, 1906 | | 61 | 835 | 11 | 907 |
| *Vertigo milium* (Gould, 1840) | | | 768 | | 768 |
| *Punctum minutissumum* (I. Lea, 1841) | 113 | 398 | 164 | | 675 |
| *Vertigo alabamensis* Clapp, 1915 | | | 494 | 64 | 558 |
| *Striatura meridionalis* (Pilsbry & Ferris, 1906) | | 413 | 25 | 46 | 484 |
| *Gastrocopta pentodon* (Say, 1821) | 6 | 258 | 156 | 45 | 465 |
| *Euconulus trochulus* (Reinhardt, 1883) | | | 216 | | 216 |
| *Euconulus chersinus* (Say, 1821) | | | 120 | 3 | 123 |
| *Gastrocopta contracta* (Say, 1822) | | | 109 | | 109 |
| *Glyphyalinia solida* (H. B. Baker, 1930) | | 15 | 64 | 19 | 98 |
| *Glyphyalinia* sp.[2] | | 28 | 63 | | 91 |
| *Vertigo oralis* Sterki, 1898 | | | 61 | 6 | 67 |
| *Hawaiia miniscula* (A. Binney, 1840) | | | 53 | | 53 |
| *Glyphyalinia luticola* Hubricht, 1966 | | 28 | 12 | 3 | 43 |
| *Vertigo conecuhensis* Clapp, 1915 | | | | 39 | 39 |
| *Gastrocopta tappaniana* (C. B. Adams, 1842) | 4 | | 28 | | 32 |
| *Zonitoides arboreus* (Say, 1816) | 12 | 5 | | 14 | 31 |
| *Euconulus fulvus* (Müller, 1774) | 20 | | | | 20 |
| *Vertigo ovata* Say, 1822 | | | | | 20 |
| *Vertigo ovata* Say, 1822 | | | 20 | | 20 |
| *Neohelix solemi* Emberton, 1988 | 1 | | 18 | | 19 |
| *Ventridens cerinoideus* (Anthony, 1865) | | | 19 | | 19 |
| *Vertigo cristata* (Sterki, 1919) | 13 | | | | 13 |
| *Nesovitrea electrina* (Gould, 1841) | 6 | | | | 6 |
| *Vertigo perryi* Sterki, 1905 | 5 | | | | 5 |
| *Gastrocopta riparia* Hubricht, 1978 | | | 3 | | 3 |
| *Helicodiscus parallelus* (Say, 1817) | | | 3 | | 3 |
| *Troidopsis soelneri* (J. B. Henderson, 1907) | | | 3 | | 3 |
| *Deroceras* sp. | | | 2 | | 2 |
| *Glyphyalinia indentata* (Say, 1823) | 1 | | 1 | | 2 |
| *Vertigo rugosula* Sterki, 1890 | | | 2 | | 2 |
| *Vertigo ventricosa* (Morse, 1865) | 2 | | | | 2 |
| *Striatura ferrea* Morse, 1864 | 1 | | | | 1 |
| *Triodopsis hopetonensis* (Shuttleworth, 1852) | | | 1 | | 1 |
| Total co-occurring individuals | 664 | 1613 | 3359 | 250 | 5886 |
| Co-occurring species richness | 13 | 9 | 26 | 10 | 34 |

[1] Data taken from 49 discrete sites of the junior author collection (lots prefixed by JCN in Table 1).

[2] Juveniles and young adults of unclear identity.

*ventricosa* were sympatric in New England, while *Vertigo milium*, *Vertigo alabamensis*, *Vertigo oralis*, *Vertigo conecuhensis*, and *Vertigo rugosula* were sympatric in the Carolina and Gulf coastal plains.

## CONSERVATION IMPLICATIONS

The data presented here show that *Vertigo malleata* is a characteristic component of the base-poor biota of the Atlantic and Gulf coastal plains, having been found in 66% of surveyed acid sites, and accounting for up to 75% of all mollusks in these sites. The abundance and widespread occurrence of *V. malleata* would seemingly suggest that it is not of immediate conservation concern. However, it appears that the species is in fact under threat because of the widespread use of fire as a management tool. Many coastal plain habitats, including those of *V. malleata* (i.e., pine woods, pine-wiregrass savanna, and pine barrens), have come to be viewed by many plant ecologists as pyrogenic (Myers, 1985; Christensen, 1988) and are being typically managed by anthropogenic fire return intervals of <5 years, with many areas being burned annually. However, such high-frequency fire management policies have been shown to exact a strong negative impact on total biodiversity, including Lepidoptera, Homoptera, Hymenoptera, Araneae, Collembola (Swengel, 1996, 1998; Harper et al., 2000), and terrestrial Mollusca (Nekola, 2002b).

The impact of fire on *Vertigo malleata* is illustrated by its distribution in the Appalachicola uplands of Florida.

We were unable to find *V. malleata* in forest that had been burned within three years, however, the presence of substantial populations in a tiny unburned inholding of mesic pine forest (Table 1 site 11), unburned mesic pine-red maple-Atlantic white cedar forest (Table 1 site 14), and unburned mesic margins of wetlands (Sites 8, 9, 12–13, 15–17) suggest that while it is not physiologically restricted to wetlands, it has become largely limited to these sites simply because they remain unburned. While these observations require further investigation, we estimate that at least 95% of the *V. malleata* population of the Apalachicola National Forest has been eliminated by management practices. Conversely, the presence of *V. malleata* in mesic bay-pine forest that had regenerated after burn (Table 1 site 10) shows that, apart from its intrinsic interest as an extreme calcifuge, this snail can potentially be used to monitor recovery from over-burning.

## ACKNOWLEDGMENTS

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# Population dynamics of the fingernail clam *Sphaerium occidentale* (Lewis, 1856) (Bivalvia: Sphaeriidae) in an intermittent pond

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## ABSTRACT

A population of *Sphaerium occidentale* (Lewis, 1856) was studied over a two-year period in an intermittent freshwater pond in southern Ontario, Canada. Sub-populations in control areas of the pond showed marked differences between the two years, which appeared to be related to different hydroperiods (34 days in 2001 vs. 94 in 2002), water temperature, and density of suspended bacteria. In the first year, there was recruitment of young into the population in April/May, but there appeared to be very little or no reproduction in the second year. Resource (decaying riparian leaves) addition and removal experiments performed in the second year had an impact on some but not all of the physico-chemical parameters measured in the pond, and also affected bacterial densities. However, there were no significant overall effects of these manipulations on subpopulations of *S. occidentale*, although there was a trend toward greater density and biomass in the resource removals during the first half of the hydroperiod. *Sphaerium occidentale* appears to be well adapted for survival in such harsh environments via a specialized physiology and, reproductively, employing a bet-hedging strategy. However, populations may occasionally be reduced to levels that may result in local extinction. To counter the latter, sphaeriids have dispersal mechanisms that allow recolonization from metapopulations.

## INTRODUCTION

Sphaeriid clams are widely distributed and many species inhabit temporary freshwater habitats. They are important components of the benthic communities of such habitats where they act as water clarifiers and organic nutrient sinks (Thorp and Covich, 2001). Sphaeriids are known to be simultaneous hermaphrodites, with the ability to self-fertilize, a trait well suited to founding and maintaining populations in temporary waters (Williams, 2006). *Sphaerium occidentale* (Lewis, 1856), commonly known as Herrington's fingernail clam, is unique among the Sphaeriidae in that it is exclusive to temporary waters (McKee and Mackie, 1981). Along with all other sphaeriids, individuals of this species brood its direct-developing young within special sacs in the inner demibranchs of the gills, from where they are eventually released as benthic juveniles (Mackie et al., 1974). Although many sphaeriids are synchronous brooders, species of *Sphaerium* are sequential brooders—that is, several sets of embryos, each in a separate stage of ontogeny, are present within the brood sacs, together, each the product of a separate spawning (Mackie, 1978). Presumably, this trait is a bet-hedging strategy conducive to releasing a subset of viable young rapidly at the beginning of a hydroperiod of uncertain length, while maintaining a reserve should the first subset be lost (Stearns 1992). Although the population dynamics of *Sphaerium occidentale* are not well known, McKee and Mackie (1981) observed that the species completed its life cycle in 24 weeks when maintained under a stable hydroperiod in the laboratory, as opposed to three years in an intermittent pond. This finding supports the hypothesis of Thorp and Covich (2001) that seasonal variation in water level drives bivalve life history traits. The purpose of the present study was to determine any relationship between hydroperiod length and the population dynamics of *S. occidentale* in an intermittent pond, and to explore other possible influences through field manipulation experiments.

## MATERIALS AND METHODS

The study population lives in an intermittent pond in Vandorf, southern Ontario, Canada. The pond is devoid of fish and has an area of approximately 1000 mm$^2$ at the beginning of hydroperiod. It is surrounded by a hay field and mixed deciduous woodland and supports emergent vegetation comprising mainly *Phalaris* grass. The pond substrate is primarily muddy and homogeneous throughout. The population was studied over a two year period

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in 2001 the pond held water for 34 days and had a maximum depth of 66 cm; in 2002 it held water for 94 days and had a maximum depth of 48 cm.

The populations were studied in six randomly chosen areas of the pond that were enclosed with watertight, circular galvanized sheet-metal walls installed prior to snowmelt in 2001. The walls were embedded 10 cm into the substratum and rose well above the water surface, forming corralled homogeneous sections of the pond each 2.4 m in diameter. Two of the enclosures were chosen at random to serve as controls. In the autumn of 2001, the locations of the control enclosures within the pond were changed in order to avoid carry-over effects, and the other four enclosures were manipulated to either receive additional riparian leaf litter (two each received a mixture of dry maple and beech leaves [~3.0 kg] that had been dried for 24 hours at 100°C), or have litter removed (~1.5±0.04 kg of leaves and other vegetation from each of the remaining two). It might be argued that the use of imperforate galvanized metal enclosures may have rendered the treatments uninhabitable (i.e., produced a container effect) for *S. occidentale*, but that is highly unlikely as clams are virtually immobile and non-selective filter feeders. Further, evidence from other taxa (e.g., ciliates) in this pond showed that the enclosures resulted in higher species richness and abundance (Andrushchyshyn et al., 2006).

The environments within the enclosures were sampled on a weekly basis beginning as soon as the pond basin filled in 2001 and again in 2002. The following parameters were measured: water depth, with a one-meter stick, and dissolved oxygen, pH, temperature, and conductivity with a portable Hach Kit spectrophotometer (DR2000; Hach Company, Loveland, Colorado, USA). Turbidity, ammonia, nitrate, and phosphorus were measured using a Hydrolab multiprobe (Hydrolab Corporation, Austin Texas, USA), and chlorophyll *a* was measured using the acetone extraction method (American Public Health Association, 1995). To assess bacterial density, a column of water extending from the bed to the surface was collected using a plastic tube; this was done at two locations within each enclosure and then combined in a bucket from which a subsample of 30 cm$^3$ was removed and stained with acridine orange. These stained samples were then filtered through a 0.2 µm Sartorius filter (Cat. No. 13007) and the bacteria counted (on ~20 fields with a concentrations of ~200 bacteria per field of view) under an epifluorescence microscope, following the method of Sorokin (1999).

Clams were sampled using a galvanized-steel box sampler (area 0.1 m$^2$) which was inserted 2 cm into the pond bed. Two such benthic samples were taken at regular intervals from random locations in the control enclosures in 2001 and from the control and treatment enclosures in 2002. All samples were put in large Ziploc bags, labeled, and preserved in 4% formalin in the field. In the laboratory, clams were removed by sieving and handpicking under a magnifying lens from samples collected on 7 April, 3 May, 10 July, and 21 August in 2001, and 7 April, 6 May, 3 June, 11 July, and 6 September in 2002. All specimens were counted, blotted on filter paper to remove excess water, and weighed to the nearest 0.0001 g using a digital balance. All specimens proved to be *Sphaerium occidentale*, and identification was confirmed by Dr. Gerald Mackie (University of Guelph, Canada). Clam lengths (anterior to posterior) were measured to the nearest 0.1 mm using a dissecting microscope fitted with an ocular micrometer, and specimens were assigned to the following four length classes: <2.5, 2.5–4.0, 4.1–5.5, and > 5.5 mm.

## RESULTS

### CONTROL POPULATIONS:

In 2001, the hydroperiod of the Vandorf pond was short (34 days, from 7 April to 17 May) and likely related to a rapid 10°C warming of the pond in the first week of May (Figure 1a, b) and low rainfall. Associated with this warming was a significant increase in the density of suspended bacteria [Figure 1c; F=7.14, p=0.02, from a repeated-measures ANOVA], perhaps partly a concentration effect, and a marked increase in the growth of individual clams (Figure 2a). From May to July, 2001, mean biomass increased from 0.33±0.02 to 2.1±0.22 g 0.1 m$^{-2}$ of pond bed area (ANOVAR F=5.95, p=0.03). At the times of sampling the dry pond bed in July and September, 2001, no additional growth was noted. In 2002, the hydroperiod was considerably longer (94 days) and started almost three weeks earlier (18 March to 19 June; Figure 1b). While water temperature attained the same maximum value as in 2001, its increase was more gradual (Figure 1a). Bacterial densities throughout 2002 were more stable, except for a minor increase in early June (Figure 1c). Clam growth during 2002 was very different from 2001 and was largely limited to shifts from size class 1 to 2 in May–June (Figure 2b; ANOVAR F=12.88, p=0.005). Biomass increased from 0.24±0.14 g 0.1 m$^{-2}$ in May to 0.88±0.39 g 0.1 m$^{-2}$ in July (ANOVAR F=15.13, p=0.0001).

Between-year comparisons suggest that while there was recruitment of young into the population in April/May of 2001 (Figure 2a), the similarity in population structure between September, 2001 and April/May, 2002 and concomitant decline in density of juveniles (Figure 2b) indicate that reproduction did not occur in 2002.

### MANIPULATED POPULATIONS:

The resource addition and removal experiments performed in 2002 had an impact on some but not all of the physico-chemical parameters measured in the Vandorf pond. Largely unaffected, compared with the control enclosures, were water temperature (although there was an increase in the resource addition enclosures in May), water depth, pH (Figure 3 a,b,c), phosphorus, and chlorophyll *a*. Affected were dissolved oxygen levels (typically

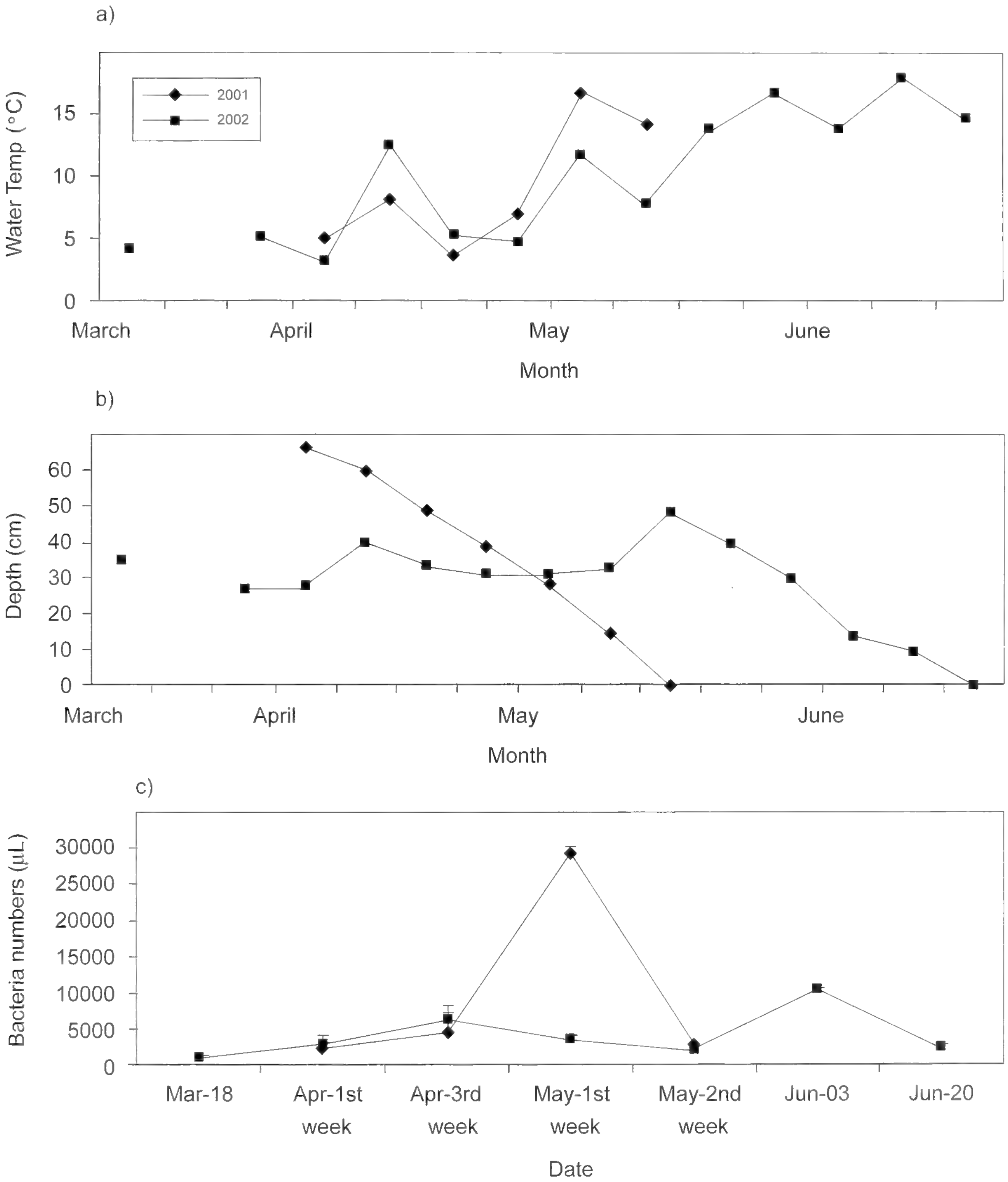

**Figure 1.** Seasonal variation in water temperature, depth, and bacterial density in the control enclosures in 2001 and 2002. Mean values are shown for the control enclosures. Error bars for bacteria indicate ±1SE ($n$ = 2).

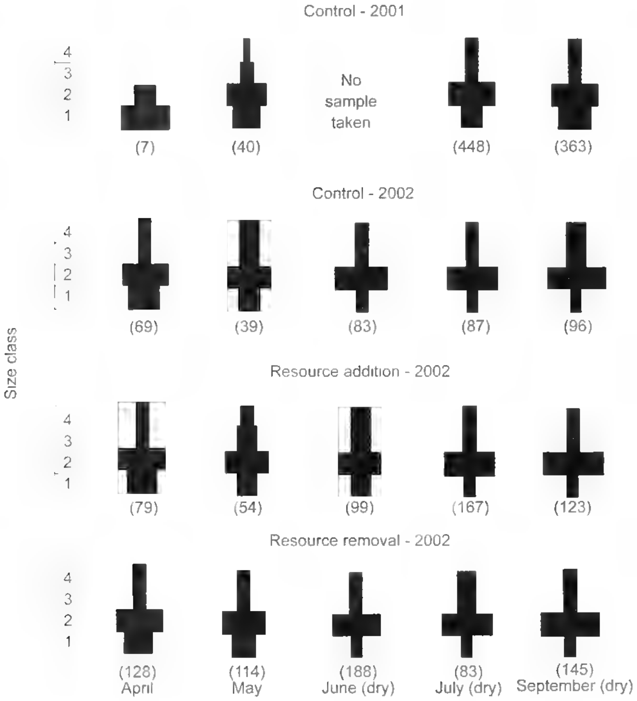

**Figure 2.** Seasonal length frequency distribution of *Sphaerium occidentale* in 2001 and 2002. Size classes 1, 2, 3, and 4 represent clams < 2.5, 4, 5.5, and > 5.5 mm, respectively, in length. Numbers in parentheses are sample sizes.

highest in the resource removal and lowest in the resource addition treatments) and nitrate (highest in the resource additions early on in the hydroperiod) (Figures 4 a,b). Bacterial densities were highest in the resource addition treatments, lowest in the resource removals, and intermediate in the controls during the first half of the hydroperiod, but more similar thereafter (Figure 4c).

Despite differences in the above parameters, there were no significant overall treatment effects on the densities or biomass of *S. occidentale*, although there was a trend towards greater density and biomass in the resource removals during the first half of the hydroperiod (Figure 5a,b). Neither did there appear to be any notable differences in the population structures in the addition and removal enclosures compared with the 2002 controls (Figure 2b,c,d).

## DISCUSSION

The sharp rise in water temperature and rapid decline in depth of the Vandorf pond in early May of 2001, accompanied by low rainfall, likely promoted the short hydroperiod in that year. Bivalve feeding filtration rates are known to be proportional to the ambient temperature (Thorp and Covich, 2001). Thus the sudden 10°C warming of the pond fortuitously allowed *S. occidentale* to benefit maximally from the high density of suspended bacteria available at that time, and to grow rapidly. However, and in spite of the longer (~3 times) hydroperiod in 2002, during this second year *S. occidentale* individuals grew much more slowly—although a growth spurt did occur during the higher temperatures reached prior to pond dry-up in June. Based on this two-year comparison, it would appear that individual clam growth does not necessarily benefit from a longer hydroperiod—indeed a shorter one may be better provided that food supply and water temperature are favorable. Thomas (1963) noted, however, that *S. partumeium* (Say, 1822) grew more under a longer hydroperiod—although its life span is 12–13 months compared with up to 3 years in *S. occidentale*. The former species may well be predisposed to continued growth in that its semelparous strategy commits it to development and reproduction under sometimes less than optimal pond conditions. *S. occidentale* appears to demonstrate more plasticity in its growth rate (McKee and Mackie, 1981), and its iteroparous strategy may allow it, on occasion, to forego a less than favourable reproductive opportunity.

Only adult (our size class 4) *S. occidentale* release offspring (McKee and Mackie, 1981). Some of the subadults present in April 2001 grew rapidly, attained size class 4, and produced large numbers of size class 1 and 2 young, as evident from the very high densities found in July 2001. As *S. occidentale* is, as previously noted, a sequential brooder it is conceivable that the high July densities may have resulted from multiple release events of young from April until the end of the hydroperiod. The same size-class proportions present in the July and September samples indicate that no further growth took place during the period when the pond bed was dry, which agrees with the findings of McKee and Mackie (1983) for this species. Further, the presence of the same distribution of size classes in April (2002) shows that there was no winter growth or container effect from the use of imperforate metal enclosures. The substantial drop in clam density between September 2001 and April 2002 likely indicates winter mortality. Throughout 2002 no significant increase occurred in the control population and this, together with modest shifts towards the large size classes by September, suggests that the population largely failed to breed in this second year. Unlike *S. partumeium*, which is more commonly found in permanent waters (Clarke, 1973), and has a semelparous, univoltine life cycle where only juveniles aestivate and the resulting adults breed and die the next spring (Way et al., 1980), *S. occidentale* can aestivate in all size classes and has the potential to breed several times and over more than one hydroperiod as pond conditions allow.

Interestingly, the initial samples collected in April, 2001 produced very few clams, and no live adults. A possible explanation for this is that when sphaeriids reach their terminal size, they do not survive a subsequent dry phase (Way et al., 1980). It is likely, then that the majority of the previous year's population had been adults at the end of the 2000 hydroperiod. The population was thus at a very vulnerable stage in early 2001, but

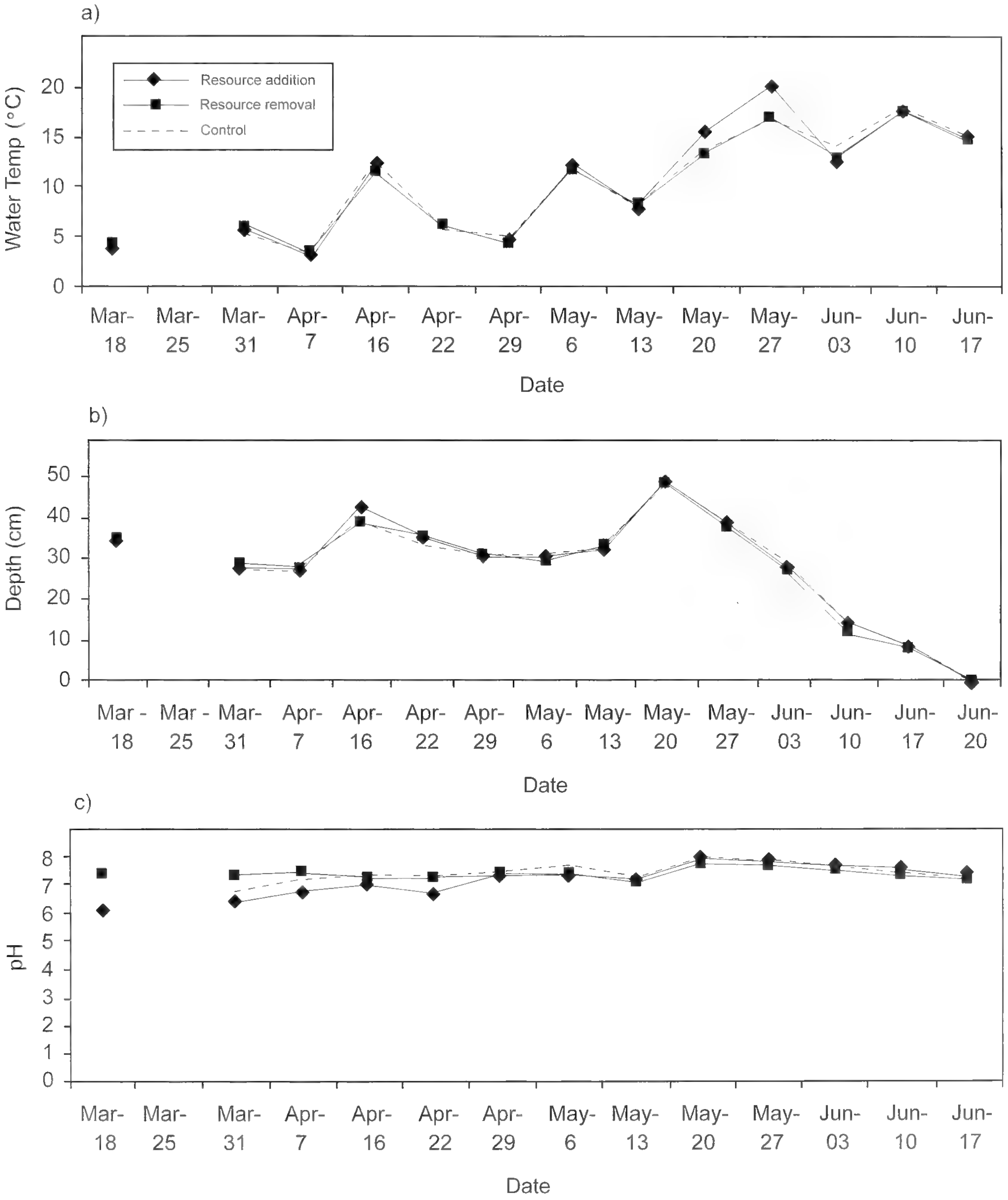

**Figure 3.** Seasonal variation in water temperature, depth, and pH in the treatment enclosures in 2002. Mean values are shown for the control, resource addition, and resource removal enclosures.

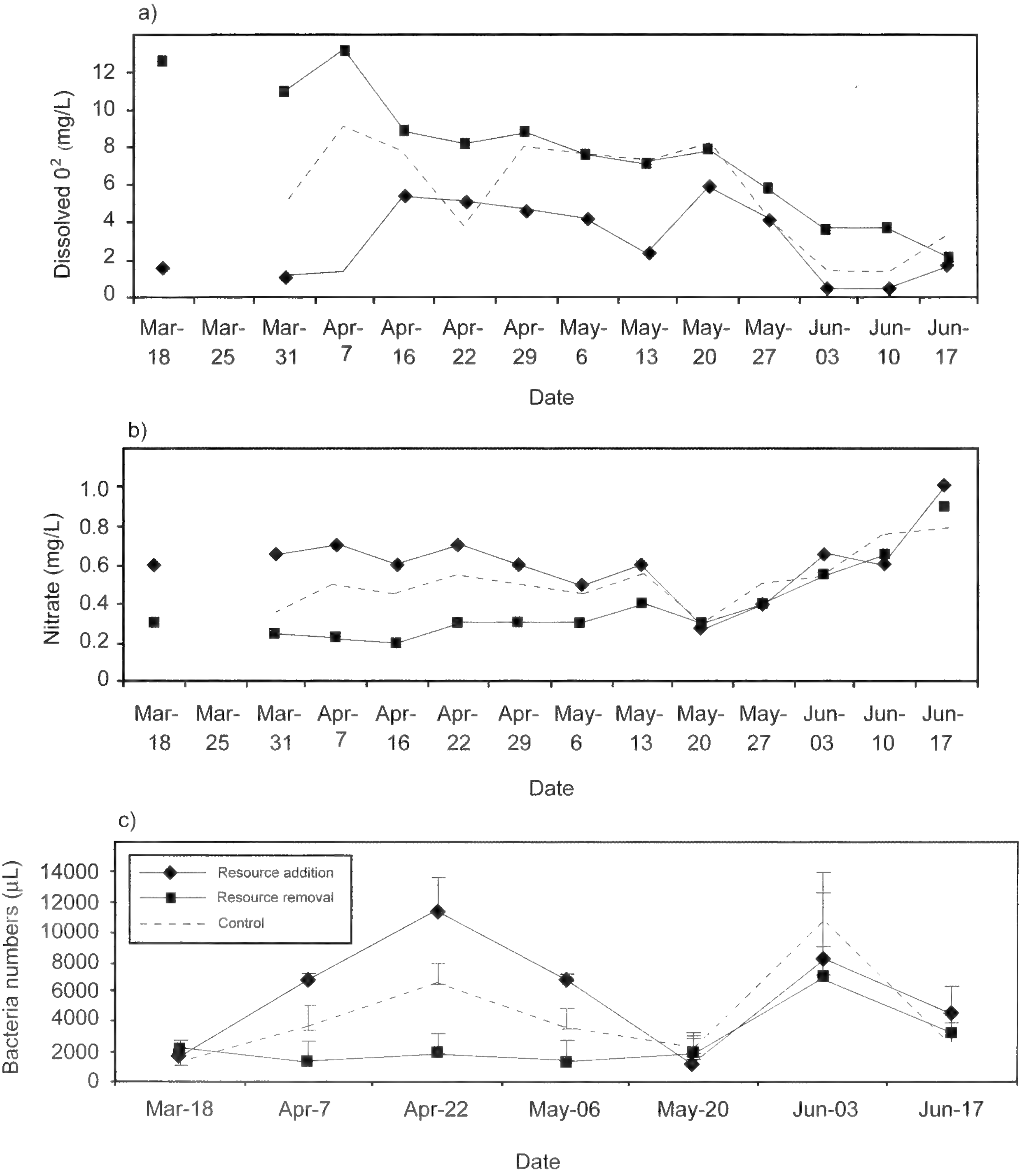

**Figure 4.** Seasonal variation in oxygen, nitrate, and bacterial densities in the treatment enclosures in 2002. Mean values are shown for the control, resource addition, and resource removal enclosures. Error bars for bacteria indicate ±1SE (*n* = 2).

was quite quickly restored by July, only to suffer substantial winter mortality in all size classes later that same year.

Removing resources from the enclosures was associated with an increase in dissolved oxygen and a lower concentration of suspended solids, although improved water clarity did not affect chlorophyll *a* production. Resource addition reduced oxygen levels and increased tur-

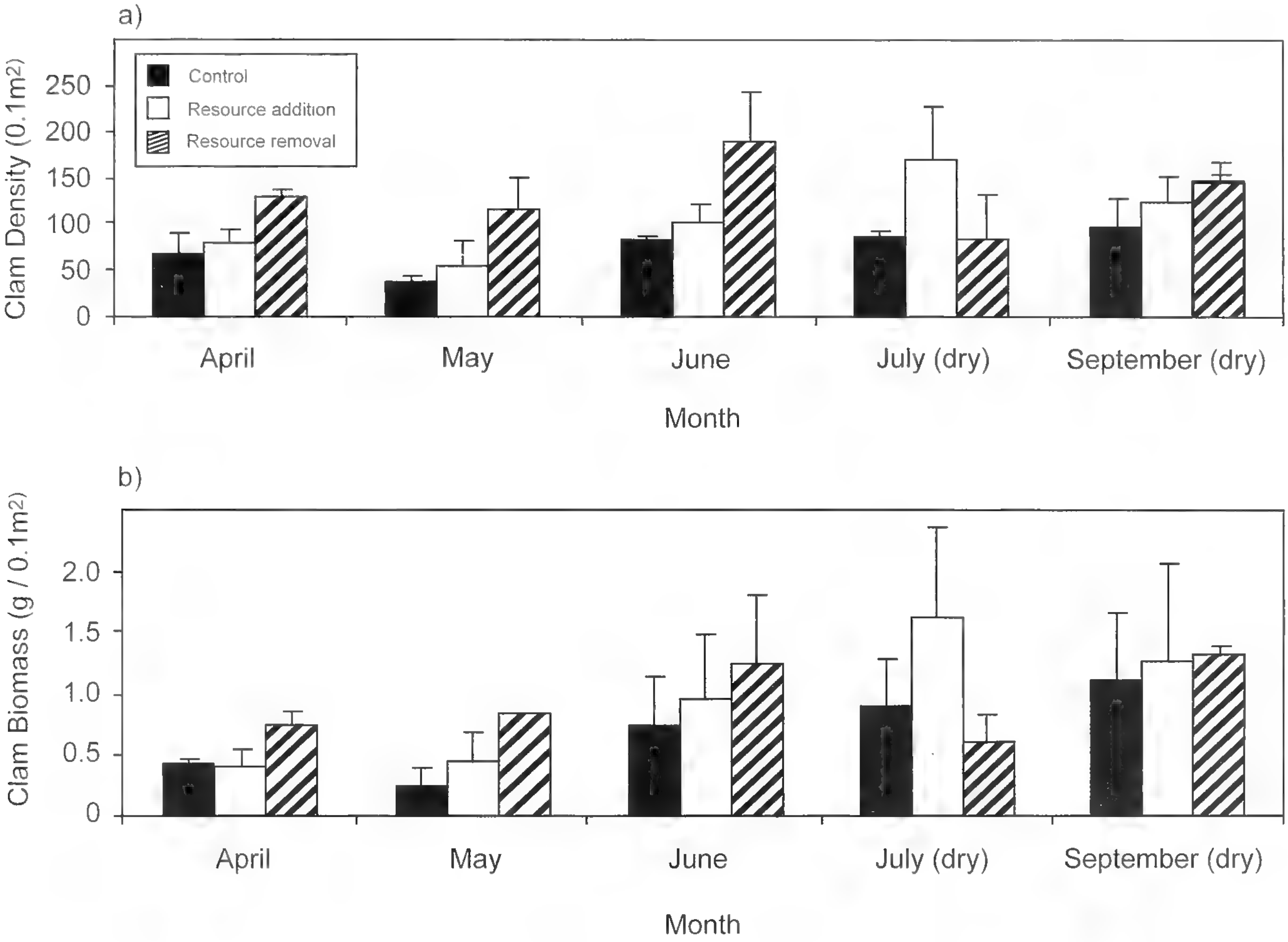

**Figure 5.** Mean values of *Sphaerium occidentale* densities in numbers 0.1 m$^{-2}$ and biomass in g 0.1 m$^{-2}$ in the treatment enclosures in 2002. Mean values are shown for the control, resource addition, and resource removal enclosures. Density and biomass bars indicate ±1SE (*n*=2) and ±1SD (*n*=2), respectively.

bidity, likely as a result of suspension of more litter breakdown products. While it might be expected that an increase in suspended food particles (including bacteria in the first half of the hydroperiod) would have benefitted the *S. occidentale* population (as shown for other detritivores, by Richardson, 1991), it is known that too high a concentration of suspended materials can interfere with the filtering and respiratory mechanisms of freshwater bivalves—although sphaeriids are known to be very tolerant of hypoxia (Thorp and Covich, 2001). Further, sphaeriids can also feed on pond bed deposits and thus a direct response to food particle manipulation may not be detectable. Despite the observed differences in the physico-chemical environments and food levels between the treatments and the controls, there were no apparent differences in the structure (size and growth) of the sub-populations. Lack of a differential response may be a reflection of the fact that intermittent ponds are normally subject to large within-year and between-year fluctuations in environmental variables (due to dilution, evaporation, etc.), and thus their inhabitants may not show population response patterns typical of those known from permanent ponds (Brönmark and Hansson, 1998).

The responses of the natural and manipulated sub-populations of *S. occidentale* in the Vandorf pond suggest that length of the hydroperiod was the major driving force on population dynamics. Further, the species exhibits a number of important adaptations that enable population survival despite large inter-year variations in its habitat, although populations may occasionally be reduced to dangerously low numbers that may result in local extinction. Sphaeriid clams are known, however, to be able to colonize/recolonize these small ponds via transportation on the bodies of more-mobile pond inhabitants (e.g., Fryer 1974). It is likely that such recolonization events from a regional metapopulation are common.

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## Research Note

# Paleoenvironmental significance of the eastern mud snail, *Ilyanassa obsoleta* (Say, 1822), from a microtidal coastal sequence of southern New England

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Reconstruction of former sea-level positions is one of the key issues in Quaternary paleoenvironmental research. Along with high-marsh peat that has been widely used for regional sea-level reconstructions due to its narrow and robust elevation range, intertidal mollusks inhabiting protected coastal embayments must also be considered as complementary reference points for the water levels. This paper presents evidence for potential use of the eastern (Atlantic) mudsnail *Ilyanassa obsoleta* (Say, 1822), as a paleoenvironmental indicator in middle Holocene deposits of southern New England.

The eastern mudsnail occupies tidal flats along the Atlantic seaboard, often occurring in dense populations on the sediment surface of intertidal mudflats or mixed flats (Brenchley, 1980; Whitlatch, 1982; Culbert and Raleigh, 2001). Their feeding habits include scavenging, predation, algal foraging, and deposit-feeding (Weiss, 1995; Kelaher et al., 2003), with feeding rhythms shown to be correlated with tidal cycles (Robertson, 1979). Native along the Atlantic seaboard, *Ilyanassa obsoleta* has been recently under stress of competitive exclusion and egg predation by invasive gastropods, such as *Littorina littorea* (Brenchley, 1982; Carlton, 1992) and has itself become an invasive species in some parts of the West Coast (Race, 1982). Although these snails are known to burrow into the substrate or migrate into shallow subtidal depths during the winter (Batchelder, 1915; Dexter, 1961; Brenchley, 1980), the depth of migration is likely to be limited by tidal range and wave energy. For example, in a microtidal coastal setting (mean tidal range: 0–2 m) where tidal flats are fronted by wave-dominated coastal barriers, the vertical habitat range of *I. obsoleta* will be relatively narrow (Whitlatch, 1982). This fact, combined with occurrence of the eastern mud snail in post-glacial deposits (past 10,000–15,000 years; Carlton, 1992), makes this species a potential indicator of former sea level.

The vertical range of a particular plant or animal species preserved in a geological record and its position relative to a specific tide level (indicative meaning; van der Plassche, 1986; Donnelly et al., 2004) can be estimated based on modern ecological response of that organism to tidal inundation. Therefore, comparison of in-situ shells of *I. obsoleta* with an adjacent reliable sea-level indicator, such as high-marsh peat, is the first step in assessing its paleoenvironmental significance. The aim of this paper is to use similar ages of *I. obsoleta* and high-marsh peat in submerged backbarrier deposits offshore Martha's Vineyard island, Massachusetts, as evidence of a potential use of this gastropod as an independent sea-level indicator.

The microtidal barrier coastlines of southern New England and Long Island have been formed in a regime of post-glacial marine transgression, with Holocene sedimentary sequences now submerged on the inner continental shelf (Rampino and Sanders, 1980; FitzGerald et al., 1994; Schwab et al., 2000). The low mean tidal range (0.7 m) and unlimited fetch offshore Martha's Vineyard island have combined to produce a high-energy, wave-dominated environment (Figure 1). Furthermore, the existence of a large glacial sand source has been conducive to the formation of coastal barriers, which at lower stands of sea level protected muddy coastal bays and fringing saltmarshes (Oldale, 2001). A recent geophysical study of the seafloor offshore Martha's Vineyard (Goff et al., 2005) offered an opportunity for study of the submerged Holocene coastal deposits that contained remains of shallow-water macrofauna, including *I. obsoleta*

High-resolution seismic imaging of the seafloor and vibracores, ranging in depth of penetration from 0.5 to approximately 2.0 m, were used to delineate a large submerged paleo-valley (Figure 1; Buynevich et al., 2002). The main valley (width: 300–500 m; depth: 1.5–7.0 m) is the offshore extension of Edgartown Great Pond, one of many proglacial spring-sapping valleys incised into the late Pleistocene glacial outwash deposits (Uchupi and Oldale, 1994). All of the sediment cores that penetrated marine sands and sampled organic-rich mud facies are confined to the paleo-valley. These deposits contain vari-

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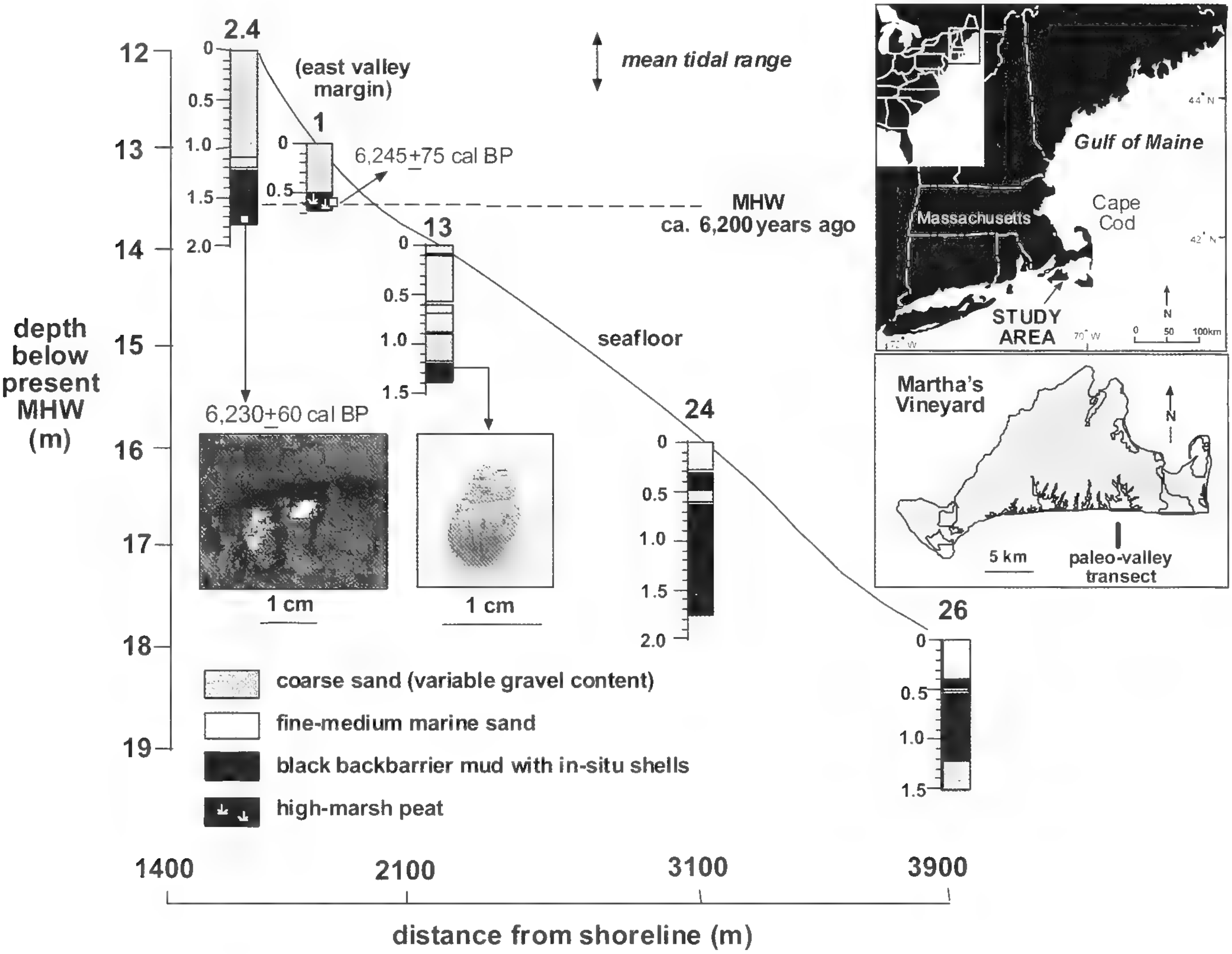

**Figure 1.** Geological section along the axis of the main valley offshore Martha's Vineyard (see inset for location) showing the occurrence of black, organic-rich backbarrier muds underlying marine sands. These facies contain in-situ gastropods and bivalves and have been sampled to a depth of at least 18 m below present sea level. Photographs: A) *Ilyanassa obsoleta* shells encased in black mud (one shell was used for dating). Saltmarsh peat recovered in the adjacent core 1 has a similar age and both dates are used to constrain the position of mean high water ca. 6,200 years ago. B) cleaned *I. obsoleta* shell from core 13 (sample depth: ~15 m below present sea level)

able amounts of organic material, occasional small burrows, as well as whole shells of *I. obsoleta* (Figure 1, photos) and shallow-water bivalves. One core through the valley margin retrieved a short section of saltmarsh peat, which suggests a low-energy backbarrier setting with saltwater access through a tidal inlet.

The age of an in-situ *I. obsoleta* shell from core 2.4 (14 m below present mean high water [MHW]) was determined with accelerator mass spectrometry (AMS) radiocarbon dating and compared to that of a saltmarsh peat from core 1 (13.5 m below MHW). A date of 6,230 ± 60 cal BP (calibrated years before present, 2σ error) of the shell provides an age for the minimum elevation of mean high tide level in this part of the valley fill. The age of 6,245 ± 75 cal BP on the saltmarsh peat ($\delta^{13}C = -15.4‰$) further constrains the paleo-MHW elevation at this location (Figure 1). Both dates plot in a relatively poorly constrained portion of the regional sea-level history, but fit well within the regional sea-level envelope of Oldale and O'Hara (1980), as well as New York and New Jersey shelf data (Stuiver and Daddario, 1963; Rampino and Sanders, 1980). The similarity between the ages of high-marsh peat and that of eastern mud snail, along with the geological context and ecology of *I. obsoleta*, demonstrates the potential of this species as a paleo-sea-level indicator. Although the elevation of muddy sediments and macrofaunal remains relative to contemporaneous sea level is less constrained than that of high-marsh peat, their association with peat and great cross-shore extent make them additional points of reference for the position of sea level. Substantial compaction by loading and vibracoring action is unlikely due to relatively small thickness of overlying sediments and basal positions of dated material in both cores, respectively.

This study demonstrates that in areas where occurrence and thickness of peat are limited, such as in microtidal settings, *I. obsoleta*-bearing muds may prove to be reliable indicators of past water levels, energy conditions, and former shoreline positions. In particular, intertidal and shallow subtidal portions of submerged valley fills provide an ideal geological setting for preserving a nearly continuous sequence of backbarrier sediments that can be used for paleoenvironmental and sea-level reconstruction.

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# Errata

In the last issue of *The Nautilus*, in the article by Thomas J. DeVries (2006), please substitute the specific epithet *mcleani* for *stucchii:*

On page 139, left-hand column, second paragraph, second line;

On page 140, legend of Figure 2, first line;

On page 146, left-hand column, sixth paragraph ("Remarks"), first line.

Due to an editorial lapse, the word *stucchii* was used unintentionally in these three instances.

## LITERATURE CITED

DeVries, T. J. 2006. The Neogene history of *Prisogaster* Mörch, 1850 (Gastropoda: Turbinidae) in South America. The Nautilus 120: 139–149.

# Notice

## THE 2007 R. T. ABBOTT VISITING CURATORSHIP

The Bailey-Matthews Shell Museum is pleased to invite applications for the 2007 R. T. Abbott Visiting Curatorship.

The Curatorship, established originally in accordance with the wishes of the late Dr. R. Tucker Abbott, Founding Director of the Shell Museum, is awarded annually to enable malacologists to visit the museum for a period of one week. Abbott Fellows are expected, by performing collection-based research, to assist with the curation of portions of the Museum's collection and to provide one evening talk for the general public. The Museum collection consists of marine, freshwater, and terrestrial specimens. A large percentage of our holdings have been catalogued through a computerized database management system; part of the catalogue is already available for searches online at: www.shellmuseum.org/collection.html. A substantial portion of the time will be available for research in the collection, but field work in southwest Florida can be arranged. The R. T. Abbott Visiting Curatorship is accompanied by a stipend of $1,500.

Interested malacologists are invited to send a copy of their curriculum vitae together with a letter detailing their areas of taxonomic expertise and research objectives, and to provide a tentative subject for their talk. Send materials to:

Dr. José H. Leal, Director
The Bailey-Matthews Shell Museum
P.O. Box 1580
Sanibel, FL 33957
jleal@shellmuseum.org

Applications for the 2007 Visiting Curatorship should be sent electronically to the above e-mail address no later than May 30, 2007, or postmarked by that date if sent by regular mail. The award will be announced by mid- to late June. Questions about the Visiting Curatorship should be sent to the e-mail address above, or by phone at:

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THE NAUTILUS publishes articles on all aspects of the biology, paleontology, and systematics of mollusks. Manuscripts describing original, unpublished research and review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of interest to the malacological community will appear in a notices section.

**Manuscripts:** Each original manuscript and accompanying illustrations should be submitted to the editor preferably via e-mail or as hardcopy in triplicate.

Text must conform to the dimensions of 8½ × 11-inch paper, double-spaced, and single-column throughout (including literature cited, tables, and figure captions). Authors should follow the general recommendations of *Scientific Style and Format—The CSE Manual for Authors, Editors, and Publishers*, available from the Council of Science Editors at www.councilscienceeditors.org. The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latinized names and other words to be printed in italics must be underlined; leave other formatting indications to the editor. Metric, not English, units are to be used. Geochronologic modifiers should be capitalized only when units are formally recognized: for instance, use Late Cretaceous but early Miocene. Likewise, only modifiers of formally recognized chronostratigraphic units are capitalized: use Lower Jurassic but upper Oligocene.

The sequence of sections should be title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). If corresponding author is not the senior author, please indicate. The abstract should summarize in 250 words or less the scope, main results, and conclusions of the article. Abstracts should be followed by a list of additional key words. All references cited in the text must appear in the Literature Cited section and vice-versa. Please follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included within the pagination of cited work. Tables must be numbered and each placed on a separate page. If in doubt, please follow a recent issue of the journal for sequence of sections and other style requirements.

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Compressed files (e.g., .jpg) may be used to facilitate transmission of files during original submission, but may not be acceptable at final submission (see below).

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# THE NAUTILUS

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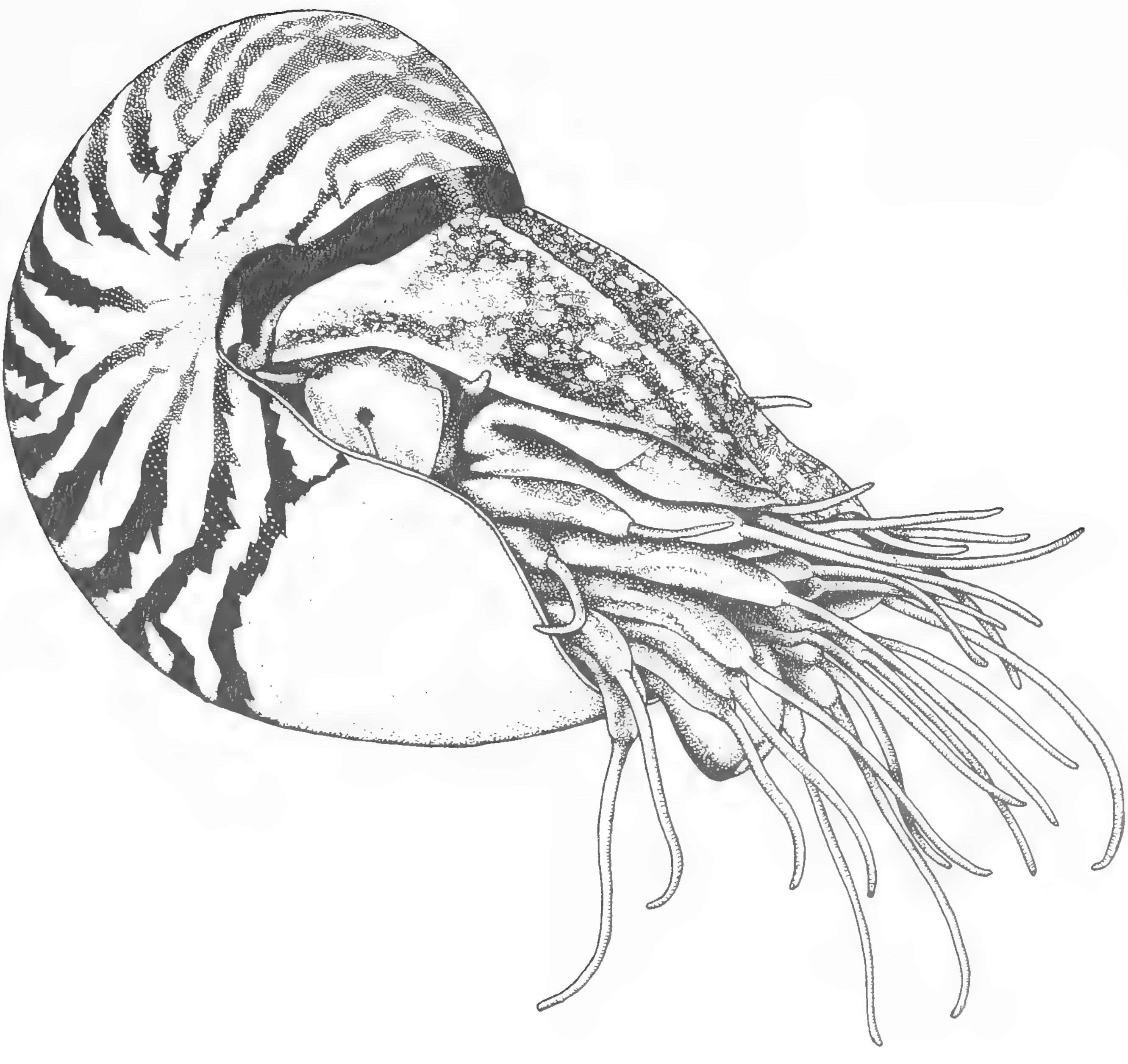

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# On the anatomy and systematics of *Juga* from western North America (Gastropoda: Cerithioidea: Pleuroceridae)

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## ABSTRACT

The family Pleuroceridae is a speciose and ecologically important family of limnic gastropods in North America and eastern Asia. *Juga* is the only native pleurocerid genus that occurs in Pacific drainage systems of Western North America, but has only recently been accepted as independent from other North American genera and may have affinities to Asian pleurocerids. As such, this genus represents a key piece to the puzzle of pleurocerid systematics. However, published accounts of *Juga* anatomy are limited to the reproductive system. Consequently, the anatomy of three species is described herein; these three taxa represent the type species of the three extant subgenera: *Juga* (*Juga*), *J.* (*Calibasis*), and *J.* (*Oreobasis*). A lectotype is designated for *Goniobasis acutifilosa* Stearns, 1890, the type species of *Calibasis*; *Melania newberryi*, the type species of *Oreobasis*, is here removed from the synonymy of *Juga bulbosa*.

This analysis confirms that *Juga* shares many anatomical features with other North American and Asian pleurocerids, but is clearly set apart from eastern North American pleurocerids in features of the ovipositor pore, radula, midgut, kidney, and pallial gonoduct. *Juga* is distinct from all other limnic cerithioideans known thus far in the form of the midgut crescentic ridge, the configuration of prostate glands, and an evagination of the kidney wall separating the main chamber and bladder. Based on information currently available, unlike molecular data, there is no morphological feature unambiguously linking *Juga* to Asian pleurocerids. Anatomically, *Oreobasis* is strikingly similar to *Juga* sensu stricto and is synonymized with it, whereas *Calibasis* is retained as a valid taxon.

## INTRODUCTION

The Pleuroceridae Fischer, 1885, is a speciose and ecologically important family of limnic gastropods occurring in North America and Eastern Asia. Despite their importance, understanding of their systematics is discouragingly incomplete. The current classification of limnic lineages within the Cerithioidea Fleming, 1822, is rooted in the works of Thiele (1928, 1929), who subdivided the heterogeneous Melaniidae Children, 1823 (an invalid name for Thiaridae Gill, 1871) into six subfamilies including the Pleurocerinae. An alternative classification advanced by Morrison (1954) distinguished only three limnic families: (i) the Pleuroceridae distributed throughout the Americas, Africa, and Asia, (ii) the Melanopsidae in Europe, and (iii) the pantropical Thiaridae. While promoting the important notion of several independent lineages, this concept heavily weighted plesiomorphic (ovipositor and oviparity) and homoplastic (brooding) features and resulted in a highly polyphyletic Pleuroceridae—a view that persisted for over three decades (e.g. Ponder and Warén, 1988). Recent work has resolved some of this confusion and supports the distinctiveness of many of Thiele's groupings (e.g. Glaubrecht, 1996, 1999; Lydeard et al., 2002; Köhler and Glaubrecht, 2001, 2003; Strong and Glaubrecht, 2002, 2003; Köhler et al., 2004; von Rintelen and Glaubrecht, 2005). However, molecular data (Lydeard et al., 2002) do not support monophyly of the Pleuroceridae as currently defined (e.g. Bouchet and Rocroi, 2005). The analysis of Houbrick (1988) based on morphological data did not include sufficient taxon sampling to adequately assess monophyly of the family.

In North America, pleurocerid diversity is highest east of the continental divide where they are represented by seven genera (*Athearnia* Morrison, 1971, *Elimia* H. and A. Adams, 1854, *Io* Lea, 1831, *Leptoxis* Rafinesque, 1819, *Lithasia* Haldeman, 1840, *Pleurocera* Rafinesque, 1818, and the extinct *Gyrotoma* Shuttleworth, 1845) and approximately 148 species currently considered valid (Johnson et al., 2005). *Juga* H. and A. Adams, 1854, with 11–12 estimated valid species (Burch, 1989; Turgeon et al., 1998; Johnson et al., 2005), is the only native pleurocerid genus that occurs in the Pacific and Interior drainages from central California to central Washington (Figure 1). Established on the basis of early teleoconch shell sculpture, four subgenera are recognized (Taylor 1966; Burch, 1989)—three are extant: *Juga* H. and A

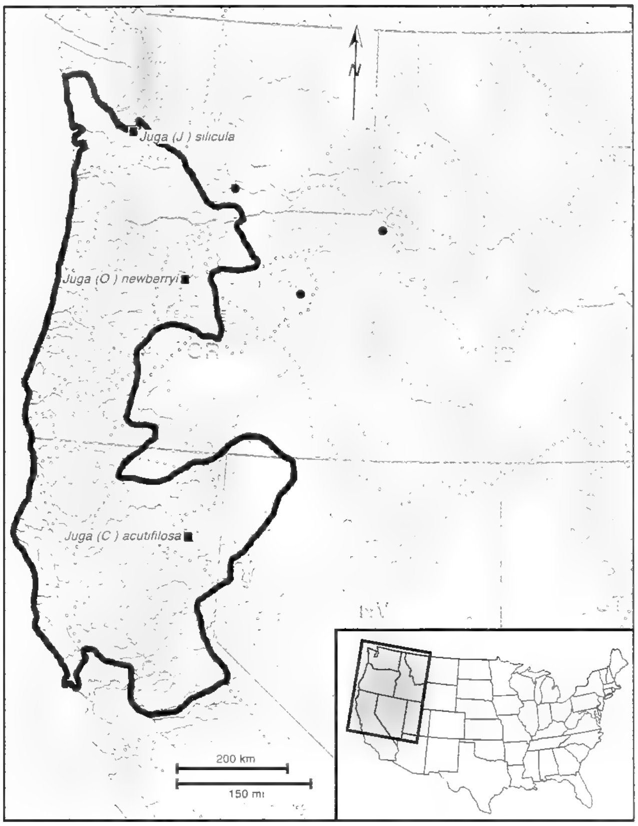


**Figure 1.** Distribution of *Juga*. Black line indicates currently known area of contiguous distribution. Black circles represent isolated sites beyond main distribution. Black squares are locations of extant subgeneric type localities and of material used in this investigation.

Adams, 1854 (with plicate early sculpture), *Calibasis* Taylor, 1966 (with lirate early sculpture), and *Oreobasis* Taylor, 1966 (with weak to no early sculpture). *Idabasis* Taylor, 1966 (with plicate and lirate early sculpture) is known only from fossils. Some east Asian species have also been assigned to *Juga*, but more recently these have been reassigned to *Parajuga* Prozorova and Starobogatov, 2004 (Starobogatov et al., 2004); however, this name is unavailable from a nomenclatural standpoint, as no type species was designated.

*Juga* has no discrete conchological feature that distinguishes it from eastern North American genera and has often been synonymized with *Goniobasis* Lea, 1862 (a junior synonym of *Elimia*) (e.g. Tryon, 1865, 1873; Pilsbry, 1899; Walker, 1918; Henderson, 1935a, b; Goodrich, 1942). Taylor (1966) was the first to restore *Juga* as a valid genus in the modern literature, primarily on the basis of its disjunct biogeographic distribution and the presence of a distinctive ovipositor (see Discussion, below). Based on recent molecular (Holznagel and Lydeard, 2000; Lydeard et al., 2002) and morphological findings (Prozorova and Raschepkina, 2004; Strong, 2005), *Juga* is supported as distinct from other North American pleurocerids and may have ties to those from eastern Asia (see Discussion, below). As such, this genus represents an important and intriguing part of the puzzle of pleurocerid systematics.

Thus, the goal of this analysis is to establish the anatomical organization for the type species of the current extant subgeneric subdivisions within *Juga*:

*Juga* H. and A. Adams, 1854: type species (by subsequent designation Baker, 1963) *Melania silicula* Gould, 1847.

*Calibasis* Taylor, 1966: type species (by original designation) *Goniobasis acutifilosa* Stearns, 1890.

*Oreobasis* Taylor, 1966: type species (by original designation) *Melania newberryi* Lea, 1860.

This also represents the first comprehensive anatomical investigation of any *Juga* species; the only information published thus far concerns female reproductive anatomy (Prozorova and Raschepkina, 2004). In the context of ongoing morphological and molecular phylogenetic analyses of pleurocerids and cerithioideans in general, this information is vitally important for assessing the affinities and relationships of taxa currently placed in the Pleuroceridae.

## MATERIALS AND METHODS

Specimens for morphological study were collected by hand or dip net, stored cold until evening, relaxed with menthol in shallow water from the same spring or stream in a broad, open container overnight, and transferred to dilute cold 4–5% formalin the next morning. Specimens were maintained in formalin for 48 hours then transferred to buffered 70% ethanol/10% glycerin/20% water for longer term storage. Voucher material is deposited in the National Museum of Natural History in Washington, DC, (USNM) and with Deixis Consultants in Seattle, WA.

Specimens were examined using a Leica MZ 12,5 binocular microscope with *camera lucida*; visualization of structures was enhanced with aqueous toluidine blue. Typically 2 to 4 specimens were examined for each organ system investigated, particularly for complex structures (i.e. midgut, nerves), as well as to assess intra-specific and/or seasonal variation in reproductive anatomy.

A comprehensive anatomical account is provided for *Juga* (*Juga*) *silicula*—the type species of the genus. Only discrete differences are detailed for *J.* (*Calibasis*) *acutifilosa* and *J.* (*Oreobasis*) *newberryi* with comparative remarks highlighting qualitative differences. As far as can be determined, near topotypic material was used for this investigation (see details below). A thorough systematic treatment of each species is not provided as a phylogenetic analysis and comprehensive revision of the genus are forthcoming (Frest et al., unpublished data).

Geographic names, road names and numbers, and land ownership data were confirmed using the DeLorme Mapping Washington, Oregon, and Northern California Atlas and Gazetteer, the latest available USGS 7.5′ series topographic maps, and National Geographic TOPO! 2006. Universal Transverse Mercator (UTM) grid coordinates are based on NAD27 (1927 North American Datum). Locality descriptions have been downloaded from Deixis Consultants MolluscDB$^{\text{TM}}$. Collector abbreviations are as follows: EJ, Edward J. Johannes; TF, Terrence J. Frest.

Institution codes cited in the text are: USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC; MCZ: Museum of Comparative Zoology, Harvard.

## RESULTS

### Pleuroceridae Fischer, 1885

### *Juga* (*Juga*) *silicula* (Gould, 1847)

**Type Material:** Three syntypes (USNM 12137) (cited as MCZ 12137 in Graf, 2001) (Figures 2–4). Johnson (1964) indicated that the largest (Figure 3) might be the specimen illustrated by Gould (1852, 1856, pl. 10, figs. 164, 164a); however, in number of whorls and overall size, the figured specimen is most likely the smallest syntype (Figure 2). As the figured specimen represents the smallest syntype, and the largest specimen mostly lacks the distinguishing axial ornament characteristic of juvenile shells, a lectotype is not here selected.

**Type Locality:** Indicated as "Nisqually, Oregon" (Gould, 1847) (see Figure 1). These specimens likely would have been collected by the Wilkes Expedition, 1838–1842, before the separation of Washington Territory from the larger Oregon Territory in 1853. This expedition started from Fort Nisqually, which was located in the current Washington State (still part of Oregon Territory in 1847). There was no rail station or city with the name "Nisqually" at that time. Thus, the river or the fort would be indicated. Johnson (1964) reported the type locality as "near present site of Tacoma, Washington" (also perpetuated by Graf, 2001), which is loosely true but unnecessarily vague and misleading as Tacoma lies outside the northern range of *Juga*, which ends just north of the Nisqually River (Pierce-Thurston Co. line)—by no mere coincidence near the approximate southern terminus of Late Wisconsinan glaciation.

The Nisqually River is a glacial flour stream originating on Mount Rainier with a depauperate freshwater mollusk fauna, despite various literature ascriptions. Its tributaries are comparatively rich, however, especially as they approach Puget Sound. "Nisqually" thus likely refers to Fort Nisqually, one of two trade outposts of the Hudson Bay Company, founded in 1833 on the Nisqually Reach directly south of Sequalitchew Creek (Hitchman, 1985)—a Puget Sound tributary northeast of the Nisqually River. In 1843 the operation was moved about 2 miles northeast, to approximately the present site of Dupont, Washington (Phillips, 1997), roughly in the same drainage. For quite some time, this was the only settlement in the area, so that the origin of Gould's specimens could be Sequalitchew Creek or one of the other nearby tributaries of the Nisqually River. Attempts to collect *Juga* from the boggy Sequalitchew Creek have been unsuccessful (Frest, unpubl. data). However, material from nearby McAllister Creek, also a Puget Sound tributary just west of the Nisqually River, has young specimens most closely resembling the types found thus far.

**Remarks:** Evidently a valid species (see also Goodrich, 1942; Burch and Tottenham, 1980; Burch, 1982a, b, 1989; Graf, 2001) but perhaps with a rather restricted range, confined to a few streams on the southeastern end of Puget Sound, near the Nisqually River.

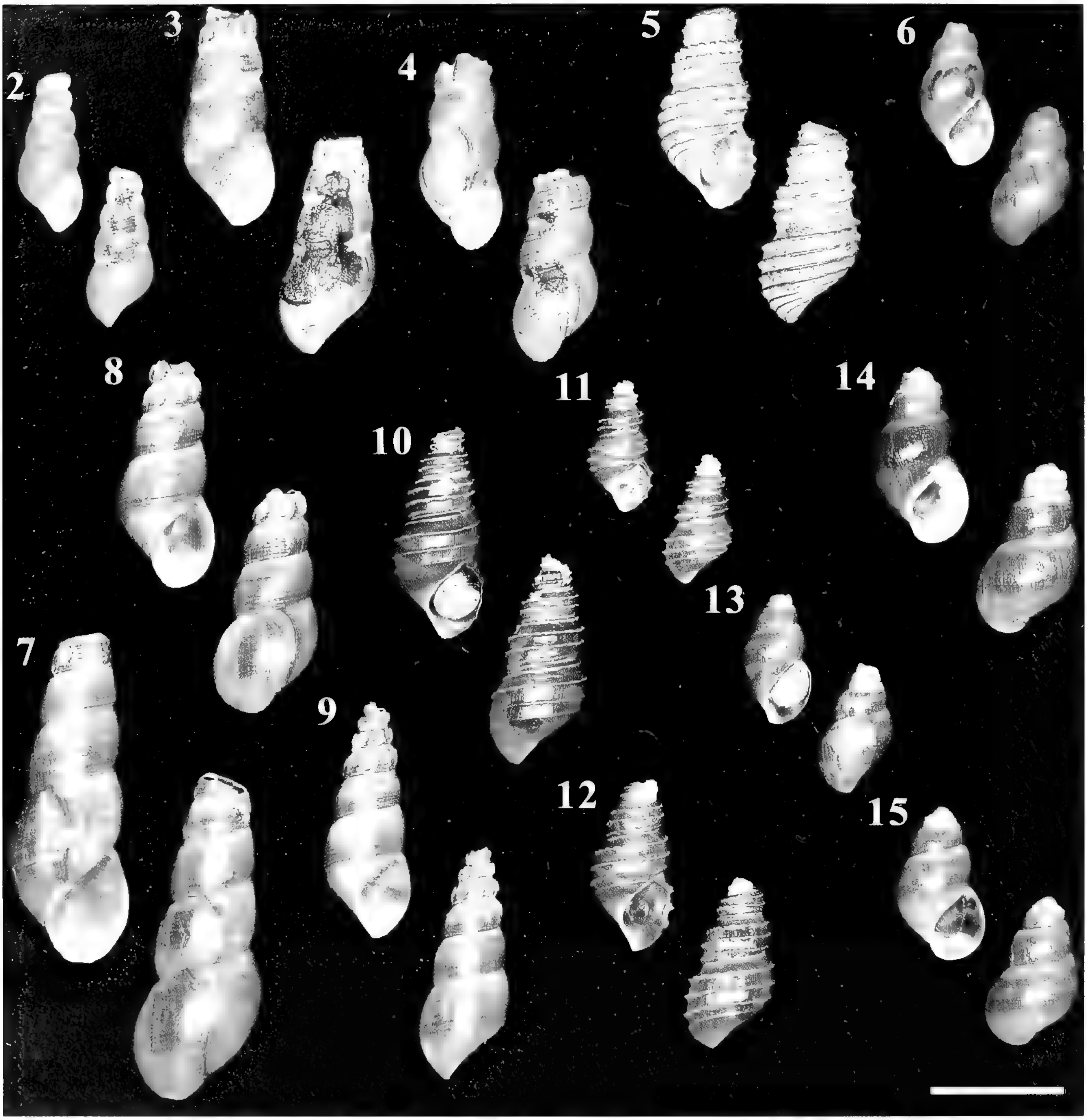
**Material Examined:** Washington: Thurston County: McAllister Creek at Steilacoom Road bridge, near McAllister Creek Hatchery, depth 0–1.22 m (Zone 10 520890E 5210540N [122°43′34″E, 47°02′59″N], Nisqually 1994 7.5′ quadrangle, elevation 1.5 m), Deixis Consultants locality #5709, 29 Sep. 2005, collected by TF, EJ (USNM 1100657) (9 specimens dissected) (see Figures 7–9).

**External Anatomy:** Operculum ovate, corneous, dark reddish brown in color, with 3.5 whorls; paucispiral with eccentric nucleus of approximately 3 whorls (Figure 16). Nucleus comprising slightly less than one half of total length (~45%).

Head-foot dark gray to black in color, with lighter gray snout tip and and pale foot sole; in females, ovipositor groove pale in color. Foot broad with wide propodium and long anterior pedal gland along anterior margin (Figure 17, **ap**). Ciliated egg groove forming longitudinally grooved tract extending from anterior tip of pallial gonoduct (**go**) and broadening continuously into shallow triangular shelf on side of neck below right cephalic tentacle (**ovp**). Ovipositor surface grooved, with folds directed medially into pore. Shallow grooved tract extending from pocket to edge of foot, short distance back from anterior pedal gland. Extensible snout (Figures 17, 18, **sn**) broad, squarish, with short triangular cephalic tentacles (**t**); tentacles also short in relaxed specimens.

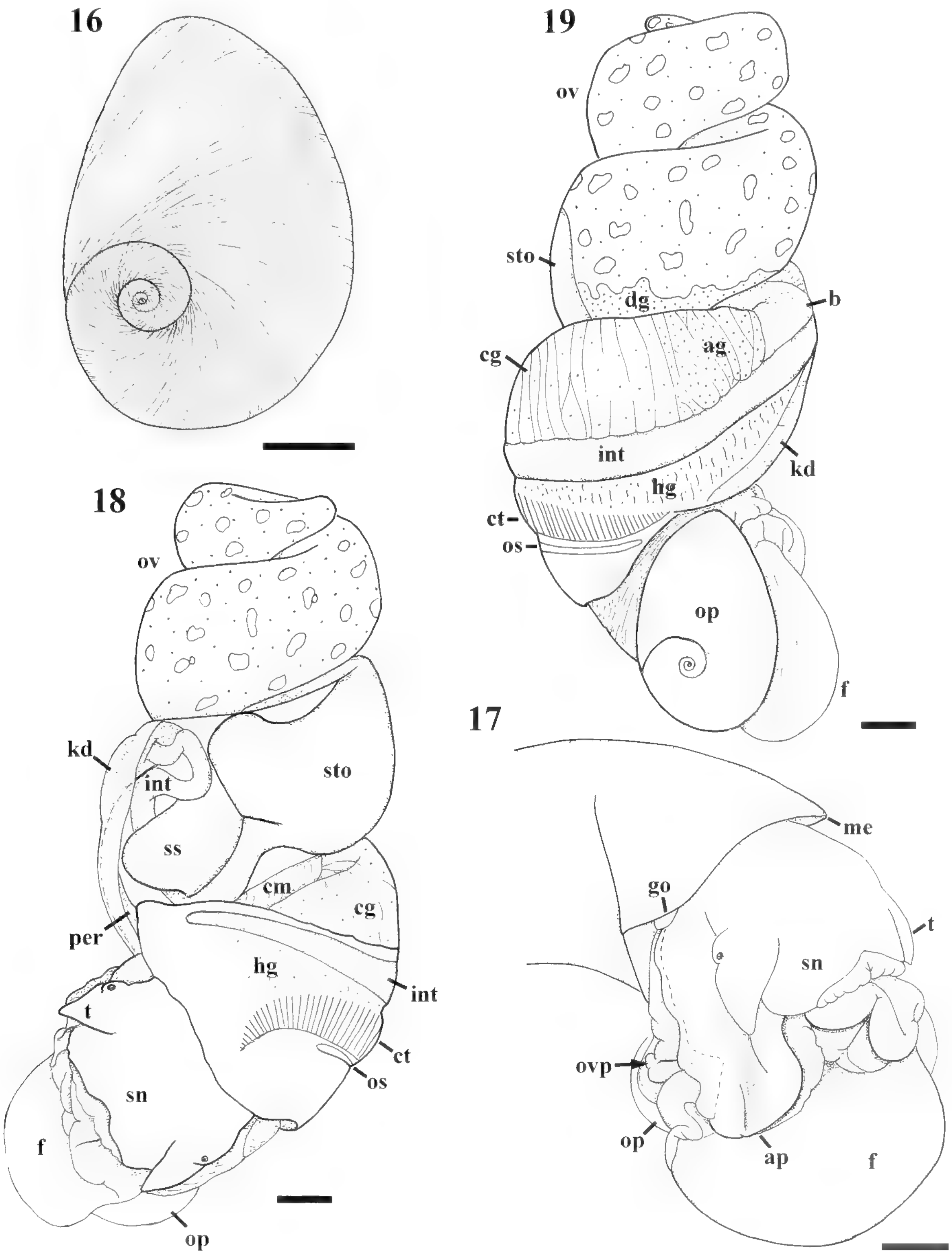
Ctenidium (Figures 18, 19, 26, **ct**) extending from posterior end of mantle cavity to near mantle edge, anteriorly curving toward the left. Osphradium forming simple ridge alongside efferent branchial vessel, sometimes with anterior tip markedly curving toward the left; osphradium undulating slightly at anterior and posterior ends, thinning posteriorly (**os**). Hypobranchial gland moderately well developed with transverse ridges, especially at posterior end of mantle cavity (Figures 18, 19, **hg**).

**Alimentary System:** RADULA: Radula comprising ~98 rows (n = 2) (Figures 20–25). Rachidian broadly rectangular, wider than tall, with smoothly rounded v-shaped lower margin and single small basal denticle at each lower, outer corner (Figure 22). Upper margin slightly concave with cutting edge bearing one large central triangular, spatulate cusp, and three stout, conical denticles on each side. Lateral teeth (Figures 20, 21, 23) with moderately short lateral extensions (slightly more than

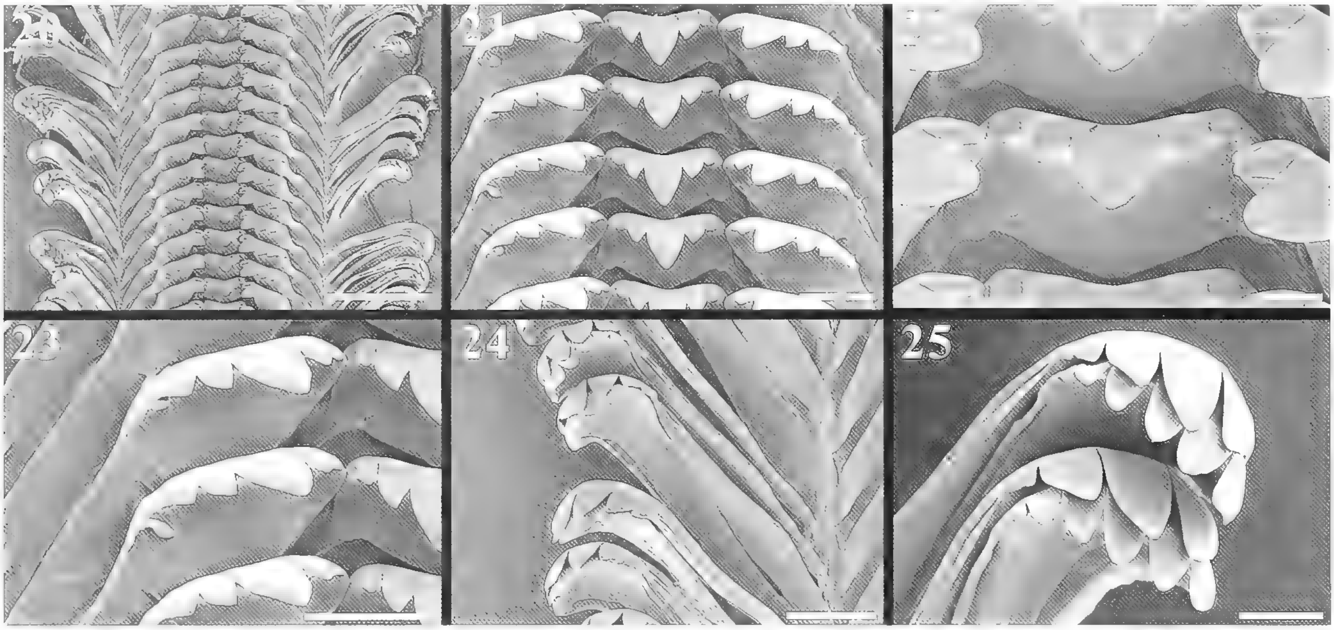


**Figures 2–15.** Shells of *Juga* species. **2–4.** *Juga* (*Juga*) *silicula* (USNM 12137, syntypes). Figure 2 is likely the figured specimen (Gould, 1852–1856, pl. 10, figs. 164, 164a). **5.** *Juga* (*Calibasis*) *acutifilosa* (USNM 60596, lectotype) (Stearns, 1890, pl. 15, fig. 9). **6.** *Juga* (*Oreobasis*) *newberryi* (USNM 118961, lectotype). **7–15.** Material examined in morphological analysis. **7–9.** *Juga* (*Juga*) *silicula* (USNM 1100659). **10–12.** *Juga* (*Calibasis*) *acutifilosa* (USNM 1100658). **13–15.** *Juga* (*Oreobasis*) *newberryi* (USNM 1100660). Scale bar = 1 cm.

half the length of lateral cutting edges), and single, prominent, spatulate cusp flanked by two inner and two to three outer denticles. Outermost denticle weakly developed and variable in shape, size, and position (Figure 23). Marginal teeth (Figures 24–25) with broadly rounded [illegible] long, slender shafts. Narrow flanges developed on outer edges of marginal teeth shafts along distal one half to two thirds. Outer flange much wider and longer on inner marginal tooth; outer flange only slightly wider on outer marginal tooth. Inner marginal teeth with six and outer marginal teeth with seven flattened denticles.



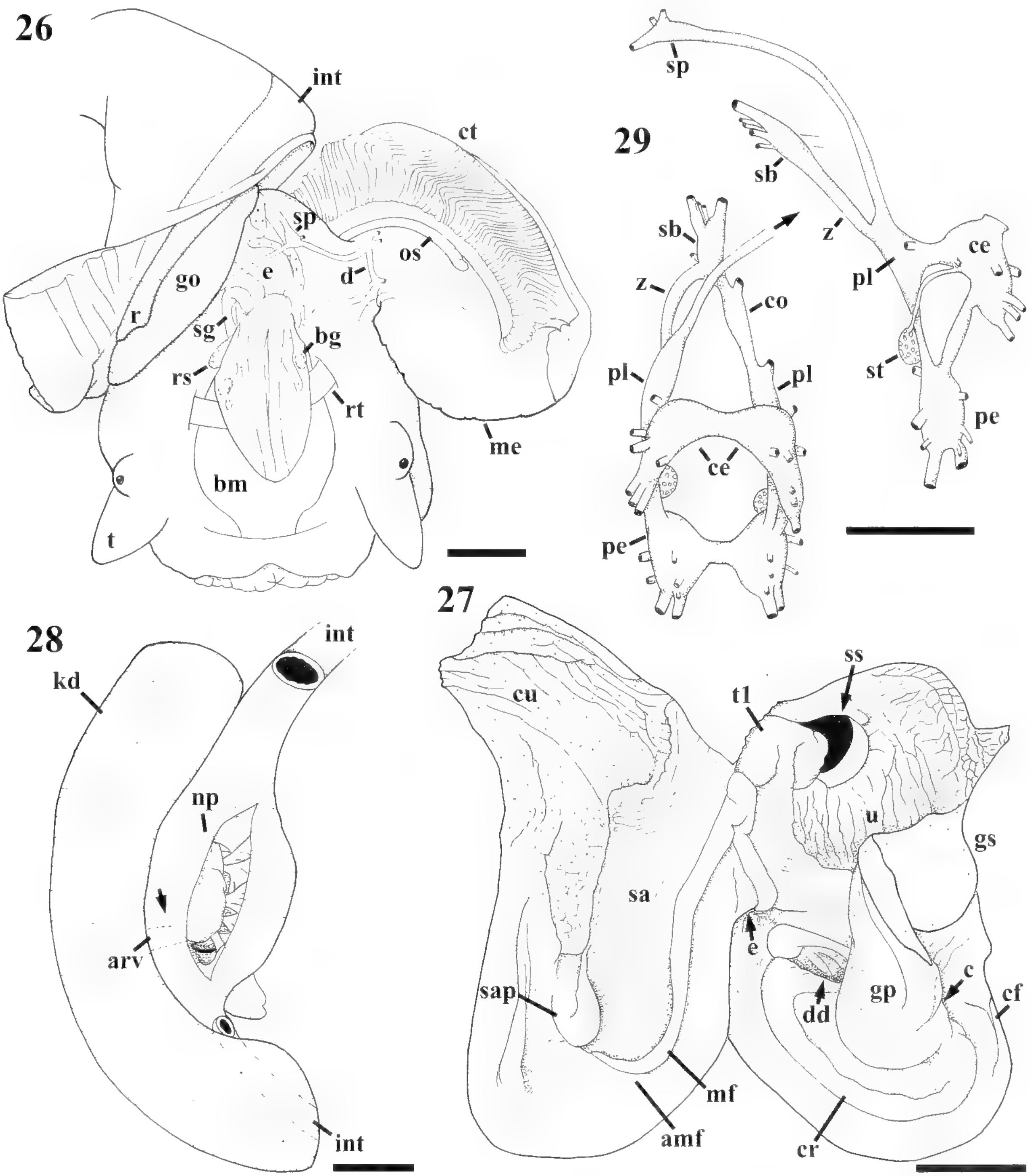
**Figures 16–19.** External anatomy of *Juga* (*Juga*) *silicula* (USNM 1100659). **16.** Operculum. **17.** Ovipositor and egg groove. Right lateral view of head-foot. **18–19.** External view of organs in visceral mass. Dotted line indicates extent of pericardium under main kidney chamber (Figure 18). Abbreviations: **ag,** albumen gland; **ap,** anterior pedal gland; **b,** bladder; **cg,** capsule gland; **cm,** columellar muscle; **ct,** ctenidium; **dg,** digestive gland; **f,** foot; **go,** pallial gonoduct; **hg,** hypobranchial gland; **int,** intestine; **kd,** main kidney chamber; **me,** mantle edge; **op,** operculum; **os,** osphradium; **ov,** ovary; **ovp,** ovipositor; **per,** pericardium; **sn,** snout; **ss,** style sac; **sto,** stomach; **t,** cephalic tentacle. Scale bars = 1 mm.



**Figures 20–25.** Radula of *Juga* (*Juga*) *silicula* (USNM 1100659). **20.** Section of anterior radular ribbon. Scale bar = 200 μm. **21.** Rachidian and lateral teeth. Scale bar = 50 μm. **22.** Detail of rachidian teeth. Scale bar = 20 μm. **23.** Detail of lateral teeth; note weakly formed outer third denticle. Scale bar = 50 μm. **24.** Marginal teeth. Scale bar = 50 μm. **25.** Detail of cutting edge of marginal teeth. Note unequal size of cusps on inner and outer teeth. Scale bar = 20 μm.

FOREGUT: Buccal mass short and robust (Figure 26, **bm**). Odontophore occupying posterior one half to two thirds of buccal cavity with small, glandular subradular organ protruding before radula. Small jaws present at anterior ends of dorsal folds; epithelium of buccal cavity between dorsal folds glandular (stippled). Dorsal folds deeply cleft along midline adjacent to odontophore; cleft receives salivary gland ducts at posterior end and shallows anteriorly. Very shallow, non-glandular buccal pouches extending underneath dorsal folds adjacent to buccal ganglia (**bg**) at rear of buccal cavity. Radular sac (**rs**) short (~4.4 mm), curving upward behind base of buccal mass, not passing through nerve ring, with tip resting against right posterior end of buccal mass. Robust buccal retractors (**rt**) inserting onto lateral walls of cephalic hemocoel anterior to nerve ring. Short, glandular mid-ventral fold forming small triangular ridge just behind odontophore in anterior esophagus, flanked by two ventro-lateral folds. Ventro-lateral folds converging short distance behind mid-ventral fold, forming rear-facing triangular depression surrounding mid-ventral fold. Paired dorsal and ventral folds continuing through long mid-esophagus (**e**) into posterior esophagus. Epithelium of mid-esophagus between dorsal and ventral folds longitudinally grooved; septate esophageal gland lacking. Posterior esophagus narrow, with numerous folds of approximately equal height. Long, tubular salivary glands (**sg**) passing through circum-esophageal nerve ring, extending to posterior esophagus.

MIDGUT: Esophagus opening under ledge on left side of midgut floor (Figure 27, **e**). Marginal fold (**mf**) extending anteriorly from esophageal aperture alongside major typhlosole (**t1**), then turning posteriorly, bordering right margin of sorting area (**sa**). Sorting area elongate, rectangular, tapering posteriorly; posterior tip curving slightly to the left around crescent-shaped sorting area pad (**sap**). Accessory marginal fold (**amf**) forming weak ridge paralleling marginal fold from near esophagus, curving around posterior margin of sorting area; posterior segment of fold variable, in some specimens intersecting straight longitudinal ridge along left posterior end of sorting area (figured), in other specimens weakly bifurcate (see e.g. Figures 37, 51). Fine parallel striations extending anteriorly from esophagus up face of major typhlosole (Figure 27, **t1**). Midgut roof to the left of sorting area coarsely folded and cuticularized (**cu**). Gastric shield (**gs**) broadly concave; shield continuous with cuticle of adjacent regions of stomach roof and floor. Glandular pad (**gp**) large, rounded posteriorly, with lightly textured surface. Slight overhanging lip of glandular pad forming shallow pocket (**c**) behind gastric shield. Crescentic ridge (**cr**) bounding wide, shallow crescentic groove. Proximal end of ridge posteriorly bordering deep pouch that receives multiple openings of digestive gland (**dd**); distally, ridge fusing to right, posterior end of glandular pad. Size of opening to digestive gland duct vestibule variable. Single, weak, irregular longitudinal fold (**cf**) along floor opposite caecum. Prominent cuticularized fold (**u**) extending from beneath right side of style sac lip (**ss**), along floor, to ridge extending from base of major typhlosole; fold bounding u-shaped depression below lip of style sac. Style sac large, communicating along entire length with intestinal groove; intestine forming prominent protuberance at distal tip of



**Figures 26–29.** Internal anatomy of *Juga* (*Juga*) *silicula* (USNM 1100659). **26.** Mantle cavity and anatomy of cephalic hemocoel. Dorsal view, anterior is below. **27.** Midgut anatomy. Dorsal view, anterior is uppermost. **28.** Kidney anatomy. Internal view of bladder. Lateral view, anterior is uppermost. Roof of bladder (below intestine) cut open to reveal interior; adjacent to incision, stippling indicates intersection of excretory tubules with roof of bladder. Arrow indicates opening in outpocketing of wall between bladder and main kidney chamber. **29.** Circum-esophageal nerve ring. Frontal view on the left, right lateral view on the right. Arrow indicates connective to supra-esophageal ganglion. Abbreviations: **amf,** accessory marginal fold; **arv,** afferent renal vessel; **bg,** buccal ganglion; **c,** caecum; **ce,** cerebral ganglion; **cf,** caecal fold; **co,** thickened connective between left pleural and sub-esophageal ganglia; **cr,** crescentic ridge; **ct,** ctenidium; **cu,** cuticularized region of stomach roof; **d,** dialyneury; **dd,** digestive gland duct vestibule; **e,** esophagus; **go,** pallial gonoduct; **gp,** glandular pad; **gs,** gastric shield; int, intestine; **kd,** main kidney chamber; **me,** mantle edge; **mf,** marginal fold; **np,** nephropore; **os,** osphradium; **pe,** pedal ganglion; **pl,** pleural ganglion; **r,** rectum; **rs,** radular sac; **rt,** buccal retractor muscle; **sa,** sorting area; **sap,** sorting area pad; **sb,** sub-esophageal ganglion; **sg,** salivary gland; **sp,** supra-esophageal ganglion; **ss,** lip of style sac; **st,** statocyst; **t,** cephalic tentacle; **t1,** major typhlosole; **u,** u-shaped fold; **z,** zygoneury. Scale bars = 1 mm

style sac where it separates from the latter (not visible dorsally; see e.g. Figure 50, **ss**). Crystalline style present.

HINDGUT: Proximal intestine (Figures 18, 19, **int**) passing below distal tip of style sac, then extending posteriorly in broad loop, partially overlying style sac, to main gastric chamber (**sto**). Intestine continuing forward, passing under posterior end of main kidney chamber (**kd**), entering pallial roof between bladder (Figure 19, **b**) and main kidney chamber (**kd**), to papillate anus near mantle margin (Figure 26, **r**).

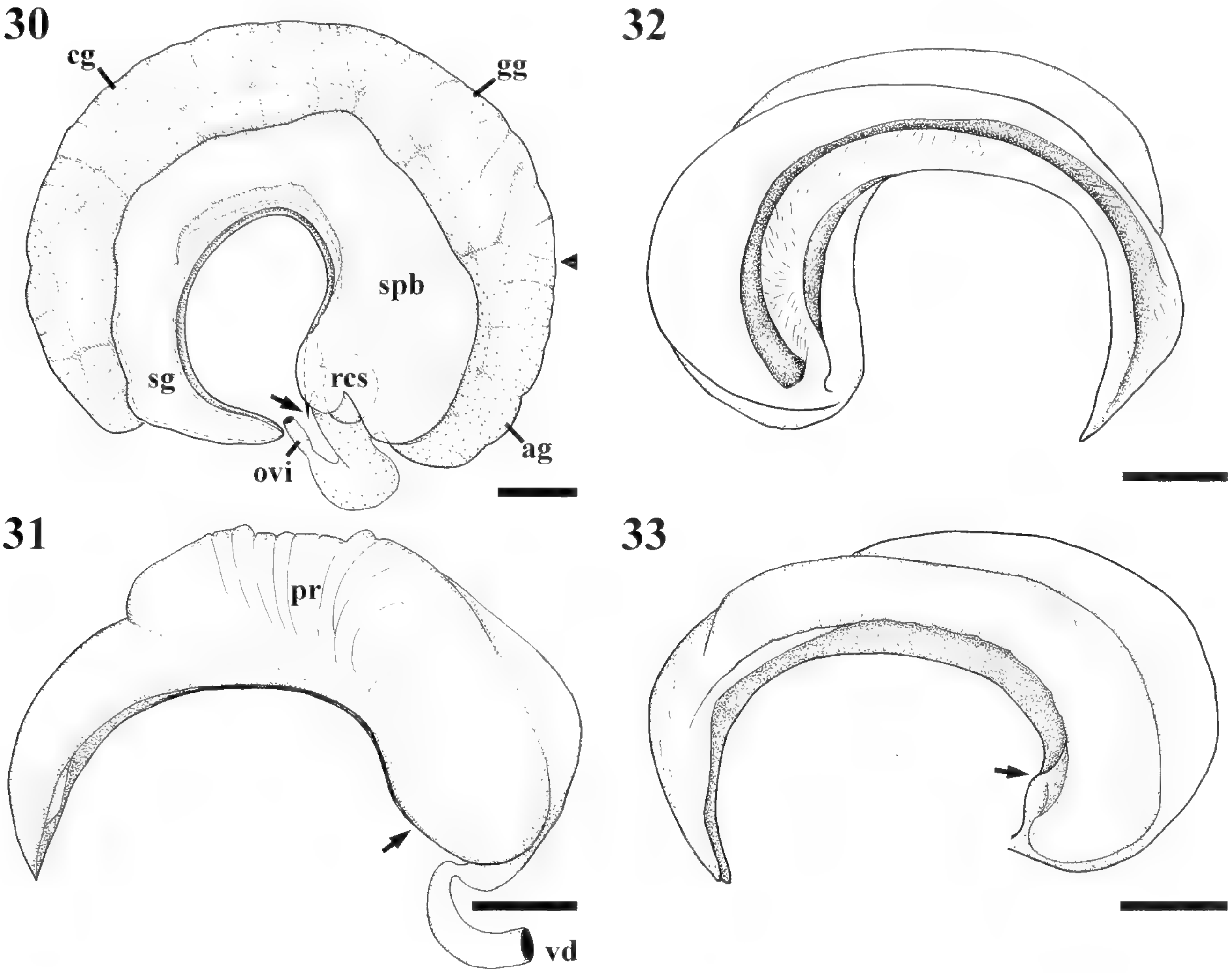
**Reno-pericardial System:** Kidney comprising two interconnected chambers (Figure 28). Main chamber (**kd**) lying along dorsal surface of body whorl, anteriorly surrounding pericardium (Figure 18, **per,** dotted line), crossing axis of body from right to left and extending short distance into pallial roof at base of mantle cavity. Main chamber occluded with excretory tubules anteriorly (within pallial roof), posteriorly, and along left margin. Central portion of main chamber with small, narrow lumen. Second chamber (exposed chamber in Figure 28) extending between pericardial chamber to right body wall below intestine, forming small bladder (Figure 19, **b**). Wall separating main chamber and bladder forming large outpocketing; small aperture within wall, just in front of afferent renal vessel, connecting main chamber and bladder (Figure 28, arrow). Bladder largely occluded by vertical sheets of excretory tissue radiating from afferent renal vessel (**arv**). Sheets of excretory tissue branching and anastomosing, and fusing to right lateral wall, floor and roof below intestine; sheets laterally enclosing outpocketing of main chamber wall. Bladder communicating to mantle cavity via large nephropore (**np**); outpocketing of main chamber wall extending into nephropore, restricting communication with mantle cavity. Bladder penetrating connective tissue along right side of body, short distance into mantle cavity. Nephridial gland absent.

Pericardium long and narrow (Figure 18, **per**, dotted line), extending to recurved intestinal loop.

**Nervous System:** Circum-esophageal nerve ring (Figure 29) lying immediately behind buccal mass, well behind base of cephalic tentacles. Cerebral ganglia (**ce**) connected by short, stout commissure, each producing seven nerves (optic, statocyst, tentacular, and 4 labial nerves). Buccal ganglia (Figure 26, **bg**) lying ventrolaterally at base of buccal mass, adjacent to retractor muscles, at outer edges of esophagus where it emerges from buccal cavity. Pleural ganglia (Figure 29, **pl**) lying behind and below cerebral ganglia, connected to cerebral ganglia by short, thick connectives. Pedal ganglia (**pe**) with two prominent anterior nerves and variable number of smaller accessory nerves (five to seven). Statocysts (**st**) with numerous statoconia present dorsally alongside pedal ganglia behind pedal connectives. Sub-esophageal ganglion (**sb**) joined to left pleural ganglion by thickened connective (**co**); connective producing one small nerve. In addition to connectives to right and left pleural and visceral ganglia, sub-esophageal ganglion producing four small nerves. Zygoneury (**z**) formed between sub-esophageal and right pleural ganglia. Long connective uniting right pleural and supra-esophageal ganglia (Figures 26, 29, **sp**), the latter lying on left side of mantle floor near midline of osphradium. Dialyneury formed between pallial nerve of left pleural ganglion and osphradial nerve of supra-oesophageal ganglion at junction of mantle roof and floor. Single visceral ganglion present between pericardium and kidney at base of mantle cavity.

**Reproductive System:** FEMALE: Gonad (Figures 18, 19, **ov**) dorsally surrounding digestive gland from tip of visceral mass to posterior end of midgut (**sto**). Oviduct emerging ventrally from ovary. Renal oviduct (Figure 30, **ovi**) entering glandular pallial oviduct at base of mantle cavity. Pallial oviduct with proximal albumen (**ag**) and distal capsule glands (**cg**). Proximal albumen gland, below pallial portion of bladder, forming u-shaped tube with glands developed dorsally along axis of fold and simple gonoductal groove between opposing flattened surfaces of glands. Anteriorly, albumen and capsule glands becoming highly glandular and thrown into complex undulating folds; gonoductal groove compressed and highly convoluted (**gg**). Albumen gland approximately one third the length of capsule gland. Pallial oviduct communicating with mantle cavity through narrow aperture along entire length (arrow), except for tubular section of albumen gland at base of mantle cavity. Above aperture, along anterior ~one fourth of oviduct, deep sperm gutter (**sg**, dashed line) present within medial lamina; gutter opening broadly to long, broadly rounded spermatophore bursa (**spb**). Bursa broadening posteriorly and extending to tubular portion of albumen gland. Behind opening to bursa, sperm gutter becoming shallow abruptly and continuing posteriorly (dashed line) as shallow groove. Near posterior end of oviduct, shallow ridge entering small rounded aperture, just inside ventral edge of medial lamina, leading to small pouch-like seminal receptacle (**rcs**). Prominent glandular protuberance from opposing inner surface of lateral lamina extending into receptacle aperture, completely filling narrow proximal portion. Thin, narrow glandular ridge extending anteriorly from protuberance along inner edge of lateral lamina; glandular ridge extending to pallial oviduct tip just inside seminal groove.

MALE: Narrow vas deferens (Figure 31, **vd**) emerging ventrally from testes, continuing forward along ventral midline of whorl. Short distal portion of vas deferens thickened and forming straight seminal vesicle. Vas deferens narrowing and curving dorsally to enter posterior end of prostate (**pr**) at base of mantle cavity. Prostate glandular, opening to mantle cavity through narrow aperture along entire length except for a short fused segment at base of mantle cavity (Figures 31, 33, arrow). Glands of medial and lateral laminae closely appressed, forming tightly interlocking tongue and groove arrange-



**Figures 30–33.** Reproductive anatomy of Juga (Juga) silicula (USNM 1100659). **30.** External, left lateral view of pallial oviduct. Anterior is to the left. Arrow indicates posterior extent of opening to gonoductal groove. "◄" indicates transition between albumen and capsule glands. **31.** External, left lateral view of prostate. Anterior is to the left. Arrow indicates posterior extent of opening to gonoductal groove. **32.** Internal view of prostate medial lamina. Anterior is to the right. **33.** Internal view of prostate lateral lamina. Anterior is to the left. Arrow indicates posterior extent of opening to gonoductal groove. Abbreviations: **ag,** albumen gland; **cg,** capsule gland; **gg,** gonoductal groove; **ovi,** renal oviduct; **pr,** prostate; **rcs,** seminal receptacle; **sg,** sperm gutter; **spb,** spermatophore bursa; **vd,** vas deferens. Scale bars = 1 mm.

ment (Figures 32, 33). Glandular tissue of medial lamina ventrally forming elongate, flattened textured fold (Figure 32), corresponding to concave ventral surface of opposing fold in lateral lamina (Figure 33). Medial lamina expanding to surround fold within lateral lamina. Dorsally and posteriorly, glands of lateral and medial laminae flaring to form flattened flange; size and shape of flange variable between individuals. Apart from fold in medial lamina, inner surface of prostate essentially smooth.

### *Juga* (*Calibasis*) *acutifilosa* (Stearns, 1890)

**Type Material:** Lectotype (USNM 60596; figured specimen in Stearns, 1890, pl. 15, fig. 9) (Figure 5), by present designation, in order to enhance the stability of the nomenclature in accordance with article 74.7.3 of the ICZN; indicated as holotype on label. Fourteen paralectotypes (USNM 60596X) in secondary type collection of USNM, indicated as paratypes on old label and as syntypes on newer label printed in 2001. Although Graf (2001) stated that the "holotype" is by original designation, Stearns figured the largest of the syntypes and provided the dimensions, but did not make an explicit type designation (designation of holotype) in the text and indicated that the description was based on examination of approximately three dozen specimens. Collected by H. W. Henshaw.

**Type Locality:** "Eagle Lake" (Stearns, 1890). Taylor (1981) corrected this to head of Willow Creek, Lassen Co., California (see Figure 1). There are no populations in the Eagle Lake drainage which includes several small tributaries that flow into the lake during winter and the only outflow is through the remnants of the Bly Tunnel. Initiated during the 1920's, the Bly irrigation project diverted water from Eagle Lake to Willow Creek at Murrer's Meadows several kilometers away in the more arid Honey Lake drainage. Today, the tunnel is mostly blocked except for an 8″(~20 cm) pipe that still allows some outflow to Willow Creek. The headwaters of Willow Creek are regarded as springs along Murrer's Upper Meadow and Bly Tunnel (Moyle et al., 1996). Graf (2001) lists the type locality as "Eagle Lake, [Lassen Co.,] California".

**Remarks:** The species varies widely in shell morphology, from populations with several strong persistent lirae to those with lirae confined to the adapical whorls. Body color also may differ drastically from population to population. Few sites show much intrapopulation variance; but adults can vary from population to population, with those at some sites highly variable and others essentially invariant. Very few populations in only a part of the range are as strongly and completely lirate as some Willow Creek (and Murrer's Upper Meadow) populations. These observations are consistent with preliminary results based on COI sequences that indicate the species, as currently recognized, is highly polyphyletic (Frest et al., unpublished data).

**Material Examined:** California: Lassen County: Willow Creek collected off dirt road (to E.), 0.40 km S. of Murrer's Lower Meadow, depth 0.05–0.20 m (Zone 10 695000E 4493820N [120°41′51″E, 40°34′26″N], Gallatin Peak 1989 7.5′ quadrangle, elevation 1509 m), Deixis Consultants locality #1484, 10 Sep. 1993, collected by TF, EJ (USNM 1100658) (4 specimens dissected) (see Figures 10–12); southern-most of three springs at N. end of Murrer's Lower Meadow, below road on E. side of meadow, E. of Eagle Lake, depth 0–0.03 m (Zone 10 694995E 4495225N [120°41′49″E, 40°35′12″N], Gallatin Peak 1989 7.5′ quadrangle, elevation 1545 m), Deixis Counsultants locality #1287, 10 Sep. 1993, collected by TF, EJ (USNM 1100659) (3 specimens dissected).

**External Anatomy:** Operculum ovate, with slightly angular tip (Figure 34). Nucleus comprising slightly less than one half of total length (~41%).

Ovipositor pore rather deep (Figure 35, **ovp**) with deep, highly grooved tract extending to edge of foot, slight distance back from anterior pedal gland (**ap**).

Mantle edge (Figure 35, **me**) crenulated, corresponding to spiral teleoconch sculpture. Ctenidium (Figure 36, **ct**) extending from posterior end of mantle cavity to mantle edge. Hypobranchial gland weakly developed (**hg**).

REMARKS: With the exception of minor individual and/or preservational differences, the external anatomy is essentially identical to *Juga silicula*. *Juga acutifilosa* differs only in that the operculum is slightly more angular and the nucleus comprises a slightly smaller proportion of the total length, the ovipositor and groove to the edge of the foot are significantly deeper and more grooved, the groove opens to the foot nearer the end of the anterior pedal gland, the gill extends slightly nearer the mantle edge, and the hypobranchial gland is much more weakly developed.

**Alimentary System:** RADULA: Radula comprising ~104 rows (n = 2) (Figures 38–43). Rachidian basal margin concave bordering bluntly rounded median projection; basal denticles lacking or only slightly developed (Figures 39, 40). Cutting edge bearing one large central conical cusp, and two stout, conical denticles on each side (Figure 40). Lateral teeth (Figures 38, 39, 41) with short lateral extensions (slightly less than half the length of lateral cutting edge), and single, prominent triangular cusp flanked by two inner triangular denticles and three to four outer denticles. Weakly developed outermost denticle may be present or absent (Figure 41). Marginal teeth (Figures 42, 43) with broadly rounded cutting edges and long, slender shafts. Inner marginal teeth with five and outer marginal teeth with six flattened denticles.

FOREGUT: Radular sac long (~6.7 mm), extending back through nerve ring approximately one half distance to supra-esophageal ganglion, then curving anteriorly with tip overlying nerve ring. Long, thin tubular salivary glands passing through circum-esophageal nerve ring, extending to posterior esophagus.

MIDGUT: Sorting area elongately triangular (Figure 37, **sa**). Accessory marginal fold (**amf**) forming weak ridge paralleling marginal fold from near esophagus, curving around posterior margin of sorting area, with weakly bifurcate posterior end. Glandular pad (**gp**) moderately large, rounded posteriorly, with coarsely textured surface. Deep pocket (**c**) extending under glandular pad behind gastric shield. Crescentic ridge (**cr**) bounding narrow, shallow crescentic groove. Style sac large; intestine forming slight protuberance at distal tip of style sac where it separates from the latter (Figure 36, **ss**).

REMARKS: In comparison to *Juga silicula*, the denticles of the rachidian and lateral teeth are typically more conical, with fewer denticles present on the rachidian and marginals, but more outer denticles present on the lateral teeth. The weakly developed outermost denticle on the lateral teeth is variably developed, and only very small. Rachidian basal denticles are lacking, or only slightly developed. The radular sac is exceptionally long in this species and the salivary glands appear narrower.

Within the midgut, in spite of the differences highlighted above, overall configuration and proportions of features are very similar between *Juga silicula* and *J. acutifilosa*, with the exception that the sorting area is more elongately triangular in shape in *J. acutifilosa*.

No significant differences in the configuration of the hindgut, with the possible exception that the hindgut dramatically widens upon entering the mantle cavity in the specimens examined for *Juga acutifilosa*. However, this may be individual variation.

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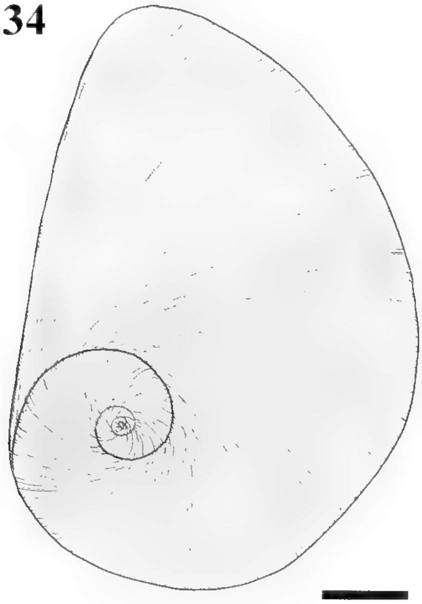

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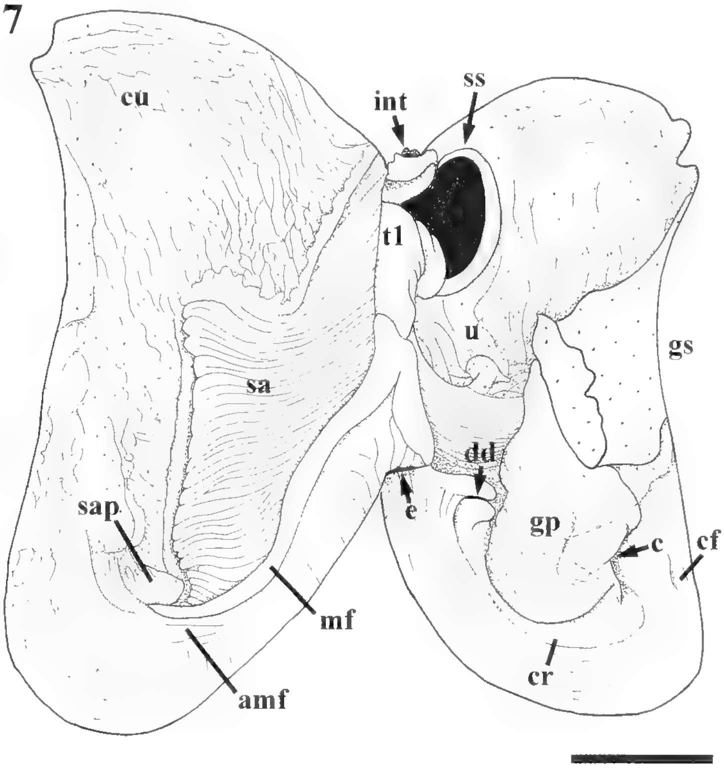

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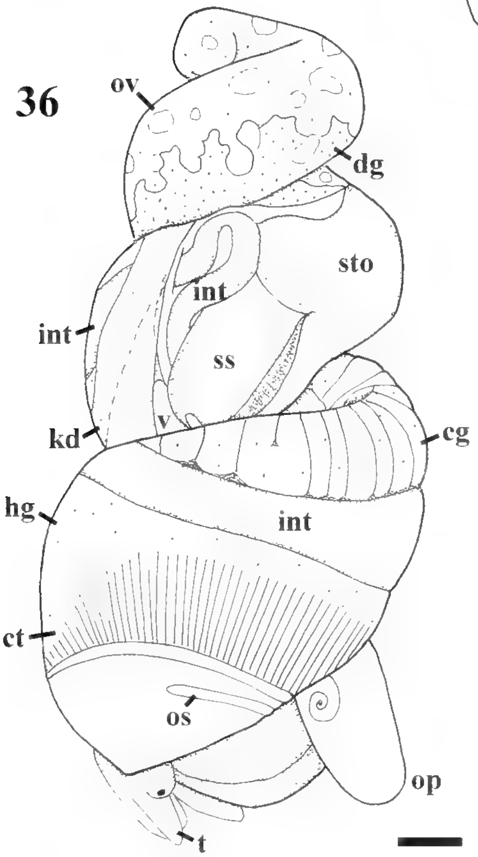

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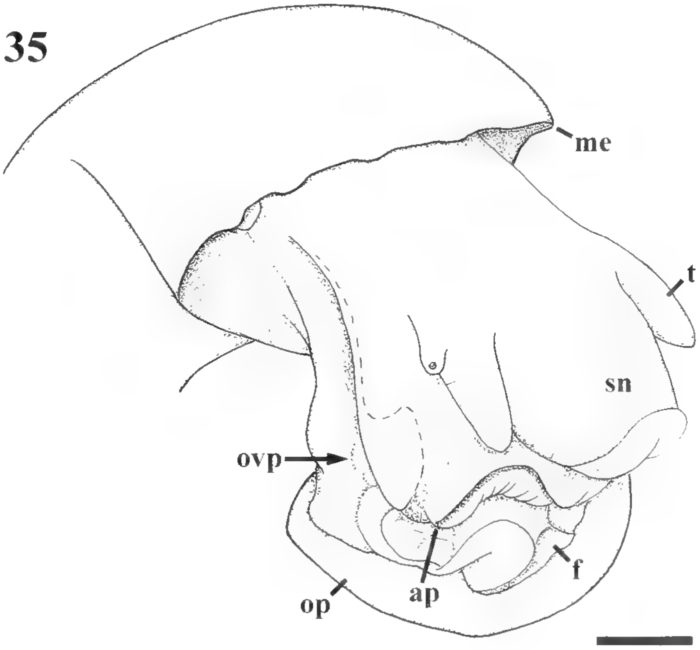
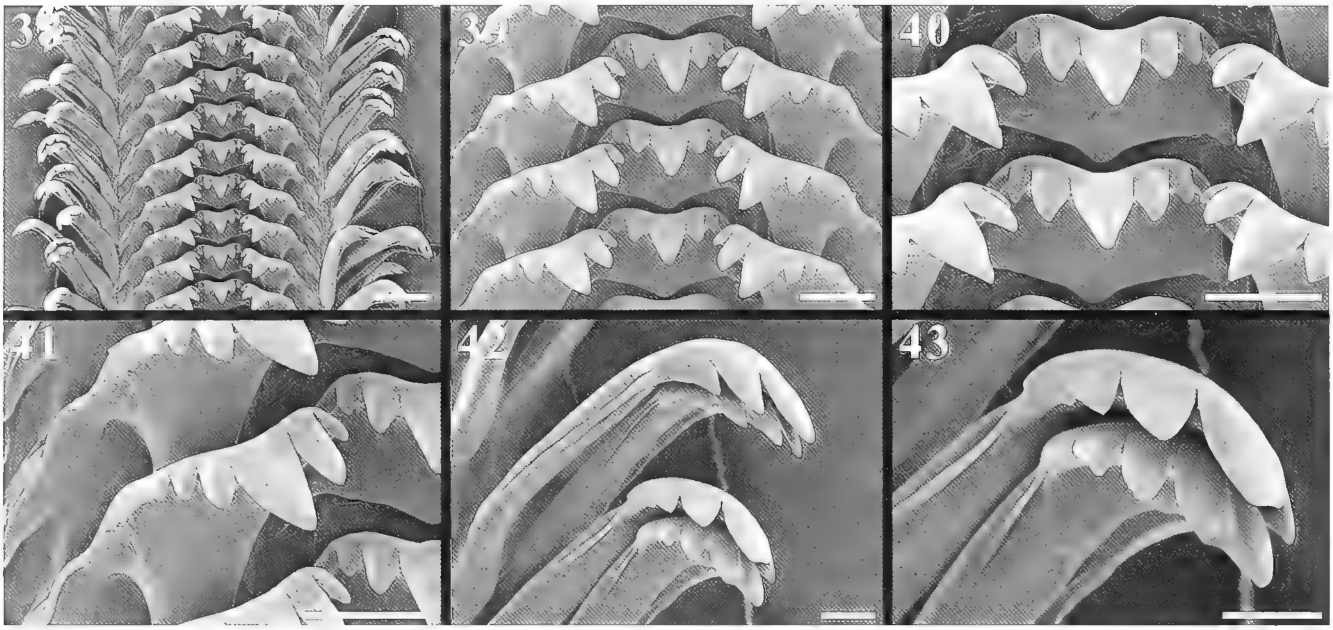


**Figures 34–37.** Anatomy of *Juga* (*Calibasis*) *acutifilosa* (USNM 1100659, except when noted). **34.** Operculum. **35.** Ovipositor and egg groove (USNM 1100658). Right lateral view of head-foot. **36.** External view of organs in visceral mass (USNM 1100658). Dotted line indicates extent of pericardium under main kidney chamber. **37.** Midgut anatomy. Dorsal view, anterior is uppermost. Abbreviations: **amf,** accessory marginal fold; **ap,** anterior pedal gland; **c,** caecum; **cf,** caecal fold; **cg,** capsule gland; **cr,** crescentic ridge; **ct,** ctenidium; **cu,** cuticularized region of stomach roof; **dd,** digestive gland duct vestibule; **dg,** digestive gland; **e,** esophageal aperture; **f,** foot; **gp,** glandular pad; **gs,** gastric shield; **hg,** hypobranchial gland; **int,** intestine; **kd,** main kidney chamber; **me,** mantle edge; **mf,** marginal fold; **op,** operculum; **os,** osphradium; **ov,** ovary; **ovp,** ovipositor; **sa,** sorting area; **sap,** sorting area pad; **sn,** snout; **ss,** style sac; **sto,** stomach; **t,** cephalic tentacle; **t1,** major typhlosole; **u,** u-shaped fold; **v,** ventricle. Scale bars = 1 mm



**Figures 38–43.** Radula of *Juga* (*Calibasis*) *acutifilosa* (USNM 1100659). **38.** Section of anterior radular ribbon. Scale bar = 100 μm. **39.** Rachidian and lateral teeth. Scale bar = 50 μm. **40.** Detail of rachidian teeth. Scale bar = 50 μm. **41.** Detail of lateral teeth. Note very weak development of tiny outer fourth denticle. Scale bar = 50 μm. **42.** Marginal teeth. Scale bar = 20 μm. **43.** Detail of cutting edge of marginal teeth. Note unequal size of cusps on inner and outer teeth. Scale bar = 20 μm.

**Reno-pericardial System:** REMARKS: Configuration of features within the kidney and density of excretory tissue essentially identical to *Juga silicula*, with the only exception being that the central lumen within the main chamber is slightly shorter.

**Nervous System:** Pedal ganglia (**pe**) with two prominent anterior nerves and four smaller accessory nerves.

REMARKS: Configuration of nervous system, including number of nerves produced by major ganglia, otherwise identical to *Juga silicula*.

**Reproductive System:** FEMALE: Proximal albumen gland (Figure 44, **ag**), below pallial portion of bladder, forming small, flattened rounded pouch with glands developed along dorsal axis; shape of pouch somewhat variable. Along anterior ~one third of oviduct, deep sperm gutter (**sg,** dashed line) present within medial lamina; gutter opening broadly to long, broadly rounded spermatophore bursa (**spb**). Behind opening to bursa, sperm gutter shallowing abruptly to shallow groove (dashed line), then rapidly becoming obsolete. Near posterior end of oviduct, small rounded aperture, just inside ventral edge of medial lamina, leading to small narrow seminal receptacle (**rcs**). Low, flatly rounded glandular protuberance from opposing inner surface of lateral lamina slightly extending into receptacle aperture. Extremely thin, glandular ridge extending from protuberance to oviduct anterior tip along inner edge of lateral lamina opposite seminal groove; ridge thickening somewhat anteriorly.

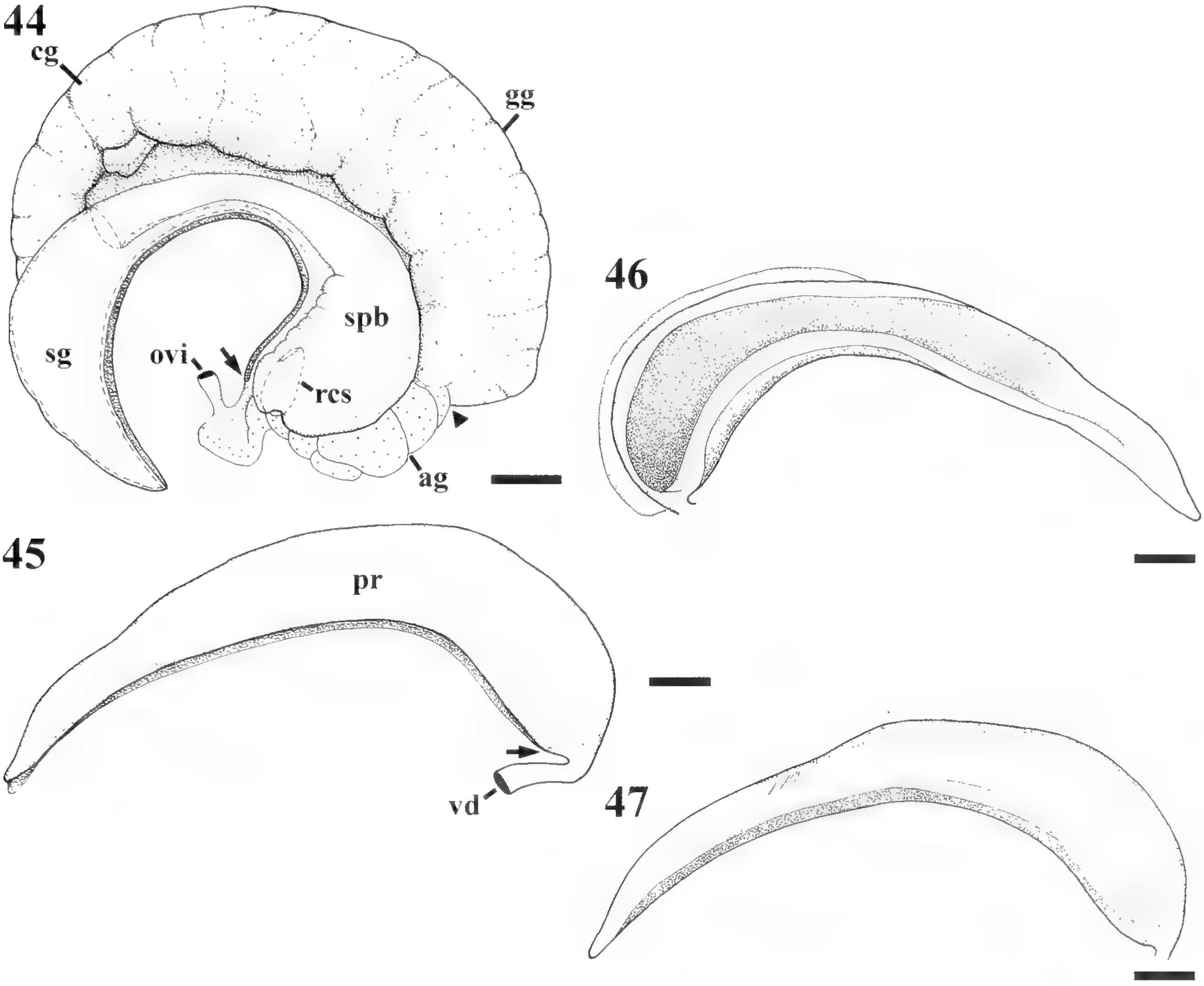
MALE: Glands of medial and lateral laminae forming loosely interlocking tongue and groove arrangement (Figures 46, 47).

REMARKS: In contrast to *Juga silicula*, the proximal albumen gland forms a small, flattened, rounded pouch. The height and shape of the pouch is variable in *J. acutifilosa*, but is distinctly smaller and slightly less glandular than the more u-shaped tube in *J. silicula*. Overall, the capsule and albumen glands are similar in proportion, but the albumen gland is slightly shorter and not as massive as that in *J. silicula*. In addition, the seminal groove is longer and deeper anteriorly but becomes obsolete before reaching the seminal receptacle, the lateral lamina glandular ridge is much weaker and the protuberance into the aperture of the seminal receptacle is more bluntly rounded than in *J. silicula*.

Male reproductive anatomy is very similar to that of *Juga silicula* in the morphology of the folds within the prostate, but the folds are not as highly developed and hence, do not tightly interlock to the same degree. In addition, the ventral fold of the medial lamina is less textured and the dorsal and posterior flange is narrower in *J. acutifilosa*.

*Juga* (*Oreobasis*) *newberryi* (Lea, 1860)

**Type Material:** Lectotype designated by Graf (2001) (USNM 118961; figured specimen in Lea, 1863, pl. 37, fig. 135) (Figure 6); indicated as holotype on label. Twelve paralectotypes (USNM 118961X) in secondary type collection of USNM; indicated as paratypes on old label and as syntypes on newer label printed in 2001. At the time of publication, the lectotype designation of Graf



**Figures 44–47.** Reproductive anatomy of *Juga* (*Calibasis*) *acutifilosa* (USNM 1100659). **44.** External, left lateral view of pallial oviduct. Anterior is to the left. Arrow indicates posterior extent of opening to gonoductal groove. "◄" indicates transition between albumen and capsule glands. **45.** External, left lateral view of prostate. Anterior is to the left. Arrow indicates posterior extent of opening to gonoductal groove. **46.** Internal view of prostate medial lamina. Anterior is to the right. **47.** Internal view of prostate lateral lamina. Anterior is to the left. Abbreviations: **ag,** albumen gland; **cg,** capsule gland; **gg,** gonoductal groove; **ovi,** renal oviduct; **pr,** prostate; **rcs,** seminal receptacle; **sg,** sperm gutter; **spb,** spermatophore bursa; **vd,** vas deferens. Scale bars = 1 mm.

was invalid as it did not follow strict guidelines concerning the language of lectotype designations after 1999. However, under Declaration 44, Amendment of Article 74.7.3 of the Code (Bulletin of Zoological Nomenclature 60(4) December 2003), Graf's lectotype designation is now valid. Collected by J. S. Newberry.

**Type Locality:** Indicated as "Upper des Chutes River, Oregon Territory" (Lea, 1860) (see Figure 1). Most likely, the lectotype came from the Deschutes R. near Bend, Oregon, even though pleurocerids are now absent this far up the river. However, *Juga newberryi* does occur in the lower Deschutes River.

REMARKS: Lea's (1860, 1862, 1863) description of *Melania newberryi* and 1863 illustration are quite accurate. As noted and illustrated by Lea, the most frequent color pattern is three yellow bands separated by three almost black. Occasionally, the lower band may be divided into two or more (Burch, 1989: fig. 452) or the dark bands may be tan in color. Alternatively, the shell may be bandless, in which case the color varies from yellowish-tan to dark tan. Lea (1863: 301) does not seem to have had any of the band-less form; recent field surveys have not revealed any "pure" populations of the band-less form, on the other hand, large populations are not likely to lack it (Frest, unpublished data).

This species is one of a small group of *Juga* with the whorls smooth throughout ontogeny which led Taylor (1966) to make it the type of *Oreobasis*. In the same publication, Taylor suggested that *J. newberryi* is a "probable" synonym of *Melania bulbosa* Gould, 1847. By 1977, Taylor (1977) had accepted this synonymy without qualification, which was followed by many authors (Burch and Tottenham, 1980; Burch, 1982a, b, 1989; Graf, 2001). However, it is not clear why the two species were considered so similar. Comparison of the types indicates that, while being similar in whorl height, the two differ in shape of the aperture, whorl profile and rate of whorl expansion, particularly for the body whorl; *J. bulbosa* generally has more than three not corroded whorls while *J. newberryi* is often more severely corroded but the early teleoconch of the latter is quite distinctive when present. A search of major museum collections failed to locate many specimens aside from the types; most museum lots ascribed to *J. bulbosa* or *J. newberryi* clearly do not belong to either.

Tryon (1865) was apparently the first to reflect on the similarity of the two, indicating the presence of bands in *Juga newberryi* as the sole separating feature, but he did not synonymize them. However, Tryon's illustration of *J. bulbosa* (e.g. 1873, fig. 496) seems to use his own specimen rather than Gould's types, even though he claimed to have had them (1873: 255). In contrast to Gould's types, the specimen figured by Tryon is rather large, strongly corroded with less than 3 whorls, and the surviving whorls appear strongly convex, with a very deep suture. It is likely a band-less form of *J. newberryi*. Thus, although long considered synonyms, the perception that the two are "exactly similar in outline" (Tryon, 1865: 246) may be due to Tryon's apparent confusion between *J. bulbosa* and bandless forms of *J. newberryi*. The scarcity of museum lots may also have contributed to the confusion about the morphology and occurrence of both taxa.

Consequently, we here remove *Juga newberryi* from the synonymy of *J. bulbosa*. At present, *J. newberryi* occurs only in the lower Deschutes River, Oregon, from about Troutdale to roughly 6 miles above the mouth, where it is replaced by *J. (Juga) plicifera*. *Juga bulbosa* is likely also a valid species, but attempts to recollect this taxon anywhere in the historically identified range have been unsuccessful (Frest, unpublished data); thus, this hypothesis cannot be tested at the moment.

**Material Examined:** Oregon: Jefferson County: Deschutes River at RM 97.2–97.4 on E side of channel, ~0.3–0.6 km S of US 26 bridge and mouth of Shitike Creek, at Rainbow Landing, depth 0–0.41 m (Zone 10 640460E 4957320N [121°13′36″E, 44°45′26″N], Eagle Butte 1962 7.5′ quadrangle, elevation 440 m), Deixis Consultants locality #2472, 13 Aug. 2000, collected by TF, EJ (USNM 1100660) (10 specimens dissected) (see Figures 13–15).

**External Anatomy:** Operculum ovate, with angular tip (Figure 48). Nucleus comprising about one third of total length (~34%).

Rather shallow ovipositor pore (Figure 49, **ovp**) with shallow, grooved tract extending to edge of foot, slight distance back from anterior pedal gland (**ap**).

Ctenidium (Figure 50, **ct**) extending from posterior end of mantle cavity to mantle edge. Hypobranchial gland (**hg**) moderately well developed with warty texture, particularly at posterior end of mantle cavity.

REMARKS: The external anatomy of *Juga newberryi* is almost identical to the two preceding species, and differs in that the operculum is more angular in shape and the nucleus is considerably smaller and more basal than eccentric; as in *J. acutifilosa*, the gill extends slightly nearer the mantle edge and the ovipositor groove opens nearer the end of the anterior pedal gland, but the pore and distal groove are considerably deeper in *J. acutifilosa* than in the other two species. The hypobranchial gland of *J. newberryi* is unique in having a warty texture.

**Alimentary System:** RADULA: Radula comprising ~106 rows (n = 2) (Figures 52–57). Rachidian with v-shaped lower margin; basal denticles lacking (Figures 53, 54). Cutting edge bearing one large central conical cusp, and two stout conical denticles on each side (Figure 54). Lateral teeth (Figures 52, 53, 55) with short lateral extensions (slightly less than half the length of lateral cutting edge), and single, prominent triangular cusp flanked by three to four inner and three to four outer denticles. Outermost denticle present, weakly developed, and variable in shape, size, and position (Figure 55). Marginal teeth (Figures 56, 57) with broadly rounded cutting edges and long, slender shafts. Inner marginal teeth with four to five and outer marginal teeth with six to seven flattened denticles.

FOREGUT: Radular sac moderately long (~6.25 mm), extending back through nerve ring, then curving upward behind base of buccal mass with tip overlying left side of nerve ring. Epithelium of mid-esophagus between dorsal and ventral folds irregularly textured.

MIDGUT: Sorting area short, broadly triangular (Fig 51, **sa**). Accessory marginal fold (**amf**) forming weak ridge paralleling marginal fold from near esophagus, curving around posterior margin of sorting area, with weakly bifurcate posterior end. Glandular pad (**gp**) moderately large, rounded posteriorly, with lightly textured surface. Crescentic ridge (**cr**) bounding shallow, broad crescentic groove. Style sac small (Figure 50, **ss**); intestine forming prominent protuberance at distal tip of style sac where it separates from the latter.

REMARKS: As in *Juga acutifilosa*, the denticles of the rachidian and lateral teeth are typically more conical in *J. newberryi* than in *J. silicula*; there are only two outer denticles on each side of the central rachidan cusp, more outer denticles on the lateral teeth, the rachidian basal denticles are lacking, and the lateral extensions are proportionally smaller. However, in contrast to *J. acutifilosa*, *J. newberryi* and *J. silicula* share a similar lower margin on the rachidian and similar development of the weak, outermost denticle on the lateral teeth. *Juga newberryi* is unique in possessing three to four inner denticles on the

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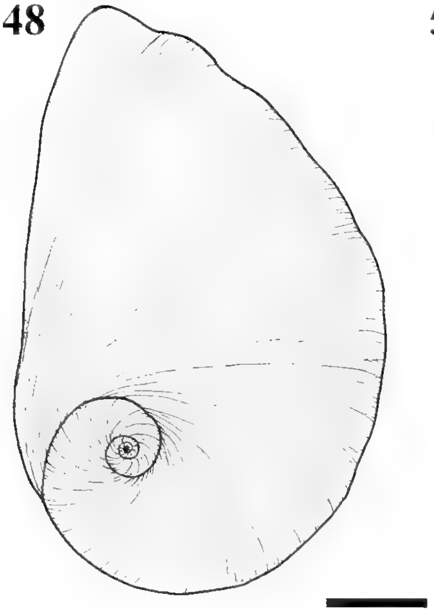

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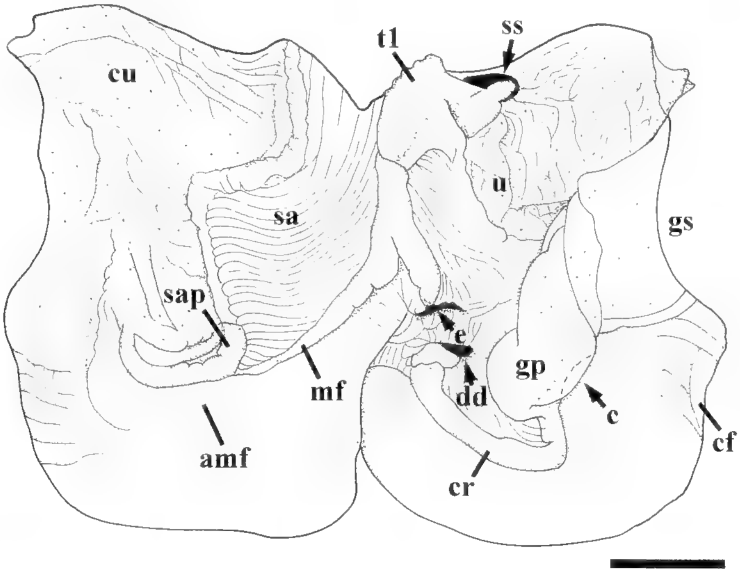

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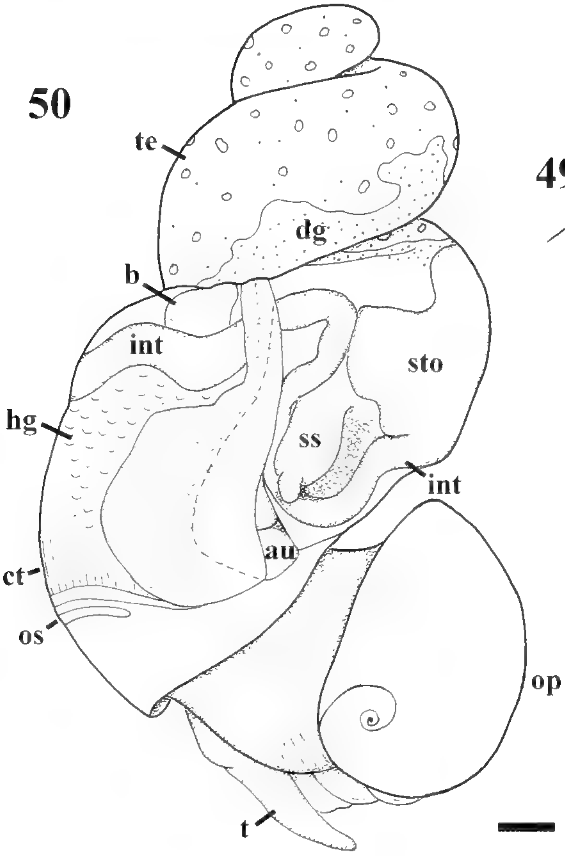

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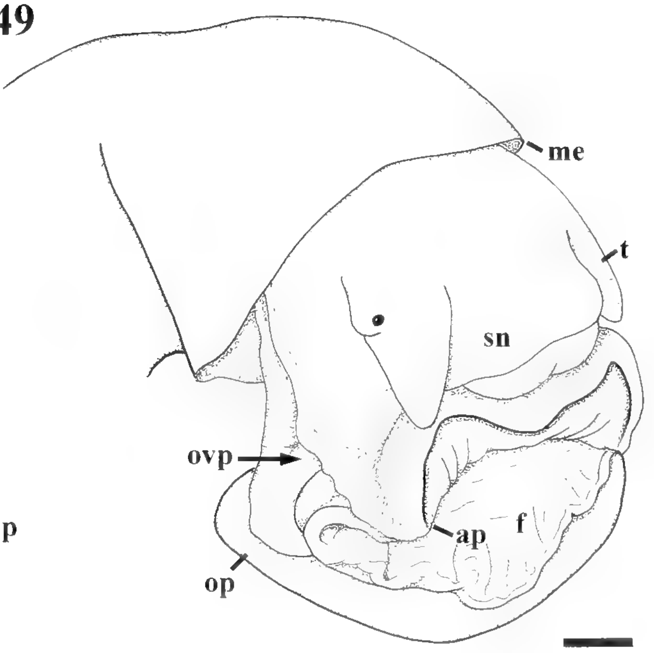
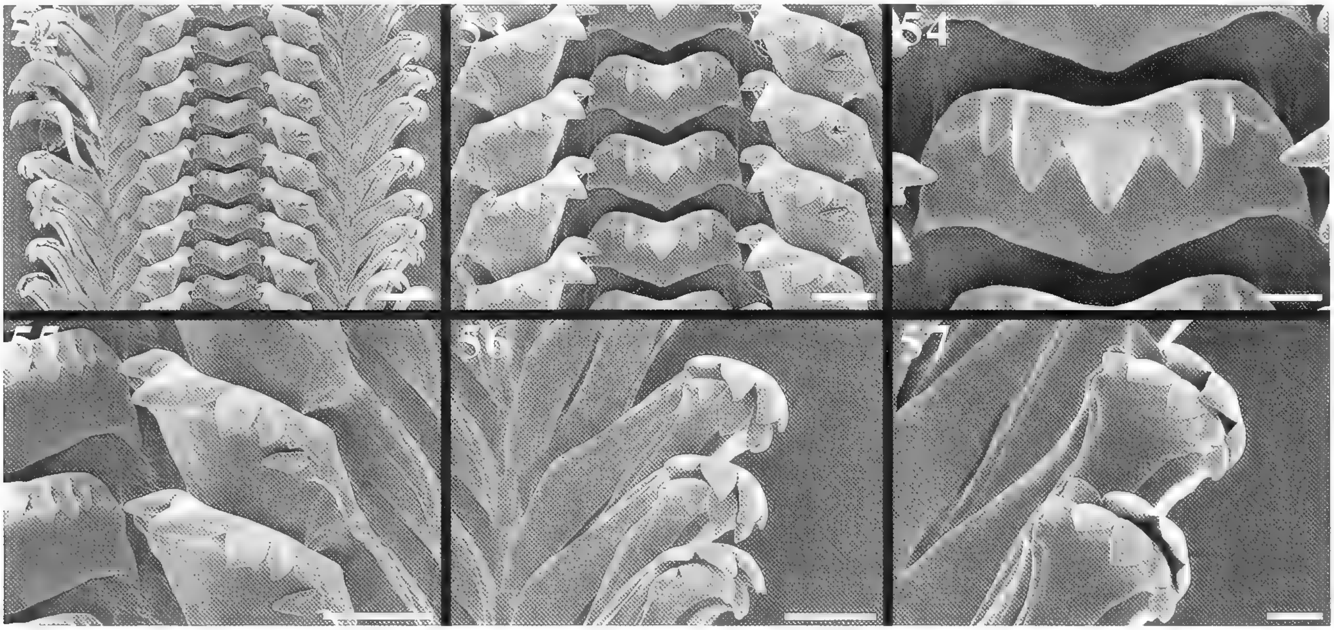


**Figures 48–51.** Anatomy of *Juga* (*Oreobasis*) *newberryi* (USNM 1100660). **48.** Operculum. **49.** Ovipositor and egg groove. Right lateral view of head-foot. **50.** External view of organs in visceral mass. Dotted line indicates extent of pericardium under main kidney chamber. **51.** Midgut anatomy. Dorsal view, anterior is uppermost. Abbreviations: **amf**, accessory marginal fold; **ap**, anterior pedal gland; **au**, auricle; **b**, bladder; **c**, caecum; **cf**, caecal fold; **cr**, crescentic ridge; **ct**, ctenidium; **cu**, cuticularized region of stomach roof; **dd**, digestive gland duct vestibule; **dg**, digestive gland; **e**, esophageal aperture; **f**, foot; **gp**, glandular pad; **gs**, gastric shield; **hg**, hypobranchial gland; **int**, intestine; **kd**, main kidney chamber; **me**, mantle edge; **mf**, marginal fold; **op**, operculum; **os**, osphradium; **ovp**, ovipositor; **sa**, sorting area; **sap**, sorting area pad; **sn**, snout; **ss**, style sac; **sto**, stomach; **t**, cephalic tentacle; **te**; testes; **t1**, major typhlosole; **u**, u-shaped fold. Scale bars = 1 mm.



**Figures 52–57.** Radula of *Juga* (*Oreobasis*) *newberryi* (USNM 1100660). **52.** Section of anterior radular ribbon. Scale bar = 100 μm. **53.** Rachidian and lateral teeth. Scale bar = 50 μm. **54.** Detail of rachidian teeth. Scale bar = 20 μm. **55.** Detail of lateral teeth; note weakly formed outer fourth denticle. Scale bar = 50 μm. **56.** Marginal teeth. Scale bar = 50 μm. **57.** Detail of cutting edge of marginal teeth. Note unequal size of cusps on inner and outer teeth. Scale bar = 20 μm.

lateral teeth. The radular sac is intermediate in length relative to the buccal mass compared to *J. silicula* with a very short sac, and *J. acutifilosa* with a very long sac.

*Juga newberryi* differs greatly from the two preceding species in the relative proportions of features in the midgut, which is significantly longitudinally compressed. Consequently, the sorting area is broadly triangular rather than elongate and the glandular pad is disproportionately smaller. Possibly reflecting the smaller size of the style sac, the opening of the style sac to the stomach is also consistently smaller.

There are no significant differences in the configuration of the hindgut between *Juga newberryi* and *J. silicula*.

**Reno-pericardial System:** REMARKS: In contrast to both preceding species, the bladder of *Juga newberryi* is compressed and less voluminous, bringing the nephropore closer to the afferent renal vessel and decreasing the length of the wall between the main chamber and the bladder. Additionally, the sheets of excretory tissue in the bladder are more numerous, and more highly branched, almost entirely occluding the lumen.

**Nervous System:** Pedal ganglia with two prominent anterior nerves and five to six smaller accessory nerves. In addition to connections to right and left pleural and visceral ganglia, sub-esophageal ganglion producing three small nerves.

REMARKS: Apart from the differences highlighted above, configuration of the nervous system is basically identical to *Juga silicula*.

**Reproductive System:** FEMALE: Capsule gland (Figure 58, **cg**) comprising approximately anterior two thirds of pallial oviduct. Along anterior ~one third of oviduct, shallow sperm gutter (**sg,** dashed line) present within medial lamina; gutter opening narrowly to long, thin spermatophore bursa (**spb**). Sperm gutter continuing

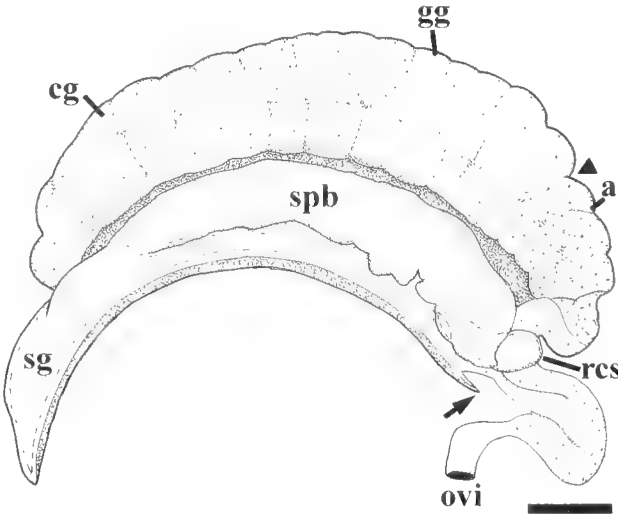


**Figure 58.** Reproductive anatomy of *Juga* (*Oreobasis*) *newberryi* (USNM 1100660). External, left lateral view of pallial oviduct. Anterior is to the left. Arrow indicates posterior extent of opening to gonoductal groove. "◀" indicates transition between albumen and capsule glands. Abbreviations: **ag,** albumen gland; **cg,** capsule gland; **gg,** gonoductal groove; **ovi,** renal oviduct; **rcs,** seminal receptacle; **sg,** sperm gutter; **spb,** spermatophore bursa. Scale bar = 1 mm.

posteriorly as shallow groove to small, narrow seminal receptacle (**rcs**). Moderate glandular protuberance from opposing inner surface of lateral lamina extending into receptacle aperture. Glandular ridge extending from protuberance to oviduct anterior tip along inner edge of lateral lamina opposite seminal groove; ridge thinning anteriorly.

REMARKS: The proximal albumen gland forms a prominent u-shaped tube that is larger than that in *Juga silicula*. The spermatophore bursa is smaller than both preceding species, but as in *J. acutifilosa*, the glandular ridge directly opposes the seminal groove and the glandular protuberance is intermediate in size between that of *J. silicula* and *J. acutifilosa*.

Apart from minor individual variation in shape and development of the prostate glands, there are no detectable discrete differences in male reproductive anatomy compared to *Juga silicula*. Some minor differences include the fact that the ventral fold of the medial lamina appears less textured as in *J. acutifilosa*, and the dorsal posterior flange appears consistently larger.

## DISCUSSION

EVALUATION OF MORPHOLOGICAL CHARACTERS: Most anatomical differences among the three species investigated herein comprise qualitative variations in size and/or shape (e.g. operculum, hypobranchial gland, ovipositor, radula, and bladder). Although often emphasized in species-level systematic studies of gastropods, male and female reproductive anatomy also displays only minor differences in shape and size of the various glands, pouches, and gutters. Additional sampling within and between *Juga* species is necessary to determine if any of these comprise discrete rather than continuous character variation. Surprisingly, the midgut offers a significant source of variation, with modifications to size of the caecum, style sac, and proximal intestine, as well as overall proportions of the gastric chamber and sorting area. This is very different from eastern North American pleurocerids with species from disparate genera displaying almost identical midgut morphologies (Strong, 2005; Strong, unpublished data). For a summary of these and other differences. see Table 1.

The only published anatomical account of any North American *Juga* is that of Prozorova and Raschepkina (2004) on the female reproductive anatomy of five undetermined *Juga* species from the Willamette River system in Oregon. That study indicated the size and shape of the seminal receptacle and spermatophore bursa can vary, which was confirmed in the present study. However, Prozorova and Raschepkina reported several additional findings that could not be confirmed here, including a sperm gutter that becomes suddenly shallow (anterior one fifth to one sixth), variable length of the opening between the gonoductal groove and mantle cavity, and asymmetrical arrangement of albumen and capsule glands. Indeed, the dorso-ventral axis (as defined by a plane extending between the gonoductal groove and the opening to the mantle cavity), is not correctly identified by these authors. Thus, they mistakenly conclude that the lateral lamina is glandular and the medial lamina is non-glandular, comprising the spermatophore bursa and seminal receptacle. Consequently, the glands of the oviduct are misinterpreted as a solid block penetrated by channels within the lateral lamina, rather than as a convoluted tube. This misunderstanding does not allow them to correctly identify the basic symmetry between the medial and lateral laminae, and the proportional development of the capsule and albumen glands along the antero-posterior axis. Instead, the albumen gland is often depicted as extending far anteriorly, dorsally overlying the capsule gland. Not only is this incorrect, it is difficult to imagine how such an arrangement would function.

ANATOMIC AND SYSTEMATIC AFFINITIES OF *JUGA*: No conchological feature unambiguously distinguishes *Juga* from eastern North American pleurocerid genera; indeed, *Juga* has often been synonymized with *Elimia* (as *Goniobasis*)—a genus widespread east of the continental divide (e.g. Tryon, 1865, 1873; Pilsbry, 1899; Walker, 1918; Henderson, 1935a, b; Goodrich, 1942). However, increasing evidence not only supports the independence of *Juga*, but suggests ties to Asian pleurocerids. In an analysis of a large segment of the mitochondrial 16S rRNA gene including representatives of five eastern North American pleurocerid genera, *Juga* falls to the base of the tree rooted on *Melanopsis praemorsa* (L.) (Melanopsidae) and *Melanoides tuberculata* (Müller, 1774) (Thiaridae) (Holznagel and Lydeard, 2000). In an analysis of cerithioidean relationships using nearly full length 16S rRNA sequences (Lydeard et al., 2002), Eastern North American pleurocerids (*Elimia*, *Pleurocera*) are supported as more closely related to *Melanopsis* than to a clade uniting *Juga* with Eastern Asian pleurocerids (*Semisulcospira* Boettger, 1886, *Hua* Chen, 1943).

Available evidence from reproductive anatomy may also support a link between *Juga* and Asian pleurocerids. A recent contribution by Strong (2005) re-described the anatomy of *Pleurocera acuta* Rafinesque, 1831 and *Elimia livescens* (Menke, 1830) with a re-evaluation of pallial oviduct homologies. Despite several erroneous accounts (Woodard, 1934; Jones and Branson, 1964; Dazo, 1965), Strong's (2005) analysis confirmed Eastern North American pleurocerids described thus far lack a seminal receptacle—a feature present in all described western North American (*Juga*) and Asian (*Hua*, *Semisulcospira*) species (Itagaki, 1960; Nakano and Nishiwaki, 1989; Prozorova, 1990; Rashchepkina, 2000; Prozorova and Raschepkina, 2001, 2004, 2005). However, as stated above, the only information available on the anatomy of *Juga* concerns female reproductive anatomy. Given the detailed description of three *Juga* species herein, it is now possible to better place this unique assemblage within the emerging anatomic and phylogenetic framework for limnic cerithioideans.

**Table 1.** Summary of anatomical differences between three species of *Juga*.

| | *Juga (Juga) silicula* | *Juga (Calibasis) acutifilosa* | *Juga (Oreobasis) newberryi* |
|---|---|---|---|
| External Anatomy: | | | |
| Operculum nucleus size (as percent of total length) | 45% | 41% | 34% |
| Ovipositor pore | Shallow | Deep, highly ridged | Shallow |
| Hypobranchial gland | Transversely ridged | Thin | Warty |
| Alimentary System: | | | |
| Dentition: | | | |
| Rachidian tooth | 3/1/3 | 2/1/2 | 2/1/2 |
| Lateral teeth | 2/1/2–3 | 2/1/3–4 | 3–4/1/3–4 |
| Marginal teeth | 6/7 | 5/6 | 4–5/6–7 |
| Rachidian basal denticle | Present | Lacking, slightly developed | Lacking |
| Rachidian basal margin | Bluntly v-shaped | Concave bordering rounded median projection | Bluntly v-shaped |
| Weakly formed outermost denticle of lateral teeth | Present | Absent | Present |
| Radular sac | Short | Long | Moderately long |
| Salivary glands | Thick, tubular | Thin, tubular | Thick, tubular |
| Sorting area | Elongately rectangular | Elongately triangular | Broadly triangular |
| Crescentic groove | Shallow, broad | Shallow, narrow | Shallow, broad |
| Caecum | Shallow | Deep | Shallow |
| Style sac | Large | Large | Small |
| Proximal intestine at base of style sac | Large protuberance | Small protuberance | Large protuberance |
| Reno-Pericardial System: | | | |
| Bladder excretory tubules | Loosely and regularly branched | Loosely and regularly branched | Densely and highly branched |
| Reproductive System: | | | |
| Proximal albumen gland | Moderately large, u-shaped tube | Small, rounded pouch | Large, u-shaped tube |
| Spermatophore bursa | Large, rounded | Moderately large, rounded | Narrow, tubular |
| Sperm gutter | Anterior one fourth of oviduct; extends to seminal receptacle as shallow groove within medial lamina | Anterior one third of oviduct; becomes obsolete before reaching receptacle | Anterior one third of oviduct; extends to receptacle as shallow groove within medial lamina |
| Lateral lamina glandular ridge | Inside seminal groove; large protuberance extending into receptacle aperture | Opposite seminal groove; low, flat protuberance extending into receptacle aperture | Opposite seminal groove; moderate protuberance extending into receptacle aperture |
| Prostate glands | Tightly interlocking | Loosely interlocking | Tightly interlocking |

*Juga*, like other pleurocerids, possesses an ovipositor involved in the deposition of the egg capsules (except the viviparous *Semisulcospira*; Itagaki, 1960) (e.g. Jewell, 1931; Woodard, 1934; Magruder, 1935b; Morrison, 1954; Jones and Branson, 1964; Prozorova, 1990; Rashchepkina, 2000; Prozorova and Raschepkina, 2001, 2004, 2005; Strong, 2005). The ovipositor pore in *Juga* forms a broad, shallow triangular shelf with a highly grooved epithelium. This is very different from the deep pore that expands medially into the foot of *Pleurocera* and *Elimia*, with parallel folds that direct the movement of ova through the pore (Strong, 2005). Indeed, this feature was cited by Taylor (1966) as justifying the independence of *Juga*. Unlike *Juga*, the distal ovipositor groove extends to the foot sole in some but not all of eastern North American pleurocerids (e.g. Van Cleave, 1932; Morrison, 1954; Strong, 2005); ovipositor morphology of Asian pleurocerids is unknown. In melanopsids, the pore is deep, glandular and complex and the distal groove does not intersect the foot sole (Bilgin, 1973; Glaubrecht, 1996) (Table 2).

Similar to other pleurocerids, the gut of *Juga* species is characterized by the presence of tubular salivary glands that pass through the nerve ring, the absence of a mid-esophageal gland, and a style sac in restricted communication with the proximal intestine (Magruder, 1935a, b; Itagaki, 1960; Dazo, 1965; Strong, 2005). Rachidian basal denticles are present in at least some Asian pleurocerids (Ko et al., 2001) and are apparently lacking in many eastern North American pleurocerids (e.g. Minton et al., 2004; Sides, 2005). However, they are easily overlooked in whole mounts and their absence from existing descriptions may be an error; for example, basal denticles are present in *Elimia livescens* (Glaubrecht, unpublished

**Table 2.** Summary of anatomical differences between *Juga* and other limnic gastropods classified in the Pleuroceridae and Melanopsidae. Details from Sunderbrink, 1929; Soós, 1936; Starmühlner and Edlauer, 1957; Itagaki, 1960; Starmühlner, 1970; Bilgin, 1973; Houbrick, 1988; Nakano and Nishiwaki, 1989; Glaubrecht, 1996; Strong and Glaubrecht, unpubl. data. NA = not applicable.

| | *Juga* | *Elimia livescens*<br>*Pleurocera acuta* | *Semisulcospira* | Melanopsidae |
|---|---|---|---|---|
| External Anatomy: | | | | |
| Ovipositor pore | Shallow, simple, weakly glandular | Deep, simple, weakly glandular | NA | Complex, highly glandular |
| Alimentary System: | | | | |
| Salivary glands | Tubular | Tubular | Tubular | Tubular/branched |
| Salivary gland position | Pass through nerve ring | Pass through nerve ring | Pass through nerve ring | Pass through/anterior to nerve ring |
| Esophageal gland | Absent | Absent | Absent? | Present |
| Digestive gland ducts | 1 | 2 | 2 | 1 |
| Caecum | Shallow/Deep | Shallow | Shallow | Deep and spiral |
| Reno-Pericardial System: | | | | |
| Bladder | Small, pallial | Small, pallial | ? | Small, pallial |
| Evagination of bladder wall | Present | Absent | ? | ? |
| Nervous System: | | | | |
| Dialyneury, Zygoneury | Zygoneury | Zygoneury | Dialyneury? | Zygoneury |
| Accessory ganglion between left pleural and sub-esophageal ganglia | Present | Present | Absent? | Present? |
| Reproductive System: | | | | |
| Ovipositor distal groove intersects foot sole | Present | Present/Absent | NA | Absent |
| Seminal vesicle | Straight | Straight | Straight | Folded |
| Proximal albumen gland | U-shaped | Straight | ? | ? |
| Gonoductal groove | Convoluted | Simple | Simple? | Simple? |
| Seminal receptacle | Present | Absent | Present | Present |
| Reproductive strategy | Oviparous | Oviparous | Viviparous | Oviparous |

data), but have not been described in the literature (e.g. Baker, 1928; Dazo, 1965). The phylogenetic significance of these features is unclear as they occur sporadically among many cerithioidean groups, including batillariids, planaxids, melanopsids, thiarids (see e.g. Thiele, 1928; Houbrick, 1987; Glaubrecht, 1996). Melanopsids differ in possessing an esophageal gland, and the salivary glands may be tubular or branched and variably pass through or by-pass the nerve ring; the radula is variable and may present a rachidian that is similar to that of pleurocerids, or may be quadrangular, robust with conical denticles and with a marked glabella (Sunderbrink, 1929; Thiele, 1928; Bilgin, 1973; Glaubrecht, 1996).

The midgut of *Juga* species diverges from eastern North American pleurocerids and other putatively closely related limnic lineages most noticeably in size and shape of the glandular pad and configuration of the crescentic ridge. In *Juga*, the glandular pad is rather narrow with a crescentic ridge that is often separated from it by a wide, shallow groove; the proximal end of the crescentic ridge borders a vestibule that receives several ducts of the digestive gland. Typically, melanopsids, paludomids, and thiarids have a broadly rounded glandular pad and a deep, narrow crescentic groove such that the crescentic ridge closely adheres to the outer edges of the pad. Although the midgut has demonstrated great utility in reconstructing relationships among cerithioidean lineages (Strong, unpublished data), midgut characters of *Juga* do not provide unambiguous evidence of affinity to any one freshwater family; the small, narrow glandular pad is rather similar to that of *Semisulcospira*, but the configuration of the crescentic ridge, particularly in *J. silicula* and *J. newberryi*, is unique among cerithioideans known thus far. The presence of a single digestive gland duct vestibule is shared between *Juga* and melanopsids, but is also found in a number of cerithioideans; other pleurocerids and paludomids have two digestive gland ducts (Strong and Glaubrecht, 2002, 2003, 2007, unpublished data; Strong, 2005).

As in paludomids (e.g. Strong and Glaubrecht, 2002, 2003) and melanopsids (Bilgin, 1973), the kidney of pleurocerids penetrates the pallial cavity (Magruder, 1935b; Itagaki, 1960; Strong, 2005), but the pallial portion of the bladder is smaller than that in the former taxa. The branching pattern of excretory tubules within the bladder is essentially identical between *Juga* and eastern North American pleurocerids, but *Juga* is unique in the outpocketing of the wall separating the main chamber and the bladder (Strong, 2005). Kidney anatomy is currently unknown for Asian pleurocerids and melanopsids

Although published accounts of pleurocerid nervous systems disagree on the number of nerves produced by various ganglia (Magruder, 1935b; Itagaki, 1960; Dazo, 1965; Strong, 2005; present study), this is often variable within species. However, the present account agrees with that of Strong (2005) that the cerebral ganglia produce seven nerves, and that there are two prominent anterior pedal nerves with a variable number of small accessory nerves (typically four to seven). The thickened connective between the left pleural and sub-esophageal ganglia, representing a small accessory ganglion, was found to give off only a single large nerve in the present study, but was found by Strong (2005) to produce one to three nerves in *Elimia* and *Pleurocera*. Strong (2005) also found the sub-esophageal ganglion to give off one to three nerves, whereas three to four nerves were found in the present study.

The most intriguing aspect of the nervous system is the presence of the accessory ganglion. It is known only from eastern North American pleurocerids (Magruder, 1935b; Strong, 2005) and now *Juga* (present study), and has not been depicted in most accounts of melanopsid (Bouvier, 1887; Soós, 1936; Starmühlner and Edlauer, 1957; Starmühlner, 1970; Bilgin, 1973; Glaubrecht, 1996) and Asian pleurocerid (Itagaki, 1960) nervous system anatomy. However, the illustration of the nerve ring of *Melanopsis frustulum* Morelet, 1856–57 (Starmühlner, 1970) and that of *M. doriae* Issel, 1866 (Starmühlner and Edlauer, 1957) clearly show a thickened connective between the left pleural and sub-esophageal ganglia, indicating that it is most likely present in melanopsids as well. Paludomids and thiarids have a much more concentrated nerve ring with the left pleural and sub-esophageal ganglia fused or in close contact (e.g. Seshaiya, 1934; Glaubrecht, 1996; Strong and Glaubrecht, 2002, 2003).

Pleurocerids and melanopsids share the same basic layout of the pallial oviduct to the exclusion of paludomids and thiarids, including the presence of a long opening to the mantle cavity, and a deep sperm gutter opening anteriorly to a spermatophore bursa and posteriorly to a seminal receptacle; as mentioned above, eastern North American pleurocerids are unique in lacking the seminal receptacle (Bilgin, 1973; Nakano and Nishiwaki, 1989; Prozorova, 1990; Glaubrecht, 1996; Rashchepkina, 2000; Prozorova and Raschepkina, 2001, 2004, 2005; Strong, 2005). Whereas in *Juga* and *Semisulcospira* the sperm gutter becomes obsolete or continues posteriorly as a shallow groove within the medial lamina (Prozorova and Raschepkina, 2004, 2005; herein), in melanopsids the sperm gutter is continuous along the ventral edge of the medial lamina and contains the opening to the receptacle at the posterior end of the oviduct (Bilgin, 1973; Glaubrecht, 1996). In *Elimia* and *Pleurocera*, a deep sperm gutter is present above the opening to the mantle cavity along its entire length, and closes posteriorly to form a short, blind spermatophore bursa.

One aspect of cerithioidean reproductive anatomy that is routinely overlooked is the configuration of the capsule and albumen glands. Strong and Glaubrecht (2002, 2003) have found that the shape of the albumen gland in paludomids is quite distinctive, and likely a synapomorphy of the family. In *Juga*, the glands and intervening gonoductal groove of the pallial oviduct are highly convoluted with a proximal albumen gland that is pouch-like or u-shaped (present study), while eastern North American pleurocerids possess glands that form two narrow bands with smooth opposing surfaces and an essentially linear proximal albumen gland (Strong, 2005). However, such potentially informative characters are undescribed for other pleurocerids and melanopsids.

Male reproductive anatomy of *Juga* is apparently quite distinct as no other male pleurocerid (indeed, no other cerithioidean) has been described with a tightly interlocking arrangement of glands (e.g. Woodard, 1934; Itagaki, 1960; Prozorova, 1990); however, a large fold within the lateral lamina may be present (Nakano and Nishiwaki, 1989; Strong, 2005). Among eastern North American pleurocerids, both the highly folded proximal portion (Woodard, 1934) and distal region of the prostate Strong (2005) have been inferred as the site of spermatophore formation. In *Juga*, there is no differentiated anterior or posterior region, but intuitively the tightly interlocking folds of the lateral and medial laminae must function in molding the spermatophore.

## CONCLUSIONS

While sharing many similarities, numerous features clearly set *Juga* apart from eastern North American pleurocerids: ovipositor pore, lateral outer cusps, midgut glandular pad and crescentic ridge, digestive gland duct vestibule, evagination of kidney wall, convoluted gonoductal groove, proximal albumen gland, seminal receptacle, interlocking prostate glands. However, as is often the case for ancient lineages, it is difficult to identify uniquely shared features that more or less unambiguously demonstrate affinity to any one limnic lineage. *Juga* is particularly difficult as many of these features not only set the genus apart from other pleurocerids, but are undocumented (ovipositor pore, kidney, pallial oviduct glands) or apparently autapomorphic among cerithioideans (crescentic ridge, evagination of the kidney wall, prostate). Nevertheless, this analysis has revealed some characters that are shared with Asian pleurocerids (midgut glandular pad, seminal receptacle), but some that are also shared with melanopsids (digestive gland duct). However, the presence of the seminal receptacle is undoubtedly plesiomorphic and uninformative in delineating relationships. Others are so heterogeneously distributed among limnic lineages, it is difficult to determine if there may be an underlying phylogenetic signal (ovipositor ventral groove, rachidian basal denticles). Unlike molecular data, given the available morphological evidence, there is no overwhelming signal linking *Juga* to Asian pleurocerids, nor for that matter linking eastern North

American pleurocerids to melanopsids (Table 2). While part of this pattern may be due to the high rate of autapomorphies, it may simply be an artifact of missing data. Clearly, one of the more significant impediments in assessing pleurocerid affinities is that comprehensive anatomical accounts of pleurocerids and melanopsids are rare, leaving many potentially informative characters unknown. Thus, it is clear that further anatomical studies within the context of ongoing morphological and molecular cladistic analyses are necessary to unambiguously resolve the question of pleurocerid monophyly and their affinities to melanopsids.

These results also have implications for the systematics of *Juga*, particularly with regards to the validity of current subgeneric subdivisions. Although all three taxa possess unique features that clearly distinguish them from one another, *J. silicula* and *J. newberryi* are strikingly anatomically similar and share many features to the exclusion of *J. acutifilosa*: 1) shallow, weakly ridged ovipositor pore, 2) similar rachidian basal margin, 3) similar development of weak, outermost denticle of the lateral teeth, 4) thick, tubular salivary glands, 5) shallow, broad crescentic groove, 6) shallow caecum, 7) large proximal intestine protuberance on base of style sac, 8) u-shaped proximal albumen gland, and, 9) tightly interlocking prostate glands (Table 1). In conclusion, the anatomical data do not support separation of *Juga* sensu stricto and *Oreobasis* and *Oreobasis* is thus here synonymized with *Juga* sensu stricto; *Calibasis* is sufficiently distinct to merit retention as a valid taxon. The question of the rank of these taxa is, of course, highly subjective. But given what is known about anatomical differentiation among other pleurocerid genera, it could reasonably be argued that *Juga* sensu stricto and *Calibasis* be recognized at the rank of genus.

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# Discriminating shells of *Gastrocopta pentodon* (Say, 1822) and *G. tappaniana* (C. B. Adams, 1842) (Gastropoda: Pulmonata) with an example from the Delmarva Peninsula, eastern USA

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## ABSTRACT

The North American pupilloid land snails *Gastrocopta pentodon* and *G. tappaniana* have similar shells that can be difficult to separate, which raises the question of whether they represent two species or environmentally influenced variants of one species. In 1906, Vanatta and Pilsbry presented 53 drawings of shells of the two species to facilitate separation, but differences therein were subtle. Discriminant function analysis of measurements from their illustrations gave a discriminant function classifying 96% correctly, with minimal overlap between groups shown by factor analysis. The function revealed both forms on the Delmarva Peninsula, again with minimal factor analysis overlap. Bimodality of morphology does not reflect sexual dimorphism in these hermaphrodites.

The two forms maintained their distinct morphologies where they co-existed, supporting the concept of separate species. Reports of the forms in habitats of different wetness could indicate separate species with different moisture preferences or one species with moisture-influenced morphology. We found the two forms to show distinct morphologies in medium wet areas, further supporting the concept of separate species.

Regarding habitat wetness, we confirmed Delmarva *Gastrocopta tappaniana* in wetter areas, whereas *G. pentodon* occurred in a wide range of moistures, but tending to be found in drier areas. Our surrogate measure of habitat wetness relying on plant moisture requirements should be useful in future studies. Geographically, *G. tappaniana* tended to occur along the SE Delmarva Atlantic coast while *G. pentodon* ranged more widely

In an application of the discriminant function, measurements from an image of the lectotype of *Gastrocopta carnegiei* classified that species with *G. pentodon*.

## INTRODUCTION

The ability to distinguish one species from another is central in biology. However, environmental variation in form can sometimes be mistaken for species-level differences in taxa including mollusks (Minton and Gunderson, 2001).

Historically, making a distinction between the North American pupilloid land snails *Gastrocopta pentodon* (Say, 1822) and *Gastrocopta tappaniana* (C. B. Adams, 1842) has been difficult (Vanatta and Pilsbry, 1906). These latter authors discussed and evaluated *G. pentodon*, *G. tappaniana*, and other similar, previously described forms. They also illustrated various modifications of form. Their paper presented drawings of 53 *Gastrocopta* specimens from eastern North America. Although Vanatta and Pilsbry identified some of their illustrated specimens as *G. pentodon* and others as *G. tappaniana*, they did not reveal their criteria for specific allocation of these individual specimens.

Vanatta and Pilsbry (1906) and Pilsbry (1948) described distinctions between *Gastrocopta pentodon* and *G. tappaniana* including differences in shell size and shape, and the number and arrangement of apertural teeth. Despite Vanatta and Pilsbry's clarification of the species differences, confusion persists and some workers have consolidated the two forms into one single species while others have kept them as separate species. Bequaert and Miller (1973: 88–90) lumped the species, stating that the holotype (actually the lectotype, selected by Clench, 1965) of *G. tappaniana* is a typical *G. pentodon*. On the other hand, Hubricht (1976: 107) also examined the type of *G. tappaniana* and concluded it was *G. tappaniana* and not *G. pentodon*. Lauriol et al. (2003) and Nekola (2004) recognized the two forms as separate species.

Our visual examination of Vanatta and Pilsbry's (1906) drawings of the 53 specimens in light of their statements comparing the two species left us uncertain that those shell characters could reliably separate the two species. Some of the *G. pentodon* seemed to have characteristics of *G. tappaniana* and vice versa (see in particular their figs. 17, 32, 45, 53). Admittedly, Vanatta and Pilsbry attempted to show variability in the forms, such that they might have chosen extreme examples.

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Multivariate statistical procedures are obviously more accessible now than they were in 1906. Factor analysis (FA) identifies the axes of major variation in a dataset and helps show whether specimens cluster into more than one group in a multidimensional space. Discriminant function analysis (DFA) can identify which variables are most useful for separating two pre-defined groups and can identify coefficients to use with the variables in a discriminant function (DF) for classifying unknown specimens. Nekola and Barthel (2002) used a similar approach.

Some researchers have suggested that *Gastrocopta pentodon* prefers drier areas and *G. tappaniana* prefers moister areas (Sterki, 1906: 134; Pilsbry, 1948: 888–890; Hubricht, 1985: 9; Nekola, 2004). One hypothesis holds that the forms are separate species as evidenced by their different moisture preferences. An alternate hypothesis is that, since larger snails are sometimes associated with moister conditions (Goodfriend, 1986, and references therein), the two forms might simply be two ends of an environmentally influenced continuum of morphology. If environmental conditions are continuous, then randomly sampled specimens should show continuous morphological variation if they represent one environmentally influenced species or a bimodal distribution if they are two species with different moisture preferences. Furthermore, examining whether the two species maintain their separate morphologies where they co-occur would provide strong evidence whether they are two separate species.

Numerous specimens tentatively identified as *Gastrocopta pentodon* were available from a survey of terrestrial mollusks on the Delmarva Peninsula (Pearce and Italia, 2002). Examining these specimens using morphometric methods should address whether both forms occur on Delmarva and, if so, whether the forms are distinct and whether they differ in their moisture preferences.

In this paper we explore the moisture associations of the two forms on the Delmarva peninsula to examine whether specimens identified as *G. pentodon* occurred in drier habitats and whether *G. tappaniana* occurred in moister habitats. Furthermore, we look for interpretable differences in geographical distribution of the two forms on the peninsula. Finally, by examining specimens at localities where the two forms co-occur, we address whether the two forms are valid species or ecomorphs of a single species.

We address three principal questions in this paper:

(1) Are the two forms identified by Vanatta and Pilsbry (1906) distinguishable via morphometric analysis and, if so, which features discriminate between them? To answer this question, we examined selected variables from their 53 illustrations in FA and DFA.

(2) Do the *Gastrocopta pentodon* and *G. tappaniana* from the Delmarva Peninsula fall into two morphometric groups and, if so, how do the features of those two groups compare with those of the forms as identified by Vanatta and Pilsbry (1906)? To answer this question, we applied the DF from question (1) to 577 Delmarva specimens and examined results along FA axes.

(3) Does the wetness of the habitats of the *Gastrocopta pentodon* and *G. tappaniana* forms differ as previously suggested? How are they distributed on the peninsula? Does co-occurrence evidence addresses whether the two forms represent separate species or environmentally influenced morphs of the same species? To answer this question, we compared occurrences using wetness estimated from plant data and compared morphology of the forms in sympatry and allopatry.

## MATERIALS AND METHODS

**Sources of Specimens:** We examined illustrations of the 53 *Gastrocopta* shells presented by Vanatta and Pilsbry (1906), which had been drawn to the same scale presumably using a camera lucida. Their specimens were from geographically widespread areas in eastern North America. They identified the specimens as 41 *G. pentodon* and 12 *G. tappaniana*.

We examined 577 unbroken adult *Gastrocopta* shells from 130 leaf-litter samples from 123 grid squares on the Delmarva Peninsula. The number of shells measured per sample ranged from 1 to 69. The Delmarva Peninsula shells came from a study of land snails on the peninsula (Pearce and Italia, 2002) in which leaf litter samples (1–4 liters) were collected from 794 5 × 5 km grid squares, passed through sieves, and snails retained by screens 0.5 mm or larger mesh were picked and identified. We excluded juveniles (adults are easily recognized by the presence of a reflected lip and well-developed apertural teeth) to avoid introducing variability from shells of different ages and excluded the other clearly different species of *Gastrocopta* found on Delmarva. Although specimens resembling *G. pentodon* and *G. tappaniana* were found in 201 samples from 181 different grid squares on Delmarva (Figure 1) excluding broken, juvenile, or wet-preserved specimens (bodies of alcohol-preserved specimens obscured apertural features) reduced the number of measurable specimens.

Differences between the datasets: the Vanatta and Pilsbry geographic coverage is about two orders of magnitude larger (throughout eastern North America for Vanatta and Pilsbry, just the Delmarva Peninsula for Delmarva), whereas the Delmarva sample size is an order of magnitude larger (n = 53 for Vanatta and Pilsbry, n = 577 for Delmarva).

Voucher specimens are deposited at the Delaware Museum of Natural History.

**Selection and Measurement of Variables:** We took measurements from camera lucida drawings of shells, using 53 drawings by Vanatta and Pilsbry (1906) and 577 of our own drawings of specimens from the Delmarva Peninsula.

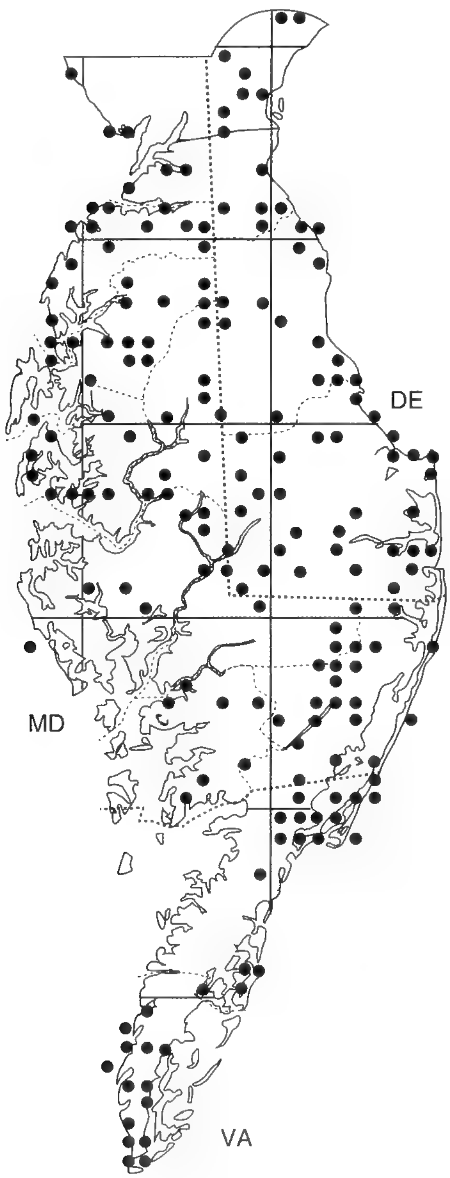

**Figure 1.** Delmarva Peninsula showing locations where specimens of *Gastrocopta pentodon* and *G. tappaniana* were found

We measured or counted 8 variables from the drawings and derived 13 additional (ratio) variables as combinations of the measured variables (Table 1, Figure 2). We excluded teeth on the parietal wall from the count of teeth because whereas only one parietal tooth is present in *Gastrocopta tappaniana*, either one or two parietal teeth can be present in *G. pentodon* (Pilsbry, 1948: 889). Aperture height was measured from the middle of the parietal callus.

We included derived variables because ratios succinctly describe shape, which is not described by original measurements. Because ratios are more intuitive, including ratios in this analysis should give a more useful result for separating these species. Although ratios can theoretically produce non-normal distributions, the ranges of our variables are limited so they can be used in FA and DFA. We did not check for normality or transform variables because FA and DFA are robust against non-normality (Mardia, 1971; Hagiuda and Shigemasu, 1996).

In order to reduce the number of variables to about 1/5 the number of specimens (Hair et al., 1998), and to determine the set of variables that have the greatest chance of separating the species as defined, we used non-parametric Mann-Whitney U-tests to compare measurements of each variable on the two *Gastrocopta* forms as defined (Table 1) and used the variables that showed significant differences between the two groups in further analyses.

**Statistical Techniques:** DFA and FA were performed using SAS version 8.02 (SAS Institute Inc., Cary, NC). We used DFA to determine the variables most useful in discriminating between the two forms using stepwise, backward, and forward methods for variable selection. The three methods gave similar sets of variables to use in separating the species, giving us confidence that two recognizable groups exist in the data set. Then SAS applied the DF to the analyzed specimens to determine reclassifications and percent correct classification. We applied those DF coefficients to measurements of the 577 specimens from the Delmarva Peninsula to determine which forms occur there.

We used FA to examine graphically whether two morphological groups of individuals are evident among the specimens, using the variables determined by the DFA. We used FA with principal components (essentially the same as principal component analysis with rotation). We accepted the first three axes, applied varimax rotation, and plotted specimens on the factor axes.

**Distinctness of the Forms:** To further study distinctness of the two forms, in addition to examining FA plots, we examined whether individual samples from Delmarva contained mostly one form of *Gastrocopta* or if forms tended to be randomly distributed among samples. To examine whether this non-randomness represents two species, or one environmentally influenced species, we examined their morphologies in sympatry. If the forms are two morphologically distinct species, then their morphologies should remain distinct and mixed samples, containing both forms, should exhibit bimodal morphology. If the forms are a single species with environmentally dependent morphology, morphology should not show bimodality under intermediate environmental conditions; in intermediate conditions, morphology should be intermediate.

To verify the names being applied to the two forms, we measured and compared the lectotype of *Gastrocopta tappaniana*. To examine visually how it compares with the other specimens, we plotted the pseudo-factor scores (calculated from lectotype measurements using results of FA on the 53 specimens, rather than including it in an analysis with the other 53 specimens) for the lectotype where it would appear on the factor plots generated for

**Table 1.** Variables recorded on *Gastrocopta pentodon* and *G. tappaniana*. Derived variables relate to shape. Bold p-values indicate variables showing significant difference (Mann-Whitney U test) between forms as identified by Vanatta and Pilsbry (1906). Measured variables are in millimeters.

| Variable | Type | Description | p-Value between forms |
|---|---|---|---|
| aph/bdh | Derived | Aperture height/body whorl height | 0.6863 |
| aph/h | Derived | Aperture height/shell height | 0.0629 |
| *aph* | Measured | Aperture height | **0.0003** |
| *bdh* | Measured | Body whorl height | **0.0001** |
| *bdh/h* | Derived | Body whorl ht/shell ht | **0.0145** |
| bdh/w | Derived | Body whorl height/shell width | 0.1948 |
| h | Measured | Shell ht | 0.0660 |
| hat | Measured | Hat height (height above penultimate whorl) | 0.2464 |
| *hat/h* | Derived | Hat height/shell height | **0.0029** |
| *hat/spr* | Derived | Hat height/spire (spire = hat height + penultimate whorl height) | **0.0007** |
| *pnlth* | Measured | Penultimate whorl height | **0.0126** |
| pnlth/bdh | Derived | Penultimate whorl height/body whorl height | 0.6100 |
| pnlth/h | Derived | Penultimate whorl height/shell height | 0.2177 |
| *pnlth/hat* | Derived | Penultimate whorl height/hat | **0.0007** |
| pnlth/pnltw | Derived | Penultimate whorl height/penultimate whorl width | 0.9915 |
| *pnltw* | Measured | Penultimate whorl width | **0.0002** |
| pnltw/h | Derived | Penultimate whorl width/shell height | 0.0742 |
| pnltw/w | Derived | Penultimate whorl width/shell width | 0.7823 |
| *tthxpar* | Counted | Number of teeth excluding those on the parietal (upper) wall | **0.0000** |
| *w* | Measured | Shell width | **0.0002** |
| w/h | Derived | Shell width/shell height | 0.1313 |

just the 53 specimens. Second, we performed DFA to determine how it classified.

**Moisture Association of the Forms:** To examine the relationship of the forms with the moisture in their environment, we calculated a surrogate index of wetness using plants noted at the collecting sites. Because plant species differ in their long-term moisture requirements, estimating environmental moisture from plant data should provide a biologically meaningful measure of long-term moisture availability.

Wetland facultative indicator status of many North American plant species is available at USDA-NRCS (2004) by geographical regions. The plants are assigned to one of five categories depending on how obligated they are to wetlands. For each plant species at a locality, we assigned a score of 5 for the wettest facultative indicator rank, 1 to the driest, and 2, 3, or 4 to the three intermediate ranks on the website (adding 0.3 for a "+" and subtracting 0.3 for a "–"). We calculated the mean facultative indicator rank of all the plants recorded at each locality and used this mean as a surrogate index of wetness at the locality.

To test the hypothesis that *Gastrocopta pentodon* occurs in drier and *G. tappaniana* in moister areas we divided the wetness score for specimens into three parts, with the middle part representing 25% of the specimens, and the other two parts being approximately equally divided. Then we examined the number of individuals in each of the three wetness areas as a function of their DF scores.

**Geographical Distribution of the Forms:** We examined a map of localities of specimens identified by the DF to see whether the two forms tended to show interpretable geographic patterns on the peninsula. Of the 130 samples, 106 were only *Gastrocopta pentodon* or *G. tappaniana*; the 16 that were predominantly *G. pentodon* were scored as *G. pentodon*, the 2 that were predominantly *G. tappaniana* were scored as *G. tappaniana*, and we omitted the 5 samples containing equal numbers of the two forms. We recognize that geographical location and wetness might not be independent.

## RESULTS

**Distinctness of 53 Specimens:** DFA of the 53 specimens as defined by Vanatta and Pilsbry (1906) determined coefficients for four variables to separate the two forms of *Gastrocopta* (Table 2). To use these coefficients to determine an unknown specimen, first multiply each DF coefficient by the corresponding variable value for that specimen, and then sum all these results. If the result is negative, then the specimen is more likely *G pentodon*, and if greater than zero, the specimen is more likely *G. tappaniana*. For example, specimen 1 in Vanatta and Pilsbry (1906) has the following measurements (mm)/count: bdh = 0.942, hat/h = 0.267, pnlth/hat = 0.645, tthxpar = 4. Multiplying these values by the DF coefficients and adding them yields –8.068, indicating that the specimen classifies as *G. pentodon*.

The DF correctly classified 51 (96.2%) of the 53 speci-

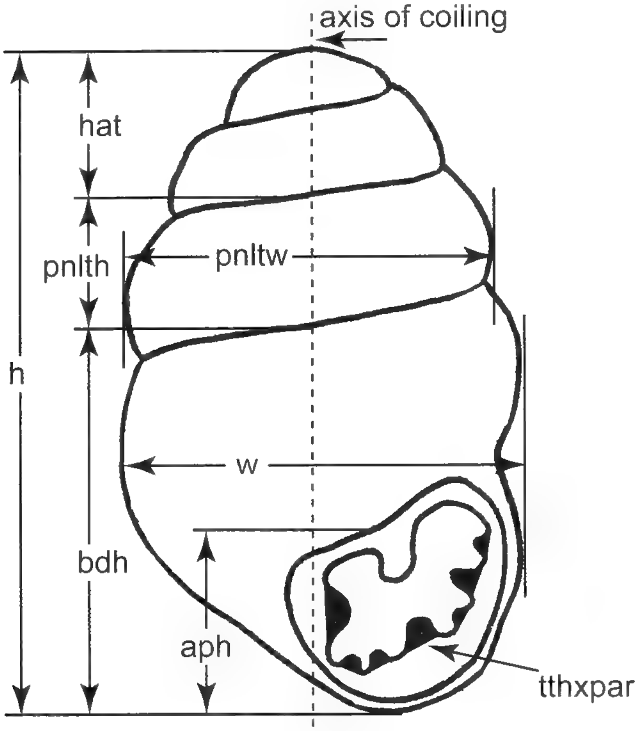

**Figure 2.** Variables measured on *Gastrocopta* spp.: **aph** = aperture height [measured from base of outer lip to midpoint of callus connecting the two lip insertions], **bdh** = body whorl height, **h** = shell height, **hat** = height of shell above penultimate whorl, **pnlth** = penultimate whorl height, **pnltw** = penultimate whorl width, **tthxpar** = number of apertural teeth excluding those on the parietal (upper) wall, **w** = shell width. Dimensions are measured perpendicular or parallel to axis of coiling.

mens that had been used to create the function: 39 of the 41 Vanatta and Pilsbry-identified *G. pentodon* classified as identified, and all 12 of the 12 *G. tappaniana* classified as identified.

In FA, of the 53 specimens, the first three eigenvalues using the four variables explained 98.1% of the variation. Two shape variables (hat/h, pnlth/hat) loaded strongly on factor 1, one size variable (bdh) loaded strongly on factor 2, and one variable (tthxpar) loaded strongly on factor 3 (Table 3). This result, in which shape loaded strongly on factor 1, contrasts with the usual FA pattern in which factor 1 is size and factor 2 is shape. The four variables were all important for explaining variation in the dataset, as evidenced by high communality scores (sum of squares of factor loadings [SS], ranging from 0.961 to 1.000). Figure 3 plots specimens on factors 1 and 2, and factors 2 and 3, showing that *G. tappaniana* (solid squares) occupies a portion of morphospace at the edge of and somewhat overlapping with *G. pentodon* (hollow diamonds). Thus, although the two forms overlap, they generally occupy separate portions of morphospace.

**Table 2.** Discriminant function (DF) coefficients for separating the two forms of *Gastrocopta* using four variables

| Variable | Coefficients |
|---|---|
| Constant | −77.5711 |
| bdh | 26.82807 |
| hat/h | 70 |
| pnlth/hat | 33.85039 |
| tthxpar | 0.92107 |

**Table 3.** Loadings for the four variables on the three factors from factor analysis (FA) of 41 *Gastrocopta pentodon* and 12 *G. tappaniana* specimens illustrated by Vanatta and Pilsbry (1906), using the rotated factor method. Bold loadings indicate the main variables loading on each factor. Percent variance explained is after varimax rotation.

| | Factor 1 | Factor 2 | Factor 3 |
|---|---|---|---|
| pnlth/hat | **0.96674** | 0.00425 | 0.16676 |
| hat/h | **−0.96086** | −0.08634 | −0.17608 |
| bdh | 0.04651 | **0.98561** | 0.16166 |
| tthxpar | 0.21990 | 0.17578 | **0.95955** |
| Variance explained | 1.908 | 1.010 | 1.006 |

Shells scoring higher on factor 1 have a relatively smaller hat to total height, and a relatively taller penultimate whorl relative to hat height. Shells scoring higher on factor 2 have a larger body whorl height. The third factor reflects number of teeth, and shells classified as *Gastrocopta tappaniana* had 7 non-parietal teeth, in contrast to *G. pentodon*, which had a variable number of teeth.

**Distinctness of 577 Specimens:** Applying the DF coefficients to the Delmarva specimens classified 475 specimens as *Gastrocopta pentodon* and 102 as *G. tappaniana*.

In FA of the 577 Delmarva specimens, the first three eigenvalues using the four variables selected by the DFA explained 98.0% of the variation. Two shape variables (hat/h, pnlth/hat) loaded strongly on factor 1, one size variable (bdh) loaded strongly on factor 2, and one variable (tthxpar) loaded strongly on factor 3 (Table 4). The four variables were all important for explaining variation in the dataset, as evidenced by high communality scores (SS ranging from 0.957 to 1.000). Figure 4 plots specimens on factors 1 and 2, and factors 2 and 3, showing that the two species occupy generally separate portions of morphospace with minimal overlap.

Interpretation of factors 1 and 2 are the same as for the Vanatta and Pilsbry results. The third factor, largely reflecting number of teeth, shows variability in both forms, but shells classified as *Gastrocopta tappaniana* tend not to have the minimum number of teeth. The specimens plot in distinct columns in this analysis because number of teeth was discreet; the columns appear more distinct in this analysis than in the analysis of Vanatta and Pilsbry data because teeth loaded much more strongly on factor 3 in this Delmarva analysis.

**Distinctness in Sympatry and Type Material:** The species composition of samples from Delmarva (contain-

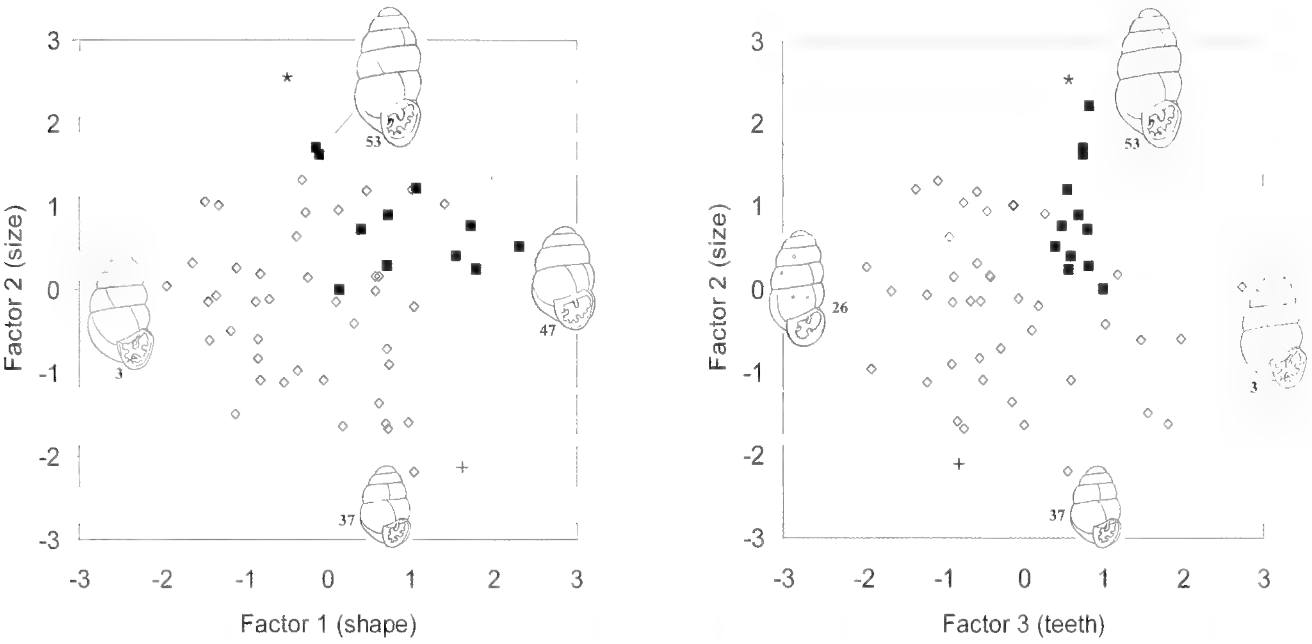

**Figure 3.** Factor analysis (FA) plots of 53 specimens on factors 1 and 2 (left) and factors 2 and 3 (right). Hollow diamonds represent *Gastrocopta pentodon* and solid squares are *G. tappaniana* as identified by Vanatta and Pilsbry (1906). The shell image shows, to the right on factor 1, a relatively smaller hat to total height and a relatively taller penultimate whorl relative to hat height; higher on factor 2 shows a larger body whorl height; to the right on factor 3 shows shells with more apertural teeth. Asterisk (★) indicates position of lectotype of *G. tappaniana* and plus symbol (+) indicates position of the lectotype of *G. carnegici*. Numbers beside shell images correspond to specimen numbers from Vanatta and Pilsbry (1906).

ing 5 or more specimens) was non-random. Samples tended to be composed primarily of one species or the other (Figure 5), instead of mostly mixed samples that would be expected with random mixing. By the DF, 28 of 39 samples were composed of a single species. In testing whether the two forms maintain their distinctness in sympatry, we examined the FA plot (factors 1 and 2) of samples from Delmarva that the DF identified to contain both forms (mixed samples). Figure 6 shows good separation of the two coexisting forms, supporting the idea that the two forms are separate species. The separation of the two forms in the mixed-only samples is as good as the separation in all samples (compare Figures 4 and 6).

We performed two tests to determine whether one of the two morphologically discrete forms we identified on Delmarva corresponds to type material of *Gastrocopta tappaniana* (we could not locate type material of *G. pentodon*). First, on the FA plots (Figure 3), the lectotype of *G. tappaniana* was located in the section of the graph with specimens classified by Vanatta and Pilsbry as *G. tappaniana*. Second, the lectotype of *G. tappaniana* was classified as *G. tappaniana* by the DF.

**Table 4.** Loadings for the four variables on the three factors from factor analysis (FA) of 577 specimens from the Delmarva Peninsula, using the rotated factor method. Bold and underlined loadings indicate the main variables loading on each factor.

| | Factor 1 | Factor 2 | Factor 3 |
|---|---|---|---|
| pnlth/hat | **0.97099** | 0.13158 | 0.03672 |
| hat/h | **−0.94900** | −0.23783 | −0.01636 |
| bdlh | 0.22451 | **0.97414** | 0.00912 |
| tthxpar | 0.03081 | 0.00861 | **0.99948** |
| Variance explained | 1.895 | 1.023 | 1.001 |

**Moisture Association and Geographical Distribution of Forms on Delmarva:** The 22 samples having 5 or more specimens with only *Gastrocopta pentodon* (as classified by the DF) were from areas drier (wetness factor $\bar{x} = 2.62$, sd = 0.46) than the 6 samples having 5 or more specimens with only *G. tappaniana* (wetness $\bar{x} = 3.14$, sd = 0.30) (t-test, $p = 0.006$). Mean wetness factor for all 471 specimens classified by the DF as *G. pentodon* was 2.59 (sd = 0.44) and that for the 100 *G. tappaniana* was 2.95 (sd = 0.44, t-test, $p < 0.00005$). The histogram in Figure 7 shows the number of individuals by their DF score separately for each of three wetness classes. The vast majority of *G. tappaniana* (positive DF) occur in medium or wet areas. On the other hand, *G. pentodon* (negative DF) occur in a wide range of moisture, with a tendency to be in drier areas. In samples from medium wet areas, bimodality of forms is evident, with a hint of bimodality in the samples from dry and wet areas.

A map of localities of specimens identified by DF shows *Gastrocopta pentodon* widespread throughout the peninsula but essentially absent from the southeastern coast and barrier islands. In contrast, samples containing *G. tappaniana* were most common along the Atlantic

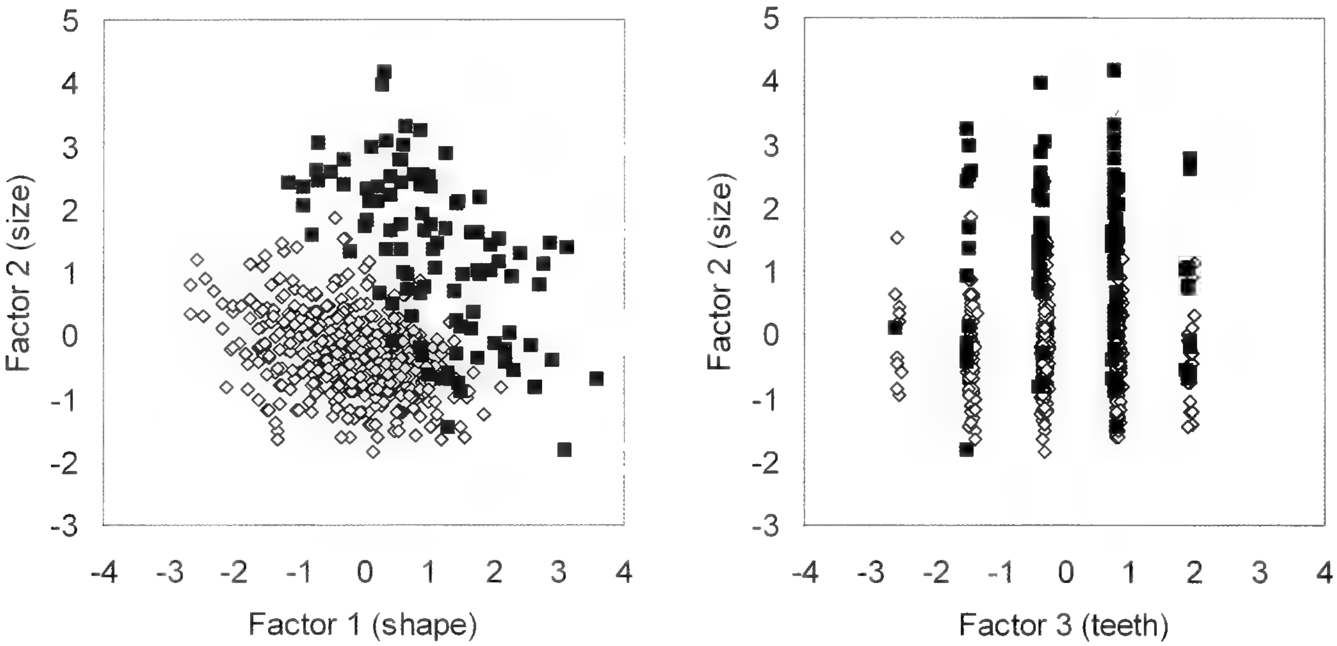

**Figure 4.** Factor analysis (FA) plots of 577 *Gastrocopta* specimens from the Delmarva Peninsula plotted on factors 1 and 2 (left) and factors 2 and 3 (right). The same variables were used as in analysis of Vanatta and Pilsbry data. Hollow diamonds represent specimens classified as *G. pentodon* and solid squares those classified as *G. tappaniana*.

Coast in southeastern Delmarva and closer to major water bodies (Figure 8). Interestingly, four Atlantic coast samples containing 5 or more specimens of only *G. tappaniana* were from four of the wettest areas, as determined by the plant moisture associations.

## DISCUSSION

These results indicate that the two forms of *Gastrocopta* can be considered separate species. DFA successfully discriminated two groups. The 53 specimens in Vanatta and Pilsbry (1906) could be separated using 4 variables and the DF classified 96% of specimens as defined. The two forms were generally distinct by FA despite some morphological overlap. When applied to the 577 Delmarva specimens, the DF identified both species on Delmarva. FA of the Delmarva specimens showed the two species occupying generally separate portions of morphospace with minimal overlap.

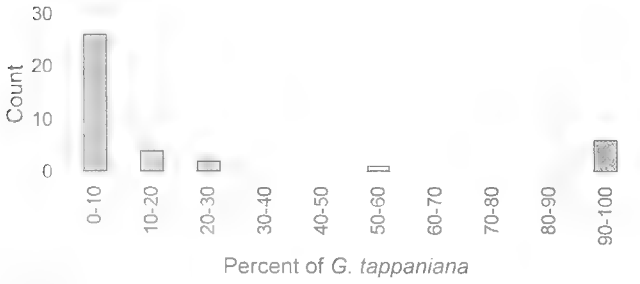

**Figure 5.** Proportion of specimens that were *Gastrocopta tappaniana* in the 39 samples containing 5 or more specimens

Even stronger evidence of separate species is that the forms maintained their distinct morphologies where they coexist. *Gastrocopta pentodon* and *G. tappaniana* from the Delmarva Peninsula showed no evidence of convergent morphology in sympatry. Moreover, the forms maintained their separate morphologies in samples from

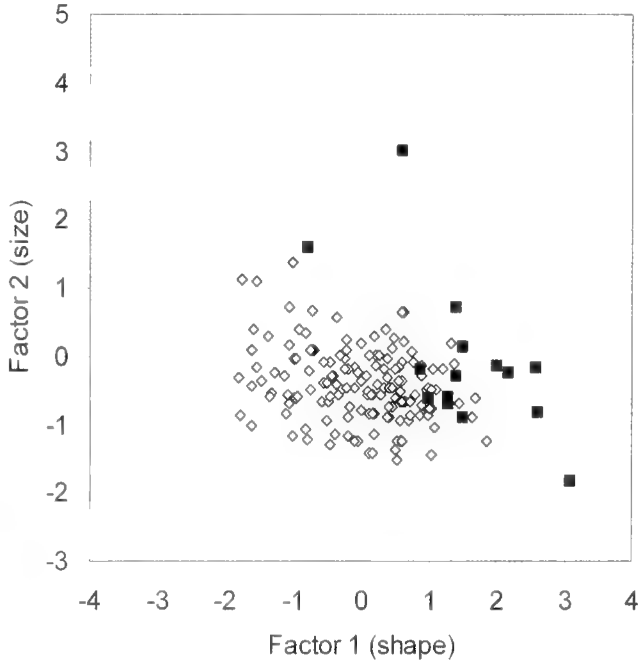

**Figure 6.** Factor analysis (FA) plot of 180 *Gastrocopta* specimens from the Delmarva Peninsula of the 11 mixed samples determined to contain both forms.

areas of intermediate wetness, further supporting the idea that the two forms are distinct species.

The dataset from Vanatta and Pilsbry (1906) and ours from Delmarva showed similar results, strengthening the conclusion that two species exist. The Delmarva dataset was more geographically restricted, but had more specimens, while the Vanatta and Pilsbry dataset was geographically broader with fewer specimens. Sources of all *Gastrocopta tappaniana* included by Vanatta and Pilsbry (1906) are from locations more concentrated in NE USA, from Washington, DC to Maine (excepting one *G. tappaniana* from Arizona), whereas their *G. pentodon* were more widespread, from Texas to Iowa and Florida to Maine. This congruence despite different geographic sampling suggests that shell morphology does not vary significantly across geography. Bimodality of morphology supports the hypothesis of two species on Delmarva and throughout the eastern USA.

*Gastrocopta tappaniana* on Delmarva occurred in samples from moister areas, whereas *G. pentodon* occurred in samples from a broad range of wetness. Sample wetness was unimodal and continuous, both for all samples and for samples containing at least 5 specimens, such that a difference in habitat by species does not seem to be an artifact of sample choice. This result confirms reports of Sterki (1906) and Pilsbry (1948) that *G. tappaniana* occurs in moister areas. However, in contrast to authors who characterized *G. pentodon* as being in drier areas, our results agree with the report of Hubricht (1985) that *G. pentodon* has a wider moisture range and can overlap in habitat wetness with *G. tappaniana*.

Geographically, *G. tappaniana* tended to occur on the SE part of the peninsula, and closer to water bodies, whereas *G. pentodon* was more evenly distributed across the peninsula, including its central part. Moistness seems to be an important influence on the distribution of *G. tappaniana*, but some other aspect of geography might also play a role in its distribution, considering that the Atlantic coast samples from the SE part of the peninsula were the moistest samples.

We examined the type specimen of *Gastrocopta tappaniana* (Museum of Comparative Zoology, Harvard, lectotype MCZ 186171, paratype [not seen] 186172) but were unable to locate type material of *G. pentodon*. For *G. tappaniana*, Pilsbry (1948: 889) stated "Type locality, Vermont, coll. Amherst College", implying that an unspecified kind of type or types was present at Amherst. Bequaert and Miller (1973) observed that the holotype [sic] was transferred from Amherst to MCZ, mistakenly stating that Pilsbry (1948) referred to it as a holotype. Clench (1965) noted that the type locality for *G. tappaniana* is Roscoe, Coshocton Co., Ohio, and not Vermont as some writers have assumed. He chose a lectotype for *G. tappaniana*: "*G. tappaniana* appears to be a synonym of *G. pentodon* (Say); the lectotype (here selected) is nearest to the figure of *pentodon* given on pl. 3, fig. 7, 1916, Manual of Conch. (2) 24: 33, and not to fig. 9 which is given as *tappaniana*. This same plate was republished in Land Mollusca of North America, vol. 2, pt. 2, fig. 477, p. 887, Mono. no. 3, Acad. Nat. Sci. Philadelphia, 1948."

We find it peculiar that Clench intended to choose a lectotype specimen of *Gastrocopta tappaniana* that was most like *G. pentodon*. Interestingly, despite Clench's bias in his choice, the lectotype is consistent with *G. tappaniana* per both of our tests: it is located among the *G. tappaniana* specimens on factor plots, and it classified as such by the DF derived in this paper.

Vanatta and Pilsbry (1906) did not reveal their objective criteria for classifying the two forms, so researchers using their paper must accept their two groups at face value. We recognize that DFA, by its nature, will find differences between nearly any groups. Therefore, to test whether the groups defined by Vanatta and Pilsbry (1906) are different from randomly selected groups, we compared the percent correct classification of the DFA results for the groups as recognized by Vanatta and Pilsbry, to 10 randomized datasets with 41 specimens in one group and 12 in the other. In contrast to the 94.3% correct classification of groups as they defined, the randomized data sets averaged 70.9% correct classification. The higher correct classification of the non-randomized groups gives us

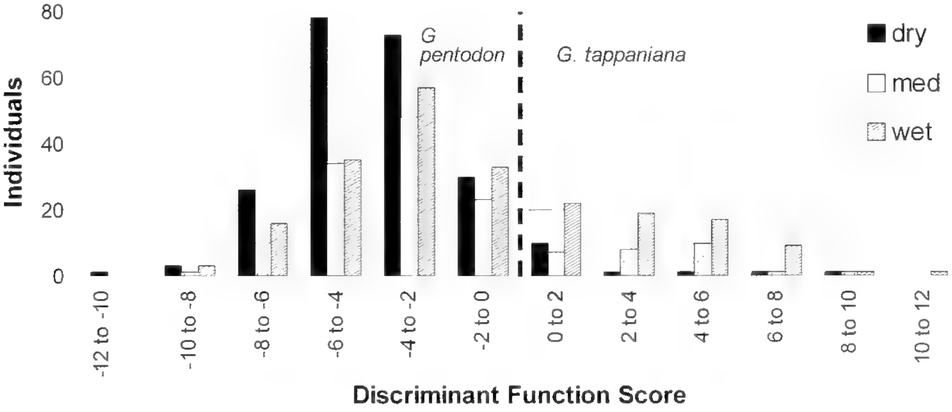

**Figure 7.** Histogram showing the number of individuals by discriminant function (DF) score, separately for each of three wetness classes.

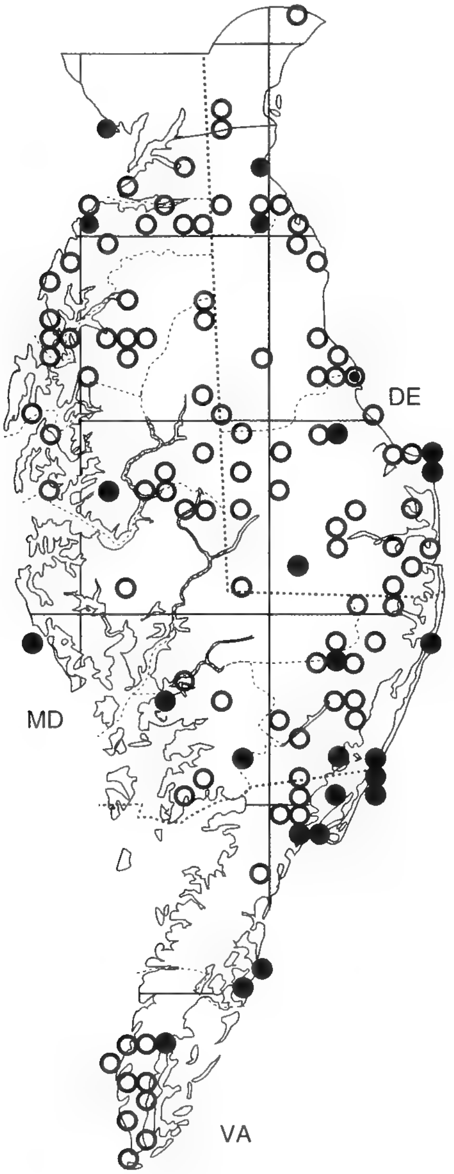

**Figure 8.** Delmarva Peninsula showing locations of 130 samples of *Gastrocopta pentodon* (open circles) and *G. tappaniana* (solid circles). Symbols on the map reflect majority rule (24 samples contained both *G. pentodon* and *G. tappaniana*; the 5 samples with equal numbers of the two species are omitted).

confidence that the two groups as defined by Vanatta and Pilsbry are non-random ($p < 0.000001$).

Some disagreement exists in the literature regarding the correct classification of *Gastrocopta carnegiei* Sterki, 1916. Sterki (1916a) described the new species as *G. minuta*, but subsequently changed the name to *G. carnegiei* because *G. minuta* was preoccupied (Sterki, 1916b). Sterki (1916a) did not designate a holotype among the three specimens, although Pilsbry (1948: 890, 892, fig. 480: 5) designated a lectotype by referring to the only unbroken specimen as the type. Turgeon et al. (1998) listed *G. carnegiei* as a valid species. Sterki (1916a) had indicated that *G. carnegiei* is similar to *G. tappaniana*, but Hubricht (1985) considered *G. carnegiei* to be a synonym of *G. pentodon*. The DF, when applied to measurements taken from the lectotype illustration of *G. carnegiei* presented by Pilsbry (1948: 892, fig. 480, image 5), classified the specimen as *G. pentodon* and the position it occupies in Figure 3 (indicated by the plus symbol) suggest it is closest to *G. pentodon*. The squat shape of the lectotype figure is like *G. tappaniana*, with its large body whorl, but it differs by a smaller shell and only 5 apertural teeth; the few whorls suggest that it might be an abnormal specimen. Although we were unable to locate the lectotype of *G. carnegiei* at Carnegie Museum of Natural History, we located the two paralectotypes, which are broken, as noted by Pilsbry (1948), so their relevant shape measurements cannot be discerned. This study suggests that *G. carnegiei* falls within the range of variation of *G. pentodon*.

Although separating the two species visually can be difficult, some characteristics might be helpful at distinguishing between them. *Gastrocopta tappaniana* tended to be larger (wider shell, wider penultimate whorl width, and taller body whorl) and regarding shape, tended to have a shorter hat (section above the penultimate whorl) relative to both shell height and spire height (hat/h, hat/spr), and a relatively taller body whorl. Regarding number of teeth, Vanatta and Pilsbry (1906) stated that all *G. tappaniana* have 7 teeth (excluding teeth on the parietal wall), whereas *G. pentodon* have 5–9 teeth. However, according to their drawings, the number of teeth for their *G. pentodon* ranged from 2–9. In contrast to their suggestion that tooth number might be a useful distinguishing character, our analysis suggested that number of teeth was not useful for separating species on the Delmarva Peninsula. A character that could be evaluated in future studies is whether the lower palatal fold of *G. tappaniana* is "usually not so long and entering as in *G. pentodon*" (Vanatta and Pilsbry, 1906; Pilsbry, 1948).

Future work could explore molecular data such as DNA sequences to verify these conclusions. Another avenue to address environmental influence on morphology would be to raise sibling specimens under different environmental conditions.

## ACKNOWLEDGMENTS

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# Upper Jurassic Pleurotomariidae (Gastropoda) from southwestern Madagascar

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## ABSTRACT

This paper describes four new species of Upper Jurassic Pleurotomariidae from southwestern Madagascar: *Obornella thompsonorum*, *Bathrotomaria annejoffeae*, *Bathrotomaria bedetteae*, and *Leptomaria takahashii*. In addition, the previously described *Leptomaria texta* Delpey, 1948, is reassigned to the genus *Obornella*. Comparison of this fauna with that of the geographically proximal Kutsch region of northwestern India reveals it to consist of representatives of wide-ranging Tethyan genera, but also to exhibit strong endemism at the species level.

## INTRODUCTION

A substantial number of well preserved Upper Jurassic pleurotomariid gastropods have recently been uncovered as a byproduct of commercial mining for ammonites in southwestern Madagascar. Six specimens, representing four species, were kindly made available to us for study by Mr. Chris Takahashi. The pleurotomariids and ammonites were dug by villagers from pit quarries near the town of Zakaraha, in southwestern Madagascar.

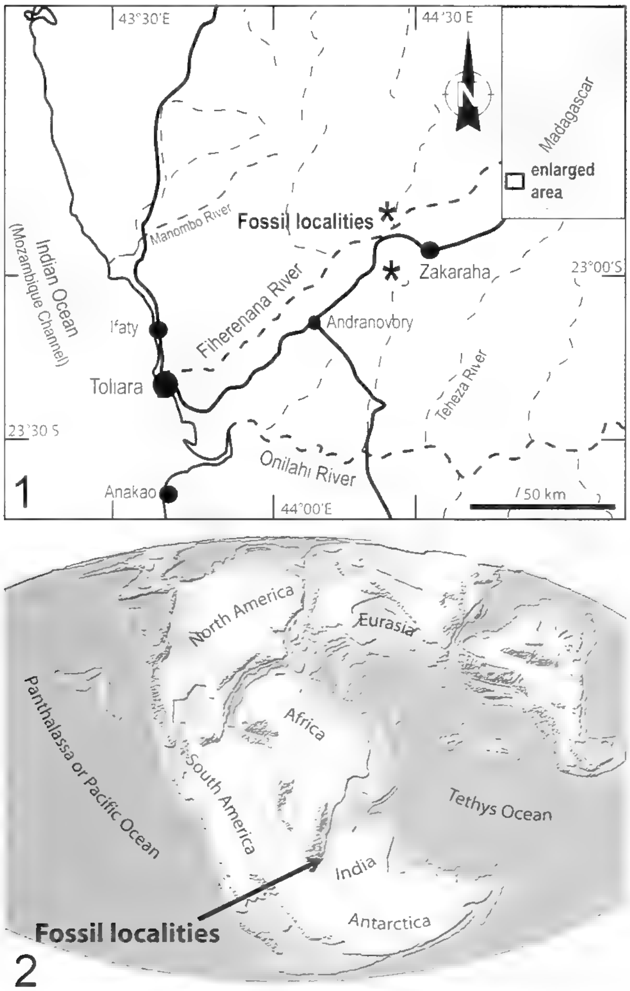
A survey of the literature on the Mesozoic gastropod fauna of Madagascar (e.g., Delpey, 1948; Collignon, 1949: Collignon, 1959; Kiel, 2006) revealed the majority of pleurotomariid species known from Madagascar to be of Cretaceous age, with only a single species, *Leptomaria texta* Delpey, 1948, reported from Jurassic strata. Although the sample available to us is of limited size and stratigraphic range, it expands our insight into the Jurassic pleurotomariid fauna of Madagascar. Like the well documented Jurassic pleurotomariid fauna of the Kutsch (also spelled Kachchh) region of western India (Jaitley et al., 2000; Das, 2002; Das et al., 2005), the Madagascar fauna reveals Tethyan affinities at the generic level, yet exhibits endemism at the species level. Both faunas evolved an increasing endemism within the Indo-Madagascan faunal province that was formed as the Tethys Ocean widened between Laurasia and eastern Gondwana, and a seaway started to develop between East and West Gondwana in the latest Jurassic (Tithonian) (Hay et al., 1999; Shome et al., 2004).

The scope of the present study is to review the Oxfordian (Upper Jurassic) pleurotomariid fauna of Madagascar, describe five species, four of them new, and to review the relationships and biogeography of these pleurotomariids.

## GEOLOGICAL SETTING

Rifting between Africa and Madagascar produced three large sedimentary basins along the west coast of Madagascar. These are, from North to South, the Ambilobe (or Diego), Mahajanga (also spelled Majunga), and Morondava basins. Sedimentation in this region commenced in the Carboniferous with the deposition of the Gondwanan Karoo sequences and equivalents. The first marine deposits resulting from the break-up of the Gondwana supercontinent are of Toarcian (late Lower Jurassic) age. From then on, alternating shallow marine, brackish, and fluviatile sediments were deposited in these basins. The pleurotomariids described here are from the Morondava basin, the southernmost of the three basins. Bio- and lithostratigraphic work in this basin is difficult because outcrops are few, index fossils are often not available, and measurable sections are usually short and difficult to correlate with each other. Consequently, only few lithostratigraphic units have been given formation names so far (Besairie and Collignon, 1972; Luger et al., 1994; Geiger and Schweigert, 2006).

The quarries that produced the specimens described here are located to the west of the town Zakaraha (also spelled Sakkara), one of them north of the Fiherenana River, the other to the south of it (Figures 1, 2). The fossiliferous layers are thin and consist of pink-yellow iron-oolithic limestones, and are overlain by grey mudstones (K. Bandel, pers. comm., 2007). The southern locality is very close, if not identical, with the "Amparambato section (VIb)" of Geiger and Schweigert (2006: 99) which was characterized by them as "a highly fossiliferous iron-oolitic limestone and sandstone bed with thin mud-stone interlayers." Accordingly, the oolitic limestones contain an abundant ammonite fauna; the overlaying mudstones contain nodosariid Foraminifera and ostracods (Geiger and Schweigert, 2006). The northern quarry is geographically close to the "Middle-Upper Oxfordian Ankilimena section (XI)" of Geiger and Schweigert (2006). This section is characterized by recurrent iron-oolitic limestones, which contain ammonites, rhynchonellids, bivalves, belemnites, echinoderms, and wood debris (Geiger and Schweigert, 2006: 103). Although Geiger and Schweigert (2006) did not report pleurotomariids or other gastropods from these sections, the remaining fossil content, their geographic position, and their lithology agrees well with that observed at the ammonite quarries visited by K. Bandel (pers. comm., 2007).



**Figures 1, 2.** Location of collection sites. **1.** Detailed map of two localities in southwestern Madagascar. **2.** Location of sites on a map of land masses during the Late Jurassic.

The ammonite fauna of these two localities, especially the presence of *Dhosaites* cf. *primus* Collignon, 1959, suggests a 'middle to upper Argovian (early Oxfordian)' age (Collignon, 1959; H. Keupp, pers. comm., 2004). The term 'Argovian' has been abandoned due to its inconsistent usage, but largely falls within the range of the Oxfordian (Zeiss, 2003). The sediments considered as 'Argovian' by Besairie and Collignon (1972) correlate with those mapped as late Callovian–early Oxfordian by Geiger and Schweigert (2006). Thus, the pleurotomariids described here are most probably of Oxfordian (Upper Jurassic) age.

## SUPRASPECIFIC CLASSIFICATION WITHIN PLEUROTOMARIIDAE

The number of genera and subgenera currently recognized within the family Pleurotomariidae (Appendix 1) has nearly doubled since the family was reviewed in the *Treatise of Invertebrate Zoology* (Knight et al., 1960). Of the 21 genera and subgenera now recognized (Figure 3), 16 are Mesozoic. Of these, five are restricted to the Triassic, three to the Jurassic, and only a single subgenus to the Cretaceous. At present, *Leptomaria* and *Conotomaria* are the only genera that are recognized as having survived from the Mesozoic into the Cenozoic. Of the seven Cenozoic genera, four survive in the Recent fauna. According to the literature surveyed, there is no chronological overlap between the Mesozoic genera and the Cenozoic genera.

As noted by a number of researchers (e.g., Hickman, 1976: 1094; Szabô, 1980: 49; Das, 2002: 99) fossil pleurotomariids are difficult to classify objectively, since the criteria upon which fossil pleurotomariid genera are defined differ conspicuously from those applied to Cenozoic genera. The monophyly and phylogenetic relationships of the surviving Cenozoic genera have been confirmed using molecular data from living representatives (e.g., Harasewych et al, 1997; Harasewych, 2002). By contrast, the relationships of Mesozoic genera and the species assigned to them are far less certain, as generic classification tends to be based on relatively few conspicuous morphological features (Table 1) especially those that are most easily derived from poorly preserved specimens and external or internal molds, while other characters are unconstrained and may vary widely. Szabô (1980: 49) commented that "almost all genera can be identified with certainty" on the basis of the shape of the whorl section and the surface of the whorls, as well as the position and width of the selenizone. Conti and Szabô (1987: 43) raised a question as to the significance of the presence or absence of an umbilicus in pleurotomariid

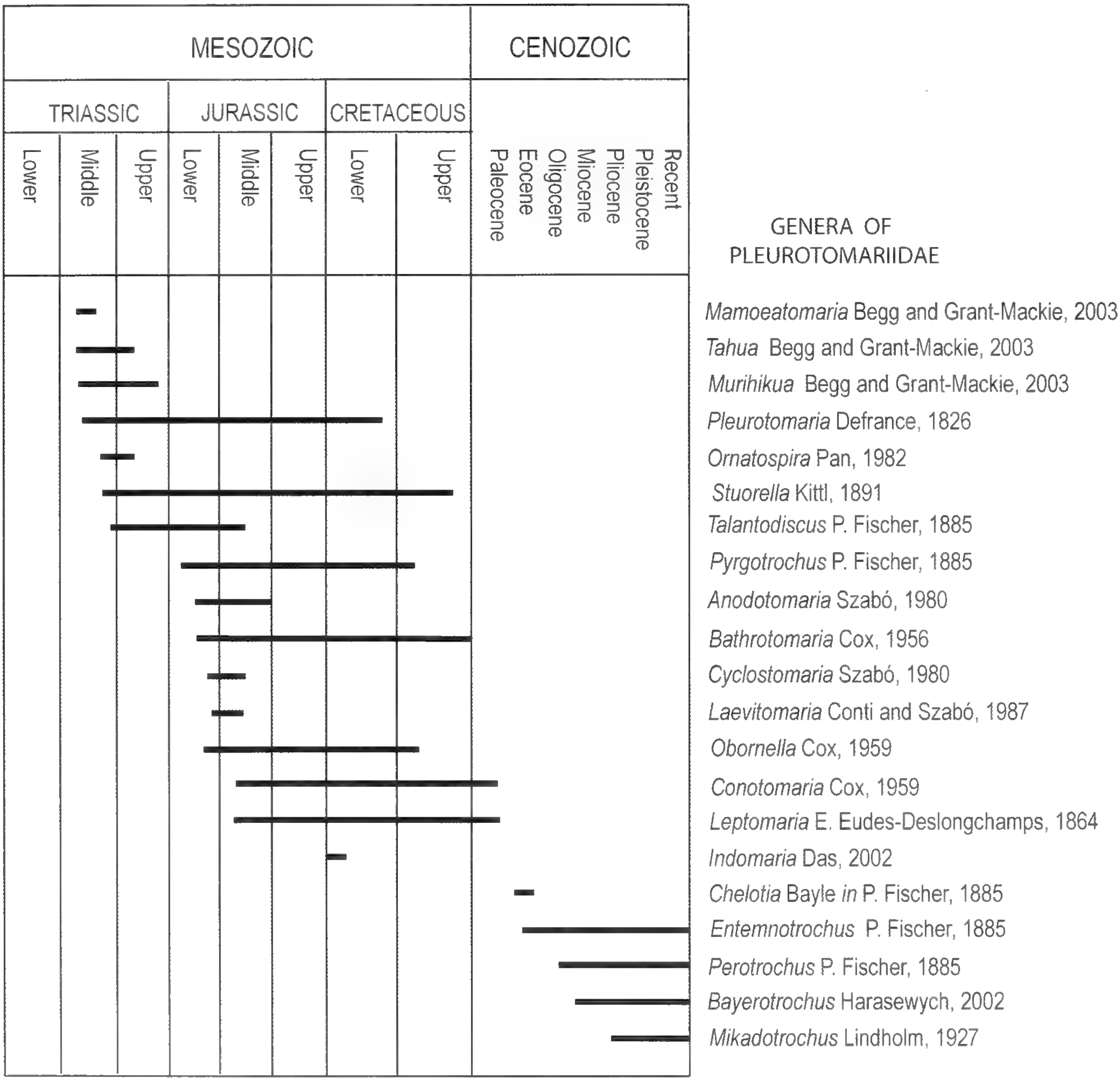


**Figure 3.** Geological ranges of the genera and subgenera within the family Pleurotomariidae, arranged by first occurrence in the fossil record

classification. The presence or absence of an umbilicus is sufficient to distinguish the most basal dichotomy among living Pleurotomariidae, yet this feature remains unconstrained and may vary widely within most Mesozoic genera and even within some "species" as they are currently diagnosed. It is therefore not surprising that fossil species are frequently reassigned from one genus to another (e.g., *Pyrgotrochus* to *Laevitomaria* Conti and Szabó, 1987: 46; *Perotrochus* to *Leptomaria*, see Das et al., 2005: 331) especially as more numerous and better preserved specimens become available.

## SYSTEMATICS

Family Pleurotomariidae Swainson, 1840
Genus *Obornella* Cox, 1959
*Obornella* Cox, 1959: 238.

**Type Species:** *Pleurotomaria plicopunctata* J. A. Eudes-Deslongchamps, 1849 (By original designation). Bajocian (Middle Jurassic) of France.

**Diagnosis:** The genus *Obornella* is characterized by a shell that is low turbiniform to sublenticular, with a nar-

**Table 1.** Genera and subgenera currently recognized within the family Pleurotomariidae and the characters used in the literature to define them.

| GENUS | Spire | Whorl profile | Selenizone | Axial shoulder sculpture | Nodes along periphery | Umbilicus | Suture | Base | Peripheral bulge | Slit | Surface sculpture |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pleurotomaria* | Gradate | 5-sided | Below shoulder | Nodes | Present/ absent | Present/ absent | Abutting | Convex | Present or absent | Broad, shallow | Spiral cords and nodes |
| *Anodotomaria* | Graduate | 5-sided | Below shoulder | Absent | Absent | Present/ absent | Abutting | Convex | Weak or absent | Broad | Spiral cords and threads |
| *Bathrotomaria* | Gradate | 5-sided | Along shouldere | Absent | Absent | Present/ absent | Abutting | Convex | Weak or absent | Narrow | Spiral or cancellate |
| *Talantodiscus* | Planspiral | 5-sided | Below shoulder | Nodes | Present | Present | Grooved | Flat | Present | Broad, shallow | Spiral threads and nodes |
| *Cyclostomaria* | Low turbiniform | Oval | Above periphery | Absent | Absent | Wide | Weakly canaliculate | Strongly convex | Absent | Narrow | Spiral cords, axial rib |
| *Indomaria* | Low turbiniform | 5-sided | Above periphery | Absent | Absent | Always present | Abutting | Convex | ? | Broad | Spiral cords, weak axial ribs |
| *Murihikua* | Gradate | 5-sided | Below shoulder | Axial ribs | Absent | ? | Abutting | ? | Absent | Narrow | Spiral cords |
| *Mamoeatomaria* | Gradate | 5-sided | Below shoulder | Nodes reduced/ absent | Absent | ? | Grooved | ? | Weak or absent | Narrow | Cancellate |
| *Tahua* | Conical | 4-sided | At mid-whorl | Absent | Present/ absent | Absent | Below periphery | Strongly convex | Absent | Narrow | Cancellate |
| *Ornatospira* | Low conical | 4-sided | At mid-whorl | Absent | Absent | Wide | Abutting | Nearly flat | Absent | Narrow | Cancellate, axial dominent |
| *Pyrgotrochus* | Conical | 4-sided | Below mid-whorl | Nodes present | Present | Absent or narrow | Flush | Flat | Present, nodose | Broad | Spiral cords, nodose bands |
| *Stuorella* | Conical | 4-sided | Just above periphery | Absent | Present | Absent or narrow | Flush | Flat | Present, nodose | Narrow | Axial costae, spiral threads |
| *Laevitomaria* | Conical | 4-sided | Below mid-whorl | Absent | Absent | Wide | Impressed | Flat | Weak or absent | Narrow | Spiral cords |
| *Obornella* | Conical | 4-sided | Near periphery | Absent | Present | Present | Abutting | Strongly convex | Weak or absent | Narrow, shallow | Cancellate, costae dominant |
| *Conotomaria* | Conical | 5-sided | At or above mid-whorl | Absent | Absent | Absent to wide | Flush | Flat | Present | Narrow, deep | Spiral cords |
| *Leptomaria* | Conical | 4-sided | At mid-whorl | Absent | Absent | Absent to wide | Abutting | Strongly convex | Weak or absent | Narrow, shallow | Spiral cords cancellate |
| *Chelotia* | Conical | 4-sided | Above mid-whorl | Absent | Absent | Wide | Flush | Flat | Weak or absent | Narrow, deep | Nodose spiral cords |
| *Entemnotrochus* | Conical | 4-sided | Above mid-whorl | Absent | Absent | Wide | Flush | Flat | Weak or absent | Narrow, deep | Spiral threads and cords |
| *Perotrochus* | Conical | 4-sided | Just below mid-whorl | Absent | Absent | Absent | Abutting | Convex | Weak or absent | Broad, shallow | Spiral cords fine or nodose |
| *Mikadotrochus* | Conical | 4-sided | Below mid-whorl | Absent | Absent | Absent | Abutting | Convex | Weak or absent | Broad, shallow | Nodose spiral cords |
| *Bayerotrochus* | Conical | 4-sided | Above mid-whorl | Absent | Absent | Absent | Abutting | Strongly convex | Weak or absent | Broad, shallow | Spiral cords and threads |

rowly open umbilicus and a strongly convex base. Surface sculpture consists of closely spaced collabral costellae (usually dominant) and spiral threads. The periphery is commonly crenate. The selenizone is narrow, smooth, often projecting onto the upper whorl face near the periphery. The labral slit is short.

**Remarks:** *Obornella* is known from strata of Toarcian (Lower Jurassic) to Oxfordian (Upper Jurassic) age (183 Ma to 156 Ma). Greatest diversity has been documented from Europe (see Gründel, 2003; Hägele, 2003), and this genus has also been reported from northeastern Iran (Majidifard, 2003) and the Kutch region of western India (Jaitley et al., 2000; Das et al., 2005).

*Obornella texta* (Delpey, 1948)
(Figure 4, reproduced from Delpey, 1948: pl. 2, fig. 1)

*Leptomaria texta* Delpey, 1948: 9, pl. 2, fig. 1.

**Original Description (Translated):** "(Height: 25 mm; diameter 31.5 mm; number of whorls: 5). The strip [selenizone] is anterior, wide relative to the last turn, and develops/changes normally until the multicarinate stage, becoming a little convex. The sculpture is latticed. An umbilicus obscured by a lamina pierces the convex base.

It is similar to *Pleurotomaria eudora* d'Orbigny, 1850, but the selenizone of this Oxfordian species is concave between two carinae, which is noticeably different from the Malagasy form. Argovian of Ankirijy (coll. Hourcq)."

**Remarks:** Unfortunately, Delpey did not specify were her type material was deposited. Inquiries at the Muséum national d'Histoire naturelle in Paris as well as the Université de Paris revealed that the specimens are not deposited in their collections. The description is minimal, and the illustration of the single, partial specimen (Figure 4) is poor, showing a specimen in which the selenizone runs along the shell periphery, with the suture adpressed along the lower edge of the selenizone. These features preclude the inclusion of this species in *Leptomaria* E. Eudes-Deslongchamps, 1864, which is characterized by convex whorls, with the selenizone at midwhorl. It is more likely that this taxon is referable to the genus *Obornella*, in which the selenizone is situated closer to the periphery. Delpey's illustration resembles the partial specimen (Jaitly et al. 2000: 39, pl. 2, figs. 8A, B) from the contemporary Dhosa Oolite Member of the Kutsch region of India that was identified as *Obornella* aff. *granulata* (J. Sowerby, 1818). Delpey's taxon is here transferred to *Obornella*, but its generic affinities remain obscure until the type, which is the only known specimen, is located.

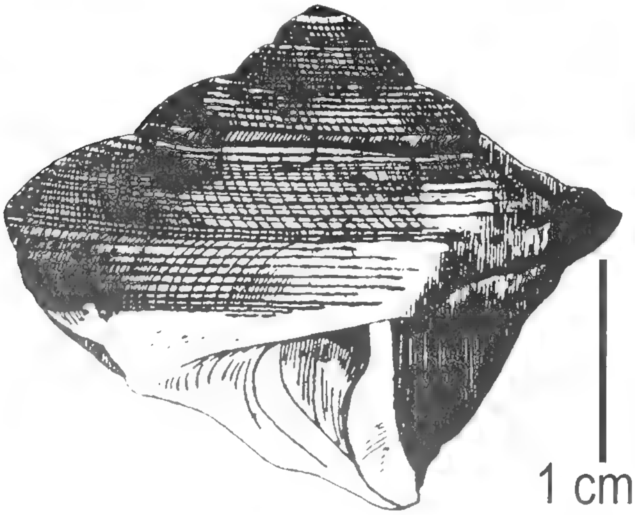


**Figure 4.** *Obornella texta* (Delpey, 1948). Reproduction of original illustration (Delpey, 1948: pl. 2, fig. 1, as *Leptomaria texta*

*Obornella thompsonorum* new species.
(Figures 5–12)

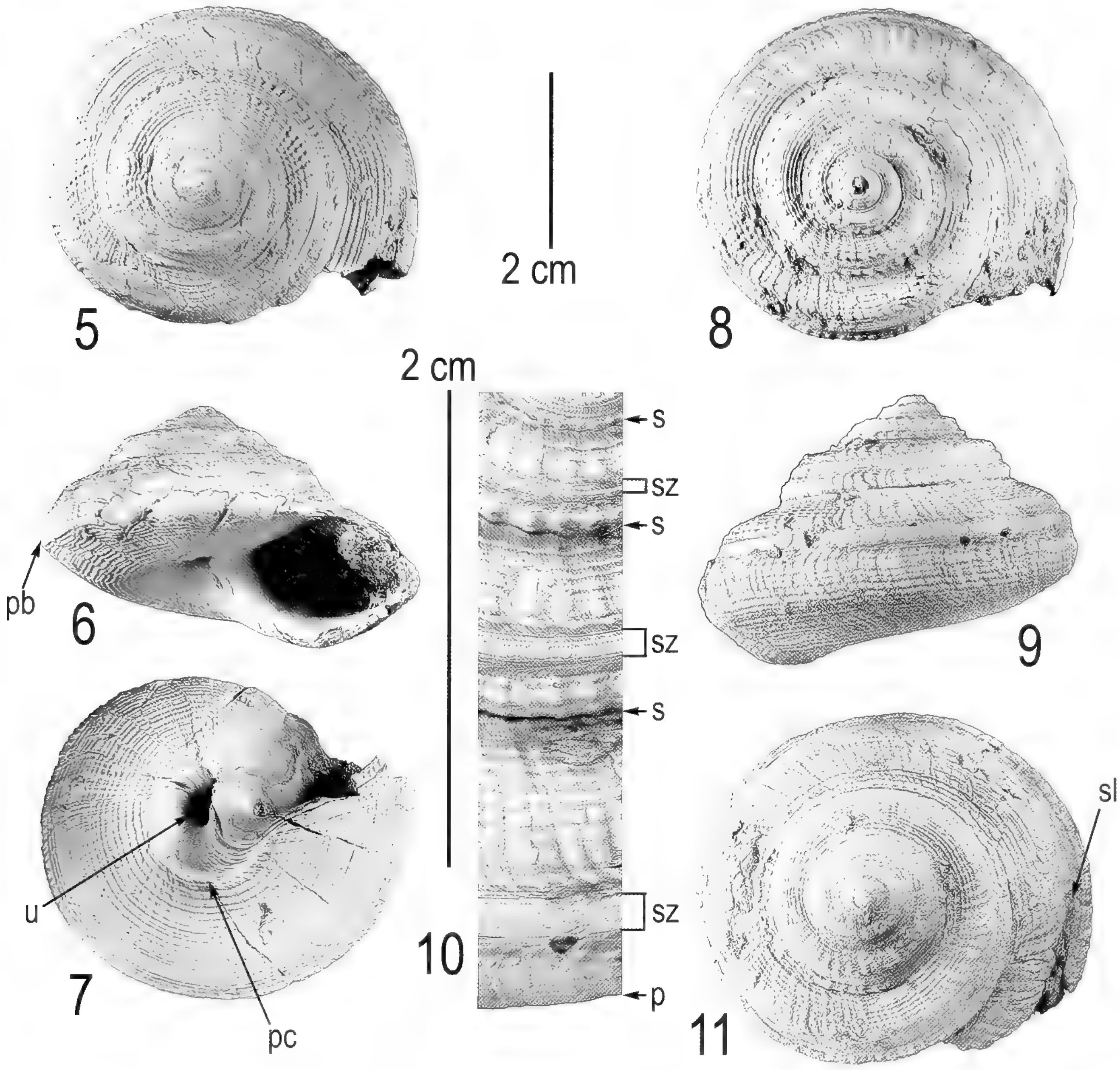
**Description:** Shell (Figures 5–12) small (holotype maximum diameter 42.2 mm, minimum diameter 34.6 mm, height 26.4 mm) low, turbiniform, consisting of approximately 7 teleoconch whorls. Base moderately convex, with narrow umbilicus (Figure 7, **u**). Spire angle 103–106°. Spire slightly convex in profile. Suture adpressed, joining previous whorl at or just below peripheral bulge (Figure 6, **pb**). Protoconch and first 3–5 teleoconch whorls eroded, only final 2–4 teleoconch whorls well preserved. Weak shoulder present on whorls 3–5, becoming convex, rounded in final two whorls. Axial sculpture of oblique radial costae most pronounced on whorls 3–5 (40–50 per whorl), weaker on subsequent whorls (80–108 per whorl), producing cancellate granules at intersections with spiral cords, especially at peripheral bulge and on either side of selenizone (Figure 10, **sz**). Number of strong, simple spiral cords 7–9 between suture and selenizone, 0–3 on selenizone, 2–4 between selenizone and peripheral bulge, 21–22 along base, between peripheral bulge and broad parietal callus (Figure 7, **pc**). Selenizone (Figure 10, **sz**) narrow, convex, with 0–3 spiral cords, and numerous strong to weak lunulae, situated just above peripheral bulge. Aperture ovate, roughly perpendicular to coiling axis. Outer lip smooth, portion below slit offset from portion above slit by 39°. Slit narrow (~2.5 mm), extending posteriorly 62° from end of suture. Lip thickest in columellar and basal region, forming broad parietal callus that partly overlaps the umbilicus.

**Type Locality:** Zakaraha, near Toliara (also spelled Tulear), southwestern Madagascar. 6–7 m below surface on plateau cut by river.

**Type Material:** Holotype, USNM 534480; paratype 1, USNM 534481; paratype 2 USNM 534482, all from the type locality.

**Age:** Oxfordian (Upper Jurassic).

**Etymology:** This new species honors Jon and Beverly Thompson for their many contributions and years of service to The Bailey-Matthews Shell Museum in Sanibel, Florida.



**Figures 5–11.** *Obornella thompsonorum* new species. **5.** Apical, **6.** apertural, and **7.** basal views of the holotype, USNM 534480. **8.** Apical and **9.** dorsal views of paratype 1, USNM 534481. **10.** Details of sculpture between suture and periphery on last three dorsal whorls of paratype 1. **11.** Apical view of paratype 2, USNM 534482. Abbreviations: **p,** periphery; **pb,** peripheral bulge; **pc,** parietal callus; **s,** suture; **sl,** posterior limit of slit; **sz,** selenizone; **u,** umbilicus.

**Remarks:** The assignment of this new species in the genus *Obornella* is provisional. The type species of *Obornella*, *Pleurotomaria plicopunctata* J. A. Eudes-Deslongchamps, 1849, from the Bajocian (Middle Jurassic) of France and England, is near one end of a morphological spectrum (see Hägele, 2003: fig. 10) that is distinguished by a low, conical spire and conspicuous axial fluting along the shell periphery and base. The other end of this morphological spectrum is characterized by shells with a higher, stepped spire, a rounder aperture, and spiral cords along the base, features reminiscent of the genus *Pleurotomaria*. *Obornella thompsonorum* more closely resembles *O. trapeza* (Hudleston, 1895: pl. 40, figs. 5a, b) and the "elevated variety" of *O. granulata* (Sowerby, 1818) illustrated by Hudleston (1895: pl. 40, figs. 1a, b) as *Pleurotomaria granulata* var. *cœlata* Deslongchamps, 1848, but differs in having a less pronounced, more rounded peripheral bulge, a spire that is stepped along intermediate whorls, and strongly beaded sculpture along both sides of the selenizone. Two

European species of *Obornella* had been reported from the Kutch fauna (Jaitly et al., 2000; Das, et al., 2005). *Obornella wuerttembergensis* (Sieberer, 1908) from Lower Jurassic [upper Bathonian] strata, is much flatter, lacks a parietal callus, and has a far broader umbilicus than *O. thompsonorum*. Specimens of *Obornella granulata* (Sowerby, 1818) from the Dhosa oolite member of the Chari Formation [Oxfordian] of Kutsch (Jaitly et al., 2000: pl. 1, figs. 5–7) resemble *O. thompsonorum* in overall proportions, but have more convex whorls between suture and periphery, far weaker axial sculpture, a broader umbilicus, and lack the distinctive parietal callus. *Obornella thompsonorum* may be distinguished from *Obornella texta* (Delpey, 1948), the only previously described pleurotomariid from the Jurassic of Madagascar, by the position of the selenizone above rather than along the periphery, and by having more prevalent sculpture, especially adjacent to the selenizone.

The shell microstructures found in *Obornella thompsonorum* (Figure 12) are similar to those of pleurotomariids from the Carboniferous (Batten, 1972), Triassic (Bandel, 1991), Jurassic (Bøggild, 1930), Cretaceous (Kiel, 2006), and Recent (Harasewych, 2002), indicating that shell microstructure is a very conservative character in this group.

Genus *Bathrotomaria* Cox, 1956

**Type Species:** *Trochus reticulatus* J. Sowerby, 1821. (By original designation). Kimmeridgian (Upper Jurassic) of England.

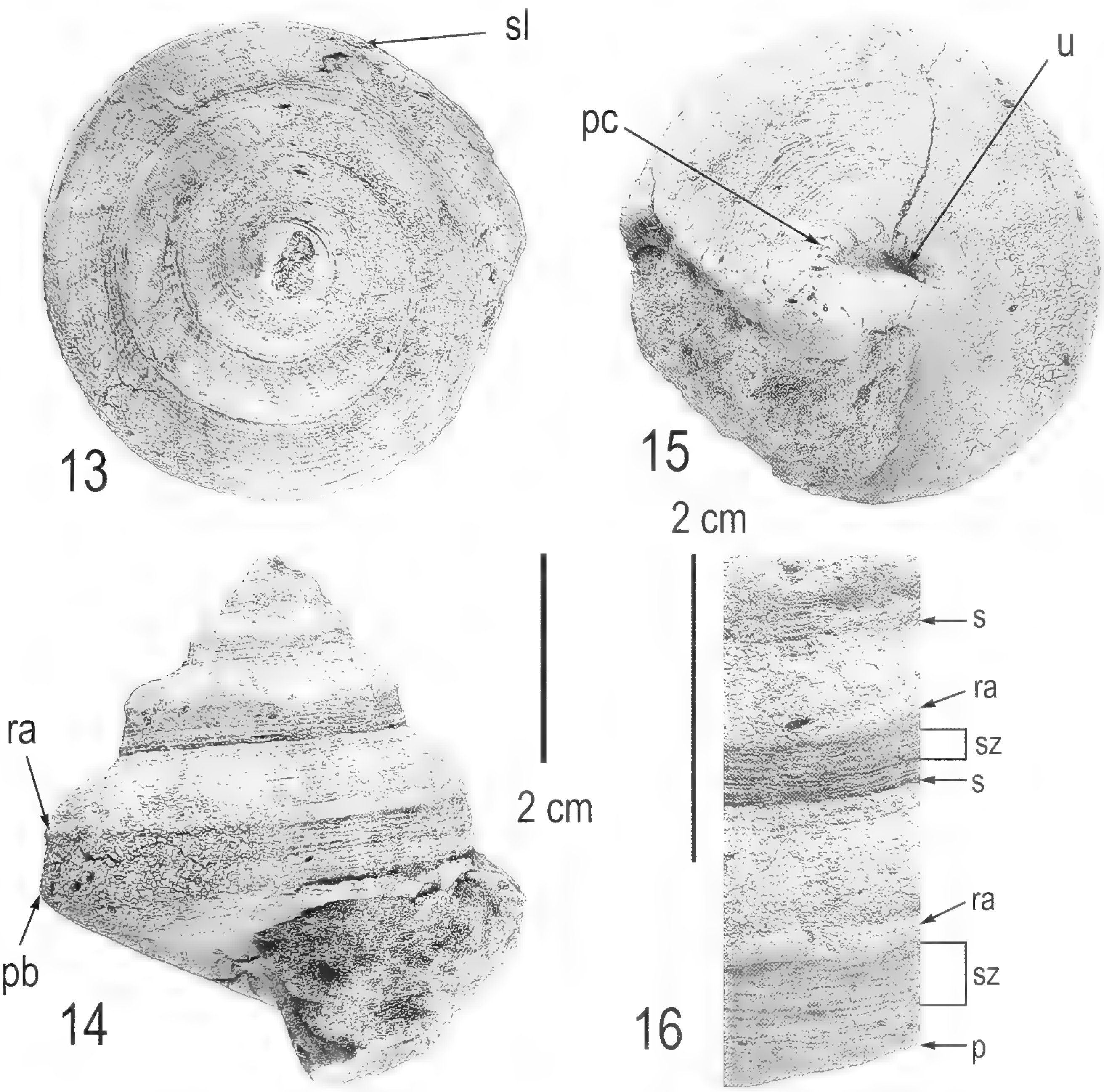
**Diagnosis:** *Bathrotomaria* can be distinguished by its usually large (to 130 mm), trochiform shell with a spire that may be elevated to depressed. The umbilicus may be broad to entirely absent. The whorl profile is usually angulate and non-tuberculate, with a broad ramp and a second carina or angulation, just overlapped on the spire. The selenizone is situated below the ramp angle. Surface sculpture of spiral cords and threads, commonly cancellate at intersection with collabral threads. The selenizone is moderately broad, the labral slit short.

**Figure 12.** SEM image of a fracture surface of the shell of *Obornella thompsonorum* new species at the aperture just below the slit, showing the transition from the simple prismatic outer layer to the nacreous inner layer. The arrows indicate areas with recrystalized shell material. Abbreviations: **Nac,** nacre; **spr,** simple prismatic crystals

**Remarks:** The oldest member of this genus is *Bathrotomaria paipotensis* Gründel, 2001, from the Sinemurian (Lower Jurassic) of northern Chile. The selenizone is narrow for the genus and the spiral sculpture is faint compared to other species. During the Middle and Upper Jurassic the genus was diverse and widely distributed from Peru (Cox, 1956) to Europe, India, and the Afro-Arabian East coast (Cox, 1960, 1965; Howarth and Norris, 1998; Das et al., 2005), and possibly also New Zealand (Gardner and Campbell, 1997), although the New Zealand record was not figured and needs confirmation. A number of species were reported from the Lower Cretaceous of the Tethyan realm, including the largest species with 130 mm diameter (Das, 2002; Kollmann, 1982, 2002). From the Cenomanian (lower Upper Cretaceous) Kiel and Bandel (2004) reported four species of *Bathrotomaria* from an intertidal rocky shore setting in Germany, the highest diversity at any Cretaceous locality. Further Upper Cretaceous records are few; the last record is from the lower Maastrichtian of France (Kollmann and Odin, 2001).

*Bathrotomaria annejoffeae* new species
(Figures 13–16)

**Description:** Shell (Figures 13–16) small for genus (holotype maximum diameter 47.7 mm, minimum diameter 43.8 mm, height 50.2 mm), with a tall, conical, strongly gradate spire, consisting of 6+ teleoconch whorls. Base weakly but evenly convex, with very narrow umbilicus (Figure 15, **u**). Spire angle 72°. Spire very slightly convex in profile. Suture weakly adpressed, joining previous whorl at or above peripheral bulge (Figure 14, **pb**). Protoconch and approximately first 2 teleoconch whorls missing. Subsequent early whorls with straight to weakly convex ramp between suture and ramp angle (Figure 14, **ra**) that becomes more inflated, convex on body whorl. Shell surface with broad, uneven, undulating rugae most evident near the suture. Axial sculpture of evenly spaced, weak axial costae (about 120 on body whorl) that produce weakly cancellate sculpture at intersections with spiral cords. Spiral sculpture (Figure 16) dominant, of 10–12 narrow, nearly abutting spiral cords between suture and ramp angle (comprised of single, smooth broad cord), 0–2 spiral cords between ramp angle and selenizone, 6–7 along selenizone, 3–4 between selenizone and peripheral bulge. Base with 36–38 spiral cords that are twice as broad as intervening spaces. Selenizone (Figure 16, **sz**) broad, weakly convex, nearly abutting ramp angle, spanning slightly more than half the distance between ramp angle and peripheral bulge. Aperture elongate, roughly pentagonal, long axis nearly perpendicular to the coiling axis. Outer lip broken. Slit broad (~3.8 mm), extending posteriorly 117° from the end of the suture. Lip thick along columellar region, with



**Figures 13–16.** *Bathrotomaria annejoffeae* new species. **13.** Apical, **14.** apertural, and **15.** basal views of the holotype, USNM 534483. **16.** Details of sculpture between suture and periphery on last three dorsal whorls of the holotype. Abbreviations: **p,** periphery; **pb,** peripheral bulge; **pc,** parietal callus; **ra,** ramp angle; **s,** suture; **sl,** posterior limit of slit; **sz,** selenizone; **u,** umbilicus.

narrow, weakly reflected parietal fold that forms a narrow parietal callus that partially occludes the umbilicus.

**Type Locality:** Zakaraha, near Toliara, southwestern Madagascar, 6–7 m below surface on plateau cut by river.

**Type Material:** Holotype, USNM 534483, from the type locality.

**Age:** Oxfordian (Upper Jurassic).

**Etymology:** This new species honors Anne Joffe in recognition of her many contributions and long service to the field of malacology, particularly to the American Malacological Union (now American Malacological Society) and most recently to The Bailey-Matthews Shell Museum in Sanibel, Florida.

**Remarks:** *Bathrotomaria* was among the most widespread and diverse of the pleurotomariid genera throughout the Middle and Upper Jurassic and Cretaceous. This is particularly true of the Jurassic fauna of the

Kutch region, from which ten species have been reported (Maithani, 1967; Jaitly et al., 2000; Das et al., 2005). Of these, five are of Oxfordian age. From its contemporary congeners within the Indo-Madagascan province, *Bathrotomaria annejoffeae* is readily distinguished from *B. tewarii* (Maithani, 1967), *B. buddhai* Das et al., 2005, *B. prasantai* Das et al., 2005, and *B. dhosaensis* Das et al., 2005 in having a proportionally taller, more gradate spire and a narrower umbilicus. In shell profile, *B. annejoffeae* more closely resembles specimens of *B. reticulata* (Sowerby, 1821) (Das et al., 2005: figs. 4, A–G) and *B. siebereri* (Jaitly et al., 2000:pl. 3, figs. 2–3) both from the Bathonian of Kutsch, and the Oxfordian *B. millepunctata* (Eudes-Deslongchamps, 1849) (Jaitly et al., 2000: pl. 3, fig. 4), but lacks granular whorl angulations of *B. siebereri* and *B. reticulata* (see Das et al., 2005:334). Das et al. (2005: 334) also noted that the Kutch specimens of *B. reticulata* lack an umbilicus (present in *B. annejoffeae*), whereas the suture of *B. siebereri* is deeply canaliculated, unlike that of *B. annejoffeae*. *Bathrotomaria annejoffeae* can also be recognized on the basis of the columellar portion of the aperture being long, straight, and nearly co-axial.

*Bathrotomaria bedetteae* new species.
(Figures 17–20)

**Description:** Shell (Figures 17–20) small for genus (holotype maximum diameter 65.0 mm, minimum diameter 58.8 mm, height 47.5 mm), with a short, broad, weakly gradate spire, consisting of 5+ teleoconch whorls. Base weakly but evenly convex, lacking an umbilicus (Figure 19). Spire angle 92°. Spire weakly convex in profile. Suture weakly adpressed, joining previous whorl at or above peripheral bulge (Figure 18, **pb**). Protoconch and approximately first 3 teleoconch whorls missing. Subsequent early whorls gradate, with straight ramp between suture and ramp angle (Figure 18, **ra**) that becomes more inflated, convex with increasing whorl number. Axial sculpture of broad, low, closely spaced, axial costae (about 56 on body whorl) that produce a coarsely cancellate sculpture at intersections of spiral cords, including weakly beaded ramp angle and peripheral bulge. Spiral sculpture codominant, of 3–4 low, broad, cords between suture and ramp angle, 0–1 spiral cords between ramp angle and selenizone, 0–1 between selenizone and peripheral bulge. Base with 17–19 finer spiral cords that are 2–4 times as broad as intervening spaces. Selenizone (Figure 20, **sz**) broad, weakly convex, nearly abutting peripheral bulge, spanning slightly more than half the distance between ramp angle and peripheral bulge. Surface without spiral cords, sculpture limited to strong lunulae. Aperture elongate, weakly pentagonal, long axis deflected from the coiling axis by 103°. Outer lip damaged, slit morphology not known. Inner lip thickest along columellar region.

**Type Locality:** Zakaraha, near Toliara, southwestern Madagascar, 6–7 m below surface on plateau cut by river.

**Type Material:** Holotype, USNM 534484, from the type locality.

**Age:** Oxfordian (Upper Jurassic).

**Etymology:** This new species honors the late Barbara A. Bedette, whose 52 years of service to molluscan paleontology at the National Museum of Natural History has benefited a multitude of researchers.

**Remarks:** *Bathrotomaria bedetteae* may be readily distinguished from *B. annejoffeae*, with which it cooccurs, on the basis of its lower, broader shell, with a weaker, more rounded ramp angle, by its coarser and more prominent cancellate sculpture that extends onto the ramp angle and peripheral bulge, and by the absence of an umbilicus. *Bathrotomaria bedetteae* is similar in profile to *B. tewarii*, *B. prasantai*, and *B. dhosaensis*, all from contemporary strata in Kutch, but differs in having a more gradate spire and a pronounced peripheral band, and in lacking an umbilicus.

Genus *Leptomaria* E. Eudes-Deslongchamps, 1864.

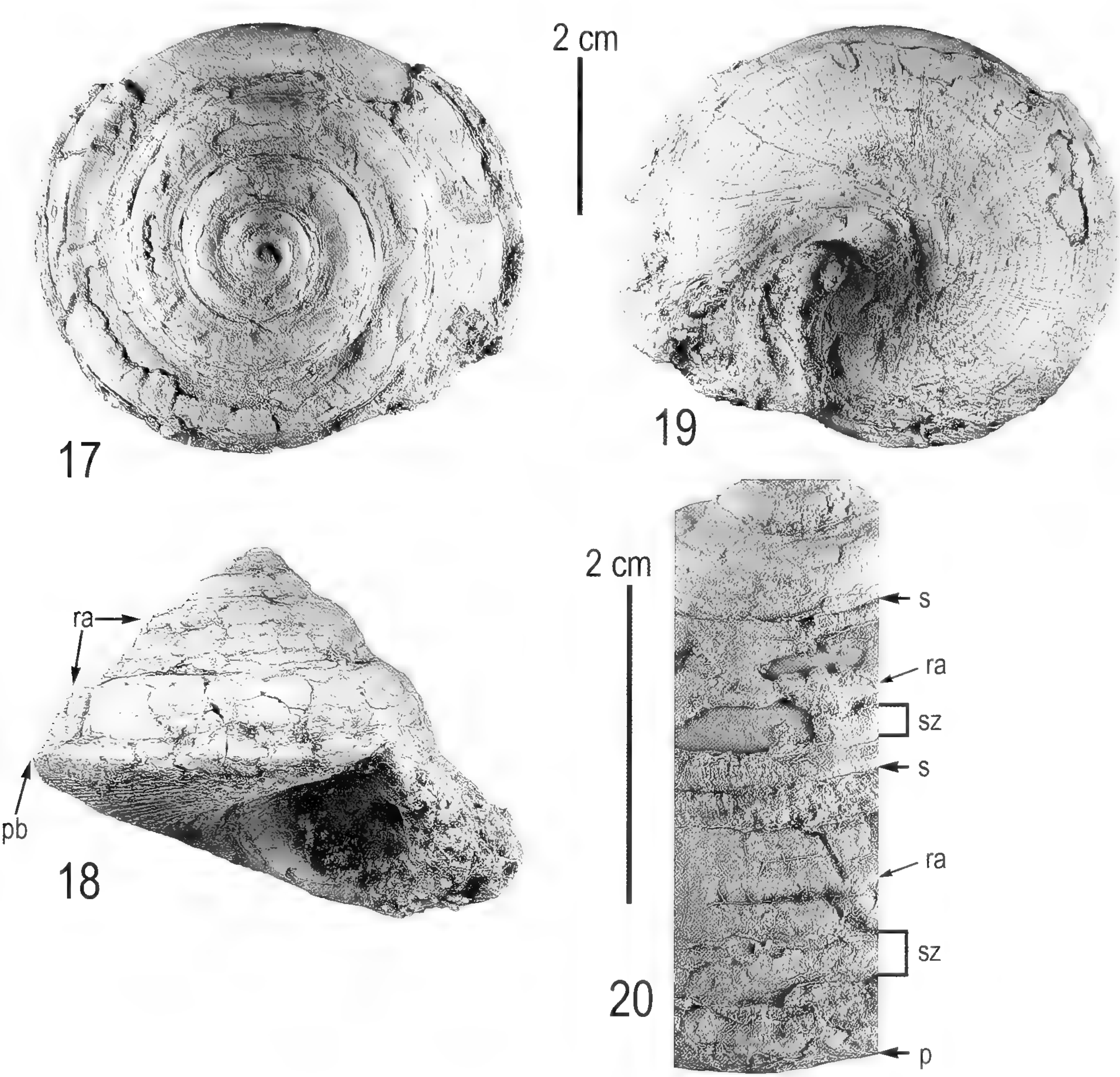
**Type Species:** *Pleurotomaria amoena* J. A. Eudes-Deslongchamps, 1849. (By original designation). Bajocian (Middle Jurassic) of France.

**Diagnosis:** Species of *Leptomaria* can be recognized on the basis of their large, turbiniform shells with low to moderately high spires and weakly to strongly rounded whorls. The umbilicus may range from broad to entirely absent. The whorl profile is rounded, lacking an angulate shoulder. The selenizone is situated at mid-whorl. Surface sculpture consists primarily of narrow spiral threads with finer axial threads forming weakly cancellate sculpture in some species.

**Remarks:** *Leptomaria* has been reported from strata ranging in age from Bajocian (Middle Jurassic, Knight et al., 1960) to Selandian (Paleocene, Kollmann and Peel, 1983). Hickman (1976) suggested that even some Eocene species may be included. Not surprisingly, the genus had a cosmopolitan distribution, with diverse faunas ranging from England (Cox, 1960) to New Zealand (Hudson, 2003). *Leptomaria* has been previously reported from Cretaceous deposits of NW Madagascar (Delpey, 1948; Collignon, 1949; Kiel, 2006). It is represented in the Jurassic fauna of Kutch (Jaitly et al., 2000; Das et al., 2005) but is not as diverse as the genera *Bathrotomaria* or *Pleurotomaria*.

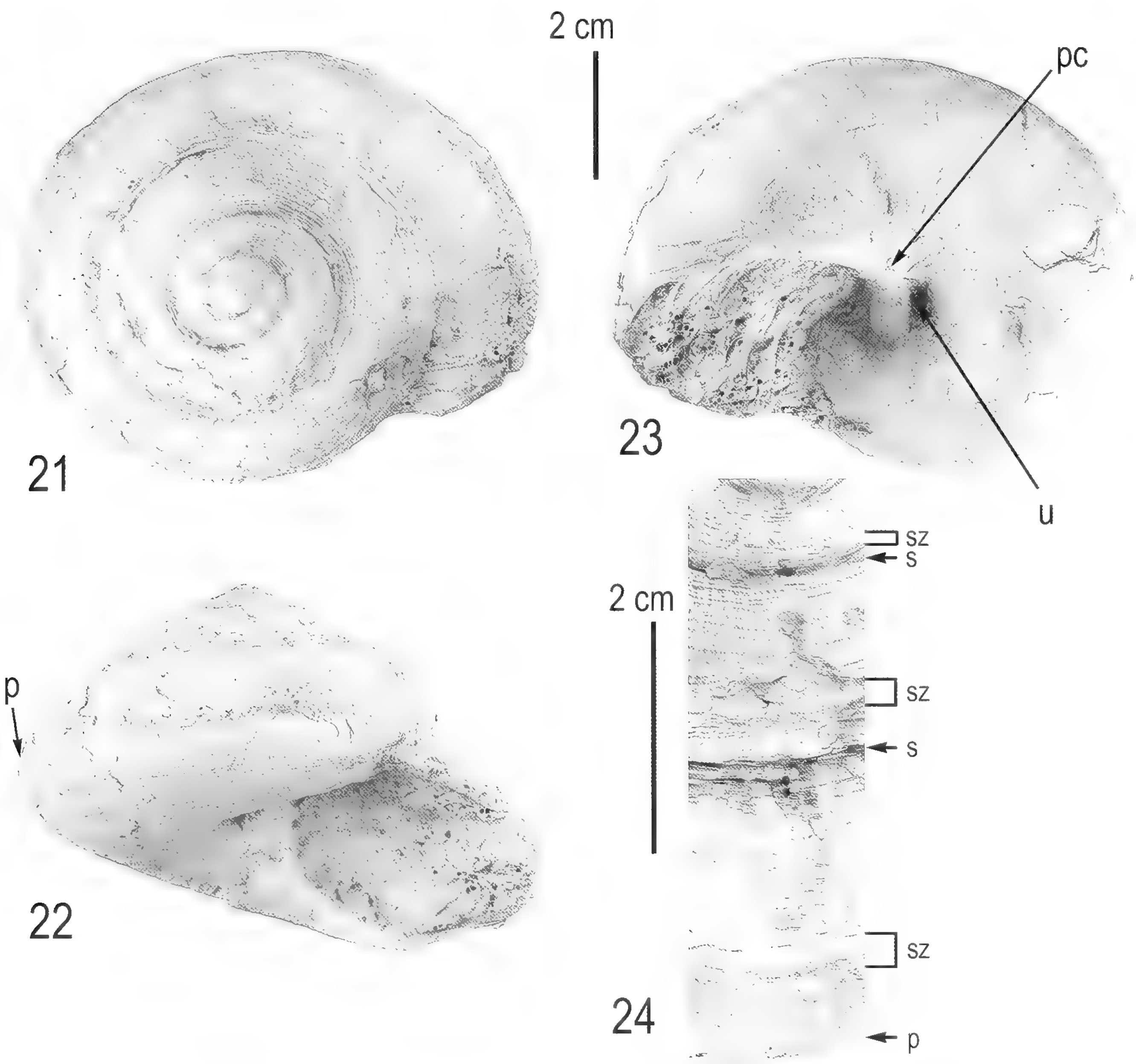
*Leptomaria takahashii* new species
(Figures 21–24)

**Description:** Shell (Figures 21–24) moderately large for the genus (holotype maximum diameter 82.4 mm, minimum diameter 67.23 mm, height 57.3 mm) low, turbiniform, consisting of approximately 6 teleoconch whorls. Base broadly and evenly convex, with very narrow umbilicus (Figure 23, **u**). Spire angle 109°. Spire strongly convex in profile. Suture (Figure 24, **s**) abutting,



**Figures 17–20.** *Bathrotomaria bedetteae* new species. **17.** Apical, **18.** apertural, and **19.** basal views of the holotype, USNM 534484. **20.** Details of sculpture between suture and periphery on last three dorsal whorls of the holotype. Abbreviations: **p,** periphery; **pb,** peripheral bulge; **ra,** ramp angle; **s,** suture; **sl,** posterior limit of slit; **sz,** selenizone.

joining previous whorl just below selenizone (Figure 24, **sz**) in early whorls, at or below periphery (Figure 22, 24, **p**) in later whorls. Protoconch and part of first teleoconch whorl eroded. Early teleoconch whorls (whorls 2–4) evenly rounded, later whorls (whorls 5–6) becoming more gradate, but evenly rounded, lacking a angular shoulder. Axial sculpture of numerous fine growth striae that produce a strongly reticulate pattern most evident between adjacent cords in region between suture and selenizone of early whorls, and broader low, axial costae that form a weakly cancellate pattern at intersections with the spiral cords. Spiral sculpture dominant, with 10 strong, closely spaced cords between suture and selenizone, 7–9 cords between selenizone and periphery, and 29–32 cords along base. Spiral cords may become broader and less distinct with increasing whorl number. Selenizone (Figure 24, **sz**) narrow, convex, situated just above periphery, with a single, median spiral cord present in early whorls, absent in later whorls, and numerous strong to weak lunulae throughout its length. Aperture evenly ovate, long axis forming an angle of 103° with coiling axis. Outer lip smooth, portion below slit offset from portion above slit by 30°. Slit narrow (~3.3 mm), extending posteriorly 81° from end of suture. Lip



**Figures 21–24.** *Leptomaria takahashii* new species. **21.** Apical, **22.** apertural, and **23.** basal views of the holotype, USNM 534485. **24.** Details of sculpture between suture and periphery on last three dorsal whorls of the holotype. Abbreviations: **p,** periphery; **pc,** parietal callus; **s,** suture; **sl,** posterior limit of slit; **sz,** selenizone; **u,** umbilicus.

thickest in columellar and basal region, forming narrow parietal callus that partly overlaps the umbilicus.

**Type Locality:** Zakaraha, near Toliara, southwestern Madagascar, 6–7 m below surface on plateau cut by river.

**Type Material:** Holotype, USNM 534485, from the type locality.

**Age:** Oxfordian (Upper Jurassic).

**Etymology:** This new species honors Mr. Chris Takahashi of Honolulu, Hawaii, in recognition of his many contributions to the study of living and fossil mollusks.

**Remarks:** *Leptomaria daityai* Das et al., 2005 (Callovian to Oxfordian of Kutch, India) occurs in coeval deposits, and most closely resembles *L. takahashii* in terms of size and general profile, but *L. takahashii* has a shorter spire, more rounded whorls, and has a very narrow rather than a wide umbilicus. Although the genus *Leptomaria* is well represented in the Jurassic fauna of the Indo-Madagascan region, most published records are either from Bathonian and Callovian strata of Kutch, or from Cretaceous deposits of Madagascar. Older taxa, including *L. fraga* (J. A. Eudes-Deslongchamps, 1849), *L. simplex* Jaitly et al., 2000, *L. pseudoumbilicata* Jaitly et al., 2000 (transferred to *Bathrotomaria* by Das et al., 2005: 340) are easily distinguished as they are smaller, and have a tall, conical whorl profile. Although the Bathonian *L. asurai* Das et al., 2005, is of comparable size, it differs in also having a tall conical profile and lacks an umbilicus.

## DISCUSSION

The species most similar to those described herein occur in contemporaneous fossil deposits of northwestern India. This is not surprising considering that the Madagascar species lived near the southern tip of a long and narrow embayment between East and West Gondwana, while northwestern Indian species lived at the northern tip of this embayment, where it opened to the Tethys Ocean (Figure 2). Although Recent pleurotomariids are restricted to hard substrates along the outermost continental shelf and upper continental slope, Mesozoic pleurotomariids inhabited sublittoral depths along the continental shelf. Studies of Upper Jurassic phytogeography have indicated that southern Madagascar was part of a warm temperate biome, while northern Madagascar and northwestern India were part of a warmer, subtropical biome (Rees et al., 2000: fig. 7C). Based on analyses of stable isotope compositions of the ammonite *Perisphinctes (Dichotomoceras)*, Lécuyer and Bucher (2006: 7, fig. 3) reported seawater temperatures ranging from 21.5°C to 24.1°C in the Morondava Basin of southwestern Madagascar, during the Oxfordian stage of the Upper Jurassic.

Extensive studies of Jurassic pleurotomariid faunas within this Indo-Madagascan Province (e.g., Cox, 1965; Jaitly et al., 2000; Das, 2005) have documented the presence of the genera *Bathrotomaria*, *Leptomaria*, *Obornella*, *Pleurotomaria*, *Anodomaria*, and *Pyrgotrochus*, the first three by far the most diverse. As additional specimens from the Jurassic of Madagascar become available, it is likely that the generic composition and diversity of this fauna will mirror that of the Kutch region of northwestern India.

## ACKNOWLEDGMENTS

We are grateful to Chris Takahashi for generously making the specimens available for study, and allowing the type material to be deposited in the collections of the National Museum of Natural History, Smithsonian Institution. We thank K. Bandel, J. Hartmann, and W. Weitschat, (all Hamburg) and H. Keupp (Berlin), for their help regarding the localities and their age; and T. A. White for providing the Jurassic paleo-map. A. Oleinik and an anonymous reviewer are acknowledged for their reviews.

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**Appendix 1.** Supraspecific taxa included in the family Pleurotomariidae, listed in the order in which they were proposed. Their type species are provided, as are known stratigraphic ranges, and geographical distributions.

*Pleurotomaria* Defrance, 1826 – Type species, *Trochus anglicus* J. Sowerby, 1818. Middle Triassic (Anisian; range extended by Begg and Grant-Mackie, 2003: 259) to Lower Cretaceous (Aptian). Cosmopolitan.

*Leptomaria* E. Eudes-Deslongchamps, 1864 – Type species, *Pleurotomaria amoena* J. A. Eudes-Deslongchamps, 1849. Middle Jurassic (Bajocian) to Paleocene (Danian). Cosmopolitan.

*Talantodiscus* Fischer, 1885 – Type species, *Pleurotomaria mirabilis* Deslongchamps, 1848. Middle Triassic (Kaihikuan ; range extended by Begg and Grant-Mackie, 2003: 259) to Middle Jurassic (Bajocian). Europe and New Zealand. Knight et al. (1960: I214) included this genus in the family Porcelliidae Broili, 1924. Subsequent authors (e.g., Szabô, 1980: fig. 3; Begg and Grant-Mackie, 2003: 229) included this genus within Pleurotomariidae.

*Pyrgotrochus* P. Fischer, 1885 – Type species, *Pleurotomaria bitorquata* J. A. Eudes-Deslongchamps, 1849. Lower

Jurassic to Upper Cretaceous (Cenomanian). Cosmopolitan.

*Perotrochus* P. Fischer, 1885 – Type species, *Pleurotomaria quoyana* Fischer and Bernardi, 1856. Oligocene to Recent. Cosmopolitan.

*Chelotia* Bayle *in* P. Fischer, 1885 – Type species, *Pleurotomaria concava* Deshayes, 1832. Eocene. Europe.

*Entemnotrochus* P. Fischer, 1885 – Type species, *Pleurotomaria adansoniana* Crosse and Fischer, 1861. Eocene to Recent. Cosmopolitan.

*Stuorella* Kittl, 1891 – Type species, *Trochus subconcavus* Münster, 1841. Middle Triassic (Ladinian) to Upper Cretaceous (Campanian; range extended by Kiel and Bandel, 2000). Europe.

*Mikadotrochus* Lindholm, 1927 – Type species, *Pleurotomaria beyrichii* Hilgendorf, 1877. Western Pacific, Pliocene to Recent.

*Bathrotomaria* Cox, 1956 – Type species, *Trochus reticulatus* J. Sowerby, 1821, by original designation. Lower Jurassic to Upper Cretaceous (Senonian). Cosmopolitan.

*Conotomaria* Cox, 1959 – Type species, *Pleurotomaria mailleana* d'Orbigny, 1843. Middle Jurassic (Bajocian) to Paleocene (Danian; range extended by Pacaud, 2004). Cosmopolitan.

*Obornella* Cox, 1959 – Type species, *Pleurotomaria plicopunctata* J. A. Eudes-Deslongchamps, 1849. Lower Jurassic (Toarcian) to Upper Jurassic (Oxfordian) Cosmopolitan.

*Anodotomaria* Szabô, 1980 [described as a subgenus of *Pleurotomaria*] – Type species *Pleurotomaria scacchi* Gemmellaro, 1874. Lower Jurassic (Pliensbachian) to Middle Jurassic (Callovian; range extended by Jaitly et al., 2000: 36). Europe to northwestern India.

*Cyclostomaria* Szabô, 1980 – Type species, *Pleurotomaria suessi* Hörnes, 1853. Lower Jurassic (Pliensbachian) to Middle Jurassic. Europe.

*Ornatospira* Pan, 1982 – Type species *Ornatospira mirifira* Pan, 1982. Triassic, China.

*Laevitomaria* Conti and Szabô, 1987 – Type species, *Pyrgotrochus? problematicus* Szabô, 1980. Lower Jurassic (Pliensbachian) to Middle Jurassic (Bajocian) Europe. Questionably included in Pleurotomariidae by the authors.

*Indomaria* Das, 2002 [described as a subgenus of *Pleurotomaria*] – Type species, *Pleurotomaria (Indomaria) umiensis* Das, 2002. Lower Cretaceous (Berriasian). Northwestern India.

*Bayerotrochus* Harasewych, 2002 – Type species, *Pleurotomaria midas* Bayer, 1964. Miocene to Recent. Cosmopolitan.

*Murihikua* Begg and Grant-Mackie, 2003 – Type species, *Murihikua tuhawaiki* Begg and Grant-Mackie, 2003, Middle Triassic (Aniasian) to Upper Triassic (Norian). New Zealand.

*Tahua* Begg and Grant-Mackie, 2003 – Type species, *Tahua waipiro* Begg and Grant-Mackie, 2003 Middle Triassic (Aniasian) to Late Triassic (Norian). New Zealand.

*Mamoeatomaria* Begg and Grant-Mackie, 2006 (new name for *Mamoea* Begg and Grant-Mackie, 2003) – Type species, *Mamoea wairakiensis* Begg and Grant-Mackie, 2003. Middle Triassic (Aniasian to Ladinian). New Zealand.

# *Sassia melpangi*, a new ranellid species (Gastropoda: Tonnoidea) from the Central Pacific

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## ABSTRACT

*Sassia melpangi* is described from bathyal depths off Oahu, Hawaii. This new species is most similar to *S. nassariformis* (Sowerby, 1902) from comparable depths off southeastern Africa, and to a lesser extent to *S. remensa* (Iredale, 1936) from the western Pacific. *Sassia melpangi* may be distinguished from all other *Sassia* on the basis of its broad, evenly rounded whorls, absence of a distinct shoulder on the varices, numerous axial ribs and spiral cords that produce an evenly reticulate surface sculpture, a broadly ovate aperture with distinctive inductura and strongly pigmented pattern along the edge of the outer lip.

## INTRODUCTION

*Sassia*, the oldest of the ranellid genera, is represented in the Upper Cretaceous deposits of the United States, Europe, and northern Africa. This genus became cosmopolitan by the Eocene and has been considered to be a basal group that gave rise to all other Ranellidae (Beu, 1998a: 800). In the Recent fauna, *Sassia* appears to have dispersed via a Tethyan distribution route, ranging from South Africa [*Sassia nassariformis* (G. B. Sowerby II, 1902)] and Japan [*Sassia semitorta* (Kuroda and Habe in Habe, 1961)] to the South Atlantic [*Sassia philomelae* (Watson, 1880)]. Greatest diversity occurs in the Indo-Pacific, with most species inhabiting outer shelf to upper slope depths (100 to 600 m). The Indo-West Pacific *Sassia* were revised by Beu (1998b: 137), who distinguished as "*Sassia* sp. nov.?" a distinctive specimen from Raevavae, French Polynesia. He mentioned examining photographs of additional specimens from Guam and Hawaii, but deferred from naming it formally until more specimens became available.

Through the kindness of Mr. Chris Takahashi, five additional specimens, all taken in traps off Oahu, Hawaii, were made available for study. Based in this new material, the taxon *Sassia melpangi* is described as a new species.

Abbreviations and acronyms used in the text are: dd, dead-collected shell; MNHN, Muséum national d'Histoire naturelle, Paris; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC.

## SYSTEMATICS

Superfamily Tonnoidea Suter, 1913
Family Ranellidae Gray, 1854
Subfamily Cymatiinae Iredale, 1913

Genus *Sassia* Bellardi, 1873

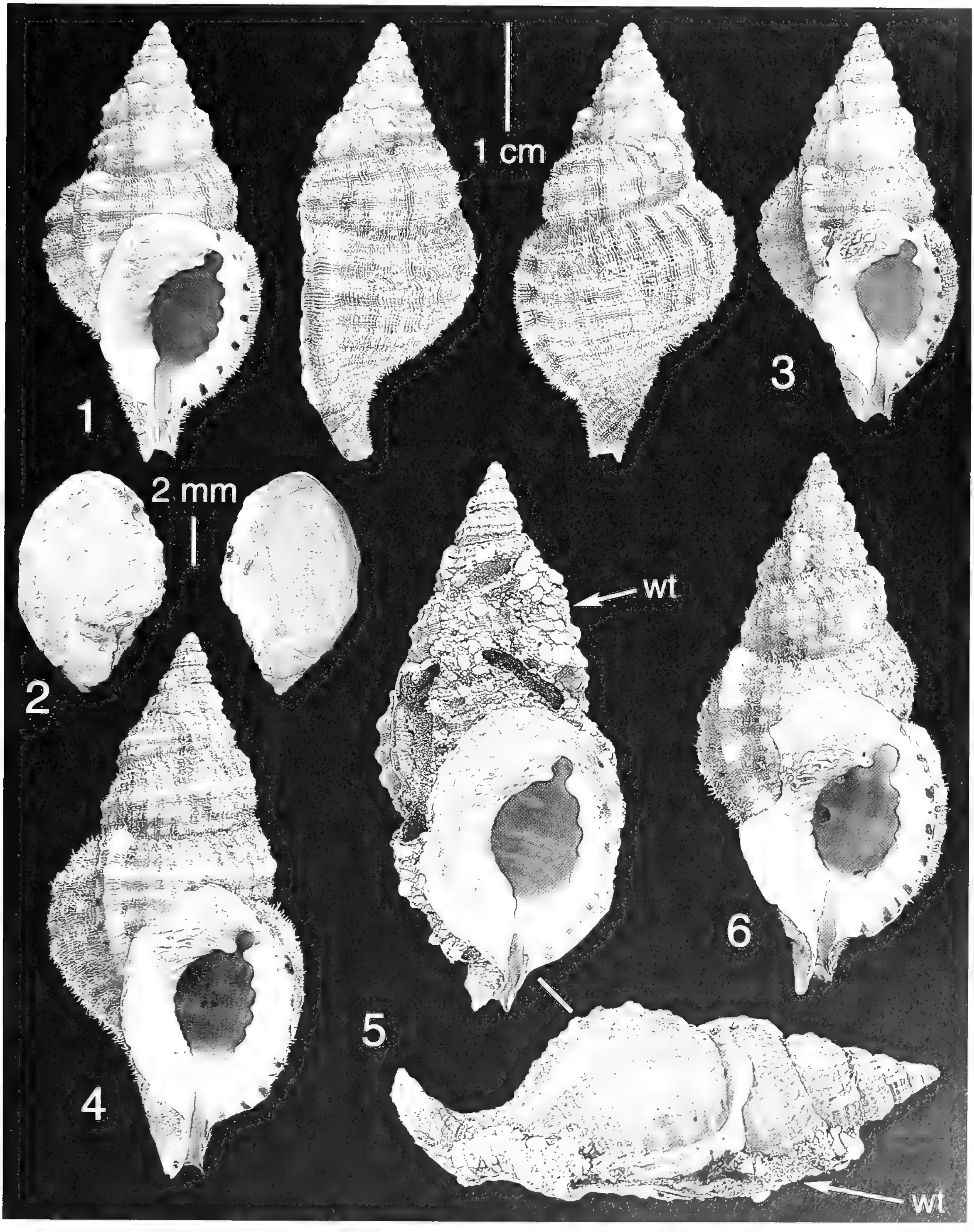
**Type Species:** *Triton apenninicum* Sassi, 1827, from the Miocene and Pliocene of Europe (by subsequent designation, Cossmann, 1903: 93). For an extensive synonymy, see Beu, 1998b: 139.

*Sassia melpangi* new species
(Figures 1–13)

*Sassia* sp. nov.? Beu, 1998: 141–142, fig. 43, 1.

**Diagnosis:** *Sassia* with up to 8 broad, evenly rounded whorls, without distinct shoulder on varices; sculpture of numerous axial ribs and spiral cords that produce an evenly reticulate surface sculpture; a broadly ovate aperture forming a distinctive inductura with ventrally reflected edges and strongly pigmented pattern along the edge of the outer lip.

**Description:** Shell (Figures 1, 3–6, 11–13) large for genus (reaching 51.7 mm; Table 1), fusiform, with tall, conical spire, large aperture, oval inductura with reflected edge, and short, open, axially oriented siphonal canal. Protoconch (Figures 12–13), tall-conical, increasing in diameter from 185 μm to 1.67 mm in 2.75 evenly rounded, glossy whorls. First half whorl smooth, followed by onset of sharp, narrow axial cords (26–29 per whorl) and 3–4 narrow, weaker, spiral cords. Transition to teleoconch abrupt, marked by change in color from amber



**Figures 1–6.** *Sassia melpangi* new species. **1.** Holotype USNM 1099759, apertural, right lateral, and dorsal views. **2.** SEMs of the inner and outer surfaces of the operculum of the holotype. **3.** Apertural view of paratype 1. **4.** Apertural view of paratype 2. **5.** Apertural and left lateral views of Paratype 3, USNM 1099760, showing adherent polychaete tubes (wt). **6.** Apertural view of Paratype 4. Scale bar (1 cm) applies to all shells. Abbreviation: wt, worm tube.

**Table 1.** Measurements of the holotype and four paratypes of *Sassia melpangi*. Linear measurements in mm.

| | HT | PT1 | PT2 | PT3 | PT4 |
|---|---|---|---|---|---|
| Shell length | 41.1 | 37.6 | 51.1 | 51.7 | 50.3 |
| Aperture length | 16.1 | 14.9 | 19.8 | 20.5 | 19.3 |
| Siphonal canal length | 7.5 | 7.4 | 9.8 | 11.2 | 9.5 |
| No. whorls, protoconch | 3.3 | 3.3 | 3.2 | 3.2 | 3.2 |
| No. whorls, teleoconch | 6.5 | 6.5 | 7.3 | 7.0 | 7.2 |
| No. cords on penultimate whorl | 5 | 4 | 5 | 5 | 5 |
| No. cords on last whorl | 8 | 9 | 9 | 8 | 9 |
| No. cords on siphonal canal | 6 | 4 | 5 | 6 | 7 |
| No. axial ribs on last whorl | 24 | 20 | 29 | 26 | 21 |
| No. axial ribs between varices | 18 | 15 | 21 | 17 | 13 |
| Spire angle | 50.0° | 48.5° | 44.8° | 45.8° | 43.0° |

to tan, loss of surface gloss, and coarsening of axial and spiral sculpture. Teleoconch of up to 8 convex, evenly rounded whorls. Suture adpressed. Axial sculpture of 13–29 weakly opisthocline to weakly prosocline ribs per whorl, as broad as interspaces, forming reticulate sculpture of hemispherical beads at intersections with strong spiral cords (3 on first whorl, 4–5 on penultimate whorl, 8–9 on last whorl, 4–7 on siphonal canal). Cords comprised of 3–5 broad fused threads with 3–9 finer threads between adjacent cords. Varices broad, strongly raised, begin after about 0.5 whorl and recur every 230–240° thereafter. Plane of inductura tangential to previous whorl, thus, varices form an angle of up to 10° with axial rib, intersecting at base of siphonal canal. Aperture large (0.38–0.40 shell length), broad (0.5–0.6 of aperture length), oval, major axis deflected from shell coiling axis by 20–23°. Outer lip reflected, forming rim of inductura, thickened, with 7 strong teeth that do not extend beyond the varix. Most adapical tooth largest, opposed to strong parietal tooth. Flaring edge of outer lip with rectangles of dark reddish brown pigment along its outer margin that are aligned with spiral cords. A broad, oval inductura with reflected edges extends over the parietal area. Parietal region with single, strong tooth that does not extend into the aperture and one or two weak folds that overlay spiral cords of previous whorl. Columella with multiple weak folds of varying lengths and angles, some ending before reaching the inductura, others short, originating on the inductura. Columellar fold at junction of siphonal canal most pronounced. Siphonal canal about half as long as aperture, axial, dorsally deflected, narrowly open, with proximal half covered by inductura. Base color cream to light tan, with axial bands of darker reddish brown, 3 bands between adjacent varices on early whorls, increasing to 6 bands between varices. Varices pigmented with reddish brown, darker on dorsal, lighter on ventral region, interrupted by slightly to much lighter bands along spiral cords. Interior of shell nacreous white, base color visible in thinner areas. Periostracum (Figure 11), thin, brown, finely lamellose, hirsute, with hairs aligned along spiral threads and growth lines. Periostracum best preserved along suture in most specimens. Operculum (Figure 2) large (> 0.8 aperture length), ovate, thin, corneous, with terminal nucleus. Radula (Figures 7–9) short (0.33 aperture length) consisting of 48–51 rows of teeth (7 per row). Rachidian teeth broad, with wide, curved basal plate, with strong central cusp flanked by 5–8 short, conical denticles. Lateral teeth broad, with stout bases, 6–8 denticles along ventral edge. Marginal teeth scythe-like, with smooth edges. Jaws (Figure 10) paired, narrow dorsally, expanded ventro-laterally, with fringed edges.

**Type Locality:** Oahu, off the north shore district of Haleiwa, muddy sand, in red shrimp traps set at 300–350 m.

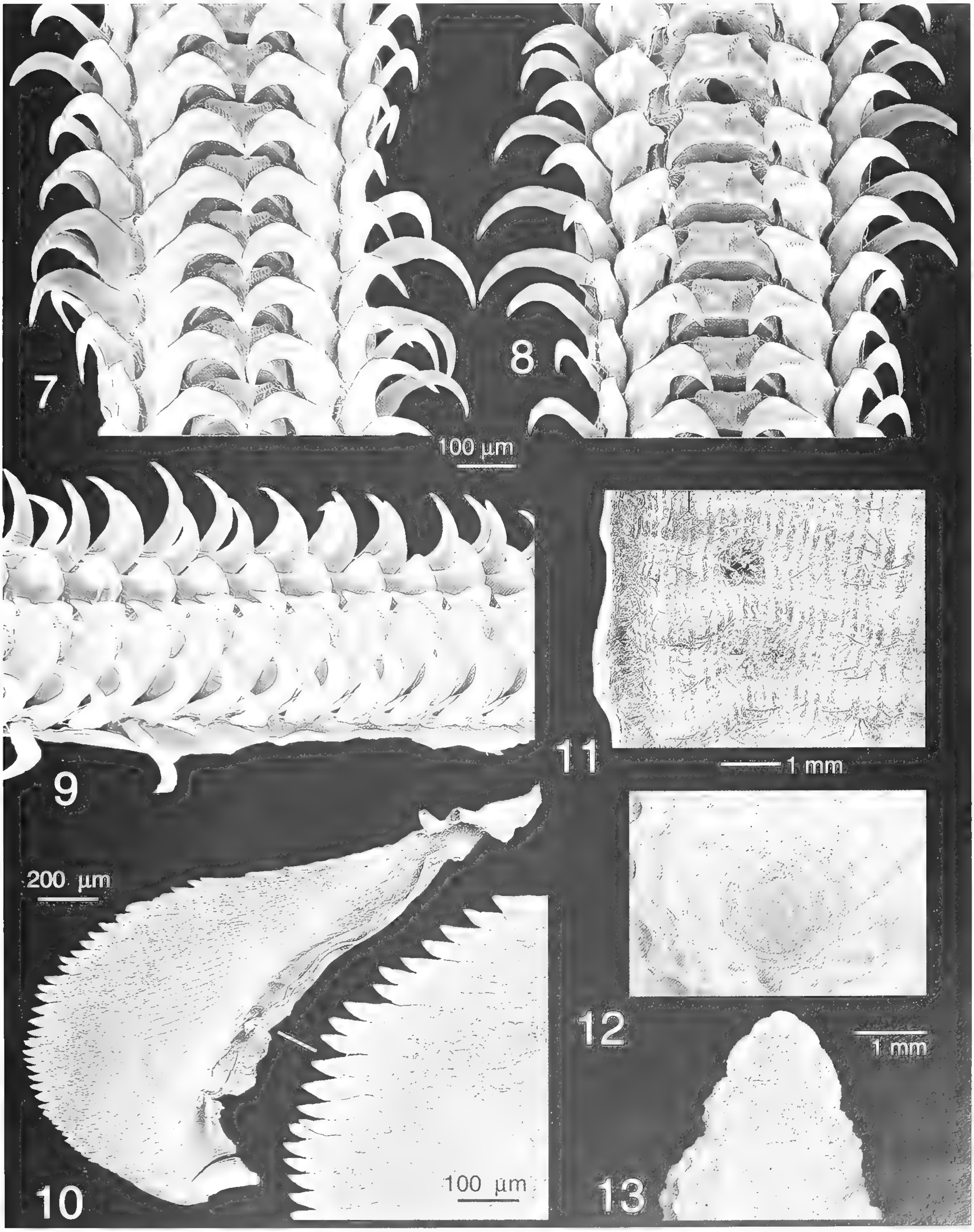
**Type Material:** Holotype, USNM 1099759; Paratype 3, USNM 1099760, Paratypes 1, 2, 4, Takahashi collection. All from the type locality.

**Additional Material Examined:** AUSTRAL ISLANDS: MNHN, Raevavae, 23°50.54′ S, 147°42.73′ W, in 400 m. BENTHAUS: stn DW 1884, Iles Marotiri, 570–620 m (1 dd); stn DW 1885, as last, 700–800 m (1 dd); stn DW 1897, ouest de Rapa, 480–700 m (2 dd); stn DW 1899, as last, 342–600 m (1 dd); stn DW 1903, Banc NE Rapa, 400–600 m (1 dd); stn DW 1923, Recif Nielsen, 360–840 m (1 dd); stn DW 1924, as last, 340–800 m (1 dd); stn DW 1925, as last, 560–790 m (1 dd); stn DW 1929, Banc Président Thiers, 350–370 m (1 dd); stn DW 1932, as last, 500–600 m (1 dd); stn DW 1933, as last, 500–859 m (2 dd); stn DW 1940, N de Raevavae, 100–460 m (3 dd); stn DW 1943, as last, 950 m (2 dd); stn DW 1945, Banc Lotus, 120–500 m (2 dd); stn DW 1951, as last, 206–450 m (1 dd); stn DW 1957, Tubuai, 558–1000 m (2 dd); stn DW 1961, as last, 470–800 m (3 dd); stn DW 1973, Banc Arago, 300–350 m (2 dd); stn DW 1974, as last, 450–618 m (2 dd); stn DW 1992, Rurutu: Mont de Lotus, 442–444 m (1 lv); stns 1997–2001, Rurutu, 200–1000 m (2 dd); stn DW 1998, cote N de Rurutu, 250–302 m (1 dd?); stn DW 1999, as last, 270–500 m (4 dd); stn DW 2000, cote N de Rurutu, 270–480 m (1 dd); stn DW 2001, port de Rurutu, 200–550 m (1 lv?); stn DW 2006, cote E de Rurutu, 35–450 m (1 dd); stn CAS 2008, cote E de Rurutu, 280–300 m (2 dd); stn DW 2018, Rimatara, 770–771 m (1 dd); stn DW 2021, Rimatara, 1200–1226 m (1 dd).

**Distribution:** *Sassia melpangi* is broadly distributed throughout the central West Pacific, from Guam to Hawaii and Raevavae in the Austral Islands, but does not occur in the Marquesas. It inhabits upper bathyal depths, with live specimens collected between 200 and 550 m.

**Etymology:** This species is named in honor of Mr. Melvin Pang, of Oahu, Hawaii, who collected the type series.

**Comparative Remarks:** The new species *Sassia melpangi* is readily distinguished from the western Pacific S.



**Figures 7–13.** *Sassia melpangi* new species. **7–9.** Radula of the holotype. **7.** Dorsal view of radula near mid-length. **8.** Dorsal view of radula near distal end, lateral teeth spread to reveal rachidian teeth. **9.** Right lateral view of radular ribbon. Scale bar = 100 µm applies to Figures 7–9. **10.** Jaw of holotype, with detail of edge. **11.** Periostracum of paratype 1, at midpoint of final varix. **12.** Apical, **13.** Lateral views of protoconch of paratype 1. Scale bar = 1 mm applies to Figures 12, 13.

*remensa* and *S. semitorta* in having: more evenly rounded whorls that lack a pronounced shoulder; the presence of more numerous, evenly spaced axial ribs that form a reticulate surface sculpture; a more evenly ovate aperture surrounded by an inductura with ventrally reflected edges; as well as a strong pigmentation pattern along the outer lip. *Sassia melpangi* most closely resembles *S. nassariformis* from southeastern Africa, with which it shares the rounded whorl profile and even cancellate sculpture. *Sassia nassariformis* can be differentiated by its shouldered varices, smaller aperture, weaker pigmentation along the outer lip, and by its thicker inductura, which is more triangular than ovate, and which is not reflected along it edges.

*Sassia melpangi* has a broad range throughout the tropical Pacific. While the type locality is off the Island of Oahu, a number of specimens are known from French Polynesia, and photographs of two specimens from Guam, Marianas Islands have been examined. This species inhabits upper bathyal depths (300–400 m). The position of worm tubes (Figure 5, wt) on the ventral surface of living specimen suggests that *Sassia melpangi* is epifaunal and inhabits hard substrates.

## ACKNOWLEDGMENTS

We are grateful to Chris Takahashi, for bringing this material to our attention, and for donating the holotype and one paratype to the National Museum of Natural History. Mr. Richard Salisbury kindly made available photographs of two specimens dredged off Guam, Marianas Islands, and Professor Alison Kay provided photographs of additional specimens dredged in Hawaii.

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# A new species of *Microcancilla* (Gastropoda: Cancellariidae) from the continental slope off northeastern Brazil

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## ABSTRACT

*Microcancilla jonasi* new species is described from deep waters off northeastern Brazil. The genus *Microcancilla* Dall, 1924, had not previously been recorded in Brazilian waters. Specimens were collected from sediment dredged as part of the REVIZEE program (Assessment of the Sustainable Potential of Living Resources in the Exclusive Economic Zone) during prospecting work on the continental slope off the state of Pernambuco at depths of 425 to 690 meters. The present study reveals that these specimens present affinities to the species *Microcancilla microscopica* (Dall, 1889), which differs from the new species, among other features, by having strong spiral sculpture between sigmoid axial ribs. In addition, a lectotype for *Cancellaria microscopica* Dall, 1889, is designated herein.

*Additional keywords: Cancellaria,* Neogastropoda, Pernambuco.

## INTRODUCTION

In his work on the gastropods collected in the West Indies (1879–80) by the U.S. Coast Survey Steamer BLAKE, Dall (1889a) described *Cancellaria microscopica* Dall, 1889, based entirely on empty shells. Dall later (1889b: 106) placed that species with a query in the genus *Admete* Kröyer in Möller, 1842. Still later, Dall erected the cancellariid genus *Microcancilla* Dall, 1924. When introducing this genus, Dall did not give a genus description, and listed only the single species *Admete* [sic] *microscopica* Dall, 1889. Until now no congeners have been reported.

Most species of *Admete* are found in shallow waters of polar regions but a few occur in deeper water in temperate zones (Harasewych and Petit, 1986; Knudsen, 1964). However, all of the taxa described as *Admete* have not been studied in detail and it is probable that some are not properly placed in this genus (Bouchet and Warén, 1985).

A recent study of deep-water Cancellaridae from the New Caledonia area (Bouchet and Petit, in preparation) shows that the central Pacific fauna contains species clearly attributable to *Microcancilla* and others that are morphologically similar to *Admete aethiopica* Thiele, 1925, from Somalia [illustrated in Verhecken (1997: 312, fig. 52)]. Intermediate between these seemingly disparate morphologies and having various features in common with them are a series of species. Verhecken (1997), in figuring the Somalia specimen, placed it in the genus *Admete* with a query but offered no other possible placement.

It is not contended here that *Microcancilla jonasi* new species, *"Admete" aethiopica* Thiele, and *Microcancilla microscopica* (Dall) are truly congeneric species. However, *Microcancilla* is considered at the moment the best available placement within the existing genera of the Cancellarioidea and such placement is provisional. Until the small deep-water species of Cancellariidae are better understood and the validity and limits of other available genus group taxa are established, we do not wish to introduce a new genus-group taxon. This problem with the available genera for small cancellariids was succinctly pointed out by Maxwell (1992: 167). *Microcancilla jonasi* new species is considered endemic to the continental slope off the state of Pernambuco, Brazil.

## MATERIALS AND METHODS

All specimens examined were obtained in 1999–2000, during oceanographic prospecting work on the continental slope off the state of Pernambuco, Brazil. No live specimens were collected. Shells were mounted on specimen stubs and exmained and photographed under a Jeol JSM 6360 Scanning Electron Microscope, at the "Instituto Tecnológico de Pernambuco (ITEP)". Shells were measured using a stereo microscope with eyepiece micrometer. The type material was deposited at the Academy Natural of Sciences, Philadelphia, USA (ANSP); Museu Nacional, Rio de Janeiro, Brazil (MNRJ); Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP); Museu Oceanográfico do Rio Grande, Rio Grande, Brazil (MORG).

## SYSTEMATICS

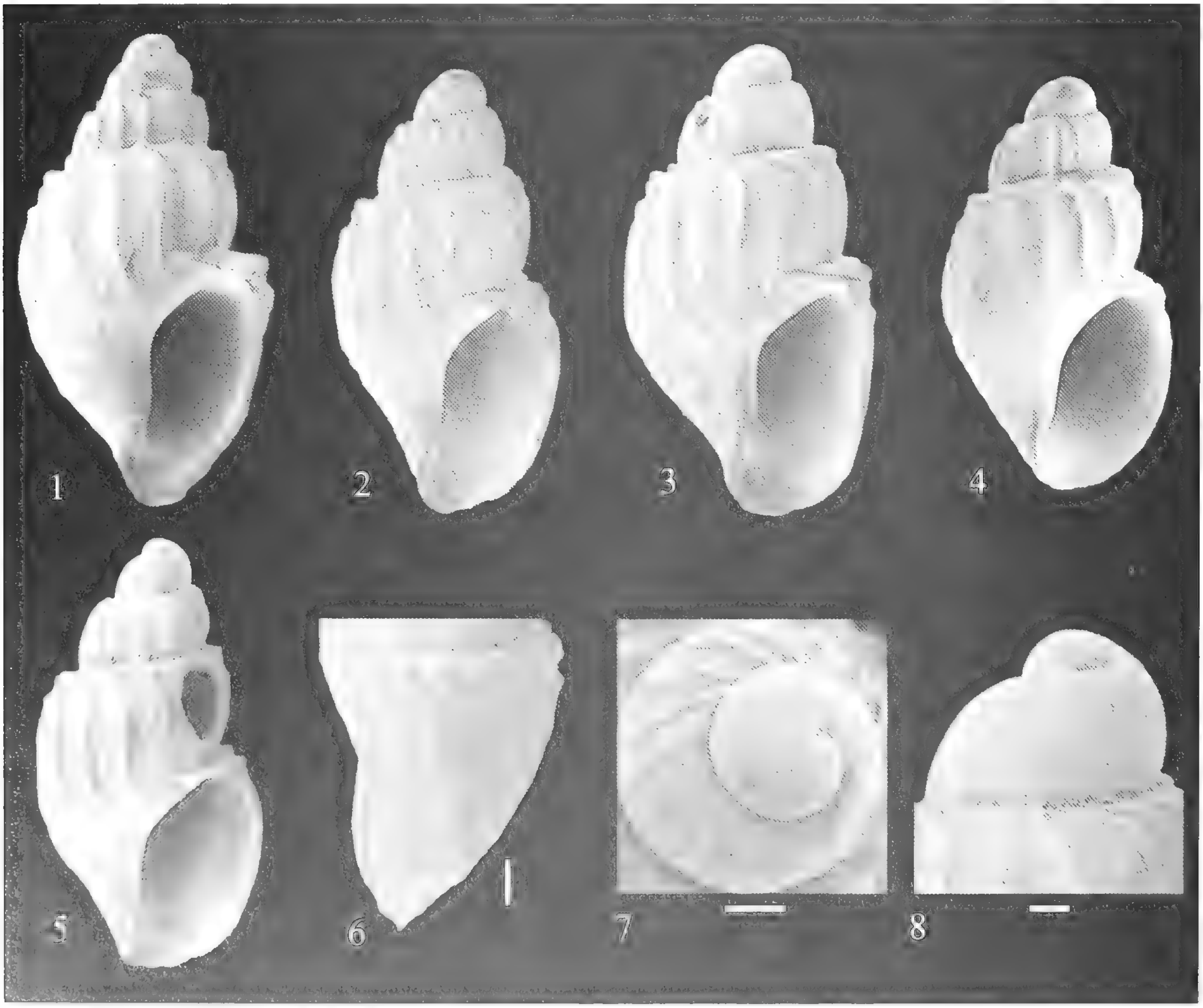
Family Cancellariidae Forbes and Hanley, 1851

Genus *Microcancilla* Dall, 1924

**Type Species:** *Admete microscopica* (Dall, 1889) [= *Cancellaria microscopica* Dall, 1889a] by original designation. Recent, Caribbean.

*Microcancilla jonasi* new species
(Figures 1–8)

**Description:** Shell conical, small, fragile, translucent, whitish, short spire. Protoconch smooth, globose, paucispiral with 1.5 whorls, terminating with the emergence of the axial sculpture of the teleoconch (Figures 7–8). Teleoconch with 2.5 slightly convex whorls. Suture well-marked, with a small, flattened subsutural region ornamented by the adapical portion of the axial ribs. On the margin of this region, there is a strongly nodular shoulder, nodules coinciding with axial ribs below, resembling a small crown. Below the shoulder, there is a second, weaker spiral cord, with nodules somewhat smaller than those of the crown on margin of a small, concave, spiral depression (Figure 6). Body whorl developed, very wide, with about 69% of the total size of the shell, sculptured with 15 to 18 rounded, regularly spaced ribs, which disappear toward the base. Interspaces ornamented by obscure threads. Base imperforate, strongly conical, with



**Figures 1–8.** Scanning electron micrographs of *Microcancilla jonasi* new species (all deposited in MORG): **1.** Holotype, apertural view, length = 4 mm; **2.** Paratype, apertural view, length: 3.28 mm; **3.** Paratype, apertural view, length = 3.12 mm; **4.** Paratype, apertural view, length = 2.85 mm. **5–8.** Paratype, length 3.60 mm. **5.** Apertural view. **6.** Subsutural view, showing strongly nodular shoulder and weak spiral cords (Figure 5). **7–8.** Protoconch (shell in Figure 5). Scale bars: Figure 6 = 500 µm; Figure 7 = 200 µm; Figure 8 = 100µm

convex contour, ornamented by 3 to 5 weak spiral cords that emerge from the interior of aperture. Aperture elliptic. Outer lip fragile and smooth inside. Inner lip strongly reflected, wide parietal region, without callus, median portion of the columella with reflected appearance, thickened upon the umbilical wall with no columellar folds. Final anterior portion of the columella inclined to the left of the shell axis.

**Type Material:** Holotype, MORG 50.716, length = 4 mm; 4 paratypes, MORG 50.718 (Figures 2–8); 3 paratypes, MZUSP 81755; 3 Paratypes ANSP 413549, 1 paratype, MNRJ 10839, Pernambuco, Brazil, D-4, 08°42.1′ S, 34°44.1′ W, 425 m, muddy bottom, 25 Mar. 2000; 2 paratypes, MNRJ 10838; 3 paratypes, MZSP 81756; 1 paratype MORG 50.717 (Pernambuco, Brazil, D-11, 08°46.5′ S, 34°44.5′ W, 690 m, muddy bottom, 18 Sep. 2000).

**Type Locality:** Continental Slope from the State of Pernambuco, northeastern Brazil, D-4, 08°42.1′ S, 34°44.1′ W, 425 m, muddy bottom, 25 Mar. 2000.

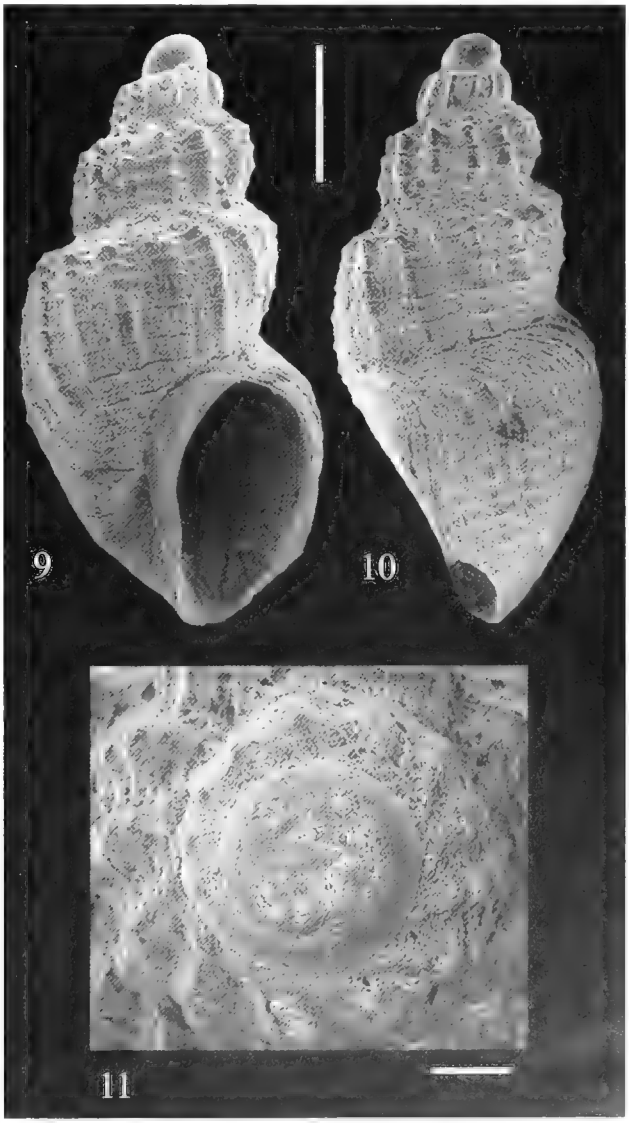
**Etymology:** The species is named after Mr. Rainer Jonas, scientific director of the Gesellschaft für Biotechnologische Forschung (GBF), Germany, for his assistance in obtaining literature and his constant support during the identification work of gastropods from the continental slope of Brazil.

**Geographic Distribution:** Endemic to the Continental Slope of the State of Pernambuco, northeastern Brazil.

**Habitat:** Muddy substrate, 425 to 690 m.

**Discussion:** *Microcancilla jonasi* new species studied here is distinguished from *Microcancilla microscopica* and ?*Admete aethiopica* based on the following characteristics: (1) sculpture of the body whorl: *M. microscopica* has a strong spiral sculpture, with subequal rather coarse threads, forming a reticulum with the axial spirals, ?*A. aethiopica* presents a wide body whorl, with a strong axial sculpture and smooth spiral bands separated by narrow grooves disappearing near the base, *M. jonasi* has strong axial ribs, sinuous and rounded, and an obscure spiral ornamentation with no reticulation; (2) Spiral ornamentation: *M. microscopica* has threads that alternate between strong and weak, crossed by raised growth threads, ?*A. aethiopica* has strong axial ribs crossed by weaker spiral threads, *M. jonasi* only presents raised axial ribs; (3) Shoulder: on *M. microscopica*, the shoulder is obsolete and the subsutural platform becomes rounded on the body whorl, ?*A. aethiopica* presents an angular shoulder, strongly nodular, and a narrow, flat subsutural platform, *M. jonasi* has a small, flat subsutural platform, bordered by a nodular shoulder with a lower depression and followed by a second subshoulder cord that is more weakly nodular; (4) Umbilicus: *M. microscopica* has a distinct, moderate umbilicus with no bounding carina or siphonal fasciole, ?*A. aethiopica* and *M. jonasi* do not possess an umbilicus; (5 Aperture: *M. microscopica* has an aperture that is rounded behind and strongly angular in front, ?*A. aethiopica* has an oval aperture, slightly square-cut adapically, *M. jonasi* has an elliptic aperture, weakly constricted behind; (6) Inner lip: *M. microscopica* has a moderately callous inner lip with one extremely faint fold about the middle, ?*A. aethiopica* has an inner lip with two very weak folds near the halfway height, *M. jonasi* has a reflected inner lip, wide parietal region, with no folds; (7) Columella: In *M. microscopica* and ?*A. aethiopica*, the columella is straight, parallel to shell axis; in *M. jonasi*, it is inclined to the left of the shell axis.

Only the type species has been allocated in *Microcancilla* since the genus was proposed. The specimen figured by Dall (1902: pl. 29, fig. 4; 1903: pl. 75, fig. 4 [same



**Figures 9–11.** Scanning electron micrographs of *Microcancilla microscopica* (Dall, 1889), lectotype, USNM 82977. **9.** Apertural view. **10.** Lateral view. **11.** Protoconch. Scale bars Figures 9, 10 = 1 mm; Figure 11 = 200 μm

drawing]) and illustrated herein (Figures 9–11) is more rounded at the anterior than in most specimens in the syntype series and also has a heavier columellar callus. Kaicher (1978: Card 1940) photographically illustrated this same specimen from the USNM type collection (USNM 62977 [sic; error for 82977]) as *Admete microscopica* (Dall), *Admete* being the genus used by Dall in 1889b and 1903. She incorrectly referred to this specimen as holotype but Dall did not designate a type specimen. The species was originally described from two localities and there are numerous specimens in the original lots. Under Article 74.5 of the current Code (International Commission on Zoological Nomenclature, 1999) Kaicher's statement does not qualify as a lectotype designation. In order to rectify this, USNM 82977, off Yucatan, 366 m (originally 200 fathoms), is here **designated lectotype of** *Cancellaria microscopica* Dall, 1889. The **type locality** thus becomes restricted to **Campeche Bank, off Yucatan, Mexico**.

## ACKNOWLEDGMENTS

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Dr. M. G. Harasewych, National Museum of Natural History, Smithsonian Institution, Washington, DC, kindly furnished the SEM of *Microcancilla microscopica* (Dall) and reviewed the manuscript.

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# A new species of *Gerdiella* (Gastropoda: Cancellariidae) from the South Atlantic Ocean off Brazil with discussion of an undescribed species

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## ABSTRACT

Two rare species of Cancellariidae were identified during the study of material from oceanographic dredge hauls undertaken in 2000 by the fishing vessel NATUREZA in deep waters off the state of Pernambuco, Brazil. The species belong to the genus *Gerdiella* Olsson and Bayer, 1972. *Gerdiella alvesi* new species is similar to *Gerdiella cingulata* Olsson and Bayer, 1972, as both have strong, nodular ornamentation that is coarsely cancellated and a heavily thickened, lirated outer lip. A second species, *Gerdiella* sp., is identified based on the protoconch, cancellated ornamentation and the presence of two columellar folds, distinguished from the species described herein by its ornamentation and the absence of a subsutural keel.

*Additional keywords: Mericella*, Neogastropoda, bathyal, Pernambuco

## INTRODUCTION

The family Cancellariidae Forbes and Hanley, 1851, is represented by a large number of fossil and recent gastropods distributed among diverse marine regions throughout the world. The group inhabits subtidal to bathyal sandy and muddy bottoms of tropical and temperate regions, with the greatest diversity found along the eastern Pacific coast of the Americas and the central Indo-Pacific area (Harasewych and Petit, 1982). In the western Atlantic Ocean, the number of known species is still relatively small especially with regard to the Brazilian coast (see for instance Harasewych et al. 1992).

The genus *Gerdiella* Olsson and Bayer, 1972, was introduced to include three species described by these two authors from bathyal depths of the Florida Straits and south of Jamaica. These species are: *Gerdiella gerda* from the Straits of Florida, 648–622 m; *G. santa* from the Straits of Florida, 648–622 m; and *G. cingulata* from S of Jamaica, 549–530 m. Another specimen of *G. cingulata*, collected in 1961 by R/V OREGON, sta. 3552, 130 miles ESE of New Orleans, Louisiana, 29°07′ N, 88°05′ W, trawled in 732 m, is now catalogued as USNM 811462. No additional species of *Gerdiella* have been discovered until now.

The genus *Mericella* Thiele, 1929, was introduced by Thiele to accommodate the bathyal *Mericella jucunda* (Thiele, 1925) from off Tanzania. He originally placed the species in *Cancellaria* (*Merica*). *Mericella bozzetti* Petit and Harasewych, 1993, was described from off Somalia. Petit and Harasewych at the same time placed *Cancellaria* (*Merica*) *paschalis* Thiele, 1925, in the genus *Mericella*. *Mericella paschalis* was described from a broken fragment, but recently collected material from off of Mozambique allowed Verhecken and Bozzetti (2006: 15–16) to confirm the allocation of the species in *Mericella*.

In a recent paper, Verhecken and Bozzetti (2006) placed *Gerdiella* in the synonymy of *Mericella* Thiele, 1929. As observed by those two authors, *Mericella* was discussed by Olsson and Bayer in the original description of *Gerdiella*. Verhecken and Bozzetti (2006: 17) stated that the two genera are "very much alike conchologically, the main differences being the relative spire height and the suture form." They also considered relative aperture heights, observing that, as *Gerdiella* has a shorter aperture, the ratio in this latter genus agrees "with Petit and Harasewych (1993: 223) who consider a value of >0.5 a diagnostic feature for *Mericella*." Verhecken and Bozzetti did not point out that Petit and Harasewych used additional characters to differentiate these genera. Verhecken and Bozzetti also stated that "there are no important differences in shell characteristics that would justify a separation between *Mericella* and *Gerdiella*." Although shown on their table, the text does not mention the fact that *Gerdiella* species have axial ribs on the protoconch. However, in an earlier work Verhecken (2002:

513) stated that "protoconch characters are not considered of diagnostic importance at generic level by this writer." We disagree with that approach, especially when protoconch characters allow for the distinction of western Atlantic taxa from those from the Indian Ocean. We consider *Gerdiella* to be a valid genus with species known at present only from the western and southern Atlantic Ocean.

The geographical grouping of *Mericella*, with all known species being from off eastern Africa, and *Gerdiella*, with all known species being from the western and southern Atlantic, is obvious.

Verhecken and Bozzetti (2006: 17) mentioned that the eastern Pacific *Cancellaria corbicula* Dall, 1908, was placed in *Gerdiella* by Kaicher (1978: card 1952). We do not agree with that placement as the species has a smooth protoconch and an aperture height greater than one-half shell height. Its generic placement remains in doubt.

Verhecken (2002: 512) studied three juvenile and fragmented shells collected from the Continental Slope of Pernambuco, northeastern Brazil, during probes of the CHALLENGER EXPEDITION in 1873. Those specimens were considered by him to be conspecific and the possibility that they represent a new species of *Gerdiella* was mentioned. We agree with Verhecken that more and better specimens are needed for identification to be confirmed.

In this paper we describe a fourth species of *Gerdiella* from the Western Atlantic, collected from the Continental Slope off Pernambuco, Brazil. This is the first definite record of the genus for the South Atlantic. The soft parts and radula are as yet unknown, but the conchological characters are sufficient to justify the naming of a new species.

## MATERIALS AND METHODS

All specimens examined were obtained by the research vessel NATUREZA along the Continental Slope off Pernambuco during oceanic prospecting work for the Research and Management Center of Fishing Resources of the Northeastern Coast—CEPENE/IBAMA. At the Malacology Laboratory of the Universidade Federal Rural de Pernambuco, the specimens were sorted under a stereomicroscope, cleaned in a diluted detergent solution, rinsed in distilled water, and air-dried. Shells were measured using a stereomicroscope with eyepiece micrometer and photographed with a Nikon COOLPIX 885 digital camera. Scanning electron micrographs were made using a Jeol JSM 6360 Scanning Electron Microscope at the Electron Microscope Laboratory of the "Instituto Tecnológico de Pernambuco (ITEP)".

Abbreviations used: ANSP, Academy of Natural Sciences, Philadelphia; LMUFRPE, Laboratório de Malacologia da Universidade Fedral Rural de Pernambuco, Brazil; MNRJ, Museu Nacional, Rio de Janeiro, Brazil; MORG, Museu Oceanográfico do Rio Grande, Rio Grande do Sul, Brazil; MZUSP, Museu de Zoologia da Universidade de São Paulo, Brazil.

## SYSTEMATICS

Family Cancellariidae Forbes and Hanley, 1851
Genus *Gerdiella* Olsson and Bayer, 1972

**Type Species:** *Gerdiella gerda* Olsson and Bayer, 1972 by original designation. Recent, Caribbean.

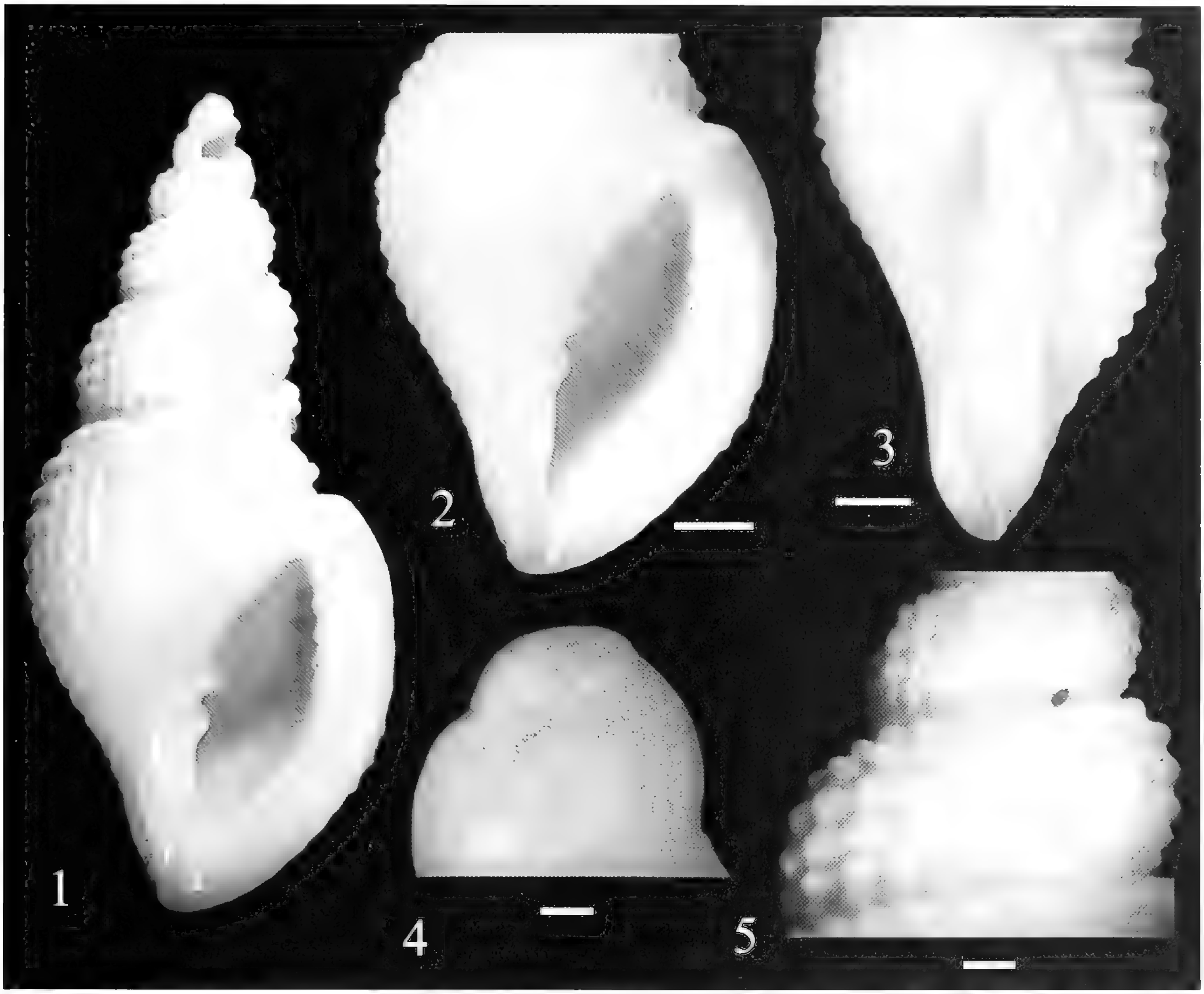
### *Gerdiella alvesi* new species
(Figures 1–5)

**Description:** Shell fusiform, stout, white, strongly ornamented axially and spirally, entirely marked by growth lines between spiral cords. Protoconch globose, cap-shaped, with 1.5 whorls, ornamented by numerous microscopic spiral threads and weak axial ribs on final portion. Transition to teleoconch marked by strong raised axial rib. Nucleus small when compared with rest of protoconch, which is inflated. Teleoconch with 5.5 whorls. Spire narrow, smaller than body whorl. Whorls rounded, strongly ornamented, with reticulated sculpture. Spiral cords intersect the equally strong axial ribs, forming strong nodules with a pustulose aspect, which progressively increase in size toward body whorl. First whorl with 20–22 axial ribs and 6–7 spiral cords, more often 6. Second whorl with 20 axial ribs and 7 spiral cords, third whorl with 22 axial ribs and 7 spiral cords, fourth whorl with 26 axial ribs and 7 spiral cords, fifth whorl with 32–33 axial ribs and 4 spiral cords. Body whorl with 32 axial ribs and 4 upper spiral cords. Suture strongly constricted, bordered by a strong, nodular, subsutural spiral cord. Base imperforate, strongly conical and gently convex, ornamented by 15 nodular spiral cords, 5 of which form siphonal fasciole. Aperture elliptical, fusiform, narrow at terminations. Peristome shiny, very thick and strongly expanded. Outer lip thick, with a broad posterior sinus, with12 denticles, most anterior denticle more elongated. Parietal region strongly reflected, with internal nodules. Columella gently concave, with two pronounced, rounded folds, the adapical fold slightly larger. Siphonal canal short and narrow in distal extremity.

**Type Material:** Holotype, MZUSP 78932 [Length 22 mm, Width 8.3 mm]; juvenile shells: 1 paratype, ANSP 413550; 3 paratypes, MORG 50.688; 2 paratypes, MNRJ 10718; 4 paratypes, MZUSP 78933. All from type locality, 18 Nov. 2000.

**Type Locality:** Northeastern Brazil, off the State of Pernambuco, 08°46.5′ S, 34°44.5′ W, muddy bottom, 690 m.

**Geographical Distribution:** Continental slope off Pernambuco, 08°46.5′ S, 34°44.5′ W, northeastern Brazil.



**Figures 1–5.** *Gerdiella alvesi* new species, holotype MZSP 78932, length = 22 mm. **1.** Apertural view; **2.** Detail of aperture; **3.** Lateral view showing profile of outer lip. **4.** Protoconch. **5.** View of ornamentation of second and third teleoconch whorls. Scale bars. Figures 2, 3, 5 = 500 μm; Figure 4 = 200 μm

**Etymology:** Named in honor of Dr. Marcos Souto Alves of the Biology Department, in the field of Zoology at the Universidade Federal Rural de Pernambuco (UFRPE) for having sent the first author under an internship at the Malacology Laboratory of the UFRPE.

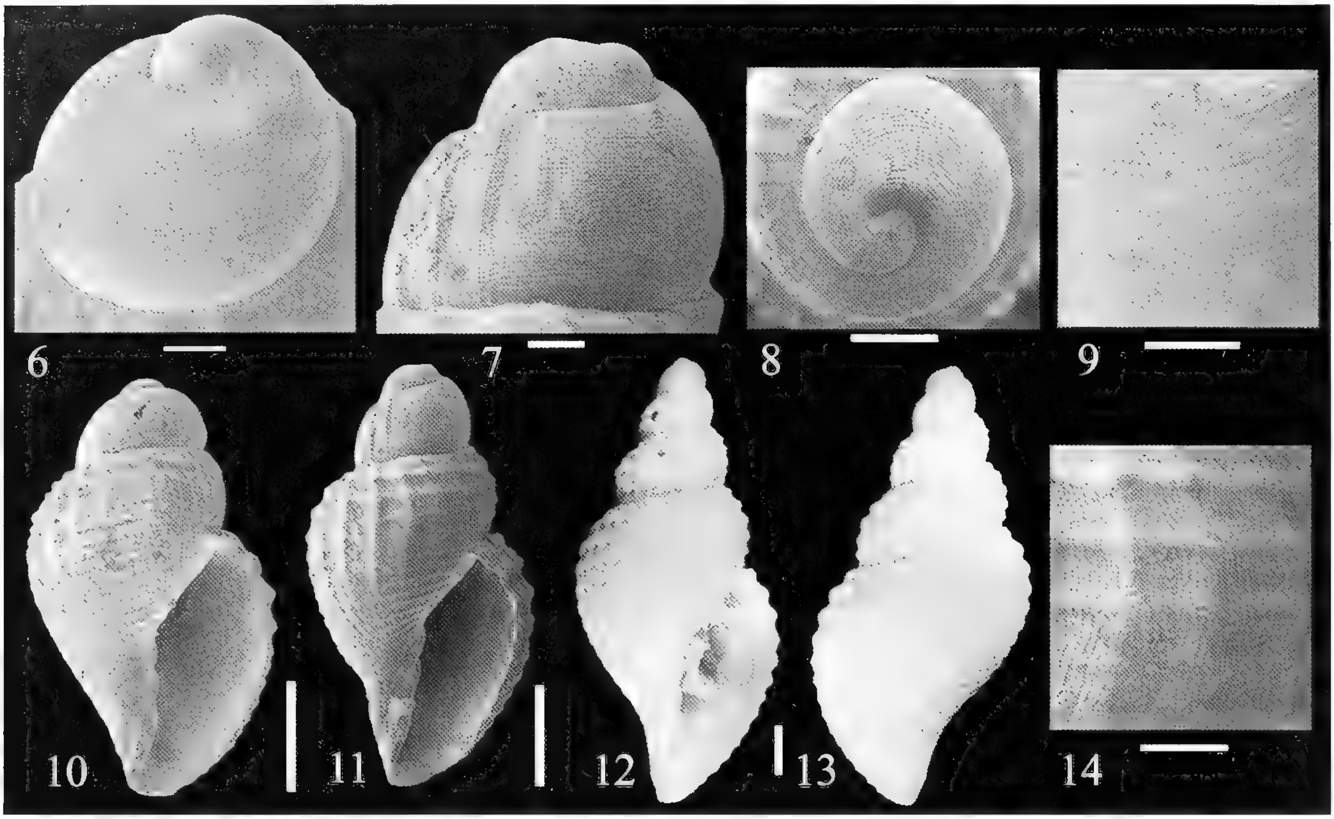
**Remarks:** The protoconch of the holotype is not well illustrated as it is damaged. Nonetheless, we were able to characterize the protoconch of juvenile specimens of the new species (Figures 6–11).

*Gerdiella* sp.
Figures 15–19

**Material Examined:** One damaged specimen, MZUSP 78934, length 18.3 mm, off the state of Pernambuco, northeastern Brazil, 08°46.5′ S, 34°44.5′ W, muddy bottom, 690 m, 18 Nov. 2000.

**Geographical Distribution:** The Continental Slope off Pernambuco, northeastern Brazil.

**Remarks:** The single specimen of *Gerdiella* sp. may represent a new species. However, we prefer not to name it as the shell is damaged and eroded. The protoconch of this species has the same characteristics, and the same number of whorls, as *Gerdiella alvesi*. This specimen has two equal and very narrow columellar folds, slightly different from those of *G. alvesi*. The first, second and third post-nuclear whorls are rounded and ornamented by finely cancellated axial ribs and spiral cords, forming small nodules at their intersections, similar to those of *Gerdiella gerda* and *Gerdiella santa*. The axial ribs are thicker than the spiral cords, (9 on the body whorl), as opposed to 6 for *G. alvesi*. The subsutural cord is weak on the first and second whorls of the teleoconch



**Figures 6–14.** Juveniles of *Gerdiella alvesi* new species. **6–8.** Protoconch under SEM, MORG 50.688; **9.** SEM of protoconch of paratype MORG 50.688 showing microscopic spiral threads. **10–11.** SEM of paratypes MORG 50.688. **12–13.** Paratype, MZUSP 78933. **14.** SEM of paratype MORG 50.688 showing growth lines. Scale bars: Figures 6–8 = 200 μm; Figure 9 = 50 μm; Figures 10–13 = 500 μm; Figure 14 = 50 μm.

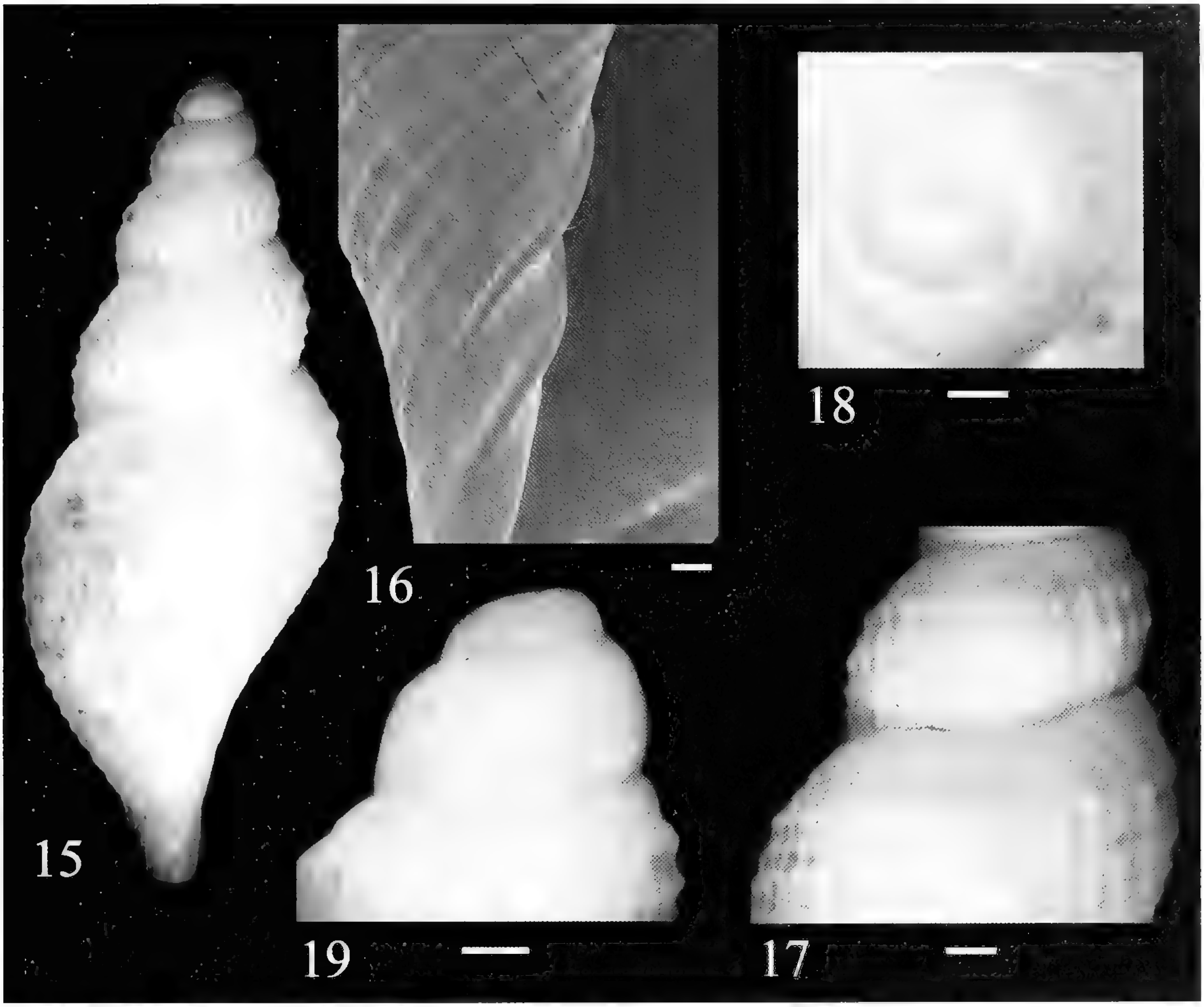
The subsutural region is flat, encompassing the first and second spiral cords, which do not form a shoulder. There are seven spiral cords on the first and second whorls, and 10 on the third. There are 27, 30, and 36 axial ribs on the first, second and third post-nuclear whorls, respectively. In relation to *G. alvesi*, *Gerdiella* sp. has the same number of spiral elements on the first and second post-nuclear whorls. This number is higher, however, on the third whorl. The number of axial ribs on the first three whorls of the teleoconch of *G. alvesi* is less than that of *Gerdiella* sp.

## DISCUSSION

The conchological characters of *Gerdiella* sp. cannot be completely and conclusively compared to any of its congeners until better material is collected for study at the species level. The analysis presented above distinguishes this species from the unnamed shell figured by Verhecken (2002: figs. 9, 10) by the greater number of axial and spiral ribs and threads on the first and second whorl. *Gerdiella alvesi* stands out from its congeners by the strong, uniform axial and spiral ornamentation, which forms large, rounded nodules that are quite pronounced, especially on the body whorl. The heavily thickened outer lip is very similar to that of *Gerdiella gerda*, principally on the sigmoid contour, and is lirated in the same way as *Gerdiella cingulata*, but not as coarsely as described by Olsson and Bayer (1972: 879). Two columellar folds are present on all the species. In both *G. cingulata* and *G. alvesi* the adapical fold is larger and there are no tubercles between the folds in the latter of the two species. In *G. alvesi,* there is no projection of the parietal callus on the outer lip, which is present in *G. gerda* and *G. santa*. Among the *Gerdiella*, the spire of *G. alvesi* has the least number of whorls and lacks varices.

## ACKNOWLEDGMENTS

We are deeply grateful to: Enílson Cabral of the Research and Management Center of Fishing Resources of the Northeastern Coast—CEPENE/IBAMA—for his personal efforts in the collection of sediment from the Continental Slope off northeastern Brazil and for the donation of all this conchological material to the Malacology Laboratory of the Universidade Federal Rural de Pernambuco, Brazil; Fernanda Emanuele, Instituto Tecnológico de Pernambuco (ITEP) for taking the electron scanning micrographs; Mr. Richard Boike for an early translation of the text into English. Dr. M. G. Harase-



**Figures 15–19.** *Gerdiella* sp., MZSP 78934, length = 18.3 mm. **15.** Abapertural view. **16.** Columellar folds under SEM. **17.** View of ornamentation and subsutural flattening of the second and third teleoconch whorls. **18–19.** Protoconch. Scale bars: Figures 16, 18, 19 = 200 μm; Figure 17 = 500 μm.

wych, National Museum of Natural History, Smithsonian Institution, Washington, DC, kindly reviewed the manuscript.

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# Book Review

## *Land and Freshwater Molluscs of Brazil*

*Luiz Ricardo L. Simone.* 2006. Land and Freshwater Molluscs of Brazil. Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil. 390 pp., including over 1100 text-figures. ISBN 859066700-6. 8.5 by 11 in. Hardback; in English. $125 from US booksellers; 92.5 to 94 € in Europe.

This large-scale work is a timely and sorely needed remedy for one of the most stark deficiencies in the global inventory of molluscan biodiversity. The author has recruited no less than 70 identified collaborators and used the resources of 27 prominent institutional collections to formulate a presentation of 1074 native and 33 introduced species-level molluscan taxa inhabiting the land and fresh waters of Brazil and/or nearby areas. The composition of this native non-marine fauna (about 700 terrestrial and over 370 aquatic, over 950 gastropods, and 116 pelecypods) invites comparison with other areas such as the USA, where freshwater clams are notably more speciose, and non-marine snails occur in roughly comparable diversity.

The work is organized thus: a one-page Introduction, four pages of legends and acknowledgements, a Table of Contents, which is a systematic outline of taxa treated, 278 pages of consistently formatted illustrations and companion text blocks in telegraphic style, a bibliography of 2696 titles, and an index of all taxa from phylum to species-level, the later presented with trivial name first.

The format is simple and efficient. The Introduction indicates the method of presentation of taxa, each consecutively numbered in a conventional phylogenetic sequence (genera non-alphabetical in family unit, but species alphabetical within genus). The reiterative eye-catching marginal icons (up to four) in each text block are explained: geographic distribution (blue globe); literature citations (red printed page); source of companion figure, each of which is like-numbered (green eyeball); a non-critical synonymy (equal sign on orange); and "N.B." for random notations when appended. The English diction is deficient on this page, but the author's intent is generally comprehensible.

One defining feature of the work is enunciated in the Introduction: Simone characterizes the figures as "normally based on type specimens." Close perusal confirms this as the case, with name-bearing types from virtually all of the cited (27) institutional collections being depicted in dedicated photographs. For the exceptions, it is apparent that paratypes, voucher specimens, iconotypes, and other levels of authenticity were assiduously pursued and exploited; for the slug groups this proved generally impossible. The photographs are generally of high fidelity, with appropriate magnification to facilitate identification. About three dozen photographic vignettes, mostly of living snails, appropriately placed at various points add a dimension of vitality.

Bibliographic citations are arranged in near flawless alphabetical-chronological sequence and numbered consecutively. One or more such numbers appear in each text block, and an attempt is made to code them with one to six lower case code letters indicating if the work contained a description, figure, etc. Regrettably there are many omissions of the important "o" code, which indicates "original," as in description. The concerned reader must alphabetically search the bibliography using author and date expressed after the binomen at the heading of such entries. Perhaps unfortunately, the works of d'Orbigny and Pilsbry are particularly prone to this oversight. The fidelity of the citations appears to be excellent, although *Bahiensis miliola* (no. 591) appears to date from d'Orbigny, 1837, rather than 1835 as stated (Pilsbry, 1901: 32; Sherborn and Griffin, 1934). A minor and easily remediable bibliographic nuisance is the lack of identification of the G. B. Sowerbys by generation.

In the course of the work several generic reassignments (clearly marked as "n. comb.") are installed and *nomina nuda* revealed. Species no. 1071, *Byssanodonta riograndensis* (Ihering and Morretes, 1949), is thus designated, but a photograph of an ANSP specimen accompanies this entry. Even though the Code (ICZN, 1999: Article 13.1.1), since 1930, has not recognized a binomen and figure indication in the absence of a written description as basis for an available name—in this instance attributable to Simone—an explanation for his treatment of this apparent taxon would be welcome by the reader. Does Simone think this is a valid, unnamed taxon?

The specimen figure on p. 309 captioned *Lamellaxis clavinulus* (Potiez and Michaud, 1838) appears not to be that species but *L. micrus* (d'Orbigny, 1835), which is treated as *Allopeas micra* [sic] on p. 184. On p. 312, Europe is given as the origin of the non-native *Bradybaena similaris* (Férussac, 1821). It is more likely from eastern Asia.

There are technical problems with the typesetting such as wholesale deletion of dozens of single letters, particularly noteworthy on page 23, and the occasional misspelling or improper diacritical mark can be a minor distraction.

The foregoing minor critique notwithstanding, Simone's book is monumental. It is a prodigious work in both scope and the quality of the research. It is certain that all serious workers will find it indispensable in the understanding of the extensive and complex Neotropical malacofauna. On another plane, its application to the analysis of other major world faunas will impel us to a better appreciation of the systematics, evolution, zoogeography, and macroecology of nonmarine Mollusca on a global scale.

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**Manuscripts:** Each original manuscript and accompanying illustrations should be submitted to the editor preferably via e-mail or as hardcopy in triplicate.

Text must conform to the dimensions of 8½ × 11-inch paper, double-spaced, and single-column throughout (including literature cited, tables, and figure captions). Authors should follow the general recommendations of *Scientific Style and Format—The CSE Manual for Authors, Editors, and Publishers*, available from the Council of Science Editors at www.councilscienceeditors.org. The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latinized names and other words to be printed in italics must be underlined; leave other formatting indications to the editor. Metric, not English, units are to be used. Geochronologic modifiers should be capitalized only when units are formally recognized: for instance, use Late Cretaceous but early Miocene. Likewise, only modifiers of formally recognized chronostratigraphic units are capitalized: use Lower Jurassic but upper Oligocene.

The sequence of sections should be title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). If corresponding author is not the senior author, please indicate. The abstract should summarize in 250 words or less the scope, main results, and conclusions of the article. Abstracts should be followed by a list of additional key words. All references cited in the text must appear in the Literature Cited section and vice-versa. Please follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included within the pagination of cited work. Tables must be numbered and each placed on a separate page. If in doubt, please follow a recent issue of the journal for sequence of sections and other style requirements.

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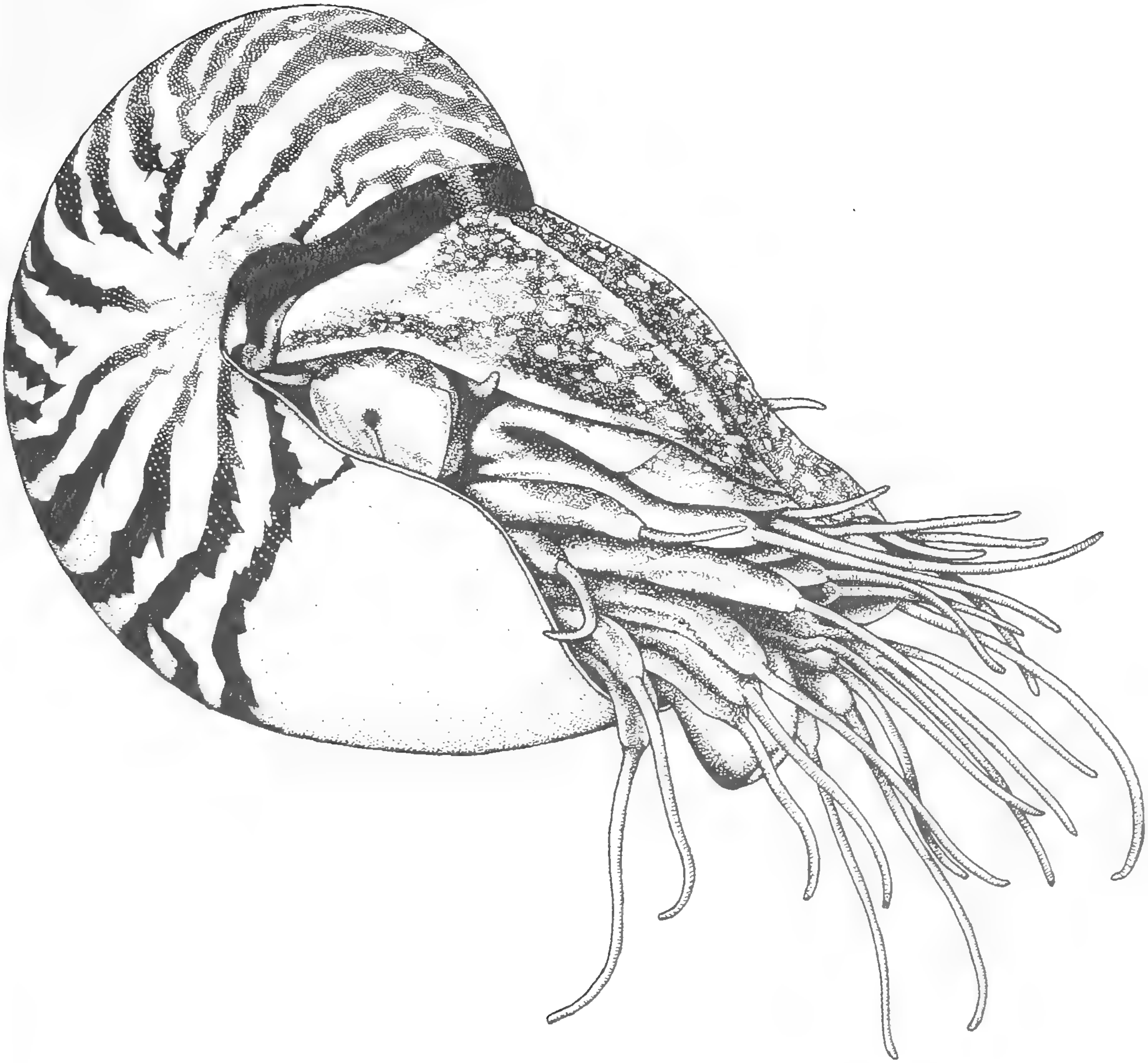

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CONTENTS

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NATIONAL
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# The Epitoniidae (Gastropoda: Ptenoglossa) from the lower Alum Bluff Group (lower to middle Miocene) of Florida, with descriptions of nine new species

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## ABSTRACT

A comprehensive study of the family Epitoniidae that exists in the lower to middle Miocene portion of the Alum Bluff Group of Florida (USA) was conducted. A total of 14 species was examined. Of these, 12 are considered valid members of the family Epitoniidae. They include three previously described species, *Amaea gardnerae*, *Cirsotrema cirritum*, and *Epitonium virginiae*, plus nine new species. Seven of the new species were collected from the Chipola Formation and two from the Shoal River Formation. One new species is assigned to the genus *Cirsotrema*, two are assigned to the genus *Opalia*, and six are assigned to the genus *Epitonium*.

*Cirsotrema* previously reported from the Chipola Formation as *Cirsotrema dalli*, a Pleistocene to Recent species, has been described as a new species. *Epitonium alaquaense* reported from the upper Miocene Choctawhatchee Formation (upper Alum Bluff Group) and questionably placed in the Shoal River Formation fauna by Gardner (1947) is no longer recognized as a Shoal River Formation species and *Gegania acutissima* has been placed with the *Architectonica*-like members of the family Mathildidae.

*Additional Keywords:* Miocene, Chipola Formation, Shoal River Formation, *Cirsotrema*, *Opalia*, *Epitonium*, Chipola River, Tenmile Creek, Farley Creek

## INTRODUCTION

The family Epitoniidae has an extensive history with representatives dating back to the early Mesozoic. According to Clench and Turner (1950), the group appears to have reached its peak of diversity during the Eocene and Miocene epochs. In Florida (USA), members of the family are well represented in early Miocene deposits and, to a lesser extent, in middle Miocene deposits of the Alum Bluff Group.

The Alum Bluff Group consists of five named stratigraphic units (Figure 1). From oldest to youngest these units are the Chipola Formation, Oak Grove Sand, Shoal River, Choctawhatchee, and Jackson Bluff formations (Huddlestun, 1984). All of the Alum Bluff strata occur in outcrops in the western portion of the Florida panhandle (Figure 2). The lower Miocene Chipola Formation was deposited approximately 18 mya (Jones et al., 1993) and outcrops along Tenmile, Farley, and Fourmile creeks, and the Chipola, Yellow, Choctawhatchee, and Apalachicola rivers. To date, most Chipola Formation specimens have been collected from Tenmile, Farley, and Fourmile creeks, and the Chipola River. Collections of fossil specimens from the Oak Grove Sand along the Yellow River and the Chipola Formation along the Apalachicola River are limited, given that these locations typically can only be accessed during very low water levels. According to Vokes (1989), Tenmile Creek, Farley Creek, and Chipola River complex alone encompasses over 7.5 miles (~12 km) of Chipola Formation exposures. The middle Miocene Shoal River Formation was deposited approximately 12 mya (Jones et al., 1993). All known Shoal River Formation outcrops are west of the Chipola Formation exposures with most of the collecting areas situated along the Shoal River in Walton County. Overviews of the geology, stratigraphy, and paleontology of the Chipola and Shoal River formations can be found, respectively, in Vokes (1989) and Portell et al. (2006).

Gardner (1947), as part of her monographic treatment of the molluscan fauna of the Alum Bluff Group, discussed three species belonging to the family Epitoniidae. These species were *Epitonium* (*Spiniscala*) *virginiae* (Maury, 1910), *Epitonium* (*Clathrus*) *alaquaense* (Mansfield, 1935), and *Gegania acutissima* (Dall, 1892). However, only two of these taxa are herein considered to belong to the family Epitoniidae. *Epitonium virginiae* was collected from a Chipola Formation site along the east bank of the Apalachicola River. It was described by Maury (1910) from a single, extremely small (3.7 mm maximum height × 1.5 mm maximum width) specimen that was part of the Cornell University Collection (now deposited at the Paleontological Research Institution). *Epitonium alaquaense*, recorded by Mansfield (1935)

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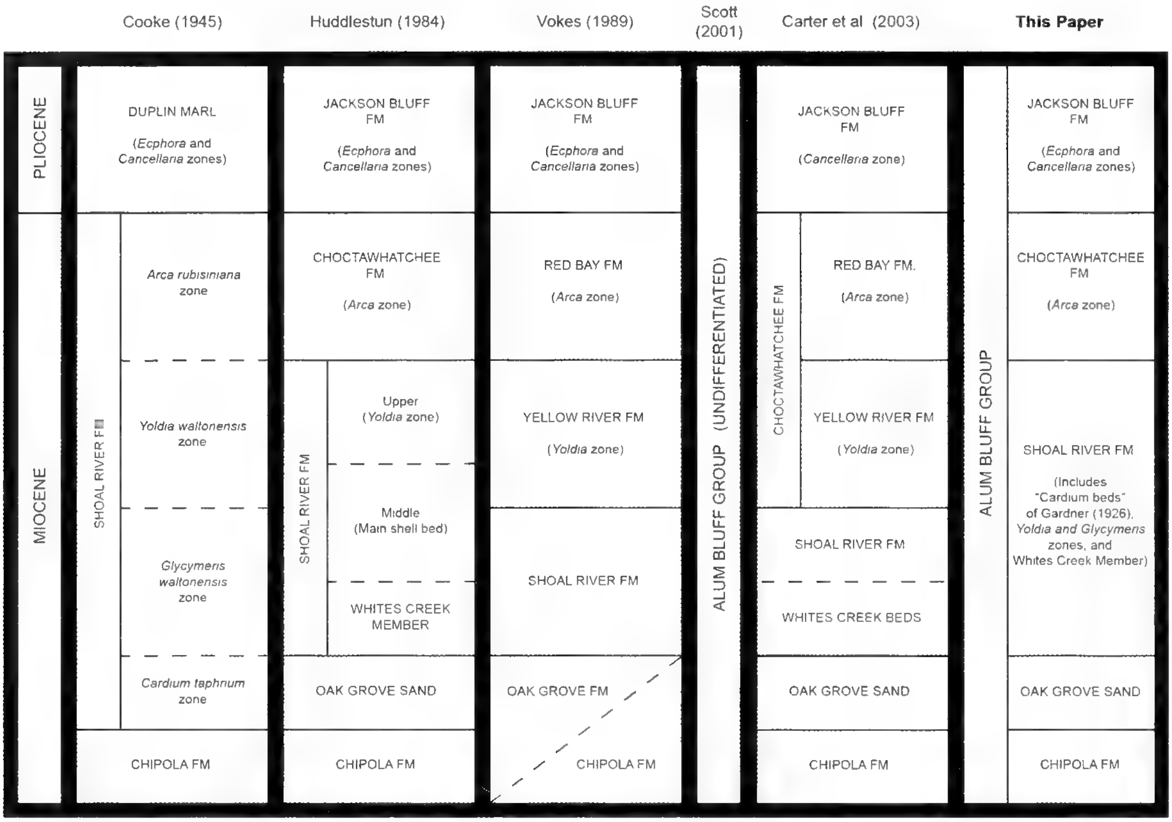


**Figure 1.** Alum Bluff Group stratigraphic nomenclatural history and correlation (in part). Modified from Portell et al. (2006).

from the *Arca* zone of the Choctawhatchee Formation, is late Miocene (Huddlestun, 1984). When Gardner (1947) collected a shell fragment similar to Mansfield's shell at a Shoal River site she included it as part of the lower Alum Bluff Group as defined by Cooke (1945). The collective evidence now suggests that *E. alaquaense* should not be listed as part of the fauna of the lower Alum Bluff Group (see Figure 1). The reasons for this are twofold. First, an extensive examination of the Chipola and Shoal River formation fossils in the Florida Museum of Natural History (including Tulane University and Florida Geological Survey collections), Paleontological Research Institution, Smithsonian's National Museum of Natural History, American Museum of Natural History, The Academy of Natural Sciences, Alabama Geological Survey, and private collections during this study did not uncover a single specimen that could be referred to as *E. alaquaense*. Second, Gardner (1947: 577) stated that she collected her shell fragment from "a horizon slightly higher than the typical Shoal River formation." Based upon this remark and that no additional specimens similar to *E. alaquaense* were ever found in the abovementioned collections, it seems fair to assume that Gardner's specimen belonged to strata younger than the Shoal River Formation; most probably to the upper Miocene Choctawhatchee Formation.

Dall (1892) described *Tuba acutissima* and placed it in the family Mathildidae. Gardner (1947) replaced the genus *Tuba* with *Gegania* and tentatively assigned it to the family Epitoniidae because she felt that its morphological characteristics more closely coincided with the suborder Ptenoglossa. Gardner's generic assignment of *Gegania* was based upon the shell similarity to *Gegania pinquis* Jeffreys, 1884, a species collected during the Porcupine Expedition off Cape Mondego, Portugal. However, the genus *Gegania* has since been assigned to *Architectonica*-like members of the family Mathildidae (Vaught, 1989).

In addition to the three species of Epitoniidae listed for the Alum Bluff Group, Gardner (1947: 575) reported shell fragments belonging to "at least a dozen" species. Gardner stated that most of the specimens were so imperfectly preserved that only subgeneric determinations could be made. Four of the unidentified epitoniids came from the Aldrich Collection (housed at Johns Hopkins University) and the remaining species were from Gardner's collection. Eleven of the fragments were obtained from Shoal River Formation localities and two were collected from Chipola Formation sites. Gardner placed eleven of the fragments in the genus *Epitonium*, one in the genus *Scalina*, and one in the genus *Gegania*. Six were placed in the subgenus *Hyaloscala*, two in *Spiniscala*, three in *Cinctiscala*, and one in *Nodiscala*.

It is apparent from Gardner's (1947) discussion on the Epitoniidae of the Alum Bluff Group that future work remained to be done on the family. Since her publication, three additional species of Epitoniidae have been reported from the Chipola Formation. These are *Cir-*

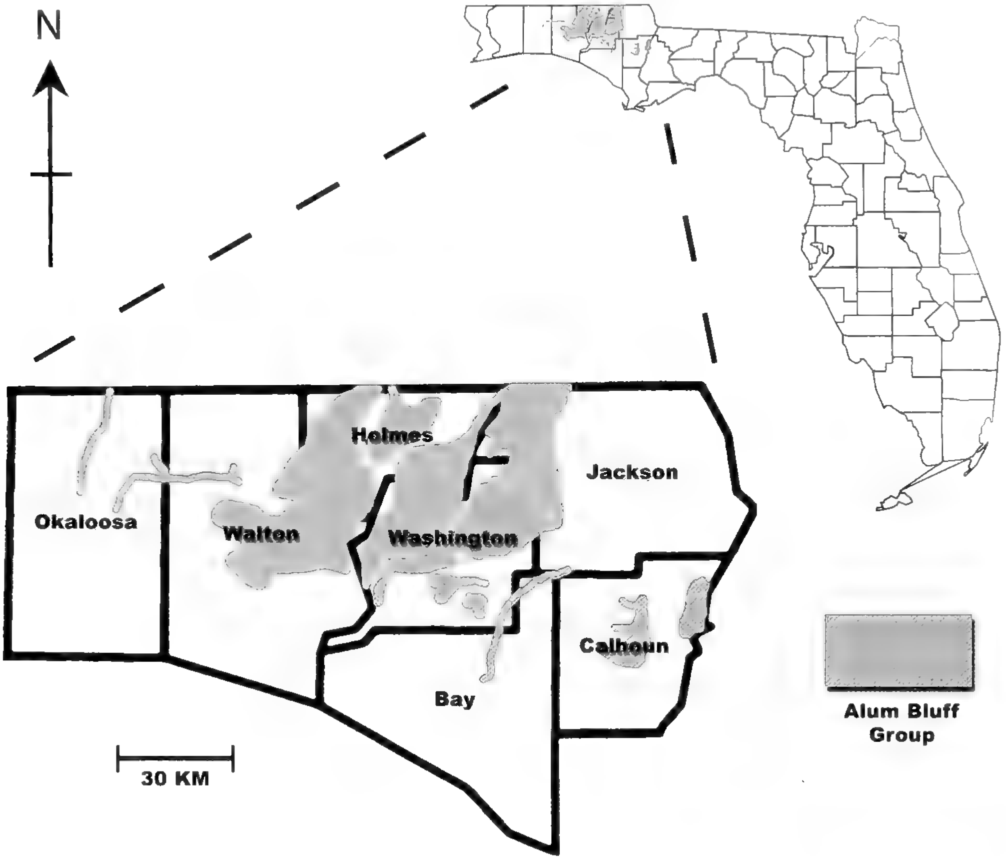


**Figure 2.** Map of Florida showing counties with Alum Bluff Group sediments found at or near the surface.

sotrema dalli Rehder, 1945; *Scalina gardnerae* (Olsson, 1967); and *Cirsotrema cirritum* Duerr, 2004. *Cirsotrema dalli* is an extant species reported to have undergone little morphological change since the early Miocene (Olsson, 1967). *Scalina gardnerae* was described by Olsson (1967) from a single large specimen collected from McClellan's Farm in Calhoun County, Florida. It is a fairly common species, and since its discovery, it has been found at numerous Chipola Formation sites by the authors and other investigators. *Cirsotrema cirritum* is a much less common species collected at a few sites along Tenmile and Farley creeks and the Chipola River (Duerr, 2004).

Scattered among the material in museums and private collections are a large number of epitoniids from the Chipola and Shoal River formations of Florida that have been amassed over the last fifty years. Since many of the recently collected specimens are in excellent shape, we have undertaken the task of identifying and describing the new species and providing better descriptions and updated taxonomic placements of existing ones. As will be evidenced in this paper, many of these epitoniids have shell structures that are similar to those of extant and fossil species from Florida, the Caribbean, western Europe, and the eastern Pacific.

According to Clench and Turner (1951), DuShane (1979), Kilburn (1985), Nakayama (2003), Robertson (1983a; 1983b; 1993), Weil et al. (1999), and others, current classification of the Epitoniidae is based upon shell characteristics. For this study, morphological features such as shell size (height and width), number and shape of the nuclear whorls, number and shape of teleoconch whorls, number and placement of the costae on the body whorl, presence or absence of varices, type of sculpturing on the body whorls, shape of the aperture, shape and thickness of the outer lip, depth of the suture, presence of punctae, and the spire angle were used to help differentiate species. Spire angles were measured from photographs. A vertical line was drawn through the axis of the shell and a protractor was used to determine the angle between the margins of the body whorls on both sides of the shell.

Additionally, in order to ascertain whether or not the Chipola Formation species of *Cirsotrema* is the same as the Recent *Cirsotrema dalli*, we closely examined the varices on both forms. As noted by Weil et al. (1999) and others, the presence or absence of varices can be a key diagnostic feature for some species of *Epitonium*. We believe that the structural configuration and the number of varices that appear within a specific generic group, such as in certain *Epitonium*, will change over geologic time and that this morphological difference between the Recent and fossil forms is significant enough to justify naming the fossil form as a separate species. In part, this decision to use the changes observed in varix count as a diagnostic feature at the species level is based upon the precedence of using the number, shape, and configuration of varices as a method of identifying different species and genera in the family Muricidae. This technique has been used broadly by muricid gastropod investigators (Herbert, 2005, and references therein).

Besides examining the varices on *Cirsotrema dalli*, we also abraded the external portion of an uncatalogued Recent shell in order to compare its underlying sculpture with that of its fossil counterpart.

Even though many of the epitoniids examined are in excellent shape, the task of classifying them and placing them into their appropriate generic and subgeneric groupings was challenging. This is, in part, because there is very little natural history information on Recent species that provide insight into how these animals grow and how their growth is impacted by environmental conditions. Subsequently, we have relied heavily upon the combined works of numerous past investigators to help us with this decision making process. These researchers included, but were not limited to: Brunet (1995), de Boury (1909), Clench and Turner (1950; 1951; 1952), DuShane (1979; 1988), Gardner (1947), Kilburn (1985), Nakayama (2003), Robertson (1983a; 1983b; 1993), Weil et al. (1999), and Woodring (1959).

At the generic and subgeneric levels of classification many investigators have widely divergent opinions about in which group a specific epitoniid should be placed. According to Clench and Turner (1950), de Boury's work on Epitoniidae left behind a long list of generic and subgeneric names with only the types available for diagnostic analysis. This list includes seven generic and 19 subgeneric names (Weil et al., 1999). It was Clench and Turner's (1950) opinion that de Boury became confused about the overlapping characteristics of the Epitoniidae and rather than trying to place them into existing categories, he established new genera and subgenera for them. To date, this confusion with overlapping characteristics appears to have continued with the list of generic and subgeneric extant Epitoniidae alone being expanded to 34 and 38 names, respectively (Weil et al., 1999). For our classification purposes we have decided to adhere, as closely as possible, to the more conservative phylogenetic scheme followed by Clench and Turner (1950) rather than the more recently expanded version used by Weil et al. (1999) and Nakayama (2004).

With fossils, placement of certain epitoniids into appropriate generic and subgeneric groups has been hampered by erosion (taphonomic degradation). This process removes surface sculpturing present on living specimens and exposes subsurface characteristics that are remarkably different. In this paper, an example of the impact erosion has on the external features of a shell is illustrated with the new species *Epitonium conwaiae*.

We have tried to survey all the pertinent descriptions and illustrations of both fossil and Recent epitoniids. For taxonomic comparison purposes the most significant literature came from publications dealing with the descriptions of Recent and fossil species collected from the United States, Central and South America, the northwest Atlantic, European continent, and the eastern Pacific.

Institutional abbreviations used herein are: USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC; UF: Florida Museum of Natural History (FLMNH), University of Florida, Gainesville; TU: Tulane University, (formerly housed in New Orleans, Louisiana and now housed at the FLMNH); PRI: Paleontological Research Institution, Ithaca, New York; ANSP: The Academy of Natural Sciences, Philadelphia, Pennsylvania; and BMSM: The Bailey-Matthews Shell Museum, Sanibel Island, Florida. Because of privacy rights of landowners, specific locality data for specimens described below are not given. However, specific locality information is available to qualified researchers upon written request to portell@flmnh.ufl.edu.

## SYSTEMATICS

Superfamily Janthinoidea Lamarck, 1812
Family Epitoniidae Berry, 1910
Genus *Amaea* H. and A. Adams, 1853

**Type Species:** by subsequent designation, *Scalaria magnifica* Sowerby, 1844.

Subgenus *Scalina* Conrad, 1865
*Amaea gardnerae* (Olsson, 1967)
(Figures 3–9)

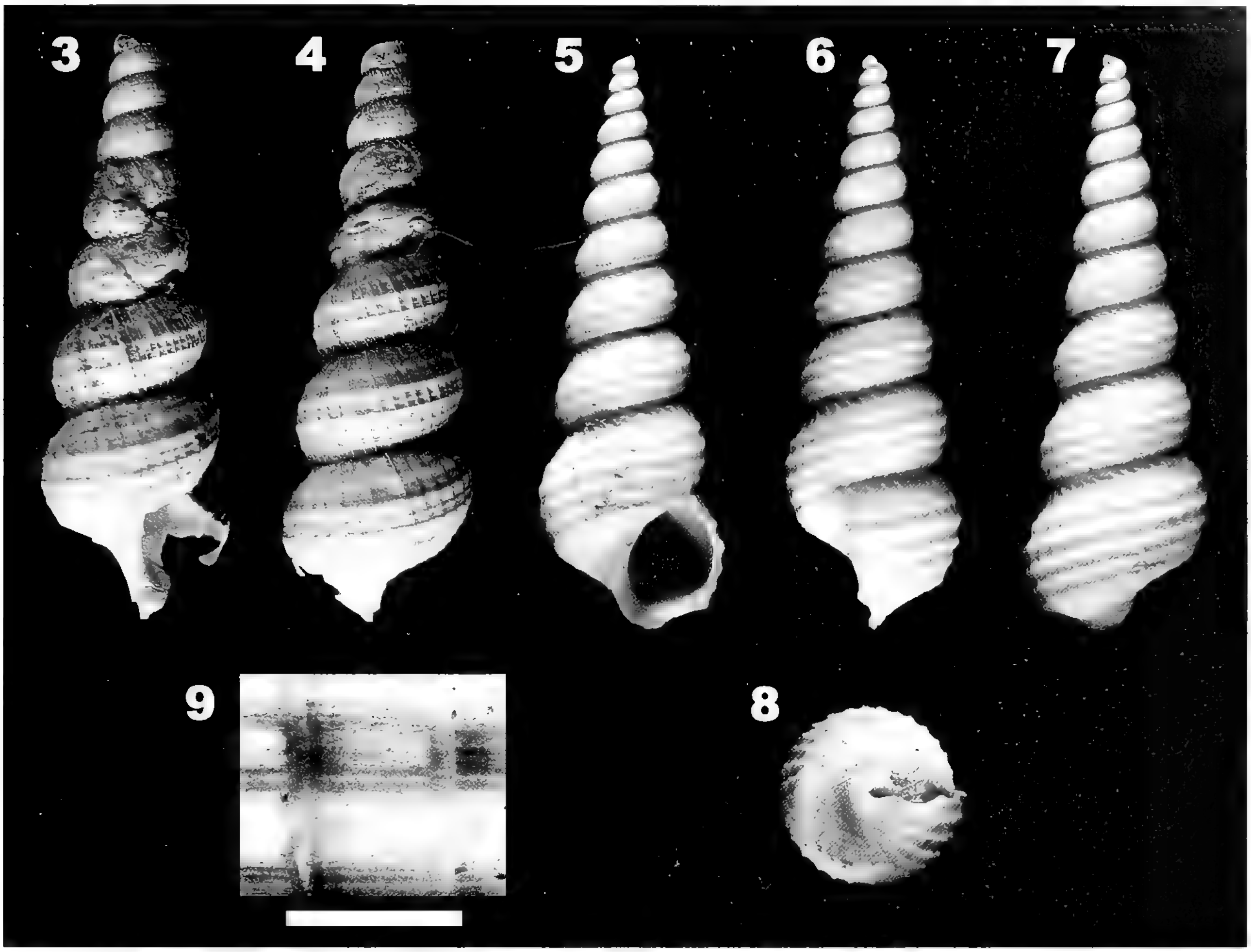
**Description:** Shell large, turriculate; protoconch missing; nine or ten teleoconch whorls. Spire angle 19.5°. Whorls convex, relatively thin, with cancellate sculpture. Cancellate pattern created by four spiral cords crossed by smaller, evenly spaced axial costae; square spaces within cancellate sculpture possess textured pattern created by fine overlapping axial and spiral threads. Suture deeply impressed. Basal cord well-defined, surface slightly elevated and sculptured with thin spiral and axial threads. Sculpture below basal disc lacks elevated spiral cords. Umbilicus absent.

**Holotype:** USNM 645180, maximum height 47.5 mm, maximum width 14.4 mm.

**Type Locality:** McClellan Farm, Calhoun County, Florida.

**Other Material Examined:** UF 117045, 1 shell, Tenmile Creek 04 (CA020) (= Tulane University locality TU 951), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; UF 117087, 1 shell, locality and formation same as preceding; UF 91459, 16 shells, Tenmile Creek 03 (CA017) (= Tulane University locality TU 546), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation.

**Distribution:** *Amaea gardnerae* is a fairly common Chipola Formation species. It is abundant at several col-



**Figures 3–9.** *Amaea gardnerae* (Olsson, 1967). **3–4.** Apertural and abapertural views of holotype USNM 645180 originally named *Scalina gardnerae* Olsson, 1967. Since its original description the specimen has degraded; maximum height 47.5 mm, maximum width 14.4 mm. **5–8.** Apertural, lateral, abapertural, and basal views of UF 117045 shown for comparison to holotype (USNM 645180) and other Chipola and Shoal River formation epitoniid species; maximum height 17.85 mm, maximum width 5.4 mm. **9.** Magnified view of sculpture of teleoconch of UF 117045. Scale bar = 0.6 mm.

lection sites along Tenmile Creek but is less abundant along Farley Creek and the Chipola River. Thus far, there are no reports of it having been collected along the Yellow or the Apalachicola rivers.

**Etymology:** Named for Julia A. Gardner, a pioneer researcher on Chipola Formation mollusks.

**Discussion:** Gardner (1948) reported an epitoniid fragment from the Chipola Formation which she assigned to the genus *Scalina*. Olsson (1967) later described this species as *Scalina gardnerae*. A more thorough analysis of additional specimens of *S. gardnerae* now indicates that it should be placed in the genus *Amaea*. DuShane (1988) noted that members of the genus *Amaea* are larger than any known *Scalina* and have a less distinct basal cord. In addition, DuShane observed that in the genus *Amaea*, the sculpture above and below the basal cord is different. Unfortunately, the poor condition of the type specimen described by Olsson makes it difficult to tell what the sculpturing was like in the vicinity of the basal cord. Subsequent specimens, however, have revealed that the sculpturing above and below the basal cord is different in *S. gardnerae* (Figures 5, 8).

Clench and Turner (1950), Weil et al. (1999), and Nakayama (2003) have all placed epitoniids with the shell sculpture described by Olsson (1967) for *Scalina gardnerae* into the genus *Amaea*. We are in complete agreement with this placement and have assigned Olsson's epitoniid to that genus.

Weil et al. (1999) has identified eight subgeneric forms of the genus *Amaea*. These subgenera are distinguished from one another by the types of sculpture that appear above and below the basal cord. Nakayama (2003) in his review of northwest Pacific epitoniids retained six of the subgenera listed by Weil et al. (1999). Among the six subgenera listed for the genus *Amaea* by Nakayama (2003), the present authors have assigned the Chipola Formation species to the subgenus *Scalina*. According to

Nakayama (2003) and Weil et al. (1999) members of this subgenus possess convex body whorls with a cancellate sculpture of spiral cords and axial ribs.

Representatives of the genus *Amaea* have been reported from a number of other fossil locations. These include *Scala (Opalia) reticulata* Martin, 1904, from the Miocene Calvert Formation of Maryland, *Amaea (Scalina) ferminiana* (Dall, 1908) from the Pliocene Esmeraldas beds of Ecuador, *Scala (Acrilla) wiegandi* (Böse, 1910) from Mexico and the Miocene Chagres Formation of Panama (formerly Canal Zone), *Scalina pseudolerogi* (Maury, 1925) from the Pliocene of Trinidad, *Epitonium (Ferminoscala) manabianum* (Pilsbry and Olsson, 1941), and *Epitonium (Ferminoscala) eleutherium* (Pilsbry and Olsson, 1941) from the Pliocene fauna of western Ecuador, *Scalina boylae* (Olsson, 1967) from the Pliocene Tamiami Formation of Florida, and *Scalina kendacensis* Jung, 1971, from the Miocene Kendeace Formation of Carriacou. *Amaea ferminiana*, originally described from the Recent of Baja California, is an offshore species. It ranges from Mexico south to Peru (Weil et al., 1999). DuShane (1988) considered *E. eleutherium* and *S. wiegandi* to be synonymous with *A. ferminiana* and suggested that *S. pseudolerogi* as well as some other fossil species of *Amaea* may be synonymous with *A. ferminiana*. Comparison of *A. gardnerae* with *A. ferminiana* clearly illustrates that the two species are not synonymous. *Amaea ferminiana* possesses six to nine spiral cords of uniform thickness on the body whorls, while *A. gardnerae* possesses four broad primary cords with finer cords in between. The costae on *A. gardnerae* are also less prominent then they are on *A. ferminiana*. Comparison of *Amaea mitchelli* (Dall, 1896), a Recent western Atlantic species, to *A. gardnerae* was also made. *Amaea mitchelli* has 6–7 primary spiral cords on the body whorls (four of which are closely spaced below the whorl mid-line and two to three that are evenly spaced above) as compared to *A. gardnerae* which has four evenly spaced primary spiral cords.

Genus *Cirsotrema* Mörch, 1852

**Type Species:** *Scalaria varicosa* Lamarck, 1822, by monotypy.

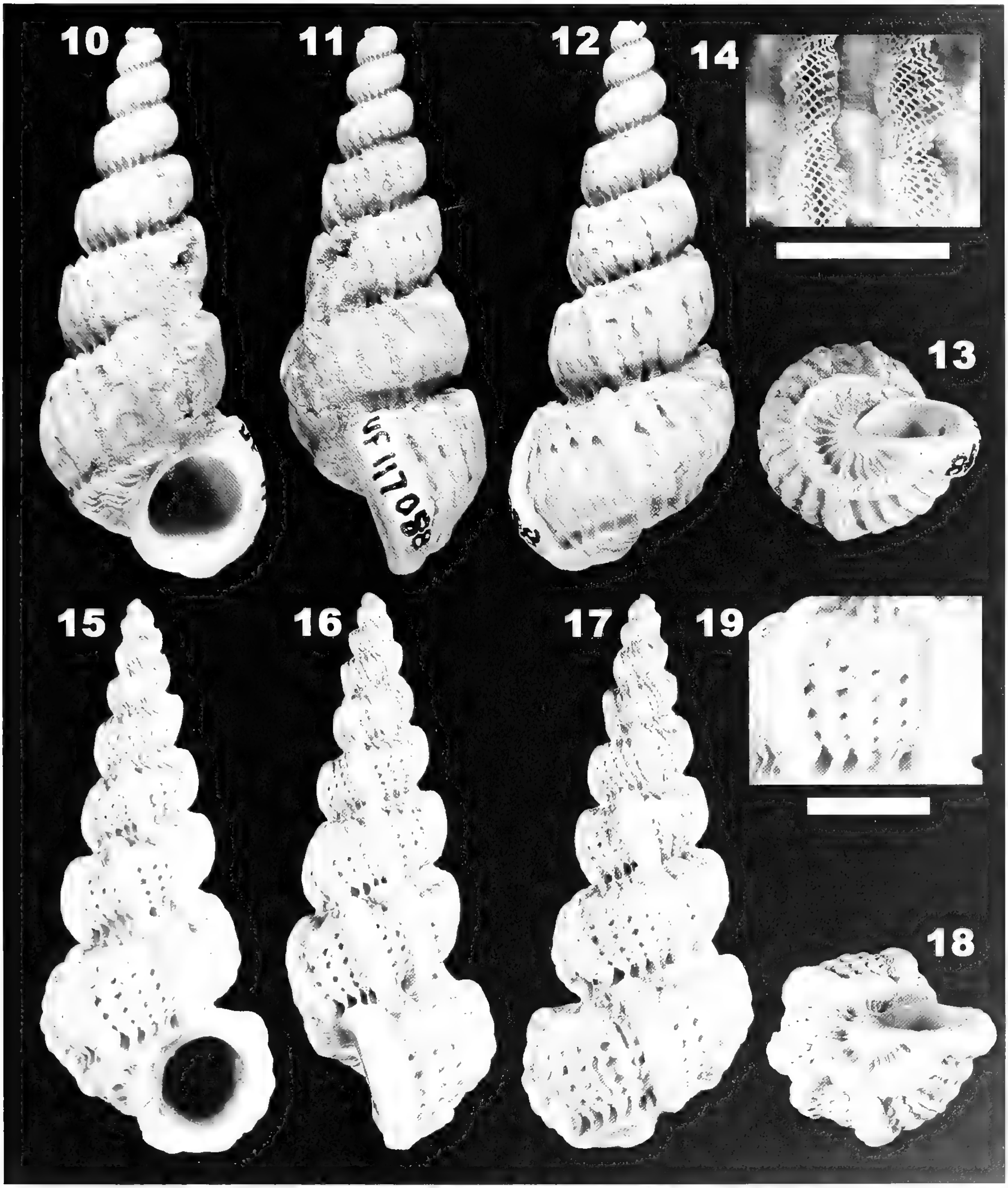
*Cirsotrema chipolanum* new species
(Figures 10–14)

**Description:** Shell large, turriculate, protoconch missing; seven to eight teleoconch whorls. Spire angle 27°. Whorls slightly convex, strongly shouldered and joined. Primary underlying sculpture present on teleoconch whorls consists of slightly elevated vertical ribs. Suture deep, covered by external sculpture. Seventeen to 23 sinuous, inclined, feather-like, broad costae on body whorls. Edges of foliated costae occasionally touch the preceding ones giving the shell surface a pitted appearance. In other instances foliated costae are slightly separated from one another. When feather-like costae separate from each other, five slightly elevated spiral cords seen on body whorls. Spiral cords, and spaces between them, possess numerous distinct spiral threads. Thin vertical threads intersect spiral threads, creating faint cancellate pattern. Varices formed from accretion of foliated costae; varices poorly developed and only slightly elevated. Apical end of costae with pointed nodes. Surface of costae pitted with obliquely arranged small holes. Three or four obliquely arranged, slightly elevated, narrow cords traverse each costa. Oblique cords on costae less pitted than remainder of surface area. Base of each costa stem-like, attached to a broad, crenulated, basal cord. Basal disk composite, created by a large outer basal cord with crenulated edges; a middle circle of narrow linear pits; and an inner columellar cord with a crenulated edge. Aperture subcircular. Columella short and arched. Lip margin thickened, pitted in unworn specimens. Less eroded specimens possess a slightly elevated node on the posterior outer margin of the lip.

**Holotype:** UF 117088, maximum height 32.9 mm, maximum width 15.0 mm.

**Type Locality:** Tenmile Creek 03 (CA017) (= Tulane University locality TU 546), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation.

**Paratypes:** UF 117089, 1 shell, locality and formation same as holotype; UF 91490, 5 shells, locality and formation same as holotype; UF 84575, 7 shells, Tenmile Creek 01 (CA002) (= Tulane University locality TU 830), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; UF 95161, 1 shell, Tenmile Creek 04 (CA020) (= Tulane University locality TU 951), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; UF 85383, 1 shell, Chipola 09 (CA018) (= Tulane University locality TU 547), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; UF 13966, 1 shell, Chipola 03 (CA005), Chipola River (exact collection site unknown), Calhoun County, Florida, Chipola Formation; UF 94650, 1 shell, Tenmile Creek 02 (CA003) (= Tulane University locality TU 70), Altha West Quadrangle USGS 7.5′ Series (1982), Calhoun County, Florida, Chipola Formation; UF 84444, 1 shell, Farley Creek 03 (CA009) (= Tulane University locality TU 825), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; UF 91356, 1 shell, Chipola 07 (CA015) (= Tulane University locality TU 554), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; USNM 534489, 1 shell, Tenmile Creek 01 (CA002) (= Tulane University locality TU 830), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; USNM 534490, 2 fragments, locality and formation same as preceding; USNM 534491, 2 fragments, Tenmile Creek 05 (CA021) (= Tulane University locality TU 998), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; USNM 534492, 1 shell, Farley Creek 03 (CA009)



**Figures 10–19.** *Cirosotrema chipolanum* new species and *Cirsotrema dalli* Rehder, 1945. **10–13.** *Cirsotrema chipolanum*; apertural, lateral, abapertural, and basal views of holotype UF 117088; maximum height 32.9 mm, maximum width 15.0 mm. **14.** Magnified view of sculpture of teleoconch of holotype UF 117088. Scale bar = 2.85 mm. **15–18.** *Cirsotrema dalli* Rehder, 1945 apertural, lateral, abapertural, and basal views of UF 238698; maximum height 32.8 mm and maximum width 13.8 mm. **19.** Magnified view of sculpture of teleoconch of UF 238698. Scale bar = 5.0 mm. UF 238698 live collected off Egmont Key, Pinellas County Florida at about 52 m depth

(= Tulane University locality TU 825), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; USNM 534493, 10 shells, Tenmile Creek 03 (CA017) (= Tulane University locality TU 546 and USGS 2212 "one mile west of Bailey's Ferry"), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; USNM 534494, 8 shells, same locality and formation as preceding.

**Distribution:** *Cirsotrema chipolanum* is a fairly common species. It is locally abundant at several Chipola Formation collecting sites along the Chipola River and Tenmile and Farley creeks. The fact that it has not been reported from the Oak Grove Sand along the Yellow River or from Chipola Formation sites along the Apalachicola River may simply reflect the degree of difficulty collecting these localities at the appropriate periods of low water level.

**Etymology:** Named for the Chipola River.

**Discussion:** The genus *Cirsotrema* has an extensive evolutionary history. Sohl (1964) established the genus *Striaticostatum* to represent a Cretaceous form of *Cirsotrema* that lacked the faint spiral striations on the body whorl. By the Eocene the genus *Cirsotrema* was well established with numerous species being described from different localities (Dockery, 1980; Harris and Palmer, 1946; Palmer, 1937). Currently, among extant forms, two species of *Cirsotrema* exist in the western Atlantic (Weil et al., 1999). These are *Cirsotrema dalli* Rehder, 1945 and *Cirsotrema pilsbryi* McGinty, 1940.

Two species of *Cirsotrema* have also been reported from lower Miocene Chipola Formation. Olsson (1967) identified a specimen collected along the west bank of the Chipola River south of Tenmile Creek as *C. dalli* and more recently Duerr (2004) described *Cirsotrema cirritum* from material collected at several different Chipola Formation sites. Olsson (1967) stated that after close examination of the Chipola Formation *Cirsotrema* he found practically no differences between it and the extant species currently living in the western Atlantic. Since Olsson's (1967) analysis of the Chipola *Cirsotrema*, over 50 additional specimens have been collected from a variety of Chipola locations. When most of these specimens were closely scrutinized it became apparent to the present investigators that the Chipola Formation *Cirsotrema* studied by Olsson (1967) was not *C. dalli*.

As noted by Clench and Turner (1950), the sculpturing on the body whorls of representatives of the genus *Cirsotrema*, is extremely complicated. It was suggested by Clench and Turner, and observed in the present work, that two layers of sculpturing are present on the body whorls of *Cirsotrema dalli*. There is an outermost one that consists of foliated costae that may or may not join each other along their convoluted edges and a secondary layer of laminated costae and spiral cords. Because of this dual type of sculpture Clench and Turner warned against identifying different species of *Cirsotrema* from beach worn specimens.

Often with fossil specimens it is difficult to find shells that have not been eroded. However, a sufficient number of well-preserved Chipola Formation *Cirsotrema* were discovered which allowed a more detailed comparison between the fossil form of this genus and its Recent counterpart. These detailed studies lead to the following observations:

First, when the underlying sculpture of the Chipola Formation *Cirsotrema* was exposed no difference was discovered between it and the underlying sculpture exhibited by *C. dalli*.

Second, although varices are present on both the Chipola Formation *Cirsotrema* and its Recent counterpart, the varices on the Chipola Formation species are clearly not as well developed as those of Recent *C. dalli*. In fact, the varices on *C. chipolanum* are at times so poorly formed that it is difficult to identify them as varices. In *C. dalli* the costae are fused together to form a pronounced, elevated ridge (Figures 15–19) that, in well-preserved specimens, has a slightly crenulated margin. Conversely, with *C. chipolanum* the varices consist of little more than one or two slightly raised costae (see Figures 10–13). In addition, even in instances where two costae are fused together to form a varix, the fusion is often not complete and a distinct line of demarcation can be seen.

Third, when a comparison of the number of varices in relation to the height of the shell was undertaken with well-preserved specimens of *C. dalli* and *C. chipolanum*, and a least squares regression analysis was done on the two species, the results showed a significant correlation between the height of the shell and the number of varices with *C. dalli* (0.922), and a low correlation between shell height and the number of varices with *C. chipolanum* (0.499). Table 1 below provides the statistical results of this study and a comparison of the number, size range, average size, varix range, and average number of varices of the specimens used in the analysis.

As a result of the regression analysis two other differences between the varices of the two species was also noted. Although the varices appeared at random intervals on the body whorls of both species, in *C. chipolanum* the first varix did not appear until after the third teleoconch whorl, while in *C. dalli* varices would appear just after the protoconch. In addition, when the number of varices

**Table 1.** Results of least squares regression analysis comparing shell height with the number of varices found in *C. dalli* and *C. chipolanum*.

| | *C. dalli* | *C. chipolanum* |
|---|---|---|
| No. of specimens examined | 23 | 16 |
| Correlation coefficient | 0.922 | 0.499 |
| Range of shell height (mm) | 5.8–37.5 | 5.0–44.2 |
| Mean height (mm) | 15.31 | 17.21 |
| Range of varices | 2–27 | 0–10 |
| Mean no. of varices | 8.82 | 4.75 |

was compared between the different species it was discovered that *C. dalli*, on average, had significantly more varices than *C. chipolanum* [$\bar{X}$ = 8.82 vs. 4.75].

Table 2 below summarizes the structural differences in shell morphology between *C. dalli* and *C. chipolanum*. In addition to comparing the differences between the shape and number of varices between species, the table also compares the number of teleoconch whorls, the number and arrangement of costae, the spire angles, the arrangement of the costae, and the placement of varices on the body whorls.

Another point worth noting is that *C. dalli* and *C. chipolanum* came from very different environments. *Cirsotrema dalli* lives in cooler continental shelf waters at depths of 37 to 227 m (Clench and Turner, 1950) while *C. chipolanum* thrived in a shallow, warm, tropical, reef habitat. Although not a great deal is known about how the environment and food supply impact the growth of wentletraps [Robertson (1983a) and Weil et al. (1999)], there has been sufficient studies done on the family Muricidae (Vokes, 1973) that will allow us to speculate as to the reasons for the number and structural differences observed between the varices of *C. dalli* and *C. chipolanum*. According to Vokes (1973) varix (axial growth ridge) development in muricids occurs during resting stages in shell formation. These stoppages may come about as the result of food shortages or perhaps as the result of environmental changes. The weaker development and lower number of varices in *C. chipolanum* may indicate that this species lived in a rather stable environment where there were a large number of prey species for it to consume. Conversely, *C. dalli* has more and better developed varices (growth stoppages) which may be due to lack of prey or perhaps increased predation pressures.

In all probability, *C. chipolanum* is the ancestral form of *C. dalli*. It is the opinion of the investigators that *C. chipolanum* probably retreated from the coastal waters into the deeper offshore waters during intervening ice ages where it gradually evolved into the extant, and morphologically similar, *C. dalli*.

Clench and Turner (1950) did not assign a subgeneric name to this genus even though de Boury (1909) did. Clench and Turner's reason for not using subgenera is not stated, but in all probability the authors did not think that structural differences between members of this genus were sufficient to warrant their use.

**Table 2.** A comparison of the structural differences in shell morphology between *C. dalli* and *C. chipolanum*.

| | *C. dalli* | *C. chipolanum* |
|---|---|---|
| No. of specimens examined | 23 | 16 |
| Teleoconch whorls | 9–10 | 7–8 |
| Spire angle | 26.5° | 27.0° |
| Costae arrangement | touching | sometimes separated |
| Mean no. of costae | 20.6 | 19.1 |
| Range in costae number | 18–23 | 17–21 |
| Range in varix number | 2–27 | 0–10 |
| Mean varix number | 8.82 | 4.75 |
| Varix placement | start on 1st body whorl | start on 3rd body whorl |

Since Clench and Turner's publication, Weil et al. (1999) and Nakayama (2003) have assigned a number of subgenera to the genus *Cirsotrema*. It is interesting to note that between these authors there is not complete agreement as to which subgenera are valid. For example, Nakayama (2003) used the subgenus *Boreoscala* to describe cold-water species that possess thickened, non blade-like costae, while Weil et al. (1999) raised the subgenus *Boreoscala* to the generic level. In addition, Weil et al. questions the use of *Elegantiscala* as a subgenus of *Cirsotrema* while Nakayama retained this subgenus and used it for many of the species of *Cirsotrema* he described from the northwest Pacific.

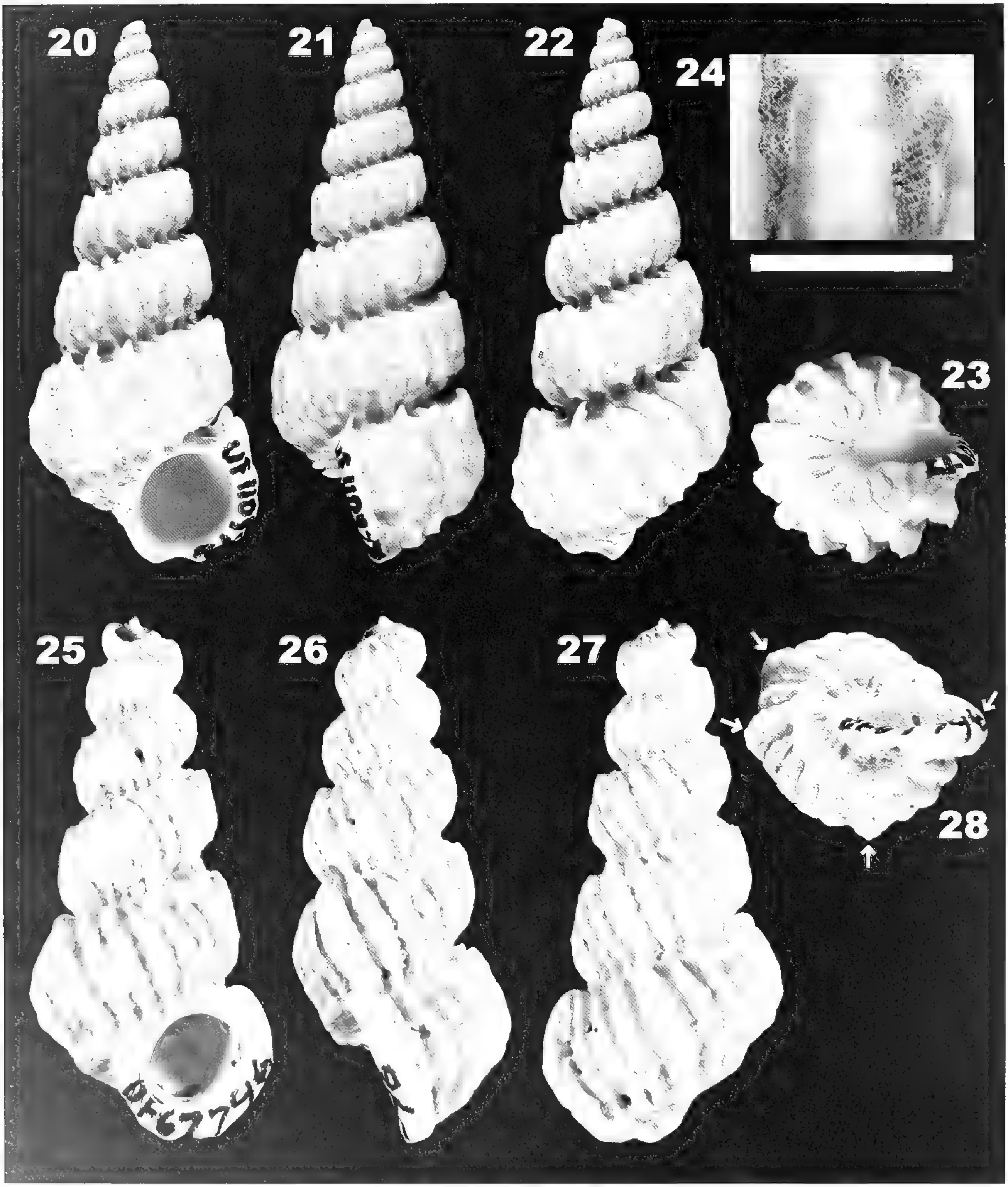
The present authors have followed the more conservative approach used by Clench and Turner (1950), Abbott (1974), Duerr (2004), and Landau et al. (2006) and have not assigned a subgenus to the new Chipola Formation species.

*Cirsotrema togatum* (Hertlein and Strong, 1951) is morphologically similar to *C. chipolanum*. Duerr (2004) considers *C. togatum* to be a western cognate of *C. dalli*. *Cirsotrema togatum* has also been reported from the Pliocene Esmeraldas beds of northwestern Ecuador by Pitt (1981) and DuShane (1988). *Cirsotrema chipolanum* differs from *C. togatum* in that it has fewer and less distinct spiral cords on the body whorls and the varices are much less developed.

*Cirsotrema woodringi* Olsson, 1967, reported from the Miocene Gatun Formation of Panama and the Pliocene Tamiami Formation at Sunnyland, Florida, is similar to *C. chipolanum*. The main difference between *C. woodringi* and *C. chipolanum* is that *C. woodringi* lacks the inclined spiral sculpture that is present on the flat outer surface of the costae in *C. chipolanum*.

*Cirsotrema cirritum* Duerr, 2004
(Figures 20–28)

**Description:** Shell medium to large. Turriculate. Much of protoconch missing. Last protoconch whorl transitions from a smooth surface into wavy axial lamellae that gradually enlarge into thickened foliated costae. Spire angle 27°. Eight strongly shouldered teleoconch whorls present. Suture deep. Thirteen crenulated, recurved, axial costae present on last body whorl. Apical ends of axial costae sharp. Costae made up of multiple wavy lamella that possesses a fine irregular diamond-shaped pattern that is inclined adaperturally. Costae separated by wide intercostal spaces. Intercostal spaces possess five rounded spiral cords. Cords and intervening spaces have a cancellate sculpture created by overlapping vertical and horizontal threads. Anterior reflected projections of costae on last body whorl form a basal ridge with a crenulate outer margin. Costae on basal ridge not fused. Varices absent. Columella short and arched. Aperture subcircular. No umbilicus.



**Figures 20–28.** *Cirsotrema cirritum* Duerr, 2004. **20–23.** Apertural, lateral, abapertural, and basal views of holotype UF 110972; maximum height 28.5 mm, maximum width 11.8 mm. **24.** Magnified view of sculpture of teleoconch of UF 110972. Scale bar = 2.75 mm. **25–28.** Apertural, lateral, abapertural, and basal views of paratype UF 67746; maximum height 29.6 mm, maximum width 13.4 mm. **Note:** Arrows point to apparent varices on paratype UF 67746; thus based upon description by Duerr (2004, p. 154–155) denoting a key diagnostic feature of no varices, this paratype was mistakenly identified. In our opinion UF 67746 is representative of *C. hipolanum* new species.

**Holotype:** UF 110972, maximum height 28.5 mm, maximum width 11.8 mm.

**Type Locality:** Tenmile Creek 01 (CA002) (= Tulane University locality TU 830), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation. Note: Duerr (2004) erroneously listed the GPS coordinates of 29° 30.05′ N, 85° 11.00′ W for this locality and provided no datum. These coordinates are approximately 17 km south of Saint Vincent Island, Florida in the Gulf of Mexico. Additionally, Duerr (2004) listed the type locality as in the SE1/4 of Sec. 7. It should have read SE1/4 of Sec. 12.

**Other Material Examined:** UF 112019, paratype, Farley Creek 03 (CA009) (= Tulane University locality TU 825), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; UF 67746, paratype, locality and formation same as preceding; BMSM 15301, paratype, Tulane University locality TU 458, Chipola Formation; USNM 534499, 2 shells, Tenmile Creek 03 (CA017) (= Tulane University locality TU 546), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation.

**Etymology:** The name *cirritum* is derived from the Latin *cirrus* meaning "filamentous" which refers to the fringed costae of this species.

**Discussion:** One of the key diagnostic features of *C. cirritum* is its lack of varices. However, when comparing the paratypes of *C. cirritum* with the holotype, one paratype, identified as *C. cirritum*, was discovered to possess varices that were similar to those observed in *C. chipolanum* (see Figures 25–28). This discovery generated some confusion and resulted in an exhaustive investigation to determine if only one species of *Cirsotrema* (*C. cirritum*) existed in the Chipola Formation or if there were two distinct species and a mistake had been made with the selection of one of the paratypes of *C. cirritum*. The conclusion drawn from this analysis was that there are two different species of *Cirsotrema* in the Chipola Formation and that the *C. cirritum* paratype (UF 67746) was mistakenly selected.

When examining the different species of the Chipola Formation *Cirsotrema* it is easy to see how this mistake occurred. The varices on *C. chipolanum* sometimes can be easily overlooked without careful examination under a microscope. A summary of differences between *C. cirritum* and *C. chipolanum* is found in Table 3.

**Table 3.** A comparison of the structural differences in shell morphology between *C. cirritum* and *C. chipolanum*.

| | *C. cirritum* | *C. chipolanum* |
|---|---|---|
| Mean varix number | 0 | 4.75 |
| Costae number | 13 | 17–21 |
| Foliated costae | widely separated | closely packed |
| Basal ridge | costae not fused | costae fused |

*Cirsotrema cirritum* is a fairly rare species that has been obtained from only three fossil localities: one each on the Chipola River (TU locality 458), Tenmile Creek (TU locality 951), and Farley Creek (TU locality 825).

As Duerr (2004) noted, *C. cirritum* is a fairly distinctive species that bears some resemblance to several types of Recent Indo-Pacific Epitoniidae. Among the comparable Recent species, Duerr (2004) reported were *Cirsotrema plexis* Dall, 1925, *Cirsotrema fimbriatulum* (Masahito et al., 1971), *Cirsotrema rugosum* (Kuroda and Ito, 1961), and *Cirsotrema excelsum* Garcia, 2003.

Among fossil species *C. cirritum* is most similar to the Miocene species *Cirsotrema undulatum* (Jung, 1965) from the Paraguaná Peninsula, Venezuela. *Cirsotrema undulatum* is a medium-size shell with six to eight post-nuclear whorls that possess thin, widely spaced axials (Jung, 1965). *Cirsotrema cirritum* differs from *C. undulatum* by having fewer axial costae on the body whorls (13 versus 17–21) and five spiral cords on each body whorl versus four.

The presence of two species of *Cirsotrema* in the tropical Chipola Formation environment is consistent with what currently exists in Florida offshore waters today. According to Clench and Turner (1950), both *C. dalli* and *C. pilsbryi* can currently be found in deep water off the Florida coast.

Genus *Opalia* H. and A. Adams, 1853

**Type Species:** by subsequent designation, *Scalaria australis* Lamarck, 1822.

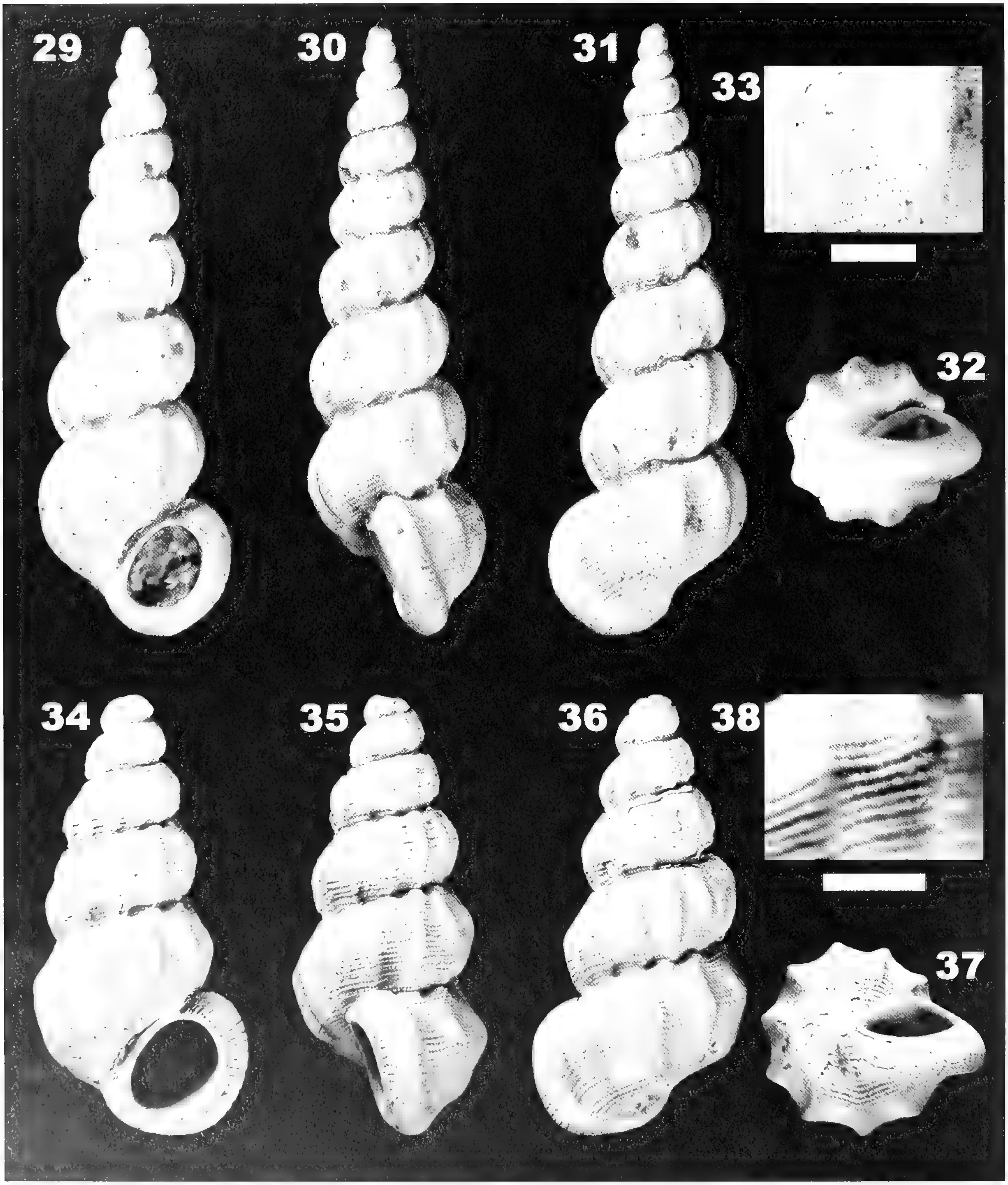
Subgenus *Nodiscala* de Boury, 1889
*Opalia politesae* new species
(Figures 29–33)

**Description:** Shell small, slender; 2.5 smooth protoconch whorls, 8 convex teleoconch whorls. Spire angle 20°. Twelve to 13 rounded axial costae on last teleoconch whorl. Shell surface covered with fine horizontal and vertical threads giving surface a pitted appearance. Pitted surface absent on distal surface of axial costae. Costae terminate at the suture, creating a crenulated ridge. Sutures moderately impressed. No basal ridge present. No varices. Aperture oblique, subcircular, surrounded by thick rounded lip. Inner portion of lip encircled by a thin, unsculptured rim. Outer portion possesses fine vertical threads that radiate outwards towards periphery. No umbilicus. Columella short and arched.

**Holotype:** UF 114913, maximum height 5.5 mm, maximum width 1.7 mm.

**Type locality:** Tenmile Creek 03 (CA017) (= Tulane University locality TU 546), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation.

**Paratypes:** USNM 534495, USNM 534496 and UF 113897, 1 shell each, protoconchs missing, locality and formation for each specimen the same as holotype; USNM 534497, 1 shell, protoconch missing, Tenmile



**Figures 29–38.** *Opalia politesae* new species and *Opalia mica* new species. **29–32.** *Opalia politesae*; apertural, lateral, abapertural, and basal views of holotype UF 114913; maximum height 5.5 mm, maximum width 1.7 mm. **33.** Magnified view of sculpture of teleoconch of UF 114913. Scale bar = 0.41 mm. **34–37.** *Opalia mica*; apertural, lateral, abapertural, and basal views of holotype UF 66077; maximum height 4.0 mm, maximum width 1.5 mm. **38.** Magnified view of sculpture of teleoconch of UF 66077. Scale bar = 0.33 mm.

Creek 01 (CA002) (= Tulane University locality TU 830), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; UF 67499, 3 shells, Chipola 01 (McClelland's Farm) (CA001) (= Tulane University locality TU 457), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; UF 114914, 2 shells, locality and formation same as holotype; UF 114922, 3 shells, Tenmile Creek 04 (CA020) (= Tulane University locality TU 951), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation.

**Distribution:** Although *Opalia politesae* is one of the more common epitoniids found in the Chipola Formation, its distribution appears limited to the reef paleoenvironments found along Tenmile Creek and the Chipola River.

**Etymology:** Named for Greta Polites, an avid student and collector of Chipola and Shoal River formation fossils.

**Discussion:** According to Clench and Turner (1950: 231) members of the genus *Opalia* have "Spiral sculpture usually of exceedingly fine incised threads which may or may not be finely pitted." In addition, the genus also possesses relatively low, heavy costae, no umbilicus, and a thick outer lip divided into a thin inner unsculptured ring and a thicker finely pitted one. In the subgenus *Nodiscala* the sutures are crenulated and the basal cord is absent.

Gardner (1947) reported the subgenus *Nodiscala* from Eocene deposits in Australia. However, there is no evidence of the genus *Opalia* from the Eocene of the United States. MacNeil and Dockery (1984) reported a number of different species of *Opalia* from the lower Oligocene Mint Spring Formation of Mississippi. According to Gardner (1947: 578), the subgenus *Nodiscala* is "peculiarly characteristic of the Miocene of central Europe" and she also noted that several species have been found in the Pliocene of Italy. Landau et al. (2006) reported a number of fossil *Nodiscala* from a wide range of European localities. These fossils have been found in deposits that date from the early Miocene to the late Pleistocene. DuShane (1979) lists *Opalia borealis* as possibly coming from Miocene deposits of the northeastern Pacific region. All of the remaining *Opalia* studied by DuShane (1979) came from Pliocene and Pleistocene formations. In the Caribbean, Maury (1917) reported a single specimen of *Epitonium textuvestitum* from Pliocene deposits in Santo Domingo (Dominican Republic). The description of this species given by Maury (1917) clearly indicates that it belongs to the genus *Opalia*. Both Campbell (1993) and Petuch (1994) have assigned this species to the genus *Opalia*. Campbell's specimen came from Pliocene deposits in Hampton, Virginia and Petuch's specimen was reported from the Pliocene deposits of the former APAC shell pits in Sarasota, Florida.

*Opalia politesae* is one of the more abundant species of Epitoniidae in the Chipola Formation where it is a unique representative of this genus. In overall contour and shape it bears some resemblance to the fossil *O. textuvestitum* but it lacks varices and has fewer costae on the body whorl. Among Recent species *O. politesae* is most similar to *Opalia burryi*, which ranges from south Florida through the West Indies to Trinidad. However, *O. politesae* is a much smaller and more slender species that has fewer body whorls (8 versus 9–11) and fewer costae on the body whorls (12–13 versus 14) than its Recent counterpart. The close similarity between *O. politesae* and *O. burryi* suggests that *O. politesae* is probably the ancestral form of *O. burryi*.

*Opalia mica* new species
(Figures 34–38)

**Description:** Shell short, stocky; one smooth protoconch whorl present, four teleoconch whorls. Nine to ten costae on last teleoconch whorl. Spire angle 29°. Costae sharply angulated, forming a node at the periphery of the body whorl. Shell surface crossed with fine horizontal and spiral threads that give the surface a pitted appearance. Pitted sculpture covers entire surface of axial costae. Costae terminate at the suture creating a crenulated ridge. Sutures moderately impressed. No basal ridge present. No varices. No umbilicus. Aperture oblique, subcircular, surrounded by a thick lip. Inner portion of lip encircled by thin, smooth rim. Outer part of lip possesses fine vertical threads that radiate outward towards the periphery. Vertical threads on lip overlapped by fine threads that give the lip a pitted appearance. Columella short and arched.

**Holotype:** UF 66077, maximum height 4.0 mm, maximum width 1.5 mm.

**Type Locality:** Shoal River Grotto (WL004) (= Tulane University locality TU 69A), New Harmony Quadrangle USGS 7.5′ Series (1987), Walton County, Florida, Shoal River Formation.

**Paratypes:** UF 114924, 1 specimen, and UF 88160, 3 specimens, locality and formation same as holotype.

**Distribution:** *Opalia mica* is a rare species but thus far has only been obtained from the type locality.

**Etymology:** Name alludes to its diminutive size.

**Discussion:** *Opalia mica* is structurally very different from *O. politesae*. It is broader and smaller than the Chipola Formation species and possesses sharply angulated costae. Gardner (1947) reported fragments of this species from the Shell Bluff location along the Shoal River in Walton County, Florida. The most comparable fossil form to *O. mica* is the Miocene species *Opalia* cf. *scacchi* (Hoernes, 1856) reported from Austria (Nordsieck, 1972). In size and overall form the two species are very similar; however, *O. mica* has deeper sutures, lacks rounded varices, and does not possess the sutural spiral cords present in the European taxon.

Among extant forms *O. mica* is similar to *O. pumilio* *morchiana* Dall, 1889. Both the Chipola Formation and Recent species are small and have costae that are sharply angulated at the periphery of the body whorl. However, *O. mica* lacks varices, has a more acute spire angle (29° versus 37°), and only has four teleoconch whorls compared to seven for *O. pumilio morchiana*.

Genus *Epitonium* Röding, 1798

**Type Species:** by subsequent designation, *Turbo scalaris* Linnaeus, 1758.

Subgenus *Asperiscala* de Boury, 1909
*Epitonium virginiae* (Maury, 1910)
(Figures 39–46)

**Description:** Shell small, attenuate; 3 smooth, glossy, protoconch whorls, 6–7 convex teleoconch whorls separated by deep sutures. Spire angle 35°. 8–9 costae on last teleoconch whorl. Costae prominent, blade-like, slightly oblique with coronate shoulders. Fine spiral threads on body whorl crossed by faint axial growth line. No varices. Umbilicus absent. No basal cord. Aperture oval.

**Holotype:** PRI 3467 (formerly in Cornell University collection), maximum height 3.75 mm, maximum width 1.5 mm.

**Other Material Examined:** UF 95695, 1 shell, Chipola 13 (CA027) (= Tulane University locality TU 458), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; UF 89251, 4 shells, Chipola 28 (CA066) (= Tulane University locality TU 548), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; UF 103784, 1 shell, Tennile Creek 06 (CA023) (= Tulane University locality TU 456), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; UF 72341, 1 shell, Shoal River Grotto (WL004) (= Tulane University locality TU 69A), New Harmony Quadrangle USGS 7.5′ Series (1987), Walton County, Florida, Shoal River Formation.

**Type Location:** Bailey's Ferry, Calhoun County, Florida.

**Distribution:** *Epitonium virginiae* is one of the more common species of Epitoniidae found in the Chipola Formation. It is also found in the Shoal River Formation where it appears to be extremely rare. A total of 59 specimens of *E. virginiae* were examined from ten Chipola Formation collection sites in Calhoun and Liberty counties. The only Shoal River example of *E. virginiae* was obtained from UF locality WL004 (= TU 69A) in Walton County.

**Etymology:** Unknown.

**Discussion:** Members of the genus *Epitonium* are small, thin, generally slender turriculate shells with a wide range of different sculptured characteristics. Some have body whorls that are attached while others do not. A basal ridge may be present or absent, the costae may be thin and blade-like or thick and rounded, and spiral sculpturing may or may not be present. This high degree of structural variability within the genus has caused researchers to organize its members into numerous subgenera.

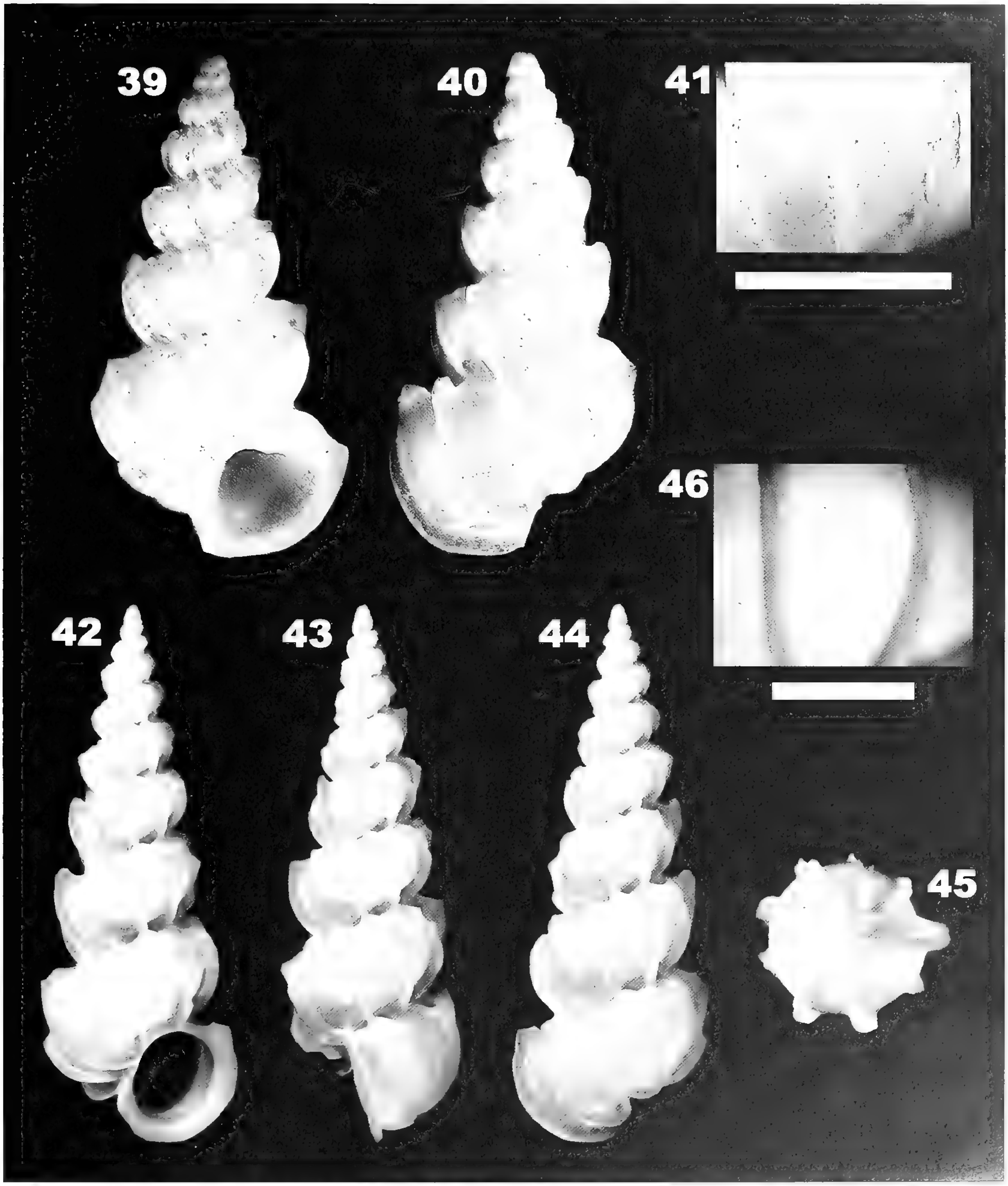
Epitoniidae with blade-like costae, spiral thread-like cords on the body whorls, and an absence of a basal ridge were assigned to the subgenus *Asperiscala* by de Boury (1909). Members of the subgenus *Asperiscala* have been reported from deposits as old as Cretaceous (Wade, 1926).

Clench and Turner (1952) kept the subgenus *Asperiscala* and assigned to it all epitoniids with spiral cords and either blade or cord-like costae. DuShane (1979: 91), because of "Certain morphological differences from those of *Epitonium s.s.*", elevated *Asperiscala* to full generic rank when she described the family Epitoniidae in the northeastern Pacific. According to Kilburn (1985), however, the type species of *Asperiscala* is not representative for this taxon. Kilburn reported that the type species of *Asperiscala* described by de Boury (1909) had cancellate sculpture. Subsequently, Kilburn assigned epitoniids with only spiral sculpture to the subgenus *Parviscala*. Weil et al. (1999) and Nakayama (2003) retained *Asperiscala* as a subgenus but limited its use to epitoniids that resembled *Parviscala* that have an open umbilicus and sutures with peaked costae. Herein, we have retained the use of *Asperiscala* in the sense of Clench and Turner (1952), pending resolution of the problems cited above. But unlike its use in Weil et al. and Nakayama, *Asperiscala* is herein used to represent members of the genus *Epitonium* that have spiral sculpture that may or may not be intersected with faint axial threads or narrow cords.

A more detailed analysis of larger specimens of *E. virginiae* revealed the presence of fine vertical lines that intersect the slender spiral threads on the body whorls (Figure 46). The absence of this feature in Maury's description was more than likely due to the small size of the specimen she examined.

Of all the Chipola Formation species of *Epitonium* examined, only *E. virginiae* was encountered in the younger Shoal River Formation. It is apparently a rare species in this unit given that numerous collecting trips to several different Shoal River Formation sites by different collectors have yielded just one specimen. Close examination of this specimen revealed that its shell structure is fundamentally the same as that of the Chipola Formation species.

Several fossil species similar to *E. virginiae* have been collected from different localities including the Caribbean, Central and South America, and Spain. *Epitonium* (*Asperiscala*) *venezuelense* (Weisbord, 1962) from the upper Miocene Mare Formation of northern Venezuela comes closest in overall morphological characteristics to *E. virginiae*. Both species have prominent blade-like, slightly oblique costae with coroneted shoulders, and both have spiral threads in the interspaces between the axial costae that are crossed by fine axial filaments. The



**Figures 39–46.** *Epitonium virginiae* (Maury, 1910). **39–40.** Apertural and abapertural views of holotype PRI 3467, maximum height 3.75 mm, maximum width 1.5 mm. **41.** Magnified view of sculpture of teleoconch of PRI 3467. Scale bar = 1.0 mm. **42–45.** Apertural, lateral, abapertural, and basal views of UF 95695; maximum height 6.9 mm, maximum width 2.45 mm. **46.** Magnified view of sculpture of teleoconch of UF 95695. Scale bar = 0.55 mm.

two species differ from one another in that *E. virginiae* has more impressed sutures, the costae of *E. virginiae* do not become obsolescent near the posterior suture, and the angle of the spire is slightly wider in *E. virginiae* (35° versus 32°).

Other fossil species similar to *E. virginiae* include *Epitonium loripanum* Pilsbry and Olsson, 1941, from the Pliocene of Ecuador, *Epitonium amosbrowni* Pilsbry, 1921, from the Miocene of the Dominican Republic, *Epitonium* cf. *gabbi* (de Boury) Woodring, 1959, from the Gatun Miocene of Panama (Canal Zone), and *Epitonium muiricatoides* (Sacco, 1891) from the early Pliocene of Spain. The Chipola Formation species differs from *E. amosbrowni*, which has 16 axial costae on the last whorl versus 8–9 for *E. virginiae*, from *E.* cf. *gabbi*, which has more pronounced and numerous spiral threads on its body whorls, and *E. muiricatoides*, which lacks spiral cords on the body whorls.

A close comparison of *E. loripanum* with *E. virginiae* suggests that they may be the same species. Both have the same body shape, the presence of faint spiral threads on the body whorls, the same number of teleoconch whorls, thin ribs with coronated shoulders, and lack an umbilicus.

Among extant species, *E. virginiae* is most similar to *Epitonium denticulatum* (Sowerby, 1844). However, *E. virginiae* is more slender and has fewer axial costae.

*Epitonium incomitatum* new species
(Figures 47–51)

**Description:** Shell small, thin, turriculate. Protoconch missing; 6 strongly convex teleoconch whorls separated by deep sutures. Spire angle 31°. Thin, low, reflected costae on last teleoconch whorl numbering 24. Costae on each succeeding whorl slightly offset from the one above. Numerous spiral cords on body whorl. No varices. No basal ridge. Umbilicus present. Outer lip of aperture thin. Aperture suboval.

**Holotype:** UF 91452, maximum height 5.0 mm, maximum width 2.2 mm.

**Type Locality:** Tenmile Creek 03 (CA017) (= Tulane University locality TU 546), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation.

**Distribution:** Only known from the type locality.

**Etymology:** The name is derived from the Latin word *incomitatus* meaning unaccompanied or alone. It refers to the unique specimen (holotype).

**Discussion:** *Epitonium incomitatum* is an extremely fragile shell. In shell sculpture it is similar to *Parviscala*, a subgenus retained by Weil et al. (1999) and Nakayama (2003). Gardner (1947) reported a fragment of this shell in the Chipola Formation and assigned it to the subgenus *Crisposcala*. A fragment similar to *E. incomitatum* was also reported from the upper part of Gatun Formation in Panama (Canal Zone). Woodring (1959) tentatively identified this species as *Epitonium rushii* (Dall, 1889). Weil et al. listed *E. rushii* as synonym of *Epitonium striatissimum* Monterosato, 1878. Among fossil western European species *E. incomitatum* is most similar to *Epitonium pulchellum* (Bivona, 1832) which has been reported from the middle Miocene in Italy (Cavallo and Repetto, 1992). *Epitonium incomitatum* differs from its European counterpart by having less elevated varices and less prominent spiral cords on the body whorls.

Among extant species, *E. incomitatum* is most similar to *E. striatissimum*, a rare species found in shallow water off Cape Hatteras. *Epitonium incomitatum* differs from *E. striatissimum* in that the body whorls are more inflated (the angle formed with the spire is 31° versus 25° for *E. striatissimum*) and the spiral cords on the body whorl are much broader and less numerous.

*Epitonium incomitatum* also bears some resemblance to *Epitonium multistriatum* Say, 1826, a species that ranges from Massachusetts to Texas. It differs from this species by possessing more numerous costae on the last body whorl (25 versus 16–19) and by having broader spiral cords on the body whorls. In addition, in *E. incomitatum* the costae are less abundant in the early whorls, while *E. multistriatum* the costae are more numerous in the early whorls (as many as 43 in some specimens).

*Epitonium regina* new species
(Figures 52–56)

**Description:** Shell small, turriculate; three smooth, glossy protoconch whorls, eight slightly angular body whorls separated by a moderately deep suture. Spire angle 23°. Eleven narrow, low, slightly reflected costae on last teleoconch whorl. Costae occasionally offset with costae on preceding whorl. Numerous faint, spiral cords on body whorls intersected by faint spiral threads. No basal cord. No umbilicus. No varices. Aperture thin, suboval.

**Holotype:** USNM 534487, maximum height 6.1 mm, maximum width 2.1 mm.

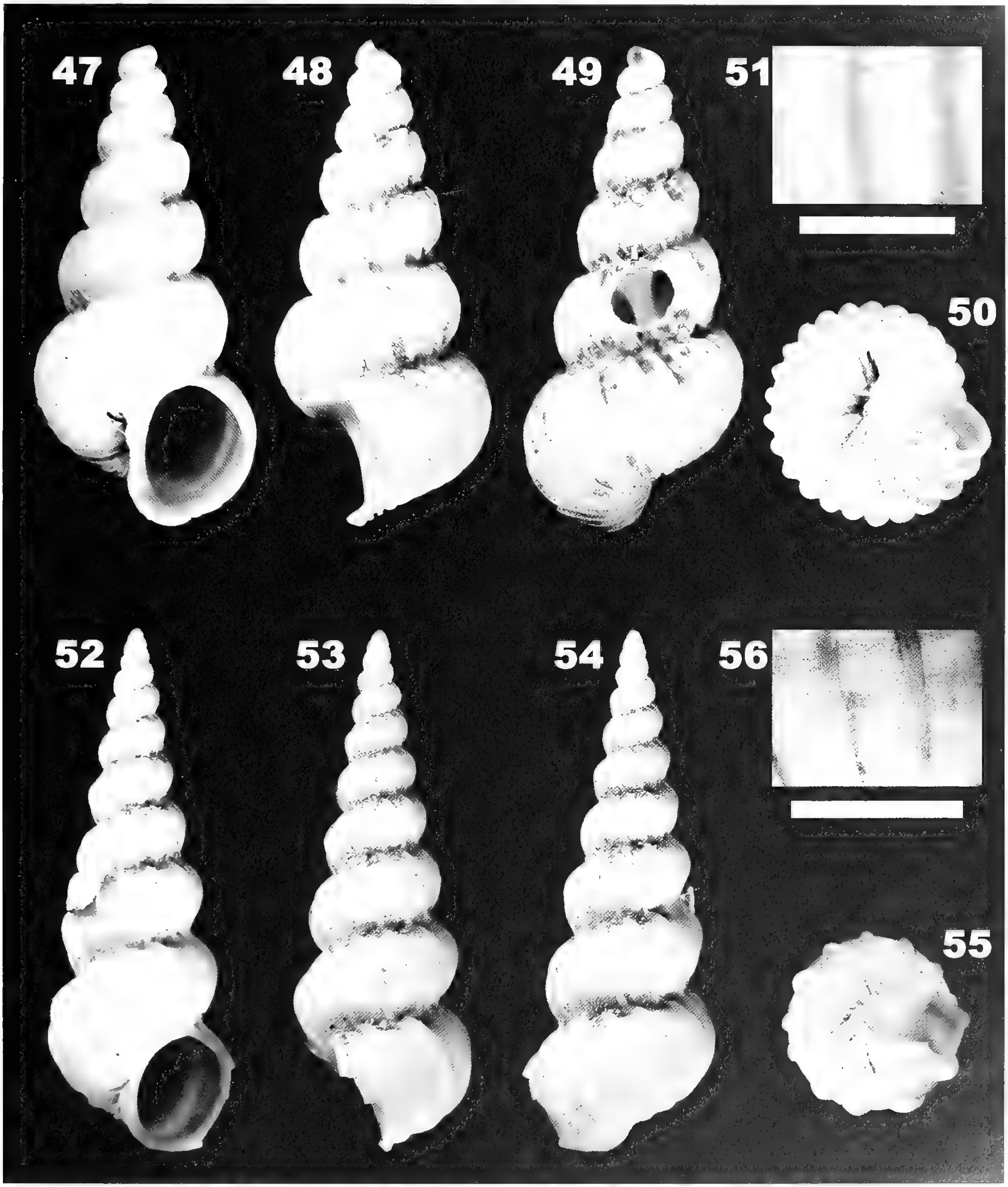
**Type Locality:** Farley Creek 03 (CA009) (= Tulane University locality TU 825), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation.

**Paratype:** UF 67498, 1 specimen, Chipola 01 (CA001) (McClelland's Farm) (= Tulane University locality TU 457), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation.

**Distribution:** Collected only from the type locality.

**Etymology:** Named from the Latin word *regina*, meaning queen, an allusion to the stately appearance of this species.

**Discussion:** Among Recent species, *E. regina* bears a slight resemblance to *Epitonium obliquum* (Sowerby, 1847), however *E. regina* has a cancellate pattern be-



**Figures 47–56.** *Epitonium incomitatum* new species and *Epitonium regina* new species. **47–50.** *Epitonium incomitatum*, apertural, lateral, abapertural, and basal views of holotype UF 91452; maximum height 5.0 mm, maximum width 2.2 mm. **51.** Magnified view of sculpture of teleoconch of UF 91452. Scale bar = 0.41 mm. **52–55.** *Epitonium regina*, apertural, lateral, abapertural, and basal views of holotype USNM 534487; maximum height 6.1 mm, maximum width 2.1 mm. **56.** Magnified view of sculpture of teleoconch of USNM 534487. Scale bar = 0.65 mm

tween costae on the body whorls, lacks elevated costae near the sutures, and has no umbilicus.

Among fossil species *E. regina* bares some resemblance to *Epitonium smithfieldensis* Mansfield, 1929 and *Epitonium dupliniana* (Olsson, 1916). *Epitonium smithfieldensis* was reported from the Pliocene Yorktown Formation of Virginia. Like the Chipola Formation species it is ornamented with marginally reflected slender varices and the number of varices on the last body whorl is 12. However, *E. smithfieldensis* does not have any spiral sculpture and its varices are united at the suture. *Epitonium dupliniana* was reported from the middle Pliocene Duplin Formation of North Carolina (Olsson, 1916). Like *E. regina*, it has a thin shell with low varices and spiral sculpturing on the body whorls that is intersected by vertical threads. It differs from the Chipola Formation species in that the varices on *E. regina* are broader and more cord-like than they are in *E. dupliniana*. Also, the upper shoulder on each of the varices of *E. dupliniana* has a small hook-like projection, a feature not present on the varices of *E. regina*.

Subgenus *Epitonium* Röding, 1798

**Type of Subgenus:** *Tubo scalaris* Linnaeus, 1758 by subsequent designation, Suter, 1913.

*Epitonium conwaiae* new species
(Figures 57–66)

**Description:** Shell small, attenuate; 3.5 smooth protoconch whorls. Spire angle 30°. Six-and-a-half moderately convex teleoconch whorls separated by a depressed suture. Seven to nine low, moderately broad, T-shaped costae on last body whorl. Costae gradually increase in width as aperture approached. Costae angled at shoulders. Body whorls smooth but eroded specimens exhibit numerous, fairly broad spiral cords on body whorls. No basal cord, umbilicus, or varices. Aperture suboval, outer lip slightly expanded and thickened.

**Holotype:** UF 113894, maximum height 3.2 mm, maximum width 1.2 mm.

**Type Locality:** Shoal River Grotto (WL004) (= Tulane University locality TU 69A), New Harmony Quadrangle USGS 7.5′ Series (1987), Walton County, Florida, Shoal River Formation.

**Paratypes:** UF 67208, 9 shells, Shell Bluff 01 (WL002) (= Tulane University locality TU 69), New Harmony Quadrangle USGS 7.5′ Series (1987), Walton County, Florida, Shoal River Formation; UF 89549, 1 shell, locality and formation same as preceding; UF 117092, 2 shells, locality and formation same as preceding; UF 89638, 29 shells, locality and formation same as preceding; UF 72340, 1 shell, locality and formation same as holotype; UF 88170, locality and formation same as holotype

**Distribution:** *Epitonium conwaiae* is known only from the type locality and from the Shell Bluff on Shoal River.

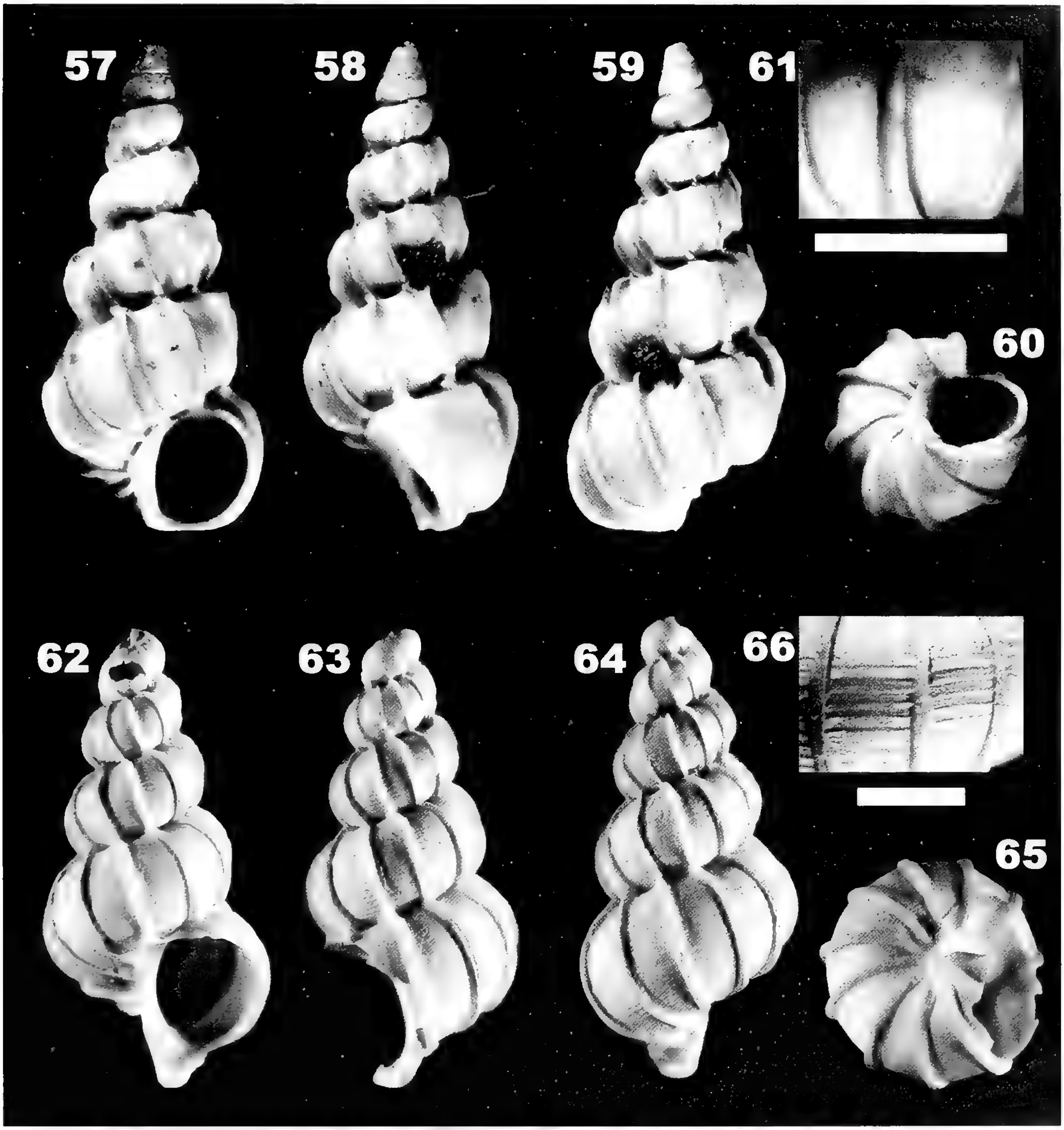
**Etymology:** Named for Wendy Conway a long time field associate of the authors and an avid collector of Chipola and Shoal River formation fossils.

**Discussion:** *Epitonium* with and without an umbilicus and possessing smooth body whorls and no basal cord were assigned to the subgenus *Epitonium* by Clench and Turner (1951). Later researchers, including Weil et al. (1999) and Nakayama (2003) subdivided *Epitonium* with smooth body whorls into a number of subgenera. For example, those with smooth body whorls, no umbilicus, and peaked costae were assigned to the subgenus *Hirtoscala*, while *Epitonium* with smooth body whorls, peaked costae and a slit-like umbilicus were placed into the subgenus *Lamelliscala*. Additionally, those with smooth body whorls, no umbilicus, and thick costae were assigned to the subgenus *Nitidiscala*.

Although probably in the minority, we find the need for splitting out the genus *Epitonium* into so many additional subgenera based upon minor morphological differences probably counterproductive to the establishment of a more realistic classification system. Clench and Turner (1951) warned researchers about this problem when they reported the difficulties de Boury experienced with his attempts to split out different members of the family. Rather than add to the confusion that exists with this taxonomic group, we have reverted to using the broader subgeneric name of *Epitonium* as defined by Clench and Turner (1951).

When compared to Recent species, non-eroded specimens of *Epitonium conwaiae* (Figures 57–61) are most similar to *Epitonium humphreysii* Kiener, 1838, which ranges from Cape Cod Massachusetts south to Florida (excluding the Florida Keys) and into the Gulf of Mexico from Cape Romano to Texas. Fossil specimens of *E. humphreysii* have also been reported from upper Miocene deposits of the Entrerriense Formation of the Chubut Province, Argentina (Brunet, 1995). Both the Shoal River Formation species and its Recent and fossil counterpart have flattened costae which are variable in width, both lack sculpturing on the body whorls, and each species has a similar number of costae on the last body whorl. The Shoal River Formation species differs from *E. humphreysii* by having more deeply impressed sutures, more angular costae on the shoulder of the body whorls, and much smaller average size.

In eroded specimens of *E. conwaiae* (Figures 62–66), the body whorls reveal a sculpture of broad spiral cords most similar to *Epitonium championi* Clench and Turner, 1952, a rare epitoniid that inhabits intertidal and near-shore waters from Cape Cod to North Carolina. Both the Shoal River Formation form and *E. championi* have flattened, cord-like costae which are variable in width and both have spiral sculpturing which consists of numerous flattened spiral cords. The Shoal River Formation species, however, differs from *E. championi* by having more deeply impressed sutures, a greater number of costae on the last body whorl (11 versus 8 or 9) and a



**Figures 57–66.** *Epitonium conwaiae* new species. **57–60.** Apertural, lateral, abapertural, and basal views of holotype UF 113894; maximum height 3.2 mm, maximum width 1.2 mm. **61.** Magnified view of sculpture of teleoconch of UF 113894. Scale bar = 0.7 mm. **62–65.** Apertural, lateral, abapertural, and basal views of paratype UF 72340; maximum height 4.2 mm, maximum width 2.0 mm **61.** Magnified view of sculpture of teleoconch of UF 72340. Scale bar = 1.26 mm. UF 72340 is an eroded specimen figured here to compare sculptural differences between it and unworn holotype UF 113894

greater angle between the spire and the outer shoulders of the shell (30° versus 20°).

Among fossil species, well-preserved specimens of *E conwaiae* are most similar to *Epitonium boltoni* Gardner, 1948, from the Pliocene Tar River deposits in North Carolina. Like *E. conwaiae*, *E. boltoni* possesses smooth spiral whorls, has thickened slightly raised costae and lacks an umbilicus and basal cord. However, *E. conwaiae* differs from *E. boltoni* by having more impressed sutures, more angular costae on the dorsal surface of each body whorl and fewer numbers of costae on the last body whorl (9 versus 12).

The eroded form of *E. conwaiae* also bears some similarities to *Epitonium alaquaense* collected and described by Mansfield (1935) from the late Miocene strata of Vaughan Creek in Walton County, Florida. Gardner (1947: 577) reported collecting a partial specimen from Walton County from "a horizon that was slightly higher than the typical Shoal River formation." These investigators were not able to locate Gardner's shell fragment but were able to borrow Mansfield's holotype (USNM 373149) for comparative purposes (see Figures 67–68). Unfortunately, the holotype was broken, which made the comparative study a bit more difficult than expected. Nevertheless, examination of the shells showed that *E. conwaiae* differs in several ways from *E. alaquaense*. *Epitonium conwaiae* is more slender than *E. alaquaense* and has 3.5 nuclear whorls versus 2.5 for *E. alaquaense* and the number axial ribs on the post-nuclear whorls on *E. conwaiae* range from 7–9 while the number of axial ribs on *E. alaquaense* ranges from 9–12. Current evidence suggests that that *E. alaquaense* is not found in the younger Shoal River Formation since none of the specimens examined were similar to Mansfield's shell.

The eroded form of *E. conwaiae* is also similar to the fossil species *Epitonium santodomingonum* Pilsbry, 1921, from the Pliocene beds of Santo Domingo (Dominican Republic) and *Epitonium antillarum* (de Boury, 1909) from Pliocene beds in Virginia and North Carolina (Gardner, 1948) and Florida (Olsson and Harbison, 1953). Like *E. conwaiae*, both fossil Pliocene species possess numerous spiral cords on the body whorls, lack a basal ridge, and both have low, well developed costae on the body whorls which increase in width near the aperture. *Epitonium conwaiae* differs from *E. santodomingonum* by having fewer costae on the last body whorl (9 versus 18) and an absence of varices on the last whorl of the shell. *Epitonium antillarum* differs from *E. conwaiae* by possessing fewer varices (7–9 versus 10–13), fewer teleoconch whorls (6 versus 8–9), thinner costae on the body whorls, a thinner lip surrounding the aperture, and a more acute spire angle (22° versus 30°). It should be noted that *E. antillarum* is no longer considered a valid species. In 1909, de Boury assigned the species *antillarum* to the epitoniid *Scalaria turricula* Sowerby, 1844. However, the shell Sowerby (1844) described had already been named by d'Orbigny (1842) as *Scalaria candeana*. Subsequently, Clench and Turner (1952) rectified de Boury's mistake by recognizing *E. antillarum* as *Epitonium candeanum*. Of further note, the shell described by Clench and Turner (1952) as *E. candeanum* does not fit the description of *E. antillarum* given by Gardner (1948) and later listed by Olsson and Harbison (1953) in their treatise on *Pliocene Mollusca of Southern Florida*. According to Clench and Turner (1952), *E. candeanum* has thinner and more numerous costae (18–25 versus 10–13) on the body whorls than does the species described by Gardner (1948) as *E. antillarum*. In all probability the *Epitonium* described by Gardner (1948) is a new species. It is beyond the scope of this paper to rectify this error and any effort to do so is being left to the work of future investigators.

*Epitonium hoerleae* new species
(Figures 69–73)

**Description:** Shell medium height, sturdy, turriculate; 3.5 smooth, glossy, protoconch whorls, 7.5 convex teleoconch whorls separated by deep suture. Spire angle 24°. Eight to nine thin costae on last body whorl. Costae slightly reflected backwards. At the whorl shoulder costae are slightly expanded and form a cusp-like node. Costae connected to one another at the suture, forming an oblique angle to the shell's central axis. Extremely faint spiral threads on glossy body whorls. No umbilicus. No basal cord. Aperture suboval. Outer lip of aperture thin and reflected backwards.

**Holotype:** USNM 534488, maximum height 8.8 mm, maximum width 3.2 mm.

**Type locality:** Tenmile Creek 03 (CA017) (= Tulane University locality TU 546), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation.

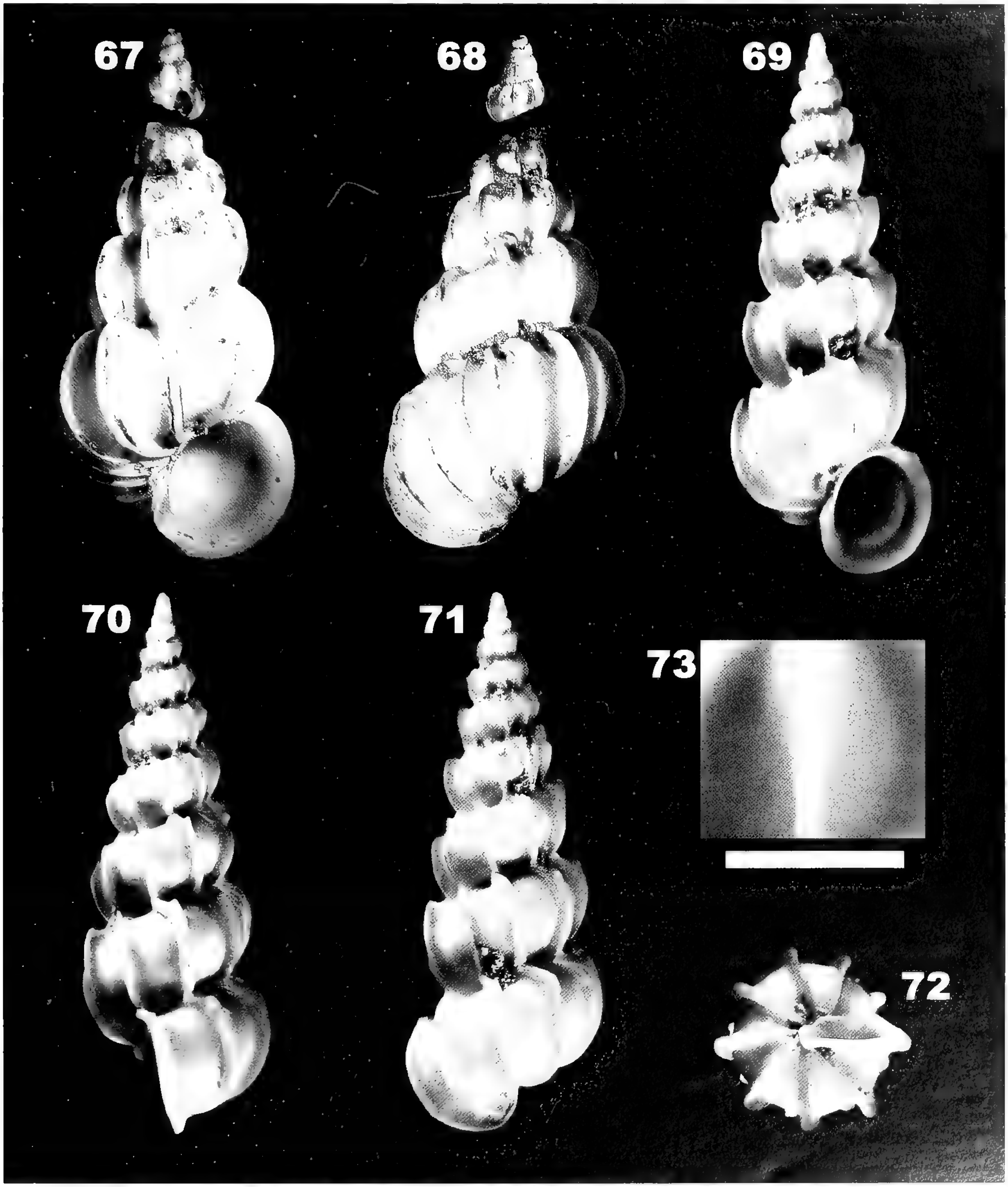
**Paratypes:** USNM 534498, 1 shell, locality and formation same as holotype; UF 84579, protoconch missing and aperture broken, Tenmile Creek 01 (CA002) (= Tulane University locality TU 830), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; UF 101862, 1 shell, protoconch missing and aperture broken, Tenmile Creek 13 (CA058) (= Tulane University locality TU 1097), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; UF 99083, 1 shell, Chipola 23 (CA037) (= Tulane University locality TU 711), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; UF 94317, 2 shells, Chipola 13 (CA027) (= Tulane University locality TU 458), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation.

**Distribution:** *Epitonium hoerleae* is a very common, widely distributed species. It has been found at the type locality of Tenmile Creek as well as along Farley Creek and the Chipola River.

**Etymology:** The species was named in honor of Shirley Hoerle, one of the pioneer researchers of Chipola Formation mollusks.

**Discussion:** Clench and Turner (1951) placed epitoniids that possessed glossy whorls and extremely faint spiral threads into the subgenus *Epitonium*. This classification has been retained with *E. hoerleae*.

Among recent species *E. hoerleae* is most similar to *Epitonium foliaceicostum* d'Orbigny, 1842, which inhabits offshore waters in the Caribbean and along Florida's east coast. Both the fossil species and its Recent counterpart have glossy body whorls with faint spiral threads, approximately the same number of costae on the last body whorl (8–9 versus 7–8), and a slightly reflected



**Figures 67–73.** *Epitonium alaquaense* Mansfield, 1935, and *Epitonium hoerleae* new species. **67–68.** *Epitonium alaquaense* apertural and abapertural views of holotype USNM 373149 shown for comparison to *E. connieae*. **69–72.** *Epitonium hoerleae* apertural, lateral, abapertural, and basal views of holotype USNM 534488, maximum height 8.8 mm, maximum width 3.2 mm. **73.** Magnified view of sculpture of teleoconch of USNM 534488. Scale bar = 0.95 mm.

aperture lip. *Epitonium hoerleae* differs from the Recent shell by having a greater number of nuclear whorls (3.5 versus 1.5), less elevated costae and a more slender body configuration.

A comparison of *E. hoerleae* with a number of fossil species shows that it most closely resembles *Epitonium fargoi* Olsson and Harbison, 1953, which was described from the Plio-Pleistocene Caloosahatchee Formation of south Florida as well as *Epitonium proximus* (de Boury, 1890) which was described from the early Pliocene of France and the middle Pliocene of England (Harmer, 1920–1925). Both *E. hoerleae* and *E. fargoi* have convex, glossy, body whorls, approximately the same number of costae on the last body whorl (8 versus 9), the costae are reflected backwards, and both have a small cusp-like node on the upper shoulder. *Epitonium hoerleae* differs from *E. fargoi* in that it has a more expanded reflected outer lip, lacks a thickened cord on the inner lip, its costae are thinner and more blade-like and the spire angle in *E. hoerleae* is less acute (24° versus 20°) than its Pliocene counterpart. The European species, *E. proximus*, differs from *E. hoerleae* in that it is larger and more slender than its American counterpart and has more varices on the body whorl (11–13 versus 8–9).

*Epitonium kallistos* new species
(Figures 74–78)

**Description:** Shell small, turriculate; 3.5 smooth, glossy, protoconch whorls, 6.5 convex teleoconch whorls separated by a deep suture. Six moderately thickened, slightly recurved costae on last body whorl. Spire angle 25°. Costae connected to one another at suture forming an oblique angle with the central axis. Costae lack a cusp-like node on the shoulder of body whorl. Body whorls smooth and glossy. No umbilicus; basal cord absent. No varices. Aperture suboval, lip slightly thickened and recurved.

**Holotype:** UF 44614, maximum height 6.8 mm, maximum width 2.3 mm.

**Type Locality:** Tenmile Creek 02 (CA003) (= Tulane University locality TU 70), Altha West Quadrangle USGS 7.5′ Series (1982), Calhoun County, Florida, Chipola Formation.

**Distribution:** *Epitonium kallistos* is known only from the type locality.

**Etymology:** Name is derived from the Greek word *kallisto* meaning most beautiful.

**Discussion:** Among Recent and fossil epitoniids, *E. kallistos* is most similar to *Epitonium unifasciatum* (Sowerby, 1844), a species that today ranges from southern Florida to the Lesser Antilles (Clench and Turner, 1951). *Epitonium unifasciatum* has also been reported from the upper Miocene deposits of the Entrerriense Formation of Chubut Province, Argentina (Brunet, 1995). Like its Recent and fossil counterpart, *E. kallistos* has smooth, shiny, convex whorls, the aperture is suboval, there is no basal ridge, and the outer lip of the aperture is reflected backwards. *Epitonium kallistos* differs from *E. unifasciatum* by having fewer costae on the last body whorl (6 versus 7 – 9), a greater spire angle (25° versus 20°), more deeply impressed sutures, and the costae on the body whorls are more elevated.

Subgenus *Gyroscala* de Boury, 1887
*Epitonium vokesae* new species
(Figures 79–83)

**Description:** Shell small, turriculate; three smooth, glossy, bulbous protoconch whorls, 5.5 moderately convex teleoconch whorls. Suture moderately impressed. Spire angle 27°. Eight to nine slightly raised, blade-like costae on body whorl. Costae sinuous, not joined at suture with costae on preceding whorl. Distinct, narrow, basal ridge present. No varices. No umbilicus. Outer lip missing.

**Holotype:** UF 113898, maximum height 4.3 mm, maximum width 1.6 mm.

**Type Locality:** Tenmile Creek 04 (CA020) (= Tulane University locality TU 951), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation.

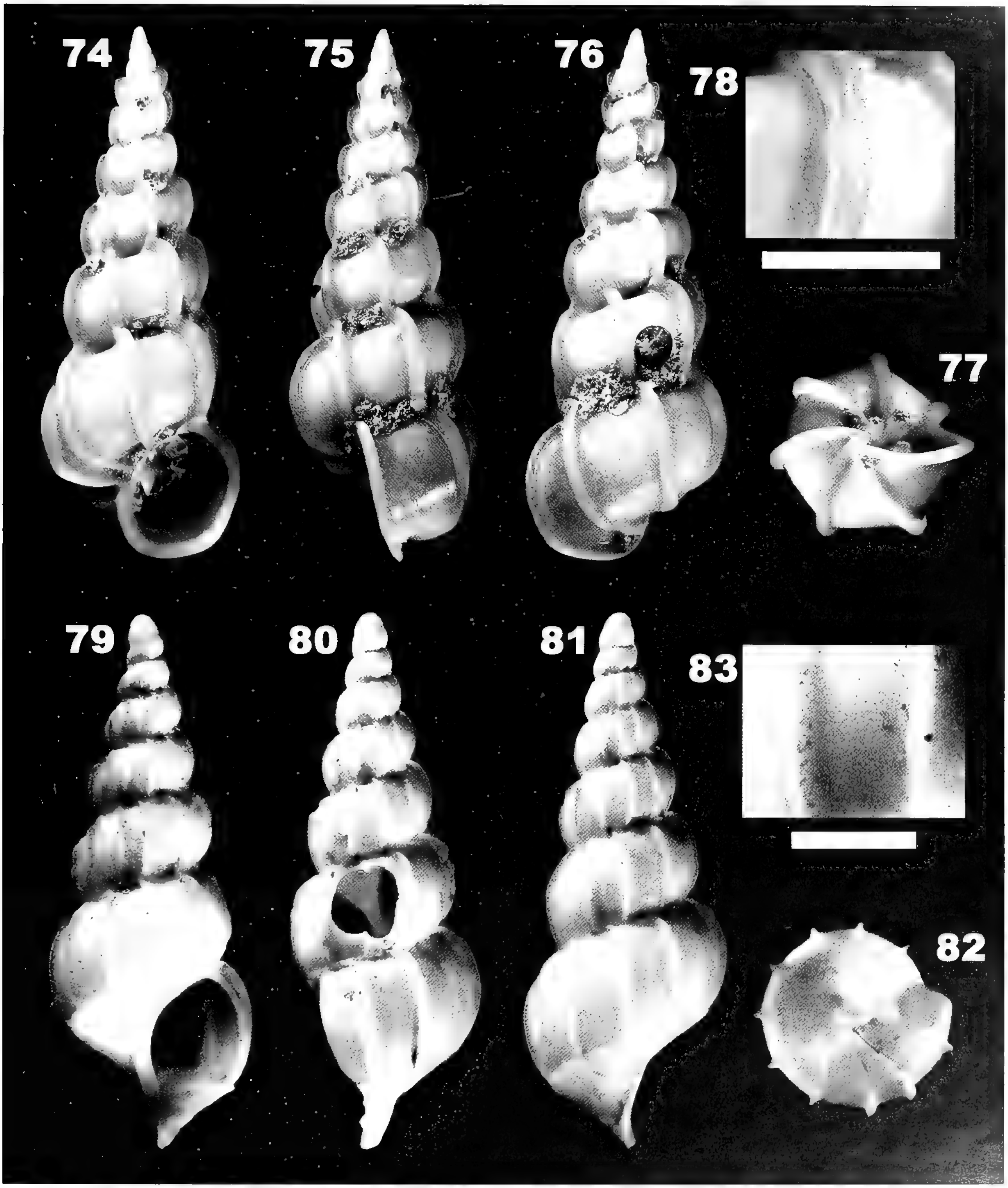
**Paratypes:** UF 114957, 1 shell, Tenmile Creek 03 (CA017) (= Tulane University locality TU 546), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation; UF 99136, 1 shell, spire missing, Chipola 23 (CA037) (= Tulane University locality TU 711), Clarksville Quadrangle USGS 7.5′ Series (1945), Calhoun County, Florida, Chipola Formation.

**Distribution:** *Epitonium vokesae* has only been collected along Tenmile Creek and the Chipola River.

**Etymology:** Named in honor of Dr. Emily Vokes, a leading researcher of the family Muricidae and a mentor to the many who have studied Chipola Formation fossils.

**Discussion:** *Epitonium* of the subgenus *Gyroscala* possess a smooth protoconch of about three whorls, high axial lamellae, gently convex smooth body whorls, a well defined, thin basal cord and a thickened peristome (Kilburn, 1985).

Thiele (1929) and a number of other European workers have made *Gyroscala* subordinate to *Cirsotrema*. Clench and Turner (1951) and Abbott (1974) retained de Boury's (1887) taxonomic classification of *Gyroscala* as a subgenus of *Epitonium*. Kilburn (1985) followed the lead of Australian and Japanese malacologists and accorded *Gyroscala* full generic status. According to Nakayama (2003), the presence of a basal cord in *Gyroscala* justifies raising this epitoniid to generic level. Once *Gyroscala* was raised to generic status, a number of investigators suggested establishing subgenera. Kilburn, for example, suggested two subgenera (*Boreoscala* and *Circuloscala*), while Nakayama suggested three (*Fragiliscala*, *Pomiscala*, and *Circuloscala*). As noted earlier, Nakayama al-



**Figures 74–83.** *Epitonium kallistos* new species and *Epitonium vokesae* new species. **74–77.** *Epitonium kallistos*, apertural, lateral, abapertural, and basal views of holotype UF 44614; maximum height 6.8 mm, maximum width 2.3 mm. **78.** Magnified view of sculpture of teleoconch of UF 44614. Scale bar = 0.81 mm. **79–82.** *Epitonium vokesae*, apertural, lateral, abapertural, and basal views of holotype UF 113898, maximum height 4.3 mm, maximum width 1.6 mm. **83.** Magnified view of sculpture of teleoconch of UF 113898. Scale bar = 0.37 mm.

ready used *Boreoscala* as a subgenus for *Cirsotrema*. To further complicate the issue Weil et al. (1999) elevated *Gyroscala* to the generic level but avoided using any subgenera. Until a more comprehensive study has been done with *Gyroscala*, we have decided to retain *Gyroscala* as a subgenus of *Epitonium* as suggested by de Boury and retained by Clench and Turner.

Representatives of the subgeneric group *Gyroscala* are not very common. There are three reported living species of the subgenus *Gyroscala* in the western Atlantic. *Epitonium lamellosum* Lamarck, 1822, is found from Lake Worth, Florida, to the Lesser Antilles, as well as from France to South Africa. Recently, Garcia (2002), reported *E. lamellosum* from the Indo-Pacific to California. *Epitonium rupicola* Kurtz, 1860, is found from Provincetown, Massachusetts, in the Atlantic to the Texas coast in the Gulf of Mexico, whereas *Epitonium xenicima* Melvill and Standen, 1903, is a circum-global species (Garcia, 2006). None of the Recent western Atlantic species appear similar to the Chipola Formation species which is much more slender, lacks varices on the last whorl, has far fewer costae on the body whorls, and possesses a very distinctive, bulbous protoconch.

There are three fossil species similar to *E. vokesae*. One is *Epitonium aciculum* (H. C. Lea, 1843) which, according to Campbell (1993), was misidentified by Gardner (1948) as *E. pratti*. The species comes from the Pliocene Yorktown Formation in Virginia and North Carolina as well as the Plio-Pleistocene Waccamaw Formation in North Carolina. *Epitonium vokesae* is more slender than the Virginia and North Carolina species. In addition, it has far fewer costae on the body whorl (9 versus 16–25). The other two fossil species similar to *E. vokesae* are an unnamed specimen from the Miocene Chagres Formation of Panama (Woodring, 1959) and *Epitonium magnolianum* (Olsson, 1916) from the lower to middle Pliocene deposits from North and South Carolina and Georgia. Both the Chipola Formation and Panama fossil species lack spiral sculpturing, have low sinuous costae on the body whorls, and a suppressed basal disk. The Chipola Formation species differs from the Panama fossil in that it is much more slender and has far fewer costae on the body whorl (9 versus 21). *Epitonium vokesae* is also a much more slender species than *E. magnolianum* and lacks varices.

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# Molecular phylogeny of some Indo-Pacific genera in the subfamily Turrinae H. Adams and A. Adams, 1853 (1838) (Gastropoda: Neogastropoda)

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## ABSTRACT

We have carried out a phylogenetic analysis of a group of Indo-Pacific species in the subfamily Turrinae (Swainson, 1840) using 12S mitochondrial ribosomal RNA gene sequences. Most of the species analyzed are conventionally assigned to one of three genera, *Turris* Röding, 1798, *Gemmula* Weinkauff, 1875 or *Lophiotoma* Casey, 1904. The molecular analysis revealed that while the species of *Turris* and *Gemmula* analyzed in this study comprise monophyletic groups, the species presently assigned to *Lophiotoma* definitely do not constitute a monophyletic assemblage and can be separated into two very distinctive groups of species based on the molecular analysis. The species presently designated as *Lophiotoma tayabasensis* Olivera, 2004, *Lophiotoma panglaoensis* Olivera, 2004, *Lophiotoma indica* (Röding, 1798) and *Lophiotoma bisaya* Olivera, 2004, are related to *Lophiotoma* (*Unedogemmula*) *unedo* (Kiener, 1839 in 1834–80) by molecular criteria, and are clearly widely separated from *Turris*, *Gemmula* or *Lophiotoma* (as redefined). We propose that *Unedogemmula* (MacNeil, 1960) be recognized as a full genus: *Unedogemmula unedo* (Kiener, 1839 in 1834–80) is the type species, and the species above are transferred from *Lophiotoma* to *Unedogemmula*

## INTRODUCTION

Venomous gastropods comprise three groups: the cone snails, the auger snails or terebrids and the "turrids", classically included in a single family, Turridae (H. Adams and A. Adams, 1853); these families are generally assigned to the superfamily Conoidea (Ponder and Waren, 1988; Taylor, Käntor, and Sysoev, 1993). It has been apparent for some time that the "turrids" comprise the largest species group in the superfamily (see for example, Powell, 1966); however, the groundbreaking work of Bouchet and co-workers (Bouchet et al., 2002; 2004) in New Caledonia, has provided evidence that >90% of Conoidean biodiversity probably resides in the "turrids" (broadly defined).

"Turrids" are problematic at all levels: not only are they a megadiverse group (>10,000 species) with a large fraction of species that remain undescribed, but the phylogenetic relationships within the group are poorly understood. The number of different "turrid" genera that have been proposed is >600; although in traditional molluscan taxonomic work all turrids had been assigned to the family Turridae, in most of the more recent systematic treatments, the group has been split into 3–6 different families (Taylor et al., 1993; Bouchet and Rocroi, 2005). However, some standard taxonomic treatments retain the old nomenclature (see for example Kohn, 1998).

To complement our ongoing study of turrid venoms (see for example Watkins et al., 2006) we initiated a study of "turrid" molecular phylogeny; the first results at the generic level are reported below. The genus *Turris* Röding, 1798, is the nominate genus of the family Turridae, with *Turris babylonia* (Linnaeus, 1758) as the type species. This is an exclusively Indo-pacific genus. However, there has been inconsistency in the definition of those genera which are traditionally grouped together with *Turris* in the subfamily Turrinae. Two other groups largely from the Indo-Pacific, *Lophiotoma* Weinkauff 1875, and *Gemmula* Casey, 1904, are included in the

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subfamily by most workers; in the western Atlantic and eastern Pacific, the genus *Polystira* Woodring, 1928, is also thought to have a close affinity to *Turris* (the type species for these genera are *Lophiotoma acuta* (Perry, 1811), *Gemmula hindsiana* (Berry, 1958) and *Polystira albida* (Perry, 1811)). Additionally, a number of other groups (such as *Turridrupa* (Hedley, 1922)) are regarded as turrine by most workers.

A major motivation for these studies is to investigate the toxin genes expressed in the venom ducts of conoidean gastropods. Among the different groups of turrids, we have initially concentrated on studying the gene products expressed in the venom ducts of species in the subfamily Turrinae, since they are larger and more easily collected than are most other turrid groups. We hope to correlate the gene families expressed in venom ducts with the molecular phylogeny of the species analyzed. Thus, the molecular analysis reported below has focused on larger Indo-Pacific species in the subfamily Turrinae, e.g. *Turris*, *Lophiotoma* and *Gemmula* spp. The data that we present below demonstrates that two groups of species presently assigned to the genus *Lophiotoma*, which appear to be closely related by shell morphology, prove to be unexpectedly divergent when evaluated by molecular criteria and need to be placed in different genera.

**Table 1.** List of species analyzed in this study.

| Species | Locality |
|---|---|
| *Lophiotoma acuta* (Perry, 1811) | Buenavista, Marinduque, Philippines |
| *Lophiotoma bisaya** Olivera, 2004 | Batangas, Philippines |
| *Lophiotoma cerithiformis* (Powell, 1964) | Oahu, Hawaii |
| *Lophiotoma cingulifera* (Lamarck, 1822) | Cawoy, Olango Island, Philippines |
| *Lophiotoma indica** (Röding, 1798) | Aligway Is. Dipolog, Philippines |
| *Lophiotoma jickelii* (Weinkauff, 1875) | Cawoy, Olango Island, Philippines |
| *Lophiotoma olangoensis* Olivera, 2002 | Cawoy, Olango Island, Philippines |
| *Lophiotoma panglaoensis** Olivera, 2004 | Panglao Is. Bohol, Philippines |
| *Lophiotoma polytropa* (Helbling, 1779) | Bataan, Luzon, Philippines |
| *Lophiotoma tayabasensis** Olivera, 2004 | Sogod, Cebu, Philippines |
| *Lophiotoma unedo** (Kiener, 1839 in 1834–80) | Panglao Is. Bohol, Philippines |
| *Gemmula speciosa* (Reeve, 1843) | Batangas, Philippines |
| *Gemmula diomedea* Powell, 1964 | Sogod, Cebu, Philippines |
| *Gemmula rosario* Shikama and Hayashi, 1977 | Sogod, Cebu, Philippines |
| *Gemmula lisajoni* Olivera, 2000 | Sogod, Cebu, Philippines |
| *Gemmula sogodensis* Olivera, 2005 | Sogod, Cebu, Philippines |
| *Turris garnonsii* (Reeve, 1843) | Cawoy, Olango Island, Philippines |
| *Turris grandis* (Gray, 1833) | Sogod, Cebu, Philippines |
| *Turris normandavidsoni* Olivera, 2000 | Sogod, Cebu, Philippines |
| *Turris babylonia* (Linnaeus, 1758) | Cawoy, Olango Island, Philippines |
| *Turris spectabilis* (Reeve, 1843) | Cawoy, Olango Island, Philippines |
| *Turris totiphyllis* Olivera, 2000 | Cawoy, Olango Island, Philippines |
| *Polystira albida* (Perry, 1811) | Bay of Campeche, Mexico |
| *Drillia regius* (Habe and Murakami, 1970) | Panglao Is., Bohol, Philippines |

* These species are proposed to be transferred from *Lophiotoma* to *Unedogemmula* (see text).

## MATERIALS AND METHODS

**Specimen Collection:** Species analyzed in this study, shown in Table 1, were mostly collected by commercial shell collectors in the Philippines, except for *Polystira albida* (Perry, 1811), a generous gift of Drs. Estuardo Lopez Vera and Ed Heimer, and *Lophiotoma cerithiformis* (Powell, 1964), which was collected in Oahu, Hawaii. Specimens of each were preserved either in RNAlater® (Ambion Inc., Tx) or 95% ethanol, and DNA extracted as described below. In most cases, the digestive gland was used as the source of DNA; however, for alcohol preserved specimens where the shell had not been cracked, the digestive gland was often degraded, and DNA was extracted from foot tissue.

Identification and sequencing of clones encoding 12S mitochondrial rRNA gene segments: Genomic DNA was prepared from tissue (~20 mg) from each turrid species using the Gentra PUREGENE DNA isolation kit (Gentra Systems, Minneapolis, MN) according to the manufacturer's standard protocol. Genomic DNA from each species (~10ng) was used as a template for polymerase chain reaction (PCR) with oligonucleotides corresponding to 12S-I (5′ TGC CAG CAG YCG CGG TTA ) and 12S-III (5′ AGA GYG RCG GGC GAT GTG T) mitochondrial rRNA segments (Oliverio and Mariottini, 2001). The 5′ and 3′ primers included adapters GGAGACAU and GGGAAAGU respectively for annealing to the cloning vector pNEB206A. The PCR cycling profiles were as follows: initial denaturation (95°C, 60s); followed by 40 cycles of denaturation (95°C, 20s); annealing (55°C, 20s) and extension (72°C, 30s). The PCR products were purified using the PureLink PCR Product Purification Kit (Invitrogen Life Technologies, Carlsbad, California) following the manufacturer's suggested protocol. The eluted DNA fragments were digested with uracil specific excision reagent, annealed to pNEB206A vector (USER™ Friendly Cloning kit, New England BioLabs, Inc., Beverly, Massachusetts) and the resulting products transformed into competent DH5α cells (Sambrook and

Russell, 2001). Plasmid DNAs were isolated from ampicillin resistant colonies and the nucleic acid sequences of the inserts determined using ABI DNA sequencer with ABI Big Dye chemistry (Foster City, CA). DNA sequences have been submitted to GenBank and the accession numbers are: EF467333, EF467334, EF467335, EF467336, EF467337, EF467338, EF467339, EF467340, EF467341, EF467342, EF467343, EF467344, EF467345, EF467346, EF467347, EF467348, EF467349, EF467350, EF467351, EF467352, EF467353, EF467354, EF467355, and EF467356.

**Sequence Analysis:** Nucleic acid sequences (the longest of which had 593 nucleotides) were aligned manually using MEGA version 3.1 (Kumar, 2004). One tree was created from two independent runs using the software program MrBayes (Huelsenbeck, 2001; Ronquist, 2003). 5,000,000 trees were made in each run, 50,000 of which were saved. Two hundred and fifty of each of those 50,000 were also discarded as burn-in. Each run had four chains (one cold and three heated). The two independent runs were combined into a single tree where branches were preserved if they were found in 70% or more of those trees not discarded. The standard deviation after 5,000,000 generations was $2.401 \times 10^{-3}$. A general time reversible (GTR) model was used, with the rate variation of some sites kept invariable and the remaining rates drawn from a gamma distribution. The other tree was created using the software program PHYML (Guindon, 2003). A thousand trees were obtained using nonparametric bootstrap analysis and combined into a single tree where branches were preserved if they were found in 70% or more of the given trees. A GTR model was used, with the base frequency estimates found empirically and the proportion of invariable sites estimated. Four substitution rates were used, with the gamma distribution parameter estimated.

## RESULTS AND DISCUSSION

**PCR Amplification of 12S Sequencing:** The sequences of 12S rDNA from 23 species in the subfamily Turrinae (see Table 1) were obtained as described above. The 12S sequence of a *Drillia* species, *Drillia regius* Habe and Murakami, 1970), was used as the outgroup for the phylogenetic analysis. The sequences obtained are shown in Table 2; these were aligned for maximal overlap.

**Phylogenetic Analysis:** A phylogenetic tree, shown in Figure 1, was constructed as described under Methods. The species that are presently assigned to two of the major turrine genera, *Turris* and *Gemmula,* appear as monophyletic clades in the phylogenetic tree obtained through Bayesian methods. However, the *Lophiotoma* species analyzed clearly split into two distinct, well-separated groups.

Thus, the species presently assigned to *Lophiotoma* analyzed in this study do not appear to constitute a monophyletic assemblage. A large separation is found between two groups of *Lophiotoma* species; one group includes *Lophiotoma unedo* (Kiener, 1839 in 1834–80), *Lophiotoma tayabasensis* Olivera, 2004, *Lophiotoma panglaoensis* Olivera, 2004, *Lophiotoma indica* (Röding, 1798), and *Lophiotoma bisaya* Olivera, 2004. These species appear to be much more divergent from the *Turris* and *Gemmula* branches than the other group of *Lophiotoma*, which includes the type species of *Lophiotoma*, *Lophiotoma acuta* (Perry, 1811); the latter comprises two sub-branches, one branch including species such as *Lophiotoma cingulifera* (Lamarck, 1822), assigned by many systematists to the subgenus *Xenuroturris* Iredale, 1929, which is regarded as a separate genus by some workers (Powell, 1966).

**Generic Classification and Nomenclature:** The unexpected phylogenetic separation between two groups of species conventionally assigned to the genus *Lophiotoma*, makes the present assignment of these species into the conventional Indo-Pacific turrine genera, *Turris*, *Lophiotoma*, and *Gemmula* inconsistent with the phylogenetic tree shown in Figure 2. One potential solution would be to lump these Indo-Pacific genera together under one genus, *Turris*, and use subgeneric designations for each large clade of species (this might be called the "*Conus* alternative"; the major group of Indo-Pacific Turrinae comprise a phylogenetic branch that does not appear to be more divergent by molecular criteria than is the divergence within the species presently assigned to the genus *Conus;* Espiritu, 2001). Although this alternative may have some merit, the substantial literature referring to species in the traditional genera *Turris*, *Gemmula*, and *Lophiotoma* (including a significant paleontological component of the research literature) would make this a radical (and probably impractical) alternative.

Because *Lophiotoma acuta* is the designated type species for the genus *Lophiotoma*, the species presently in *Lophiotoma* that are in the branch not including *L. acuta* require a new generic designation. There are two generic/subgeneric designations potentially available for the group. One is a name proposed originally by Powell, *Lophioturris* Powell, 1964; Powell envisioned *Lophioturris* as a genus allied to *Lophiotoma* with *Lophiotoma indica* (Röding, 1798) as type. *Lophioturris* was set up specifically for forms that have blunt paucispiral protoconchs; since most of the species in this clade have polygyrate (multispiral) protoconchs, *Lophioturris* does not seem to be an appropriate taxonomic designation (see Powell, 1964, for a discussion of differences in protoconch morphology).

The other available generic name for this group of species (which would have priority) is *Unedogemmula* MacNeil 1960: as originally proposed, *Unedogemmula* was a separate genus, with *Undogemmula unedo* (Kiener, 1839 in 1834–80) as type. However, Powell relegated *Unedogemmula* to be a subgenus of *Gemmula*. Subse-

**Table 2.** Alignment of 12S rDNA sequences. 1. *Lophiotoma cerithiformis*. 2. *Lophiotoma cingulifera*. 3. *Lophiotoma olangoensis*. 4. *Lophiotoma tayabasensis*. 5. *Lophiotoma unedo*. 6. *Lophiotoma polytropa*. 7. *Lophiotoma jickelii*. 8. *Lophiotoma panglaoensis*. 9. *Lophiotoma indica*. 10. *Lophiotoma bisaya*. 11. *Turris totiphyllis*. 12. *Turris spectabilis*. 13. *Turris babylonia*. 14. *Turris grandis*. 15. *Turris normandavidsoni*. 16. *Turris garnonsii*. 17. *Gemmula sogodensis*. 18. *Gemmula diomedea*. 19. *Gemmula speciosa*. 20. *Lophiotoma acuta*. 21. *Gemmula lisajoni*. 22. *Gemmula rosario*. 23. *Polystira albida*. 24. *Drillia regius*.

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1  TGCCAGCAGT CGCGGTTAGA CCGAGAAATT AAGTCATAT  AAGAATGGTA AAAAGACAGT TAGAC---GT A-A-ATTGAT TTGAAGTTTT ATCT-GATTT TCTTATAGAA AAGTAAAATT TATATATAAG -AAT-ATA-A TTTAATTGAA AACTATGAAG TTGAATCTGT GATGCCCTGG AGGGAAACTG GGATTAGATA CCC [203]
2  TGCCAGCAG  CGCGGTTAGA CCGAGAAATT AAGTCATATT AAGAATGGTA AAAAGACAGT TAGACATAGT ATT-ATTAAT CTAAAGTT-T ATTT-GATTT TCTTATAAAA AAGTAAAATT TGTATATGAG -AAT-ATA-A TTTAGTTAAA AACTGTAAAG TTGAATCTGT GATATCCTGG AGGGAAACTG GGATTAGATA CCC [203]
3  TGCCAGCAGT CGCGGTTAGA CCGAGAAATT AAGTCATAT  AAAAATGGTA AAAAGACAGT TAGAC----- GTAAATTGAT TTAAAGTT-T GTCT-GATTT TCTTATAGAA AAGTAAAATT TACATATAAG -AAT-ATA-A TTTAATTGGA AACTATGAAG TTGAATCTGT GATGCCCTGG GGGGAAACTG GGATTAGATA CCC [203]
4  TGCCAGTAGT CGCGGTTACA CCAAGAAATT AAGTCATAT- TTAAATGGTA AAAAGACAGT TAGAC----- ATTAGATA-T TTAAAGC--T TTTT-GA-CC TTTTATATAG AAGTAAAATT TATATATAAA -TGT-GTA-A TTTAACAATA -GTTGTAAAG TTGAATCTGT GACAGCCTGG AGGGAAACTG GGATTAGATA CCC [203]
5  TGCCAGTAGT CGCGGTTACA CCAAGAAATT AAGTCATAT- TTAGATGGTA AAAAGACAGT TAGAC----- ATTAGATA-T TTAAAGC--T TTTT-GA-CC TTTTATATAG AAGTAAAATT TATGTATAAA -TGC-GTA-A TTTAACAATA -GCTATAAAG TTGAATCTGT GACAGCCTGG AGGGAAACTG GGATTAGATA CCC [203]
6  TGCCAGCAGT CGCGGTTACA CCGAGAAGTT AAGTCATATA AATAATGGTA AAAAGGCAGT TAGAC----- ATA-ATTAAT TTTTAGG--T TTACTTA-AC TTTTATAAAA AAGTAAAATT TGTATATAAT -TGT-ATA-T TTTAATTAAG -ACTGTAAAG TTGAATCTGC GATCGCCTGG AGGGAAACTG GGATTAGATA CCC [203]
7  TGCCAGCAGC CGCGGTTACA CCAAAGAGTT AAGTCATAT- AATAATGGTA AAAAGACAGT TAGAC----- ATA-ATT--T TT-AAGG--T TTACTTA-GC TTTTATAGAA AGGTAAAATT TGTATATAAT -TGT-ATA-T TTTAATAAAA -ACCGAAAAG TTGAATCTGT GACAGCCTGG AGGGAAACTG GGATTAGATA CCC [203]
8  TGCCAGCAGT CGCGGTTACA CCAAGAAATT AAGTCATAT  TTAGATGGTA AAAAGACAGT TAAAC----- ATTAAATA-T TCAAAG---C TTTTTGA-CT TTTTATAAAG AAGTAAAATT TATATATAAA -TGT-ATA-A TTTAACAACA -GCTGTAAAG TTGAATCTGT GACAGCCCGG AGGGAAACTG GGATTAGATA CCC [203]
9  TGCCAGCAGC CGCGGTTACA CCAAGAAATT AAGTCATAC- TTAAATGGTA AAAAGACAGT TAGAC----- ATTAAATA-C TCAAAG---C TTTTTGA CT TTTTATATAG AAGTAAAATT TATATATAAA -TGT-GTA-A TTTAACAATA -GCTATAAAG TTGAATCTGY GACAGCCTGG AGGGAAACTG GGATTAGATA CCC [203]
10 TGCCAGCAGT CGCGGTTACA CCAAGAAATT AAGTCATAT- TTAAATGGTA AAAAGACAGT TAGAC----- ATTAAATA-T CCAAAG---C TTTTTGA-CC TTTTATACAG AAGTAAAATT TAGATATAAA -TGT-GTA-A TTTAACAATA -GCTATAAAG TTGAATCTGT GACAACCTGG AGGGAAACTG GGATTAGATA CCC [203]
11 TGCCAGCAGT CGCGGTTATA CCGAGAAATT AAGTCATAT- TTTAACGGTA AAAAGACAGT TAGAC----- ATA-ATTG-T TTTAGG---T TTCTTGA-CT TCCTATAAAA AGGTAAAATT TGTATATAAT -AAT-GAA-A TTTAATTTTA AACCGTAAAG TTGAATCTGT GACAGCCTAG AGGGAAACTG GGATTAGATA CCC [203]
12 TGCCAGCAGT CGCGGTTATA CCGAGAAATT AAGTCATAT- TTTAACGGTA AAAAGACAGT TAGAC----- ATA-ATTG-T TTTAGG---T TTCTTGA-CT TCCTATAAAA AGGTAAAATT TGTATATAAT -AAT-GAA-A TTTAATTTTA AACCGTAAAG TTGAATCTGT GACAGCCTAG AGGGAAACTG GGATTAGATA CCC [203]
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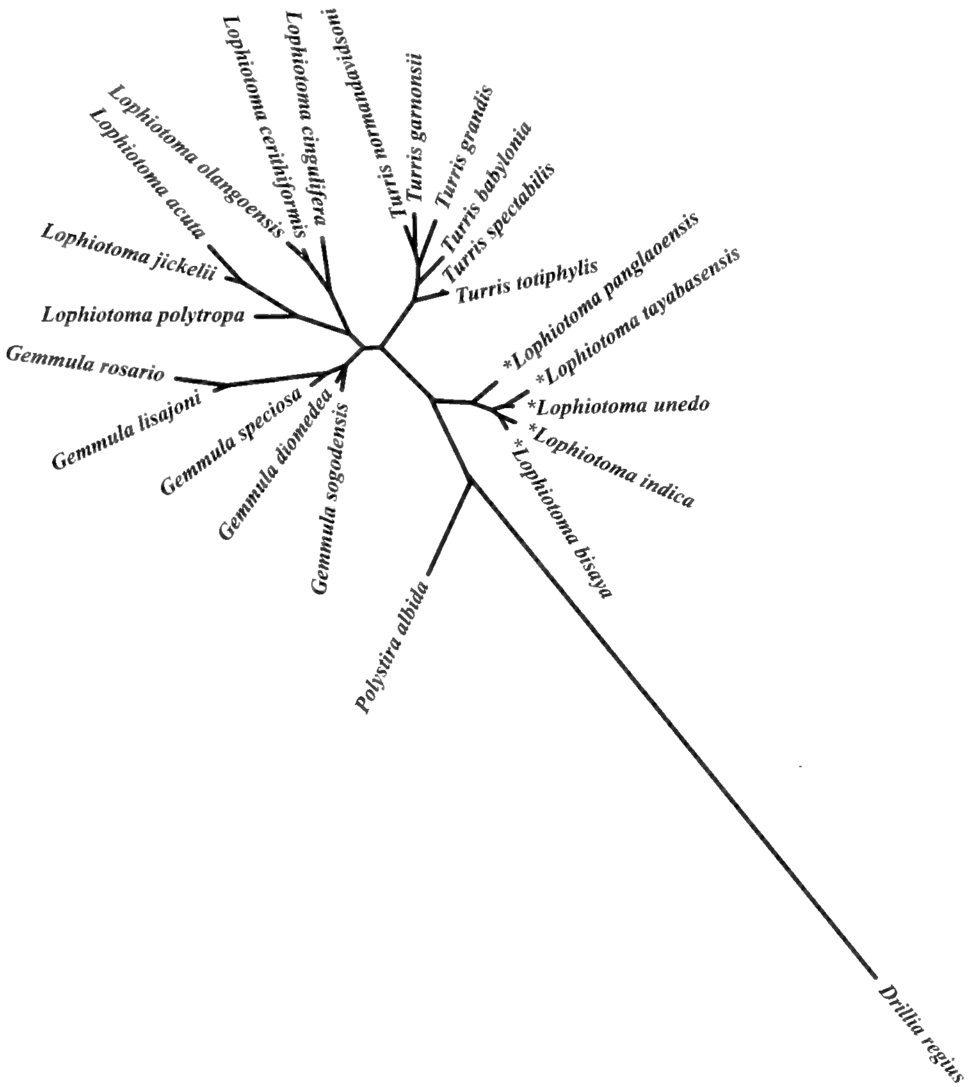

**Figure 1.** Phylogenetic tree of species listed in Table 1. A tree based on 12S rDNA sequences was constructed (see Methods). Species from three Indo-Pacific families in the subfamily Turrinae were analyzed (*Turris*, *Gemmula*, *Lophiotoma*). In addition, one Atlantic species, *Polystira albida* and a species in the subfamily Drillinae (or Clavinae), *Drillia regius* were included. Note that the species of *Lophiotoma* are split into two widely separated groups. As discussed in the text, species marked by an asterisk are proposed to be moved to another genus. *Lophiotoma jickelii* and *Turris grandis* are non-standard taxonomic assignments for the figured specimens: these are widely regarded as synonymous to *Lophiotoma acuta* and *Turris crispa*, respectively (see Powell, 1964). However, the molecular data clearly separates *Lophiotoma acuta* and *Lophiotoma jickelii*, and the type of *Turris crispa* is sufficiently divergent from the form shown that using *Turris grandis* seems a preferable name for this species.

quently, Kilburn (1983) suggested that based on general shell morphology, *Unedogemmula* seems much closer to species traditionally assigned to *Lophiotoma*, and that it should more appropriately be regarded as a subgenus of *Lophiotoma*; this suggestion has been adopted in most of the recent taxonomic treatments of turrine genera.

The molecular results reported above demonstrate that *Unedogemmula unedo* is indeed closely related to some of the species most taxonomists presently include in *Lophiotoma*, (such as *Lophiotoma indica*, *Lophiotoma bisaya*, and *Lophiotoma tayabasensis*). Furthermore, the molecular analysis clearly shows that there is no justification for designating *Unedogemmula* as a subgenus of either *Gemmula* or *Lophiotoma*, since *Unedogemmula unedo* is in a very divergent branch of the phylogenetic tree. Thus, our results support the original designation of *Unedogemmula* as a full genus, although the species comprising the genus need to be somewhat redefined. *Unedogemmula unedo* is the type species, and the larger, strongly maculated forms previously assigned to *Lophiotoma* (such as *Lophiotoma indica*, *Lophiotoma tayabasensis*, and *Lophiotoma bisaya*) are transferred to *Unedogemmula* from *Lophiotoma*. A recent analysis of Philippine forms related to these species, clarifying the relationships between these forms and the *Unedogemmula unedo* group, was recently published (Olivera,

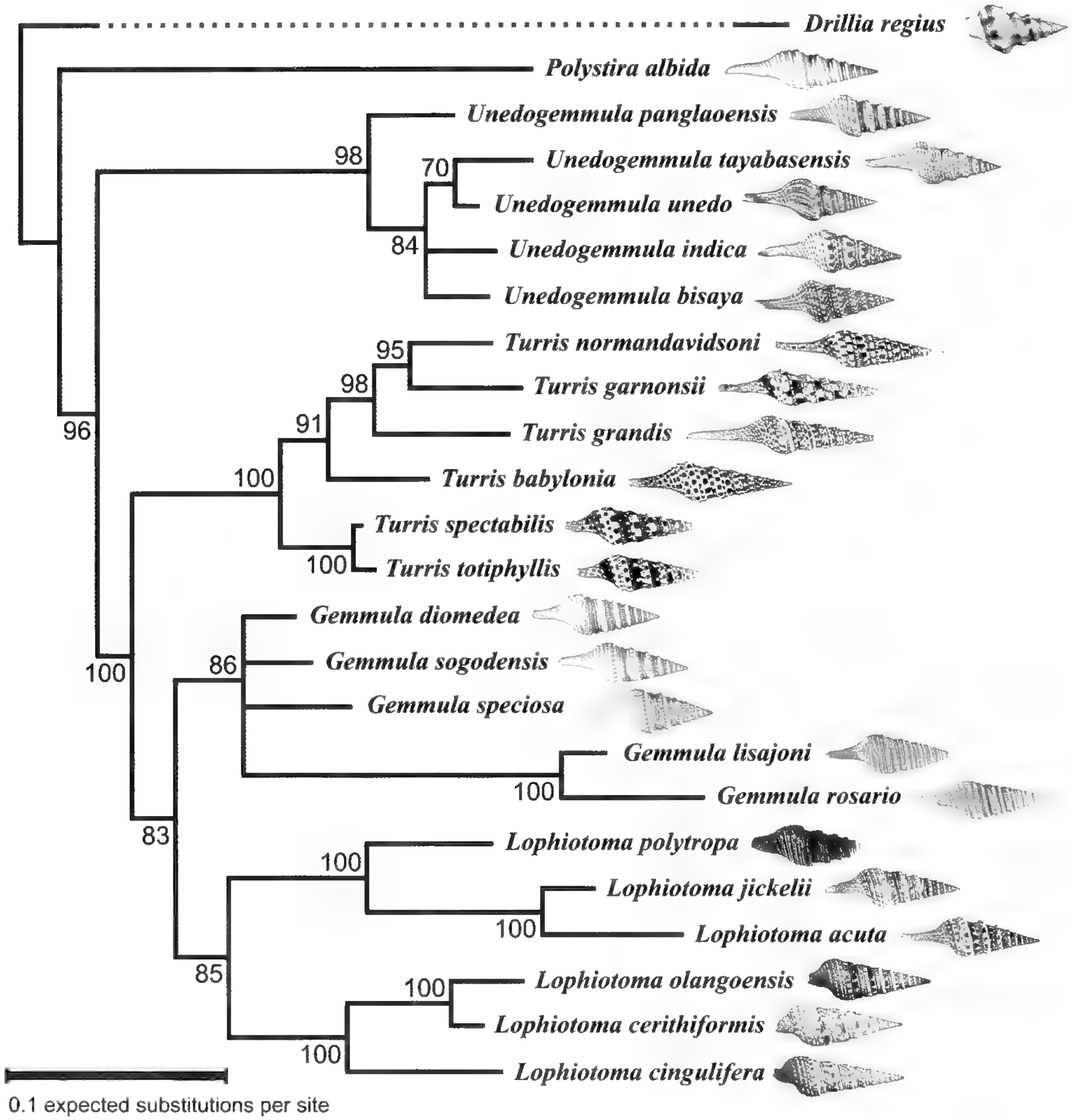

**Figure 2.** The phylogenetic tree in Figure 1 is re-plotted, except that the confidence limits are included (calculated after 10 million generations). Note that all the major groups are highly supported; as is explained in the discussion, one of the groups formerly assigned to *Lophiotoma* is now regarded as a full genus, *Unedogemmula*, with *Unedogemmula unedo* as type species; thus, in this figure, these species (still labeled *Lophiotoma* in Figure 1) are designated as *Unedogemmula* spp.

2004) it seems likely that all of the species level taxa treated in that work are properly placed in the genus *Unedogemmula*, as redefined below, although this should be verified by obtaining molecular data for those species.

### Genus *Unedogemmula* MacNeil, 1960

**Description:** Shell large, 30–105mm, fusiform with tall spire, long, straight, anterior canal unnotched. Protoconch variable from blunt paucispiral to multispiral, often with the transitional part of the larval shell decorated with brephic axials or axially costate whorls. Sinus is peripheral, deep, and narrow at the termination of the sinus rib.

**Remarks:** The genus has shell morphology with strong similarities to *Lophiotoma*; most species have a smooth peripheral keel but, in some species, there are distinct peripheral granulations. In other species, these granulations continue to the body whorl, but these tend toward obsolescence in most forms. In contrast to *Lophiotoma*, the peripheral keel does not consist of two raised cords at the edges with a depressed area in the center; rather, in some forms, there is a single smooth rib exhibiting a variable level of peripheral granulation.

In order to test the veracity of the proposals based on the Bayesian analysis and outlined above, a second approach to the phylogenetic analysis of the sequences was also carried out. A Maximum Likelihood method was employed as described under Methods. The results of this analysis are shown in Figure 3. The separation of the species described above originally in *Lophiotoma* into two distinct groups is strongly supported using this analysis. Thus, both methods support raising *Unedogemmula* to a full genus, as described above. The analyses differ, however, in the results with *Gemmula*; the maximum likelihood method does not group all of the species analyzed into a single monophyletic clade, but into two groups of species. Thus, given this discrepancy between the two methods, the monophyly of *Gemmula* clearly requires further investigation.

A brief summary of a proposed revision of Indo-Pacific genera in the subfamily Turrinae is given in Table III. The cladogram in Figures 2 and 3 give support to *Turris* and *Unedogemmula*. However, *Lophiotoma* (redefined to exclude the species transferred to *Unedogemmula*) has two branches, both strongly supported; the conjoining of the branches has less than 90% support in the Bayesian analysis, and is not supported above the cutoff level

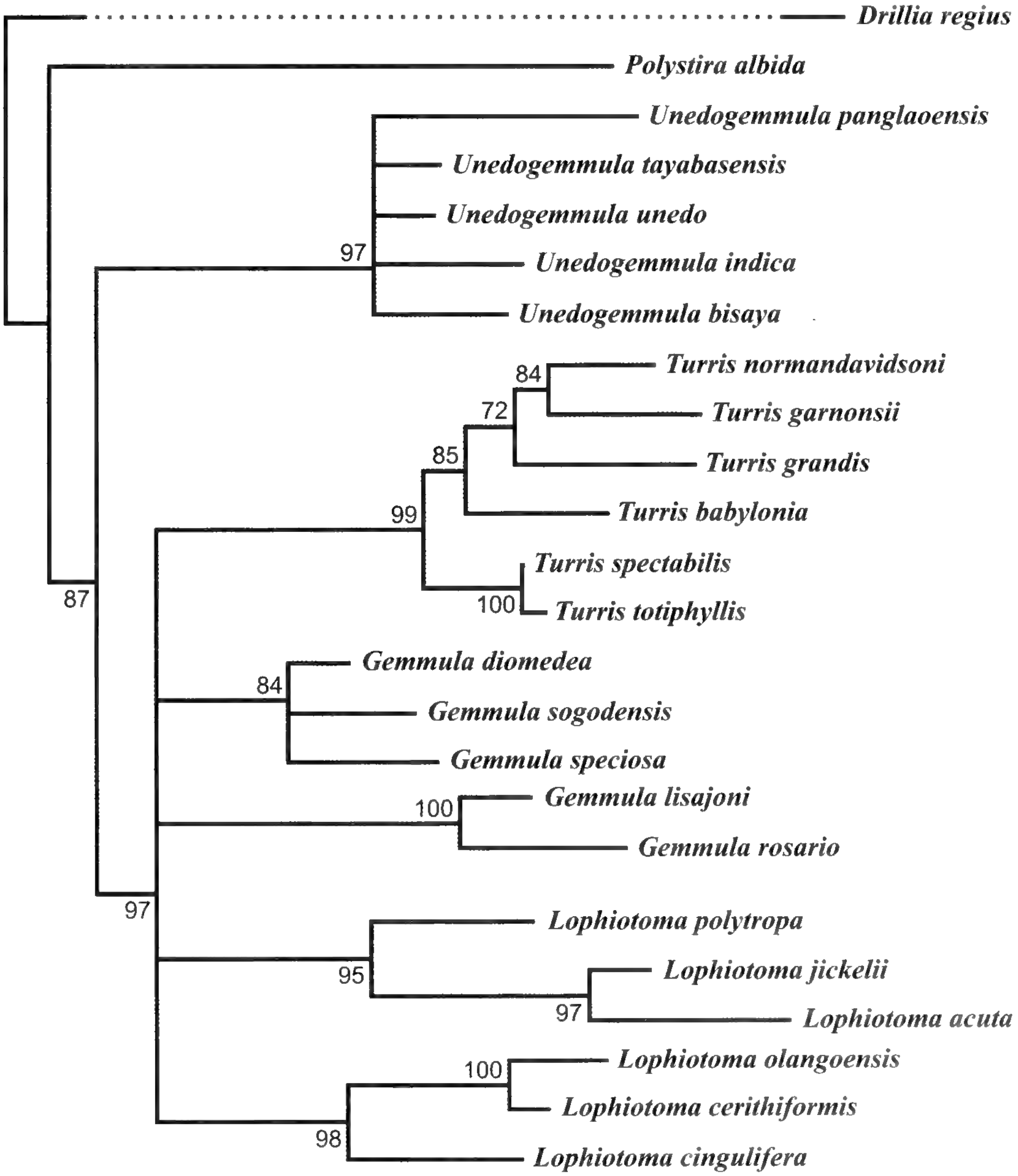

**Figure 3.** Phylogenetic tree of species listed in Table 1 This tree was made using the same sequence alignment as that used for the tree in Figure 1, but was constructed using the PHYML software program.

(70%) in the Maximum Likelihood analysis. Given these data, the solution would be to split *Lophiotoma* into two separate genera, *Lophiotoma* and *Xenuroturris*. We feel that at this time the more conservative approach of retaining the genus *Lophiotoma*, and dividing it into two subgenera, *Lophiotoma* (s.s.) and *Xenuroturris* (with *Lophiotoma* (*Lophiotoma*) *acuta* and *Lophiotoma* (*Xenuroturris*) *cingulifera* as types, respectively) is preferable until a wider range of species has been analyzed. There are a number of species (presently in *Lophiotoma*) that are problematic to assign (such as *Lophiotoma ruthveniana* (Melvill, 1923)), and we believe that a molecular analysis of these forms needs to be carried out before we fully understand the relationship between *Lophiotoma* (s.s.) and *Xenuroturris*. It may well turn out that, when the analysis is completed, the separation between the two branches (*Lophiotoma* and *Xenuroturris*) will be definitive; at that point, separating the two groups of species into different genera will be justified.

The major conclusion from this work is that *Unedogemmula* should be recognized as a full genus, and is a sister group to the major branch that includes *Turris*, *Gemmula*, and *Lophiotoma* (as redefined).

## ACKNOWLEDGMENTS

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# Reproductive biology of the nudibranch *Doris fontainei* d'Orbigny, 1835 (Gastropoda: Opisthobranchia) from the Magellanic Region

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## ABSTRACT

The present study describes the egg deposition, embryonic and larval development, and reproductive behavioral traits of the South American dorid nudibranch *Doris fontainei* d'Orbigny, 1835, observed in laboratory under controlled conditions. Behavior during copulation and spawning was recorded using a digital video camera. Copulation and spawning lasted 2–4 h and 22–23 h, respectively. The spawned mass reached 1.80 m in length and was coiled in a counter-clockwise direction from the centre with one edge affixed to the substrate. The ribbon contained numerous small capsules, each having 2–4 eggs of about 86 μm in diameter. Intracapsular egg development lasted about 14 days at 14.5°C, culminating with the release of up to 1.25 million veliger larvae per egg mass. The new veliger larvae showed incipient development of the foot and a relatively small protoconch (ca. 158 μm), indicating they enter a planktotrophic phase. A comparison with other nudibranchs, and particularly with dorids, suggests that *D. fontainei* has an annual cycle whose egg mass fits a morphological pattern typical of the family. The characteristics of its encapsulated development show it is one of the most fecund species among those having this pattern, which also explains, in part, its geographical dispersion from Peru in the Pacific to northern Argentina in the Atlantic.

*Additional Keywords:* Nudibranchia, reproductive behavior, multiple embryos, planktotrophic development

## INTRODUCTION

An interesting characteristic of nudibranch gastropods is their capacity to produce conspicuous and delicate egg masses, which can be obtained in laboratory through adequate maintenance of adult individuals. The pattern of early development of these egg deposits is a basic trait in the life histories of the different species. These patterns, which can be determined through observations under controlled conditions, may also provide new elements to better typify and distinguish species whose taxonomic status is still debated.

Hurst (1967) has grouped the egg deposits of opisthobranchs into three morphological types in accordance with the morphology of the ribbon, mode of attachment, and alignment of the capsules. However, Thompson (1967) defined three developmental larval strategies: planktotrophy, lecithotrophy, and direct development.

Although there is general knowledge about egg deposition and definition of some developmental parameters for different species worldwide, the reproductive biology of the rich and diverse nudibranch assemblages inhabiting the coasts of South America is still poorly known. *Doris fontainei* d'Orbigny, 1835, is a widely distributed and common nudibranch from the South American coast. This sea slug inhabits the extensive littoral fringe of the SE Pacific (Peru and Chile), spanning the entire Magellanic region, to latitude 38°S in northern Argentina, following cold Antarctic currents to depths of 70 m (Muniain et al., 1991; Muniain, 1997; Schrödl, 1997a, b; 2000). As with other dorids occurring along this stretch of coastline, *D. fontainei* has been subjected to several taxonomic revisions, including a recent re-assignment based on detailed anatomical studies (Valdés and Muniain, 2002).

An exploratory sampling for nudibranchs on the coast near Valdivia, Chile (40°S), allowed us to collect and maintain living specimens of *D. fontainei* in the laboratory and observe their reproductive behavior, including copulation, spawning, some aspects of individuals behavior after completion of egg deposition, and planktotrophic larval stage.

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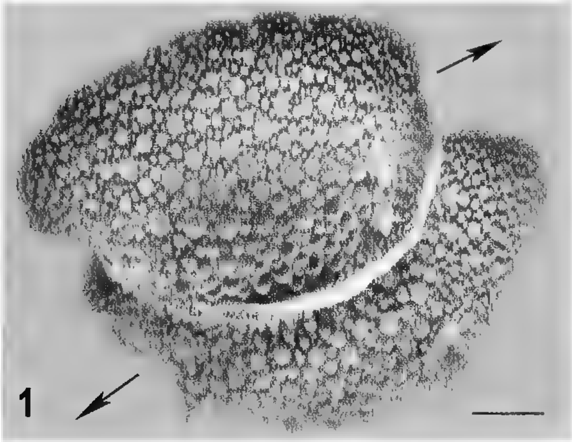
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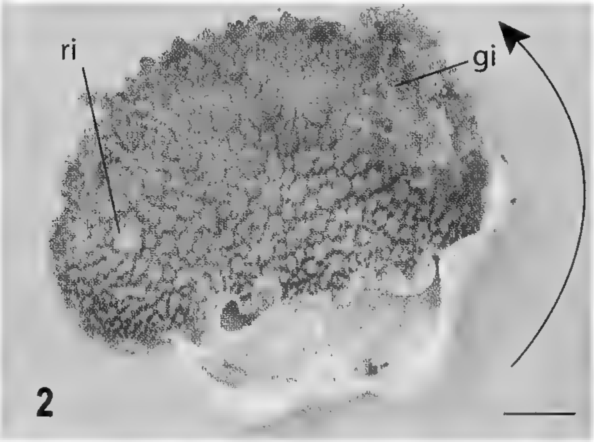
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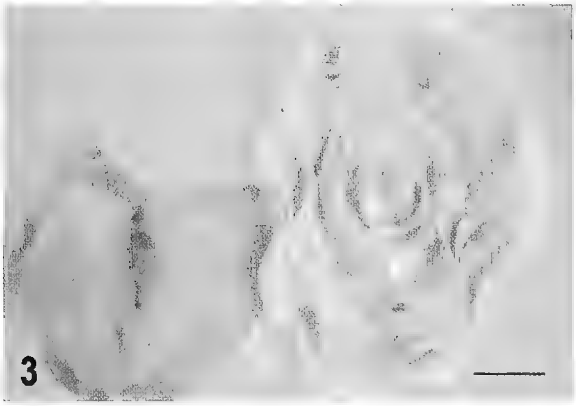
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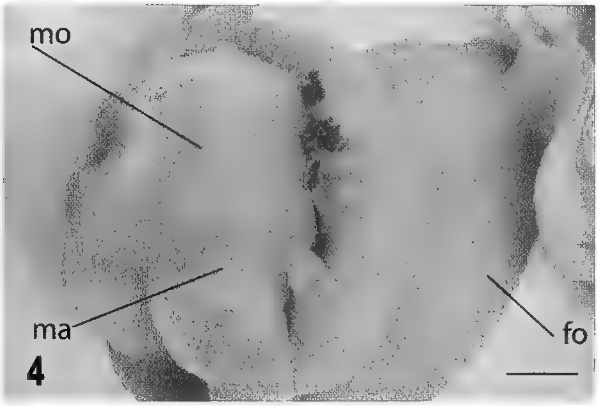
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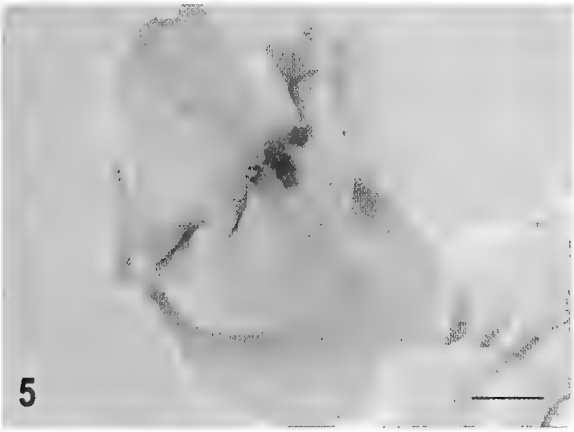
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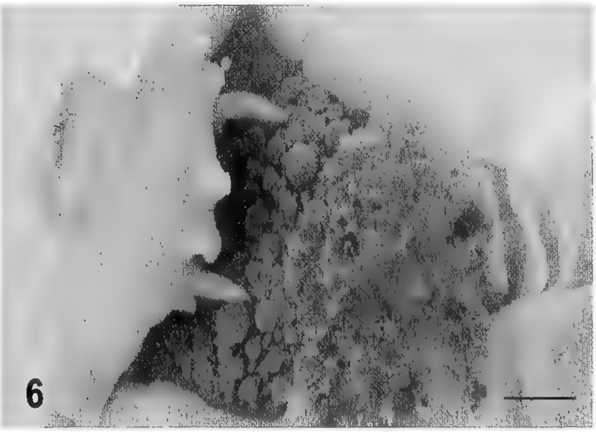
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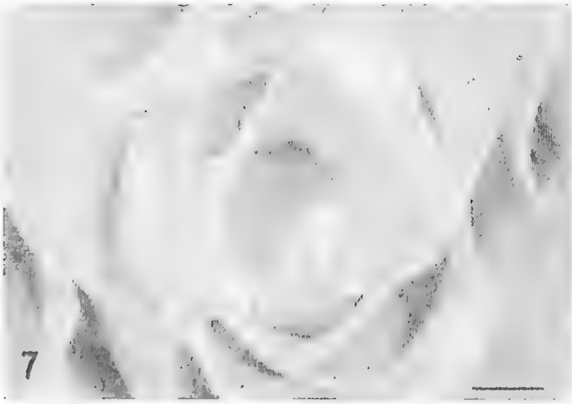
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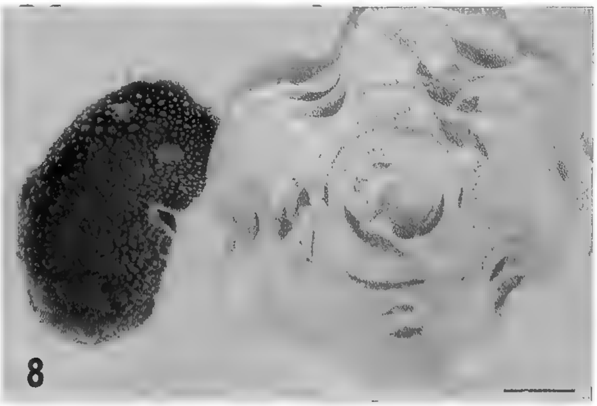
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## MATERIALS AND METHODS

A total of six specimens of *Doris fontainei* were collected from Los Molinos (40°S), Valdivia, (Chile), by scuba diving to depths of 3–6 m from 4–16 March 2001. The water temperature at the sampling site was 14–15°C. To obtain information on the copulatory and reproductive behavior of *Doris fontainei*, the specimens were maintained in aquaria containing aerated seawater at approximately 14.5°C, at the Zoological Institute of the Universidad Austral de Chile, Valdivia. Egg masses deposited on the aquarium walls were cultured in the original container without dislodging the egg mass. Routine isothermal seawater changes were made daily with water filtered to 1 μm. Egg development was monitored until hatching. Egg samples were preserved in 6% formalin in seawater for further microscopic studies, which included counting and measuring the capsules and the eggs and embryos contained inside them. Most of the information presented in this study was recorded by photography and digital video during maintenance of living individuals. Complementary observations were made using preserved material. Voucher material was deposited in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" under accession number MACN 36542.

Egg deposits were described from macroscopic observations as well as using a Zeiss Axiostar stereoscopic microscope equipped with a digital camera and imaging software at Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". The number of eggs per capsule were determined using repeated counts in randomly chosen locations throughout of the egg ribbon. Development was observed under microscope and each developmental stage illustrated, particularly that of the trocophore and middle veliger; mean numbers of embryos per capsule, and their size relation to the size of the capsule were calculated. Capsular volume (V) was determined (in $\mu m^3$) based on measurements of capsular length and width, assuming that the depth axis was equivalent to the width axis. The radii ($r_1$, $r_2$, $r_3$), and the volume was calculated using the formula:

$$V = 4/3\pi \times r_1 \times r_2 \times r_3.$$

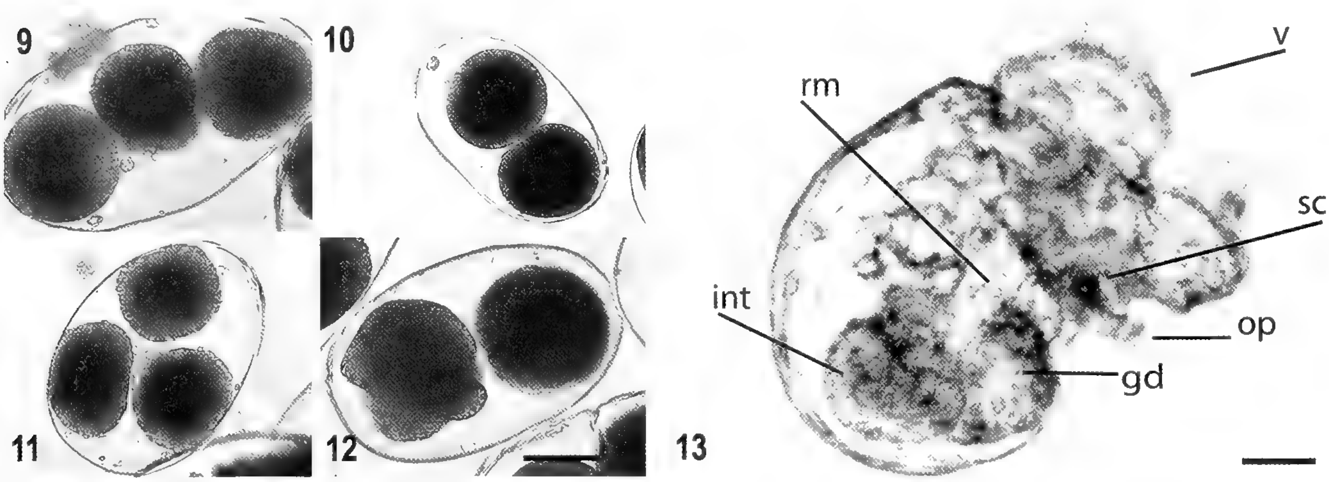
Sixty capsules previously separated in groups according to the number of embryos they contained were randomly extracted from the gelatinous matrix and measured as mentioned above.

The diameters of 40 eggs at the unsegmented zygote stage were measured. Descriptions of the development included three embryonic stages: trochophore, middle to advanced veliger, and pre-hatching veliger; each stage was photographed and measured (n = 30). The total number of eggs in a deposit was estimated indirectly by counting egg capsules in two different 5 mm-wide segments of the egg ribbon. For this purpose representative segments of the ribbon were isolated by cutting them with a scissor and carefully extracting individual capsules from the gelatinous matrix of each segment. The mean number of eggs per cm of egg ribbon was determined, and the total number of eggs in the deposit was calculated based on the length of the entire ribbon. The ribbon length was determined by measuring the length of its unattached free edge from the photographic images, taking into account the photo scale. The approximate number of embryos in the egg ribbon was estimated multiplying the number of egg capsules by the average number of embryos they contained; the total number of embryos was estimated following the same procedure as for eggs. The development period was determined in an egg deposit maintained under controlled temperature, and was considered to start at egg deposition and finish at the initiation of hatching. Recently hatched larvae were observed under stereoscopic microscope.

## RESULTS

**Copulatory and Spawning Behavior:** Copulation and post-copulation behavior of two of the six specimens collected and maintained in aquaria was observed (Figures 1–8). During copulation, nudibranchs had the right sides in contact at the level of the genital openings, with the heads in opposite directions (Figure 1). Copulation lasted between 2 and 4 hours, with the animals in total contact; penises were not visible because they were obscured by the mantle, although there was a conspicuous penial papilla, as described by Muniain et al. (1991) and Valdés and Muniain (2002). One individual of 76.2 mm in length began to spawn in a counter-clockwise direction (sinistral) at 16:00 h on 13 Mar. 2001 and finished at 15:00 h on 14 Mar. 2001 (23 h) at a temperature of 14.7°C. During spawning, movement was very slow, with the rhinophores contracted within the sheaths and the branchial tuft exposed but motionless. Following deposition of the egg mass in the center of the aquarium, the nudibranch slowly moved to one side. A second specimen, 64 mm in length, began to spawn two hours after collection on 16 Mar. 2001, showing sinistral oviposition, and terminated at 11:00 on 17 Mar. 2001, after a total spawning time of 22 h (Figure 2). Following complete spawning, the slug remained almost immobile, contracting and completely invaginating very slowly, with only the posterior portion of the foot adhered to the

**Figures 1–8.** *Doris fontainei* d' Orbigny, 1835, reproductive behaviour captured from digital video. **1.** Copulation maintained in aquaria. Scale bar = 1 cm. **2–3.** Specimens showing sinistral oviposition (counter-clockwise direction). Scale bars: Figure 2 = 1 cm; Figure 3 = 1.5 cm. **4.** Detail of the post-spawned behavior. Scale bar = 1 cm. **5.** After half and hour immobile, the nudibranch slowly returning to a normal position. Scale bar = 0.5 mm. **6.** Detail of rhinophores and gills exposed again. Scale bar = 1 cm. **7.** Detail of the free border and scattered spaces of the spiral ribbon. Scale bar = 2 cm. **8.** Complete spawn, specimen (64 mm). Scale bar = 1.5 cm. Abbreviations: **gi,** gills; **ma,** mantle; **mo,** mouth; **ri,** rhinophores; **fo,** foot



**Figures 9–13.** *Doris fontainei* d' Orbigny, 1835. **9–12.** Details of the ovoidal capsule with 2 and 3 eggs. The volume of the capsule increases with the number of embryos, 3 embryos is the most common number. Scale bar = 45 μm. **13.** Hatching planktotrophic larva, right lateral view. Typical coiled shell (type 1, Thompson, 1961). Scale bar = 25 μm. Abbreviations: **int,** intestine; **op,** operculum; **rm,** retractor muscle; **sc,** statocyst; **v,** velum.

substrate (Figures 3, 4). The ventral surface of the mantle completely covered the organism, which raised so as to show the anterior portion of the foot. The nudibranch remained in this position for about half an hour (Figure 5), slowly returning to a normal position, extending the rhinophores, unrolling the mantle, and slowly crawling away from the egg deposit (Figure 6). This behavior was completely recorded with digital video from 11:00 to 12:10 hrs on 17 Mar. 2001 (Figure 8).

**Egg Mass and Larval Development:** The egg mass formed a spiral ribbon of concentric rings consisting of five to seven revolutions around a central point (Figures 3, 8). The free border of the ribbon was undulated, unlike the attached border, which was straight (Figure 7). The undulations of the free border coincided with concentric rings of the ribbon. Both the egg deposits obtained in the laboratory and those collected in the field were pink. The latter were typically positioned under rocks or in shaded areas.

The egg mass exhibited some mucous areas without egg capsules (Figure 7). The egg capsules were arranged linearly along the spiral ribbon, and were joined by a fine cord (chalaza) that served to maintain the spiral configuration. Randomly scattered spaces without capsules occurred in the egg ribbon and in its different median portions. The egg deposit from the 64-mm specimen was formed in six revolutions around the center, with a maximum diameter of 10 cm; it was 13.4 mm in height, and an estimated 1.8 m in length (Figure 8).

Mean egg diameter was 86.5 ± 4.7 μm. The capsules contained multiple embryos, although single embryos appeared occasionally. The number of embryos in capsules ranged from 2 to 5, 3 embryos being clearly the most common number (Figures 9–12). The first count based on 338 capsules, containing trochophores, gave an average number of 3 embryos per capsule. A second count, of 361 capsules (containing intermediate veligers), produced an average number of 3.18 embryos per capsule. The average of the 2 counts was about 3.1 embryos per capsule.

The capsules tended to be ovoid, exhibiting some more irregular shapes when crowded. The volume of an egg capsule increased with the number of embryos it contained (Figures 9, 11). As expected, the eggs demonstrated typical spiral cleavage. Measurements of the different stages were as follows: trochophore = 99.35 ± 5.5 μm (n = 20), advanced encapsulated veliger = 116.25 ± 12.55 μm (n = 20), and hatched veliger larva = 158.1 ± 7.16 μm (n = 10). Hatching of typically planktotrophic veligers began 14 days after incubation, at an average temperature of 14.5°C. These veligers measured a mean of 150 μm (n = 20) in prostomial length, with the protoconch sinistrally coiled, with ¾ to 1 whorl at hatching. At hatching, the larvae had no eyes nor propodium rudiment, although the velum, velar retractor muscle, larval kidney, nephrocysts, operculum, and cephalopedal alimentary apparatus were developed (Figure 13).

The total number of larvae released from the egg mass was estimated indirectly through observations under controlled conditions. Microscope-aided counts carried out on 2 transects of the egg ribbon showed an average of 2236 egg capsules per cm. With an estimated length of ca. 1.8 m (indicated above), the entire egg deposit contained about 402480 capsules, and with the above estimate of 3.1 embryos per capsule, the entire egg deposit contained about 1.25 million embryos, resulting in the same number of developed planktotrophic veliger larvae a few days later.

## DISCUSSION

The present study describes some of the traits that typify the life history of *D. fontainei*, specifically in regard to its reproductive pattern. Its relatively large body size suggested *a priori* that the species would have an annual cycle, with one generation per year, and the spawning characteristics fell into Class A, following the classification and corresponding attributes of dorid nudibranchs provided by Hurst (1967).

The characteristics of the encapsulated development described in the present study agree with the embryonic developmental pattern observed in most of the Doridacea, based on information summarized by Thompson (1967) that typifies the three basic developmental stages observed in that group of nudibranchs. The embryonic development observed in *D. fontainei* fits Type-1 pattern of this scheme. Free planktotrophic larvae are released at hatching, there are multiple relatively small embryos per capsule, and the period of embryonic development leading to hatching of weakly developed veliger larvae is comparatively short.

Based on information on related species (Thompson, 1958; 1967; Strathmann, 1987; Goddard, 2005) most dorids with planktonic life cycles have eggs ranging between 60 and 130 μm in size, many of which are in the 70–90 μm range, in agreement with values found for *D. fontainei*. There is also agreement in the number of embryos produced per spawning, with values as high as several hundred thousand embryos per spawning in the most fecund species, such as *Acanthodoris pilosa* (Abildgaard, 1789) and *Archidoris pseudoargus* (Rapp, 1827) (both reviewed by Thompson, 1967). Accordingly, *D. fontainei* is a highly fecund dorid, given that it produces over a million eggs per spawning. This notably exceeds the numbers reported for other species in the group; the closest species is *A. pseudoargus*, which spawns 645000 eggs (Colgan, 1914, cited in Thompson, 1967). The duration of embryonic development (pre-hatching) in planktotrophic species can be as short as 6 to 10 days, and rarely exceeds one month (Thompson, 1967). The development period of 15 days found for *D. fontainei* falls within the range expected for dorids with planktotrophic development. Another trait coinciding with the Type-1 pattern of development are the characteristics and degree of development of the veliger larvae hatched from the egg deposits of *D. fontainei*. As Thompson (1967) and Todd et al. (2001) mentioned for species showing this pattern, typical characteristics include absence of eyes or propodial rudiment, but presence of a developed velum, retractor muscle, larval kidney, operculum, and cephalopedal digestive system, which were the most notable traits observed by us.

Based on observations of lecithotrophic dorids of the genera *Adalaria*, *Dendronotus*, *Discodoris*, *Tritonia* (Thompson, 1958; 1961; 1962; 1976; Gohar and Abul-Ela, 1959; Roginsky, 1962; Todd, 1979) and of the direct-developing species *Cadlina laevis* Linnaeus, 1767 (Roginsky, 1962; Thompson, 1967), the eggs are 200 and 400 μm in size, respectively, and the total number of embryos per spawn is clearly lower (aprox. 15000 to 50000), reaching only a few hundreds in species with direct development.

As indicated above, it is clear that *D. fontainei* has multiple embryos per egg capsule, but given the lack of information, we do not know if this condition is common within Doridacea, although Thompson (1967) mentions it as a frequent characteristic among the opisthobranchs that have planktotrophic larvae and Type-1 development. Among the studies of reproductive aspects in other species of Magellanic opisthobranchs, the presence of multiple embryos was noted in the saccoglossan *Elysia patagonia* Muniain and Ortea, 1997, which completes development with the formation of planktotrophic larvae (Muniain and Ortea, 1997; Muniain and Penchaszadeh, 2000; Muniain et al., 2001).

Given the large number of embryos that *D. fontainei* produces, enclosure of more than one embryo per egg capsule is probably an efficient mechanism for reducing the energetic cost of these egg masses compared to the relatively large benefits of maximizing the numbers of larvae generated per spawning.

Although there is little information available on some species in this region, the development of *D. fontainei* can be compared with that of other dorids that occur on the Chilean coast, such as *Peltodoris marmorata* (Bergh, 1898) (cited as *Anisodoris rudberghi*). It has eggs of 80 μm in diameter and a larger number of eggs per capsule (5–23), as well as a pre-hatching veliger of 125 μm in length, and its embryonic development occurs in only 10 days at 14–16°C (Brokordt, 1992).

The large number of larvae produced by *D. fontainei* suggests a possibly high degree of larval mortality and, associated with this, a potentially effective mechanism for extensive larval dispersal. Wide dispersal can maintain gene flow among populations as well as the extensive geographical dispersal (Schrödl, 1997a, b; 2000; Valdes and Muniain, 2002) shown by this nudibranch in comparison with other species on the South American coast.

There are no records in the literature of detailed observations on the behavioral mechanisms accompanying spawning of nudibranchs. The intriguing post-hatching behavior shown by a specimen of *D. fontainei* in the present study deserves further laboratory research with a higher number of individuals to determine whether behavior has a given pattern at this stage of the reproductive process.

The duration of the spawning process (22–23 h) associated with the relatively long, highly fecund egg ribbon of *D. fontainei* may imply the generation of some form of physiological imbalance, which the animal strives to overcome through the behavioral event observed at the culmination of oviposition. Whether this behavior results from an inordinate energy demand compared to that occurring in other species of nudibranchs is unknown. Evaluations made in prosobranchs have shown the high relative energetic cost involved in making benthic egg masses (Perron, 1981; 1982).

Studies on the chemical ecology of this species have shown that it biosynthesizes repellent compounds that accumulate only in the mantle tubercles (Muniain, 1997

Gavagnin et al., 1999). If this behavior is confirmed under laboratory conditions, further studies should also evaluate its possible occurrence in natural conditions, where the nudibranch would be exposed to predation throughout the entire stage.

Nudibranchs can be considered semelparous (despite spawning repeatedly in a season) in that once they have reached maturity, their period of spawning is inevitably followed by apparent genetically programmed post-reproductive death (Todd et al., 2001). Therefore, reproduction must be fully successful in the single opportunity presented to these animals, which will probably not be able to survive until another reproductive season to repeat the process. Such is the high cost of reproductive activity for the individual. The broad geographic distribution of *D. fontainei* makes it a useful species for future studies of possible geographic variations in its pattern of embryonic development. Further studies including related nudibranch species in the region should be conducted. For example, studies of the dorid *Adalaria proxima* (Alder and Hancock, 1854) have shown that the egg diameter and other embryonic and larval traits could show intraspecific variation, reflecting the adjustment of its populations to a given range of variability in environmental conditions where the species is distributed (Jones et al., 1996; Todd et al., 2001).

## ACKNOWLEDGMENTS

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# Two new modern records of the southern oyster drill *Stramonita haemastoma floridana* (Conrad, 1837) in Chesapeake Bay, USA

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## ABSTRACT

Live southern oyster drills, *Stramonita haemastoma floridana* (Conrad, 1837), have been collected from two Chesapeake Bay western shore tributaries. Four specimens were collected between Brown Shoal and Thomas Rock in the lower James River in February 2005. Thirteen live southern oyster drills were collected from Back River in April 2006. Identification of these drills as *Stramonita haemastoma floridana* has been confirmed using DNA bar-coding data. Southern oyster drills collected in Chesapeake Bay are genetically nearly identical to populations from the Atlantic coast, and differ significantly from populations from the Azores and from the Gulf of Mexico. These collections mark the first reported records of live southern oyster drills from within the Chesapeake Bay estuary. It is unknown if these drills represent isolated introductions or expansions of the northern range this species. Water temperature patterns in Chesapeake Bay and the Mid-Atlantic Bight from 1990–2005 are similar to those observed in the late 1950s when *Stramonita haemastoma floridana* was first found living in Chincoteague Bay, Maryland.

*Additional Keywords:* Range extension, water temperature, Cape Hatteras, zoogeography, DNA bar-coding

## INTRODUCTION

The southern oyster drill *Stramonita haemastoma floridana* (Conrad, 1837) is a predatory gastropod typically found in association with populations of the oyster *Crassostrea virginica* Gmelin, 1791 (e.g., Burkenroad, 1931; Butler, 1985). A population from the Atlantic coast of the United States was described as *Purpura floridana* Conrad, 1837, but later regarded to be a subspecies of the broadly ranging *Stramonita haemastoma* (Linnaeus, 1767), a morphologically diverse taxon that has been reported to span the temperate and tropical coasts of the eastern and western Atlantic as well the eastern Pacific.

The name *Stramonita haemastoma haemastoma* (type locality: Tenerife, Canary Islands, fixed by Clench, 1947: 76) has been applied to the populations ranging from the Channel Islands southward to Senegal, the western Mediterranean, the Madeira, Canary and Cape Verde Islands in the eastern Atlantic (Clench, 1947: 76; Poppe and Goto, 1991: 141), the Azores (Morton et al., 1998), Trinidad southward to Uruguay in the western Atlantic (Clench, 1947: 76), and from Baja California southward to Peru in the eastern Pacific by some (e.g., Clench, 1947) but not all (e.g., Keen, 1971: 549) researchers. *Stramonita haemastoma floridana* (type locality: Hypoluxo Island, Lantana, Florida, see Clench, 1947: 77) was reported to range from North Carolina southward to Yucatan and the West Indies, and throughout the Caribbean as far south as Trinidad (Clench, 1947: 76), or extending to Brazil (Abbott, 1974: 180). The name *Stramonita haemastoma canaliculata* (Gray, 1839) (type locality originally but erroneously listed as China) has been applied to a distinctive morphological variant prevalent throughout the Gulf of Mexico (e.g., Abbott, 1974: 180). Some three dozen names have been variously partitioned and synonymized for the many geographically circumscribed shell phenotypes belonging to the *Stramonita haemastoma* complex (see Rosenberg, 2005).

North American records of *Stramonita* have generally been divided into two subspecies, *Stramonita haemastoma floridana* from the Atlantic coastline, and *Stramonita haemastoma canaliculata* from the Gulf of Mexico; such division is based on shell characters (Abbott, 1974; Butler, 1985). *Stramonita haemastoma canaliculata* has been differentiated morphologically on

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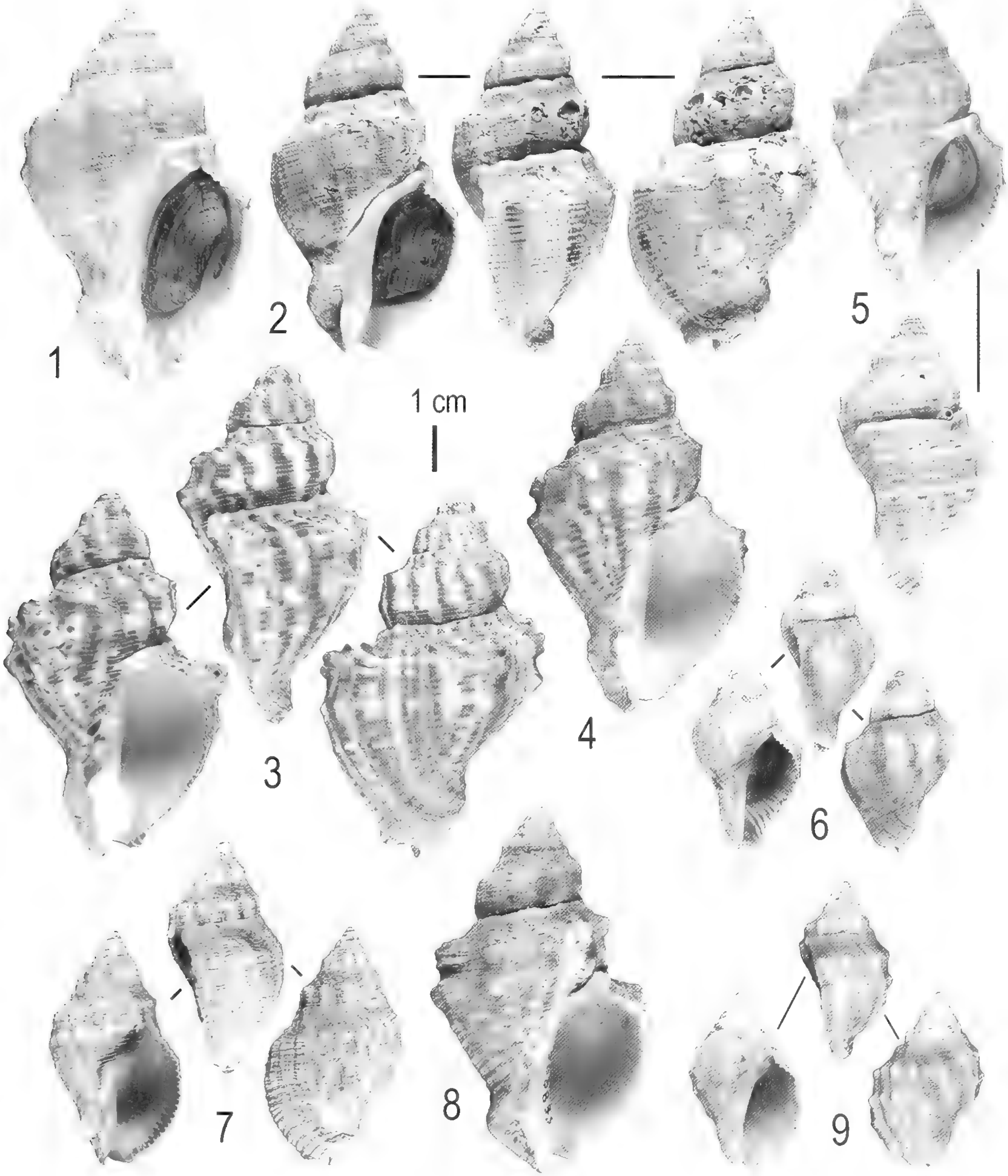

**Figures 1–9.** *Stramonita* spp. **1–6.** *Stramonita haemastoma floridana* (Conrad, 1837). **1.** USNM 618840, Willis Wharf, Hog Island Bay, Northumberland Co., Virginia, trapped in 2.4 m depth. September 15, 1955, ex-F. W. Sieling. **2.** USNM 1091020, oyster reefs just below Deep Creek, Lower James River, Virginia, in approximately 3 m, February 2005. **3.** Male and **4.** female specimen, USNM 1091021, Back River, Virginia, in commercial crab pots set in 3 m, April 2006. **5.** USNM 416874, Fort Macon, North Carolina. **6.** USNM 1099258, Sand bar on north side of Fort Pierce Inlet, E of Little Jim Island, Ft. Pierce, Florida. 6 August 2004. **7.** *Stramonita canaliculata* (Gray, 1839). USNM 1099259, St. Andrews Bay, Florida, rip-rap near campsites. **8.** *Stramonita haemastoma haysae* (Clench, 1927). USNM 568834, Barataria Bay, Louisiana. **9.** *Stramonita haemastoma haemastoma* (Linnaeus, 1767). USNM 1099260, intertidal rocks. Vila Franca do Campo, São Miguel, Azores, 26 July 2006.

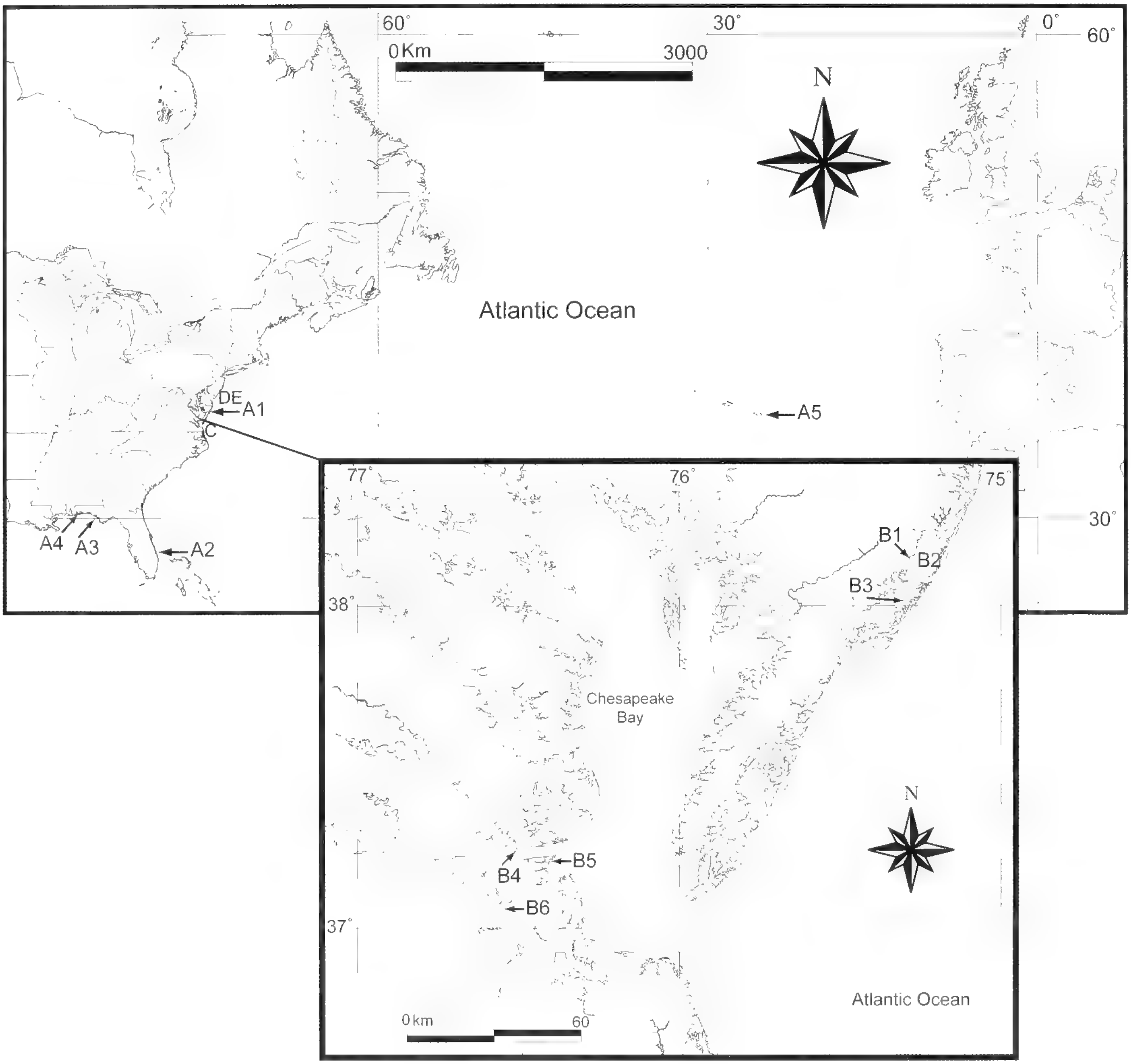

**Figure 10.** Map of the Atlantic Ocean depicting the southeastern coast of the United States, Chesapeake Bay region [inset], and the Azores Islands, showing collection sites for *Stramonita* specimens and water-temperature data. Sites are identified as follows: Delaware lightship and buoy stations (DE), Chincoteague, VA (A1), Chesapeake lightship and buoy stations (C), Fort Pierce Inlet, FL (A2), St. Andrew's Bay, FL (A3), Pensacola, FL (A4), and São Miguel, Azores (A5). Within the Chesapeake Bay region Chincoteague, VA (B1), Maryland DNR monitoring station XBM1849 (B2), Maryland DNR monitoring station XBM 1301 (B3), Virginia Institute of Marine Science, Gloucester Point, VA (B4), Back River, VA (B5), James River near Deep Creek (B6).

the basis of its larger size, presence of strong, rugose shoulder nodules, and its deeply channeled suture. Several authors (e.g., Butler, 1954; Gunter, 1979; Walker, 1982) had reported that differences in shell morphology are neither consistent nor concordant with geographical patterns and concluded that subspecific distinction was not warranted. More recently, Liu et al. (1991) confirmed that characters of shell and radula were not taxonomically informative, but demonstrated that *Stramonita* from the northern Gulf of Mexico could be differentiated from populations of the Atlantic coast at "a level that is characteristic of congeneric species" using allozyme electrophoresis. Other recent studies have explored the effectiveness of the east Florida ecotone as a barrier to gene flow between Atlantic and Gulf coast populations for a variety of taxa (for reviews, see Avise, 2000; Wise et al., 2004). Vermeij (2001: 701) reviewed the Recent and fossil species of *Stramonita*, and suggested that the *Stra-*

**Table 1.** Samples of *Stramonita* spp. used in this study.

| Taxon | Locality | Voucher specimens USNM | Number of specimens sequenced | GenBank accession number |
|---|---|---|---|---|
| *Stramonita canaliculata*(1) | Pensacola, FL | 888709 | 1 | U86330 |
| *Stramonita canaliculata* | St. Andrew's Bay, FL | 1099259 | 1 | EU073061 |
| *Stramonita haemastoma haemastoma* | São Miguel, Azores | 1099260 | 2 | EU073051–EU073052 |
| *Stramonita haemastoma floridana* | Ft. Pierce Inlet, FL | 1099258 | 2 | EU73053–EU073054 |
| *Stramonita haemastoma floridana* | Deep Creek, VA | 1091020 | 3 | EU073055–EU073057 |
| *Stramonita haemastoma floridana* | Back River, VA | 1091021 | 3 | EU073058–EU073060 |

(1) Sequence data from Harasewych et al., 1997

*monita haemastoma* complex may consist of as many as four western Atlantic and two eastern Atlantic species. He also noted similarities (bifid crenulations along the outer lip) between some specimens of *S. canaliculata* and *S. bifida* Vermeij, 2001, from the Cantaure Formation (early Miocene, Venezuela).

Although the northern limit of *Stramonita* along the eastern United States has generally been reported as Oregon Inlet, North Carolina (Wells and Grey, 1960; Butler, 1985), living individuals (Figure 1) and recent historical specimens (empty shells) were collected from locations in the Maryland and Virginia waters of Chincoteague Bay (Figure 10, A1) in 1955 and 1956 (Sieling, 1955; 1960), extending the northern range boundary for this animal along the US Atlantic coast. Sieling (1960) suggested that the southern oyster drills were introduced into Chincoteague Bay with transplanted oysters. Subsequent surveys of Assateague Island and Chincoteague Bay by Counts and Bashore (1991), Homer et al. (1997), and Prezant et al. (2002) reported living *S. haemastoma floridana* from these habitats as recently as 1996 (Prezant et al., 2002). Counts and Bashore (1991) categorized *S. haemastoma floridana* as "rare" and linked the relative decline in abundance and distribution of this drill with the decline in local oyster resources from 1960 to 1989. Prezant et al. (2002) report living *S. haemastoma floridana* in their survey and collected specimen(s) from Memorial Park, Maryland.

Living species of *Stramonita* have not previously been reported from the interior of the Chesapeake Bay (Andrews, 1956; Wass, 1972) in modern time, although *S. h. canaliculatum* had occurred in Chesapeake Bay, Maryland, and *S. h. floridana* had reached southern New Jersey during the exceptionally warm Sangamonian Stage (80,000 to ca. 220,000 yr BP) of the Pleistocene (Petuch 1997: 53). Ruiz et al. (2000) reported *S. haemastoma* as an established resident in the Chesapeake Bay region on the basis of the Chincoteague Bay, Maryland-Virginia,

**Table 2.** Summary of water temperature data sources from 1950–2005 for Delaware (DE, Figure 10) and Chesapeake (C, Figure 10). Sea surface temperature (SST), bottom temperature (BT) and air temperature at the water surface (AT) were used.

| Station | Year(s) | Data | Station type | Depth | Source |
|---|---|---|---|---|---|
| Delaware/Winter Quarter | 1955–60 | SST, BT | Winter Quarter lightship | 24–29 m | 1 |
| | 1961–70 | SST, BT | Delaware lightship | 30 m | 2 |
| | 1970–84 | SST | One degree quadrangles | NA | 3, 4, 5 |
| Chesapeake | 1984–2005 | AT, SST | NOAA buoy 44009 | 28 m | 6 |
| | 1950–1971 | SST | Chesapeake lightship | 20 m | 7, 8 |
| | 1971–84 | SST | One degree quandrangles | NA | 3, 4, 5 |
| | 1985–2005 | AT, SST | NOAA buoy CHLV2 | 11.6 m | 9 |

1. Winter Quater lightship data archive. East Coast USCG lightship/Lightstations. MBLWHOI Library data archives, Woods Hole, MA. http://dlaweb.whoi.edu/lightship/lightships_winterqtr.html
2. Delaware lightship data archive. East Coast USCG Lightship/Lightstations. MBLWHOI Library data archives, Woods Hole, MA. http://dlaweb.whoi.edu/lightship/lightships_delaware_html
3. 1966–1974. The Gulf Stream. U.S. Naval Oceanographic Office, Vols 1–9.
4. 1975–1980. gulfstream. U.S. Dept. of Commerce, NOAA, National Weather Service. Vols. 1–6.
5. 1981–94. Oceanographic Monthly Summary. U.S. Dept. of Commerce, NOAA, National Weather Service/National Earth Satellite Service. Vols. 1–14.
6. Delaware Bay, Buoy 44009. http://www.nodc.noaa.gov/BUOY/44009.html.
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9. Chesapeake Light, VA, Buoy CHLV2. http://www.nodc.noaa.gov/BUOY/chlv2.html.

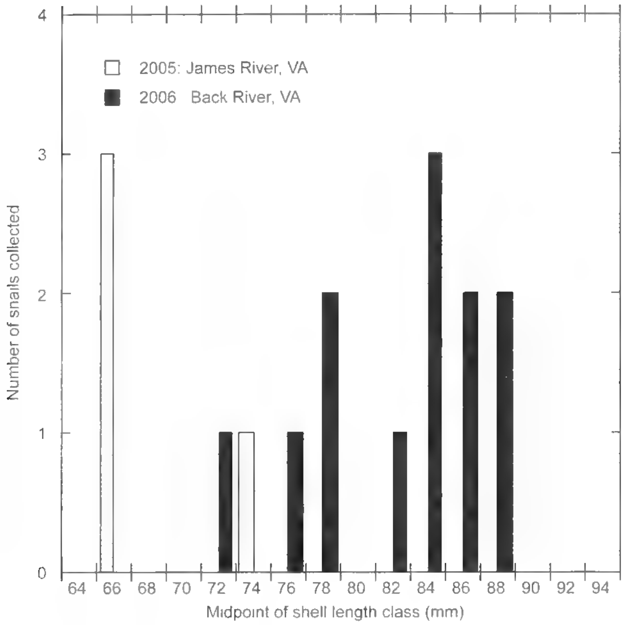

**Figure 11.** Length frequency distribution of live *Stramonita haemastoma floridana* specimens collected from Back River, VA (2006) and the James River, VA near Deep Creek (2005).

and Hog Island Bay, Virginia, collections reported by Sieling (1960) (P. Fofonoff, Smithsonian Environmental Research Center, personal communication). Distribution patterns of many molluscan species along the US Atlantic coast are directly related to water temperature with Cape Hatteras acting as a natural zoogeographic boundary (Franz and Merrill, 1980a, b). Wells and Gray (1960) reported *S. h. floridana* on two subtidal shipwrecks south of Cape Hatteras, North Carolina, but found none on the four shipwrecks they examined north of Cape Hatteras. Wells (1961) described regular collections of resident *S. h. floridana* from intertidal oyster reefs in the vicinity of Beaufort and Cape Lookout, North Carolina.

Southern oyster drills begin laying eggs at water temperatures between 20 and 30°C (Stickle, 1999). At water temperatures less than 10–12.5°C southern oyster drills stop feeding on bivalves, bury into the substrate, and become inactive (Bulter, 1954; Gunter, 1979; Garton and Stickle, 1980; Stickle, 1999) until water temperatures rises. While the upper lethal thermal limit for southern oyster drills is 35 to 40° C (Brown and Stickle, 2002), the lower lethal thermal limit for southern oyster drills is unknown.

This report documents the first collections of living *Stramonita haemastoma floridana* from within the Chesapeake Bay estuary. We characterize both groups of southern oyster drills collected in the Chesapeake Bay genetically (cytochrome *c* oxidase I "DNA bar-coding") and compare these data to sequences derived from representative specimens from the southeastern (Indian River Inlet) and northwestern (St. Andrew's Bay, Pensacola) coasts of Florida, as well as from samples from São Miguel, Azores. The presence of these drills in Chesapeake estuarine habitats is analyzed in the context of a long term (1950–2005) coastal bottom water temperature data set and two independently collected estuarine bottom water temperature data sets (Chincoteague Bay, Maryland and Virginia, 1951–56; McGary and Seiling, 1953; Seiling, 1957; York River, Virginia, 1986–2005; VIMS, 2006) in order to relate the observed Chesapeake collections with environmental/climate conditions in known drill habitats along the Atlantic coast and in Chincoteague Bay.

## MATERIALS AND METHODS

**Sample Collection:** Four living *S. haemastoma* (Figure 2) were collected in the lower James River, Virginia, in the Chesapeake Bay from oyster (*Crassostrea virginica*) reefs just below Deep Creek (Figure 10, B6) at a depth of approximately 3 m in February 2005 and were turned in to the Virginia Institute of Marine Science (VIMS) rapa whelk [*Rapana venosa* (Valenciennes, 1846)] bounty program (see Harding and Mann, 2005, for bounty program details). All four *Stramonita* speci-

**Table 3.** Nucleotide (above diagonal) and amino acid (below diagonal) differences between samples in the portion of the cytochrome *c* oxidase I gene (591 aligned positions, corresponding to positions 73 to 664 in the complete mitochondrial genome of *Ilyanassa obsoleta* [Genbank NC 007781])

| Sample | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1) *S. canaliculata* Pensacola, FL | — | 0 | 126 | 126 | 123 | 123 | 123 | 122 | 124 | 124 | 123 | 122 |
| 2) *S. canaliculata* St. Andrew's, FL | 0 | — | 126 | 126 | 123 | 123 | 123 | 122 | 124 | 124 | 123 | 122 |
| 3) *S. h. h aemastoma* Azores 1 | 8 | 8 | — | 5 | 56 | 55 | 55 | 58 | 56 | 56 | 56 | 56 |
| 4) *S. h. haemastoma* Azores 2 | 7 | 7 | 1 | — | 57 | 56 | 56 | 61 | 57 | 57 | 57 | 57 |
| 5) *S. h. floridana* Ft. Pierce Inlet, FL1 | 7 | 7 | 3 | 2 | — | 2 | 2 | 7 | 3 | 5 | 3 | 3 |
| 6) *S. h. floridana* Ft. Pierce Inlet, FL2 | 7 | 7 | 3 | 2 | 0 | — | 0 | 5 | 1 | 3 | 1 | 1 |
| 7) *S. h. floridana* Deep Creek, VA1 | 7 | 7 | 3 | 2 | 0 | 0 | — | 5 | 1 | 3 | 1 | 1 |
| 8) *S. h. floridana* Deep Creek, VA2 | 8 | 8 | 2 | 3 | 1 | 1 | 1 | — | 6 | 8 | 6 | 6 |
| 9) *S. h. floridana* Deep Creek, VA3 | 7 | 7 | 3 | 2 | 0 | 0 | 0 | 1 | — | 4 | 2 | 2 |
| 10) *S. h. floridana* Black River, VA1 | 7 | 7 | 3 | 2 | 0 | 0 | 0 | 1 | 0 | — | 4 | 4 |
| 11) *S. h. floridana* Black River, VA2 | 7 | 7 | 3 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | — | 2 |
| 12) *S. h. floridana* Black RIver, VA3 | 7 | 7 | 3 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | — |

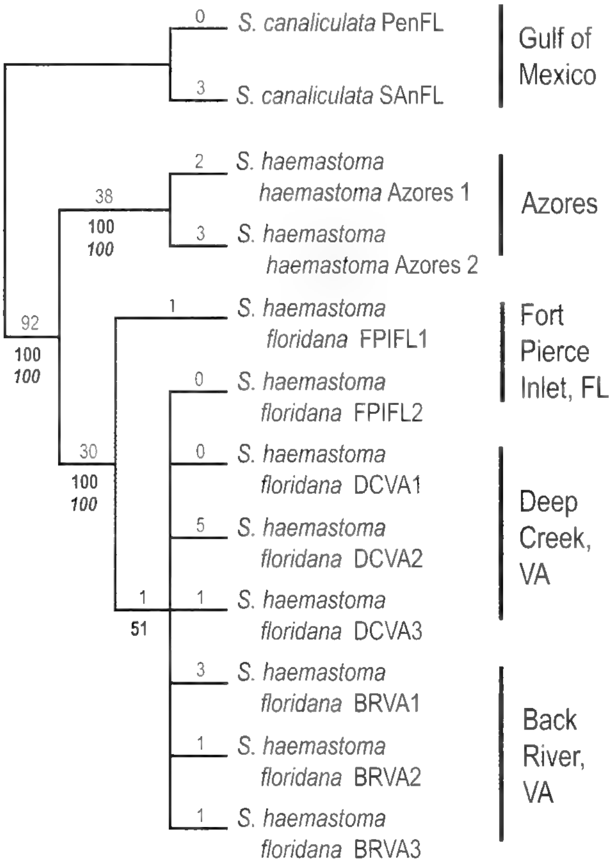

**Figure 12.** Strict consensus of four most parsimonious trees (l = 176; ci = 0.955; ri = 0.960) resulting from an exhaustive search using maximum parsimony (PAUP 4.0b10) based on 591 bp of cytochrome *c* oxidase I sequences. Branch lengths from one of the four most parsimonious trees are above the branches, bootstrap (**bold**) and jackknife (***bold italic***) proportions are below the branches.

mens were collected in a single oyster dredge tow. Thirteen living *S. haemastoma* (Figures 3–4) were collected in Back River, Virginia, (Figure 10, B5) in April 2006 and were also turned into VIMS via the rapa whelk bounty program. The 2006 collection was made using commercial crab pots (wire mesh cubes with approximately 0.5 m sides) baited with northern quahogs [*Mercenaria mercenaria* (Linnaeus, 1758)] deployed at a depth of 3 m. Shell lengths of specimens (mm, maximum dimension tip of the spire to bottom of the siphonal canal) were measured upon receipt at VIMS. Voucher specimens from both Chesapeake collections have been deposited in the National Museum of Natural History, Smithsonian Institution (USNM, Table 1).

**DNA Bar-coding:** Three specimens from each Chesapeake collection were frozen and transported to the laboratory, where DNA was extracted from red buccal muscles of each animal using Qiagen DNEasy kits according to the manufacturer's protocol. A portion of the mitochondrial gene for the DNA bar-coding region of the cytochrome *c* oxidase I gene was amplified using Sigma JumpStart RedTaq ReadyMix and Meyer's (2003) degenerated versions of the Folmer et al. (1994) HCO and LCO primers for the samples listed in Table 1. The resulting PCR products were cleaned using magnetic beads [Agencourt, manufacturer's protocol] and sequencing reactions were run on ABI 3730 sequencers that were set up according to manufacturer's instructions. Sequences were manually checked/corrected and assembled using Sequencer™ 4.1 (Gene Codes Corp.), then aligned with Clustal W (Higgins et al., 1994) using default settings, and their relationships analyzed using PAUP 4.0b10 (Swofford, 2002). Pairwise comparisons of sequences and amino acids were performed using Mega 3.1 (Kumar et al., 2004).

**Water Temperature Data:** COASTAL HABITATS: Water temperature data from 1950–2005 were used to describe mean monthly bottom water temperatures (BT, C°) for two stations in the Mid-Atlantic Bight (Delaware/Winter Quarter and Chesapeake) (Figure 10, Table 2). Daily sea surface and bottom water temperature data from the Delaware/Winter Quarter (1961–70) and Chesapeake (1958–71) lightship stations were used to calculate the average monthly observed difference between sea surface temperature (SST) and bottom water temperature (BT) on a site-specific basis. The observed average monthly SST-BT differences from the daily lightship data were used to estimate average monthly BT at these sites during years after 1971 when only SST was available (Table 2).

Hourly air temperature (AT) and SST data from NOAA buoys (1985–2005) were used to calculate the observed difference between average monthly AT and average monthly SST for Delaware Light and Chesapeake Light. The observed average monthly AT-SST differences from the buoy data were used to estimate hourly SST for these sites during months after 1984 when only AT was available.

Average residuals for annual BT from the long-term (1950–2005) average annual BT were calculated for each site in which at least 9 months of data were available. Monthly average bottom water temperatures (with standard error of the mean) were calculated for each of 12 months for all sites. Monthly BT estimates from 1970 to 1983 (Delaware) and 1984 (Chesapeake Light,) use a single published monthly average (Table 2) while monthly BT estimates from NOAA buoys (Table 2) are averages calculated from hourly readings with n values >400 per month.

**Estuarine Habitats:** Water temperature data collected at Public Landing, Maryland, in Chincoteague Bay from McGary and Sieling (1953) and Sieling (1957) were used to calculate average monthly water temperatures (with standard error of the mean) during the period 1951–1956. Modern (2001–2004) water temperature data from Chincoteague Bay stations south of Robins Marsh (XBM8149) (Figure 10, B2) and near the MD-VA border (XBM1301) (Figure 10, B3) were obtained from

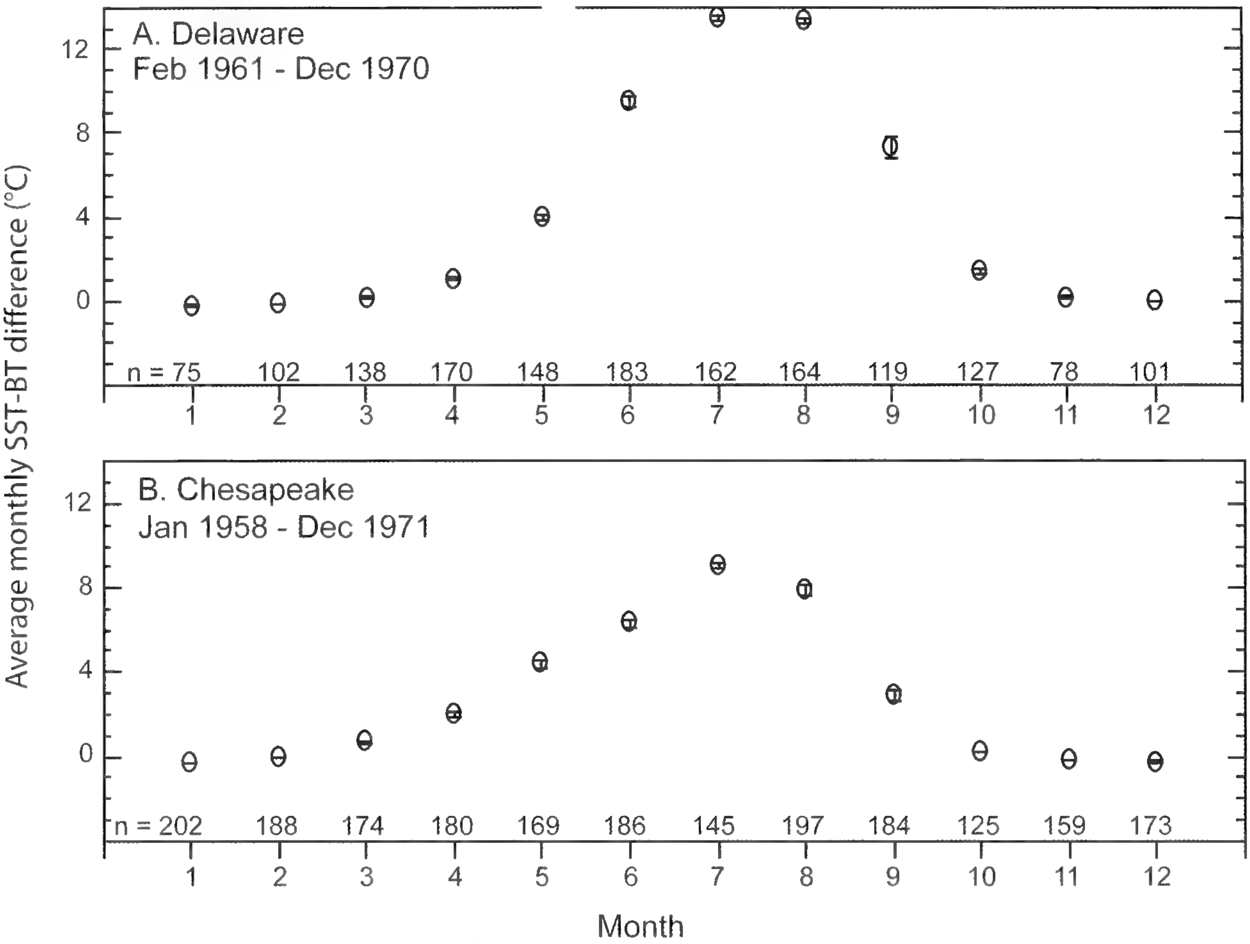

**Figure 13.** Average monthly difference between sea surface temperature (SST) and bottom water temperature (BT) from lightship data (Table 2) for Delaware (A) and Chesapeake (B) lightships. Error bars indicate standard error of the mean. N values (number of daily SST-BT pairs used to estimate the SST-BT differences) at each site are presented above the X axis in each panel.

the Maryland Department of Natural Resources Eyes on the Bay web site (http://mddnr.chesapeakebay.net/bay_cond/). Water depth at all (historical and modern) of these Chincoteague Bay sites is 3 m or less. Seiling (1954) reported less than a degree Celsius variation between surface and bottom water temperatures and the data presented in McGary and Seiling (1953) and Seiling (1957) from sites throughout the estuary confirm the well-mixed nature of these non-channel habitats.

The Virginia Institute of Marine Science (VIMS) at Gloucester Point, Virginia (Figure 10, B4) maintained a water temperature monitoring station from 1986 through September 18, 2003, (arrival of Hurricane Isabel) that recorded bottom water temperatures (°C) at a depth of 2–3 m. The VIMS Molluscan Ecology program has maintained an environmental monitoring station located within 200 m of the original VIMS station since January 2005 that records bottom water temperatures (°C) at depths of 2 m. Hourly water temperature averages were obtained from the VIMS data archive (1986 to Sep 2003) and the VIMS Molluscan Ecology program environmental data archive (2005) and used to calculate monthly residuals from the 1986–2005 mean and average monthly bottom water temperatures (with standard error of the mean).

## RESULTS

**Morphology:** The southern oyster drill specimens collected from the James River in February 2005 ranged in size from 66.4 to 75.6 mm shell length with an average shell length of 69.0 ± standard error of the mean 2.21 mm. Southern oyster drills collected in April 2006 from Back River had shell lengths ranging from 73 to 89 mm with an average shell length of 83.3 ± 1.41 mm. Size frequency distributions for both collections (Figure 11) indicate that all specimens were adults (sexually mature; Burkenroad, 1931; Butler, 1985) and represent the upper end of the size distribution typically found in Louisiana habitats (Brown and Richardson, 1987; Brown et al., 2004). These large individuals have probably reached a size refuge from most local predators including blue crabs (*Callinectes sapidus*, see the work of Turra et al., 2005, using *C. danae* preying on *S. haemastoma*) and are certainly capable of eating oysters >50 mm shell height (Garton, 1986; Brown and Richardson, 1987).

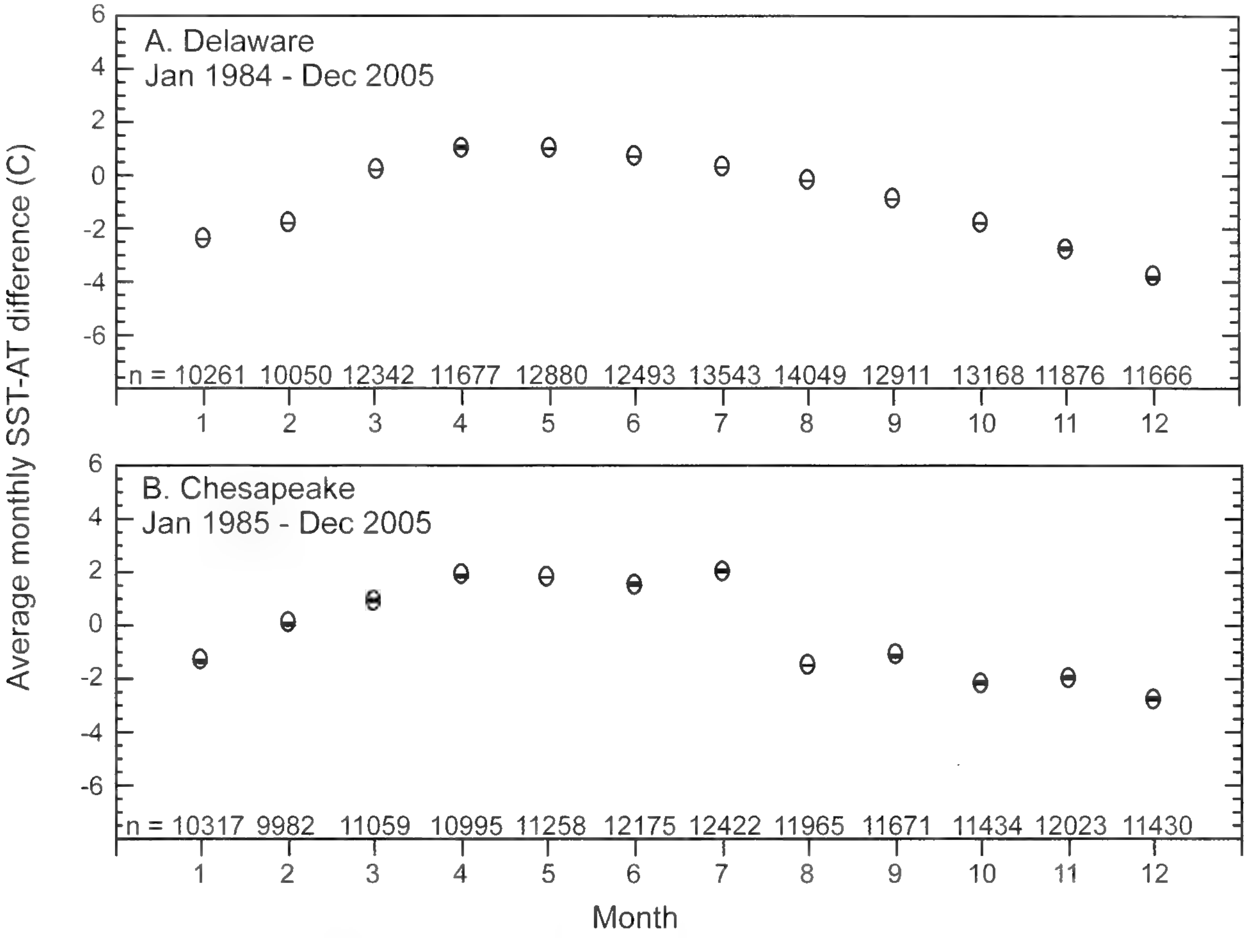

**Figure 14.** Average monthly difference between sea surface temperature (SST) and air temperature (AT) from NOAA buoys (Table 2) for Delaware (A) and Chesapeake (B) buoys. Error bars indicate standard error of the mean. N values (number of daily SST-AT pairs used to estimate the SST-AT differences) at each site are presented above the X axis in each panel.

**DNA Bar-coding:** Comparisons of a 591 base-pair portion of the mitochondrial gene for cytochrome *c* oxidase I from the samples listed in Table 1 revealed that specimens of *Stramonita* collected within Chesapeake Bay were genetically very similar or identical to specimens collected from Fort Pierce Inlet, on the southeastern coast of Florida, but differed substantially from Azorean samples and even more so from specimens from the northwestern coast of Florida (Table 3). Maximum parsimony analyses of the 144 phylogenetically informative sites using the exhaustive search algorithm yielded four equally parsimonious trees (length = 176; ci = 0.955; ri = 0.960). Figure 12 illustrates strict consensus tree of these four trees, including results of bootstrap and jackknife analyses.

**Water Temperature Data:** COASTAL HABITATS: Average annual bottom water temperatures in the period 1950–2005 for the two stations along the US Atlantic coast followed a latitudinal trend and were lower (9.81°C, SEM = 0.15, 600 months of data) at Delaware than at Chesapeake (12.30°C, SEM = 0.21, 596 months of data). The differences between SST and BT recorded by the lightships (approximately 1956–71) show the seasonal development of the thermocline at Delaware and Chesapeake beginning in April and persisting until October with the most pronounced differences between surface and bottom water temperatures occurring in July and August (Figure 13) when these stations experience surface temperatures that are at least 7° C higher than bottom temperatures. Air temperatures recorded by the Delaware and Chesapeake NOAA buoys (Table 2) are 1–2° warmer than SST from April through July (Figure 14).

Examination of annual average residual bottom water temperatures from the average long-term (1950–2005) bottom water temperatures at coastal stations (Figure 15) shows that both sites experienced above average water temperatures during the late 1950s. Multiple consecutive years between 1970–1980 and, again, in the period 1995–2005. Estimated bottom water temperatures for 2002 were among the highest observed during the period 1950–2002 for Delaware and Chesapeake Bays. Delaware and Chesapeake, both north of Cape Hatteras, experience water temperatures of 10°C or less eight and five months out of the year, respectively (Table 4A)

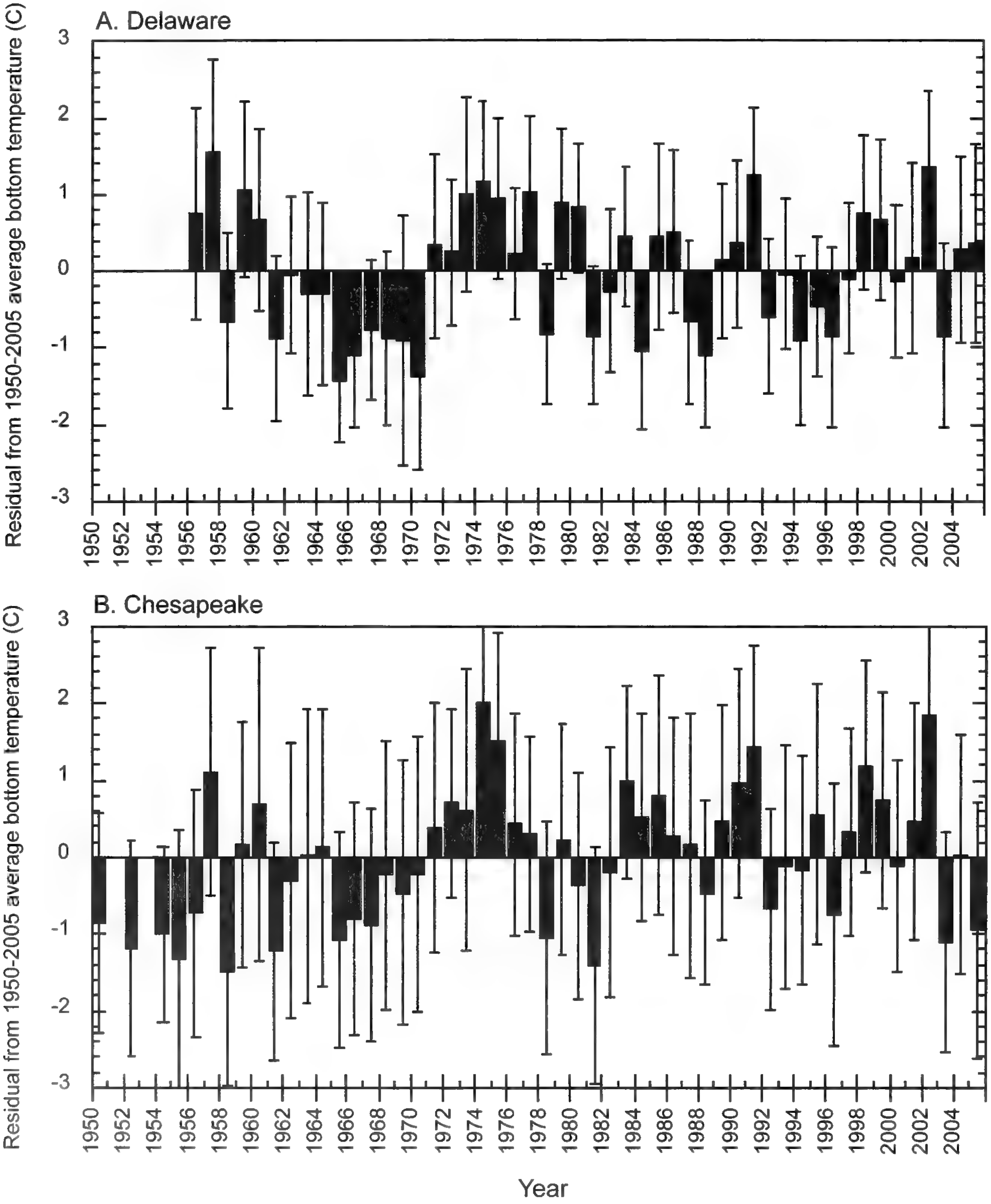

**Figure 15.** Annual average residual bottom temperature (BT) from the long term (1950–2005) average bottom temperatures for Delaware (A) and Chesapeake (B). Long term average data for each site are presented in Table 4. The error bars represent the standard error of the mean in degrees Celsius

**Table 4.** Summary of average monthly bottom water temperatures for coastal stations (A, 1950–2005) and estuarine stations (B) shown in Figure 10 and discussed in text. Standard error of the mean for each value is given in parentheses.

A.

| Month | Delaware | Chesapeake |
|---|---|---|
| Jan | 6.99 (0.22) | 6.96 (0.24) |
| Feb | 5.25 (0.20) | 5.60 (0.23) |
| Mar | 5.58 (0.18) | 6.12 (0.21) |
| Apr | 7.02 (0.15) | 8.31 (0.20) |
| May | 8.88 (0.22) | 11.02 (0.21) |
| Jun | 9.33 (0.18) | 14.34 (0.21) |
| Jul | 9.45 (0.15) | 14.93 (0.20) |
| Aug | 10.69 (0.20) | 16.72 (0.25) |
| Sep | 14.62 (0.29) | 20.27 (0.20) |
| Oct | 16.56 (0.20) | 19.11 (0.21) |
| Nov | 13.57 (0.15) | 11.02 (0.21) |
| Dec | 10.06 (0.18) | 10.41 (0.23) |

B.

| Month | Chincoteague Bay, Public Landing, MD (1951–56) | Chincoteague Bay, XBM8149 (2001–04) | Chincoteague Bay, XBM1301 (2001–04) | York River, Gloucester Point, VA (1986–2005) |
|---|---|---|---|---|
| Jan | 4.14 (0.36) | 5.3 | 5.7 | 5.32 (0.36) |
| Feb | 6.22 (0.33) | 5.25 | 5.38 | 5.55 (0.47) |
| Mar | 9.76 (0.35) | 9.65 | 9.9 | 8.46 (0.33) |
| Apr | 14.57 (0.43) | 15.53 | 15.85 | 13.61 (0.30) |
| May | 20.1 (0.38) | 18.65 | 18.87 | 18.86 (0.26) |
| Jun | 24.08 (0.38) | 27.25 | 26.33 | 23.91 (0.26) |
| Jul | 27.77 (0.32) | 26.1 | 25.85 | 26.96 (0.18) |
| Aug | 27.2 (0.26) | 27.42 | 27.65 | 27.11 (0.18) |
| Sep | 23.6 (0.40) | 22.95 | 22.93 | 23.99 (0.59) |
| Oct | 17.32 (0.50) | 14.55 | 14.6 | 19.28 (0.33) |
| Nov | 10.72 (0.38) | 15.1 | 15.68 | 13.56 (0.24) |
| Dec | 5.64 (0.39) | 5.2 | 5.5 | 8.36 (0.54) |

ESTUARINE HABITATS: Annual average residual bottom water temperatures from the York River at Gloucester Point, Virginia were higher than the 1986–2005 annual average (16.23 ± 0.56°C) in 10 of the 18 years for which data are available (Figure 16) including 2005.

The relatively shallow (3 m or less) estuarine habitats examined in Chincoteague and Chesapeake Bays experience a seasonal average monthly water temperature cycle appropriate for their latitudes (Table 4B) with water temperatures less than 10°C observed December through March. The same pattern was observed in Chincoteague Bay during 1951–1956 (Table 4B).

## DISCUSSION

The collections of live *Stramonita* from the James River (2005) and Back River (2006) mark the first modern record of this predatory gastropod from the Chesapeake Bay interior. The morphology of these specimens, particularly their larger size, deeply channeled suture, and the presence of strong, rugose shoulder nodules in the Back River samples, is similar to that of some populations from the northern Gulf of Mexico [particularly the form named *Stramonita haemastoma haysae* (Clench, 1927) (Figure 8)]. This, in turn, has raised questions about whether these animals were introduced into Chesapeake Bay, and the possible source of such introductions. However, the results of the "DNA bar-coding" study clearly indicate that the Chesapeake *Stramonita haemastoma floridana* are genetically very similar to, and in one case indistinguishable from, a population of *Stramonita haemastoma floridana* from southeastern Florida. There seems little doubt that the source of the Chesapeake *Stramonita haemastoma floridana* populations lies along the eastern seaboard of the United States. Less clear is whether these populations were introduced into Chesapeake Bay with oysters, as had been suggested by Sieling (1960) for the Chincoteague *Stramonita*, or if their presence is due to a northward expansion of the range of *Stramonita haemastoma floridana* due to warmer ocean temperatures.

The "bar-coding" data also indicate that the east-coast *Stramonita* are well differentiated from, yet more similar to *Stramonita* from the Azores than to specimens from the northern Gulf of Mexico (Figure 12). Provisional taxonomic consequences of this study are to recognize the Azorean populations as *Stramonita haemastoma haemastoma*, to retain the usage of *Stramonita haemastoma*

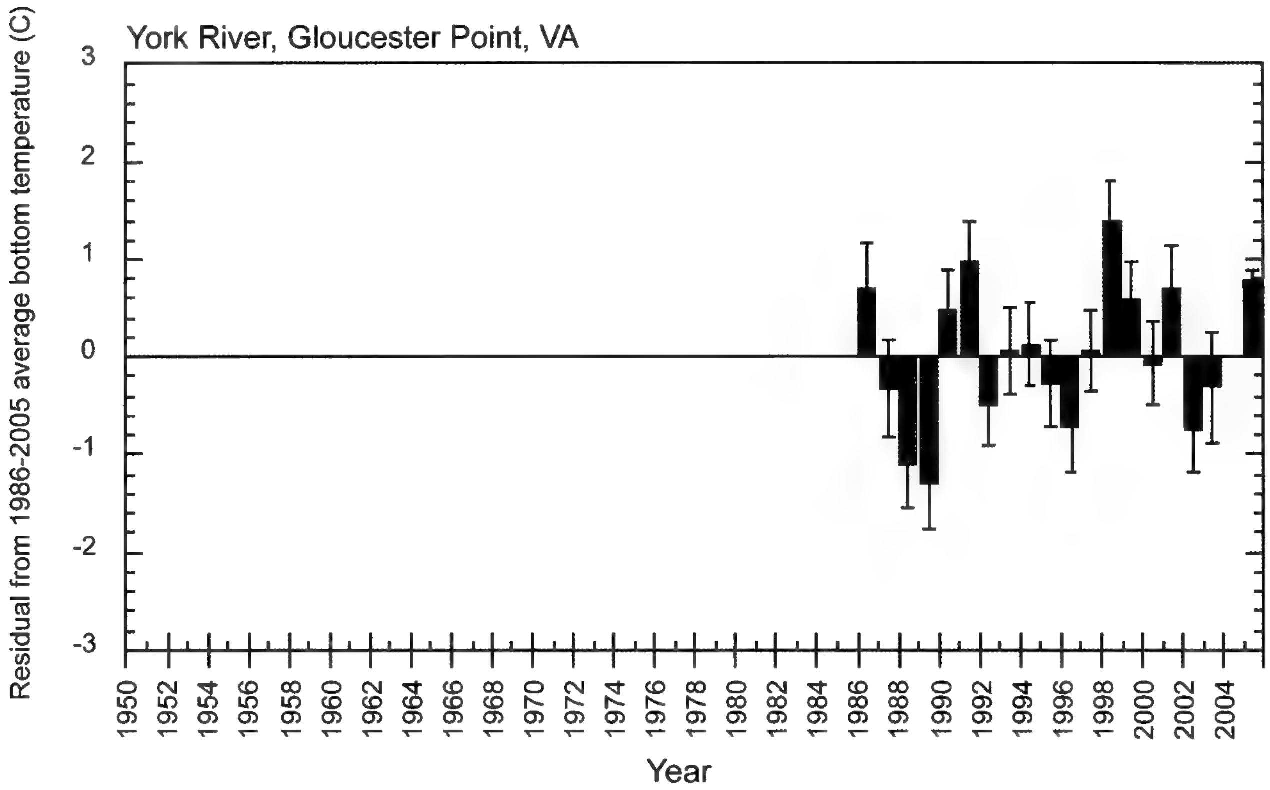

**Figure 16.** Annual average residual bottom temperature (BT) from the long term (1986–2005) average bottom temperatures (16.23 °C, standard error of the mean 0.56 °C) recorded at Gloucester Point, Virginia. The error bars represent the standard error of the mean in degrees Celsius.

*floridana* for the populations from the eastern United States, and to distinguish the populations from the northern Gulf of Mexico as *Stramonita canaliculata*, as advocated by Liu et al. (1991). Detailed analyses of this species complex over its entire geographic range are clearly required to better understand its biogeography and taxonomy.

Water temperature patterns in Chesapeake Bay habitats and along the coast of the lower Mid-Atlantic Bight since the late 1990s have been above average as were water temperature trends observed in the period 1955–1957 when live *Stramonita* were collected on the Atlantic coast of Maryland and Virginia (Sieling, 1960). Although the lower thermal lethal limit for southern oyster drills is unknown, the fact that observed seasonal trends in bottom water temperatures in Chincoteague Bay during the period 1951–56 are within 1 to 2°C of bottom water temperatures observed in the lower York River from 1986–2005 suggests that Chesapeake Bay tributaries may have seasonal temperature regimes conducive to survival of this animal. Living southern oyster drills were collected from Chincoteague Bay by Prezant et al. (2002) during surveys between 1991 and 1996, some 40 years after the initial collection (Sieling, 1956). The very low population levels ("rare", Counts and Bashore, 1991) of southern oyster drills observed in Chincoteague Bay since 1988–89 have been attributed to a decline in local oyster resources (Counts and Bashore, 1991) rather than unfavorable water temperatures. The tributaries of the lower Chesapeake Bay have resident populations of bivalves commonly eaten by *Stramonita* including mussels and oysters (Butler, 1985; Garton, 1986; Brown and Richardson, 1987). Several of these tributaries are also sites of focused oyster restoration efforts that incorporate addition of either spat on shell or broodstock oysters further expanding the potential prey field for southern oyster drills.

If these collections represent the beginning of an invasion into Chesapeake Bay tributaries, the persistence of *Stramonita haemastoma floridana* in Chesapeake Bay will be dictated by thermal tolerances as subjected to seasonal temperature cycles, while the geographic distribution will be set by salinity tolerances of adult and larvae. Adult *Stramonita haemastoma* may survive at salinities as low as 5–7 ppt (Gunter, 1979; Stickle, 1999). *Stramonita haemastoma* egg capsules survive and release viable larvae at salinities down to at least 7.5 ppt and possibly as low as 3.5 ppt (Stickle, 1999). Veliger larvae may survive up to 5 days when exposed to 10 ppt (Wells, 1961) but Roller and Stickle (1989) reported very low survival at salinities less than 15 ppt. In June 1972, heavy rains from Tropical Storm Agnes in combination with summer temperatures killed essentially all of the native oyster drills [*Urosalpinx cinerea* (Say, 1822), *Eupleura caudata* (Say, 1822)] in the upper reaches of Chesapeake Bay tributaries and reset the distributional range of the native drills to the high salinity, lower reaches of the Chesapeake Bay where natural oyster populations currently persist in only limited regions and numbers. Reestablishment of these native gastropod species to their former habitats is occurring slowly over decadal time scales and is limited by the lack of planktonic larvae for both *Urosalpinx cinerea* and *Eupleura caudata*. Reinvasion of their historic habitats by the native drills is confounded by the fact that the historically widespread distribution of oyster reef habitat has been drastically reduced in areal coverage since the early 1960s by a combination of diseases and environmental degradation. Competition for the niche vacated by the native drills during Tropical Storm Agnes already includes one large non-native gastropod, the veined rapa whelk (*Rapana venosa*) (Harding and Mann, 1999; 2005), which has planktonic veliger larvae like *Stramonita haemastoma* and is equally long-lived. Regardless of how these *Stramonita haemastoma* got to these Chesapeake tributaries, the presence of adult individuals in these tributaries adds yet another competitor for this vacant niche as well as additional predation pressure on local oyster resources.

Successful invasion of a habitat requires a breeding population and the presence of all life history stages in the new habitat (Williamson, 1996). Southern oyster drills live from 5–20 yr in Florida (Butler, 1985) with generation times on the order of 12 months (Burkenroad, 1931; Butler, 1954). The small number of specimens collected to date combined with the absence of these animals in annual fishery independent surveys of oyster reefs in the James River conducted by Harding and colleagues at VIMS and the Virginia Marine Resources Commission since the early 1990s may be an indicator that the observed southern oyster drills specimens represent small, isolated introductions that have not yet established local populations.

## ACKNOWLEDGMENTS

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# *Brachycythara beatriceae*, a new species from the Alboran Sea and the eastern Atlantic Ocean (Gastropoda: Neogastropoda: Conidae)

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## ABSTRACT

Based on shell characters, *Brachycythara beatriceae*, a new gastropod species of the family Conidae from the Alboran Sea and the eastern Atlantic Ocean, is here described. The new taxon, represented by five specimens dredged along the Spanish Mediterranean and the West Sahara coasts, is compared with the similar *Brachycythara atlantidea* (Knudsen, 1952), a species that occurs in the same geographical area. This new species is conchologically distinct and can be identified on the basis of its teleoconch shape, rib count and microsculpture, protoconch morphology, and shell color.

*Additional Keywords*: Mangeliinae, turrid, shell morphology.

## INTRODUCTION

Traditionally, the epithet "turrid" has been used as a general term referring to the numerous species belonging to the family-group Turridae H. Adams and A. Adams, 1853, sensu lato. The new taxon described in the article is assigned to the family Conidae Fleming, 1822, subfamily Mangeliinae Fischer, 1883, genus *Brachycythara* Woodring, 1928, in accordance with the revision of the superfamily Conoidea (= Toxoglossa) Rafinesque, 1815, as proposed by Taylor, Kantor, and Sysoev (1993). The genus was re-described by Powell (1966: 117), and consists of small Recent and Tertiary species that mainly occur in the Caribbean area. *Brachycythara* has been represented in the eastern Atlantic Ocean by only one species, *Brachycythara atlantidea* (Knudsen, 1952) (see Rolán and Otero-Schmitt, 1999), which has recently been reported from the Alboran Sea by Smriglio et al. 2007). I had the opportunity to examine five shells of a species that, in spite of their similarity with *B. atlantidea*, could not be considered that species. These shells, collected along the southern Spanish (Costa del Sol) and West Sahara coasts, show features typical of the genus *Brachycythara*. After a comparison with the similar and sympatric *B. atlantidea*, I believe they represent an undescribed species.

Abbreviations used are: MZB, Laboratorio di Malacologia, Museo di Zoologia dell'Università di Bologna, Italy. Private collections cited in this article are: CS-PM, Carlo Smriglio and Paolo Mariottini (Rome, Italy); SR, Stefano Rufini (Rome, Italy); FG, Franco Gubbioli (Marbella, Spain). SEM photographs were carried out at the LIME (Interdepartmental Laboratory of Electron Microscopy), University "Roma Tre", Rome, Italy.

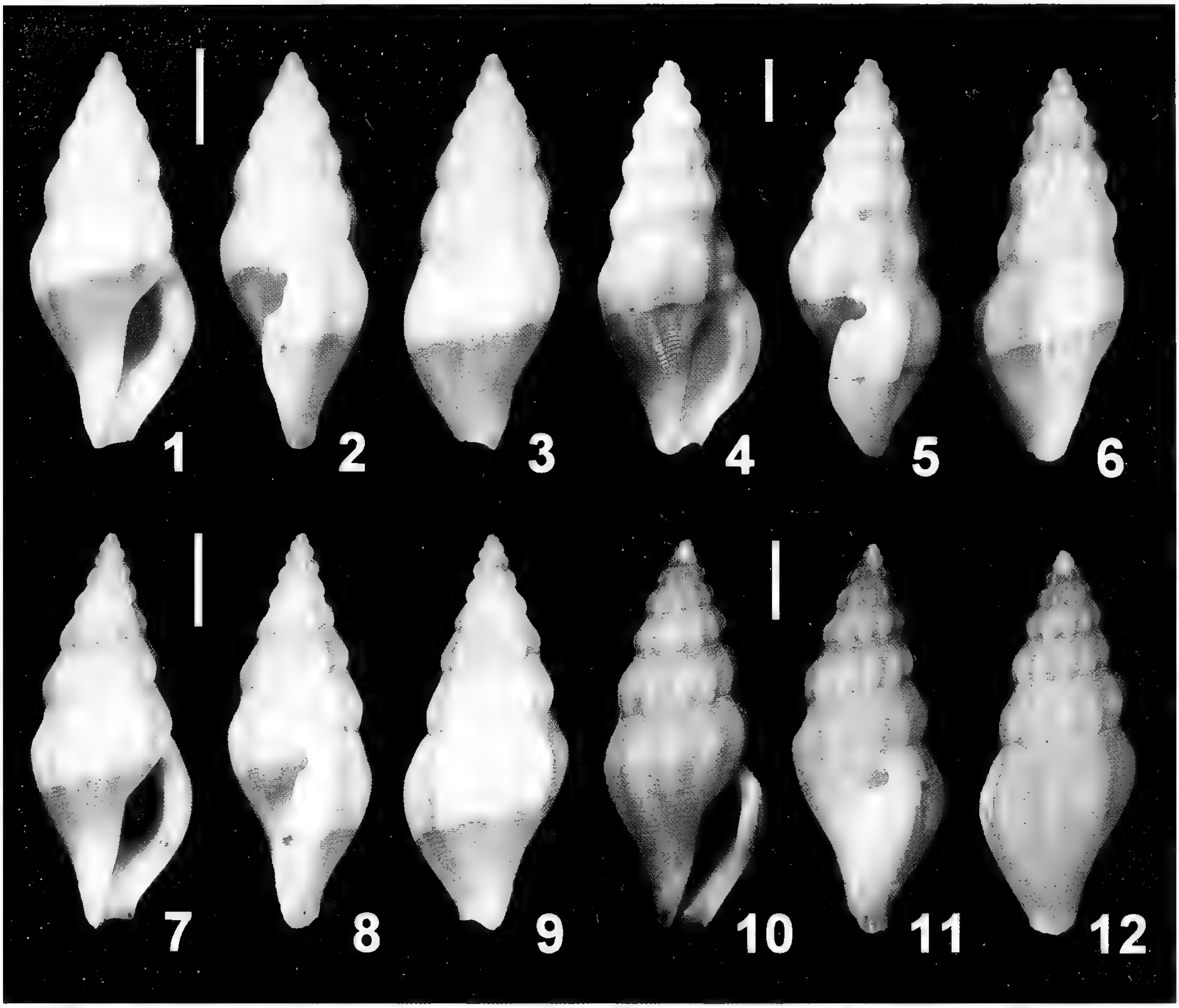
## SYSTEMATICS

Superfamily Conoidea Rafinesque, 1815
Family Conidae Fleming, 1822
Subfamily Mangeliinae Fischer, 1883
Genus *Brachycythara* Woodring, 1928

**Type Species:** By original designation, *Cythara gibba* Guppy, 1896. Woodring, 1928, Carnegie Institute Washington of Publications 385, p. 175.

*Brachycythara beatriceae* new species
(Figures 1–9; 13–20)

**Description:** Shell rather small, to 10.9 mm in length, holotype 8.6 × 3.4 mm, biconical, elongate-fusiform, solid, spire about half total height. Protoconch multispiral, dome shaped, of 3–3.5 strongly convex whorls, first 1.5–2 whorls smooth, remainder whorls reticulated with oblique axial costae crossed by spiral ribs of about equal width; protoconch indicative of planktotrophic larval development. Diameter of protoconch about 700–750 μm. Protoconch-teleoconch transition not well marked. Teleoconch of 5–6 whorls, weakly angulate near middle of spire, sutural ramp gently concave, whorl sides gently convex; last whorl about 2/3 shell length. Axial sculpture consisting of 7–8 prominent, slightly opisthocline, flexuous, and narrowly rounded axial folds; folds regularly spaced, with much broader interspaces, reaching from suture to suture on spire but fading out after crossing the

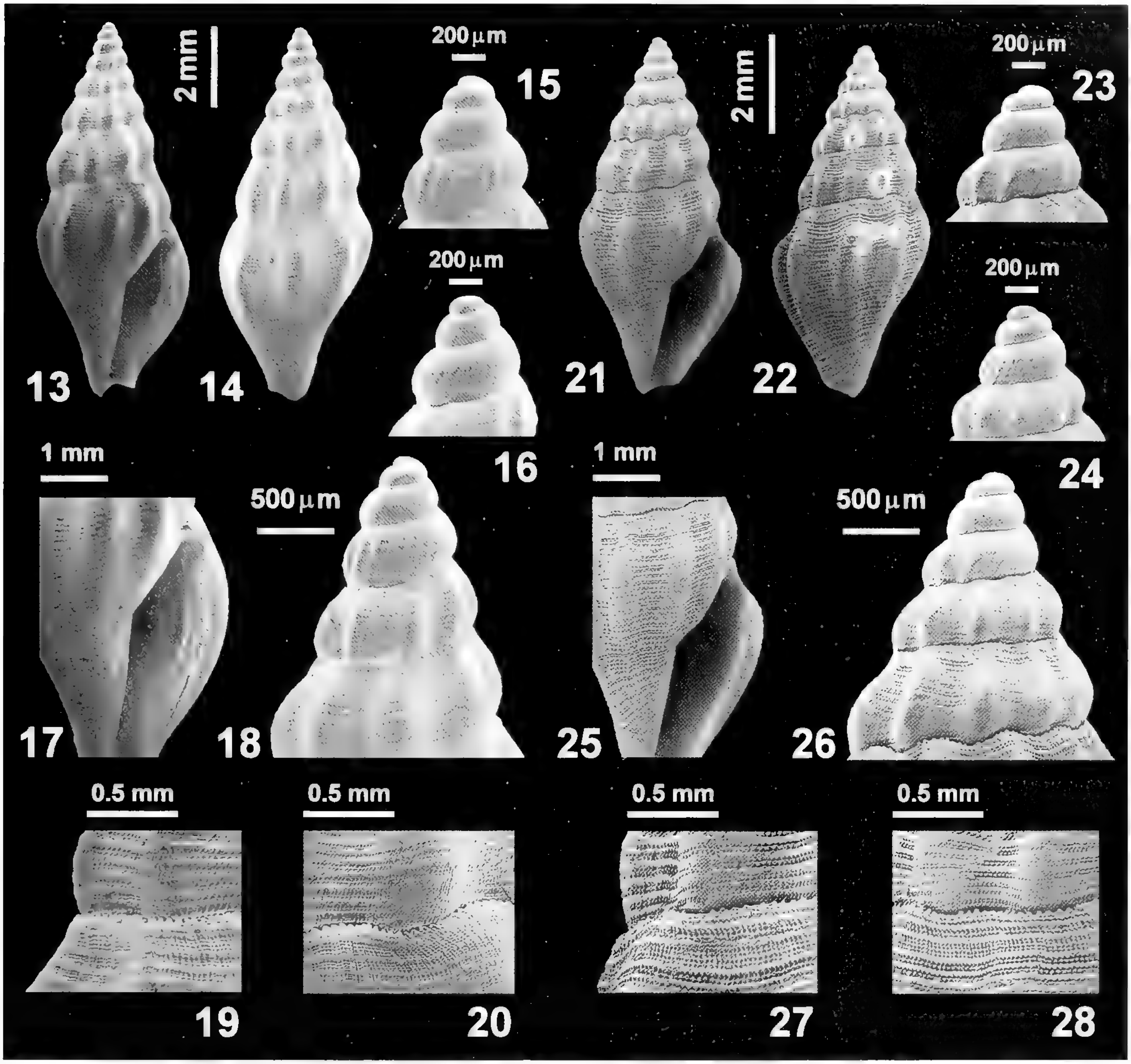


**Figures 1–12.** Shells of *Brachycythara* species. **1–3.** *Brachycythara beatriceae* new species, holotype, 8.6 × 3.4 mm, MZB 31032, Spain, Alboran Sea, off Marbella, 36°28′ N, 4°52′ W, 30–40 m. **4–6.** *Brachycythara beatriceae* new species, paratype A, 10.9 × 4.5 mm, CS-PM, Spain, Alboran Sea, off Malaga, 36°33′ N, 4°22′ W, 50 m. **7–9.** *Brachycythara beatriceae* new species, paratype B, 9.3 × 3.7 mm, FG, coast of West Sahara, 50–60 m. **10–12.** *Brachycythara atlantidea* (Knudsen, 1952), specimen L, 9.5 × 3.6 mm, FG, coast of West Sahara, 30–60 m. Scale bars: 2 mm.

shoulder slope and at about the middle of the base. Spiral sculpture of numerous, very fine threads that densely alternate with bigger interspaces; the subsutural thread shows well-marked axial denticles. At higher magnification, it can be observed that each interspace consists of several (up to five) row of rounded tiny granules, each one linked axially to the upper and lower thread by a very fine connection. Aperture narrow, ovate, about one third of the shell height. Siphonal canal short, narrow, and open. Inner lip with a moderately developed parietal callus pad. Outer lip thin or variced, according to the stage of growth, whether the lip coincides with an axial rib or an interspace. Anal sinus marked, arcuate on shoulder slope. Shell color white, with a brown band on lower half of body whorl (juvenile and subadult shells uniformly white); a darker spot present on the outer lip at the boundary of the white and the brown colors.

**Type Material:** Holotype (Figures 1–3), 8.6 × 3.4 mm, MZB 31032, Spain, off Marbella, 36°28′ N 4°52′ W, 30–40 m; Paratype A (Figures 4–6), 10.9 × 4.5 mm, CS-PM, Spain, off Malaga, 36°33′ N 4°22′ W, 30–40 m; Paratype B, 8.3 × 3.1 mm, SR, Spain, off Malaga, 36°33′ N 4°22′ W, 30–40 m; Paratype C (Figures 7–9; 13–20), 9.3 × 3.7 mm, FG, West Sahara, 50–60 m; Paratype D, 8.2 × 2.6 mm, FG, West Sahara, 50–60 m.

**Other Material Examined:** Shells of *Brachycythara atlantidea* (Knudsen, 1952): Specimen A, 10.2 × 4.1 mm;



**Figures 13–28.** Shell morphological details of *Brachycythara* species by SEM photographs. **13–14.** *Brachycythara beatriceae* new species, paratype B. **15–20.** Details of the larval whorls and the shell sculpture. **21–22.** *Brachycythara atlantidea* (Knudsen, 1952), spec. F. **23–28.** Details of the larval whorls and the shell sculpture

Specimen B, 9.2 × 3.7 mm; Specimen C, 7.5 × 3.4 mm; Specimen D, 8.2 × 3.6 mm; Specimens A–D from Spain, off Estepona, 36°25′ N, 05°09′ W, 150–250 m; Specimen E, 7.7 × 3.4 mm, from Spain, off Adra, 36°45′ N, 03°01′ W, 80–150 m; Specimen F (Figures 21–28), 7.4 × 3.2 mm; Specimen G, 10.2 × 4.4 mm; Specimens F–G from Spain, off Malaga, 36°33′ N, 04°22′ W, 50 m; Specimen H, 10.5 × 4.3 mm; I, 9.3 × 3.6 mm; Specimens H–I from Spain, off Marbella, 36°28′ N, 04°52′ W, 30–40 m; Specimen L (Figures 10–12), 9.5 × 3.6 mm; M, 8.2 × 3.4 mm; Specimen N, 6.3 × 2.6 mm; Specimens L–N dredged along the coast of West Sahara; 30–60 m. Specimens A–G, N are deposited in CS-PM collection, specimens H–M in FG collection.

**Type Locality:** Alboran Sea, Spain, off Marbella, 36°28′ N, 4°52′ W, 30–40 m depth.

**Distribution:** Alboran Sea (Costa del Sol, Spain) and eastern Atlantic Ocean (West Sahara)

**Habitat:** The dredged specimens were from muddy bottoms

**Etymology:** This species is named after the author's daughter.

**Remarks:** *Brachycythara beatriceae* new species shows several shell diagnostic features (shape and sculpture of the protoconch and the teleoconch) that match the ones described by Powell (1966: 117, plate 18, fig. 7) for the genus *Brachycythara*, an amphiatlantic group of Recent to Miocene/Pliocene species whose distribution ranges from the Caribbean to the coast of West Africa (Powell, 1966; Rolán and Otero-Schmitt, 1999). *Brachycythara atlantidea* (Figures 10–12, 21–28) has been the only species belonging to this genus known to occur in the eastern Atlantic Ocean (Rolán and Otero-Schmitt, 1999) and in the Alboran Sea (Smriglio et al., 2007). *Brachycythara beatriceae* and *B. atlantidea* show close similarities, but the two taxa can be easily separated on the basis of several shell morphological differences, as summarized in Table 1. Furthermore, at high magnification the complicated spiral microsculpture of *B. beatriceae* shows finer threads, smaller and more numerous granules in each interspace. The finding of three specimens of *B. beatriceae* from two localities off the Spanish coast (Alboran Sea) indicates that this species can be added to the Recent Mediterranean malacofauna, while the collecting depth suggests that it is a circumlittoral species. As a final conclusion, the genus *Brachycythara* is at the present represented by two sympatric species distributed in the Alboran Sea and the eastern Atlantic Ocean, *Brachycythara atlantidea* and *Brachycythara beatriceae*.

**Table 1.** Comparisons of shell features between *B. beatriceae* and *B. atlantidea*.

| Morphological characters | *B. beatriceae* | *B. atlantidea* |
|---|---|---|
| Prontoconch diameter size (in μm) | 700–750 | 600–650 |
| Protoconch number of whorls | 3–3½ | 3 |
| Teleoconch axial folds (last whorl) | 7–8 | 9–10 |
| Shell color | white with a basal brown band | uniformly yellowish-brown |

## ACKNOWLEDGMENTS

I am grateful to Mr. Carlo Smriglio and Dr. Marco Oliverio (Dipartimento di Biologia Animale e dell'Uomo, Università di Roma "La Sapienza", Rome, Italy) for their critical comments and advice on the present paper. I would like to express my deep gratitude to Mr. Franco Gubbioli (Marbella, Malaga, Spain) and to Dr. Stefano Rufini (Dipartimento di Biologia, Università di Roma "Tor Vergata", Rome, Italy) for kindly supplying type material of *B. beatriceae* and specimens of *B. atlantidea*. Dr. Andrea Di Giulio (Dipartimento di Biologia, Università di "Roma Tre", Rome, Italy) is acknowledged for SEM photographs, which were carried out at the LIME (Interdepartmental Laboratory of Electron Microscopy, Università di "Roma Tre", Rome, Italy). I am very indebted to two anonymous referees for useful suggestions and corrections to the manuscript.

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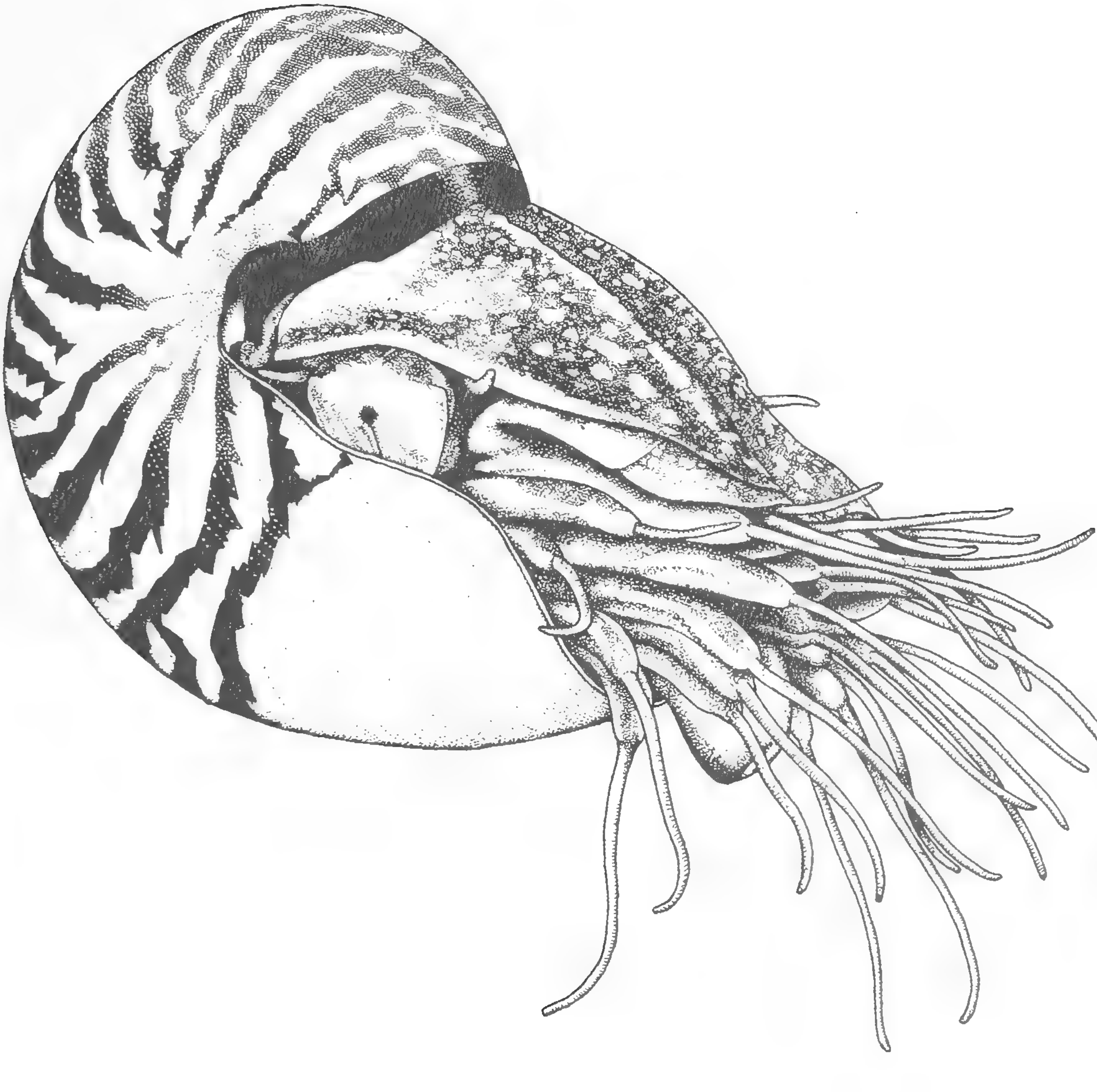

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# Late Cenozoic Tegulinae (Gastropoda: Trochidae) from southern Peru

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## ABSTRACT

Four new fossil tegulines (Gastropoda: Trochidae) are described from southern Peru [*Chlorostoma quipua* new species (late Miocene to late Pliocene), *Intistoma pirqua* new genus, new species (early Pliocene), *Cantallocostoma panistostum* new genus, new species (late Miocene to early Pliocene), *Tegula* (s.l.) *masiasi* new species (early to middle Miocene)], as are Pliocene and Pleistocene occurrences of the extant *Chlorostoma atrum* (Lesson, 1830), *C. luctuosum* (d'Orbigny, 1841), *Cantallocostoma quadricostatum* (Wood, 1828), *Agathistoma patagonicum* (d'Orbigny, 1835), *T.* (s.l.) *melaleucos* (Jonas, 1844), and *T.* (s.l.) *tridentata* (Potiez and Michaud, 1838). These data show that the Peruvian chlorostomine group is too ancient to be a Pliocene sister group to Caribbean-Atlantic agathistomines; indicate additional eastern Pacific groups of tegulines exist with roots reaching into the Miocene; and further demonstrate the success of *A. patagonicum* as a widespread and long-lived teguline in austral waters. A small radiation of Peruvian chlorostomines during the late Pliocene coincided with a molluscan mass extinction event in the Peruvian Faunal Province.

*Additional Keywords:* Mollusk, *Tegula*, *Chlorostoma*, *Agathistoma*, Miocene, Pliocene, Cenozoic, Pisco Basin, Taxonomy

## INTRODUCTION

Seven extant teguline species (Gastropoda: Trochidae) inhabit the cool coastal waters of the Peruvian Faunal Province. They are, according to their traditional nomenclature, *Tegula atra* (Lesson, 1830), *T. luctuosa* (d'Orbigny, 1841), *T. euryomphala* (Jonas, 1844), *T. ignota* Ramírez-Böhme, 1976, *T. tridentata* (Potiez and Michaud, 1838), *T. quadricostata* (Wood, 1828), and *T. patagonica* (d'Orbigny, 1835) (Alamo and Valdivieso, 1997; Véliz and Vasquez, 2000). An eighth species, *Tegula melaleucos* (Jonas, 1844), a species from warmer waters of northern Peru, does appear rarely at southern Peruvian latitudes. This teguline fauna is as diverse as that of the warm-water Panamic Faunal Province (Keen, 1971; Alamo and Valdivieso, 1997), although with mostly different species, and is more speciose than the teguline fauna of the Magellanic Faunal Province (four species), which is a subset of the Peruvian fauna (Forcelli, 2000).

The geological record of tegulines from the Peruvian Faunal Province is meager. *Tegula luctuosa*, *T. atra*, and *T. tridentata* are listed in Herm's (1969) study of Pliocene and Pleistocene mollusks from Chile. *Tegula luctuosa* and *T. melaleucos* were reported from upper Pliocene and Pleistocene beds of northern Peru (DeVries, 1986). Four new species of tegulines, considered to have early to middle Miocene age (DeVries and Frassinetti, 2003; Finger et al., 2007), have been described from the Navidad Formation of central Chile by Nielsen et al. (2004).

This paper documents four new fossil species and several previously known Recent species of tegulines in Neogene deposits of southern Peru, including the oldest known teguline from Peru, the early Miocene *Tegula* (s.l.) *masiasi* new species; creates two new genera of tegulines, *Cantallocostoma*, new genus, and *Intistoma*, new genus, each with a newly described Neogene fossil species in the Peruvian Faunal Province, *Cantallocostoma panistosum* new species and *Intistoma pirqua* new species, and each having a modern representative in the eastern Pacific Ocean, the Peruvian *C. quadricostatum* and Californian *I. aureotinctum* (Forbes, 1852); adopts a full generic status for *Tegula* (*Chlorostoma*); and provides evidence for a late Miocene origin of a western South American group of *Chlorostoma* species.

## GEOLOGY

The late Cenozoic marine stratigraphy of southern Peruvian forearc basins has been described by Dunbar et al (1990) and DeVries (1998). Teguline-bearing deposits crop out west of Nazca and throughout the Sacaco Basin (Fig. 1). These bioclastic conglomerates and sandstones which were assigned to the La Planchada and Pisco for-

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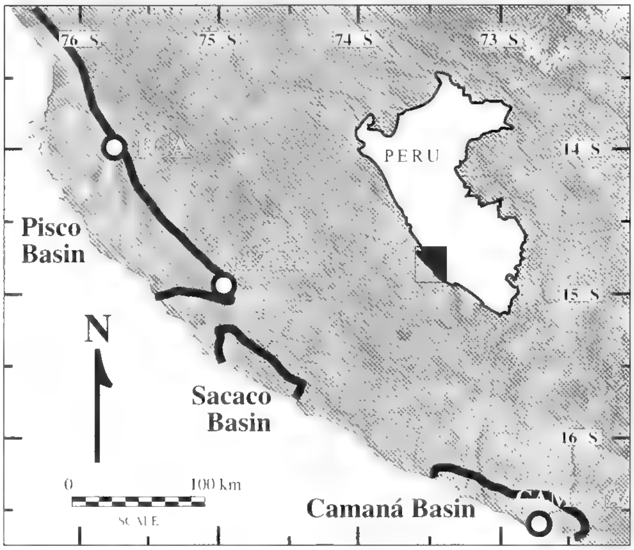


**Figure 1.** Location of onshore portions of Cenozoic forearc basins in southern Peru. New fossil species of *Tegula* are from Cenozoic deposits west and south of Nazca.

mations by Beaudet et al., 1976, and Muizon and DeVries, 1985, respectively, represent high-energy foreshore and intertidal environments lying close to mountainous paleo-shorelines and quieter foreshore and inner shelf environments lying hundreds to thousands of meters from paleo-shorelines defined by the beginning of the Andean foothills.

## MATERIALS AND METHODS

Most Peruvian specimens described in this study were found by the author. Comparative material was studied at the Natural History Museum of Los Angeles County, Los Angeles, California, USA (LACM). Locality and sample descriptions are listed in the appendix. Lengths (L) and widths (W) are measured in millimeters, with dimensions of broken specimens enclosed by parentheses. A non-standard orientation for photographs of some specimens has been necessary to reveal important characters. Some figured specimens were coated with ammonium chloride. Types and numbered specimens, including those figured, are deposited at the Orton Geological Museum, Ohio State University, Columbus, Ohio USA (OSU); the Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM INV); and the Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington (UWBM). The prefixes "DV" refers to DeVries localities, "JM" to localities of J. Macharé (Instituto Geológico Minero y Metalúrgico, Lima, Peru), and "WJZ" to localities of W. J. Zinsmeister (Purdue University, Indiana, USA).

## SYSTEMATICS

Superfamily Trochoidea Rafinesque, 1815
Family Trochidae Rafinesque, 1815
Subfamily Tegulinae Kuroda, Habe and Oyama, 1971
Genus *Tegula* Lesson, 1835

**Type Species:** *Trochus elegans* Lesson, 1835 (by monotypy) (= *Trochus pellisserpentis* Wood, 1828). Recent, Pacific coast of Central America.

**Remarks:** Resolving the difficult subfamilial placement of Tegulinae within Trochoidea (Hickman and McLean, 1990; Bouchet and Rocroi, 2005) is beyond the scope of this paper. *Tegula* itself has been assigned to three different subfamilies over the past century, but most taxonomists now refer it to the undiagnosed Tegulinae Kuroda, Habe, and Oyama, 1971 (Hickman and McLean, 1990). Only one extant teguline species, *Tegula pellisserpentis* (Wood, 1828), pertains to *Tegula* (s.s.) (Keen, 1971). Its combination of features (densely packed and heavily beaded spiral cords, tightly twisted columella, and numerous teeth extending from the columella across the apertural floor) is not seen in other species assigned to *Tegula*, so *T. pellisserpentis* is herein considered to be the monotypic representative of *Tegula* (s.s.), an opinion shared by J. H. McLean (pers. comm., 2006). Taxa often considered as subgenera of *Tegula*, e.g., *Chlorostoma* and *Agathistoma*, are elevated to generic status in this paper in accord with the practice of some authors (e.g., Arnold, 1907; Higo et al., 1999) and the opinion of J. H. McLean (pers. comm., 2006).

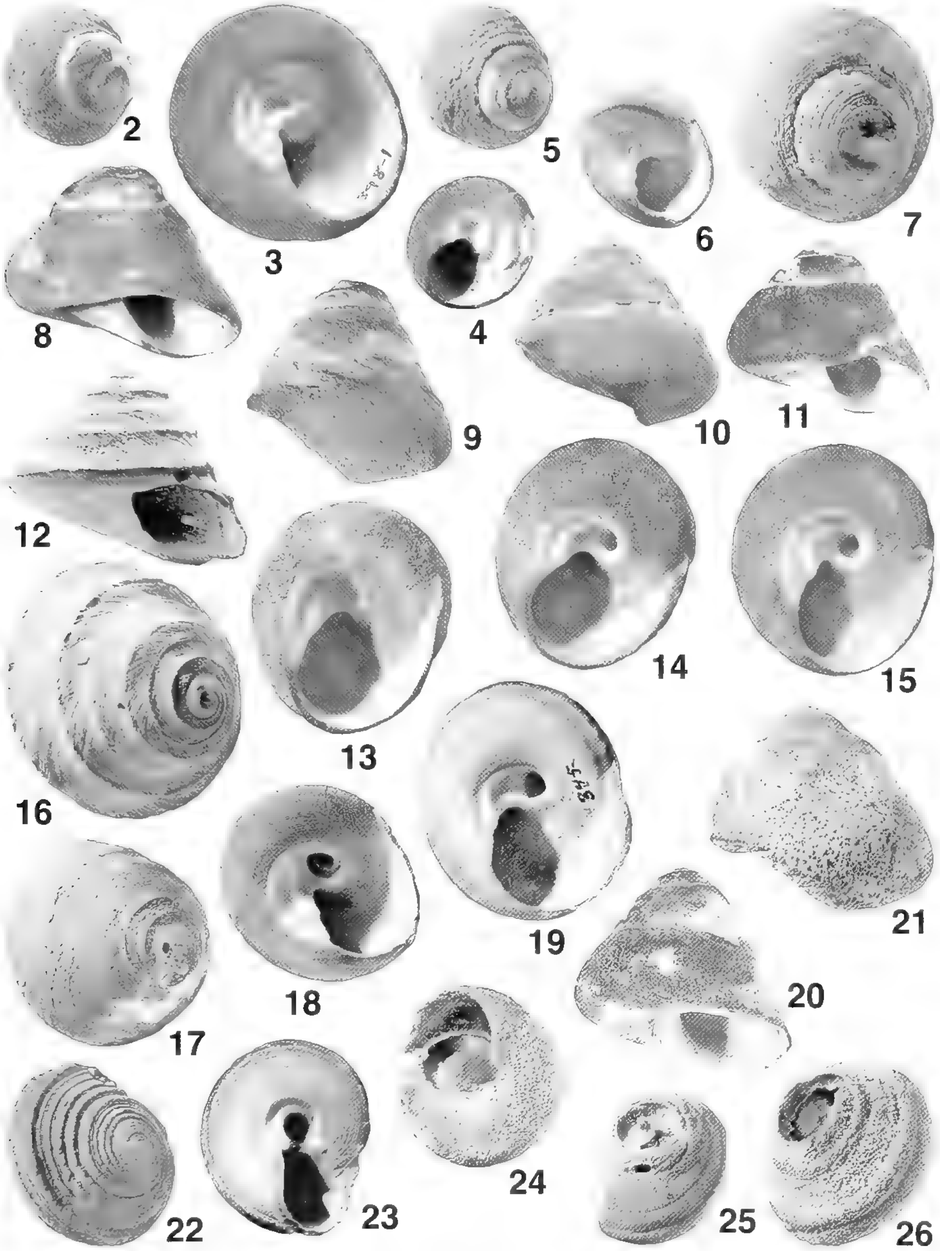
Genus *Chlorostoma* Swainson, 1840

**Type Species:** *Trochus argyrostomus* Gmelin, 1791 (by subsequent designation, Herrmannsen, 1846). Recent, Japan.

**Remarks:** Swainson (1840) erected *Chlorostoma* as a subgenus of *Trochus* Linnaeus, 1758, to include species with a "remarkably oblique" aperture, a very deep umbilicus, and one or two teeth on the outer (= lower part of inner?) lip. He assigned two species to *Chlorostoma*: *Trochus* (*Chlorostoma*) *argyrostoma* (= *Tegula argyrostoma* of authors) and *Trochus* (*Chlorostoma*) *umbilicaris* [= *Gibbula umbilicaris* (Linnaeus, 1758)]. Herrmannsen (1846) implicitly limited the definition of *Chlorostoma* by choosing *T. argyrostoma* as the type species. Examination of LACM material from the western North Pacific Ocean [*C. argyrostoma*, *C. lischkei* (Tapparone-Canefri, 1874), *C. rusticum* (Gmelin, 1791), *C. turbinatum* (A. Adams, 1853), *C. xanthostigma* (A. Adams, 1853)] shows that adult chlorostomine umbilici can be either open or closed. In the view of Grant and Gale (1931), *Chlorostoma* should be further restricted to toothed species having ventricose whorls, a nacreous interior, and a dark purplish exterior. This diagnosis makes possible the identification of Recent chlorostomine taxa from both sides of the North Pacific Ocean and in the eastern South Pacific Ocean.

*Chlorostoma atrum* (Lesson, 1830)
(Figures 2–4, 7–9, 13)

*Trochus ater* Lesson, 1830, vol. 2, pt. 1, p. 344, Mollusques, pl. 16, fig. 2; d'Orbigny, 1840: 409; Philippi, 1844, Abbildun-



**Figures 2–4, 7–9, 13.** *Chlorostoma atrum* (Lesson, 1830). **2.** UWBM 97863, DV 1372-1, Recent, oblique spire view, width = 9.8 mm. **3.** UWBM 97855, DV 398-1, Recent, basal view, width = 30.7 mm. **4.** UWBM 97863, oblique basal view. **7.** MUSM INV 126, DV 1252-1, early Pleistocene, oblique spire view, width = 27.1 mm. **8.** UWBM 97855, apertural view. **9.** UWBM 97860, Paracas Hotel, Recent, lateral view, length = 22.2 mm. **13.** UWBM 97860, oblique basal view, width = 23.4 mm. **Figures 5, 6.** *Chlorostoma funebralis* (A. Adams, 1855). UWBM 97862, south of La Jolla, California, Recent, width = 13.4 mm. **5.** Oblique spire view. **6.** Oblique basal view. **Figures 10–12, 14–19.** *Chlorostoma luctuosum* (d'Orbigny, 1841). **10.** UWBM 97864, Paracas Hotel, Recent, lateral view, length = 20.2 mm. **11.** UWBM 97865, Paracas Hotel, Recent, apertural view, length = 20.5 mm. **12.** UWBM 97866, Hueco La Zorra, Peru, Recent, apertural view, length = 21.6 mm. **14.** UWBM 97864, oblique basal view, width = 23.7 mm. **15.** UWBM 97865, basal view, width = 24.4 mm. Figure 16. UWBM 97866, oblique spire view, width = 28.5 mm. **17.** UWBM 97867, Lomas, Peru, Recent, oblique spire view, width = 26.4 mm. **18.** UWBM 97867, oblique basal view. **19.** UWBM 97868, Chile, Pleistocene, oblique basal view, width = 37.3 mm. **Figures 20, 21.** *Chlorostoma euryomphalum* (Jonas, 1844). UWBM 97871, DV 1599-1, Recent, length = 26.0 mm. **20.** Apertural view. **21.** Lateral view. **Figures 22, 23.** *Chlorostoma ignotum* (Ramírez-Böhme, 1976). UWBM 97872, Pelluhue, Chile, Recent, width = 17.5 mm. **22.** Oblique spire view. **23.** Basal view. **Figures 24–26.** *Chlorostoma quipua* new species. **24.** UWBM 97873, DV 1254-Bal 6, late early Pliocene, basal view, width = 17.3 mm. Note faint protractive stripes on base. **25.** MUSM INV 136, DV 571-1, syntype, late Miocene, oblique spire view, width = 17.0 mm. **26.** UWBM 97873, oblique spire view.

gen und beschreibungen neuer oder wenig gekannter Conchylien, v. 1, p. 188, pl. 5, fig. 6; Philippi, 1846, Die Kreiselschnecken oder Trochoideen, p. 198, pl. 30, fig. 1; Hupé, 1854, p. 142, Malacologia, pl. 4, fig. 2.

*Monodonta atra* Lesson.—Potiez and Michaud, 1838: 319, pl. 29, figs. 14, 15.

*Tegula atra* Lesson.—Dall, 1909: 239, pl. 24, fig. 4; Carcelles and Williamson, 1951: 262; Aldea and Valdovinos, 2005: fig. 8B.

*Chlorostoma ater* Lesson.—Mörch, 1850: 20.

*Tegula* (*Chlorostoma*) *atra* (Lesson, 1830).—Marincovich, 1973: 24, fig. 42; Alamo and Valdivieso, 1997: 13, fig. 25; Guzmán et al., 1998: 35, fig. 22; Forcelli, 2000: 61, fig. 87; Véliz and Vasquez, 2000: 759, fig. 1B.

*Trochus moestus* Jonas, 1844: 113; Philippi, 1846, Abbildungen und beschreibungen neuer oder wenig gekannter Conchylien, v. 2, pl. 6, fig. 5; Philippi, 1846, Die Kreiselschnecken oder Trochoideen, p. 199, pl. 30, fig. 2; Hupé, 1854: 147, Malacologia, pl. 4, figs. 3, 3a, 3b.

*Tegula moesta* (Hupé, 1854).—Dall, 1909: 239; Alamo and Valdivieso, 1997: 14.

*Chlorostoma minor* Mörch, 1850: 20.

**Diagnosis:** Shell width about 40 mm; last whorl broadly rounded, including shoulder; keels lacking. Umbilicus of juvenile and adult shells white, closed; umbilicus with two well exposed spiral cords, the adaxial cord terminating in a columellar tooth.

**Material Examined:** UWBM 97855, DV 398-1, Recent, L = 25.0, W = 30.7; UWBM 97856, DV 398-1, lot of 2; UWBM 97857, DV 1252-1, L = 11.8, W = 18.6; UWBM 97858, DV 1418-1, latest Pliocene, L = (22.2), W = 30.2; UWBM 97859, DV 463-1, late Pleistocene, lot of 2; UWBM 97860, Paracas Hotel, Recent, L = 22.2; W = 23.4; UWBM 97861, Ipun, Chile, Recent, lot of 2; UWBM 97863, DV 1372-1, Recent, L = 8.0, W = 9.8; MUSM INV 126, DV 1252-1, early Pleistocene, L = (19.2), W = 27.1; MUSM INV 127, DV 1418-1, L = 31.4, W = 36.6; MUSM INV 128, DV 463-1, lot of 2.

**Occurrence:** Late Pliocene to middle Pleistocene: southern Peru to southern Chile. Late Pleistocene: southern Peru, Chile, southern Argentina. Recent: northern Peru to southern Chile, southern Argentina (G. Pastorino, pers. comm., 2002).

**Remarks:** Specimens of *Chlorostoma atrum* can exceed 40 mm in width and are generally smooth-shelled and purple-black, either entirely or dorsally, only. The last whorl is always broadly rounded; it lacks the keeled spiral cords present on specimens of *C. luctuosum*. The base on some specimens of *C. atrum* has weak spiral threads; the spire of some also has one or more narrow spiral grooves that produce as many as 15 intervening low broad spiral cords (Figure 7), not unlike the spiral sculpture of the Californian *C. funebralis* (A. Adams, 1855) (Figures 5, 6).

The adult shell of *Chlorostoma atrum* is usually distinguished from that of other Peruvian chlorostomines by its closed umbilicus. [G. Collado (pers. comm., 2005) notes that juveniles of *C. luctuosum* and adults of the small *Tegula* (s.l.) *tridentata* occasionally have closed umbilici.] The white umbilical area on specimens of *C. atrum* has two spiral cords. A white inner cord rises from beneath the umbilical callus and terminates on the edge of the columella as a thickened tooth. A weakly developed white outer cord traces the boundary of the umbilical area and becomes flattened on the columella, not quite protruding far enough to produce a tooth. Rarely, one or two weak spiral spurs develop between the two umbilical cords in a nacreous area that lies adaperturally of a thin, glossy, umbilical veneer. They, too, do not extend far enough to produce columellar teeth.

*Chlorostoma luctuosum* (d'Orbigny, 1841)
(Figures 10–12, 14–19)

*Trochus luctuosus* d'Orbigny, 1841, v. 5, p. 409, pl. 76, figs. 16–19; Philippi, 1846, Die Kreiselschnecken oder Trochoideen, p. 153, pl. 25, figs. 4, 5; Hupé, 1854: 143.

*Tegula luctuosa* Orbigny.—Dall, 1909: 239; DeVries, 1986: 512, pl. 27, figs. 3, 4; Guzmán et al., 1998: 36, fig. 23; Véliz and Vasquez, 2000: 762, fig. 1D; Alamo and Valdivieso, 2000: 14; Aldea and Valdovinos, 2005: fig. 8E.

**Diagnosis:** Shell width to 35 mm. Last whorl with one to three spiral cords or keels. Adult umbilicus open; juvenile umbilicus usually open; umbilicus with two well exposed umbilical spiral cords, the adaxial cord terminating in a columellar tooth.

**Material Examined:** OSU 37596, DV 240-23, latest Pliocene, L = 19.5, W = 23.9; UWBM 97864, Paracas Hotel, Recent, L = 20.3, W = 23.7; UWBM 97865, Paracas Hotel, Recent, L = 20.5, W = 24.4; UWBM 97866, Hueco La Zorra, Recent, L = 21.6, W = 28.5; UWBM 97867, Lomas dump, Recent, L = (20.6), W = 26.4; UWBM 97868, WJZ 345, Chile, Pleistocene, L = 26.8, W = 37.3; UWBM 97869, DV 382-1, Pleistocene, L = (20), W = 28.4; UWBM 97870, WJZ 345, L = (35.0), W = 43.1; MUSM INV 129, DV 382-1, L = 20.6, W = 31.1; MUSM INV 130, JM 8220, Pleistocene, lot of 2.

**Occurrence:** Late Pliocene to upper Pleistocene: northern Peru to Tongoy, central Chile. Recent: Galapagos Islands to Concepción, central Chile (southern limit from LACM collections).

**Remarks:** Specimens of *Chlorostoma luctuosum* are large and purple-black, either entirely or dorsally, only. Adult specimens are generally distinguished from specimens of *C. atrum* by having an open umbilicus and from both *C. atrum* and *C. euryomphalum* by having one to three primary spiral cords or keels: one near the base of the whorl, forming the periphery (Figure 12); another about one quarter of the distance anteriorly from suture to suture (Figure 12); and a third occasionally developed just anterior to the periphery (Figure 19). Some specimens of *C. luctuosum* are also covered with tertiary spiral threads (Figures 17, 18). The thin umbilical veneer and columellar teeth are identical to those on specimens of *C. atrum*, as are the umbilical cords, except that they are exposed coiling deep into the umbilicus.

*Chlorostoma euryomphalum* (Jonas, 1844)
(Figures 20, 21)

*Trochus euryomphalus* Jonas, 1844: 113; Philippi, 1844, Abbildungen und beschreibungen neuer oder wenig gekannter

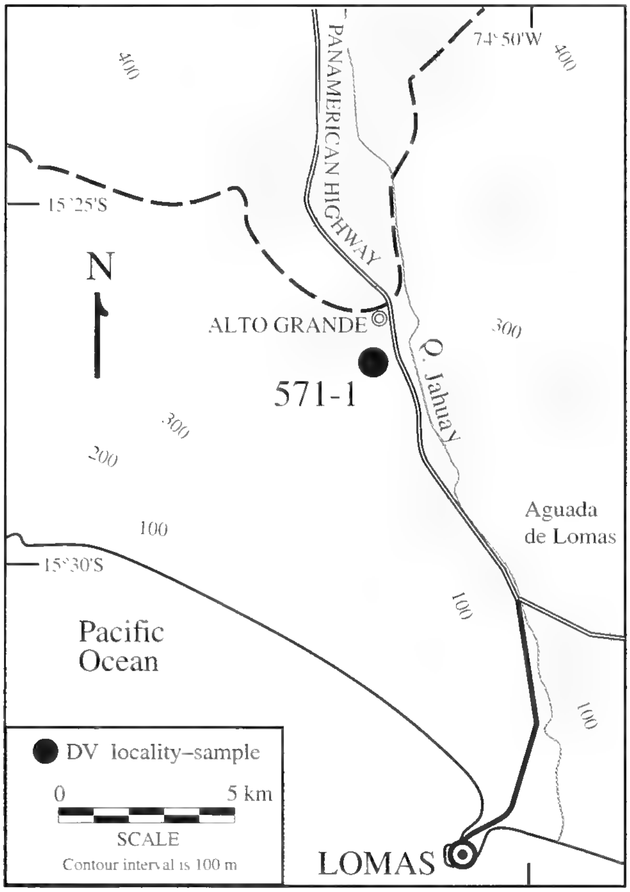


**Figure 41.** Type locality (DV 571-1) of *Chlorostoma quipua* new species.

Conchylien, v. 2, p. 27, pl. 6, fig. 4; Philippi, 1846, Die Kreiselschnecken oder Trochoideen, p. 155, pl. 25, fig. 7.
*Tegula euryomphala* (Jonas, 1844).—Carcelles and Williamson, 1951: 262.
*Tegula euryomphalus* [*sic*] (Jonas).—Dall, 1909: 239; Alamo and Valdivieso, 1997: 14.
*Tegula euryomphala* (Jones, 1844) [*sic*].—Guzmán et al., 1998: 36, fig. 25; Véliz and Vasquez, 2000: 762, fig. 1E; Aldea and Valdovinos, 2005: fig. 8C.
*Trochus kieneri* Hupé, 1854, p. 144, Malacologia, pl. 4, figs. 1, 1a, 1b.

**Diagnosis:** Shell width to 35 mm. Last whorl broadly rounded. Umbilicus white, open; umbilicus with two well exposed spiral cords, the adaxial cord terminating in a columellar tooth.

**Material Examined:** UWBM 97871, DV 1599-1, Recent, L = 26.0, W = 29.9.

**Occurrence:** Late Pleistocene: Northern to central Chile. Recent: Southern Peru to central Chile.

**Remarks:** Specimens of *Chlorostoma euryomphalum* are large, purple-black, and characterized by a broad open umbilicus and broadly rounded whorls. They differ from specimens of *C. atrum*, which have a closed umbilicus, and *C. luctuosum*, which have one or more angular spiral cords or keels. On some specimens of *C. luctuosum*, however, including Recent Peruvian and Chilean examples from LACM collections, Pleistocene Chilean specimens from WJZ collections, and upper Pliocene Peruvian specimens from northern Peru, the spiral cords are so weak that assigning the material to *C. luctuosum* or *C. euryomphalum* is problematic.

*Chlorostoma ignotum* (Ramírez-Böhme, 1976)
(Figures 22, 23)

*Tegula ignota* Ramírez-Böhme, 1976: 3, figs. 1–6; Forcelli, 2000: 61, fig. 88; Véliz and Vasquez, 2000: 762, fig. 1F; Aldea and Valdovinos, 2005: fig. 8D; Collado and Brown, 2005: 131.

**Diagnosis:** Shell width to 30 mm. Outer layer slate colored. Sculpture consists of several well developed, unbeaded, primary spiral cords. Umbilicus open.

**Material Examined:** UWBM 97872, La Rinconada, Pelluhue, Chile, Recent, L = 11.1, W = 17.5; UWBM 97906, Ipun, Chile, Recent, L = 29.4, W = 32.6.

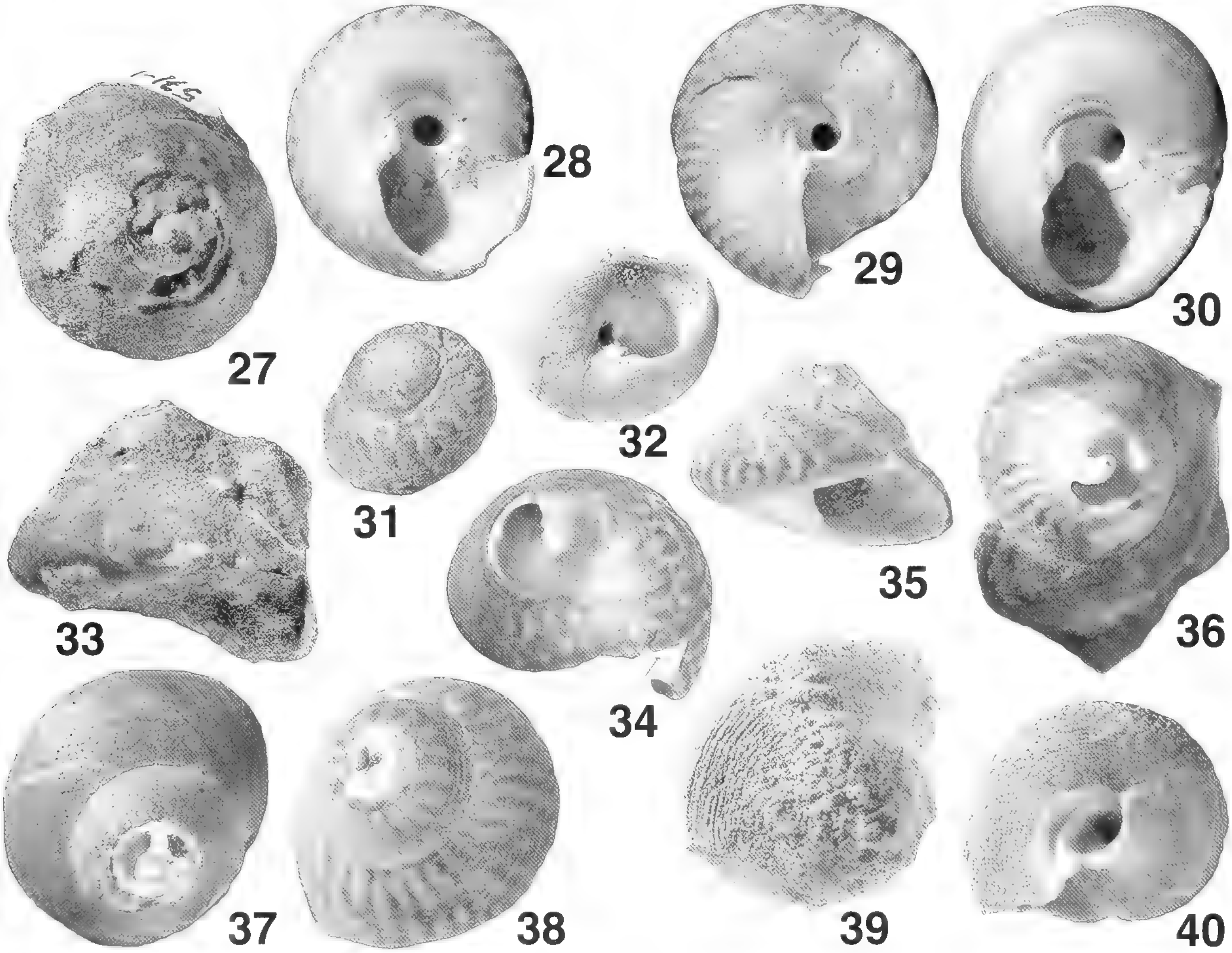
**Occurrence:** Recent: central to southern Chile.

**Remarks:** *Chlorostoma ignotum* is known only as a Recent species from Chile (e.g., Collado and Brown, 2005). Specimens of *C. ignotum* differ from those of other extant chlorostomines of the Peruvian Faunal Province in two significant respects: they lack the purple-black outer shell layer of *C. atrum*, *C. luctuosum*, and *C. euryomphalum*, being rather slate colored, and they have numerous, prominent, well-differentiated primary and secondary spiral cords between the periphery and suture and to a lesser extent on the base. The well-exposed umbilical cords, thin umbilical veneer, and columellar teeth are identical, however, with those of other species of South American *Chlorostoma*, and the strong spiral cords (Figure 22) are like those seen on rare specimens of early Pliocene *C. quipua* new species (Figures 25, 26; see below).

*Chlorostoma quipua* new species
(Figures 24–40)

**Diagnosis:** Adult whorls purple-black dorsally; spire and base usually light brown, commonly with dark brown protractive stripes or mottling. Umbilicus narrow, open.

**Description:** Shell up to 30 mm wide. Spire angle about 80 degrees. Periphery near base, sharply rounded to slightly angular. Sutures appressed. Protoconch unknown; teleoconch with five flat-sided to slightly convex whorls. Axial sculpture absent or rarely with rugose protractive ribs. Thin growth lines strongly prosocline. Spiral sculpture of 20 muted spiral threads posterior to periphery; rarely with three to five spiral grooves separating four to six broad low spiral cords or without spiral sculpture. Twenty to 30 evenly spaced spiral threads on base of juvenile specimens, muted or obsolete on adult whorls. Outer shell layer purple-black on adult whorls, tan or light brown on spire whorls and base. Protractive and rarely retrotractive wrinkled brown stripes usually



**Figures 27–40.** *Chlorostoma quipua* new species. **27.** MUSM INV 131, DV 571-1, syntype, spire view, width = 28.4 mm. **28.** MUSM INV 133, DV 1635-2, early Pliocene, basal view, width = 16.0 mm. **29.** UWBM 97880, DV 1635-2, basal view, width = 16.6 mm. **30.** UWBM 97879, DV 1635-2, basal view, width = 18.5 mm. **31.** UWBM 97890, DV 1598-1, early Pliocene, oblique spire, width = 11.2 mm. **32.** UWBM 97883, DV 1284-1, Pliocene, oblique basal view, width = 8.9 mm. **33.** UWBM 97876, DV 571-1, syntype, apertural view, length = 22.7 mm. **34.** UWBM 97880, oblique spire view. **35.** MUSM INV 133, apertural view. **36.** UWBM 97881, DV 1029-1, early Pliocene, spire view, width = 17.4 mm. **37.** UWBM 97879, oblique spire view. **38.** MUSM INV 135, DV 1029-1, oblique spire view, width = 11.3 mm. **39.** UWBM 97878, DV 809-1, Pliocene, spire view, width = 22.1 mm. **40.** MUSM INV 132,DV 809-1, basal view, width = 19.0 mm.

present on base and less often on spire. Inside edge of outer lip smooth. Umbilicus open, narrow; umbilical veneer thin. Columella with thick inner tooth at end of well-exposed white spiral umbilical cord. Weak outer tooth adjacent to floor of aperture at end of thin spiral cord following outer margin of umbilical area. Small parietal flange barely overhanging umbilicus.

**Type Locality:** DV 571-1, Alto Grande, about one km south of intersection with abandoned paved road to San Juan de Marcona, on south facing hillside west of Panamerican Highway; one of several shell banks of the Pisco Formation (Figure 41). Locality inaccurately referred to as El Jahuay in Muzon and DeVries (1985). 15°26′57″S, 74°52′06″W (Acarí 1:100,000 quadrangle). Middle upper Miocene.

**Type Material:** (All DV 571-1, all syntypes) UWBM 97876, L = 22.7, W = 27.3; UWBM 97877, L = (17), W = (25.1); MUSM INV 131, L = (18.9), W = 28.4; MUSM INV 136, L = (10.2), W = 17.0.

**Other Material Examined:** UWBM 97873, DV1254-Bal 6, late early Pliocene, L = (11.0), W = 17.3; UWBM 97874, DV 1254-Bal 10, late Pliocene, L = (4.8), W = 10.4; UWBM 97875, DV 1254-Bal 10, L = (14.1), W = 24.4; UWBM 97878, DV 809-1, Pliocene, L = 15.4, W = 22.1; UWBM 97879, DV 1635-2, early Pliocene, L = 12.2, W = 18.5; UWBM 97880, DV 1635-2, L = (11.3), W = 16.6; UWBM 97881, DV 1029-1, early Pliocene, L = (12.3), W = (17.4); UWBM 97882, DV 1029-1, L = (12), W = 16.7; UWBM 97883, DV 1284-1, Pliocene, L = (5.2), W = 8.9; UWBM 97890, DV 1598-1, early

Pliocene, L = 8.4, W = 11.2; MUSM INV 132, DV 809-1, L = 16.8, W = (19.0); MUSM INV 133, DV 1635-2, L = 11.2, W = 16.0; MUSM INV 134, 1635-2, lot of 2; MUSM INV 135, DV 1029-1, L = 6.9, W = 11.3.

**Occurrence:** Middle late Miocene to early late Pliocene: southern Peru.

**Etymology:** "Quipua," Latinized version of "quipu," Inca counting device of braided and knotted strings, evoked by the wrinkled brown stripes on the base and spire of this species.

**Remarks:** Specimens of *Chlorostoma quipua* differ from those of *C. euryomphalum* and *C. luctuosum* by having a narrower umbilical area, smaller parietal flange, and protractive brown stripes. Specimens of *C. quipua* lack the keeled spiral cords of *C. luctuosum* and closed umbilicus of *C. atrum*. Some specimens of *C. quipua*, both Miocene and Pliocene, have broad spiral cords (Figure 25) like those seen on the juvenile whorls of some specimens of *C. atrum* (Figure 7). A single specimen from upper Pliocene beds above Playa Huacllaco (Figure 26) has spiral cords as pronounced as the raised spiral cords on specimens of the modern Chilean *C. ignotum* (Figure 22). Some lower Pliocene specimens near Yauca (Figure 31) have coarse protractive axial ribs like those on some Asian chlorostomines.

Specimens of *Chlorostoma quipua* superficially resemble those of *C. gallina* (Forbes, 1852), a Pliocene-to-Recent species from California and Baja California (Grant and Gale, 1931; McLean, 1978), and *C. rugosum* (A. Adams, 1853), a Recent species from the Gulf of California (Keen, 1971). Specimens of all three species have some degree of purple-black color and protractive stripes on the spire and/or base. Specimens of *C. gallina* and *C. rugosum*, however, are more ventricose laterally and basally and have weak to prominent protractive axial ribs and stripes posterior to the base. Specimens of *C. gallina* usually have a closed umbilicus.

Shells of *Chlorostoma quipua* are found in upper Miocene beach deposits near Alto Grande (DV 571-1; see Muizon and DeVries, 1985) with specimens of *Chorus frassinetti* DeVries, 1997, and *Acanthina obesa* DeVries, 2003 (DeVries, 1997, 2003). Lower Pliocene specimens of *C. quipua* occur together with specimens of the muricid gastropods, *Concholepas kieneri* Hupé, 1854; *Xanthochorus ochuroma* DeVries, 2005; and *Herminespina saskiae* DeVries and Vermeij, 1997; and the turbinid gastropod, *Prisogaster mcleani* DeVries, 2006 (DeVries, 2005, 2006; DeVries and Vermeij, 1997).

### Genus *Cantallocostoma* new genus

**Type species:** *Trochus quadricostatus* Wood, 1828. Recent. Peru and Chile.

**Diagnosis:** White to brown outer shell layer. Three to five beaded primary spiral cords. Umbilicus open, broad. Two adaxially situated spiral umbilical cords terminating in columellar teeth. Parietal wall vertical, without parietal flange overhanging umbilicus.

**Description:** Shell up to 35 mm in diameter. Whorls ventricose to quadrate; periphery weakly bicarinate. Spiral sculpture of three to five primary spiral cords broken into beads; interspaces with two to five continuous or weakly beaded tertiary threads. Base with four to five beaded or non-beaded primary spiral cords and intervening secondary cords and tertiary threads. Umbilical area white, tabulate, sharply defined, with margin of umbilical area flaring towards aperture as steeply inclined wall. Umbilicus open, broad, with two spiral umbilical cords situated adaxially, the innermost thicker; each cord terminating in columellar tooth. Third tooth sometimes present at base of columella. Umbilical veneer variably developed. Columella thin, upright, without parietal flange overhanging umbilicus. Floor of aperture with ledge but without teeth. Inner lip sometimes with four to six closely spaced low teeth.

**Occurrence:** Late Miocene to Pleistocene: southern Peru. Recent: northern Peru to Chile.

**Etymology:** "Cantalloc," site near Nazca, Peru, where subterranean aqueducts are reached from ground level by pre-Incaic stonewall-lined spiral paths that resemble the spiral umbilical cords of this genus.

**Remarks:** Specimens of *Cantallocostoma* differ from those of Asian, Californian, and Peruvian *Chlorostoma* by having beaded spiral cords and two adaxially situated umbilical spiral cords. They differ from specimens of *Intistoma* new genus, by having closely spaced beads and lacking a subsutural band of well-developed protractive nodes. Specimens of *Cantallocostoma* differ from tegulines traditionally assigned to *Agathistoma* by lacking hallmarks of that genus: "narrow open umbilicus, a smooth or finely beaded spiral sculpture, and a variegated surface coloration" (Olsson and Harbison, 1953: 351).

### *Cantallocostoma quadricostatum* (Wood, 1828)
(Figures 42–45, 47–49)

*Trochus quadricostata* Wood, 1828: 16, pl. 5, fig. 16.

*Trochus quadricostatus* Wood.—Philippi, 1846, Die Kreiselschnecken oder Trochoideen p. 154, pl. 25, fig. 6.

*Tegula quadricostata* (Wood, 1828).—Véliz and Vasquez, 2000 759, fig. 1A; Aldea and Valdovinos, 2005: 8F.

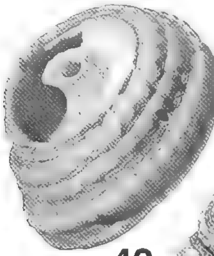
*Tegula quadricostata* Gray.—Dall, 1909: 240; Alamo and Valdivieso, 1997: 14.

*Monodonta catenifera* Potiez and Michaud, 1838: 318, pl 29 figs. 12–13.

*Trochus torulosus* Philippi, 1843, Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien, v. 1, pl 2, fig. 12.

**Diagnosis:** Low spire, white to cream-colored with purple along edges of sculptural elements. Sculpture of three to five prominent primary beaded spiral cords.

**Material Examined:** UWBM 97884, DV 1372-1, Recent, L = (14.4), W = 23.9; UWBM 97885, DV 1372-1, L = (13.3), W = (20.8); UWBM 97886, DV 1713-1, early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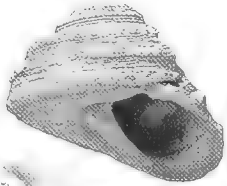
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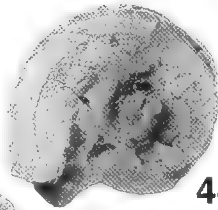
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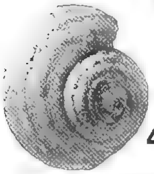
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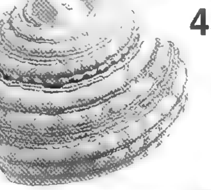
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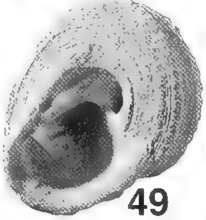
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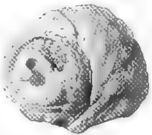
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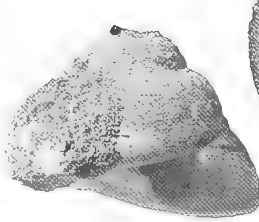
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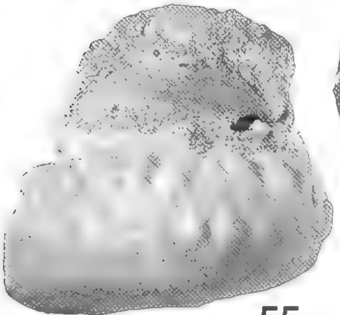
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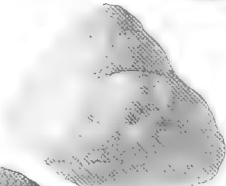
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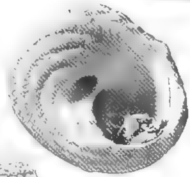
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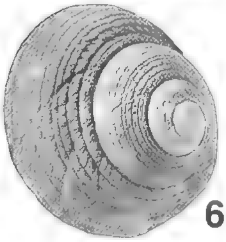
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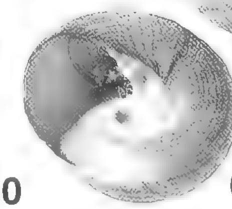
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**Figures 42–45, 47–49.** *Cantallocostoma quadricostatum* Wood, 1828. **42.** UWBM 97884, DV 1372-1, Recent, oblique spire view, width = 23.9 mm. **43.** UWBM 97886, DV 1713-1, early Pleistocene, apertual view, width = 21.5 mm. **44.** MUSM INV 137, DV 1355-1, late Pliocene, basal view, width = 16.0 mm. **45.** UWBM 97884, oblique basal view. **47.** UWBM 97885, DV 1372-1, oblique lateral view, width = 20.8 mm. **48.** UWBM 97887, DV 1355-1, oblique spire view, width = 18.1 mm. **49.** UWBM 97886, oblique basal view. **Figures 46, 50–54.** *Cantallocostoma panistostum* new species. **46.** MUSM INV 141, DV 1635-2, early Pliocene, oblique spire view, width = 14.3 mm. **50.** UWBM 97891, DV 571-1, late Miocene, oblique spire view, width = 14.9 mm. **51.** UWBM 97889, DV 1598-1, syntype, oblique lateral view, width = 33.7 mm. **52.** UWBM 97889, oblique basal view. **53.** UWBM 97889, apertural view. **54.** MUSM INV 139, DV 1598-1, syntype, basal view, width = 24.9 mm. **Figures 55–57.** *Intistoma pirqua* new species. UWBM 97892, DV 470-1, syntype, early Pliocene, length = 38.9 mm. **55.** Lateral view. **56.** Apertural view (lighting from upper right). **57.** Oblique basal view. **Figures 58, 59.** *Intistoma aureotinctum* (Forbes, 1852). South of La Jolla, California, Recent. **58.** UWBM 97896, lateral view, length = 20.0 mm. **59.** UWBM 97897, oblique basal view, width = 17.8 mm. **Figures 60–63.** *Agathistoma patagonicum* (d'Orbigny, 1835). **60.** UWBM 97893, Argentina, Recent, oblique spire view, width = 15.4 mm. **61.** UWBM 97893, oblique basal view. **62.** UWBM 97895, DV 1032-2, late Pliocene, lateral view, width = 12.7 mm. **63.** UWBM 97895, oblique spire view.

Pleistocene, L = (14.5), W = 21.5; UWBM 97887, DV 1355-1, late Pliocene, L = 12.6, W = 18.1; UWBM 97888, DV 1355-1, L = (10.0), W = 16.1; MUSM INV 137, DV 1355-1, L = (8.9), W = 16.0; MUSM INV 138, DV 1355-1, L = 14.1, W = (19).

**Occurrence:** Late Pliocene: southern Peru. Recent: northern Peru to Chile.

**Remarks:** The number of primary beaded spiral cords on the last whorl of *Cantallocostoma quadricostatum* varies between three and five. Most modern specimens have two widely spaced primary spiral cords on the anterior half of the whorl and two closely spaced primary spiral cords adjacent to the posterior suture (Figure 42). Some specimens have an additional primary spiral cord between the two anterior spiral cords (Figure 47); other specimens have one of the two posteriormost primary spiral cords missing (Figure 43). The six known late Pliocene specimens from southern Peru (Figure 48) and single early Pleistocene specimen (Figure 43) have three primary spiral cords.

*Cantallocostoma panistostum* new species
(Figures 46, 50–54)

**Diagnosis:** Exterior uniformly pale brown; spiral sculpture of three beaded spiral cords. Basal spiral cords bunched towards umbilical area.

**Description:** Shell nearly 35 mm in diameter. Spire angle about 70 degrees. Periphery at base, sharply rounded. Sutures impressed. Protoconch unknown. Teleoconch with five quadrate whorls. Axial sculpture absent except for intermittently rugose prosocline growth lines. Spiral sculpture of closely beaded spiral cord at base and two posterior spiral rows of more widely spaced beads, about 25 per whorl, bracketing shoulder. Posterior beads sometimes slightly protractively elongate. Interspaces rarely with beaded secondary spiral cords; usually with wavering tertiary spiral threads. Base weakly convex, with six to ten closely spaced spiral cords adjacent to umbilical area. Outer shell layer pale brown, without color pattern. Inner edge of outer lip smooth. Umbilicus open, wide, with two adaxially situated spiral cords. Umbilical veneer thin. Innermost umbilical cord prominent, second cord thin; each terminates in columellar tooth. Third tooth at base of columella nearly obsolete. Columella thin; parietal flange absent.

**Type Locality:** DV 1598-1, roadcut along Panamerican Highway, shell beds exposed along descent from north into Río Yauca valley (Figure 64). 15°39′49″S, 74°31′50″W (Yauca 1:100,000 quadrangle). Lower Pliocene.

**Type Material:** (DV 1598-1, all syntypes) UWBM 97889, DV 1598-1, L = (25.2), W = 33.7; UWBM 97890, DV 1598-1, L = 8.4, W = 11.2; MUSM INV 139, DV 1598-1, L = (13.7), W = 24.9; MUSM INV 140, Panamerican roadcut at Yauca, early Pliocene, L = (17.9), W = 33.3.

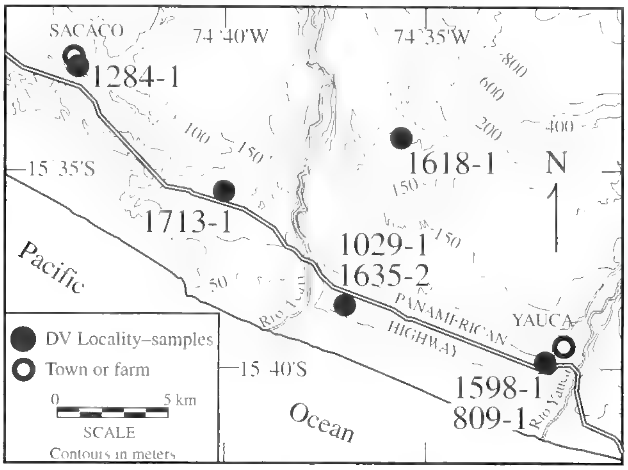


**Figure 64.** Type locality (DV 1598-1) of *Cantallocostoma panistostum* new species and other teguline localities between Sacaco and Yauca.

**Other Material Examined:** UWBM 97891, DV 571-1, late Miocene, L = 10.4, W = 14.9; MUSM INV 141, DV 1635-2, early Pliocene, L = 8.8, W = 14.3.

**Occurrence:** Late Miocene to early Pliocene: southern Peru.

**Etymology:** "Panis," Latin noun meaning "bread," and "tostum," Latin neuter past participle-adjective meaning "toasted," referring to the bread-crust color of this species.

**Remarks:** The light brown color of the outer shell layer on specimens of *Cantallocostoma panistostum* resembles that of specimens of *Tegula hemphilli* Oldroyd, 1921, a late Pliocene-to-Pleistocene species from California (Grant and Gale, 1931). Specimens of *T. hemphilli* and numerous other Miocene and Pliocene Californian teguline species with similar coloration lack the two umbilical spiral cords close to the axis and are covered by numerous closely spaced primary spiral cords, none of which are beaded.

Specimens of *Cantallocostoma panistostum* are found in upper Miocene nearshore sandstones with *Chlorostoma quipua*; *Chorus frassinetti* DeVries, 1997; *Acanthina obesa*; and *Xanthochorus stephanicus* DeVries, 2005; and in lower Pliocene cobbly bioclastic gravels associated with the mouth of the paleo-Río Yauca with disarticulated valves of an undescribed *Anadara* species, venerid bivalves, *Chlorostoma quipua*, *Xanthochorus ochuroma*, and *Concholepas nodosa* Möricke, 1896.

Genus *Intistoma* new genus

**Type species:** *Trochus aureotinctus* Forbes, 1852. Pleistocene to Recent, California.

**Diagnosis:** Spiral sculpture of subsutural band of thick protractive nodes and peripheral and sub-peripheral primary spiral cords. Base with three thick, primary spiral cords. Umbilicus open.

**Description:** Shell up to 45 mm wide, spire angle about 75 degrees. Whorls four to five in number, quadrate to carinate; sutures weakly impressed. Protoconch unknown. Sculpture of thick rounded protractive axial ribs intersecting with an equally thick spiral cords, producing a broad subsutural spiral band of elongate protractive nodes, a near-basal peripheral band of stubby protractive nodes more numerous than nodes in the subsutural band, and a sub-peripheral primary spiral cord with little axial modification. Tertiary threads sometimes present; often corrugated by slightly raised strongly oblique lamellar growth lines. Umbilicus open. Columella thin; parietal flange erect to slightly overhanging umbilicus; parietal callus small. Umbilical veneer thick, covering all but wedge-shaped adapertural portion of umbilical wall. Umbilical spiral cord submerged in umbilical wall, emergent terminally as prominent columellar tooth. Smaller second columellar tooth sometimes present abaxially adjacent to first tooth.

**Etymology:** "Inti," the Inca sun god, with a nod to California's sunshine and the sunset-orange color inside the umbilicus of the type species, *Intistoma aureotinctum*.

**Occurrence:** Late Miocene or early Pliocene: southern Peru. Early Pleistocene to Recent: California.

**Remarks:** The new genus, *Intistoma*, is proposed for two very similar species: the Pleistocene-to-Recent Californian *Intistoma aureotinctum* and the early Pliocene Peruvian *I. pirqua* new species. Specimens of both species differ from those of nearly all other teguline taxa by possessing three thick primary spiral cords on the base, rather than cords that are more numerous and thinner. Specimens of *Intistoma* additionally differ from those properly assigned to *Agathistoma* by lacking teeth on the floor of the aperture and the inner edge of the outer lip and by lacking closely spaced beaded primary spiral cords.

*Intistoma aureotinctum* has been considered the extant representative of a lineage of Californian Neogene tegulines (Addicott, 1970) that includes the early Miocene *Tegula dalli arnoldi* Addicott, 1970, the late Miocene *Tegula nashae* Clark, 1915, and Pliocene *Tegula hemphilli* Oldroyd, 1921. Specimens of fossil Californian species do have a subsutural band of elongate protractive nodes, as do specimens of *Intistoma*, and some have thick peripheral spiral cords, but none have the distinctive intistomine combination of thick basal spiral cords and tertiary spiral threads across the entire surface of the whorls

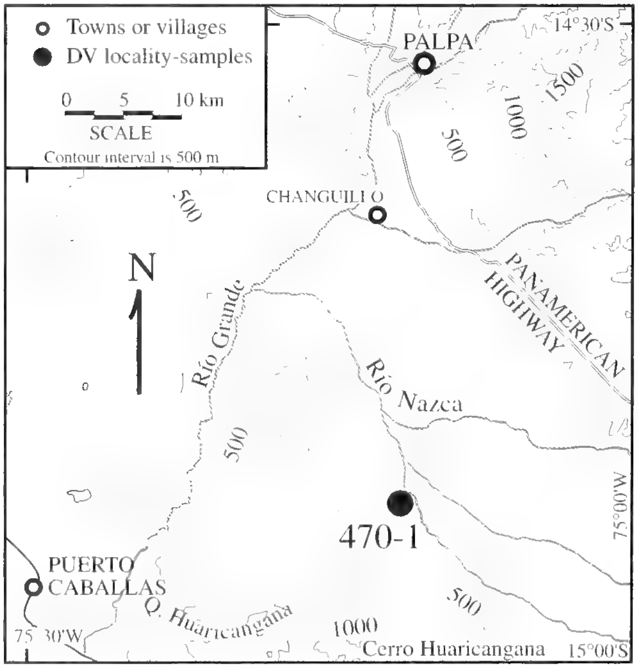
*Intistoma pirqua* new species
(Figures 55–57)

**Diagnosis:** Shell large, weakly bicarinate, with posterior row of protractive nodes. Base of shell with three broad spiral cords. Umbilicus open.

**Description:** Shell large, width more than 40 mm; spire angle about 60 degrees. Whorls ventricose, weakly bicarinate; sutures deeply impressed. Protoconch unknown; early spire whorls missing; teleoconch of at least three whorls. Last whorl with sculpture of about 18 elongate protractive ribs on posterior half of whorl; with about 21 circular to slightly protractively elongate nodes at periphery, two-thirds the distance from suture to base; and with a continuous low broad spiral cord at edge of base. Base with three low broad spiral cords, innermost cord bordering umbilical area and twice as wide as other two cords. Faint traces of secondary spiral cords in interspaces laterally and basally. Aperture oblique, outer lip and colabral growth lines moderately prosocline (40 degrees). Umbilicus open. Columella with at least one tooth, directed basally; anterior portion partly excavated, partly missing. Floor of aperture partly missing; no teeth evident.

**Type Locality:** DV 470-1, above rocky road from Hacienda Tunca to Quebrada Huaricangana; hillside of brown sandstone (Figure 65). 14°56′ S, 75°09′ W (Palpa 1:100,000 quadrangle). Upper Miocene or lower Pliocene.

**Type Material:** (DV 470-1, syntypes, late Miocene or



**Figures 65.** Type locality (DV 470-1) of *Intistoma pirqua* new species.

early Pliocene) UWBM 97892, L = (38.9), W = 43.4; MUSM INV 142, L = (32), W = (42).

**Occurrence:** Late Miocene to early Pliocene: southern Peru.

**Etymology:** "Pirqua," Latinized version of "pirqa," Quechua word for "wall," referring to the similarity of this species's sculpture and Incaic stone walls.

**Remarks:** The type specimens of *Intistoma pirqua* closely resembles specimens of *I. aureotinctum* (Figures 58, 59), differing principally by being twice the size in all dimensions and by having better developed nodes on the peripheral spiral cord. The specimens of *I. pirqua* were found together with specimens of *Chlamys simpsoni* (Philippi, 1887) and *Panopea coquimbensis* (d'Orbigny, 1842), both species from lower Pliocene beds in Chile (Herm, 1969) and southern Peru (Muizon and DeVries, 1985).

Genus *Agathistoma* Olsson and Harbison, 1953

**Type Species:** *Trochus viridulus* Gmelin, 1791 (by original designation). Recent, Caribbean and northeastern South America.

**Remarks:** One of two Recent specimens of *Agathistoma patagonicum* from Argentina (UWBM 97893) lacks an open umbilicus (Figure 61), as do some specimens of the Pliocene Sierra Laziar outcrops in Argentina (Ihering, 1907), suggesting either that the character is not diagnostic for all species of *Agathistoma* (Olsson and Harbison, 1953) or that the species in question might not be a member of the *Agathistoma* group.

*Agathistoma patagonicum* (d'Orbigny, 1835)
(Figures 60–63)

*Trochus* (*Monodonta*) *patagonicus* d'Orbigny, 1835, vol. 3(4), p. 155; d'Orbigny, 1840, vol. 5(3), p. 408, pl. 55, figs. 1–4.
*Neomphalius patagonicus* (Orb.). —Ihering, 1907: 400.
*Tegula patagonica* Orbigny.—Dall, 1909: 240; Alamo and Valdivieso, 1997: 14; Forcelli, 2000: 62, fig. 89.
*Tegula* (*Agathistoma*) *patagonica* (d'Orbigny, 1835).—Rios, 1985: 20, pl. 9, fig. 77; Del Río, 1998: 27, pl. 1, figs. 16–17.
*Trochus corrugatus* Philippi, 1844, Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien, v. 1, p. 67, pl. 2, fig. 7.
*Trochus fuscesens* Philippi, 1844, Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien, v. 1, p. 92, pl. 3, fig. 8.
*Trochus orbignyana* Pilsbry, 1900: 110; Carcelles, 1945: 38, pl. 1, figs. 6, 7, 12–15.

**Material Examined:** UWBM 97893, Cabo dos Bahías, Chubut Province, Argentina, Recent, L = 11.2, W = 15.4; UWBM 97894, Cabo dos Bahías, Chubut Province, Argentina, Recent, L = 11.6, W = 14.6; UWBM 97895, DV 1032-2, late Pliocene, L = (9), W = 12.7.

**Diagnosis:** Shell under 20 mm wide. Sculpture of closely spaced beaded primary spiral cords with intercalated secondary cords; beading sometimes obsolete. Columella with three teeth; umbilicus open or closed.

**Occurrence:** Late early to middle Miocene: Argentina (Ihering, 1907). Late Pliocene: southern Peru. Recent: northern Peru to Chile, southern Brazil to Argentina.

**Remarks:** A single incompletely preserved specimen of an agathistomine was found between Yauca and Chala in bioclastic deposits just below the highest marine terrace at 200 meters above sea level. Associated taxa that are either locally or entirely extinct [*Prisogaster valenciai* DeVries, 2006; *Acanthina triangularis* DeVries, 2003; *Chorus giganteus* (Lesson, 1830); *Concholepas camerata* DeVries, 2000; *Xanthochorus xuster* DeVries, 2005] are indicative of a late Pliocene age (DeVries, 1997; 2000; 2003; 2005; 2006).

The closely spaced beaded spiral cords on the southern Peruvian agathistomine resemble those on specimens of *Agathistoma verrucosum* McLean, 1970, and *A. pictum* McLean, 1970, Panamic species which presently range as far south as northern Peru (Alamo and Valdivieso, 1997), but the base of the Peruvian Pliocene specimen is not as flattened as it is on specimens of the northern Peruvian species and the spiral cords are more closely spaced, suggesting an assignment to *A. patagonicum*.

Genus or Subgenus indeterminate

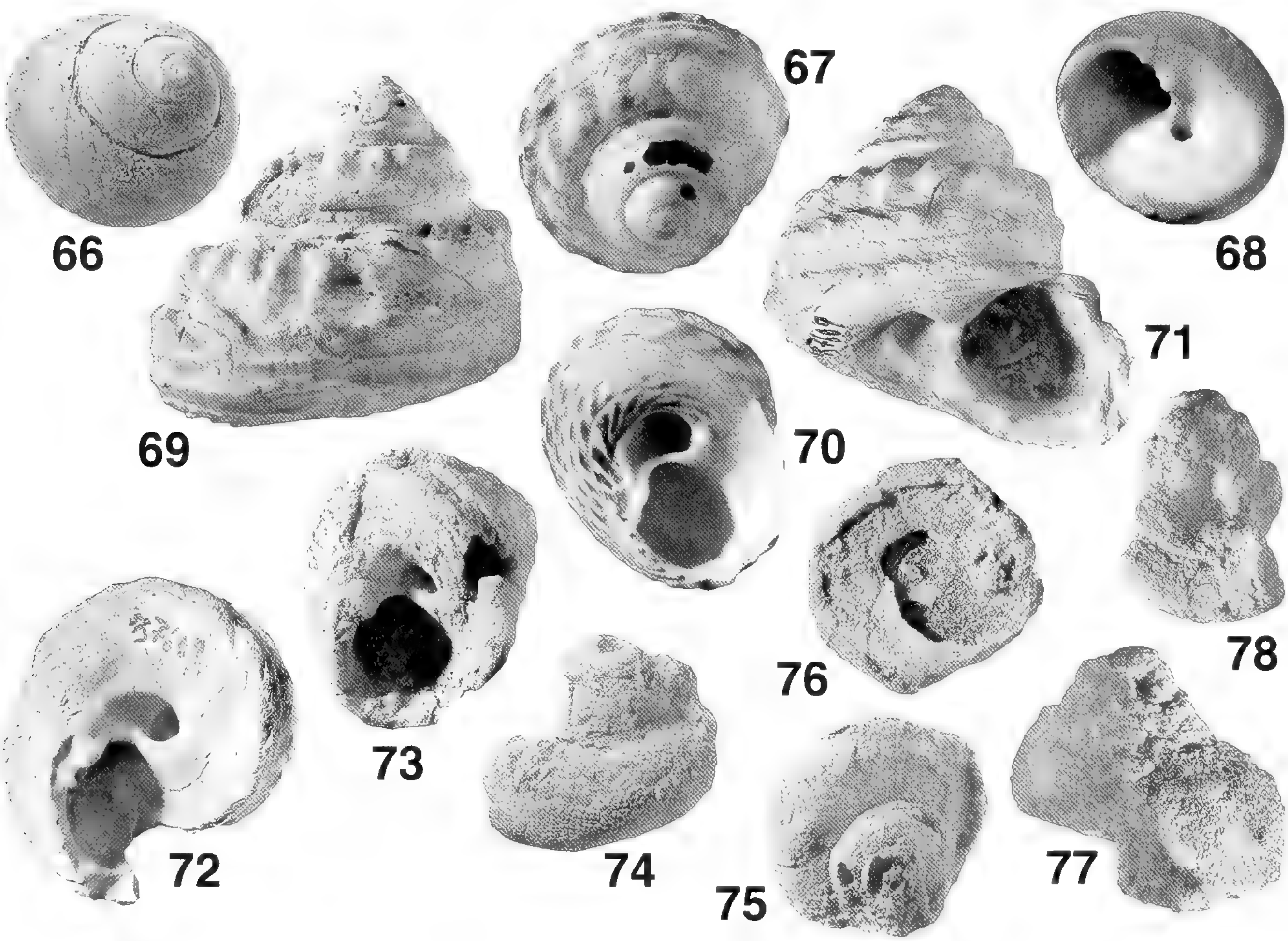
*Tegula* (s.l.) *tridentata* (Potiez and Michaud, 1838)
(Figures 66, 68)

*Monodonta tridentata* Potiez and Michaud, 1838, vol. 1, p. 321, pl. 29, figs. 16–17.
*Trochus tridentatus* Potiez and Michaud.—Philippi, 1846, Die Kreiselschnecken oder Trochoideen, p. 153, pl. 25, fig. 3.
*Tegula tridentata* (Potiez and Michaud).—Dall, 1909: 176; Carcelles and Williamson, 1951: 262; Herm, 1969: 91; Aldea and Valdovinos, 2005: fig. 8G.
*Tegula* (*Chlorostoma*) *tridentata* (Potiez and Michaud, 1838).—Marincovich, 1973: 24, fig. 43; Véliz and Vasquez, 2000: p. 761, fig. 1C; Guzmán et al., 1998: 36, fig. 24; Forcelli, 2000: 90, fig. 60.
*Trochus tridens* Hupé, 1854: 145.

**Material Examined:** UWBM 97898, DV 1372-1, Recent, L = 7.0, W = 9.9; UWBM 97899, DV 401-1, Recent, lot of 5; UWBM 97900, DV 381-5, middle Pleistocene, L = (11.7), W = 14.0.

**Occurrence:** Middle Pleistocene: southern Peru to central Chile. Recent: northern Peru to southern Chile.

**Remarks:** *Tegula tridentata* is a small, high-spired, purple-black species with an excavated white base. The exterior is usually smooth, but some specimens have low broad primary spiral cords on juvenile whorls. A narrow open umbilicus is bordered by a white columella with three teeth. The two teeth closest to the axis lie at the end of umbilical spiral cords, the outermost of which is mostly submerged beneath a thick umbilical veneer. The third tooth is situated adjacent to the floor of the aper-



**Figures 66, 68.** *Tegula* (s.l.) *tridentata* (Potiez and Michaud, 1838). UWBM 97898, DV 1372-1, Recent, width = 9.9 mm. **66.** Oblique spiral view. **68.** Oblique basal view. **Figures 67, 69–72.** *Tegula* (s.l.) *melaleucos* (Jonas, 1844). **67.** UWBM 97901, Paracas Hotel, Recent, oblique spire view, width = 23.9 mm. **69.** OSU 37609, DV 211-3, late Pleistocene, lateral view, length = 28.2 mm. **70.** UWBM 97901, oblique basal view. **71.** OSU 37609, apertural view. **72.** OSU 37609, oblique basal view, width = 29.0 mm. **Figure 73.** *Tegula* (s.l.) (?) *rubroflammulata* (Koch in Philippi, 1843). OSU 37610, DV 341, early Pleistocene, oblique basal view, width = 22.0 mm. **Figures 74–78.** *Tegula* (s.l.) *masiasi* new species. **74.** UWBM 97904, DV 478-1, early Miocene, lateral view, length = 16.6 mm. **75.** UWBM 97903, DV 1019-1, holotype, middle Miocene, oblique spire view, width = 15.9 mm. **76.** UWBM 97903, basal view. **77.** UWBM 97905, DV 1648-1, early Miocene, lateral view, length = 14 mm. **78.** UWBM 97905, basal view showing edge of umbilical area, width = 16.9 mm.

ture. The inside of the outer lip often has four to six short elongate teeth. In the latter three characters the species resembles *Cantallocostoma quadricostatum*, with which it has been grouped using mitochondrial DNA sequences by Hellberg (1998), who placed the species with *Agathistoma*. In its color and obsolete spiral sculpture, however, "*tridentata*" specimens greatly resemble Peruvian species of *Chlorostoma*, to which they were assigned by Marincovich (1973) and Guzmán et al. (1998). The only fossil example of *T. tridentata* in Peru comes from a middle Pleistocene marine terrace bed near San Juan de Marcona, southern Peru.

### *Tegula* (s.l.) *melaleucos* (Jonas, 1844)
(Figures 67, 69–72)

*Trochus melaleucos* Jonas, 1844: 169; Philippi, 1846, Die Kreiselschnecken oder Trochoideen, p. 185, pl. 28, fig. 16.
*Tegula melaleucos* (Jonas). —Dall, 1909: 239.
*Tegula* (*Agathistoma*) *melaleucos* (Jonas, 1844).—Keen, 1971: 340, fig. 106; Alamo and Valdivieso, 1997: 13, fig. 22.
Not *Tegula* (*Agathistoma*) *melaleucos* (Jonas, 1844).—DeVries, 1986: 515, pl. 27, figs. 1, 2, 10, 12 [possibly *Tegula* (s.l.) *rubroflammulata* (Koch in Philippi, 1843)].

**Material Examined:** OSU 37609, DV 211-3, late Pleistocene, L = 28.2, W = 29.0; UWBM 97901, Paracas Hotel, Recent, L = 17.3, W = 23.9; UWBM 97902, northern Peru, Recent, L = (11.5), W = 20.1. Specimens assigned to *Tegula melaleucos* by DeVries (1986) but more likely belonging to *Tegula* (s.l.) *rubroflammulata*: OSU 37610, DV 341, early Pleistocene, L = 22.0, W = 22.0; OSU 37611, DV 341, L = (14.8), W = (18.0).

**Occurrence:** Recent: northern Peru; rarely in southern Peru.

**Remarks:** Specimens of *Tegula melaleucos* are characterized by a strongly bicarinate periphery, a line of protractive nodes between the periphery and suture, and protractive brown stripes laterally and basally, where they spiral into an open umbilicus. A single spiral cord emerges from the umbilicus and is truncated by a columellar ridge that ends in a basally projecting tooth. A second prominent tooth protrudes at the juncture of the columella with the floor of the aperture, and additional small teeth may occur along the edge of a beveled ledge that passes just inside the floor of the aperture.

Imperfectly preserved specimens of *Tegula* from the uppermost Pliocene / lower Pleistocene Mancora Tablazo of northern Peru (Figure 73; DeVries, 1986; 1988) have less impressed sutures and more convex profiles than typical specimens of *T. melaleucos* and nodes near the suture that are not protractive. These specimens are better referred to *T. rubroflammulata*, a Recent species that had been reported to range only as far south as Colombia (Keen, 1971).

*Tegula* (s.l.) *masiasi* new species
(Figures 74–78)

**Diagnosis:** Spire whorls with broad spiral cords; umbilicus narrow, open; shell lacking purple-black outer layer.

**Description:** Shell conical, up to 16 mm wide. Spire angle about 70 degrees. Periphery at base; angular. Sutures appressed to impressed. Protoconch unknown; teleoconch with at least four flat-sided to convex whorls. Axial sculpture absent; colabral growth lines strongly prosocline. Spiral sculpture absent or with several broad, low spiral cords on spire. Outer shell layer lacking purple-black color. Base flattened to weakly convex, without visible spiral sculpture. Inner side of outer lip smooth. Umbilicus open. Columella thin, with at least one tooth at end of umbilical cord. Parietal flange barely overhanging umbilicus.

**Type Locality:** DV 1019-1, Gramonal, about one-half km east of mouth of Quebrada Gramonal, on bluff overlooking road to Fundo Santa Rosa (Figure 79). 14°45′50″S, 75°30′22″W (Lomitas 1:100,000 quadrangle). Lower middle Miocene.

**Type Material:** UWBM 97903, DV 1019-1, holotype, early middle Miocene, L = (7), W = 15.9.

**Other Material Examined:** UWBM 97904, DV 478-1, early Miocene, L = 16.6, W = (21.8); UWBM 97905, DV 1648-1, early Miocene, L = 14.0, W = 16.9; MUSM INV 143, DV 1648-1, L = 14.6, W = 19.8

**Occurrence:** Early to early middle Miocene: southern Peru.

**Etymology:** Named in honor of Antonio Masias, petroleum geologist from Arequipa, Peru, who has provided advice on Peruvian matters since we both attended Oregon State University in 1977–1978.

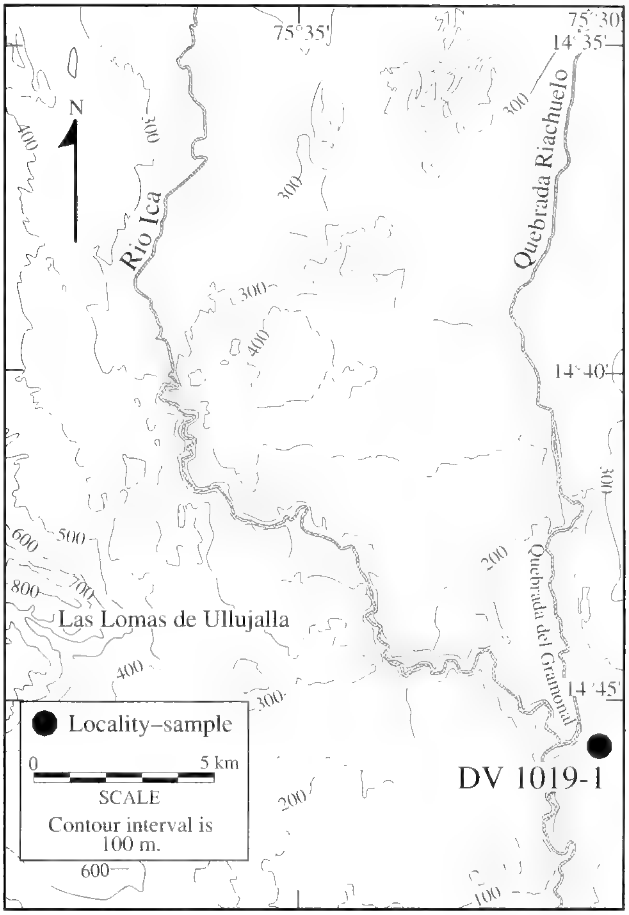


**Figure 79.** Type locality (DV 1019-1) of *Tegula* (s.l.) *masiasi* new species.

**Remarks:** Specimens of *Tegula* (s.l.) *masiasi* are the oldest known tegulines from the Pisco Basin; they occur near the base of a depositional sequence that unconformably underlies the Pisco Formation near Cerros Colorado (Figure 78), which implies the lower portion of the uppermost Oligocene to lower middle Miocene Chilcatay Formation (DeVries, 1998), as well as a few tens of meters above the base of the Pisco Formation, which indicates an early middle Miocene age (DeVries and Schrader, 1997). Despite the poor state of preservation, it does appear that these early and middle Miocene specimens are not chlorostomines, which first appear with their purple-black outer shell layer in beds at Alto Grande at about 9–10 Ma (Muizon and DeVries, 1985; DeVries and Schrader, 1997).

## DISCUSSION

Fossils found since 1990 offer a new perspective on the origin of Tegulinae. Tegulines had been thought to have arisen during the early or middle Miocene (Hickman and McLean, 1990), based on knowledge of fossil taxa from Japan and California [e.g., *Tegula thea* Nomland, 1917, and *T. varistriata* Nomland, 1917, Santa Margarita beds, California, upper Miocene (Nomland, 1917); *T. dalli* Arnold, 1907, and *T. dalli* var. *inornata* Arnold, 1907, Topanga Group, California, middle Miocene (Arnold, 1907; Yerkes and Campbell, 2005); *T. dalli arnoldi* Addicott, 1970, Olcese Sand, California, uppermost lower Miocene (Addicott, 1970; Sanchez and Prothero, 2003)]. The discovery of *T. jeanae* Squires and Saul, 2005, a late Campanian species from the Chico Formation of California with many attributes of *Chlorostoma* (ventricose whorls, black-brown outer shell layer, absence of beaded spiral cords), recasts discussions of teguline phylogeny (Squires and Saul, 2005). A flat-sided, spirally beaded Cretaceous teguline, the late Maastrichtian *T. ovallei* Philippi, 1887, from central Chile (Bandel and Stinnesbeck, 2000), further demonstrates the pre-Miocene diversity and geographic distribution of tegulines.

As a consequence of these Cretaceous discoveries, an evolutionary scenario rejected by Hickman and McLean (1990), which placed the plesiomorphic *Tegula* near the base of the trochid group, gains credence, whereas scenarios inspired by the molecular data of Hellberg (1998) that presumed a strictly late Neogene timeline for teguline phylogeny are undermined by these Cretaceous data, as well as by early, middle, and late Miocene occurrences of tegulines in Peru.

The following observations provide some further constraints on phylogenetic hypotheses related to Tegulinae.

## PERUVIAN CHLOROSTOMINE GROUP

The Peruvian chlorostomine group is comprised of four modern species: *Chlorostoma atrum*, *C. ignotum*, *C. euryomphalum*, and *C. luctuosum*. Gradations of sculpture indicate the latter two species may be one; *C. luctuosum* would be the senior synonym. Adding *C. quipua* extends the record of Peruvian chlorostomines to 9 Ma (Muizon and DeVries, 1985). This late Miocene occurrence precludes Hellberg's (1998) molecularly based hypothesis that these chlorostomines appeared in western South America during the late Pliocene and constitute a sister group to a North Atlantic Pliocene group of *Agathistoma* species.

The flattened base, open umbilicus, and spiral threads of *Chlorostoma quipua* indicate that it is most closely related to the modern *C. luctuosum*. Some specimens of *C. quipua* from upper Pliocene beds above Playa Huacllaco also have broad spiral cords like those on some specimens of modern *C. atrum*. A single upper Pliocene Huacllaco specimen has strongly convex spiral cords like those on specimens of the modern Chilean *C. ignotum*. This morphological variation suggests the onset of a radiation of South American chlorostomines near the end of the Pliocene. The late Pliocene was also a time of species-level molluscan mass extinction throughout the Peruvian Faunal Province (DeVries, 2001).

The origin of chlorostomines in Peru and Chile is not known. Tegulines are found, rarely, in lower and middle Miocene beds of southern Peru (*T.* (s.l.) *masiasi*; Figures 74–78), but they do not resemble late Neogene Peruvian *Chlorostoma*. Of Chilean Miocene species assigned to *Chlorostoma* (Nielsen et al., 2004), none exhibit the purple-black outer shell layer that characterizes the type species of *Chlorostoma* and most modern Peruvian chlorostomines. At three mm in length, *Tegula austropacifica* Nielsen, Frassinetti, and Bandel, 2004, is extraordinarily small for a chlorostomine. *Tegula chilena* Nielsen, Frassinetti, and Bandel, 2004, lacks the flattened base of chlorostomine species. *Tegula matanzensis* Nielsen, Frassinetti, and Bandel, 2004, resembles Californian specimens of *C. funebralis*, as the authors note, but the specimen lacks critical portions of the columella from which a better comparison can be made.

Chlorostomines appeared in southern Peru at the same time as the turbinid genus, *Prisogaster* Mörch, 1850 (DeVries, 2006), and mollusks with Panamic affinities (DeVries, 2006), an immigration pattern consistent with either a western North American or boreal Asian origin for the group. Molecular data (Hellberg, 1998) indicate Peruvian chlorostomines are more similar to Californian than Asian taxa. Shell characters are equivocal on this point. Protractive stripes, present on specimens of the oldest Peruvian chlorostomine, *C. quipua*, are also seen on some specimens of Californian *C. gallina*, *C. rugosum*, and Asian *C. nigerrimum* and *C. rusticum*. Protractive ribs, which occur in rare examples of *C. quipua*, are found on some specimens of the Californian "*Tegula*" *brunnea* and several Asian species. Imbricate subsutural spiral cords, which occur rarely on juvenile whorls on specimens of *C. atrum*, are most characteristic of the Californian *C. funebralis* (Figures 5, 6), are weakly developed on specimens of the Californian *C. gallina* and *C. rugosum*, and are not seen on specimens of Asian species.

Peruvian chlorostomines are distinguished from all Californian chlorostomines and all Asian taxa except a few specimens of *C. rusticum* by possessing a very thin and expansive umbilical veneer that does not bury the spiral umbilical cord. A thicker umbilical veneer drapes across the spiral umbilical cords in Californian and Asian specimens, largely burying the spiral umbilical cord and leaving visible only a blunt adaxial columellar tooth, a tooth at the base of the columella, and an intervening depressed nacreous wedge (e.g., *Chlorostoma funebralis*; Fig. 6). Peruvian chlorostomines also lack a second well developed tooth at the base of the columella, a character usually seen on Californian and Asian chlorostomine specimens (Fig. 6). These two derived characters–thin umbilical veneer, obsolete basal columellar tooth–may indicate that Peruvian chlorostomines are a sister group to Californian+Asian chlorostomines, with a common ancestor in the North Pacific Ocean older than late Miocene.

## *CANTALLOCOSTOMA* GROUP

*Cantallocostoma* is an endemic western South American genus characterized by beaded spiral cords and two adaxially situated spiral umbilical cords. *Cantallocostoma panistostum* appears first in upper Miocene beds of southern Peru with other Panamic species (DeVries, 2002). It and the extant *C. quadricostatum* are unlike any Neogene or Recent teguline from Peru or Chile. Specimens of *Cantallocostoma* share with specimens of *Intistoma* the presence of two adaxially situated spiral umbilical cords (mostly covered by a thick umbilical veneer in specimens of *Intistoma*) and an erect columella with little in the way of a parietal flange or callus. Genetic data of Hellberg (1998), however, show no close affinity between *C. quadricostatum* and *I. aureotinctum*.

### INTISTOMA GROUP

*Intistoma* has been created to include two very similar species, the modern Californian *I. aureotinctum* and early Pliocene Peruvian *I. pirqua*. Their distinctive spiral sculpture (strong bicarinate periphery, protractive subsutural nodes, three broad basal spiral cords), absence of a purple-black outer shell layer, absence of apertural teeth, and the isolation of *T. aureotinctum* in mtDNA phylogenies (Hellberg, 1998) indicate that neither *Chlorostoma* nor *Agathistoma* properly encompass these taxa.

Two other groups, one consisting of the modern northern Peruvian / Panamic *Tegula* (s.l.) *melaleucos* and possibly *T.* (s.l.) *rubroflammulata*, the other comprising Miocene and Pliocene species from California [e.g., *T.* (s.l.) *dalli*], exhibit the distinctive subsutural spiral row of protractive nodes of *Intistoma*, but both lack the three broad basal spiral cords that characterize the new genus. The Californian Neogene species also lack the differentiation of spiral sculpture (coarse primary spiral cords, fine tertiary spiral threads overrunning primary spiral cords and interspaces) that is visible on well-preserved specimens of *I. aureotinctum*.

### *Tegula* (s.l.) *tridentata* (Potiez and Michaud, 1838)

*Tegula* (s.l.) *tridentata* is a small teguline with a record in Peru and Chile extending no farther back than the middle Pleistocene. The distinctive purple-black exterior is shared with Peruvian chlorostomines, but the arrangement and number of columellar teeth is like that of Panamic species of *Agathistoma*. Mitochondrial DNA data (Hellberg, 1998) are not helpful on this point of phylogeny, as *T.* (s.l.) *tridentata* usually clusters with *Cantallocostoma quadricostatum*, which it resembles in only one significant shell character: two adaxial umbilical spiral cords, both terminating in a columellar tooth. For now, the proper phylogenetic assignment of *T.* (s.l.) *tridentata* remains elusive.

### AUSTRAL *AGATHISTOMA*

Panamic agathistomines, which are so speciose in warm waters of the Panamic Faunal Province, have been notably unsuccessful in penetrating the cold waters of the Peruvian Faunal Province. The only fossil agathostomine from western South America is a specimen from upper Pliocene beds of southern Peru assigned to *Agathistoma patagonicum*. A Miocene agathistomine reported from central Chile, *Agathistoma antiquum* Nielsen, Frassinetti, and Bandel, 2004, a Miocene occurrence of *A. patagonicum* reported from Argentina (Ihering, 1907; del Río, 1998), and an extensive record of modern *Agathistoma patagonicum* from southern Brazil to southern Argentina, including the Magellanic waters of Argentina (Carcelles and Williamson, 1951), if the synonymy of *A. fuscesens* and *A. orbignyana* with *A. patagonicum* is accepted (Forcelli, 2000), may point to a Miocene austral origin for the subgenus (Nielsen et al., 2004), rather than the Pliocene western Atlantic origin suggested by Hickman and McLean (1990). Alternatively, the monophyly of *Agathistoma* might be suspect; compact, beaded, multi-toothed austral tegulines with or without open umbilici might constitute a long-lived sister group to a group of Caribbean and Central American species.

## CONCLUSIONS

Pre-late Miocene tegulines in southern Peru are exceedingly rare, poorly preserved, and bear little resemblance to late Neogene or extant taxa. During the early late Miocene, at least two lineages of tegulines, *Chlorostoma* and *Cantallocostoma*, entered Peruvian waters. It is unclear whether these two genera originated in California or Asia. Other trochids, namely *Diloma* Philippi, 1845, are thought to have dispersed across the Equator and across the Pacific Ocean from Australia, rafted by buoyant fragments of the brown kelp, *Durvillaea* Bory de Saint-Vincent, 1826 (Donald et al., 2005). Species of Peruvian *Tegula* likewise live upon on brown kelp (*Lessonia* Bory de Saint-Vincent, 1825) (Véliz and Vasquez, 2000; V. Mogollon, pers. comm., 2006), and thus may have been rafted to western South America from California or Asia in the same manner as *Diloma*.

Species of *Chlorostoma* and *Cantallocostoma* remained relatively unchanged until the end of the Pliocene, when a mass extinction swept away 80 percent of molluscan species in the Peruvian Faunal Province (DeVries, 2001). At that time, chlorostomines experienced a mini-radiation in southern Peru or Chile, with one species, *C. atrum*, eventually spreading to southern Argentina (Carcelles and Williamson, 1951). *Cantallocostoma panistostum* was replaced at the same time by the modern *C. quadricostatum*.

Another lineage of tegulines, represented by the early Pliocene *Intistoma pirqua*, appeared on Peruvian shores by the early Pliocene. Although the genus is now extinct in Peru, it persists in California in the guise of *I. aureotinctum*. It is likely that these species, with their broad basal spiral cords, are not related to the "*dall*" lineage of Californian tegulines that ranged from the early Miocene to Pliocene (Addicott, 1970).

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## APPENDIX

Locality-samples. GPS = latitude and longitude coordinates obtained by a hand-held GPS unit. GE = coordinates obtained from satellite images available on-line from Google Earth™.

| | |
|---|---|
| DV 211-3 | Punta Lobitos, northern Peru, western point, terrace surface midway between sea cliff and inshore edge of deposit. 04°27′12″S, 81°17′25″W (GE; Lobitos 1:100,000 quadrangle). Upper Pleistocene. |
| DV 341-1 | Quebrada Mogollon, northern Peru. Upper coquina of Mancora Tablazo. Lower Pleistocene. |
| DV 381-5 | San Juan-Lomas road, km 47.5. Uppermost coquina. 15°22′59″S, 75°03′11″W (San Juan 1:100,000 quadrangle). Middle Pleistocene. |
| DV 382-1 | San Juan / Lomas road, kilometer marker 50, flat-topped knoll south of highway. 15°22′02″S, 75°05′26″W (San Juan 1:100,000 quadrangle). Remnant of marine terrace. Upper Pleistocene. |
| DV 398-1 | Playa Canastones, Bahia de la Independencia, Peru (Punta Grande 1:100,000 quadrangle). Recent. |
| DV 401-1 | Hueco La Zorra, north end of beach. 14°02′31″S, 76°15′51″W (Punta Grande 1:100,000 quadrangle). Recent. |
| DV 463-1 | Lower terrace, five km north of Chala (Chala 1:100,000 quadrangle). Upper Pleistocene. |
| DV 470-1 | Above rocky road from Hacienda Tunca to Quebrada Huaricangana; hillside of brown sandstone. 14°56′ S, 75°09′ W (GE; Palpa 1:100,000 quadrangle). Lower Pliocene. |
| DV 478-2 | Lomas Chilcatay, northeast end of outcrop. 14°11′42″S 76°06′57″W (Punta Grande 1:100,000 quadrangle). Chilcatay Formation, lower Miocene. |
| DV 571-1 | Alto Grande, about one km south of intersection with abandoned paved road to San Juan de Marcona, on south-facing hillside west of Panamerican Highway; one of several shell banks. 15°26′57″S, 74°52′06″W (Acarí 1:100,000 quadrangle). Middle upper Miocene. |
| DV 809-1 | Yauca, roadcut on western side of Panamerican Highway as it descends to valley floor. 15°39′49″S, 74°31′50″W (Yauca 1:100,000 quadrangle). Pisco formation. Lower Pliocene. |
| DV 1019-1 | Gramonal, about one-half km east of canyon mouth. 14°45′50″S, 75°30′22″W (Lomitas 1:100,000 quadrangle). Middle Miocene. |
| DV 1029-1 | Yauca Depression, west of Pana merican Highway. 15°39′29″S, 75°35′08″W (GPS, Yauca 1:100,000 quadrangle). Lower Pliocene. |
| DV 1032-2 | Morro Abra de los Chaparrinos, descending from highest terrace level, north and south of second curve in Panamerican Highway. 15°52′59″S, 74°10′05″W (Chala 1:100,000 quadrangle). Upper Pliocene. |
| DV 1252-1 | Quebrada de la Vaca, roadcut along Panamerican Highway, south of south wall, uppermost terrace above non-marine deposits. 15°48′56″S, 74°18′50″W (GPS; Chala 1:100,000 quadrangle). |
| DV 1254-Bal 6 | Section along Panamerican Highway, ten km southeast of Chala and above Playa Huacllaco. 35 meters above basement rocks in measured section. 15°53′25″S, 74°09′52″W (GPS; Chala 1:100,000 quadrangle). Upper lower Pliocene. |
| DV 1254-Bal 10 | Section along Panamerican Highway, ten km southeast of Chala and above Playa Huacllaco. 47.5 meters above basement rocks in measured section. 15°53′25″S, 74°09′52″W (GPS; Chala 1:100,000 quadrangle). Upper Pliocene. |
| DV 1284-1 | Sacaco, shell banks southwest of north-south road to farmhouse (chacra). 15°33′03 S′, 74°43′50″W (GE; Yauca 1:100,000 quadrangle). Lower Pliocene. |
| DV 1355-1 | Quebrada Pongo, one km upstream from juncture with Quebrada Caracoles. 15°30′22″S, 74°45′40″W (GPS; Yauca 1:100,000 quadrangle). Upper Pliocene. |
| DV 1372-1 | Rocky beach on northwestern side of Punta Lomas (Acarí 1:100,000 quadrangle). Recent. |
| DV 1418-1 | East side of Acarí Depression, 15°34′50″S, 74°36′59″W (GPS; Yauca 1:100,000 quadrangle). Upper Pliocene |

| | |
|---|---|
| DV 1598-1 | Roadcut along Panamerican Highway, descent from north into Yauca. Shell beds. 15°39′49″S, 74°31′50″W (GPS; Yauca 1:100,000 quadrangle). Lower Pliocene. |
| DV 1599-1 | Hueco La Zorra, north end of beach (see DV 401-1). Recent. |
| DV 1635-1 | Yauca Depression, west of Panamerican Highway. 15°39′33″S, 75°34′54″W (GPS; Yauca 1:100,000 quadrangle). Lower Pliocene. |
| DV 1648-1 | Westward-facing side of valley, southwest of Cerros Colorado. 14°22′25″S, 75°53′52″W (GPS; Punta Grande 1:100,000 quadrangle). |
| DV 1713-1 | Marine terrace on east side of Panamerican Highway north of road to Acarí. 15°36′09″S, 74°41′08″W (GPS; Yauca 1:100,000 quadrangle). Lower Pleistocene. |
| JM 82-19 | Cerro El Huevo, northeast of San Juan de Marcona. 15°18′ S, 75°09′ W (San Juan 1:100,000 quadrangle). Upper Pleistocene. |
| JM 82-20 | Cerro El Huevo, northeast of San Juan de Marcona. 15°18′ S, 75°09′ W (San Juan 1:100,000 quadrangle). Upper Pleistocene. |
| WJZ 345 | Coquimbo, Chile. Pleistocene. Approximately 29°58′ S, 71°20′ W (GE). |
| Isla Ipun | Isla Ipun, Chile, shores of eastern embayments. 44°38′ S, 74°44′ W (GE). Recent. |
| Paracas Hotel | Beach south of Hotel Paracas, facing Bahía Paracas, southern Peru. 13°50′09″S, 76°15′ 19″W (GE, Pisco 1:100,000 quadrangle). |

# Three new species of *Paryphantopsis* (Gastropoda: Pulmonata: Charopidae) from the Nakanai Mountains, New Britain, Papua New Guinea

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## ABSTRACT

Recent surveys (February–March, 2005) of the terrestrial snail fauna of the Nakanai Mountains, central New Britain, Bismarck Archipelago have uncovered several undescribed species, including three new species of *Paryphantopsis*, a diverse genus of charopid snails, previously believed to be endemic to mainland New Guinea and adjacent islands of the Louisiade Archipelago. The three species are described using shell, genital, and radular morphology. Although the land snail fauna of New Britain is arguably the best sampled in Papua New Guinea, there has been little sampling in the interior mountains of the Nakanai, Whiteman, Baining, and Willaumez ranges, which harbor previously undetected species of terrestrial snails.

*Additional Keywords:* Pulmonata, Charopidae, *Paryphantopsis*, New Britain, Papua New Guinea

## INTRODUCTION

This is the third in a series of reports on the results of recent field surveys for terrestrial mollusks from Papua New Guinea. The previous two reports focused on species of *Paryphantopsis* from the eastern peninsula of mainland New Guinea (Slapcinsky, 2005) and nearby islands of the Louisiade Archipelago (Slapcinsky, 2006). This report reviews *Paryphantopsis* species collected during three weeks of field surveys in February and March 2005 from the Nakanai Mountains northwest of Pomio, East New Britain Province, Papua New Guinea (Figure 1). *Paryphantopsis*, a diverse genus of charopid snails endemic to New Guinea and surrounding islands, is comprised of 23 described species (Solem, 1970; Slapcinsky, 2005; Slapcinsky, 2006) that are distributed from Papua (Irian Jaya) to the Louisiade Archipelago and that, prior to this study, were not known from New Britain

Nearly all species of *Paryphantopsis* have distributions stricted to single mountain ranges or islands where they are found in hilly or mountainous terrain from 60 to 4000 meters elevation. In upland habitats they can be the most abundant snail species reaching densities of more than 10 individuals per square meter on Sudest and Rossel Islands in the Louisiade Archipelago (personal observation). Despite their small size (4–12 mm), their bright yellow body coloration and diurnal activity in exposed locations on tree trunks, vegetation and rotting wood make them among the most obvious snail species. These showy snails are under-sampled and recent surveys have nearly doubled the number of recognized species. Further sampling in New Guinea and surrounding islands will certainly uncover additional species of *Paryphantopsis* as well as many other more cryptic snail species.

New Britain, a large volcanic island, 35145 km$^2$, extending from 148° to 152° E longitude and from 4° to 7° S latitude, emerged in the late Miocene (8–10 mya). The island's basement rocks were deposited by volcanic activity, between the upper Eocene and the middle Oligocene. Volcanic activity ceased in the early Miocene leading to regional subsidence and the deposition of extensive reef complexes. At the end of the Miocene, subduction of the Solomon plate under the Bismarck plate led to renewed volcanism, resulting in a chain of young arc volcanoes along the northwestern coast of New Britain (Woodhead et al. 1998). At the same time, reef complexes along the south and eastern coasts of the island were rapidly uplifted, creating extensive karst mountains. One of these ranges, the Nakanai Mountains, contains the Southern Hemisphere's deepest caves, some nearly 1200 meters in depth (Audra et al. 2001). New Britain's isolation, complex geology, and extensive raised limestone have allowed the radiation of a diverse and largely endemic land snail fauna (Rensch, 1934; 1937) that is among the best surveyed in Papua New Guinea. However, rough karst terrain and lack of roads have limited nearly all surveys to coastal lowlands, and most taxa from interior mountains of the Nakanai, Whiteman, Baining, and Willaumez ranges are still poorly surveyed (Beehler,

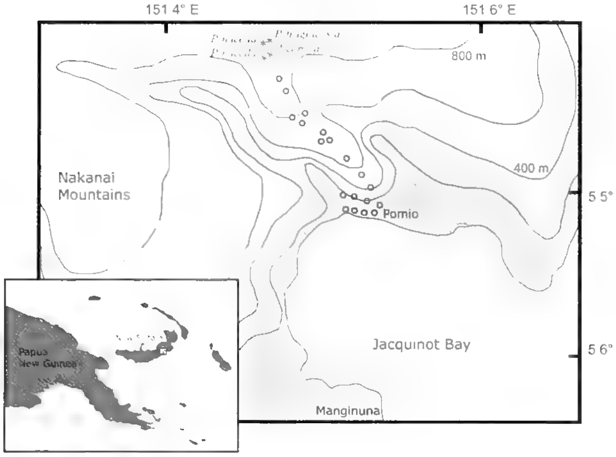


**Figure 1.** Distribution of *Paryphantopsis* in New Britain, Papua New Guinea; o = other sites sampled.

1993), even for macrofauna such as mammals (Flannary, 1995: 12) and birds (Orenstein, 1976). The invertebrate fauna of New Britain's interior mountains is almost entirely unknown. This is disturbing because intensifying land usage, including logging and the establishment of oil palm plantations (McAlpine and Fryne, 2001), threatens to deforest extensive areas of New Britain before they can be adequately inventoried, potentially leading to largely undocumented losses in biodiversity.

## MATERIALS AND METHODS

Specimens were hand-collected, drowned overnight, and then preserved in 75% ethanol. Gross anatomical dissections were made under 75% ethanol using a dissecting microscope. Radulae were isolated from dissected buccal masses using 5% sodium hypochlorite solution. Scanning electron micrographs of radulae were made using a Field Emission SEM. Line drawings of the genital anatomy were made from digital images, and measurements were taken using an ocular micrometer. Shell measurements were made as figured in Slapcinsky (2005). The following abbreviations are used in figures of genital anatomy: AT = atrium, DI = diverticulum, EP = epiphallus, OV = free oviduct, PE = penis, PG = prostate gland, PP = penial pilasters, PR = penial retractor muscle, SD = spermathecal duct, SP = spermatheca, VA = vagina, VD = vas deferens. Terminology of vegetation types follows Paijmans (1976). Specimens are deposited in the following institutions: Bernice P. Bishop Museum, Honolulu (BPBM); Florida Museum of Natural History, Gainesville (UF); Natur-Museum Senckenberg, Frankfurt (SMF); Papua New Guinea National Museum, Port Moresby (PNGNM); Wroclaw University Museum of Natural History (MNHW).

## SYSTEMATICS

Family Charopidae Hutton, 1884
Genus *Paryphantopsis* Thiele, 1928

**Type Species:** *Flammulina* (*Paryphantopsis*) *lamelligera* Thiele, 1928, by original designation.

*Paryphantopsis corolla* new species
(Figures 2–7, Table 1)

**Holotype:** UF 366508, J. Slapcinsky, 25 February 2005.

**Paratype:** UF 366453 (1 specimen), J. Slapcinsky, 25 February 2005.

**Type Locality:** Papua New Guinea, East New Britain Province, New Britain, 12 km northwest of Marmar Village on the trail to Pakia Village, 5.432° S, 151.460° E, 900 meters altitude (Figure 1).

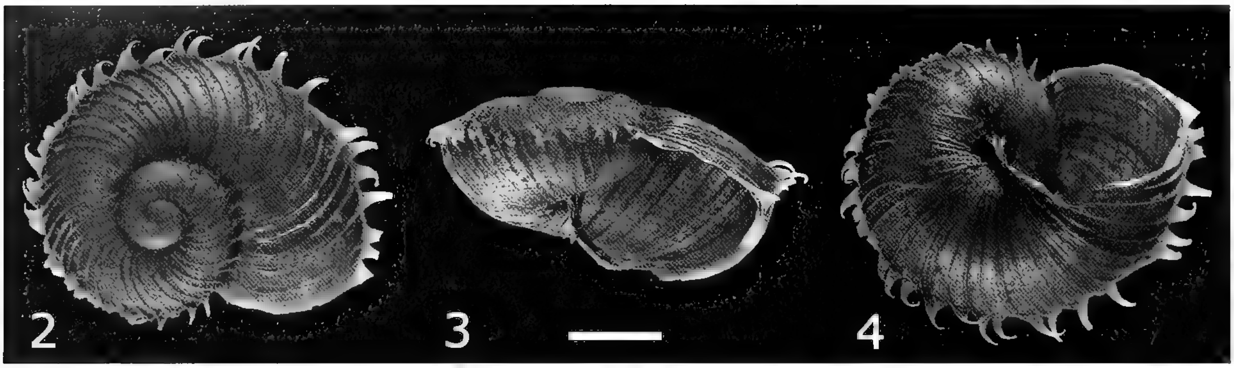
**Habitat:** Collected in mixed hill forest on vegetation within 1 m of the ground.

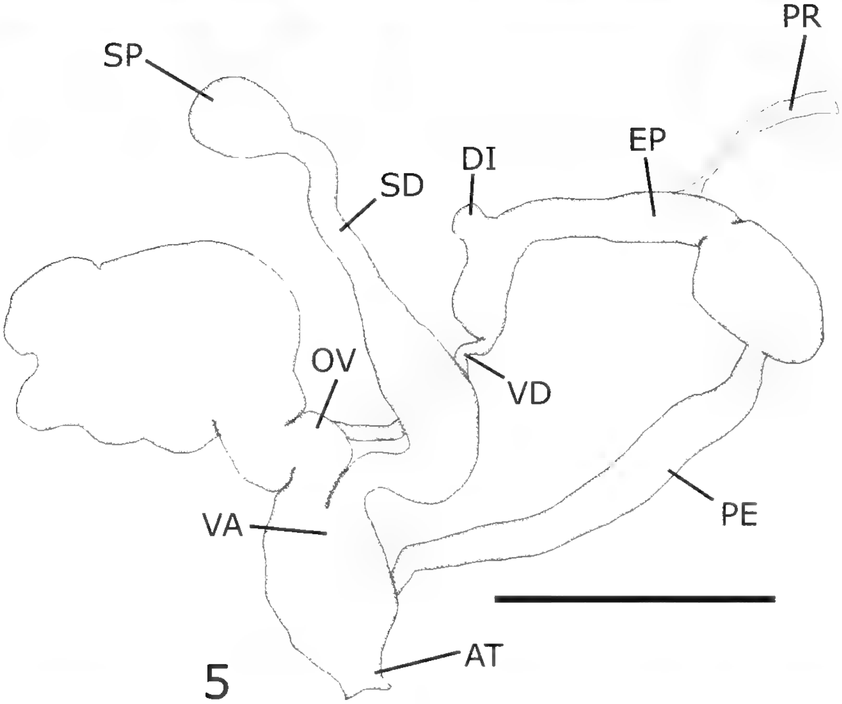
**Description:** The adult shell is depressed-globose, small for the genus, 3.5–3.6 mm (mean = 3.55, see Table 1 for sample size and standard deviation) in diameter and 2.2–2.3 mm (mean = 2.25) in height, with 2.5–2.6 (mean = 2.55) rapidly expanding whorls (Figures 2–4). The apical surface of the whorls flattens between the deep suture and the shell periphery which is slightly angular a little above its mid-point. The basal surface of the whorl is evenly rounded from the angular periphery to the umbilicus. The spire is slightly elevated, 0.1–0.2 mm (mean = 0.15). Teleoconch whorls descend slowly and regularly and shell height/diameter ratio is 0.61–0.66 (mean = 0.63). Approximately 1.3 rounded protoconch whorls are sculptured with 13 rows of spiral

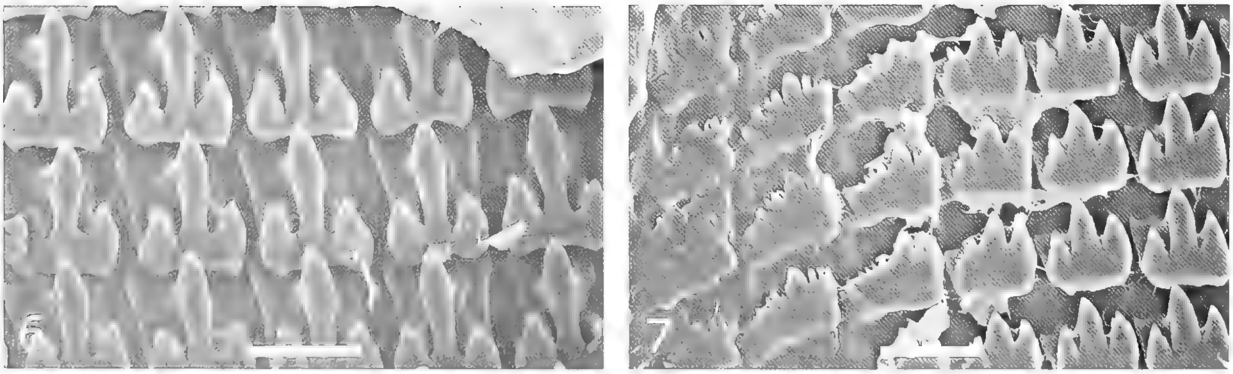
**Table 1.** Measurements in mm of undamaged adult shells of three species of *Paryphantopsis*.

| Species | N | | H | D | SH | SD | AH | AW | W |
|---|---|---|---|---|---|---|---|---|---|
| *P. corolla* | 2 | Mean ± SD | 2.25 ± 0.07 | 3.55 ± 0.07 | 0.15 ± 0.07 | 1.60 ± 0.00 | 1.60 ± 0.00 | 2.15 ± 0.07 | 2.55 ± 0.07 |
| | | Range | 2.2–2.3 | 3.5–3.6 | 0.1–0.2 | 1.6–1.6 | 1.6–1.6 | 2.1–2.2 | 2.5–2.6 |
| *P. fragilicosta* | 6 | Mean ± SD | 3.43 ± 0.18 | 5.00 ± 0.20 | 0.13 ± 0.05 | 2.33 ± 0.12 | 2.48 ± 0.16 | 2.92 ± 0.16 | 3.00 ± 0.09 |
| | | Range | 3.2–3.7 | 4.8–5.3 | 0.1–0.2 | 2.2–2.4 | 2.3–2.7 | 2.8–3.2 | 2.9–3.1 |
| *P. nucella* | 10 | Mean ± SD | 3.75 ± 0.32 | 5.22 ± 0.23 | 0.18 ± 0.04 | 2.06 ± 0.20 | 2.78 ± 0.27 | 3.16 ± 0.22 | 2.81 ± 0.12 |
| | | Range | 3.3–4.1 | 4.9–5.7 | 0.1–0.2 | 1.8–2.5 | 2.4–3.3 | 2.9–3.6 | 2.6–3.0 |

N = number of specimens, H = height, D = diameter, SH = spire height, SD = spire diameter, AH = aperture height AW = aperture width, W = number of whorls







**Figures 2–7.** *Paryphantopsis corolla*. **2–4.** Shell, Holotype UF 366508. Scale bar = 1 mm; Figure **5.** Genitalia, UF 366453. Scale bar = 1 mm. **6–7.** SEMs of radula, UF 366453. **6.** Central and lateral teeth. **7.** Marginal teeth. Scale bars = 10 μm.

pits, which continue on the teleoconch where the pits elongate nearly fusing to form incised spiral lines. These apical pits are typical of nearly all species of *Paryphantopsis* as, for example, in *Paryphantopsis louisiadarum* (see Solem, 1959: plate 13, fig 6). Approximately every third growth line is accentuated with a periostracal extension that bears a sharply pointed triangular process at the shell periphery. These processes are approximately 0.2 mm in length and 0.3 as wide at the base. The protoconch and teleoconch whorls are uniformly brown except for the columellar edge of the peristome and umbilicus, which are slightly darker brown. A reflection of the peristome covers approximately 0.4 of the umbilicus. The aperture is large and ovate with an aperture:width to aperture:height ratio of 1.31–1.38 mm (mean = 1.34).

The external body color is bright yellow in life and there are no bands or other color patterns. Specimens preserved in ethanol fade to uniform cream. The head is short similar to other species of *Paryphantopsis* and the posterior of the foot is slightly shorter than average for the genus.

The vas deferens is 0.2 the diameter of the head of the epiphallus which bears a short subapical diverticulum approximately 0.1 the length, and 0.6 the diameter of the epiphallus where they join (Figure 5). The apical 0.7 of the epiphallus is uniform in diameter; the basal 0.3 is twice as wide and ovoid. The penial retractor muscle is long and originates at the diaphragm, inserting 0.6 the way to the base of the epiphallus. The penis is approximately the same length as the epiphallus and the same diameter as the apical 0.7 of the epiphallus. The penis, narrow apically, widens slightly below the apex, and tapers basally to 0.2 the diameter of the atrium where they join. The atrium, widest at the insertion of the penis, narrows abruptly by 0.6 at the gonopore. The vagina narrows slightly at the junction with the free oviduct and spermathecal duct. The S-shaped free oviduct is 1.2 times the width of the spermathecal duct at their junction with the vagina. The diameter of the spermathecal duct doubles from its junction with the vagina distally to 0.4 the length, then narrows to 0.4 its greatest diameter at 0.7 the length, and remains narrow to the junction with the ovate spermatheca.

The central teeth of the radula (Figure 6, second from the right) are tricuspid, 7–8 μm wide and 11–12 μm long, of similar shape and length but slightly narrower and shorter than the first laterals, 8–9 μm wide and 12–13 μm long (Figure 6). The mesocones of both the centrals and first laterals are tall and slender, and project beyond their basal plates. The ectocones of the central teeth are trigonal and symmetric. Ectocones and endocones of the laterals are trigonal and about 0.5 the height of the mesocones. The endocones of the laterals are slightly larger but otherwise of similar shape to their ectocones. The first 5 teeth to the left and right of the central row are similar to the first lateral teeth, the next 3 teeth on either side grade in shape and are difficult to classify as either lateral or marginal teeth. The last 4 marginal teeth are wider, 10–11 μm wide, and shorter 7–8 μm long (Figure 7). Both the endocones and ectocones of the marginal teeth are irregularly multicuspid. The endocones are 0.9–0.8 as tall as the mesocones and usually bear 3 cusps, although these are sometimes divided into additional cusps. The ectocones sit on a rectangular base and are divided into 5 or more cusps that are 0.7 to 0.8 the height of the mesocones.

**Remarks:** The only other *Paryphantopsis* species with shells bearing periostracal processes are: *P. abstrusa* Slapcinsky, 2005; *P. fultoni* (Coen, 1922); *P. lebasii* Slapcinsky, 2005; *P. lamelligera* (Thiele, 1928); *P. striata* (Fulton, 1902); *P. yawii* Slapcinsky, 2005; and *P. yelensis* Slapcinsky, 2006. However, the periostracal processes in *P. corolla* do not overlap unlike *P. fultoni* and *P. yawii*, and are sharply pointed unlike *P. lebasii*. Also, the processes are prominent unlike *P. abstrusa* and *P. yelensis*. Finally, the shells of *P. lamelligera* and *P. striata* are more than twice the size of *P. corolla*. *Paryphantopsis corolla* has an epiphallus that is basally robust unlike all other *Paryphantopsis* species for which the genital anatomy is known except for *P. nucella* and *P. misimensis* Slapcinsky, 2006. In contrast to *P. corolla*, *P. nucella* has an apically inflated penis in addition to a large dark glandular area on the spermathecal duct, and *P. misimensis* lacks an apical diverticulum. The ectocones of the marginal teeth sit on a rectangular extension of the tooth, unlike all other *Paryphantopsis* for which the radular morphology is known other than *P. fragilicosta* and *P. nucella*.

**Etymology:** The species name is from the Latin feminine noun *corolla* and describes the shells resemblance to a small garland or crown.

*Paryphantopsis fragilicosta* new species
(Figures 8–13, Table 1)

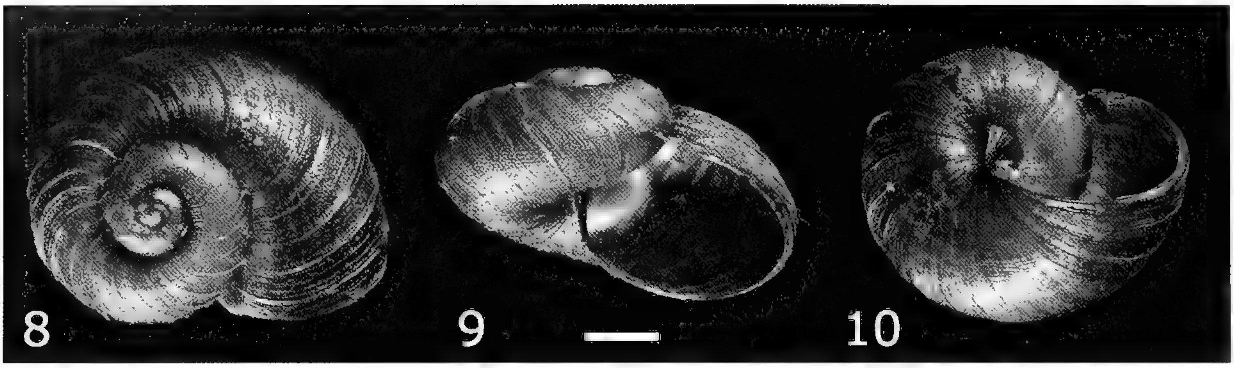
**Holotype:** UF 383995, J. Slapcinsky, 28 February 2005.

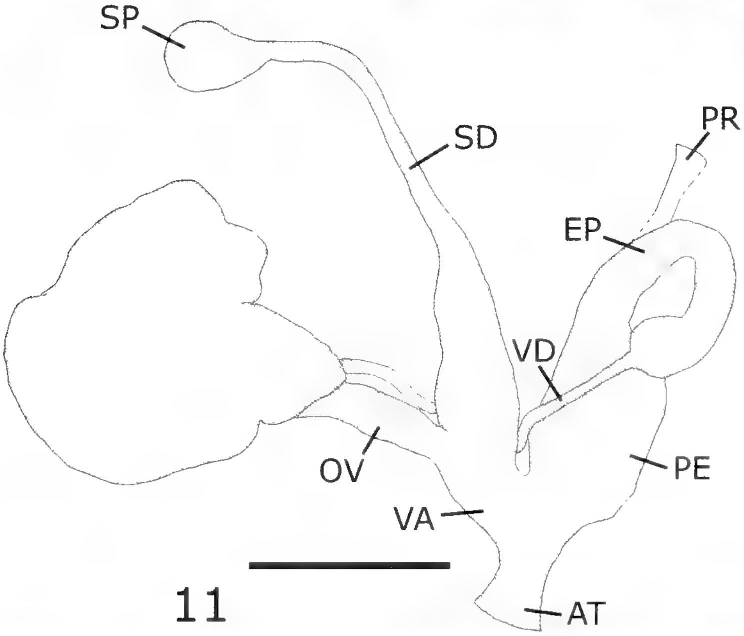
**Paratypes:** Papua New Guinea, East New Britain Province, type locality, J. Slapcinsky, 28 February 2005, BPBM 282461 (2 specimens), PNGNM (1 specimen), UF 366505 (4 specimens), UF 366507 (9 specimens).

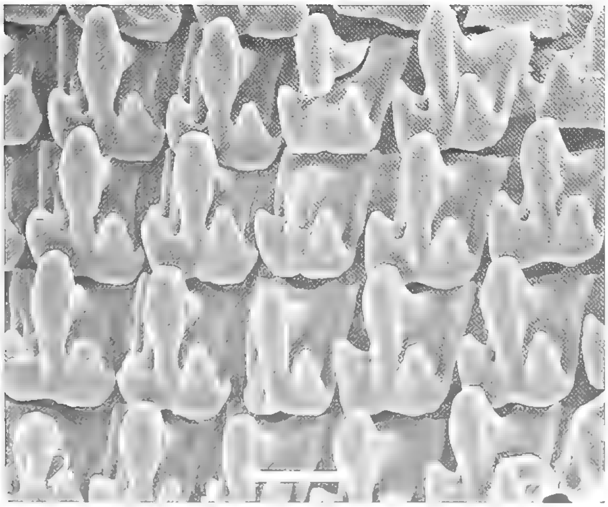
**Type Locality:** Papua New Guinea, East New Britain Province, New Britain, Saukale, 13 km northwest of Marmar Village on the trail to Pakia Village, 5.426° S, 151.453° E, 910 meters altitude (Figure 1).

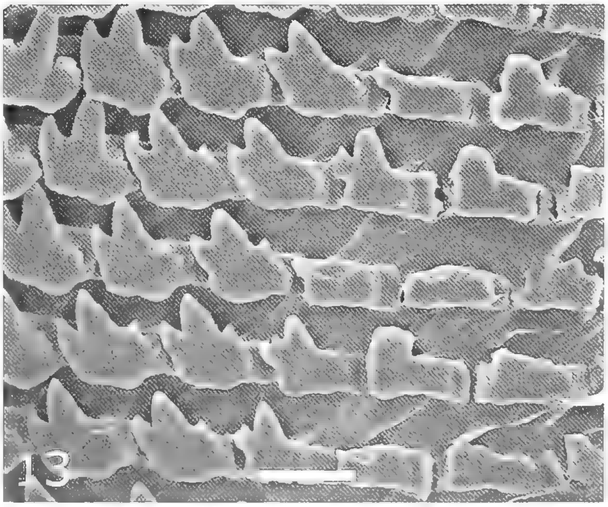
**Habitat:** Collected in mixed hill forest on vegetation within 1 meter of the ground.

**Description:** The adult shell is globose to depressed-globose, average size for the genus, 4.8–5.3 mm (mean = 5.00, see Table 1 for sample size and standard deviation) in diameter and 3.2–3.7 mm (mean = 3.43) in height, with 2.9–3.1 (mean = 3.00) rapidly expanding whorls (Figures 8–10). The suture is deeply impressed and the shell periphery is evenly rounded. The spire is slightly elevated, 0.1–0.2 mm (mean = 0.13). Teleoconch whorls descend slowly and regularly until the end of the body whorl, which descends slightly more rapidly. The shell









**Figures 8–13.** *Paryphantopsis fragilicosta.* **8–10.** Shell, Holotype UF 383995. Scale bar = 1 mm. **11.** Genitalia, UF 366507. Scale bar = 1 mm. **12–13.** SEMs of radula, UF 366507. **12.** Central and lateral teeth. **13.** Marginal teeth. Scale bars = 10 µm.

height:diameter ratio is 0.65–0.71 (mean = 0.69). There are approximately 1.4 evenly rounded protoconch whorls sculptured with 13 spiral rows of small pits which continue on the teleoconch where the pits elongate nearly fusing to form discontinuous spiral striae. Short periostracal extensions that do not bear periostracal processes are present approximately every four growth lines. These extensions are often worn or absent in older adult shells. The protoconch and teleoconch whorls are usually uniformly brown, shiny, and translucent, although older worn shells can be dull brown, opaque, with a white protoconch. The umbilicus is closed or nearly closed by a reflection of the peristome. The aperture is large and ovate, with an aperture:width to aperture:height ratio of 1.08–1.28 (mean = 1.18).

The external body color is bright yellow in life and there are no bands or other color patterns. Specimens preserved in ethanol fade to uniform cream. The head is short similar to other species of *Paryphantopsis* and the posterior of the foot is of average length for the genus.

The vas deferens is 0.2 the diameter of the slightly inflated head of the epiphallus which does not bear a diverticulum (Figure 11). The epiphallus is approximately 1.5 the length and 0.5 the diameter of the penis and widens only slightly at the junction with the penis. The penial retractor muscle is moderate in length, originating from the diaphragm and inserting at the basal 0.3 of the epiphallus. The penis is robust and of uniform width apically, narrowing basally to 1.2 the width of the atrium just before their junction. The atrium narrows slightly and then broadens between the vagina and gonopore. The vagina broadens slightly at its junction with the free oviduct and spermathecal duct. The straight free oviduct is 0.5 the width of the spermathecal duct at their junction with the vagina. The spermathecal duct is relatively wide basally, tapering to 0.3 its basal diameter at its midpoint, and remaining narrow until the junction with the ovate spermatheca.

The central teeth of the radula (Figure 12, middle row) are tricuspid, 8–9 μm wide, and 12–13 μm long, of similar shape and length but slightly narrower and shorter than the first lateral teeth, 10–11 μm wide and 14–15 μm long (Figure 12). The mesocones of the central and first lateral teeth are tall, slender, and project slightly beyond their basal plates. The ectocones of the central teeth are trigonal and symmetric. Ectocones and endocones of the lateral teeth are trigonal and about 0.5 the height of the mesocones. The endocones of the lateral teeth are slightly larger but otherwise of similar shape to their ectocones. The first 10 teeth to the left and right of the central row are similar to the first laterals. The next 3 on either side grade in shape and are difficult to classify as either lateral or marginal teeth. The last 4 marginal teeth are slightly wider, about 11–12 μm wide, and shorter, 7–10 μm long (Figure 13). The base of the unicuspid or bicuspid endocones of the first and second marginal teeth is reduced, and they originate from the side of their mesocones. The ectocones are reduced, and their rectangular bases are usually devoid of cusps. The third and fourth marginal teeth often lack all cusps and are reduced to rectangular bases.

**Remarks:** The only other *Paryphantopsis* species with shells that have periostracal extensions on the growth lines and no processes at the margin are: *P. arcuata* Jutting, 1964; *P. dauloensis* Solem, 1970; *P. filosa* Jutting, 1964; *P. koragae* Slapcinsky, 2005; *P. latior* Jutting, 1964; *P. matawanensis* Slapcinsky, 2005; *P. platycephala* Jutting, 1964; and *P. pygmaea* (Bavay, 1908). *Paryphantopsis fragilicosta* is larger than *P. filosa*, is less depressed than *P. dauloensis*, has a higher spire than *P. latior* and *P. platycephala*, and has stronger spiral sculpture than *P. pygmaea* and *P. arcuata*. *Paryphantopsis fragilicosta* lacks an apical diverticulum, unlike all *Paryphantopsis* species for which the genital anatomy is known, except for *P. louisiadarum*, *P. misimensis*, and *P. vanatinensis*, which are much larger, as well as *P. lebasii* and *P. yawii*, which have long periostracal processes. The ectocones of the marginal teeth of *P. fragilicosta* sit on a rectangular extension of the tooth, unlike all other *Paryphantopsis* for which the radular morphology is known other than *P. corolla* and *P. nucella*. It differs from these species by having very few or no cusps on the marginal teeth.

**Etymology:** The species name derives from the combination of the Latin adjective *fragilis* meaning crackling or easily broken and the feminine noun *costa* meaning rib, and refers to the shells fragile periostracal extensions.

*Paryphantopsis nucella* new species
(Figures 14–19, Table 1)

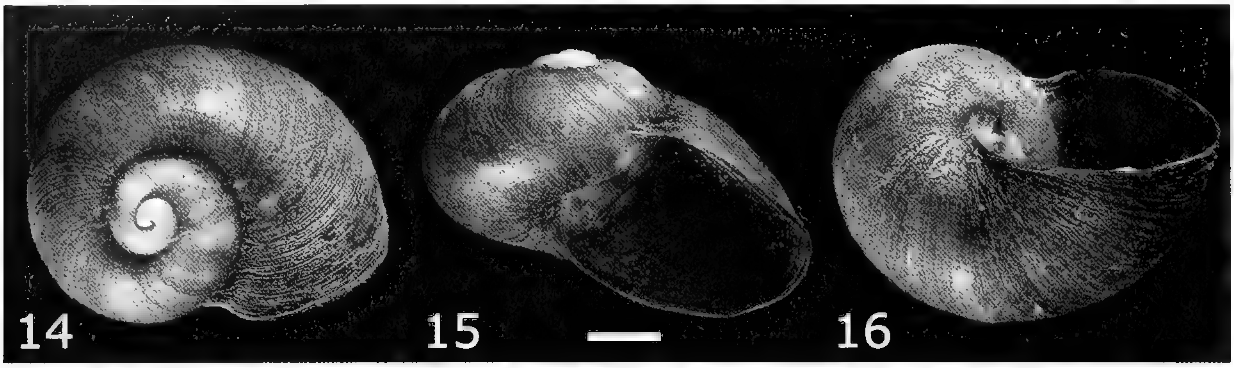
**Holotype:** UF 383996, J. Slapcinsky, 28 February 2005.

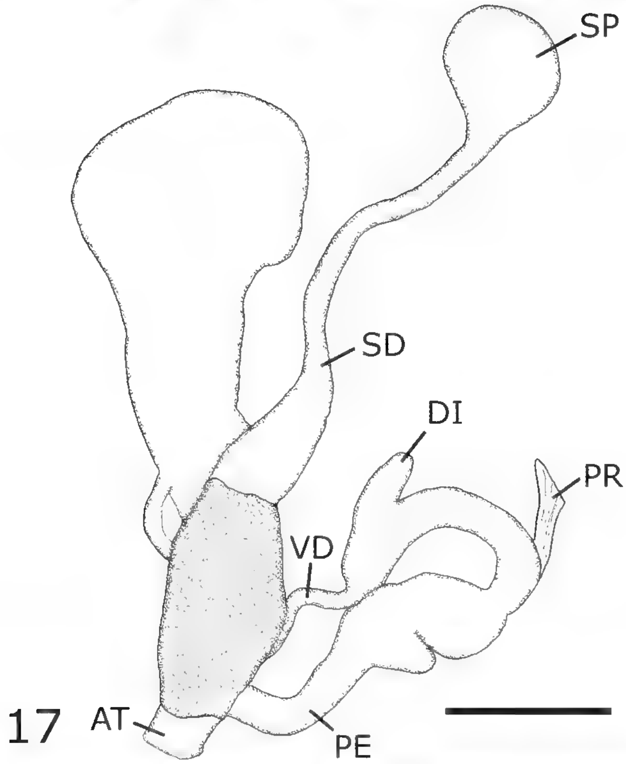
**Paratypes:** Papua New Guinea, East New Britain Province, New Britain: BPBM 282462 (2 specimens), MNHW MP 1001 (2 specimens), PNGNM (2 specimens), SMF 329401 (2 specimens) UF 383993 (34 specimens), UF 383994 (3 specimens), type locality, J. Slapcinsky, 28 February, 2005; UF 366504 (5 specimens), UF 366506 (7 specimens), 12 km northwest of Marmar Village on the trail to Pakia Village, 5.432° S, 151.460° E, 900 meters altitude, J. Slapcinsky, 25 February 2005

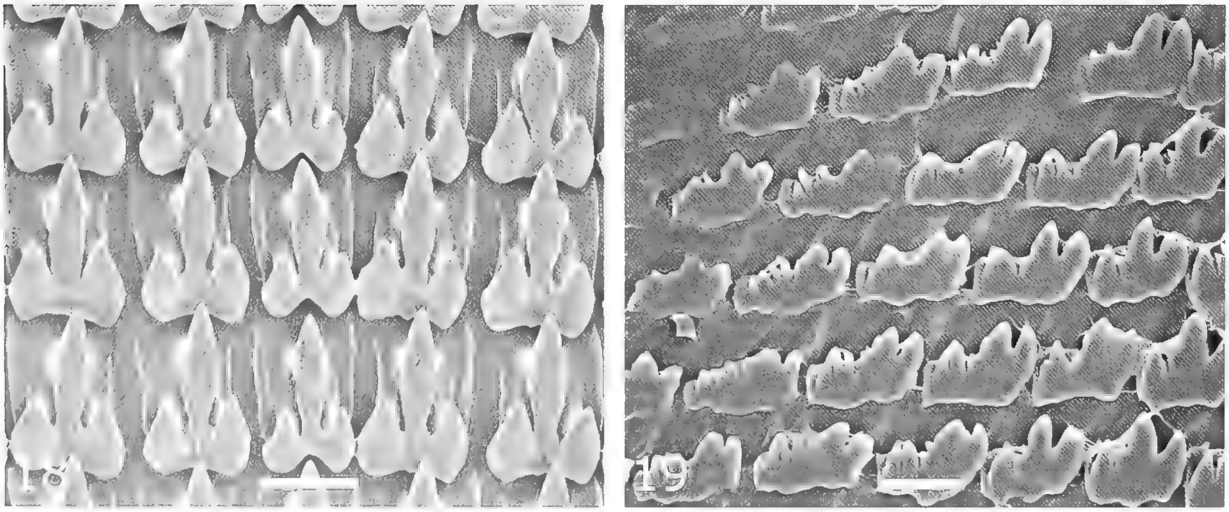
**Type Locality:** Papua New Guinea, East New Britain Province, New Britain, Saukale, 13 km northwest of Marmar Village on trail to Pakia Village, 5.426° S, 151.453° E, 910 meters altitude (Figure 1).

**Habitat:** Collected in mixed hill forest on vegetation within 1 meter of the ground.

**Description:** The adult shell is globose to depressed-globose, average for the genus, 4.9–5.7 mm (mean = 5.22, see Table 1 for sample size and standard deviation) in diameter and 3.1–4.1 mm (mean = 3.75) in height with 2.6–2.9 (mean = 2.81) rapidly expanding whorls (Figures 14–16). The apical surface of the shell whorls







**Figures 14–19.** *Paryphantopsis nucella.* **14–16.** Shell, Holotype UF 383996. Scale bar = 1 mm. **17.** Genitalia, UF 383993. Scale bar = 1 mm. **18–19.** SEMS of radula, UF 383993. **18.** Central and lateral teeth. **19.** Marginal teeth. Scale bars = 10 μm

are flattened between the deeply impressed sutures and the submedian shell periphery, which gives the shell a somewhat angular appearance. The spire is slightly elevated, 0.1–0.2 mm (mean = 0.18). The teleoconch whorls descend slowly and regularly until the end of the body whorl and more rapidly near the aperture. Shell height:diameter ratio is 0.62–0.78 (mean = 0.72). There are 1.5 evenly rounded protoconch whorls sculptured with spiral rows of small pits. Approximately 14 rows can be seen on the apex of shells. These pits become elongated on the teleoconch whorls nearly fusing to form weak incised spiral striae. Spiral striae weaken, becoming obsolete on the final 0.30 of the body whorl where shell sculpture becomes predominated by growth lines all of which are accentuated with short periostracal extensions that do not bear peripheral processes. The protoconch is white, and teleoconch whorls gradually darken from yellow brown to brown. The umbilicus is closed by a reflection of the peristome. The aperture is ovate except for the flattened apical surface and has an aperture:width to aperture:height ratio of 0.94–1.25 (mean = 1.14).

The external body color is bright yellow in life and there are no bands or other color patterns. Specimens preserved in ethanol fade to uniform cream. The head is short similar to other species of *Paryphantopsis* and the posterior of the foot is slightly shorter than average for the genus.

The vas deferens is 0.2 the diameter of the head of the epiphallus, which bears an apical diverticulum that is approximately 0.3 the length and 0.7 the diameter of the midpoint of the epiphallus (Figure 17). The apical 0.7 of the epiphallus is uniform in diameter; the basal 0.3 is ovoid and twice as wide. The penial retractor muscle is moderate in length originating from the diaphragm and inserting 0.6 the way to the base of the epiphallus. The penis is 0.7 the length of the epiphallus. Its apical 0.3 is as robust as the base of the epiphallus and narrows rapidly basally. The basal 0.7 of the penis is 0.3 narrower than the apex and uniform in diameter to the junction with the atrium. The atrium is 1.5 times wider than the penis at their junction and remains constant in diameter to the gonopore. The vagina expands slightly at the junction with the free oviduct and spermathecal duct. The free oviduct is broad, not folded, and approximately the same diameter as the base of the spermathecal duct. The basal 0.3 of the spermathecal duct is wide and surrounded by darkly pigmented glandular tissue. The basal 0.5 of the spermathecal duct tapers apically to 0.2 of its original diameter and remains narrow until the junction with the ovate spermatheca.

The central teeth of the radula (Figure 18, middle row) are tricuspid, 10–11 µm wide and 14–15 µm long, and of similar shape and length, but are slightly narrower and shorter than the first lateral teeth, 11–12 µm wide and 16–17 µm long (Figure 18). The mesocones of the central and first lateral teeth are tall and slender, and project beyond their basal plates. The ectocones of the central teeth are trigonal and symmetrical. Ectocones and endocones of the lateral teeth are trigonal and about 0.5 the height of the mesocones. The endocones of the lateral teeth are slightly larger but otherwise of similar shape to their ectocones. The first 12 teeth on either side of the central row are similar to the first laterals. The next three on either side grade in shape and are difficult to classify as either laterals or marginals. The last four teeth are clearly marginals and are irregularly multicuspid, wider, about 13–14 µm wide, and shorter, 8–9 µm long (Figure 19). The endocones are as tall as the mesocones and are usually unicuspid, but sometimes bear 2 or 3 cusps. The ectocones sit on a rectangular base and are usually divided into 2–6 cusps that are 0.6 to 0.7 the height of the mesocones.

**Remarks:** *Paryphantopsis nucella* is similar to only *P. koragae* in having short periostracal extensions on all growth lines; these growth lines do not bear processes at the shell periphery. The shell of *P. koragae*, however, differs in having the shell periphery above, rather than below, the midpoint of the whorl. *Paryphantopsis nucella* is unique among *Paryphantopsis*, for which the genital anatomy is known, in having a large glandular area on the base of the spermatheca and having both an apically robust penis and a basally robust epiphallus. The ectocones of the marginal teeth sit on a rectangular extension of the tooth, unlike all other *Paryphantopsis* for which the radular morphology is known other than *P. corolla* and *P. fragilicosta*.

**Etymology:** The species name derives from the Latin feminine noun *nucella* and describes the shells resemblance to a small nut.

**Discussion and Conclusions:** Despite previous intensive surveys for terrestrial snails in coastal New Britain, much of the diversity of the island's interior mountains may remain to be described. More exploration is clearly needed in the Nakanai Mountains, where uplifted karst terrain has promoted the development of a unique and diverse snail fauna. Our cursory surveys, which did not penetrate deeply into, or reach high elevations in the Nakanai Mountains, uncovered several previously unreported species, including the three *Paryphantopsis* species described here. Most species of *Paryphantopsis* appear to be restricted to single mountain ranges or islands. The absence of these three species from relatively intensively surveyed coastal areas suggest they are endemic to the Nakanai Mountains. It is likely that other endemic species will be found in the Whiteman, Baining, and Willaumez ranges of New Britain. The Charopidae were until recently, considered a minor component of the terrestrial mollusk fauna of New Guinea (Solem, 1983). Our surveys (Slapcinsky, 2005; 2006) suggest charopid species radiations on New Guinea and surrounding islands rival the spectacular radiations exhibited by this family in the oceanic Pacific (Solem, 1983).

Based on shell and genital morphology, the relationships among the three *Paryphantopsis* species on New Britain are unclear. *Paryphantopsis corolla* and *P. nu-*

*cella* share several unusual traits that may indicate a common origin. In both species, the marginal ectocones are divided into numerous irregular cusps, the base of the epiphallus is robust, and an apical diverticulum is present on the epiphallus. *Paryphantopsis fragilicosta*, on the other hand, lacks these characters but has a large, globose shell that can be difficult to differentiate from that of *P. nucella*. However, all three New Britain species share unique rectangular bases to their marginal teeth, a possible synapomorphy. If so, characters that have been historically used to determine monophyly, i.e. genital and shell morphology, appear to be rapidly evolving and variable in this group. Additional morphologic and genetic characters are necessary before a clear picture of the relationships between *Paryphantopsis* species within New Britain and the adjacent New Guinea mainland can be resolved.

## ACKNOWLEDGMENTS

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# *Mysella gregaria* new species, a bivalve (Galeommatoidea: Montacutidae) commensal with an intertidal burrowing sea anemone from North Carolina, USA

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## ABSTRACT

*Mysella gregaria* new species (Bivalvia: Galeommatoidea: Montacutidae) is described from Wrightsville Beach, North Carolina, USA. Several individuals were collected from the body column of an intertidal burrowing unidentified actinian. The morphology of the shell and soft parts is described and compared with other species of the genus from the W. Atlantic Ocean and with other bivalves associated with solitary anthozoans. *Mysella gregaria* is a ctenidial brooder and specimens are either males or females; no true hermaphrodites were found. Contrary to many less social commensal bivalves, reproduction in *M. gregaria* does not involve sperm storage. We suggest that this may be correlated with the species' gregariousness.

*Additional Keywords:* Mollusca, reproduction, anatomy, sperm morphology, gregariousness.

## INTRODUCTION

During intertidal collecting on a muddy sand flat at Wrightsville Beach, North Carolina, USA, one of us (TF) collected a number of galeommatoidean bivalves from 8–10 cm long specimens of an unidentified burrowing actinian. The host species was rare, as not more than an estimated 5–8 specimens were found during occasional visits to the locality in the period from October 1970 through July 1975. Unfortunately, none of them were preserved for later identification. Only two of the collected actinians had commensal bivalves attached.

Many bivalves of the superfamily Galeommatoidea have a commensal life style as they live together with species of bottom-dwelling marine invertebrate hosts such as other bivalves, polychaetes, sipunculans, echiurans, crustaceans, and echinoderms. Commensal associations between bivalves and solitary anthozoans are restricted to three known cases (Yamamoto and Habe, 1961; Ponder, 1971; Oliver, 1993) and it was therefore judged to be of interest to examine the present association more closely. The study has disclosed that the bivalves represent a new species of *Mysella* Angas, 1877, a genus that comprises both commensal and free-living bivalves and species that are commensal on certain conditions, free-living on other conditions (Ockelmann and Muus, 1978).

## MATERIALS AND METHODS

Thirty-two bivalves were retrieved from the skin of a host specimen collected on 9 July 1975. The site of collection was a sandy mud tidal flat in Banks Channel, Wrightsville Beach, North Carolina, and the approximate coordinates are longitude 77.8° W and latitude 34.2° N. The anemones were dug from the lower intertidal zone during a spring low tide. The number associated with the second host and the date of collection was not noted. The behavior of the bivalves after removal from the host was not studied, but it was observed that they detached easily. Seventeen of the bivalves were preserved in Heidenhain's Susa for several hours. This procedure decalcifies the shells and the sizes given based on measurements of the mantle are therefore approximate. Three other bivalves were fixed in 70% ethanol and used for the description of the shell and for type material. Six specimens were embedded in Araldite and cut into 2-μm thick serial sections that were stained with toludine blue. Seven other specimens were embedded in Paraplast, sectioned, and the 8-μm thick serial sections stained with hematoxylin and eosin (H+E). Ultrathin sections were performed on the testis of one of the males. These sections

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were contrasted with uranyl acetate and lead citrate and examined in a JEOL 100SX electron microscope. Scanning electron micrographs were made using a JEOL JSM-6335F SEM. Photos of the type specimens of *Mysella casta* (Verrill and Bush, 1897) (USNM 77632) and *M. barbadensis* Dall, 1899 (USNM 95703) were used for comparison with *M. gregaria*. Shell length (SL) and height (SH) are given to the nearest 0.1 mm.

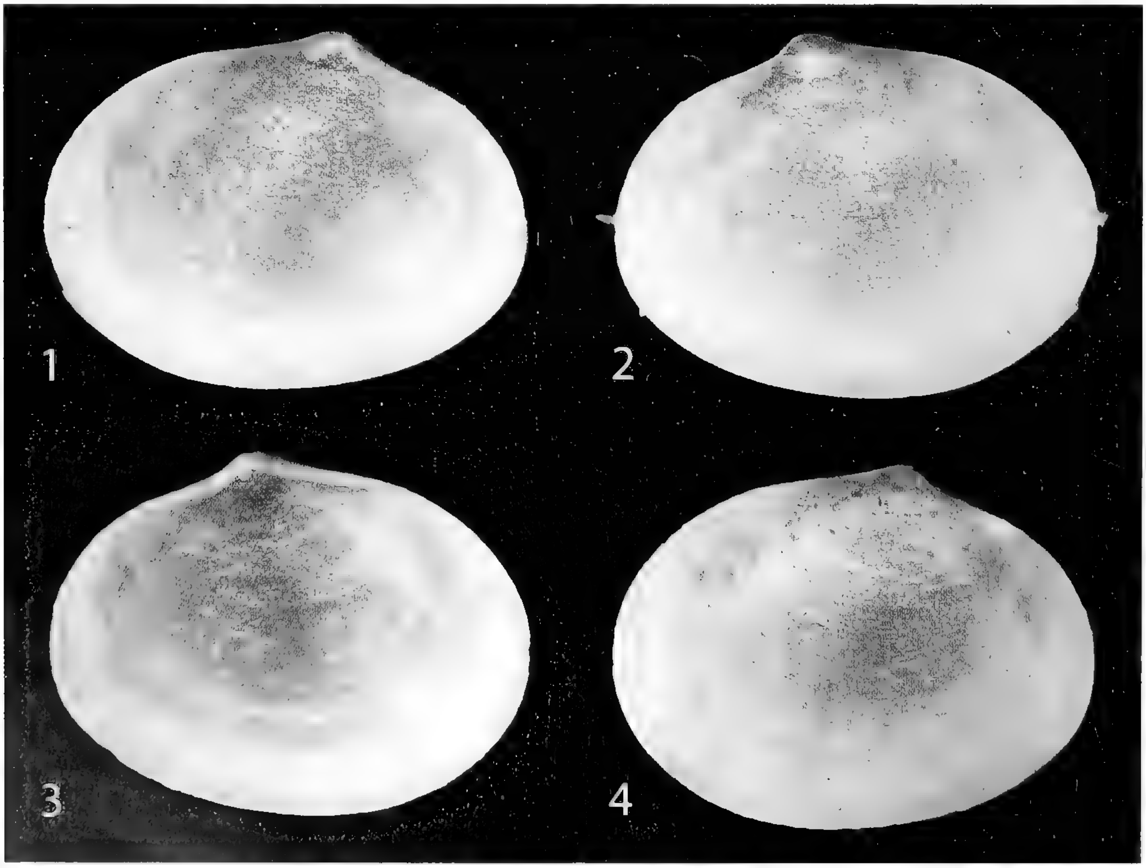
## SYSTEMATICS

Family Montacutidae Clark, 1855
Genus *Mysella* Angas, 1877

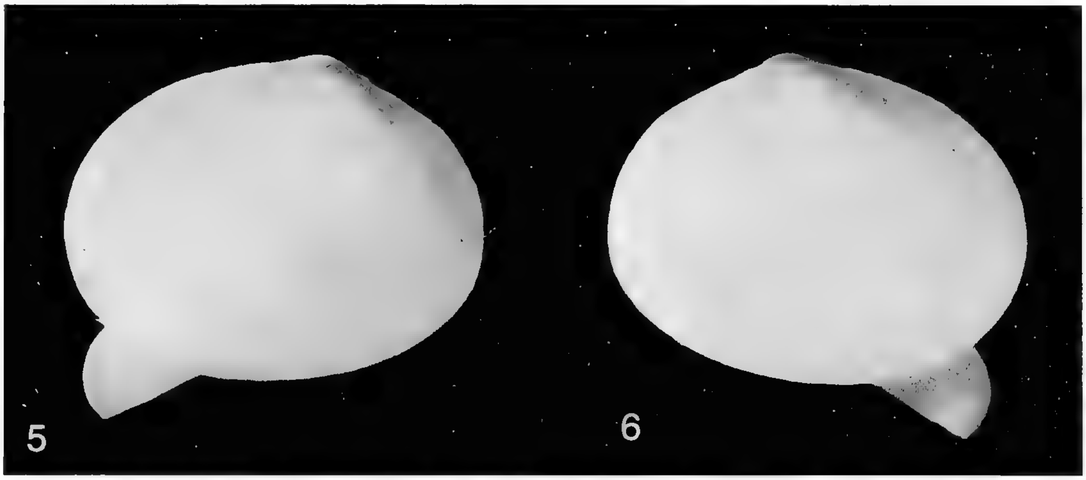
*Mysella gregaria* new species
(Figures 1–20)

**Description:** SHELL (Figures 1–10): Observations were made on three shells. The SL of twenty measured specimens varied from 3.0 to 6.0 mm. The measurements SL×SH in the type material are 4.5×3.6 mm, 5.1×3.8 mm, and 5.5×4.3 mm. The outline is almost perfectly oval, slightly higher in the anterior part, all margins being evenly rounded. The valves are relatively flattened, very thin, semitransparent, and with a light-brown to grey-brown periostracum, which is darkest in the dorsal part. There are no coatings of ferruginous deposits. The surface is smooth, with very fine commarginal lines and even finer radial striae. No growth checks were ever visible. The interior surfaces of the valves are polished. The umbos are not very prominent and placed slightly toward the posterior region. In the right valve there are two diverging teeth; the anterior tooth is elongate-subtriangular and more prominent than the narrower, posterior one. They are separated by a stout ligament placed immediately below umbo in a triangular resilifer. The left valve is edentulous but has a produced dorsal margin that fits into the teeth of the right valve. The anterior adductor scar is subtriangular, the posterior more oval, both fused with the respective foot retractor scars. The pallial line is relatively broad and lacks a pallial sinus.

MANTLE (Figure 11): The mantle folds are fused far behind and for a short distance to separate the mantle opening into an inhalant-pedal aperture and an exhalant aperture. While the first forms a long slit along the four-fifths of the length of the ventral side, the exhalant aperture is very small and located far posteriorly. Since live animals were not observed, we do not know whether, or to which extent, the mid mantle fold may cover the outside of the shell or whether there are any siphons. The mantle edges bear minute papillae that are most distinct



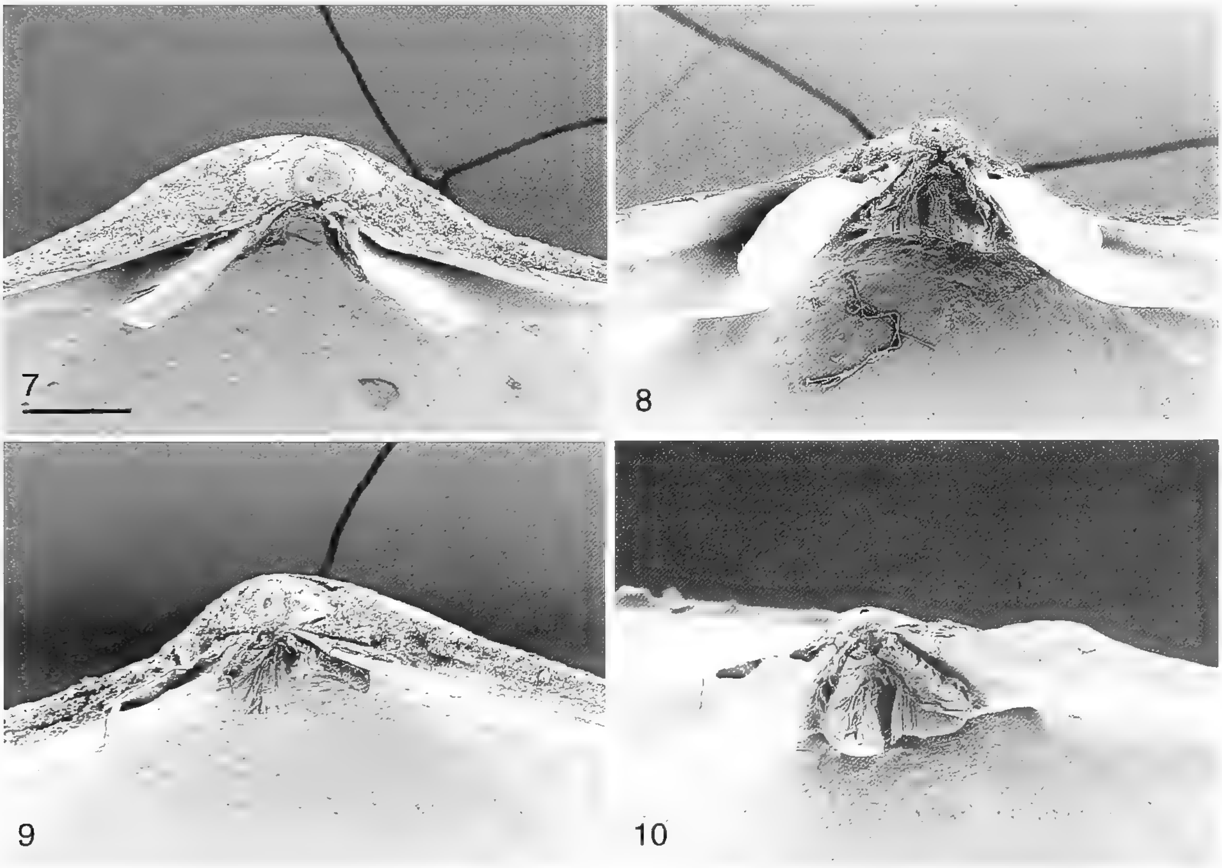
**Figures 1–4.** *Mysella gregaria*. Cleaned shell of holotype. **1.** Right shell seen from inside. **2.** Right shell seen from outside. **3.** Left valve seen from inside. **4.** Left shell seen from outside. Shell length 5.1 mm



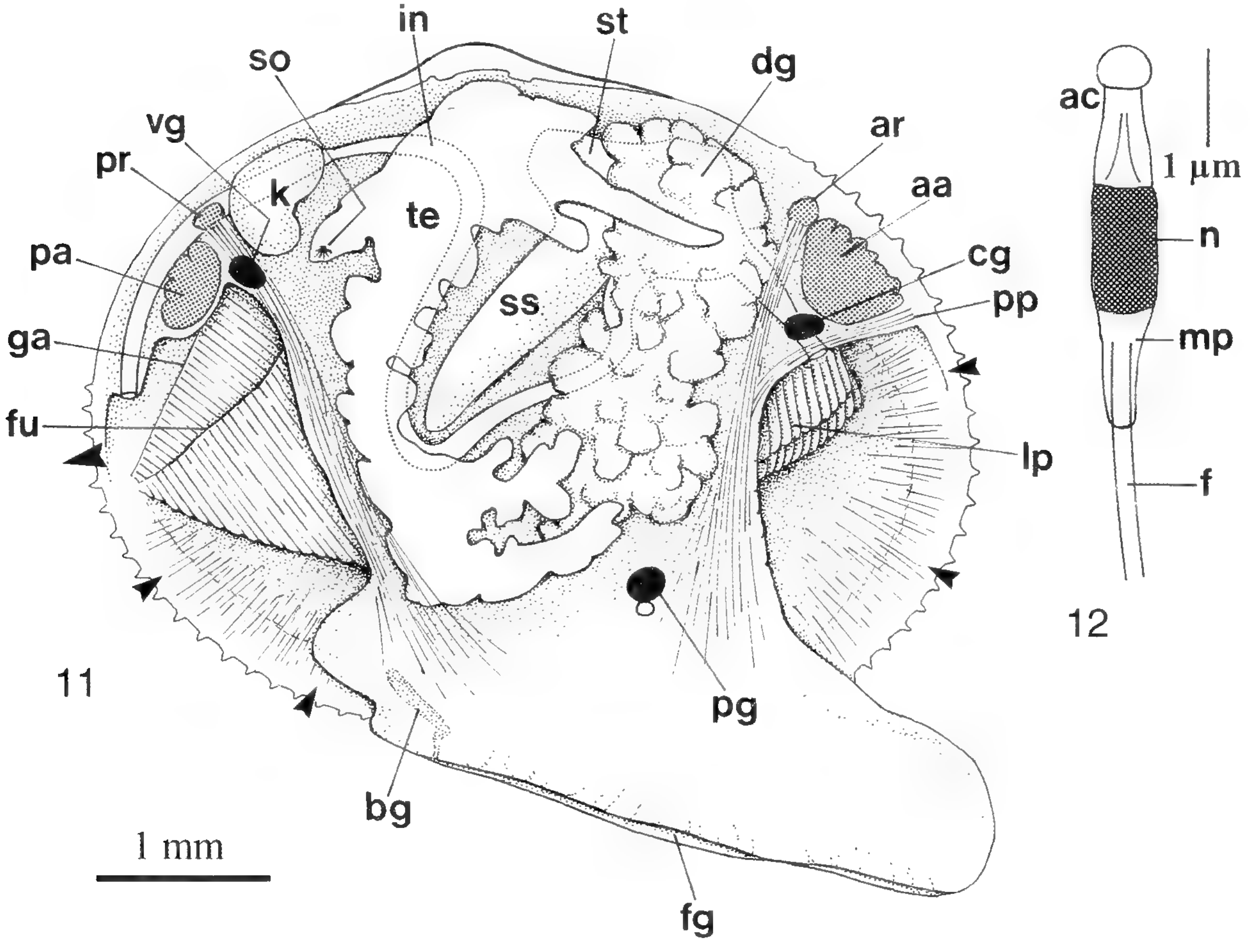
**Figures 5, 6.** *Mysella gregaria.* Paratype, outside view of left **(5)** and right sides **(6).** Shell length 4.5 mm.

in the dorso-anterior sector. A typical, ciliated rejection fold is located just anterior to the end of the inhalant-pedal opening.

MUSCULATURE (Figures 11, 13): The anterior adductor muscle is the larger of the two and is subtriangular in outline, whereas the smaller posterior adductor is more oval. A small pedal protractor muscle is located ventrally and clearly outside the anterior adductor muscle. The two pedal retractor muscles are equally large and of moderate size. They terminate in the base of the foot,



**Figures 7–10.** *Mysella gregaria.* Holotype, SL 5.1 mm. Scanning electron micrographs of right hinge seen in direct view **(7)** and slightly tilted from below **(8)** and of left hinge seen in direct view **(9)** and slightly tilted from below **(10).** Scale bar represents 200 μm.



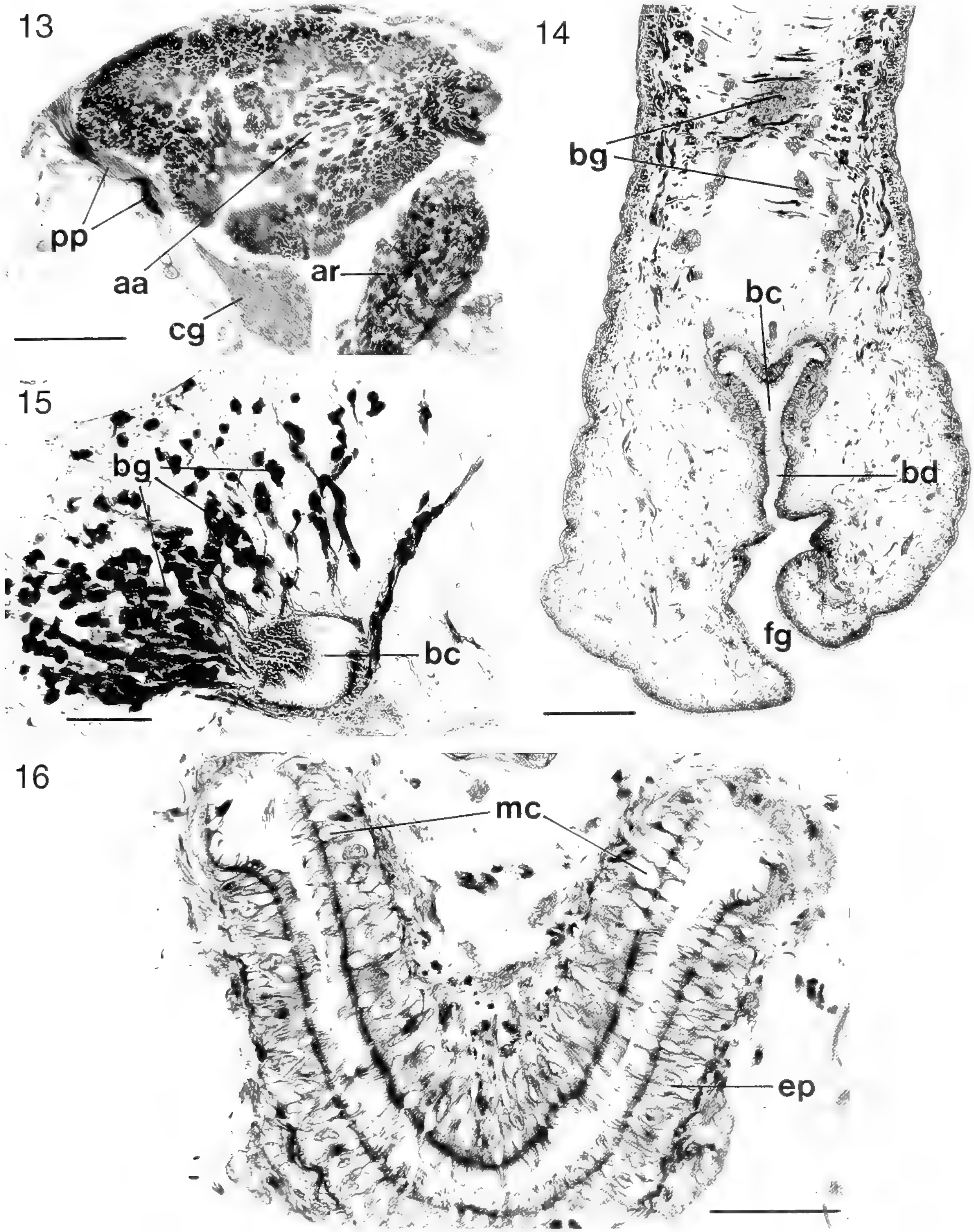
**Figures 11, 12.** *Mysella gregaria*. **11.** Anatomy of male, right valve, mantle and gill removed, heart and pericardium omitted. **12.** Light microscopic representation of sperm cell. Abbreviations: **aa,** anterior adductor muscle; **ac,** acrosome; **ar,** anterior pedal retractor muscle; **bg,** byssus gland; **cg,** cerebral ganglion; **dg,** digestive gland; **f,** flagellum; **fg,** foot groove; **fu,** fusion of left and right demibranch behind visceral mass; **ga,** gill axis; **in,** intestine; **k,** kidney; **lp,** labial palps; **mp,** middlepiece; **n,** nucleus; **pa,** posterior adductor muscle; **pg,** pedal ganglion and statocysts; **pp,** protractor pedis muscle; **pr,** posterior pedal retractor muscle; **so,** sexual opening; **ss,** style sac; **st,** stomach; **te,** testis; **vg,** visceral ganglion. Arrowheads indicate water entering along the inhalant-pedal opening and exiting through the exhalant opening.

while only a few fibers spread further into the foot. There are almost no muscle fibers serving the byssus gland.

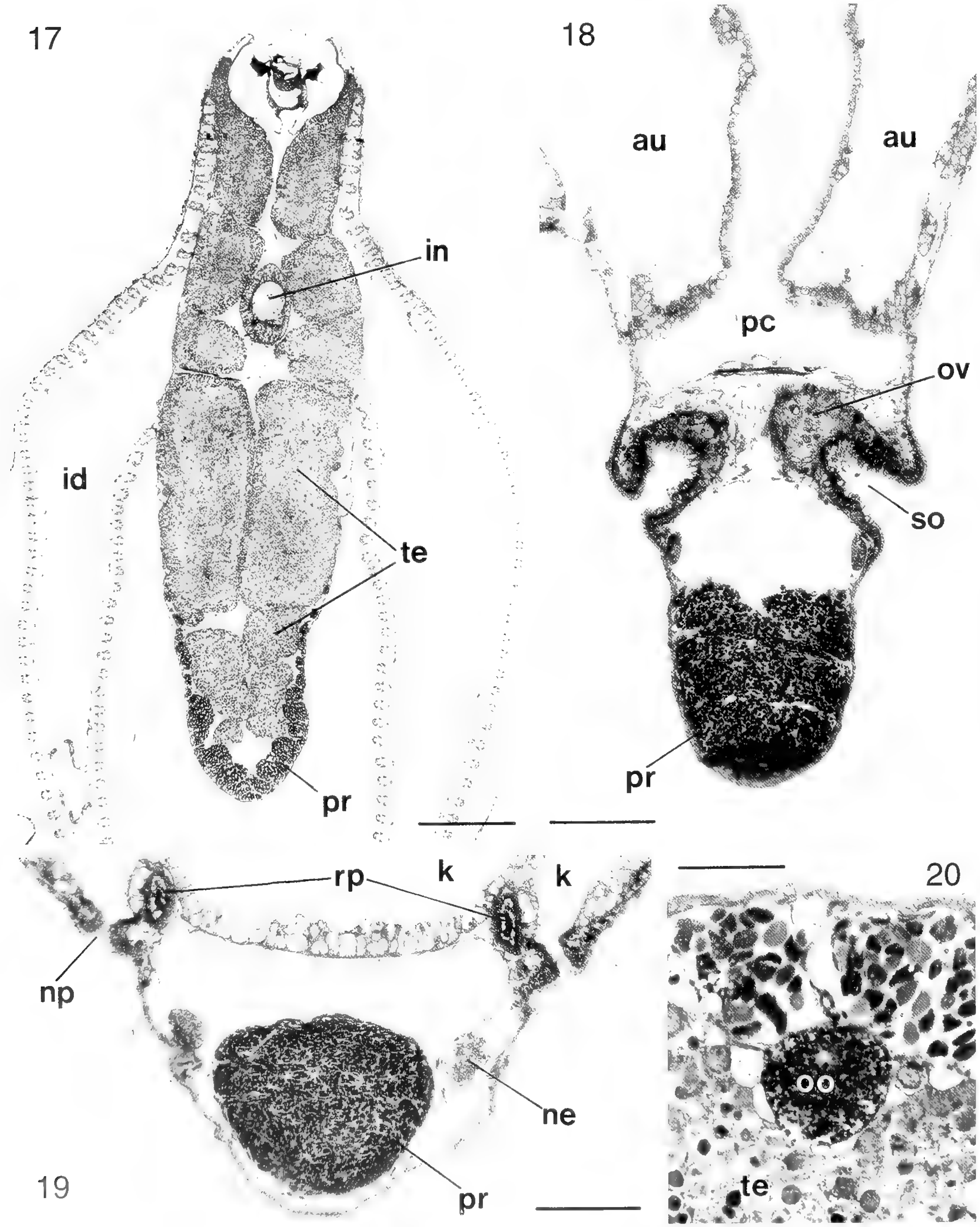
FOOT AND BYSSUS GLAND (Figures 11, 14–16): In preserved specimens, the foot extends forward and a little beyond the shell margin. It is bluntly rounded in front. The ventral side is distinctly ciliated and has a furrow that extends from in front of the heel to tip of the foot. In some specimens a blackish pigment spot can be seen at the very tip of the foot. The very small byssus cavity appears Y-shaped in transversal sections as it consist of a right and left slit which both discharge into the median furrow by way of a single duct. The lining epithelium is composed of a mixture of ciliated and of mucous-producing goblet cells. A group of more distant glandular cells terminate between the cells of the byssus cavity epithelium through long, slender ducts. Although such cells are normally involved in the formation of byssal threads, none were ever seen either in sections or on whole animals. The nature of the glandular epithelium indicates that slime threads, rather than normal byssal threads are produced by the byssus gland.

GILLS (Figures 11, 17): The gill axis, which runs from near the umbo, has an oblique course backward. Each gill is triangular. An outer demibranch is entirely absent and only the inner one is present. The ascending lamellae of the left and right demibranch are fused behind the foot, more anteriorly to the lateral sides of the visceral mass. Both gills are fused to the mantle edges immediately in front of the exhalant opening. A food groove is only present along the ventral edges of each gill. Interlamellar junctions are present, but they are very few, whereas interfilamentary bridges are numerous and occur regularly. Right and left hypobranchial glands of normal size occur well inside the exhalant aperture. A pair of relatively large labial palps lies on either side of the mouth. Their opposing surfaces are provided with 9–10 ciliated ridges.

ALIMENTARY CANAL (Figure 11): The esophagus is a



**Figures 13–16.** *Mysella gregaria.* **13.** Sagittal section of a male (SL 3.0 mm) showing the course of the protractor pedis muscle (**pp**). **14.** Transverse section of a male (SL 4.3 mm) through the foot and the opening of the byssus cavity (bc). **15.** Byssus gland cells (**bg**) opening into byssus cavity **16.** Transverse section through byssus cavity of the male shown in **Fig. 14.** Abbreviations: **aa,** anterior adductor muscle; **ar,** anterior pedal retractor muscle; **bc,** byssus cavity; **bd,** byssus duct; **bg,** byssus glandular cells; **cg,** cerebral ganglion; **ep,** epithelium of byssus cavity; **fg,** foot groove; **mc,** mucous cells. 2-µm thick Araldite sections stained with toluidine blue (**13, 14** and **16**) and 8-µm thick paraplast sections stained with H+E (**15**). Scale bars represent 100 µm (**13–15**) and 30 µm (**16**).



**Figures 17–20.** *Mysella gregaria*. Transversal section of male (SL 4.3 mm) (**17**) and of female (**18, 19**). **20.** Testis with abortive oocyte (**oo**). Abbreviations: **au**, auricles; **id**, inner demibranch; **in**, intestine; **k**, kidney; **ne**, nerve; **np**, nephridiopore; **ov**, posterior wall of ovary; **pc**, pericardial cavity; **pr**, posterior pedal retractor muscle; **rp**, renopericardial canal; **so**, sexual opening; **te**, testis. 2-μm thick Araldite sections stained with toluidine blue. Scale bars represent 200 μm (**17**), 100μm (**18, 19**) and 50 μm (**20**).

short curved tube. The stomach is relatively capacious and heavily cuticularized. The style sac forms a wide posterior continuation from the stomach, is elongated conical, nearly as long as the stomach, and directed postero-ventrally. It is placed within the right side of the visceral mass. The intestine leaves from the underside of the stomach near its connection to the style sac, runs alongside the style sac and forms a loop around its tip, then turns dorsally between left and right parts of the gonad to loop backwards to the rectum The boundary between the ciliated intestine and the unciliated rectum is marked by a sharp transition zone dorsal to the posterior adductor.

The digestive gland is mainly located ventral to the stomach and around the posterior part of the esophagus. In addition to a large ventral communication with the stomach, there are also smaller openings into it.

REPRODUCTIVE SYSTEM (Figures 11, 17, 18, 20): Eight sectioned bivalves (SL = 3.0–5.6 mm) were males, while three other sectioned bivalves (SL = 4.1–6.0 mm) were females. No truly hermaphroditic specimens were found, but a few mature oocytes were present in the testis of one of the males (Figure 20).

All males were sexually mature. The very large testis occupies the posterior half of the visceral mass being replaced more anteriorly by the style sac, stomach, and digestive gland. The general shape as seen in decalcified specimens is relatively constant. A large undivided posterior portion gives rise to right and left halves that surround the intestine and extend ventrally to send a few short branches forward. Two other forwardly directed finger-shaped branches embrace the stomach. The paired spermiducts issue from the most posterior, undivided part of the testis. They are short but have prominent funnel-shaped and heavily ciliated openings into the suprabranchial chamber. Spermatogenesis proceeds everywhere along the walls of the different portions of the testis. There is no special chamber for storing the mature sperm which, in a non-orientated manner accumulate in huge numbers in the central parts of the different portions of the testis. Many spherical to ovoid cells, 5–7 μm in diameter, lie scattered among the mature sperm. These cells have a centrally placed nucleus plus one or two inclusions. We were unable to discover how these cells arise and if they are in the any way associated with the spermatogenesis.

Because of the insufficient fixation the TEM micrographs were of low quality. They nevertheless show enough details to illustrate the general ultrastructure of the flagellate sperm cells (Figure 11, B). The acrosome is 1.4–1.5 μm long and basally (near the nucleus) 0.6 μm broad. It is divided into a terminal subspherical body (0.4×0.6 μm) and a slightly tapering acrosomal vesicle, which is basally deeply invaginated to accommodate a filamentous subacrosomal material. The nucleus is 0.7–0.8 μm across and 1.2–1.3 μm in length. The 1.4–1.5 μm long middle piece was extremely ill-preserved without any identifiable mitochondria but seems from a broad base near the nucleus to taper backwards.

The female sexual openings (Figure 18) are identical in size and structure to those of the male. Two females were obviously spent, but one of them had retained a few abortive oocytes (diameter ca. 60 μm) within the ovary and a few embryos in the suprabranchial chamber. Except for this, none of six decalcified but unsexed specimens examined in transparent light (SL = 4.0–5.6 mm) were brooding ova or larvae. No structures for storing foreign sperm were found in any of the sectioned bivalves.

EXCRETORY SYSTEM (Figures 11, 18, 19): Left and right halves of the kidney communicate in the median plane for a short distance. Each one is composed of several smaller and larger sacs with glandular walls. Anterolaterally the kidney opens directly to the suprabrancial chamber through two ciliated nephroducts, which are uncharacteristically short and have porous nephridiopores placed not far from the genital opening. Rather far behind within the kidney, two long straight and heavily ciliated renopericardial canals run forward to open into the forward and ventral part of the pericardium.

HOST RELATIONS: All 32 individuals were attached onto the body column of a single sea anemone, whereas the number attached to a second host was not noted. None were found on any of the other host specimens from the same site, which suggests that the species is gregarious. It was observed that the attachment to the host was very loose as several of the bivalves had fallen off during the collection. This corresponds with the conclusion that no true byssus threads are produced and that attachment rather takes place by means of slime threads.

**Holotype:** BIV-445 (Zoological Museum, University of Copenhagen), a cleaned shell, SL = 5.1 mm.

**Paratypes:** BIV-446, a shelled animal, SL = 4.5 mm; USNM 1107828 (National Museum of Natural History, Washington, DC), a shelled animal, SL = 5.5 mm; all from type locality, 9 July 1975.

**Type Locality:** Banks Channel, Wrightsville Beach, North Carolina, USA. (ca. 77.8° W, 34.2° N), lower intertidal zone during spring low tide, sandy mud substratum, 9 July 1975. Thirty-two specimens were attached to a single host.

**Etymology:** the species name is derived from the Latin *grex*, flock, and refers to the gregarious life style of the new species.

## DISCUSSION

**Identification:** The details of the shell and hinge allocate the species into the genus *Mysella* (family Montacutidae) and indicate that it is close to the North Atlantic *M. bidentata* (Montagu, 1803). In *M. gregaria* the protractor pedis muscle is inserted immediately ventral to the anterior adductor as in *M. bidentata* (Montagu, 1803) and in *Montacutona compacta* (Gould, 1861), in contrast to the condition in another group of montacutids, in which it splits the adductor in dorsal and ventral portions (Jespersen et al., in press). *Mysella* has often been combined with *Rochefortia* Velain, 1877, but the two differ with respect to the dimensions of the teeth of the right valve (Coan et al., 2000; Holmes et al., 2006). In species of *Mysella* the right valve has a stout transverse tooth anterior to the resilifer and a posterior tooth is either small or absent. In *Rochefortia* the right valve has two subequal diverging teeth, which would place *M. gregaria* in *Rochefortia*. The distinction ignores the available soft anatomical characters which, especially in species with a *Rochefortia* type of hinge, vary considerably: A small outer demibranch is present in some (*M. tumida* (Carpenter, 1864), *M. verrilli* (Dall, 1899), and *M. sovaliki* McGinitie 1959), absent in other (*M. bidentata* and *M. gregaria*). The esophagus is a simple tube in all the species except for *M. verrilli*, in which it forms a suctorial proboscis. Foreign sperm are either not stored (*M. gregaria* and *M. verrilli*), attached directly to the gill surface (*M. tumida*), or stored in an unpaired pouch-shaped seminal receptacle within the visceral mass (*M. bidentata*) or in paired receptacles in the outer demibranch (*M. sovaliki*). A new definition of the genus *Mysella* will probably be called for as additional data on the anatomy of a wider range of species will bring about a complete rearrangement of the genus and its included species.

From the described species of *Mysella* from the East American waters, *M. gregaria* may be distinguished by the following characters: *M. planulata* (Stimpson, 1857) has a very prominent hinge and the umbo is placed more posteriorly. It attaches to buoys and wharf pilings or occurs in muddy sand of the *Zostera* community (Abbott, 1974; Franz, 1973). In *Mysella ovata* (Jeffreys, 1881) the umbo is extremely protruding and placed far posteriorly. It occurs in depths of 183 to 287 m. The shell of *M. triquetra* (Verrill and Bush, 1898) is equilateral and the posterior part of the shell is distinctly rostrate, not evenly rounded. *Mysella verrilli*, a deep water species, has the umbo placed far posteriorly and the esophagus is developed as a suctorial proboscis (Allen, 2000). In *M. striatula* (Verrill and Bush, 1898), both teeth are delicate and very narrow, the anterior tooth is shorter, and the very small umbo is located more posteriorly than in *M. gregaria*. The shell of the following two species were studied from photos provided by the National Museum of Natural History, Smithsonian Institution (USNM): The anterior part of a left valve of *M. barbadensis* Dall, 1899 (USNM 95703) is almost three times as long as the posterior part (in contrast to the claim that it is shorter as described by Dall, who obviously mistook a left valve for a right one). The left valve of the type of *M. casta* Verrill and Bush, 1898 from North Carolina (USNM 77632) is more elongate (SH:SL = 7:10) than the valves of *M. gregaria* (SH:SL = 7.8:10) and the anterior end relatively longer. Nevertheless, among the East American species, the shell of *M. casta* is the one most similar to *M. gregaria*.

**Comparison with North Atlantic/Arctic species of *Mysella*:** Conchologically *M. gregaria* resembles *M. bidentata* (Montagu, 1803) but differs anatomically in that the latter has an unpaired seminal receptacle and dimorphic sperm (Jespersen and Lützen, 2001). The shell of *M. cuneata* (Verrill and Bush, 1898) is distinctly asymmetrical, as the right valve shows a slight concavity with a consequent skewness along the ventral margin (Gage, 1968). In *M. tumidula* (Jeffreys, 1866), the posterior shell margin is distinctly angular, not evenly rounded. *Mysella moelleri* (Mörch, 1877) and *M. sovaliki* both differ from *M. gregaria* in the hinge structure and, more significantly, in having preserved a small outer demibranch (Petersen and Lützen, in press). *Mysella planata* (Dall in Krause, 1885) has a thick shell, in which the left valve has the dorsal line modified into two teeth, and the right valve shows only one, anterior tooth (van Aartsen, 1996).

**Comparison with Other Bivalves Associated with Anthozoans:** Commensalism between bivalves and anthozoans is rare. *Nipponomontacuta actinariophila* Yamamoto and Habe, 1961, is small Japanese bivalve that has been found attached immediately outside the ring of tentacles of *Halcampella maxima* Hertwig (Actiniaria: Halcampoididae). Details of the relationship are not known, except that three specimens sitting close together outside the ring of tentacles were illustrated by Habe (1973). Although the outline of the shell and the position of the umbo in *N. actinariophila* are somewhat similar to the studied species, the hinges are clearly different, as teeth are only present in the left valve in *N. actiniariophila*, not, as in *M. gregaria*, on the right valve. *Montacutona ceriantha* Ponder, 1971, from *Cerianthus* sp. (Ceriantharia) in Moreton Bay, E Australia, is easily separated from *M. gregaria* in that each valve has four cardinal teeth and a small outer demibranch is present. Furthermore, *M. ceriantha* is attached to the interior of the tube of the host, not to the body, and in a small numbers (Table 1) (Ponder, 1971). A third bivalve, *Halcampicola tenacis* Oliver, 1993, from Rottnest Island off Perth, SW Australia has a hinge similar to *Montacuta*, the right valve with a strong anterior cardinal merging with a submarginal lateral ridge and an obsolete posterior cardinal. The left valve has anterior and posterior strongly projecting marginal extensions which fit into the right valve (Oliver, 1993). Besides, the ligament has a lithodesma and there is a small outer demibranch. A single bivalve was found on each of six hosts (*Halcampoides* sp., Actiniaria: Halcampoididae) among 20 collected. It seems fairly obvious that all four anthozoan-associated bivalve species are not specifically interrelated .

**Reproduction:** Eight of the sectioned bivalves (SL = 3.0–5.6 mm) were sexually mature males and three other (SL = 4.1–6.0) were females. The females were spent but one had retained a few embryos in the suprabranchial chamber which shows that this species, like other galeommatoideans, is a ctenidial brooder. A few mature oocytes, left over from a previous ovulation, were present in

**Table 1.** Mean number of commensal bivalves per host specimen and reproductive specializations in montacutid bivalves. Abbreviations: **dw,** dwarf males; **sp,** spermatophores; **sr,** seminal receptables; **ss,** sperm sacs; **tt,** testis transplantation.

| Bivalve species | Mean no. per host specimen | Host species | Reproductive specializations | References |
|---|---|---|---|---|
| *Montacuta percompressa* | 1 | Holothurioidea | tt | Fox et al., 2007 |
| *Peregrinamor ohshimai* | 1 | Crustacea | sr, dw | Lützen et al., 2001a |
| *Salpocola philippinensis* | 1 | Sipuncula | tt? | Lützen et al., in press |
| *Halcampicola tenacis* | 1 | Anthozoa | ? | pers. comm. (Graham Oliver) |
| *Litigiella pacifica* | 1–3 | Sipuncula | sr | Lützen and Kosuge, 2006 |
| *Montacutona ceriantha* | 1.8 | Anthozoa | sr | Ponder, 1971 |
| *Entovalva lessonothuriae* | < 2 | Holothurioidea | sp | Kato, 1998; Lützen et al., 2005 |
| *Pythina arcuata* | ca. 2 | Brachiopoda | sr | pers. comm. (JL) |
| *Anisodevonia ohshimai* | 1.8–2.7 | Holoturioidea | sp | Kosuge, 2001; Lützen et al., 2005 |
| *Nipponomysella subtruncata* | 2.5 | Sipuncula | sr, ss | Lützen et al., 2001b |
| *Tellimya ferruginosa* | < 3 | Echinoidea | tt | Fox et al., 2007 |
| *Mioerycina coarctata* | 3.8 | Sipuncula | sr | Gage, 1979 |
| *Mysella cuneata* | 5 | Sipuncula | sr | Gage, 1968 |

one of the males, which could indicate that females may change sex and that the species shows hermaphroditic tendencies. The species in all probability reproduces by outcrossing, since none of the sectioned bivalves showed truly simultaneous hermaphroditic characteristics.

All galeommatoideans brood the ova in a ctenidial brooding chamber consisting of the inner and, if present, the outer demibranch. This is also where fertilization takes place. In a normally-filtering bivalve the gills and the currents they generate do not favor a casual intake of sperm suspended in the water. The ciliary activity of the gills probably functions as a barrier for penetration of most sperm cells and the only other access to the brooding chamber is against the flow of filtered water expelled through the exhalant aperture. Many species have overcome these difficulties by bulk transfer of sperm in containers of different nature to the female's suprabranchial chamber (see Ó Foighil, 1985a, for a review). Exactly how they do this is not understood except in a single case (Ó Foighil, 1985b). Some species have minute dwarf males that are permanently and intimately associated with the much larger female and still other produce sperm of two types that form spermatozeugmata. Some of that spermatozeugmata is probably capable of independent mobility. None of these methods of a precise transfer of sperm occur in *M. gregaria*. The testis is exceptionally large in the species, and we speculate that the resulting high production of sperm cells may compensate for the inevitable loss suffered during the transfer between the opposite sexes of sperm cells that are simply broadcast into the water.

Sperm transferred to a female (or hermaphrodite) are often stored for a considerable period either on the gills or in seminal receptacles of various types and location. We think it is likely that there may be some correlation between the presence or absence of storing devices and the chance of encountering bivalves of the opposite sex. The commensal galeommatoid bivalves are sequestered along with their host into a microhabitat that they probably never leave. A few examples show that the number of montacutid bivalves present per host (or host burrow) is usually small (Table 1). Except for *H. tenacis,* which has not been anatomically studied, all these species have evolved various measures that allow long-time storage of sperm in the female (or hermaphrodite), which effectively enhance the chances that spawned ova can be fertilized even if no sexual partners are around. Conversely, in a highly social species, like *M. gregaria*, such mechanisms are evidently much less needed. It would be interesting to study the relation between the sizes of the micro-populations in other Montacutidae that neither exhibit sperm transfer nor sperm storage. Unfortunately, besides the present species, the known cases are limited to two species with unknown spatial distribution, *Tellimya tenella* (Lovén, 1846) and *Mysella moelleri* (Fox et al. 2007; Petersen and Lützen, in press).

The present study has shown the need for further information on the anatomy as a tool of a better understanding of the taxonomy, which, to a much too large extent, has been based only on shell characters. More data are also wanted on the numerical relations between hosts and commensals and, above all, analyses on the sexual behavior of commensal bivalves are in very high demand.

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# *Corbula tarasconii*, a new species of Corbulidae (Bivalvia) from offshore Brazil

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## ABSTRACT

*Corbula tarasconii*, a new species of Corbulidae is described from material collected along the Brazilian coast. No living specimens are known and only shell characters were compared with the most similar *Corbula* species from the western Atlantic and eastern Pacific oceans. Short, ventrally curving rostrum and sculpture of low, rounded commarginal ribs having their bases about three times broader than the interspaces are the most important diagnostic characteristics of *C. tarasconii*. These characters distinguish the new species from other western Atlantic and eastern Pacific Corbulidae.

*Additional Keywords: Corbula tarasconii*, Corbulidae, Bivalvia, taxonomy, Brazilian littoral, new species.

## INTRODUCTION

During a research project carried out by the two senior authors on *Corbula* Bruguière, 1797, occurring in Brazilian sea waters, specimens of an unknown species were found in samples made at four different localities between southern Bahia state and northern Rio de Janeiro state. Working independently, the last two authors found the same unknown bivalve among the benthic fauna collected during field research on the continental shelf of northern Bahia state. Careful examination of all specimens gathered by the four authors, plus comparison with the nominal species hitherto published in the literature, led to us to conclude that the specimens represent a new species.

Corbulids are readily recognized by their small size usually less than 20 mm in shell length) and their inequivalve condition, with the right valve larger, more convex, and overlapping the left one. All corbulids are shallow-burrowing suspension feeders inhabiting sandy, sandy-mud, or muddy substrata, usually at depths greater than 4 m (Lamprell et al., 1998).

Two living subfamilies of Corbulidae, Corbulinae Lamarck, 1818, and Lentidiinae Vokes, 1945, encompass all extant (~85) species; a few tropical representatives live in brackish rivers and streams (Coan et al., 2000). Lentidiinae is represented by species of the single genus *Lentidium* Cristofori and Jan, 1832; Corbulinae is by far more specious and includes 25 genus-level taxa (Coan et al., 2000), among which *Corbula* is the largest. Keen (1969) previously subdivided *Corbula* into 18 subgenera, several of which were rather poorly defined and in need of revision, whereas authors such as Warmke and Abbott (1961), Abbott (1974), Bernard et al. (1993), Coan et al. (2000), Mikkelsen and Bieler (2001) and Anderson and Roopnarine (2003) elevated some subgenera to generic status, a decision not shared by Coan (2002). In this latter paper, Coan (2002), considered elevating subgenera to genera premature, because the arrangement of these taxonomic categories is still fraught with inconsistencies and additional characters need to be better defined.

The genus *Corbula* has long been a source of nomenclatural confusion and many authors have been attempted to resolve it. It is beyond the scope of this paper to discuss the systematics of the entire group once Coan (2002) has already presented a consensus based on the current rules of the International Code of Zoological Nomenclature (1999).

According to Mikkelsen (2004), there are 13 species of Corbulidae in the western Atlantic, eight of which were previously cited by Rios (1994) as occurring on the Brazilian coast: *Corbula (Corbula) caribaea* d'Orbigny, 1853, *C. (C.) lyoni* Pilsbry, 1897, *C. (C.) patagonica* d'Orbigny, 1846, *C. (C.) tryoni* E. A. Smith, 1880, *C. (Caryocorbula) cymella* Dall, 1881, *C. (Caryocorbula) dietziana* C. B. Adams, 1852, *C. (Juliacorbula) cubaniana* d'Orbigny, 1853, and *C. (Varicorbula) operculata* Philippi, 1848. Revising *Varicorbula* from the western Atlantic, Mikkelsen and Bieler (2001) considered *C. (V.) operculata* cited by Rios (1975; 1985; 1994) as a synonymous with *V. disparilis* (d'Orbigny, 1842) or misidentified specimens of *V. philippii* (E. A. Smith, 1885).

In this contribution, we describe a new species of *Corbula* from Brazilian waters, based on shell characters only, because no living specimens were obtained, and we compare this new species with its most closely related species from Atlantic and Pacific waters.

## MATERIALS AND METHODS

Twenty whole shells and 56 disarticulated valves (28 right and 28 left) of the new species were collected on the Brazilian continental shelf, between northeastern Bahia state (11°58.7′ S, 36°49.2′ W), and northeastern Rio de Janeiro state (21°20′28″ S, 40°16′09″ W). Shell morphology was compared with the most closely related species known from the western Atlantic and eastern Pacific, borrowed from the Departamento de Zoologia da Universidade de São Paulo, Brazil (one lot of *Corbula aequivalvis* Philippi, 1836, and one of *C. caribaea* d'Orbigny, 1853, both without catalog number), Museu de Zoologia da Universidade de São Paulo, Brazil (*C. bicarinata* G. B. Sowerby, 1833, lot MZSP 67964), and Santa Barbara Museum of Natural History, USA (*C. marmorata* Hinds, 1843, lots SBMNH 83076, SBMNH 131640, and SBMNH 141610). Shell characters and illustrations of *C. ira* Dall, 1908, provided by Coan (2002), were the basis for comparison with those in the new species.

The holotype and 14 paratypes were deposited in the malacological collection of the Museu de Zoologia da Universidade de São Paulo (MZSP), 15 paratypes in the Museu Nacional do Rio de Janeiro (MNRJ), and 46 paratypes were deposited in the Museu Oceanográfico Prof. Eliézer de Carvalho Rios (MORG).

## SYSTEMATICS

Order Myoida
Family Corbulidae Lamarck, 1818
Subfamily Corbulinae Lamarck, 1818
Genus *Corbula* Bruguière, 1797
Subgenus *Caryocorbula* Gardner, 1926

### *Corbula tarasconii* new species

(Figures 1–18)

**Type Locality:** Off Guarapari Municipality, Espírito Santo state, 20°45′ S, 40°25′ W, Brazil, 60–65 m depth.

**Holotype:** Museu de Zoologia, Universidade de São Paulo, MZSP 84452 (Figures 1–5, 8, 11).

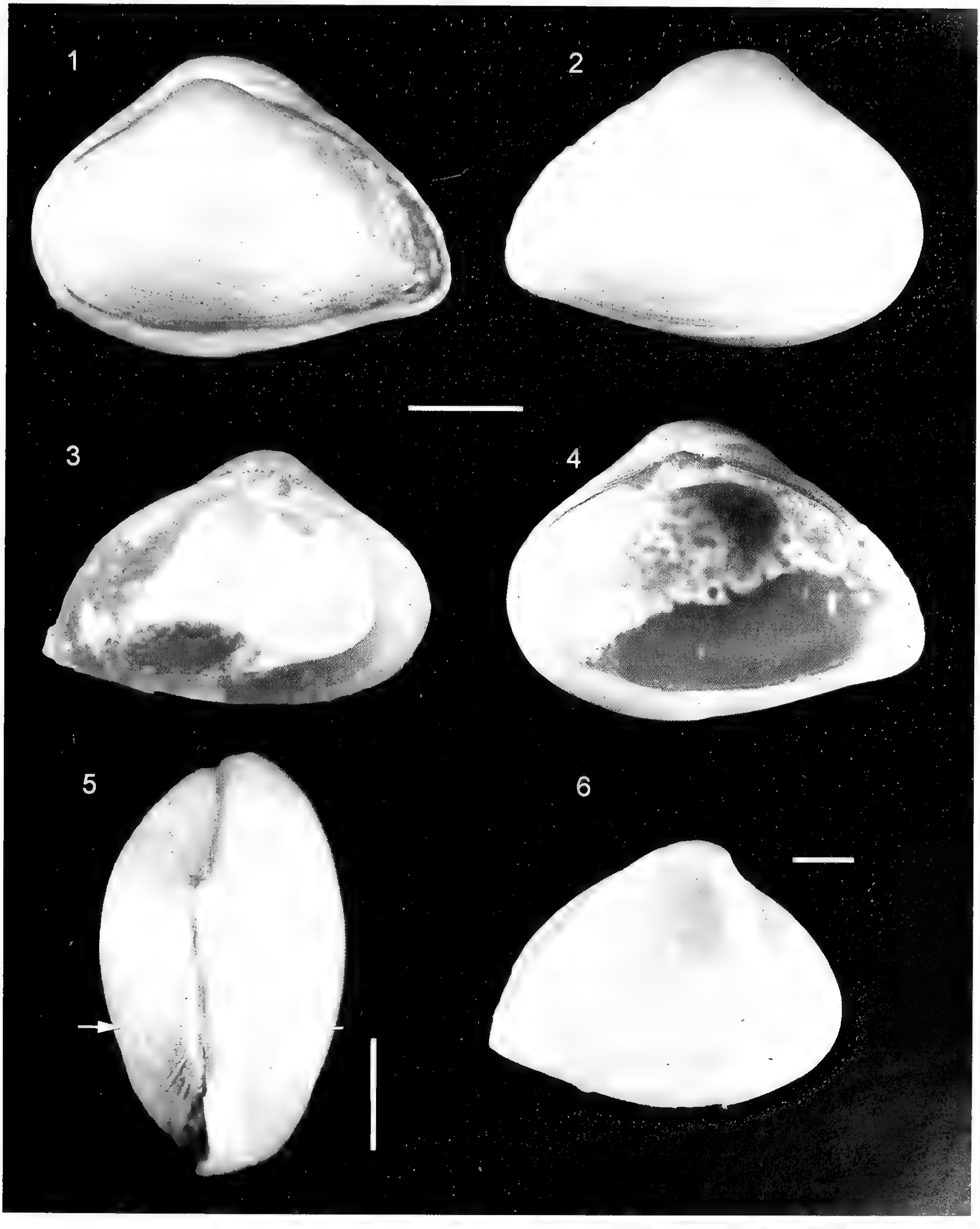
**Measurements:** 7 mm length, 5 mm height, 4 mm width.

**Paratypes:** MZSP 84453 to 84461, northeast of Bahia state, 11°58.7′ S, 36°49.2′ W, 01 Nov. 2000, 100 m (MZSP 84453: 1 complete shell; MZSP 84454 to 84461: 6 right, 2 left valves); MZSP 84462 to 84464, southeast of Bahia state to Guarapari Municipality, Espírito Santo state, 15°33′ S, 38°56′ W to 20°45′ S, 40°25′ W (MZSP 84462–84464: 3 complete shells, 1 left valve); MZSP 86026, northeast of Rio de Janeiro state, 21°20′28″ S, 40°16′09″ W, Feb.–Mar. 1992, 139 m (1 complete shell); MNRJ 11146–11157, northeast of Bahia state, 11°58.7′ S, 36°49.2′ W, 01 Nov. 2000, 100 m (MNRJ 11146, MNRJ 11147: 2 complete shells; MNRJ 11148–11157: 5 right, 5 left valves); MNRJ 11040, southeast of Bahia state, 15°53′82″ S, 38°31′09″ W, 30 Apr. 1996, 66 m (1 right, 1 left valve); MNRJ 11812, off Guarapari Municipality, Espírito Santo state, Oct. 1992, 60–70 m (1 complete shell); MORG 50792, off Boipeba Municipality, Bahia state, 13°35′18.33″ S, 38°54′48.27″ W, Feb. 2003, 41–53 m (4 complete shells); MORG 50789, off Camamu Municipality, Bahia state, 13°55′58.79″ S, 38°05′28.13″ W, 11 Dec. 2002, 52 m (7 complete shells, 16 right, 19 left valves).

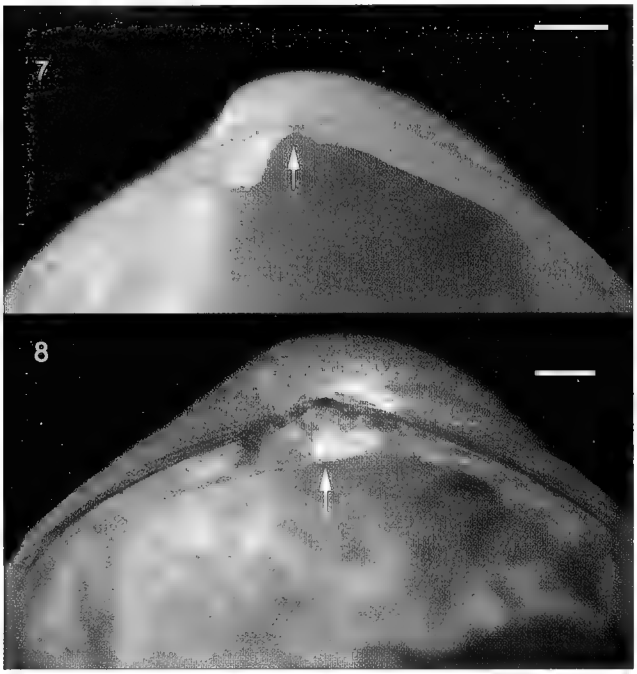
**Diagnosis:** Shell trigonal to trigonal-elongate, small (maximum length ~8 mm), thin to moderately thick, inflated, subequilateral, with a short rostrum, gently curving ventrally. Left valve smaller than right. Sculpture similar in both shell valves, comprised of low, regularly spaced rounded commarginal ribs crossed by minute, radially arranged pustules; base of commarginal ribs about three times broader than the intercostal spaces.

**Description:** Prodissoconch I and II markedly suborbicular. Prodissoconch I with a coarse and irregular surface texture under the SEM (length: 66.6 to 84.4 μm, $n = 5$); prodissoconch II with subtle growth lines (length: 189.5 to 233.2 μm, $n = 5$) and separated from the dissoconch by a sharp transitional line and change in sculpture on the latter. Dissoconch small (length: min. = 2.4 mm, max. = 8.11 mm, mean = 5.92 ± 1.36 SD [standard deviation]; height: min. = 1.7 mm, max. = 6.8 mm, mean = 4.48 ± 1.06 SD; $n = 47$; measurement taken from right valve), trigonal to trigonal-elongate, moderately thick in gerontic specimens, inflated, subequivalve, subequilateral with short rostrum.

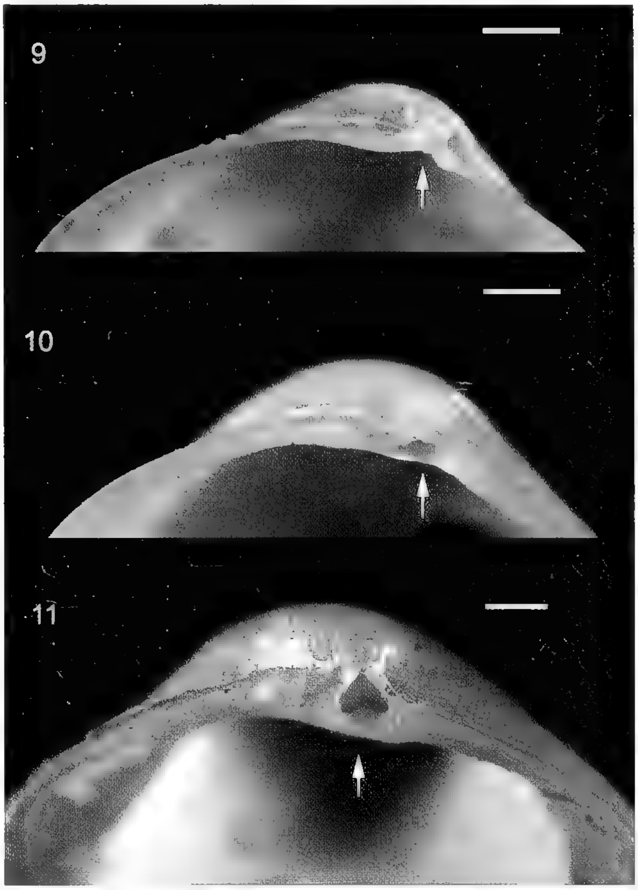
Free margin of the right valve completely overlapping the entire free margin of the left valve. Rostrum acutely rounded, gently curved ventrally. Posterior slope of each valve narrow, slightly concave, forming an acute angle (~20°) between posterior dorsal margin and the low, rounded radial keel. Radial keel an inverted, gentle sigmoid line from umbo to the posterior limit of ventral margin; plane tangential to posterior slope forming a slightly obtuse angle with the plane tangential to central slope. Valve surface, excluding the posterior slope, regularly convex, except for a slight concavity in median-ventral area, just anterior to the keels. Umbos prosogyrous, at about 36% of shell length from anterior end, aligned with cardinal tooth on right valve and cardinal socket on left valve. Anterior dorsal margin straight, ventrally directed, continuous with evenly convex anterior margin, the latter situated below median longitudinal shell axis; posterior dorsal margin slightly convex, as long as, but less steep than the anterior dorsal margin; posterior margin long, obliquely truncated, and forming a short rostrum with posterior end of ventral margin; ventral margin evenly convex, except for a straight to slightly concave portion just anterior to the radial keel. Juvenile



**Figures 1–6.** [illegible] **1–5.** Holotype MZSP 84452. **1.** Complete specimen viewed from the left valve. **2.** [illegible] of the right valve. **3.** Internal view of the left valve. **4.** Internal view of the right valve. **5.** Dorsal view to show the [illegible] (broad arrow) and escutcheon (narrow arrow). Scale bar = 2 mm. **6.** Paratype MNRJ 11154, external view of a translucent shell [illegible] scale bar = 1 mm.



**Figures 7–8.** *Corbula tarasconii.* Hinge of the right valve of a thin-shelled specimen (7) and a thick, gerontic specimen (8), showing differences in the development of the hinge plate at the resilial socket region (arrow). **7.** Paratype MNRJ 11154. **8.** holotype MZSP 84452. Scale bar = 0.5 mm.



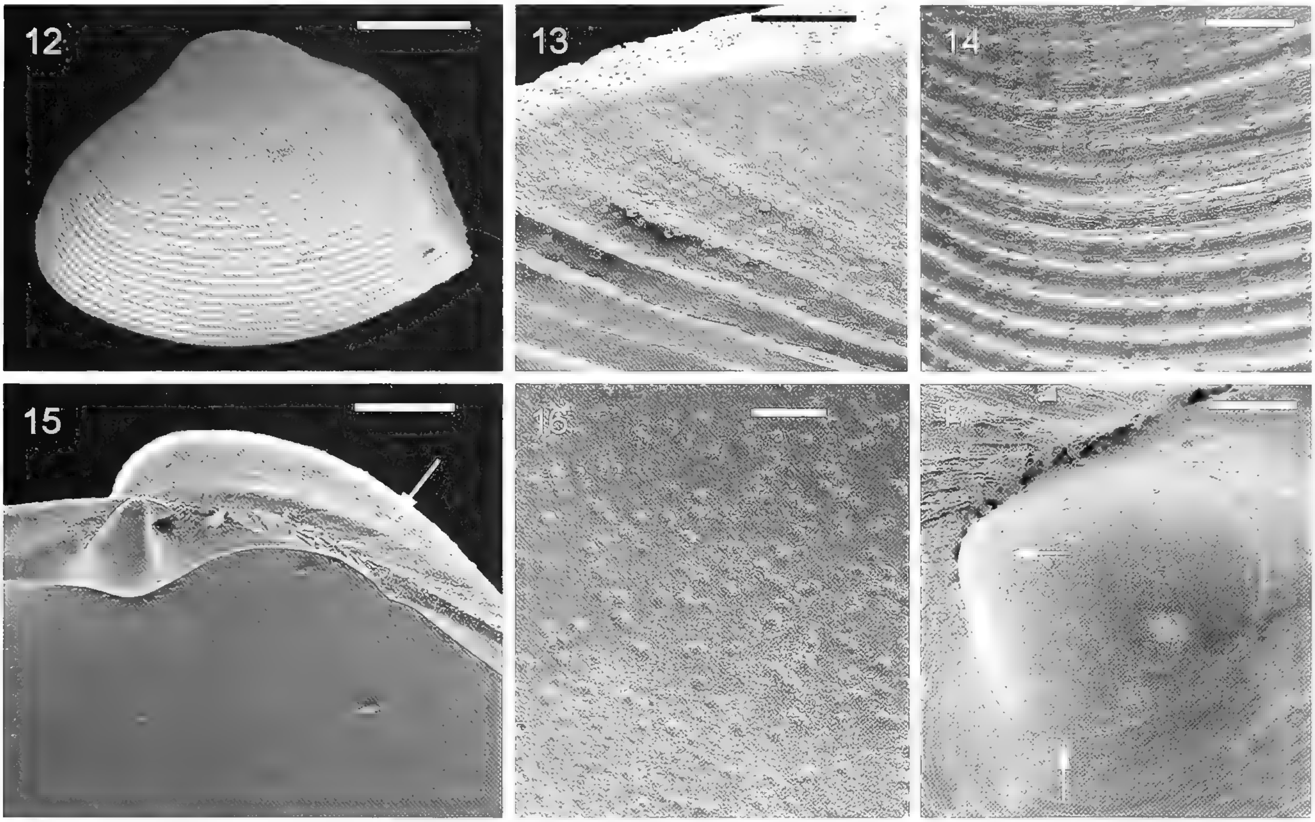
**Figures 9–11.** *Corbula tarasconii.* Hinge of the left valve of thin-shelled specimens (9–10) and a thick, gerontic specimen (11), showing differences in the development of the hinge plate at the cardinal socket region (arrow). **9.** Paratype MNRJ 11150; **10.** Paratype MNRJ 11149; **11.** Holotype MZSP 84452. Scale bar = 0.5 mm.

shells thin, whitish-translucent, turning moderately thick, and whitish-opaque as the specimens grow older; periostracum partially preserved on posterior slope, especially on left valve, missing on remaining shell area.

External sculpture similar in both shell valves, comprised of commarginal ribs crossed by minute pustules (~28.1 μm in basal diameter), the latter showing a tendency to align radially. Commarginal ribs regularly spaced, very low, rounded, with bases about three times broader than the intercostal spaces; commarginal ribs becoming moderately elevated lamellae on posterior slope of left valve only. Radial lines of pustules present all over shell surface, closer to each other on posterior slope; pustule lines visible through translucent shells. Area immediately in front of umbos sunken; lunule absent. Escutcheon lanceolate (~1/3 of shell length), delimited on right valve by a low, rounded elevation on the posterior slope, and on left valve by a slender radial rib; this slender radial rib formed by confluence and abrupt decrease in height of adjacent commarginal ribs, the last extending onto umbo almost parallel to free margin of escutcheon. Inner surface whitish, porcelaneous, crowded with randomly scattered submicroscopic pustules (~16.5 μm in basal diameter), distinguished under SEM only.

Hinge axis almost parallel to anterior dorsal margin. Right hinge plate with a cardinal tooth aligned with umbo, and a resilial socket sunken under umbonal region; cardinal tooth pyramidal, stout, with its apex curled dorsally, isosceles-triangle-shaped when viewed from its convex face; hinge plate narrow, deeply retracted at resilial socket region in thin-shelled specimens, becoming expanded, thick, and more evident as specimens grow older. Left hinge plate with a deep, trigonal cardinal socket just posterior to umbo, and a thick, short chondrophore projecting almost perpendicular to plane of hinge plate when viewed from its dorsal side; hinge plate narrow, deeply retracted at cardinal socket region in thin-shelled specimens, becoming expanded, thick, and more evident as specimens grow older. Dorsal face of the chondrophore shallowly excavated and divided into an anterior and a posterior trigonal area by a radially placed, shallow, narrow groove; posterior margin of posterior trigonal area becoming thicker and projecting as a stout, rounded, tooth-like knob as specimens grow older.

Inner face of the right shell valve bearing a well-impressed commarginal groove for reception of entire free margin of the left valve. Anterior adductor muscle scar ovate, slightly to well-impressed; posterior adductor scar rounded in frontal view, on top of a slightly to well-elevated callosity. Anterior and posterior pedal muscle scars conspicuous and fused dorsally with corresponding adductor muscle scar. Pallial line narrow, glazed, far



**Figures 12–17.** Scanning electron micrographs of *Corbula tarasconii*. **12–14.** Paratype MZSP 84454. **12.** External view of the left valve showing regularly spaced, low commarginal ribs (scale bar = 1 mm). **13.** Frontal view of the posterior slope to show pustules radially arranged and commarginal ribs turning into moderately elevate lamellae. Scale bar = 200 μm. **14.** Detail of central slope (external view) showing the tendency of the pustules to arrange themselves radially. Scale bar = 200 μm. **15–16.** Paratype MZSP 84456. **15.** Detail of the umbonal region and the hinge plate region of the right valve showing the low, rounded border of the escutcheon (arrow). Scale bar = 100 μm. **16.** Internal view to show the presence of randomly scattered pustules. Scale bar = 50 μm. **17.** Paratype MORG 50789, detail of the umbo to show the limit of both prodissoconch I and II (arrows). Scale bar = 62 μm.

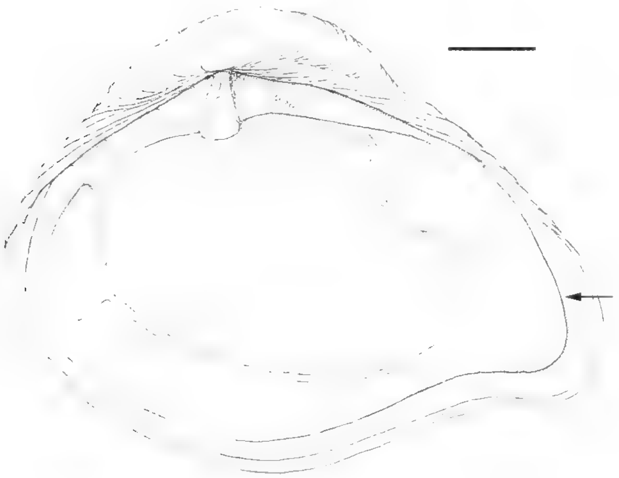


**Figure 18.** *Corbula tarasconii*. Paratype MZSP 84462. Camera lucida drawing of the inner surface of the right valve showing shell outlines, hinge, muscle scars and well impressed commarginal groove for reception of the free margin of the opposite valve (arrow). Scale bar = 1 mm.

from free border in both shell valves (farther in the right valve), especially in its anterior two thirds. Siphonal retractor muscle scar straight.

**Etymology:** This species is named after Dr. José Carlos Tarasconi, a physician interested in collection and molluscan studies, who kindly donated the specimen from his collection, herein designated as the holotype.

**Observation:** The holotype is the best preserved specimen among all complete ones; nevertheless, both shell valves have the postero-ventral portion of the ventral margin slightly broken. The brownish-red color viewed in the internal side of the holotype (Figures 3–4) was not observed among the paratypes.

**Remarks:** The presence in *Corbula tarasconii* of a small prodissoconch I (length: 66.6 to 84.4 μm), distinctly separated from the larger prodissoconch II (length: 189.5 to 233.2 μm), the latter devoid of surface ornamentation, except for growth lines. This suggests that the species has planktotrophic development according to the discussions in Jablonski and Lutz (1980) and

**Table 1.** Shell characteristics in *C. tarasconii* compared with those in its closely related species from the western Atlantic and eastern Pacific oceans. Characteristics of *C. ira* are based on Coan (2002).[*]

| | Inequivalveness | Shape | Rostrum | Keel | Sculpture | | Siphonal plates | Escutcheon | Max. size (mm) | Distribution |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Commarginal | Radial | | | | |
| *C. tarasconii* | subequivalve | trigonal to trigonal-elongate | short, ventrally curving | low, rounded | low, rounded ribs, with base wider than the intercostal spaces | pustulate | absent | RV—defined by low, rounded elevation; LV—defined by slender rib | 7.2 | western Atlantic, Brazil |
| *C. aequivalvis* | quite equivalve | subrectangular | short | sharp, stout | low to moderately high ribs, with acute apex and base width equivalent to the intercostal spaces | absent | absent | defined by sharp, elevated ribs | 16.6 | western Atlantic |
| *C. caribaea* | subequivalve | trigonal-elongate | moderately to well produced, aligned with the anteroposterior shell axis | low, rounded | RV—low, slender to rounded ribs, with base narrower than the intercostal spaces; LV—low, moderatly rounded ribs, with base width equivalent to the intercostal spaces | pustulate, present on the umbonal region only | present in most specimens | RV—defined by low, rounded elevation, LV—defined by slender rib | 11.5 | western Atlantic |
| *C. bicarinata* | quite equivalve | subquadrate to trigonal | short | sharp | low to moderately high ribs, with acute apex and base width equivalent to the intercostal spaces | absent | absent | defined by sharp ribs | 13.0 | eastern Pacific |
| *C. ira* | subequivalve | ovate-subquadrate | short | sharp | strong, rounded ribs | fine ribs | nm | defined by ridge | 13.6 | eastern Pacific |
| *C. marmorata* | subequivalve | Trigonal-ovate | moderatly to well produced, ventrally curving | rounded | strong, high ribs, with acute apex | absent | absent | defined by sharp ribs, more elevated on RV | 8.2 | eastern Pacific |

[*] nm = not mentioned; RV = right valve; LV = left valve.

Hain and Arnold (1992) on the relationships between prodissoconch morphology and modes of development.

This new species encompasses all diagnostic characteristics presented by Keen (1969) and Coan et al. (2000) both for the family Corbulidae and genus *Corbula*. Its subequivalve, trigonal to trigonal-elongate shell with moderately coarse commarginal ribs, similar on both shell valves allow the inclusion of this species in the subgenus *Caryocorbula* Gardner, 1926, as established by Anderson (1996) and Coan (2002). Beside these characteristics, *C. tarasconii* shares with *Caryocorbula* species a short chondrophore that projects almost perpendicular to the plane of the hinge plate when viewed from its dorsal side.

The allocation of *C. tarasconii* in *Caryocorbula* based in qualitative shell characters is an initial attempt to allocate the new species to one of the named subgenera. As observed by Anderson and Roopnarine (2005), *Caryocorbula* "is relatively conservative in its morphology, making qualitative methods for alpha-level taxonomy difficult." Subgenera of *Corbula* have been poorly defined and fraught with inconsistencies, and a full-scale revision of the family is long overdue (Coan, 2002). Much more studies are needed to gather new taxonomic characters, which could better define the subgenus-level categories of *Corbula* and corroborate whether *C. tarasconii* is correctly allocated to *Caryocorbula*.

Eighteen living species of *Corbula* are currently referable to the eastern Pacific (Coan, 2002) and thirteen to the western Atlantic (Mikkelsen, 2004). The western Atlantic species more closely related to *C. tarasconii* are *C. aequivalvis* and *C. caribaea*, and those of eastern Pacific water are *C. bicarinata*, *C. marmorata*, and *C. ira*.

*Corbula tarasconii* is distinguished from *C. aequivalvis* by being approximately 50% smaller in length, conspicuously inequivalve, with the posterior slope set off from the central slope by a low, rounded radial keel, sharp and stout in the latter species. The commarginal ribs in *C. tarasconii* are low, rounded, with the base about three times broader than the intercostal spaces and becoming lamellate on the posterior slope of the left shell valve, while in *C. aequivalvis* they are low to moderately high, each with a quite acute apex and basal width equivalent to the intercostal spaces. The narrow, lanceolate escutcheon, better demarcated in the left shell valve of *C. tarasconii*, is another remarkable difference distinguishing this new species from *C. aequivalvis*, which has a wide, lanceolate escutcheon, wider in the right valve, and well-demarcated in both valves by elevate ribs. The species can also be differentiated by the form and development of both the chondrophore and the right cardinal tooth. In *C. tarasconii*, the chondrophore has an inconspicuous to small tooth-like knob, and is shallowly excavated, with the dorsal face divided into two areas by a low, slender ridge; in *C. aequivalvis*, the tooth-like knob is larger and higher and the chondrophore is more projected from the free border of the hinge plate, with the dorsal face divided into two areas by a high ridge, with the anterior area deeply excavated. Viewed from its convex face, the right cardinal tooth is right-triangle-shaped in *C. aequivalvis* and isosceles-triangle-shaped in *C. tarasconii*.

*Corbula tarasconii* greatly differs from *C. caribaea* by its short, ventrally curving rostrum that in *C. caribaea* is moderately to well produced and aligned with the antero-posterior shell axis. Viewed from its inner surface, the posterior margin of the rostrum, in most individuals of the latter species, has a sinuous outline; the rostrum is frequently extended farther posterior by lateral, siphonal plates made of calcified periostracum. The rostrum of *C. tarasconii* neither has sinuous outline nor siphonal plates.

The eastern Pacific *C. bicarinata*, compared to *C. tarasconii*, has an oval-subquadrate to trigonal outline, a shallow depression on the disc area farther anterior to the radial keel and aligned with the umbo-ventral axis, and the posterior slope set off from the central slope by a sharp, stout radial keel. The right cardinal tooth with a right-triangle shape and the wider, almost fan-shaped escutcheon, set off from the posterior slope by two stout, lateral ribs in *C. bicarinata* also differentiate it from *C. tarasconii*.

Based on the figures and description given by Coan (2002), the eastern Pacific *Corbula ira* is similar to *C. tarasconii* in outline, configuration of the retractor siphonal muscle scar, umbos position, but greatly differs in its larger size and disc area sculptured with strong, less numerous, rounded commarginal and fine radial ribs.

*Corbula marmorata*, the third eastern Pacific species closely related to *C. tarasconii*, has a more elongate, trigonal-ovate shell sculptured with strong, high, and acute commarginal ribs anterior to the radial keel. Both species share a shallow depression just anterior to the posterior radial keel and a short, ventrally curved rostrum, but the former species is also differentiated by the presence of a second shallow depression aligned with the umbo-ventral axis.

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# Two new gastropod species (Neogastropoda: Drilliidae, Turridae) from the western Atlantic Ocean

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## ABSTRACT

Two new deep-water species from the western Atlantic are proposed: *Drillia* (*Clathrodrillia*) *blakensis* and *Hindsiclava rosenstielanus*. *Drillia blakensis* is nearest *Drillia* (*Clathrodrillia*) *petuchi* Tippett, 1995, and *Hindsiclava rosenstielanus* recalls *Hindsiclava polytorta* (Dall, 1881). Animal anatomy, especially foregut anatomy, is described for *H. rosenstielanus*.

*Additional Keywords:* New species, Brazil

## INTRODUCTION

The species proposed here are examples of the richness of the turrid fauna that continues to be discovered in the deep waters of the western Atlantic. Although collected in the 1960s, neither has been previously reported. The type material of *Drillia blakensis* was part of the Bullis collection, secured as by-catch from the R/V OREGON. *Hindsiclava rosenstielanus* was dredged by the University of Miami's R/V PILLSBURY, but was only recently discovered during a review of the previously unsorted portion of the mollusk collection at the University of Miami's Rosenstiel School of Marine and Atmospheric Science. It is evident that further exploration and research will continue to reveal new material.

## MATERIALS AND METHODS

Empty shells and shells with preserved animals were examined. Preserved material was dissected. Radulae were mounted on microscopic slides and stained with Prontocil + CMCP 10. Type specimens were deposited at the National Museum of Natural History and other institutions. The classification used is that proposed by Taylor, Kantor, and Sysoev, 1993, which involved a rearrangement of the traditional classification of the Turridae. Abbreviations are: ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; UMML Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC

## SYSTEMATICS

Drilliidae Olsson, 1964
Genus *Drillia* Gray, 1838

**Type Species:** *Drillia umbilicata* Gray, 1838, by subsequent designation, Gray, 1847.

Subgenus *Clathrodrillia* Dall, 1918

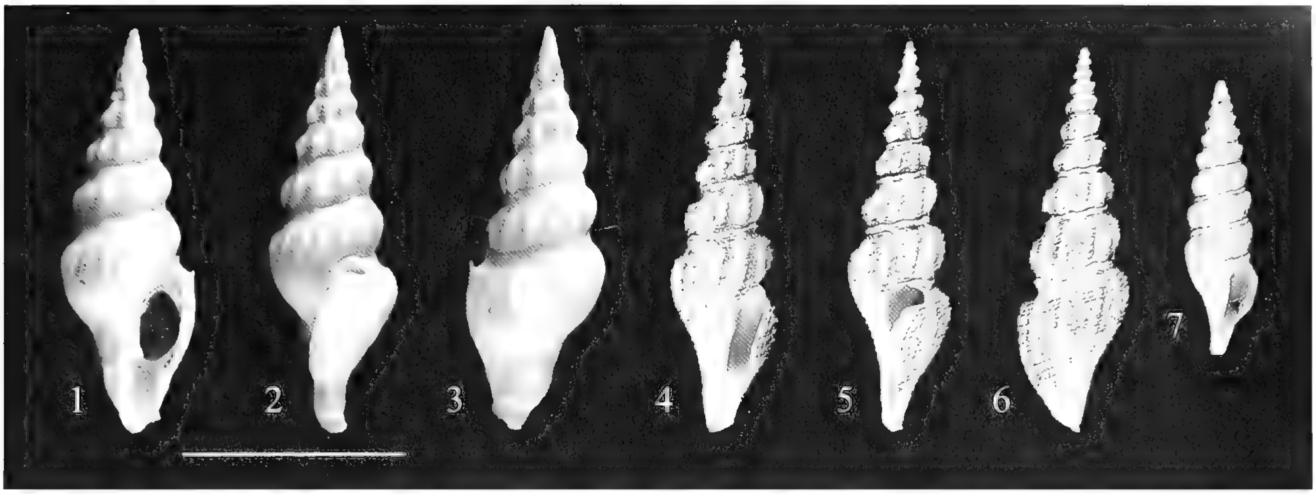
**Type Species:** *Murex gibbosus* Born, 1778, by original designation.

*Drillia* (*Clathrodrillia*) *blakensis* new species
(Figures 1–3, 8)

? Turridae sp.—Lamy and Pointier, 2001: 22, number 73, list, p. 26, photo.

**Description:** Shell of medium-size (to approximately 45 mm), elongate, fusiform, with tall spire and large body whorl measuring about 0.5 shell length. Shell tapering gradually with moderate basal constriction to moderately elongate, open, slightly notched, slightly bent right anterior canal. Protoconch decollated, teleoconch whorls ten. Whorls well-rounded, shoulder sulcus on upper third concave, suture prominent. Sculpture of rounded, regularly spaced axial ribs with equal interspaces, extending from shoulder to following whorl on spire and to base on body whorl. Ribs increase in number with shell growth, seven on early whorls, 12, narrower and closer spaced, on penultimate, ten or 11 on body whorl leading to small varix 0.25 whorl back of lip edge, two or three possibly abortive ribs following varix. Fine spiral threads overall, weaker on sulcus. Aperture parallel-sided with apically directed, U-shaped sinus posteriorly, bordered on body whorl by flat parietal tubercle. Lip sloping roundly forward below sinus, upper edge directed upward, narrowing sinus somewhat, producing spout-like appearance. Stromboid notch distinct. Color dirty-white overall, faint, pale brown peripheral band, blotch of same color on varix and spots preceding tops of axial ribs on later whorls. Operculum (Figure 8) of chestnut color, ovate with roundly pointed anterior end and terminal nucleus.

**Type Material:** Holotype, USNM 900034, 400–450 m, May 1965; three paratypes, USNM 1096708, data same



**Figures 1–7.** Drilliids and turrids. **1–3.** *Drillia (Clathrodrillia) blakensis* new species, holotype, USNM 900034, 44.8 ×16.0 mm, apertural, lateral, dorsal views. **4–6.** *Hindsiclava rosenstielanus* new species, holotype, USNM 1086746, off Riohacha, off Colombia, 44.5 × 13.6 mm, apertural, lateral, dorsal views. **7.** *Pleurotoma (Drillia) polytorta* Dall, 1881, holotype, USNM 412171, 32.6 × 9.6 mm, off Cape San Antonio, Cuba. Scale bar = 25 mm.

as for holotype, 45.7 × 16.6 mm, 44.1 × 14.7 mm, 42.5 × 16.0 mm (ex-José and Marcus Coltro collection., ex-author's collection); all dredged by R/V OREGON on type locality.

**Other Material Examined:** one specimen, Dr. Douglas Wolfe collection , 41.2 × 15.5 mm, dredged by R/V OREGON on type locality.

**Type Locality:** Blake Plateau; precise location unknown, data presumably not retained.

**Distribution:** Blake Plateau and possibly off Saba Island, Netherlands Antilles (Lamy and Pointier).

**Discussion:** *Drillia blakensis* is most similar to *Drillia Clathrodrillia) petuchi* Tippett, 1995, from which it differs in being narrower, having less robust ribs, finer spirals, a broader, non-tabulate, more sloping sulcus, and fainter color pattern. The author has not seen the shell figured in Lamy and Pointier, stated to be 48 mm in length and from 150 m depth, however it appears from the illustration to be *D. blakensis*, differing in being slightly broader, having a slightly shorter anterior canal and stronger peripheral color banding, features within intraspecific variation limits.

**Etymology:** Named after the Blake Plateau, the type locality.

Turridae H. Adams and A. Adams, 1853 (1838)

Crassispirinae Morrison, 1966
Genus *Hindsiclava* Hertlein and Strong, 1955

**Type Species:** *Clavatula militaris* Hinds, 1843, by original designation.

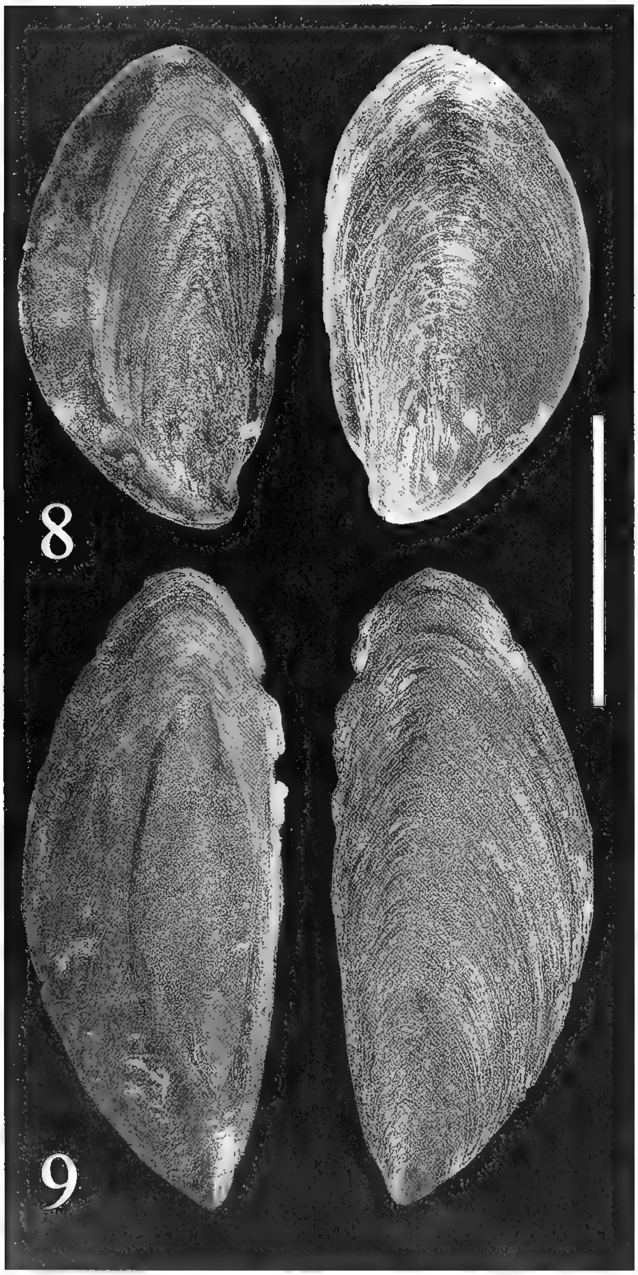
*Hindsiclava rosenstielanus* new species
Figures 4–6, 9, 10

*Crassispira polytorta* (Dall, 1881): Okutani, 1983: 304, description and figures (apertural and lateral views plus radular teeth).

?Turridae sp.—Lamy and Pointier, 2001: 22, number 71, list and photo.

**Description:** Shell of medium-size (to approximately 48 mm), elongate, fusiform, turreted, with tall spire, body whorl about 0.4 of shell length, whorls rounded below concave shoulder slope, gently constricted at base to moderately long, anterior canal open, notch lacking. Protoconch with 2.5 smooth whorls, tip central, first 1.5 whorls glossy, remainder dull-white, terminating in short portion of whorl with 4–5 axial riblets that quickly enlarge to axial ribs in adult shell. Teleoconch whorls 9–10. Aperture of parallel sides and with moderately deep, U-shaped posterior sinus on shoulder slope. Parietal tubercle absent. Suture distinct, almost channeled, slightly wavy. Subsutural cord of double threads. Axial ribs robust (11–12 on body whorl, 11 on penultimate), extending faintly across sulcus above and to next suture on spire, disappearing on base; interspaces half again as wide. Uniform, regularly spaced spiral threads (5–6 on whorl periphery) cross ribs, producing modest, laterally elongate nodules, then continue forward to anterior canal. Microsculpture of fine spiral threads, including sulcus, irregular in strength and distribution. Notch and varix lacking. Color dirty-white overall, traces of dark periostracum.

**Gross Anatomy:** Animal white, foot with upturned propodium, operculum locate d posteriorly on foot. Head bearing two tentacles, each with eye dorsally on an expansion midway from base. Penis behind right tentacle, reflected back under mantle. Respiratory siphon on left, bearing a fold, mantle edge extending across head, with moderate anal sinus on right. Gills and os



**Figures 8, 9.** Opercula, inner (left) and outer (right) views. **8.** *Drillia* (*Clathrodrillia*) *blakensis*, 7.5 mm length. **9.** *Hindsiclava rosenstielanus*, 11 mm length. Scale bar = 5 mm

phradium visible through mantle. Rectum on right. Puckered rhynchostome between and slightly below tentacles. Rhynchostomal sphincter present. Rhynchocoel with strong linear folds internally. Rhynchodeal wall circularly folded due to retraction. Proboscis long, circularly folded along its length in preserved animal due to contraction, linear folds posteriorly. Large buccal mass and cavity posterior to rhynchodeum. No sphincter seen at beginning of esophagus. Large, highly coiled poison gland and bulb in body cavity. Right and left salivary glands present. Radular ribbon ventral and posterior to buccal mass. Gland ducts and radular ribbon enter at beginning of esophagus ventrallly and posteriorly to buccal mass. Incomplete radula with approximately 40 pairs of wishbone marginal teeth (Figure 10) measuring approximately 300 μm. Operculum (Figure 9) medium amber, ovate with flat proximal side, rounded peripheral side, ends rather sharply rounded, terminal nucleus at anterior end.

**Figure 10.** *Hindsiclava rosenstielanus*, radula, teeth are 300 μm length.

**Type Material:** Holotype, USNM 1086746, west of Riohacha, off Colombia, 11°32′ N 073°23′ W, 549 m, R/V Pillsbury 781, 30 July 1968, 3 m, otter trawl, ex-UMML 30.10788; paratypes (ex-UMML): one specimen, USNM 1107006; one specimen, MCZ 359135; one specimen, ANSP 416320; seven specimens UMML 30.10788, four with animal preserved, three shells only. All from type locality.

**Other Material Examined:** USNM 902064, three specimens, off Cartagena , Colombia, (ex-José and Marcus Coltro collection, ex-author's collection); *Pleurotoma* (*Drillia*) *polytorta* Dall, 1881, USNM 412171, holotype.

**Type Locality:** West of Riohacha, off Colombia.

**Discussion:** *Hindsiclava rosenstielanus* is most similar to *Hindsiclava polytorta* (Dall, 1881) (Figure 7) reported from off Cuba. *Hindsiclava rosenstielanus* differs by its wider sulcus, doubled subsutural cord, fewer ribs (e.g., nine on sixth spire whorl versus 12 on equivalent whorl of *polytorta*), presence of fine secondary spiral threads overall, and absence of parietal tubercle. The specimen reported by Okutani, measuring 58 × 19 mm, from 328–470 m off Surinam, appears to be this species despite the larger size and the radular teeth which are dissimilar at the location of their basal attachment (drawings appear stylized). The specimen reported by Lamy and Pointier (2001) from 450 m off Point Noire, Guadeloupe, is 63 mm in length and, appears to be this species, again despite its larger size, and also despite the geographic distance of Guadalupe from the type locality of *rosenstielanus*. The specimens in USNM 902064 are identical with the type material except that the axial ribs are slightly broader.

**Etymology:** The species is named for the Rosenstiel School of Marine and Atmospheric Science, University of Miami, from which the material was obtained.

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