IDENTIFICATION OF EASTERN NORTH AMERICAN LAND SNAILS

The Prosobranchia, Opisthobranchia and Pulmonata (Actophila)

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IDENTIFICATION OF EASTERN NORTH AMERICAN LAND SNAILS

THE PROSOBRANCHIA

I. The Archaeogastropoda: HELICINIDAE

The most primitive gastropods, the prosobranch archaeogastropods, are represented in North America by one land snail family, the Helicinidae Férussac 1822. Nearly all members of the Prosobranchia have gills (ctenidia) for exchange of respiratory gases, and in this way differ from the Soleolifera (Gymnophila) and Pulmonata (Actophila and Geophila), which instead have a vascularized "lung" for respiration. But, in terrestrial and many amphibious prosobranchs (which comprise relatively very few taxa), the gill has gradually been replaced by a vascularized area of the mantle roof, which takes over the respiratory function. Thus, the land-inhabiting Helicinidae lack gills, having a pallial "lung" like the Pulmonata. In other respects the helicinids are undeniably prosobranchs.

The Helicinidae are mainly tropical and three of the four eastern North American species are found only in the south, two of them (Helicina clappi and Lucidella tantilla) being restricted to Florida. The fourth species, Hendersonia occulta, has a more northern distribution, occurring as far north as the Upper Peninsula of Michigan. In addition to the four native helicinid species, three other species have been reported (*Henry A. Pilsbry, 1948, The land Mollusca of North America (north of Mexico), Acad. nat. Sci. Philad., Monogr. 3, 2(2): i-xlvii + 521-1113; Leslie Hubricht, 1960d, Nautilus, 74(2): 82-83) as dead shells in beach drift on the coast in southern Texas: Helicina chrysocheila Binney, H. fragilis elata Shuttleworth and Lucidella lirata (Pfeiffer). However, these are Mexican species which have never been found alive north of the Rio Grande, so it is assumed that they are not members of the United States' fauna, but have been carried by Gulf currents from the south and deposited on the beaches of Padre, Mustang and Galveston islands (Paul Lewis McGee, 1965, Distribution and ecology of the terrestrial mollusks of the Texas coastal counties. Publ. by the author. 46 pp.).

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^{*}In this and following sections on identification, complete citations are given the first time a reference is cited. Subsequent citations to the same references are given only by author's last name and date.

Helicinid shells are usually wider than high and all are imperforate, the umbilical region being occupied by a callous pad. As is typical for nearly all prosobranch snails, the shell aperture is closed by an operculum when the animal is withdrawn into the shell. The opercula are either paucispiral or concentric, depending on the genus, and are layered with a rather thin calcareous deposit.

Key to the Species of Helicinidae

Shell small[†], 3 mm or less in diameter, strongly depressed (Fig. 18). Southern Florida (Fig. 19). . . . Lucidella tantilla (Pilsbry)

[The shell of *Lucidella tantilla* is glossy, has about 3½ whorls, is marked with prominent growth lines, and is faintly yellowish to white in color. The basal (axial) callus is covered with minute pits. The operculum is concentric, its nucleus located near the posterior edge.]

[The adult shell of *Hendersonia occulta* has 4½ to 5 whorls and is 6 to 8 mm in diameter. The shell varies in color from cinnamon red to pale yellow. The periphery is slightly angular, sometimes weakly keeled (particularly in younger specimens).

B. Shimek (1904, Proc. Davenport Acad. Sci., 9: 173-180; 1905, J. Geol., 13(3): 232-237; 1919, Proc. Iowa Acad. Sci., 26: 385-390; 1930, Nautilus, 43(4): 111-112) reviewed the literature and discussed the distribution, taxonomy and synonymy of Hendersonia occulta, including the reasons for rejecting H. rubella Green. The anatomy of H. occulta has been described by H. Burrington Baker (1925b, Proc. Acad. nat. Sci. Philad., 77: 273-303, pls. 7-10).

Shimek (1905: 232-233) suggested "that local variations in the minimum amount of moisture are responsible for the differences

[†]Characters used in this and subsequent keys refer to adult shells.

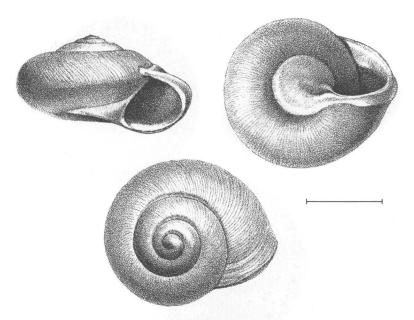
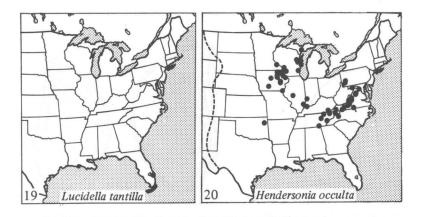


FIG. 18. Lucidella tantilla (Pilsbry). Scale line = 1 mm.



FIGS. 19, 20. Distributions of Lucidella tantilla and Hendersonia occulta.

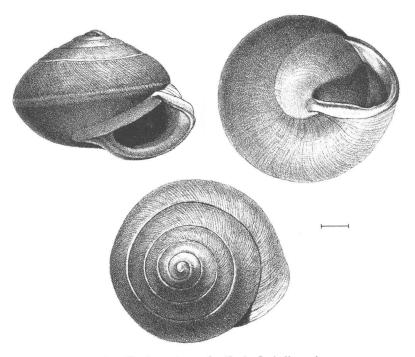


FIG. 21. Hendersonia occulta (Say). Scale line = 1 mm.

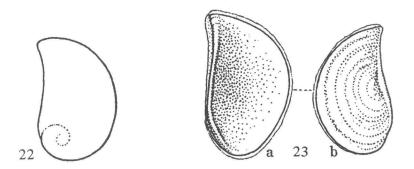


FIG. 22. External outline of the operculum of *Hendersonia occulta* (from Pilsbry, 1948). FIG. 23. Operculum of *Helicina orbiculata tropica* (from Pilsbry, 1948). a, External view; b, internal view.

in size, the smallest shells occurring in the driest and most exposed places. The average diameter of both recent and fossil forms becomes a little less as we go westward into drier regions . . . "]

Shell smooth, with very weak growth lines, and only occasionally with a few widely spaced spiral striae; operculum concentric (Fig. 23). Genus *Helicina*

3(2) Shell globose, periphery of last whorl broadly rounded; junction of columella and basal lip generally with a well-developed angle (Fig. 24). Florida west to Texas, north to Illinois and Kentucky (Fig. 25). Helicina orbiculata (Say)

[The adult shells of *Helicina orbiculata* generally have about 5 whorls, and are white to buff in color (sometimes varying to pink), often with brownish or white bands. The shell surface is dull and has rather obscure growth lines.

A western race in Arkansas, Oklahoma, Texas and Mexico, Helicina orbiculata tropica Pfeiffer, is sometimes recognized. It has a more solid shell with a thicker apertural lip and "typically having a bevelled thickening beyond the reflected lip. ... Collectors recognize that specimens not distinguishable from orbiculata are sometimes found in tropica territory. There is no hard and fast line between them. But the difference between orbiculata and tropica is not solely a matter of pH, for in wholly calcareous tracts in Florida and Alabama the helicinas retain their typical orbiculata characters. [Pilsbry did not imply that the tropica characters were the "reaction to a limestone substrate."] The modification is correlated with geographic range, therefore of subspecific significance" (Pilsbry, 1948: 1084). Similarly, Richard W. Fullington & William Lloyd Pratt, Jr. (1974, The aquatic and land Mollusca of Texas. Pt. 3. The Helicinidae, Carychiidae, Achatinidae, Bradybaenidae, Bulimulidae, Cionellidae, Haplotrematidae, Helicidae, Oreohelicidae, Spiraxidae, Streptaxidae, Strobilopsidae, Thysanophoridae, Valloniidae (Gastropoda) in Texas. Dallas Mus. nat. Hist., Bull. 1, 48 + iv pp.) mention that the tropica characteristic "is well developed in specimens from a number of localities on acid sandy soils in . . . Texas." The latter authors believe that the tropica characters are a phenotypic response to drier conditions.]

Shell more trochiform in shape, periphery of last whorl generally obtusely subangular; junction of columella and basal lip often lacking an angle, or having only a very weak one (Fig. 27). Restricted to Florida (Fig. 26)

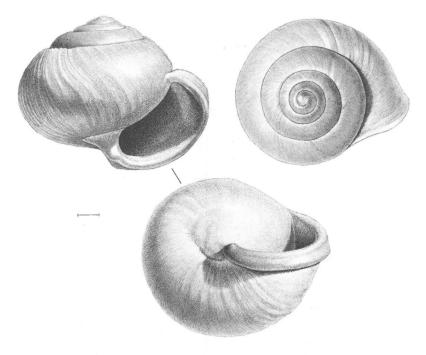
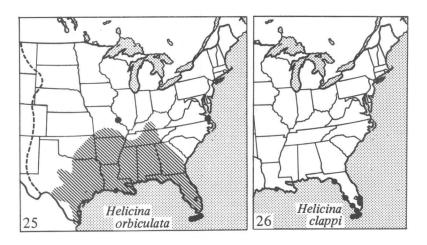


FIG. 24. Helicina orbiculata (Say). Scale line = 1 mm.



FIGS. 25, 26. Distributions of Helicina orbiculata and H. clappi.

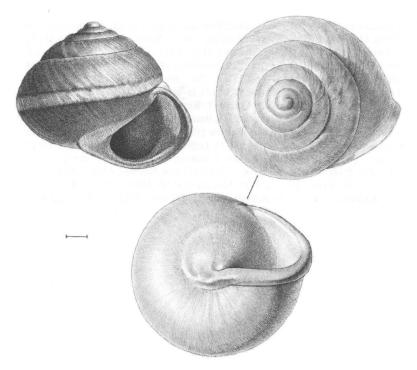


FIG. 27. Helicina clappi Pilsbry. Scale line = 1 mm.

[The adult shells of Helicina clappi have 5 to 5½ whorls, and are white, pale yellow or red in color, sometimes with several red bands. The differences in shell characters between H. clappi and H. orbiculata are rather minor. H. clappi usually has ½ to 1 more whorl and is generally larger [in Florida, where the 2 species overlap in distribution], is usually slightly less globose, the periphery of the last whorl tends to be a bit more obtusely subangular, the aperture is somewhat lower and broader, and the angle near the junction of the columella and basal lip is weaker or may be absent all together. The dorsum of the anterior head-foot region on H. clappi is darker ("blackish") than on H. orbiculata.]

Literature Sources for Geographic Distributions of Helicinidae

Helicina clappi. Pilsbry (1948).

Helicina orbiculata. Dorothy E. Beetle (1973, Sterkiana, (49): 21-33), Branley A. Branson (1961b, Proc. Okla. Acad. Sci., 41: 45-69; 1971, Sterkiana, (41): 35-40), Branley A. Branson & Donald L. Batch (1971, Sterkiana, (43): 1-9), E.P. Cheatum, Richard Fullington & Lloyd Pratt (1972, Sterkiana, (46): 6-10), Dee

Saunders Dundee & Patti Watt (1962, Proc. La. Acad. Sci., 25: 47-49), Leslie Hubricht (1956a, Nautilus, 69(4): 124-126; 1962g, Sterkiana, (8): 33-34; 1963h, Sterkiana, (10): 1-3; 1964h, Sterkiana, (16): 5-11; 1965c, Sterkiana, (17): 1-5; 1968b, Sterkiana, (32): 1-6; 1972d, Sterkiana, (45): 34-35; 1972e, Sterkiana, (45): 36; 1972f, Sterkiana, (46): 15-17; 1973, Sterkiana, (49): 11-17), Morris K. Jacobson (1952, Nautilus, 65(4): 109-114), Louis Lutz (1950a, Proc. Okla. Acad. Sci., 30: 32-35), Pilsbry (1948), Landon T. Ross (1964, Nautilus, 78(2): 50-52).

Hendersonia occulta. Beetle (1973), Branley A. Branson (1963b, Trans. Kans. Acad. Sci., 66(3): 501-512), M.S. Briscoe (1963, Sterkiana, (9): 41-48), F. Wayne Grimm (1971b, Sterkiana, (41): 51-57), Leslie Hubricht (1956c, Nautilus, 70(1): 15-16; 1968b; 1973), Lorna R. Levi & Herbert W. Levi (1950, Nautilus, 63(4): 131-138), Pilsbry (1948), Margaret C. Teskey (1954, Nautilus, 68(1): 24-28), Henry van der Schalie (1939, Occ. Paps. Mus. Zool., Univ. Mich., (399): 1-9).

Lucidella tantilla. Leslie Hubricht (1972c, Sterkiana, (45): 33), Pilsbry (1948).

II. The Mesogastropoda: POMATIIDAE, TRUNCATELLIDAE and HYDROBIIDAE

POMATIIDAE

The Pomatiidae Gray 1852 (=Pomatiasidae Pilsbry 1919, Chondropomat-idae Henderson & Bartsch 1920, Choanopom-idae Thiele 1929) are terrestrial prosobranchs, and, like the helicinids, lack a gill, having instead a vascularized portion of the mantle wall functioning as a "lung." The family is a large one, with 66 genera listed for it by D.W. Taylor & N.F. Sohl (1962, Malacologia, 1(1): 7-32). Some genera (e.g., Opisthosiphon) are characterized by a breathing tube behind the outer shell lip (Fig. 29b), which allows air to pass into the mantle cavity. The pomatiids are tropical or subtropical in distribution and are limited to the Caribbean region and northern South America. One species, Chondropoma dentatum (Say) (Fig. 28), occurs naturally in the United States (in southern Florida; Fig. 31). Another species, the Bahaman Opisthosiphon bahamensis (Pfeiffer) (Figs. 29, 30b), was found by W.H. Rush in 1897 at Key West, Florida (Pilsbry, 1948: 1077) but it apparently has not been reported since then and probably was only a temporary introduction. Earlier, W.G. Binney (1865, Land and freshwater shells of North America, pt. 3, Smithson. misc. Coll., (144), 120 + viii pp. [p. 97, fig. 195]) figured the Cuban "Ctenopoma" (=Rhytidopoma) rugulosum (Pfeiffer) from Florida, but this species also has not been found since. More recently, Fritz Haas (1947, Nautilus, 61(1): 33) reported a specimen of the Central American Adelopoma costaricense Bartsch & Morrison from an insect trap at Charleston, South Carolina. This report was later retracted by Alan Solem & Fritz Haas (1964, Nautilus, 78(2): 68-69), who suggested that the report probably resulted from a mislabelled specimen.

The Pomatiidae have elongate shells, which are usually marked with axial and often with spiral sculpture. They are frequently covered with fine riblets. Small calcareous projections at rather regular intervals just below the sutures give the shells a crenulated appearance. Often the earlier whorls break off, leaving the shells decollate in the adult stage.

[The shell of *Chondropoma dentatum* (Fig. 28) has about 4 whorls remaining in decollated adults and measures from 10 to 12 mm in length. It is dull red to light tan, and sometimes has several narrow interrupted bands or spots. The shell lacks an opening for a breathing tube behind the outer lip. The shell is umbilicate, the outer surface has both transverse and spiral sculpture, and the inner edge of the aperture is smooth and rounded.

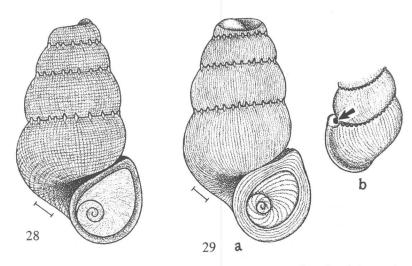


FIG. 28. Chondropoma dentatum (Say). FIG. 29. Opisthosiphon bahamensis (Pfeiffer). a, Apertural view of shell; b, dorsal view, showing opening for breathing tube. Scale line = 1 mm.

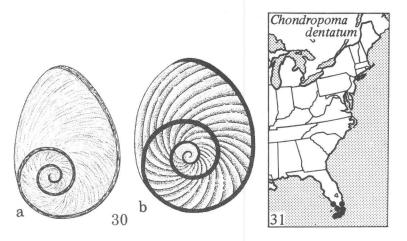


FIG. 30. Opercula of pomatiids. a, Chondropoma dentatum; b, Opisthosiphon bahamensis. FIG. 31. Distribution of Chondropoma dentatum.

The operculum is spiral and cartilaginous (Fig. 30a).

According to Pilsbry (1948: 1076), Chondropoma dentatum is closely related to C. auberianum mayense Torre & Bartsch of northern Cuba.]

Literature Source for Geographic Distribution of Pomatiidae

Chondropoma dentatum. Pilsbry (1948).

TRUNCATELLIDAE

The Truncatellidae Gray 1840 comprise species with very small, cylindrical shells, which are imperforate, usually decollate and often heavily ribbed. The operculum is subspiral (Fig. 36) and corneus, often covered with a calcareous layer. The family and its main genus, Truncatella, get their names from the characteristically truncated shell spire, which results from the upper spire being broken off at about the fourth or fifth whorl as the snails reach maturity. The truncatellids are widely distributed in tropical and subtropical areas, usually living on beaches above high tide level, often on rocks or under stones or debris. "In the Western Atlantic, Truncatella extends from the Bermudas, northern Florida and the West Indies as far south as Trinidad. The records from southern New England and North Carolina are based upon mechanical introduction by man or sporadic introductions by drift. Records from the northern Gulf of Mexico may also be chance introductions which in these areas may survive for only a short period of time" (William J. Clench & Ruth D. Turner, 1948a, Johnsonia, 2(25): 149-164). One species long recorded in North America is T. truncatula Draparnaud (="Truncatella subcylindrica (Linnaeus)" in Pilsbry (1948)), which was found by A.E. Verrill (1880, Amer. J. Sci., 20: 250) along the docks at Newport, Rhode Island ("perhaps introduced") in July, 1880, occurring among decaying seaweeds thrown up at high-water mark and on the undersides of stones. "It has failed to survive. No records of this species have been obtained since from anywhere in New England or even south of this area" (Clench & Turner, 1948a).

The latest comprehensive account of American Truncatellidae is that of Torre (1960, *Nautilus*, 73(3): 79-88). The key below is adapted from Torre.

Key to the Species of Truncatellidae

1	Shell small, 3-6 mm in length; outer apertural lip of shell generally duplex (i.e., in addition to the thickened apertural rim there is also a large, more or less prominent rib-like thickening behind the apertural lip)
	Shell larger, 6-9 mm in length; outer apertural lip of shell simple, not duplex (Fig. 32). Texas, Alabama, Florida and North Carolina (Fig. 37)
	[The truncated adult shell of <i>Truncatella caribaeensis</i> retains about 3½ whorls and is rust colored to pale cinnamon-buff. It is sculptured with many axial ribs, but often the ribs may not be strongly developed and in many specimens the ribs may be more or less obsolete. The smooth form has been improperly called <i>T. subcylindrica</i> Gray [which is not the "Helix" subcylindrica Linnaeus 1767 of Europe]. <i>Truncatella caribaeensis</i> has a rather wide distribution in the Caribbean region.]
2(1)	Ribs 17 or more on the body whorl (the shell may be nearly smooth or strongly ribbed) (Figs. 33, 34); shell lacking microscopic spiral sculpture between the ribs. Florida (Fig. 38)
	[The truncated shell with 3½ to 4½ whorls may vary in length from 3 to 6 mm. It is red-brown to amber-yellow in color. <i>Truncatella pulchella</i> "is very variable, going from a smoothish form with the duplex condition of the outer lip and peristome in a very reduced or obsolete condition [Fig. 33], to a form presenting strong axial ribs and with the duplex condition of the outer lip very prominent [Fig. 34]. This last form is what properly may be called <i>T. pulchella</i> form <i>bilabiata</i> Pfr." (Torre, 1960). <i>Truncatella pulchella</i> and its form <i>bilabiata</i> occur also on various of the West Indian islands.]
	Ribs 16 or less on the body whorl (Fig. 35); shell with microscopic spiral sculpture between the ribs. Florida (Fig. 39)
	[The shell of <i>Truncatella scalaris clathrus</i> is solid and is sculptured with 12 to 16 very prominent axial ribs on the body whorl. The truncated adult shell with $3\frac{1}{2}$ to $4\frac{1}{2}$ remaining whorls is 4.5 to 5

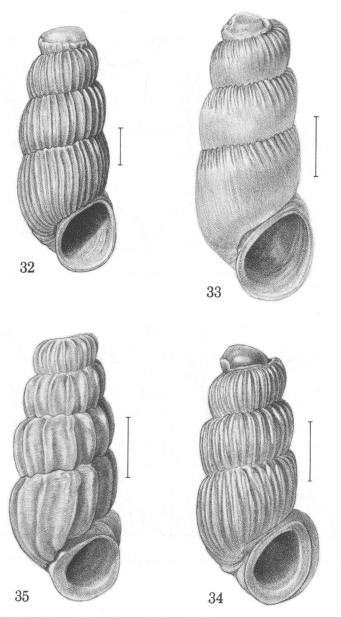


FIG. 32. Truncatella caribaeensis "Sowerby" Reeve. FIG. 33. T. pulchella Pfeiffer. FIG. 34. T. pulchella form bilabiata Pfeiffer. FIG. 35. T. scalaris clathrus Lowe. Measurement lines = 1 mm.

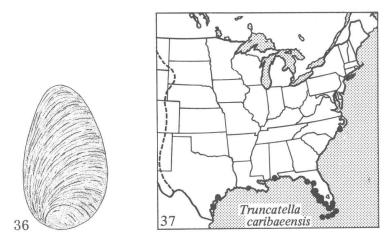
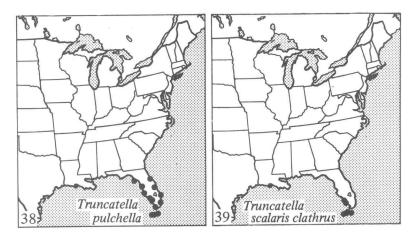


FIG. 36. Subspiral operculum of *Truncatella*. FIG. 37. Distribution of *Truncatella caribaeensis*.



FIGS. 38, 39. Distributions of *Truncatella pulchella* (including form *bilabiata*) and *T. scalaris clathrus*.

mm long. Its color is grey, buff, yellowish- or reddish-brown. The subspecies *T. scalaris clathrus* differs from *T. scalaris scalaris* (Michaud) by its more numerous ribs, having 12-16 on the body whorl, rather than the 8-11 which characterize typical *scalaris*. "Dr. Morrison thinks that the specimens coming from Florida and the Bahamas in the collection of the USNM all correspond to the form *clathrus* and none to the typical *scalaris* Michaud. I keep them separate, as distinct subspecies, although they possibly may prove to be only different extreme forms . . ." (Torre, 1960). *T. scalaris scalaris* is found in Cuba, Haiti, Jamaica and St. Croix. *T. scalaris clathrus* is found in Florida, Bermuda, Puerto Rico (?), St. Thomas (?), Cuba, Haiti and Bahamas (Torre, 1960).

Clench & Turner (1948a; 1948b, Occ. Paps. Moll., 1(13): 157-212) placed Truncatella scalaris, together with the West African T. rostrata Gould, into a separate subgenus, Tomlinitella. Torre (1960) placed two other species into this subgenus, T. bahamensis Clench & Turner of the Bahama Islands and T. barbadensis Pfeiffer of Barbados, Guadeloupe and Antigua.]

Literature Source for Geographic Distribution of Truncatellidae

Truncatella caribaeensis, Truncatella pulchella and Truncatella scalaris clathrus. Torre (1960).

HYDROBIIDAE

The Hydrobiidae Troschel 1857 are one of the most common and widely distributed gastropod families. The family is a large one, comprising some 103 genera (Taylor & Sohl, 1962). Nearly all hydrobiid species live in fresh water, although some are associated with brackish and even salt water; a few species are amphibious, and a few are essentially terrestrial in habit. Several species of the North American genus *Pomatiopsis* come under the latter category. These pomatiopsine species, together with their Oriental, Asian and South African relatives, are placed in a separate hydrobiid subfamily, the Pomatiopsinae Stimpson 1865 (e.g., see George Morgan Davis, 1967, *Malacologia*, 6(1/2): 1-143). Sometimes the group is raised to familial rank.*

Shells of hydrobiids are generally small, elongate, dextral, drab and unicolored, and have few whorls. The shells of some species have surface sculpture, and a few are spectacularly ornamented. The shell aperture is closed by an operculum, which, in *Pomatiopsis*, is paucispiral. Like the rest of the operculate land snails included here, the sexes are separate.

^{*}For example, see Theodore Gill (1863, Proc. Acad. nat. Sci. Philad., 15: 33-40), H.A. Pilsbry & James H. Ferris (1907, Proc. Acad. nat. Sci. Philad., 1906, 58: 529-567, pls. 20-22), Frank Collins Baker (1926, Trans. Wisc. Acad. Sci., Arts and Lett., 22: 192-205), George M. Davis (1979, Acad. nat. Sci. Philad., Monogr. 20: i-ix, 1-120).

But *Pomatiopsis*, unlike the other North American land prosobranchs, have gills in their mantle cavity for respiration.

Three species of *Pomatiopsis* are known from eastern North America. A fourth name, *Pomatiopsis praelonga* Brooks & MacMillan, is a synonym of *P. lapidaria*.

Key to the Species of Hydrobiidae

	,
1	Shell elongate, with relatively flattened whorls and oval aperture
	Shell more squatty, broadly conical, with rounded whorls and aperture (Fig. 40). Tennessee and southwest Virginia to southern Michigan, Illinois and Iowa (Fig. 43)
	[Pomatiopsis cincinnatiensis is more aquatic (i.e., more intolerant of low moisture levels) than the other common eastern pomatiopsine species, P. lapidaria, and is restricted to a narrow zone on the banks of rivers above the water line (see Henry van der Schalie & Lowell L. Getz, 1962, Am. midl. Nat., 68(1): 203-231).]
2(1)	Spire more acute, body whorl proportionately smaller, aperture broadly oval, umbilicus wider, more open (Fig. 41). Widely distributed in the eastern United States, with occasional occurrences west to northern Texas and New Mexico (Fig. 44)
	[Pomatiopsis lapidaria, although commonly found close to streams, has a greater tolerance to drier conditions than does P. cincinnatiensis. In addition to inhabiting stream banks, "Pomatiopsis lapidaria is found in a variety of habitats such as marshes, wooded flood plains of small creeks, grassy hummocks in low, wet pastures, and in upland artesian-fed marshes" (Dee Saunders Dundee, 1957, Misc. Publ. Mus. Zool., Univ. Mich., (100): 1-37). Elmer G. Berry (1943, Misc. Publ. Mus. Zool., Univ. Mich., (57): 1-68, pls. 1-9) reported collecting specimens on a mountain side in southern Kentucky more than 500 feet from water. Stanley T. Brooks & Gordon K. MacMillan (1940, Nautilus, 53(3): 95-97) found "P. praelonga" 100 to 500 feet above the Elk River on a rocky hillside under the dead fronds of ferns.]
	Spire more obtuse, body whorl proportionately larger, aperture narrowly oval, umbilicus nearly closed (Fig. 42). Alabama

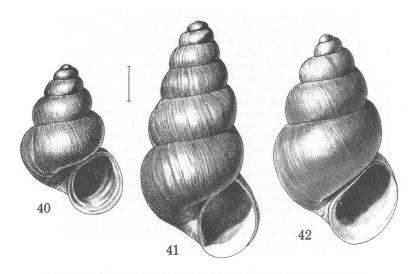
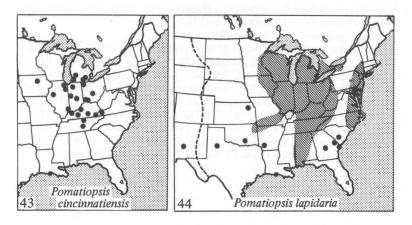


FIG. 40. Pomatiopsis cincinnationsis (Lea). FIG. 41. P. lapidaria (Say). FIG. 42. P. hinkleyi Pilsbry. Measurement line = 1 mm.



FIGS. 43, 44. Distributions of Pomatiopsis cincinnationsis and P. lapidaria.

[A.A. Hinkley discovered Pomatiopsis hinkleyi in 1894. His description of the habitat and type locality [Black Falls, above Florence, Alabama] (in Henry A. Pilsbry, 1896, Nautilus, 10(4): 37-38) was as follows: "Most of the distance from Florence to the last lock of the canal there is a steep rocky bank; a few rods from the water of the river over this bank and out of it are several small streams and springs of clear water. The species . . . was seen at most of these small streams but was not numerous except at the two falls from which they were taken. . . . They were taken from moss and decaying vegetation [not in the water] but were kept damp by the spray of the falls or by the dripping water under the rock back of the falls and saturated moss. . . . None of them were found beyond the reach of the spray but still they might have been hidden under the rubbish." These habitats are now covered by the water impounded by Wilson Dam. Hubricht (1960b, Nautilus, 74(1): 33-34) found similar shells at a dripping spring, 3 miles north of Ashland City, Cheatham Co., Tennessee, and from a swamp near Little Salkehatchie River, 4.2 miles north of Eberhardt, Bamberg Co., South Carolina. He believes that P. hinkleyi is only a wet habitat form of P. lapidaria.]

Literature Sources for Geographic Distributions of Hydrobiidae

Pomatiopsis cincinnatiensis. Frank Collins Baker (1928, The fresh water Mollusca of Wisconsin. Pt. 1. Gastropoda. Wisc. geol. & nat. Hist. Surv., Bull. 70, 507 pp.), Beetle (1973), Lowell L. Getz (1971, Sterkiana, (43): 20), Hubricht (1973), Henry van der Schalie & Dee Saunders Dundee (1955, Trans. Am. microsc. Soc., 74(2): 119-133), van der Schalie & Getz (1962).

Pomatiopsis hinkleyi. Pilsbry (1896).

Pomatiopsis lapidaria. R. Tucker Abbott (1948, Proc. U.S. natl. Mus., 98(3222): 57-68, pls. 3, 4), Baker (1928), Beetle (1973), Branson & Batch (1971), Briscoe (1963), Lorenzo E. Daniels (1902, Ind. Dept. Geol. & nat. Res., 26th ann. Rep., pp. 629-652), Dundee (1957), Dorothea S. Franzen (1944, Trans. Kans. Acad. Sci., 47(2): 261-273), F. Wayne Grimm (1961b, Nautilus, 74(3): 106-109; 1971b), Leslie Hubricht (1960b; 1964h; 1965c; 1966a, Nautilus, 79(4): 117-118; 1968b; 1970, Sterkiana, (39): 11-15; 1971a, Sterkiana, (41): 41-44; 1972d; 1972f; 1973), Jacobson (1952), Michael F. Kaplan & W. L. Minckley (1960, Nautilus, 74(2): 62), Teskey (1954), Charles B. Wurtz (1948, Nautilus, 61(3): 80-89).

THE OPISTHOBRANCHIA

The Gymnophila (Systellommatophora): VERONICELLIDAE

The gymnophile slugs have long been known to be an aberrant group, and there is still controversy regarding their systematic placement. The two land families, the Veronicellidae and the Rathouisiidae, are obviously rather closely related, although their Recent natural distributions do not overlap. The carnivorous Rathouisiidae are confined to limited areas of the Australasian region, whereas the herbivorous Veronicellidae occur naturally in the Neotropics, southeast Asia, and Africa south of the Sahara, but human commerce has distributed them throughout the tropics of the world.

Pilsbry (1948: 1062) introduced the ordinal name Systellommatophora for the veronicellid slugs, although there were earlier names available, such as Ditremata Fischer 1883, Soleolifera Simroth 1890, Teletremata Pilsbry 1898, and Digonophora Suter 1913. Pilsbry's introduction of the word Systellommatophora was undoubtedly to conform to the commonly used terms Stylommatophora (the land pulmonates) and Basommatophora (the aquatic pulmonates). However, there may be equally good reasons, as Baker (1955, Nautilus, 68(4): 109-112) suggests, for using Geophila Férussac 1812 ("as restricted") for the stylommatophoran land snails ("this return to the earliest name is because it is not preoccupied, has no different modern connotation, and is short"), Limnophila Férussac 1812 for the freshwater pulmonates, and Gymnophila Baker 1955 for the Veronicellidae, Rathouisiidae and Onchidiidae. Pilsbry's name Systellommatophora has been used to include all three gymnophilan families (e.g., G. Alan Solem, 1974a, In: Encyclopaedia Britannica, Chicago, 15th ed., Macropaedia, vol. 7, p. 947-957; 1974b, The shell makers, introducing mollusks, John Wiley & Sons, New York, 289 pp.), although Pilsbry's original definition said "Pulmonata in which the eyes are on contractile (not inversible) stalks," and "... female opening about midway of right side of hyponotum" (i.e., characters of the Veronicellidae and Rathouisiidae, but not the Onchidiidae; however, Pilsbry listed the Oncidiacea in the synonymy of Systellommatophora). Johannes Thiele (1931, Handbuch der systematischen Weichtierkunde, Gustav Fischer, Stuttgart, 1(2): 377-778 [488-489]) placed the veronicellids. together with the Asian and Australasian rathouisids, in the Stylommatophora, "stirps" Soleolifera, and more recently the marine Onchidiidae also have been included in the [order] Soleolifera (e.g., C.R. Boettger, 1955, Zool. Anz., suppl., 18: 253-280; Taylor & Sohl, 1962).

There is considerable divergence of opinion as to the systematic placement of the Gymnophila. Pilsbry (loc. cit.) stated, "This series of slugs, hitherto included in the Stylommatophora [Geophila] under various names, is far more distinct from that group than are the Basommatophora [Limnophila]." Yet, he still considered them pulmonates, and has been followed in this regard by various more recent authors, e.g., Lothar Forcart (1953, Ann. Mus. roy. Congo belge, Tervuren, ser. 8, sci. zool., 23: 1-109, pls. 1-5), Solem (1974a,b). Few now still include them in the Stylommatophora, although there are some exceptions (e.g., Louisa Stripling Peterellis & Dee S. Dundee, 1969, Trans. Am. microsc. Soc., 88(4): 547-558; Dee S. Dundee, 1974, Sterkiana, (55): 1-37). Boettger (1955) and others before him, followed by Adolph Zilch (1959, Gastropoda. Teil 2. Euthyneura. In: Schindewolf, Otto H., Handbuch der Paläozoologie, Lief. 1, pp. 1-200 [63], Gebrüder Borntraeger, Berlin-Nikolassee), Taylor & Sohl (1962), and others, placed the systellommatophoran or soleoliferan slugs with the opisthobranch groups. This placement may be more accurate, since the gymnophile slugs, at least the Onchidiidae, share more characteristics with the opisthobranchs than they do with the pulmonates (Vera Fretter, 1943, J. mar. biol. Assoc. U.K., 25: 685-720).

VERONICELLIDAE

The Veronicellidae Gray 1840 (=Vaginulidae Gill 1871) are a tropical family of primitive slugs that have their eyes on contractile (not inversible) stalks or tentacles. The mantle (notum) covers the entire back of the animal and contains neither an external nor internal shell. The body is characterized by a flattened, elongate or elongate-oval form, with the mantle laterally overhanging the narrow foot, hiding the side walls of the body. Differing from other terrestrial slugs, the anus and nephridio-pore in veronicellids are at the posterior end of the animal (see Fig. 51). This is because veronicellids are detorted gastropods, i.e., the mantle cavity has migrated to the posterior end during development, carrying with it the rectal and renal openings. In adults, the mantle cavity is completely obliterated; veronicellids lack a respiratory cavity.

Only one species, *Leidyula floridana* (Leidy), presumably originally an immigrant from Cuba, is now native to the United States. Five other species have been reported as recent introductions. Hopefully, voucher specimens of these introduced species will be kept available for verification and for future studies.

The most commonly used generic names for North American veronicellid slugs are *Veronicella* and *Vaginulus* (e.g., see H. Burrington Baker, 1925a, *Proc. Acad. nat. Sci. Philad.*, 77: 157-184, pls. 3-6; 1928, *Nautilus*, 42(2): 43-47), although several other names also have been used to varying degrees (even, curiously, the reptilian name *Vermicella* (Dee S. Dundee, 1969, *Malacologia*, 9(1): 264)). The nomenclature adopted below is that of José Willibaldo Thomé (1975, *Iheringia*, zool., (48): 3-56). The key which follows is adapted from Baker (1925a)*.

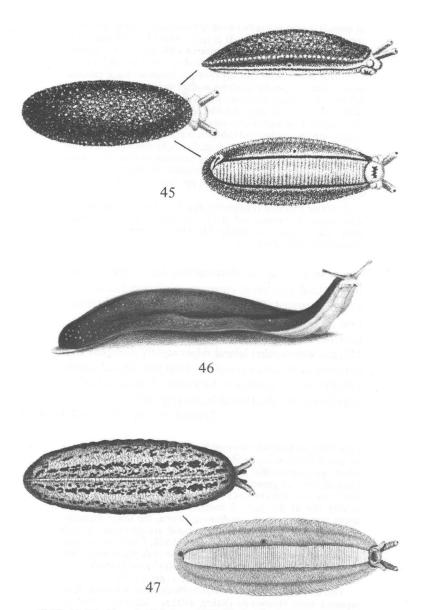
Key to the Species of Veronicellidae

Roundish anus almost median, usually protected ventrally by a dextral flap, so that the superficial crescentic slit is more or less longitudinal and usually hidden under end of even retracted foot; spermathecal stalk short and usually swollen; canalis junctor enters spermathecal sac rather than joining the spermathecal stalk (Fig. 53); verge without granulate, chalky-white glans 5

2(1) Dorsum without dark bands, even in immature specimens; vagina without accessory bursa; spermathecal stalk hard and polished, looped back and forth beneath the vas deferens; verge elongate and quite simply cylindrical (Fig.

^{*&}quot;In the following key, which may assist in their separation, color patterns are sometimes included, but warning is given that, although large lots of a single species usually show certain characteristic trends, any attempt to identify individuals on external characters alone is absolutely futile!" (Baker, 1925a: 157).

	55), with strictly apical orifice; viviparous (?). Bermuda, Jamaica (Cuba?). Intercepted at several U.S. ports; whether or not it has been successfully established in the southern United States is not known
	[This species from Jamaica was first named by H. Sloane (1725, A voyage to the islands Madera, Barbadoes, Nieves, St. Christophers and Jamaica, Publ. by the author, Vol. 2, 499 pp.), a non-binomial author. G. Cuvier (1817, Le Règne Animal distribué d'apres son organisation, pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie comparée, Vol. 2, xviii + 532 pp.) renamed the species after Sloane. Baker (1925a) identified specimens found in 1896 on bananas in Nantucket, Massachusetts, as this species. It is certain that this tropical slug could not become established in New England, but Dundee (1974) has reported it being intercepted by U.S. Department of Agriculture inspectors at ports in Florida. The dorsal mantle of Leidyula sloanei lacks dark longitudinal bands, and it is this feature that mainly distinguishes it from its subspecies schivelyae from Bermuda. Specimens of L. sloanei may attain a length of nearly 90 mm.]
	Dorsum with or without dark bands (when present, they are quite evident in all stages of maturity); vagina with large accessory bursa; spermathecal stalk softer in texture and often spirally coiled; verge with spiral or subspiral ridges (Figs. 54, 56, 57)
3(2)	Hyponotum usually light, unicolored; verge with subspiral ridges which are close together on the orificial side at the glans but diverge as they pass proximad; seminal orifice subapical (Figs. 56, 57)
	Hyponotum usually dappled with vague gray spots (Fig. 45); dorsum with light dorsomedian stripe [not shown in Férussac's (1823) original figure] but with longitudinal dark bands narrow or quite obliterated by general infuscation; verge with large glans, practically apical orifice and two fine spiral ridges which pass almost completely around its apical half (Fig. 54). Jamaica to Puerto Rico (Cuba?). Reported to be introduced into the United States



FIGS. 45-47. Veronicellid slugs. FIG. 45. *Leidyula kraussi* (from Férussac & Deshayes, 1823). FIG. 46. *L. moreleti* (from Fischer & Crosse, 1878). FIG. 47. *L. floridana* (from Binney, 1857).

[Leidyula kraussi is a rather small species, larger specimens reaching only 38 mm in length. It is rather broad for its length. The dorsal surface of the mantle is covered with very small tubercles. Its color varies from linen gray to dark brown, but it is generally very dark above, with coarsely-meshed, irregular, black reticulations. There is usually a lighter median stripe. The underside is lighter. The upper tentacles are dark, the lower ones are very thick and lighter in tint. Smaller specimens have two marginal dark zones on the dorsum, bounded mesially by longitudinal black stripes, and one median reddish-brown zone, about 1/3 the width of the animal and bisected by a median light stripe (D. de Férussac & G.-P. Deshayes, 1823, Histoire naturelle générale et particulière des mollusques terrestres et fluviatiles. II. Histoire naturelle des pulmonés sans opercule, Pt. 1, pp. i-xvi, 1-184 [96x], J.-B. Baillière, Paris; Baker, 1925a).

Leidyula kraussi was originally described from the Antilles. It also occurs in Jamaica and Haiti. Branley A. Branson (1962c, Trans. Kans. Acad. Sci., 65(2): 110-119) has reported it from a greenhouse in Oklahoma City.]

[The body of Leidyula moreleti has the tint of a dead leaf, more or less dark, browner on the back and generally tempered by a salient granulation that is a little lighter in color. Two narrow, blackish, not very pronounced bands run along the flanks and diffusely unite at the two ends of the mantle. The latter assumes a reddish tint at the edges in individuals of a darker color. The upper tentacles are of a violaceous brown, the lower tentacles, which are slightly notched and bifurcated, are light gray. Length up to 90 mm. (P. Fischer & H. Crosse, 1878, Etudes sur les mollusques terrestres et fluviatiles du Mexique et du Guatemala. Mission scientifique au Mexique et dans l'Amérique Centrale . . . , Recherches zoologiques . . . , pt. 7, vol. 1, pp. 1-702).

This species was first named from Mexico, but it has also been reported from Guatemala (Baker, 1925a). Dundee (1974) reported it from nurseries in Hidalgo and Willacy counties, Texas, in Cameron County, Texas, and as having been intercepted from Costa Rica, Honduras, Jamaica, Mexico and Panama by U.S. Department of Agriculture inspectors at ports in Florida, Louisiana, Pennsylvania, South Carolina and Texas.]

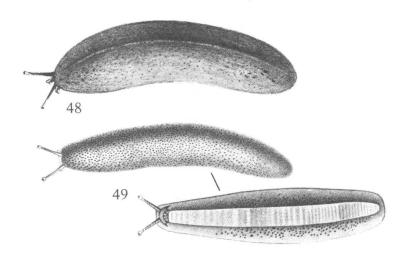
Dorsum with light, dorsomedian stripe; the two longitudinal dark bands usually broad and distinct (Fig. 47); female opening usually less than ¼ hyponotal width from foot; verge larger and more elongate, with small glans usually bent back so orifice is almost terminal, and with prominent lateral ridges that separate gradually without confluence and extend beyond apical ½ of organ (Fig. 57); oviparous. Southern Florida to Jamaica (Haiti?); introduced into Louisiana (Fig. 61) Leidyula floridana (Leidy)

[The dorsal mantle of Floridan specimens of Leidyula floridana is tan, mottled with black, and has a median whitish line running its length. Two longitudinal black mottled stripes are on each side of the median line (see Fig. 47 [from Amos Binney, 1857, The terrestrial air-breathing mollusks of the United States, and the adjacent territories of North America, Vol. 3, Plates, 40 pp., 47 pls. [pl. 67], Little, Brown & Co., Boston]). Length up to 70 mm. Although the coloration of Floridan specimens of this species is rather constant, Cuban specimens vary from the typical pattern with a reddish cast, to very dark in which the dark bands are obscured or lacking. In some, the black bands are restricted to the anterior third of the mantle, where they are solid and jet black. However, all specimens show some trace of the light dorsomedian band (Baker, 1925a).

Leidyula floridana is the only native veronicellid slug found in the United States, although it too is probably a relatively recent immigrant (from Cuba). It was originally named from Meta-leechee Key, Charlotte Harbor, on the west coast of Florida, but it is generally distributed over the Florida Keys, and on the east coast it is found as far north as Lake Worth, Florida (Pilsbry, 1948). Dee S. Dundee (1971, Nautilus, 85(2): 72) reported L. floridana to be introduced into Louisiana (Hodges Gardens, western Louisiana, and New Orleans). It is distributed generally over the western 3/4 of Cuba, and is also found in the Bahamas and

Jamaica, probably artificially introduced.]

5(1) Verge long and cylindrical (Fig. 58a), quite symmetrical except at apex; canalis junctor enters apex of spermathecal sac (Fig. 53a). Hyponotum with black spots (Figs. 48,49); tip of verge (Fig. 58b) with papillae and with prominent, reflected emarginate cap (glans) which hides the pseudacrocaul opening. Puerto Rico through northern South America to Guatemala. Reported to be introduced into the United States Diplosolenodes occidentale (Guilding)



FIGS. 48,49. *Diplosolenodes occidentale*. Fig. 48 from Fischer (1871); Fig. 49 from Guilding (1823).



FIG. 50. Angustipes ameghini, from Tallahassee, Florida, x 1.4.

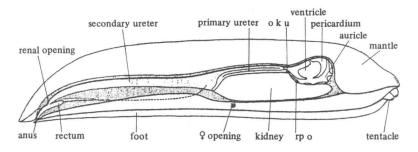


FIG. 51. Longitudinal partial section of a veronicellid slug. o k u = opening

[The mantle of Diplosolenodes occidentale is covered by slightly elevated punctuations, irregularly distributed and of a dark brown color which can be very easily distinguished from the lighter brown tint of the surface. The lower tentacles are very short, bifurcated at their tips and of a reddish-brown tint. The lower side of the mantle has the same color. It is here strewn with brown dots, but in less number than on the dorsal surface. (Férussac & Deshayes, 1823). Most specimens have a light dorsomedian stripe (shown in Fig. 48 [from M.P. Fischer, 1871, Nouv. Arch. Mus. Hist. nat. Paris, 7: 148-175, pl.11] but not in Fig. 49 [from Lansdown Guilding, 1823, Trans. Linnean Soc. London, 14: 322-324, pl. 9, figs. 9-10]). Length up to 65 mm.

This species was originally named from St. Vincent. It also occurs in Costa Rica, the Dominican Republic, Panama, and probably in Jamaica. In the United States, it has been reported in a greenhouse in Guthrie, Oklahoma (Branson, 1962c) and at Raymondville, Texas (see Dundee, 1974). Dundee, loc. cit., reports it as having been intercepted from Colombia, Ecuador, El Salvador, Guatemala, Haiti, Honduras, Mexico and Panama by U.S. Department of Agriculture inspectors at ports in Florida, Louisi-

ana, New York and Texas.]

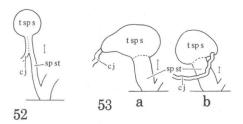
[Adult Angustipes ameghini are characterized by their jet black, velvety dorsal mantle. In juveniles, the dorsum is brown with black spots. This is not a large species, but adults may measure up to 54 mm or more in length.

This species was originally described from Paraguay. It has been restudied recently by Peterellis & Dundee (1969) and José Willibaldo Thomé (1970, *Iheringia*, zool., (39): 19-31). In the United States, Dundee (1974) has reported it to be established in Alabama, Florida, Louisiana and Mississippi.]

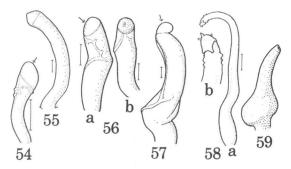
Literature Sources for Geographic Distributions of Veronicellidae

Angustipes ameghini. Dundee (1971; 1974).
Diplosolenodes occidentale. Branson (1962c), Dundee (1974).
Leidyula floridana. Baker (1925a), Dundee (1971), Pilsbry (1948).
Leidyula kraussi. Branson (1962c).
Leidyula moreleti. Dundee (1974).
Leidyula sloanei sloanei. Baker (1925a).

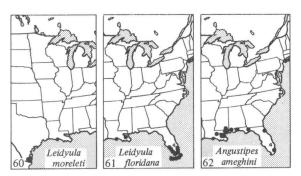
from the kidney to the ureter; rp o = renopericardinal opening. From Paul Pelseneer, 1901, Mem. Acad. roy. Sci., Lett., Beaux-Arts Belgique, 54: 1-76, 14 pls. [pl. 6, fig. 51].



FIGS. 52, 53. Spermatheca and ducts. FIG. 52. The type of spermatheca found in *Leidyula*. FIG. 53. The types found in a, *Diplosolenodes occidentale* and b, *Angustipes*. c j = canalis junctor; sp st = spermathecal stalk; t sp s = terminal spermathecal sac. Measurement lines = 1 mm. Adapted from Baker (1925a).



FIGS. 54-59. Verges of Veronicellidae. FIG. 54. Leidyula kraussi, dorsal view. FIG. 55. L. sloanei sloanei, dorsal view. FIG. 56. L. moreleti; a, lateral view, showing weaker and transverse ridges; b, orificial view. FIG. 57. L. floridana, lateral view. FIG. 58. Diplosolenodes occidentale; a, dorsal view; b, apex of verge, much enlarged. FIG. 59. Angustipes ameghini. Arrows indicate position of seminal orifice. Measurement lines = 1 mm. Figs. 54-58 are from Baker (1925a); Fig. 59 is after Gambetta (1923, Boll. Mus. Zool. Anat. comp. Univ. Torino, n.s., 38(11): 1-10).



FIGS. 60-62. Distributions of Leidyula moreleti, L. floridana and Angustipes ameghini.

THE PULMONATA

I. The Actophila (Basommatophora): CARYCHIDAE

The mainly aquatic pulmonate order Actophila has one inland family in North America, the Carychiidae, a small group of snails with minute, elongate, translucent or whitish shells. The various species usually frequent moist to wet places, often rotting logs or decaying leaves. The family includes four genera, *Carychium* of North America, the West Indies, Eurasia, Indonesia and the Philippines; *Carychiopsis* of the European Tertiary; *Zospeum* of the Balkan Peninsula; and *Coilostele* of southern Europe, Abyssinia, India, Timor and the Panuco River Valley in eastern Mexico (Pilsbry, 1948). Like other basommatophorans, the eyes of carychiid snails are sessile at the bases of contractile tentacles.

The taxonomy of the species and subspecies of Carychium in North America is still somewhat confused. Several nominal species seem to be clearly distinct, yet others are difficult to distinguish, in spite of seemingly contrary statements in the literature. For example, there is the difficulty of separating C. exiguum, C. exile and C. exile canadense, a problem that has been considered in some detail by Harold W. Harry (1951, Carvchium exiguum (Sav) of lower Michigan; morphology, ecology, variation and life history (Gastropoda, Pulmonata), Ph.D. Thesis, Univ. Mich., 154 pp.*). Harry found two extremes in shell characters of Carychium in Michigan, extremes that "are based on a combination of characters and fit rather closely the concepts of C. exiguum and C. exile canadense as now generally accepted; . . . the characters which distinguish them are mostly relative. They do not seem to segregate indepen-. . . C. exile falls into this graded series somewhere near the C. exile canadense extreme. We may . . . suppose that each colony has a gene pool which may differ from that of another colony in some respects. Possibly few, if any, colonies have a complete complement of genetic factors to be found in all colonies of the area. The variation of effective environmental factors may further complicate the situation by evoking different phenotypes from similar genotypic potentialities. ... Whether these species [and subspecies, i.e., C. exiguum, C. exile and C. exile canadense are only nominal or represent valid genetic distinctions. and thus are biological, is the significant problem. Its ultimate solution

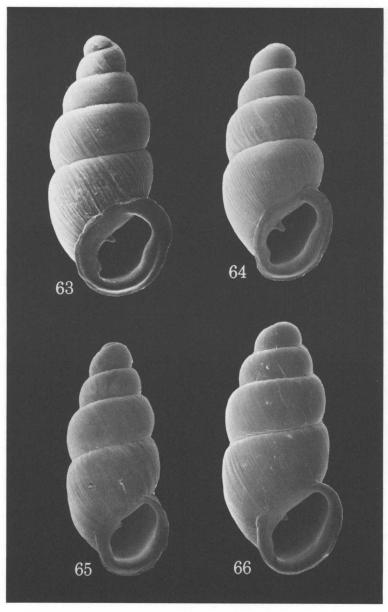
^{*}Available from University Microfilms, 300 North Zeeb Rd., Ann Arbor, Michigan U.S.A.

seems to require an investigation of the dynamic aspects of Carychium biology beyond those touched upon in this and previous studies." Harold W. Harry (1952, Nautilus, 66(1): 5-7) concluded ". . . that criteria previously used for distinguishing nominal species [of Carychium] in this area [Michigan] are not sufficient for recognizing more than one natural species." Further studies going more deeply into this problem have not been published. Accordingly, some authors (e.g., Branson, 1961b; John B. Burch, 1962, How to know the eastern land snails, Wm. C. Brown, Dubuque, Iowa, 214 pp.) have not treated C. exile and C. exile canadense as being distinct from C. exiguum. Similar problems may exist in the C. mexicanum, C. floridanum and southern C. exile forms. Further, the relationships of C. clappi to C. exile, and especially to C. exile canadense, or the relationship of C. exiguum to the cave-dwelling C. stygium, have not been adequately studied. Nevertheless, in spite of some doubt as to the validity of certain nominal species, we are treating them individually in the key on Carychium which follows, since many of the reports on distribution of Carychium in the United States recognize all or some of the questionable forms as being distinct. Obviously, the genus Carychium in North America needs much more study.

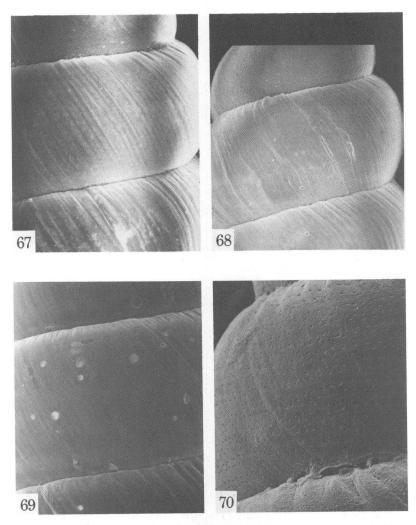
Key to the Species of Carychiidae

1	Shell without rib-striae, or striae weak and irregular; parietal lamella (also called upper lamella, superior lamella, principal internal lamella or upper columellar fold) within the last whorl not deflected sharply downward (except in western forms of <i>C. mexicanum</i>)*
	Shell, especially the last several whorls, sculptured with relatively strong, evenly spaced transverse rib-striae; parietal lamella bent sharply downward (except in C. minimum)
2(1)	Apertural lip especially thick (Figs. 63-65). South Carolina to Florida, west to Mexico and south to Guatemala (Fig. 73)
	[Carychium mexicanum is best distinguished by the heavy apertural lip of its shell. Other identifying characters — not restricted to C. mexicanum alone, but useful when considered in conjunction with the thick lip — are the smooth or only weakly striate

^{*}Shell surface sculpture of the various species are shown in Figs. 67-70, 89-92 and 107-110; parietal lamellae are shown in Figs. 75-84.



FIGS. 63, 64, 65. Carychium mexicanum Pilsbry. FIG. 66. C. exiguum (Say). All shells x ca. 42.



SHELL SCULPTURE. FIGS. 67, 68. Carychium mexicanum, x ca. 90. FIG. 69. C. exiguum, x ca. 90. FIG. 70. C. nannodes, x ca. 300.

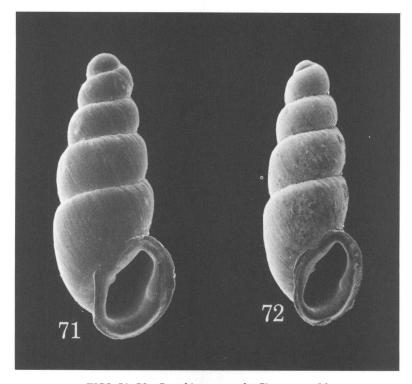
shell and its tapering apex. The shell of *C. mexicanum* varies in length from about 1.5 mm in Florida to 2 mm in Texas.

The description above follows Leslie Hubricht (1974, Malacol. Rev., 7(1): 33-34) in considering Carychium mexicanum Pilsbry and C. floridanum Clapp to be synonymous, but the two forms are lumped here with some misgivings, because it seems that a much better analysis of variation of these two nominal species and southern (especially southwestern) C. exile is necessary. While there is very little material from Florida in the collections of the Museum of Zoology, The University of Michigan, there is material from the southwestern United States, Mexico and Guatemala. None of these latter specimens (with the exception of one specimen among 14 from Tampico, Mexico) conform to George H. Clapp's (1918, Nautilus, 31: 73-75, figs. 4-6) and Pilsbry's (1948) descriptions of C. floridanum or our material from Florida.

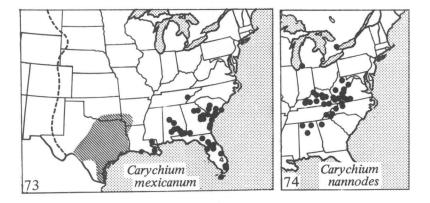
Carychium mexicanum was first named as a variety of C. exiguum by Henry A. Pilsbry (1891, Nautilus, 5: 8-10 [9]), but he (Pilsbry, 1948: 1060) later considered it to be a subspecies of C. exile, "the tropical representative of the exile stock and probably to be considered a southern subspecies of that, intergrading with it in Texas; . . . the Texan form of exile . . . resembles mexicanum in being smooth or only weakly or irregularly striate. The lobe of the lamella, one whorl within, is squarish, with the edge bent forward, the principal internal lamella being like that of C. exile." According to Hubricht (1974), "The holotype (ANSP [in the Academy of Natural Sciences of Philadelphia]) of C. mexicanum is a slightly immature shell in which the lip is expanded but not thickened, and is thus a poor specimen for the identification of a species. Other specimens from Mexico and Guatemala identified by H.A. Pilsbry as C. mexicanum do not appear to be specifically distinct from C. floridanum, having the very thick lip characteristic of that species."]

[Carychium nannodes is the smallest species of the genus in North America, its shell measuring only 1.3 to 1.5 mm in length. It has a translucent to transparent shell, with about 4½-5 whorls, which in many specimens are rather distinctly shouldered. The shell is smooth, except for fine growth lines. With high magnifications and clean shells, small spiral lines of puncta can be seen on the whorls. The base (anterior end) of the aperture is rather truncate. The upper columellar fold is small and evenly sinuate.

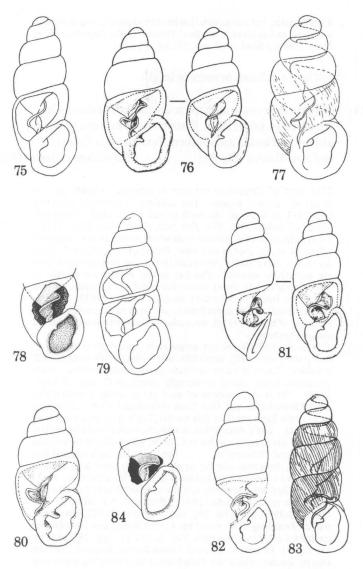
The type locality of *Carychium nannodes* is Monte Sano, about 5 miles east of Huntsville, Alabama, but this species' distribution extends northward in the mountains to Kentucky and



FIGS. 71, 72. Carychium nannodes Clapp, x ca. 56.



FIGS. 73, 74. Distributions of Carychium mexicanum and C. nannodes.



PARIETAL LAMELLAE. FIG. 75. Carychium nannodes (from Winslow, 1922). FIG. 76. C. exiguum (from Winslow, 1922). FIG. 77. C. exiguum (after Harry, 1951). FIG. 78. C. stygium. FIG. 79. C. stygium (from Hubricht, 1960i). FIG. 80. C. minimum (from Winslow, 1922). FIG. 81. C. exile (from Winslow, 1922). FIG. 82. C. exile canadense (from Winslow, 1922). FIG. 83. C. exile canadense (after Harry, 1951). FIG. 84. C. clappi.

West Virginia, and one population has been found in southwestern Michigan and another in southern Ontario (John Oughton, 1948, *Univ. Toronto Stud.*, biol. ser., 57: i-x, 1-126).]

Shell larger, 1.5 mm or more in length 4

[The shell of Carychium exiguum is elongate, whitish and has about 4½ convex whorls. The aperture is generally relatively large, 1/3 or more of the total length of the shell. Clapp (cf. Mina L. Winslow, 1922, Occ. Pap. Mus. Zool., Univ. Mich., (128): 1-16) pointed out the swollen body whorl, which gives C. exiguum a 'bellied' appearance in side view, distinguishing it from C. exile. As in the other North American forms, the first several whorls are essentially smooth. The last several whorls are weakly or faintly striate. The upper columellar lamella is S-sinuate, curving first down (near the aperture), then up (Harry, 1951). Winslow (1922) described the upper lamella as "small in proportion to the diameter of the last whorl, somewhat sinuate, but never deflected sharply downward."

The shell of Carychium exiguum is stouter than that of C. exile, and it is usually smoother, often having only faint growth wrinkles. There is some variation in sculpture, however, some specimens being nearly as strongly striate as C. exile (Pilsbry, 1948). "It is the presence of such striate shells in several lots from Pennsylvania and New York (Dutchess Co.) which permits us to apply Say's name to this species [Say's type specimens have been lost]. Say's description is ambiguous and could be applied to either the present species or C. exile, which also occurs within the limits of Philadelphia. . . . The terms [in Say's original description], 'tapering, oblong' apply better to what later authors have called exiguum; 'with minute grooved lines' to exile. Probably Say had both species; but the next authors to describe and figure the species, Gould (1841) [Boston J. nat. Hist., 3: 395-404 (398-399), pl. 3, fig. 20] and A. Binney [1852, The terrestrial air-breathing mollusks of the United States, and the adjacent territories of North America, Vol. 2, 362 pp. (pp. 286-288, pl. 53, fig. 1), Charles C. Little & James Brown, Boston, had the stouter species, which the Philadelphia conchologists apparently took to be Say's exiguum, at the time H.C. Lea described C. exile [from Wissahickon Creek, Philadelphia]. In the absence of Say's material, no longer existing, absolute certainty as to what he had is not attainable, and the identification of his early successors is accepted" (Pilsbry, 1948). According to Thomas Say (1822, J. Acad. nat. Sci. Philad., 2(2): 370-381 [375]), his specimens of "Pupa exigua" ("probably a Carychium") "were found near this city [Philadelphia] by Mr. William Hyde, and I have obtained

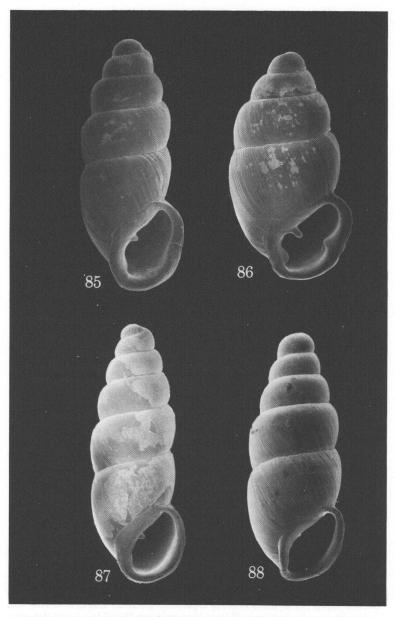


FIG. 85. Carychium exiguum (Say), x ca. 38. FIG. 86. C. minimum Müller, x ca. 38. FIG. 87. C. stygium Call, x ca. 20. FIG. 88. C. stygium, x ca. 32.

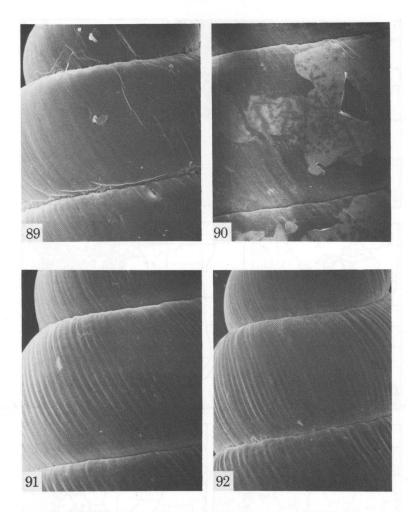
many at Harrigate [corrected by pen to "Harrowgate" in our UMMZ copy of the Journall."

The relationship of the nominal species Carychium exiguum and C. exile to each other is poorly understood, and the two are frequently difficult to separate in spite of statements as to how they are "readily distinguishable," and in spite of a great many publications - mostly distribution lists - which include one or the other or both forms. The only in-depth study of the problem is that of Harry (1951; abstracted in Harry, 1952*), an excellently illustrated and unusually detailed (for North American land snails) and penetrating analysis. He concluded "from the variation of the form, size, sculpture, internal lamellae, number of whorls and extent of resorption of the internal lamellae . . . that only one natural species [C. exiguum] is worthy of recognition in the [Michigan] material." Additionally, nothing was found in the soft anatomy that could be used to separate the nominal forms. Harry's specimens were from 60 localities and represented the conchological extremes from C. exiguum (sensu stricto) to C. exile canadense.

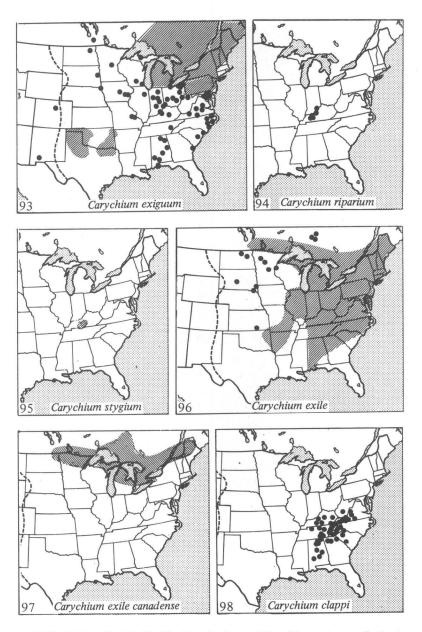
- 5(4) Shell narrow and conical, smaller (2.0 mm or less in length) (Fig. 101). Known from five localities in Kentucky and one in Indiana (Fig. 94) Carychium riparium Hubricht

["Carychium riparium is most likely to be confused with C. exile H.C. Lea. It differs in its more opaque shell, more conical spire, weaker sculpture and expanded rather than reflected outer lip. It averages smaller and more slender. The smaller specimens are almost as small as C. nannodes Clapp. In its sculpture and whitish shell it resembles C. exiguum (Say). In its internal lamellae it resembles C. nannodes. At the type locality and in Clark Co., Indiana, it was found associated with both C. exile and C. exiguum." (Leslie Hubricht, 1977, Malacol. Rev., 10(1/2): 37-52 [51].]

^{*}Neither Harry nor Branson (1961b) expressed "the belief that *C. exile H.C.* Lea was only an ecological form of *Carychium exiguum* (Say)" (see Leslie Hubricht, 1963a, *Nautilus*, 76(3): 108).



SHELL SCULPTURE. FIG. 89. Carychium exiguum. FIG. 90. C. stygium. FIG. 91. C. exile. FIG. 92. C. riparium. All figures x ca. 90.



FIGS. 93, 94, 95, 96, 97, 98. Distributions of Carychium exiguum, C. riparium, C. stygium, C. exile, C. exile canadense and C. clappi.

[The shell of Carychium stygium is translucent and shiny to opaque white, quite elongate and relatively large, measuring up to 2.6 mm in length. It has a tapering spire and 5 to 6 whorls. The outer shell surface lacks striae, having only faint growth lines. The upper columellar lamella in the body whorl forms a simple twist as in C. nannodes, and similar to C. exiguum. The columellar tooth is quite small. Although R. Ellsworth Call (1897, Am. Nat., 31(365): 377-392, pl. 10, figs. 6,7) and Pilsbry (1948) figure rather robust specimens, the shells in the single lot (from Mammoth Cave) in the Museum of Zoology, The University of Michigan, are more elongate and narrower, as are most of the shells figured by Leslie Hubricht (1960i, Trans. Ky. Acad. Sci., 21(12): 35-38. fig. 2).

Carychium stygium was found originally in Mammoth Cave among fungal (Rhizomorpha) filaments on damp old bridge timbers by Call (1897). Leslie Hubricht (1964a, Natl. speleol. Soc. Bull., 26(1): 33-35) found it feeding principally on the guano of the cave cricket Hadenoecus subterraneus (Schudder).]

[The ovoid shell of Carychium minimum is white to corneous, translucent, has about 4½ whorls and measures from 1.4 to 1.6 mm in length. It is an introduced Eurasian species which can be distinguished from native North American species by the combination of several characters: its more ovoid shape, distinct ribstriae, and more developed tooth on the outer apertural lip. Controversies as to the specific distinctness of C. minimum from the European C. tridentata are similar to the taxonomic problems between C. exiguum and C. exile in North America (cf. Harry, 1951).

W.F. Clapp (1912, Nautilus, 26(2): 24) reported Carychium minimum in a greenhouse in Norfolk Downs, Quincy, Massachusetts, and there is a lot in the Museum of Zoology, The University of Michigan, from the McAndrews Collection labeled "Carychium mariae Paul, Florida." Since C. minimum has not been reported again, this species may not have become established in North America.]

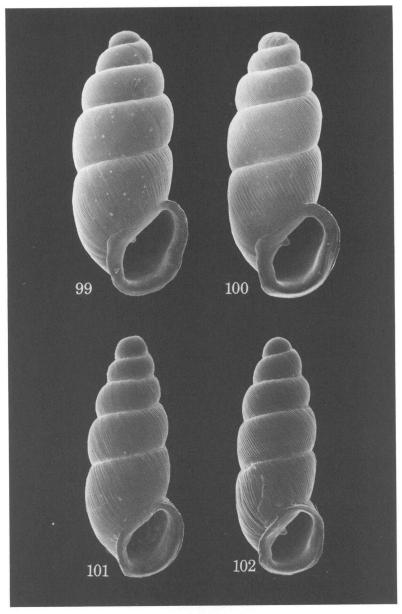


FIG. 99. Carychium exiguum (Say). FIG. 100. C. exile. FIG. 101. C. riparium Hubricht. FIG. 102. C. clappi Hubricht. All shells x ca. 38.

Shell smaller, averaging 1.75 mm in length (Fig. 100).

Eastern North America generally, except for Florida
and possibly Texas (Fig. 96) Carychium exile Lea

[The shell of Carychium exile is generally narrower than that of C. exiguum, has a smaller aperture and is usually more strongly and regularly striate. However, like C. exiguum, the shell may vary considerably. "A further difference is that in C. exile the last whorl is built forward so that, in a profile view of the aperture, the lip is even with the ventral convexity of the last whorl. In C. exiguum the belly of the last whorl projects decidedly beyond the plane of the aperture. By this peculiarity the occasional striate specimens of C. exiguum may readily be distinguished from C. exile" (Pilsbry, 1948). According to Hubricht (1963a). the best distinguishing character to separate C. exile and C. exiguum is in the outer lip. "In C. exiguum the outer lip is somewhat expanded, but in C. exile it is narrowly reflected. This appears to be a constant difference which will stand up when other characters fail." Winslow (1922) advocated using the upper columellar lamella to distinguish exile from exiguum in case other shell characters were not adequate to do so. "The deflection downward of the upper fold [in C. exile] is a very marked characteristic. . . . The upper columellar fold is very large in proportion to the diameter of the last whorl, almost touching the wall of the last whorl at the upper angle of the aperture. Typically it is bent sharply downward at its widest part, the edge turning toward the columella." However, Harry (1951) questions the ultimate value of the columellar lamellae in separating C. exiguum and C. exile. Further doubt might occur after assessing Oughton's (1948) and Stanley Truman Brooks & Gordon M. Kutchka's (1937, Ann. Carnegie Mus., (25): 155-161) accounts of variation found in the columellar folds.

8(7)	Northern in distribution, Maine to Michigan, Ontario
	and Manitoba (Figs. 97, 103, 104)

[The shells of *Carychium exile canadense* are larger than those of *C. exile exile*, i.e., averaging 2.1 x 0.75 mm vs. 1.75 x 0.6 mm, according to George H. Clapp (1906, *Nautilus*, 19: 138-140, pl. 8). Harry (1951) found that *Carychium* shells in Michigan occurred in and between two extremes of variation, at the one end *C. exiguum* and at the other *C. exile canadense*. He contrasted the two extremes as follows:

C. exiguum

C. exile canadense

Shell Form

Ovate-conic, the diameter being broader in proportion to the height.

Cylindric, the diameter being narrower in proportion to the height.

Whorls rounded.

Whorls flattened.

Sculpture

Transverse striae indefinite, weak, discontinuous, sparse.

Transverse striae strong, regular, closely spaced.

Upper Lamella

Upper lamella S-sinuate, curving first down (near the aperture) then up. Upper lamella V-sinuate, which seems to be an overemphasis of the downward flexure of the Ssinuate lamella of the other extreme.

Sinuosity occurs about 3/4 whorl inward from the aperture.

Sinuosity occurs closer to 1 whorl inward from the aperture.

Lower Lamella

Slightly expanded at about the position of maximum flexure of the upper lamella; expansion tending to an equidimensional node. Expanded also at the position of maximum flexure of the upper lamella, but distinctly quadrate, longer than broad.

Resorption

Resorption of internal whorls begins about 1 3/4 whorls from the aperture.

Resorption of internal whorls begins about 2 1/4 whorls from the aperture.

Number of Whorls

About 4 suture whorls.

About 4 1/2 to 5 suture whorls.

Size

Smaller

Larger

Harry found a graded series between the two above extremes, with *C. exile* falling somewhere near the *C. exile canadense* extreme. "We may suppose that the characters of *C. exile canadense* are merely distortions of the corresponding characters of the *C. exiguum* type. This hypothesis should have as much validity as the presumption that the extremes represent distinct biological species."

According to Clapp (1906), Carychium exile canadense is northern in distribution, confined to the 'Canadian Zone.' He gave the type locality as Kennebunkport, Maine. However, the differences between this form and C. clappi Hubricht seem to be very slight indeed, pointing to the possibility that the latter may be the southern representative of the northern canadense form.]

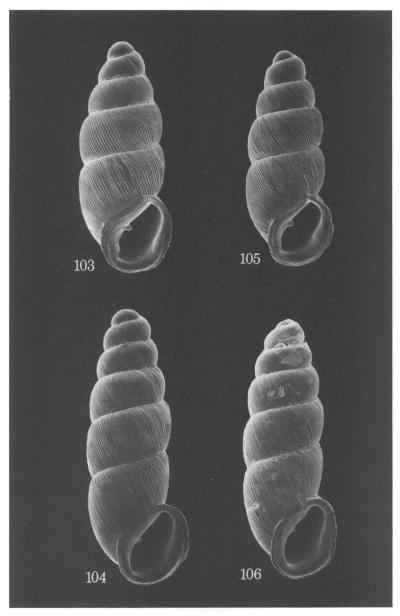
[Clapp (1906), in a paper describing Carychium exile canadense, gave the first description of C. clappi, but he did not name it. ("The only southern shells which I have seen approaching var. canadense in size is a lot collected by Herbert H. Smith in mountain forests near Princeton, Ala. These measure 1.90 x .70 mm., and are unusually heavily ribbed") A form almost identical to Clapp's unnamed one was described by Leslie Hubricht (1951b, Nautilus, 65(2): 57-59) as C. costatum from various localities in Virginia, West Virginia (type loc.: below Cane Branch Falls, 1.3 miles southeast of Gauley Bridge, Fayette Co.) and North Carolina. Carychium costatum Hubricht, preoccupied by C. [Zospeum] costatum Freyer 1856, was renamed C. clappi by Leslie Hubricht (1959, Nautilus, 73(1): 36).

Hubricht compared Carychium costatum (= C. clappi) to C. exile ("Differs from Carychium exile H.C. Lea in being larger [measurements given for the holotype as 1.9 mm (height), 0.8 mm (diameter), 0.7 mm (apertural height)], whiter, the rib-striae are higher, tending to be bluntly angular rather than rounded, and extend higher up the shell. The lip does not have the heavy thickening usually found in exile. The internal lamella is similar but the margin is more sinuous.") C. clappi, although a southern form, does not seem to be significantly distinct in shell characters from the northern C. exile canadense.]

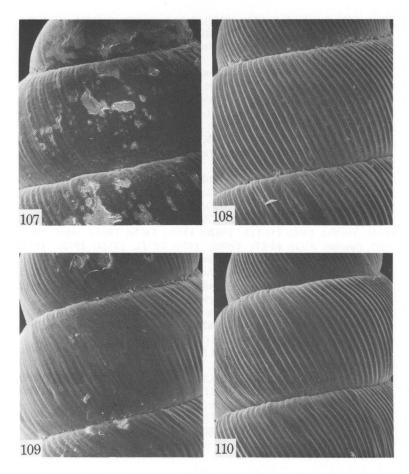
Literature Sources for Geographic Distributions of Carychiidae

Carychium clappi. Beetle (1973), Leslie Hubricht (1951b; 1952b, Nautilus, 66(1): 10-13; 1964h; 1965c; 1968b; 1970; 1971a; 1973).

Carychium exiguum (some of the records for this species may include C. exile, since some authors have not distinguished between the two forms). Robert C. Alexander (1952b, Nautilus, 66(2): 54-59), Beetle (1973), Branson (1961b; 1971), Branson & Batch (1971), Briscoe (1963), Stanley Truman Brooks (1936a, Nautilus,



FIGS. 103, 104. Carychium exile canadense Clapp. FIGS. 105, 106. C. clappi Hubricht. All shells x ca. 36.



SHELL SCULPTURE. FIG. 107. Carychium minimum. FIG. 108. C. exile canadense. FIGS. 109, 110. C. clappi. All figures x ca. 84.

49(4): 115), Brooks & Kutchka (1937), John Bayard Burch (1955, Va. J. Sci., 6(2): 154-162), Clinton J. Bushey (1950a, Nautilus, 63(4): 119-121), Clarence F. Clark (1962, Sterkiana, (6): 15-22), Daniels (1903), Fullington & Pratt (1974), Grimm (1961b; 1971b), A.W. Hanham (1899, Nautilus, 13(1): 1-6), Harry (1951), Leslie Hubricht (1952b; 1960g, Sterkiana, (2): 9-11; 1964h; 1968b; 1970; 1971a; 1972d), Kaplan & Minckley (1960), Levi & Levi (1950), Oughton (1948), William H. Over (1915, Nautilus, 29(7): 79-81, 29(8): 90-95), Pilsbry (1948), H.E. Sargent (1895, Nautilus, 9(8): 87-89), Celeste Taft (1961, Ohio Biol. Surv. Bull., 1(3): i-xi, 1-108), Teskey (1954), Bryant Walker (1906a, Rep. State Bd. geol. Surv. Michigan 1905, Lansing, Mich., pp. 431-531, 1 chart; 1928, Misc. Publ. Mus. Zool., Univ. Mich., (18): 180 pp.), Mina L. Winslow (1921, Occ. Pap. Mus. Zool., Univ. Mich., (98): 1-18), Wurtz (1948).

Carychium exile. Alexander (1952b), Beetle (1973), Briscoe (1963), Brooks (1936a), Brooks & Kutchka (1937), Clinton J. Bushey (1950b, Nautilus, 64(2): 54-55), Clark (1962), Daniels (1903), Dorothea S. Franzen & A. Byron Leonard (1943, Univ. Kans. Sci. Bull., 29-II(a): 363-439), Grimm (1971b), Leslie Hubricht (1941, Nautilus, 54(4): 111-112; 1952b; 1956c; 1962g; 1964a; 1964i; 1965c; 1967, Nautilus, 81(2): 65-67; 1968b; 1970; 1971a; 1972d; 1972e; 1972f; 1973), Aurèle La Rocque (1962, Sterkiana, (7): 23-45), A. Byron Leonard (1959, Misc. Publ. Univ. Kans., 20: 1-224), Over (1915), Pilsbry (1948), Imogene C.S. Robertson & Clifford C. Blakeslee (1948, Bull. Buffalo Soc. nat. Sci., 19(3): v-xi, 1-191, 1 map), Sargent (1895), Wurtz (1948).

Carychium exile canadense. Lorenzo E. Daniels (1909, Nautilus, 22(11): 119-121), Hanham (1899), La Rocque (1962), Levi & Levi (1950), Oughton (1948), Pilsbry (1948), Robertson & Blakeslee (1948), Winslow (1921).

Carychium mexicanum. Fullington & Pratt (1974), Hubricht (1960g; 1963a; 1963h; 1964h; 1965c; 1971a; 1973).

Carychium nannodes. Beetle (1973), Branson & Batch (1971), Brooks (1936a), Brooks & Kutchka (1937), Hubricht (1952b; 1964h; 1965c; 1968b; 1970), Oughton (1948), Pilsbry (1948), Walker (1928), Wurtz (1948).

Carychium riparium. Hubricht (1977).

Carychium stygium. Hubricht (1960i; 1964a; 1973).