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THE HYDROBIID SNAIL GENUS *MARSTONIA*

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THE HYDROBIID SNAIL GENUS *MARSTONIA*

FRED G. THOMPSON¹

SYNOPSIS: The recent species of *Marstonia* are revised, based on material in most major museum collections and on new material recently collected in the southeastern states. A total of eight species are recognized, of which five are described as new: *M. arga*, *M. ogmorhapha*, and *M. pachyta* from the Tennessee River system; *M. castor* from the Flint River system, Georgia; and *M. halcyon* from the Ogeechee River system, Georgia. Five names are placed in the synonymy of *Marstonia lustrica* (Pilsbry): *Amnicola oneida* Pilsbry, *A. winkleyi* Pilsbry, *A. perlustrica* Baker, *M. decepta* Baker, and *M. gelida* Baker. *M. olivacea* is considered a distinct species of uncertain status and is probably extinct. *Marstonia* is placed in the subfamily Nymphophilinae and is most closely related to *Cincinnatiata*. Other North American genera in Nymphophilinae include *Fonticella*, *Notogillia*, *Spilochlamys*, *Rhaphinema*, *Nymphophila*, and *Birgella*.

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INTRODUCTION

Attempts to define many genera and species of southeastern hydrobiid snails necessitates restudy of taxa long known from the north-central United States. A genus of particular note is *Marstonia* and its wide-ranging cold-temperate species *M. lustrica* (Pilsbry). Even though the species is widely distributed throughout the Great Lakes region and has been known since 1890, there exists a dearth of information on its eco-geographic variation and anatomy. All previous studies on geographic variation were confined to single states, and anatomical observations have been limited to the verge of the male. The discovery of several undescribed species of *Marstonia* in the Tennessee, Flint, Ocmulgee, and Ogeechee river systems necessitates a review of all other known taxa referable to the genus. Anatomical data provide a basis for relating *Marstonia* to other North American genera with a lobed verge, and to similar European genera about which a great deal of anatomical information is available, particularly through the studies of P. Radoman and H. D. Boeters (see references). The following study does not pretend to be definitive. Some species from the Tennessee and Coosa rivers are left undescribed because anatomical specimens of these forms are not available. Also, additional species can be anticipated in other river systems.

Marstonia was regarded as a subgenus of *Amnicola* until recently (Taylor 1960:51), as were other distinct groups of hydrobiid snails that possess small, simple, conical shells. All specific and subspecific forms of *Marstonia* described prior to 1969 were named as species of *Amnicola*. Morrison (1949:13-15) demonstrated that *Amnicola* and *Marstonia* belong to different subfamilies (see Thompson 1968:147-167). *Marstonia* currently is placed in the subfamily Nymphophilinae Taylor 1966.

When F. C. Baker (1926:195) proposed *Marstonia* as a subgenus of *Amnicola*, he included seven species: *Amnicola lustrica* Pilsbry, *A. gelida* F. D. Baker, *A. oneida* Pilsbry, *A. walkeri* Pilsbry, *A. pilsbryi* Walker, *A. greenensis* F. C. Baker, and *A. winkleyi* Pilsbry. Of these, *A. walkeri* and *A. pilsbryi* are species of *Lyogyrus* (Thompson 1968:162-163); and *A. oneida*, *A. gelida*, and *A. winkleyi* are here considered objective secondary synonyms of *M. lustrica*. *A. greenensis* is a Pleistocene fossil. Speculation about its generic affinities is fruitless, because critical anatomical data are not available for such fossil species. Taylor (1960:50) placed the Pliocene *Amnicola crybetes* Leonard 1952 in *Marstonia*, but that allocation is also purely speculative. Thus, *M. lustrica* was the only species unequivocally placed in *Marstonia* until recently when *M. agarhecta* was described (Thompson 1969:242-247).

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Marstonia F. C. BAKER 1926

Marstonia F. C. Baker 1926:195. (Type species: *Amnicola lustrica* Pilsbry 1890; see Berry 1943:29, Thompson 1969:242-243.

GENERIC CHARACTERISTICS.—This is a genus of small conical or elliptical-conical snails, in which the shell seldom exceeds 5 mm. The shell, operculum, and radula are not diagnostic at the generic level.

The shell is conical to elliptical-conical in shape, with about five whorls at maturity, and is about 0.46-0.80 times as wide as high. The periostracum is light gray. The peristome is usually complete across the parietal margin of the aperture, but occasionally it may be incomplete. Sculpturing either is absent or consists of fine incremental striations. The umbilicus may be broadly perforate or closed. The embryonic whorls protrude, with the nuclear whorl about 0.25 mm in diameter perpendicular to the initial suture. The embryonic sculpture consists of a densely folded and anastomosing series of wrinkles and pits, and is similar to that found in other bilobed American hydrobiid genera (Fig. 4).

The operculum (Fig. 25) is paucispiral, thin, membranous, transparent, ovate to modified elliptical in outline, and consists of about 2.5 whorls. The nucleus is near the left and lower third

of the outer face. The radula is taenioglossate with the following formula: $C \frac{(3-5)-1-(3-5)}{1-1}$,

L(2-4)-1-(3-5) M's (15-20). The basocones rise from the lateral angle of the tooth. The stomach lacks a tube-shaped caecal appendage on the esophageal end.

The foot is broadly rounded posteriorly and truncate anteriorly. It moves over the substrate by a gliding ciliary movement. A deep mucous slit overlies the anterior margin. A suprapedal fold and an external omniphoric fold are absent. A short, weak fold underlies the anterior half of the operculigerous lobe on each side. The eyes lie at the base of the tentacles and are raised. The snout, foot, and nape may be pigmented to varying degrees with melanin. Usually the mantle bears two diffuse black stripes over the mantle cavity. One stripe overlies or parallels the left margin of the intestine, and the other overlies or parallels the left margin of the gill. The two bands usually unite over the pericardium. Occasionally the bands are broader and almost completely cover the mantle cavity and the posterior viscera. The central nervous system is unpigmented.

The male reproductive system of *M. lustrica* is illustrated in Figure 5A. The verge originates on the nape beneath the mantle, just to the right of the middorsal line, and is innervated by the right pleural ganglion. The verge is bilobed distally, and bears a large apical lobe, a short terminal penis, and a single duct, the vas deferens. The apical lobe bears a single enlarged apical gland, although some species have an additional smaller gland near the base of the verge. The glands are apocrine. The gonad consists of 3-5 large lobes. The vas deferens I is strongly convoluted near its middle, at which point the vas wall is thickened and glandular. The prostate is fan-shaped or reniform and overlaps the posterior end of the mantle cavity. The vas deferens II is simple and is a closed duct from the prostate to the tip of the penis. A diverticulum to the mantle cavity is absent from either the vas deferens I or II.

The female reproductive system of *M. lustrica* is illustrated in Figures 6B, C. The ovary consists of three primary lobes, each of which may be divided into 2-4 secondary lobes. Each lobe is the diameter of one primary oocyte. The oviduct I is relatively short and thick, becoming narrower anteriorly. Just posterior to the wall of the mantle cavity the oviduct forms a large inverted U-shaped loop along, and transverse to, the middle of the posterior section of the pallial oviduct. The wall of the loop along this U-segment is very thick and glandular. (This glandular loop may serve as an albumen gland.) The single seminal receptacle is small, saculate, lies along the ventral margin of the posterior pallial oviduct, and enters the end of the oviduct loop by a very short duct. The seminal receptacle is homologous to the seminal receptacle 2 of Radoman (1973). The bursa copulatrix overlies the posterior mesad surface of the posterior pallial oviduct. It has a relatively long duct that is usually imbedded in the latter structure. The bursal duct enters the oviduct I just posterior to the anterior pallial oviduct. A short gonopericardial duct (GPD) connects the oviduct I to the pericardium. Neither a receptacular duct nor a bursal duct (which would connect either of these structures to the posterior mantle cavity) is present. The oviduct II is closed within the anterior pallial oviduct. The female opening is a short vaginal slit. A short omniphoric groove connects the vaginal slit to the anterior margin of the mantle collar.

GEOGRAPHIC DISTRIBUTION.—*Marstonia* is widely distributed in eastern North America, although it does not have a continuous range in that area. One species, *M. lustrica*, occurs throughout the St. Lawrence River system, the Great Lakes region, and the upper Mississippi River system. A disjunct group of species is found in the Tennessee River system in northern Alabama and adjacent Tennessee and in the Coosa River of Alabama. Three isolated species occur in the Flint, Ocmulgee, and Ogeechee river systems in Georgia. *Marstonia* probably occurs in other rivers in Georgia and Alabama.

The present distribution of *Marstonia* strongly suggests that the genus originated in the Tennessee River system and dispersed from there. This interpretation is based on the species diversity presently existing in the Tennessee River. The species there comprise a natural group, from which the more northern species, *M. lustrica*, presumably was derived during the Wisconsin Glacial Period. A second lineage invaded the coastal drainages of Georgia, probably via the Savannah River System, and evolved as a strongly differentiated species group. The time at which the coastal invasion occurred is not clear, but it probably was during the Pliocene or very early Pleistocene.

RELATIONSHIPS.—*Marstonia*, as is true of other hydrobine snails, has a single duct (the vas deferens) within the male reproductive appendage. The genus belongs to a group that also includes the North American *Nymphophila*

Taylor 1966, *Cincinnatia* Pilsbry 1891, *Fontelicella* Gregg and Taylor 1965, *Birgella* F. C. Baker 1926, *Rhaphinema* Thompson 1969, *Notogillia* Pilsbry 1953, *Spilochlamys* Thompson 1968, and perhaps *Pyrgulopsis* Call and Pilsbry 1886. The reproductive anatomies of these genera remain unstudied except for the verge. I examined internally males of all but *Fontelicella* and *Pyrgulopsis*. The males are alike in having (1) a bilobed verge with a slender terminal penis off the right margin; (2) a single duct, the vas deferens, within the verge; (3) various superficial apocrine glands on the verge, apical crest, and/or penis; (4) the verge innervated by the right pleural ganglion; and (5) a connective absent between the vas deferens and the mantle cavity. I have examined cursorily the female reproductive systems of *Notogillia*, *Spilochlamys*, *Rhaphinema*, *Cincinnatia*, and *Birgella*, and find they are basically similar to *Marstonia*. The females of these genera agree in having (1) a thick, glandular-walled loop in the oviduct I beside, and mesad to, the posterior pallial oviduct; (2) a gonopericardial duct; (3) a single seminal receptacle (SR: 2) at the base of the oviduct loop; (4) a bursa copulatrix that has a duct partially imbedded in the posterior pallial oviduct; and (5) a closed oviduct II within the anterior pallial oviduct.

The oldest and only group name proposed for the North American bilobed-verge genera is the Nymphophilinae Taylor 1966. Other North American hydrobine genera have an unlobed verge and are placed in different subfamilies. These other genera remain unstudied internally and further comments on similarities or differences are not possible.

Radoman (1973) divided the Balkan hydrobine snails into a number of families and subfamilies. The Nymphophilinae of North America are equivalent to Radoman's Orientaliidae, with its subfamilies Orientaliinae, Horatiinae, Sadlerianinae, Pseudohoratiinae, Islamiinae, Graecoanatolicinae, Pyrgulinae, Chilopyrgulinae, and Ochridopyrgulinae. These subfamilies are based on the numbers, position, and development of the seminal receptacles and the bursa copulatrix. The Nymphophilinae is most like the Pseudohoratiinae in having a single seminal receptacle 2 and a normal bursa copulatrix.

I feel that greater emphasis is placed on these divisions (families and subfamilies) of the Balkan hydrobiids than is currently justified, especially since so little is known of the anatomies of the hydrobiids from the rest of the world. In any event, Nymphophilinae Taylor 1967 is equivalent to and predates Orientaliidae Radoman 1973 and its subordinate groups.

Marstonia is more similar to North American hydrobiid genera than to any European genus. It is unique among North American groups in having a relatively simple glandular pattern on the verge and a short terminal penis. Other genera, except *Rhaphinema*, have elaborate patterns of many glands. *Rhaphinema*, like *Marstonia*, has a single large gland (the apical gland) on the apical lobe, but it differs by having both a long, slender flagellar penis and a large, globose shell with a thick rolling parietal callus and columella.

The shell of *Marstonia* is characterized by its generally narrow shape, gen-

erally perforate umbilicus, and a small, protruding apical whorl. Among the eastern North American genera with a lobed verge it overlaps in shell morphology with *Cincinnatia* and the eastern species placed in *Pyrgulopsis*. Species of *Cincinnatia* are usually more obese, and the eastern species of *Pyrgulopsis* (*letsoni*, *wabashensis*, *ozarkensis*, and *scalariformis*) are narrower than most *Marstonia*.

Marstonia consists of two species lineages. One lineage, found in the Tennessee River system and northward, has a large, squarish apical lobe and a relatively small, slender penis. The second lineage, found in coastal drainages of Georgia, has a more elongate apical lobe and a relatively robust penis.

SPECIES OF QUESTIONABLE STATUS

One lot, consisting of two specimens (UMMZ 161894), comes from the Coosa River, Etowah Co., Alabama. The shell is conical-ovate in shape, has a narrow umbilicus, and a constricted aperture. These specimens represent an undescribed species that almost certainly is a *Marstonia*. It receives no further discussion because of the scant material available.

Four species currently placed in *Pyrgulopsis* may actually belong in *Marstonia*: *P. letsoni* (Walker), *P. wabashensis* Hinkley, *P. ozarkensis* Hinkley, and *P. scalariformis* (Wolf). These are small narrow hydrobiids that have in common a carinate body whorl. The verge of *P. letsoni* is similar to that of *Marstonia*, except that it is longer, more slender, and has a small papilliform apical lobe (Berry 1943:43). The anatomy of the type species of *Pyrgulopsis*, *P. nevadensis* (Stearns), is not known. Thus the relationship of *Pyrgulopsis* to other genera remains undetermined, and the relationships of the eastern species to *P. nevadensis* need to be corroborated. The generic allocations of the eastern species placed in *Pyrgulopsis* require further anatomical studies.

KEY TO THE SPECIES OF *Marstonia*

- | | | |
|-----|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------|
| 1. | Verge with an elongate apical lobe; penis large and robust (Fig. 19, A-B). Shell minute, less than 2.7 mm long at maturity with four or more whorls | 2 |
| 1a. | Verge with a squarish apical lobe; penis short and slender (Fig. 11, A-B). Shell larger, 3.5 mm long at maturity with 4.5 or more whorls | 4 |
| 2. | Shell thin, fragile, transparent, conical, with an incomplete peristome across the parietal margin; verge with a single gland on apical lobe. Ocmulgee River System | <i>agarhecta</i> Thompson |
| 2a. | Shell thick, solid, nearly opaque, ovate-conical; with a complete peristome across parietal margin; verge with two glands, one on the apical lobe and one near the base of the verge | 3 |
| 3. | Umbilicus wide; shell broadly ovate, 0.70-0.80 times as wide as high; whorls strongly shouldered, flattened at periphery; suture descending in lateral profile. Ogeechee River System | <i>halcyon</i> n. sp. |
| 3a. | Umbilicus narrow; shell ovate-conical, 0.66-0.73 times as wide as high; whorls rounded, not strongly shouldered; suture not descending to the aperture in lateral profile. Flint River System | <i>castor</i> n. sp. |
| 4. | Shell thick, solid, nearly opaque; umbilicus closed or narrowly rimate | 5 |

- 4a. Shell thinner, transparent or translucent; openly umbilicate 6
5. Shell ovate-conical in shape, spire convex in outline; outer lip straight in lateral profile; suture shallow, whorls not shouldered. Verge with two small glands on apical lobe and a small raised gland near base of verge. Creeks, Limestone Co., Alabama *pachyta* n. sp.
- 5a. Shell nearly conical, spire straight sided; outer lip strongly curved in lateral profile; suture deep, whorls shouldered. Verge with a single large gland on the apical lobe. Tennessee River, Alabama *arga* n. sp.
6. Shell conico-terete in shape; suture deep, producing strongly shouldered whorls; outer lip slightly arched forward in lateral profile. Owens Spring, Sequatchie, Marion Co., Tennessee *ogmorhapha* n. sp.
- 6a. Shell ovate-conical or elongate-terete in shape; suture shallow, whorls not shouldered; outer lip straight in lateral profile *lustrica* (Pilsbry), *olivacea* (Pilsbry)

Marstonia arga new species

DIAGNOSIS.—The verge tapers basally and bears a single apical gland on the apical lobe. The glandular development of its verge is similar to *M. lustrica* and *M. ogmorhapha*. It further resembles the latter in having a reniform prostate. It differs anatomically from other *Marstonia* species in having the bursa copulatrix completely overlapping the posterior pallial oviduct, and in having the distal half of the bursal duct exposed.

The shell is distinct in being imperforate or at the most narrowly rimate, in having a conical spire, in having a thick callused ridge inside the aperture, and in having a strongly curved lip in lateral profile.

SHELL (FIGS. 1A-B; 6A-F).—The shell is medium-sized and conical, with a relatively large body whorl, and is about 0.52-0.63 times as wide as high. The spire is acutely conical, nearly straight-sided, and over half the length of the shell. The aperture is about 0.36-0.50 times the length of the shell. The shell is very thick and opaque or weakly translucent, with a heavy callused ridge inside the aperture. The umbilicus is weakly rimate or imperforate. The color is light grayish-brown. The surface is smooth and dull in most specimens. Occasional specimens have strong, widely spaced vertical striations and light zones that correspond to growth rest stages. There are 4.6-5.4 whorls in large specimens (4.7 in holotype). The suture is moderately impressed. The whorls tend to be flattened along the periphery. The apical whorl is about 0.25 mm in diameter, perpendicular to the initial suture, and projects above the succeeding whorl. The aperture is irregularly ovate in shape. It is about 0.86-0.96 times as wide as high, and may be slightly solute in gerontic specimens. The posterior corner is weakly angulate or bluntly rounded. The peristome extends completely across the parietal wall at maturity. The outer lip is strongly arched forward in lateral profile, projecting considerably anterior to the posterior corner and the basal margin. The basal lip is recurved slightly posterior to the columellar margin.

Measurements in mm of 10 paratypes selected to show maximum variation are as follows (measurements of the holotype are in parentheses): shell length 3.2-3.9 (3.3), shell width 2.1-2.5 (2.3), aperture length 1.4-1.6 (1.5), aperture width 1.2-1.5 (1.4).

FEMALE (FIG. 7B-C).—The lower female reproductive system is similar to that of *M. lustrica*, except for the following features. The glandular wall of the oviduct loop is comparatively thin. The seminal receptacle opens directly into the oviduct I and lacks a distinct duct. The bursa copulatrix projects completely beyond the posterior pallial oviduct. The bursal duct is exposed for about half its length below the bursa on the mesad surface of the posterior pallial oviduct.

MALE (FIG. 7A).—The vas deferens I is strongly convoluted above the prostate. The latter is about twice as long as wide and is roughly kidney-shaped. The vas deferens II is only slightly convoluted within the coelomic wall and is nearly straight within the verge and penis.

The verge is relatively long and is tapered basally. It bears a single large gland confined to the tip of the apical lobe. The penis is relatively long and slender.

OPERCULUM (FIG. 25, B).—The operculum is broad and irregularly ovate, thin, transparent, and slightly amber colored. It is paucispiral, with about 2.5 whorls. The nucleus is in the lower and right third of the face. The outer surface is weakly striate, with incremental striations.

DISTRIBUTION (FIG. 8).—*Marstonia arga* is known only from the Tennessee River in the vicinity of the Guntersville Reservoir in northeastern Alabama and from Shoal Creek. Although numerous collections of mollusks were made in creeks, rivers, and springs draining into the Tennessee River between Florence, Alabama, and Chattanooga, Tennessee, this snail was not encountered except at the above stations.

TYPE LOCALITY.—Guntersville Reservoir, at mouth of Mink Creek, 9.8 mi. SW Scotsboro, Jackson Co., Alabama. HOLOTYPE: UF 22286, collected 14 September 1973 by Fred G. Thompson. PARATYPES: UF 22287 (± 800), same data as holotype.

SPECIMENS EXAMINED.—TENNESSEE RIVER: ALABAMA. Jackson Co.: Guntersville Reservoir, 4.8 mi. SE Scotsboro (UF 22299); 4.3 mi. ESE Scotsboro (UF 22298); 5.1 mi. ESE Scotsboro (UF 22300); 11.2 mi. SW Scotsboro (UF 22302); mouth of North Sauty Creek, 7.5 mi. SW Scotsboro (UF 22289); near mouth of Sauty Creek, 8.1 mi. SW Scotsboro (UF 22301); 3.3 mi. SE Holly-wood (UF 22297). Marshall Co.: Guntersville Reservoir, Honeycomb Creek boat landing, 4.2 mi. WSW Henryville (UF 22291); south shore of bay S of Honeycomb Creek (UF 22293); small bay 2.1 mi. SW Henryville (UF 22292); Creek Reservation, between Tennessee River miles 356 and 357 (UF 22295); Mill Creek Bay, 5.5 mi. NE Guntersville (UF 22303); Town Creek Bay, 8.8 mi. NE Guntersville (UF 22288); Street Bluff Bay, 4 mi. WNW Guntersville (UF 22294); Street Bluff Bay, 3.1 mi. W Guntersville (UF 22290). SHOAL CREEK: ALABAMA. Lauderdale Co.: Shoal Creek at Lauderdale Co. Hwy. 8 (UF 22306, UF 22308). TENNESSEE. Lawrence Co.: Shoal Creek, 0.3 mi. NE Iron City (UF 22307).

REMARKS.—This species appears to be favored by the creation of large quiet bodies of water due to damming of the Tennessee River. It has not yet been found at lentic stations in the Tennessee River below the Guntersville Dam, although it undoubtedly occurs there. In Shoal Creek it was collected in quiet pools of water.

This snail was found most abundantly in beds of *Najas* in quiet, shallow water but generally not on other plants. Three genera of aquatic angiosperms form extensive colonies within the Guntersville Reservoir; *Elodea*, *Myriophyllum*, and *Najas*. Extensive search was made in beds of all three genera, and only rarely was *Marstonia arga* found on *Myriophyllum*. It was never encountered on *Elodea*. Occasional specimens were found on algae-coated cobbles in water less than two feet deep and in piles of submerged dead tree leaves.

ETYMOLOGY.—The species name *arga* is derived from the Greek *argos*, meaning white, and refers to the white aperture caused by the thick internal callus and shell wall.

Marstonia ogmorhaphae new species

DIAGNOSIS.—The verge of this species is most similar morphologically to that of *M. lustrica* and of species living in the Tennessee River System because of the enlarged, squarish apical lobe on the verge and the short, terminal penis. It is more similar to other *Marstonia* from the Tennessee River System than to *M. lustrica* in having an elongate reniform prostate. *M. ogmorhaphae* is distinguished from all other species of *Marstonia* by (1) its large size (4-5 mm), (2) its large number of whorls (5.2-5.8), (3) its deeply incised suture producing strongly shouldered whorls that are almost flat above, (4) its complete aperture that is broadly ovate in shape with a rounded posterior corner, (5) its outer lip which is slightly arched forward in lateral profile, (6) its thin shell, (7) its conical-terete shape, and (8) its enlarged bursa copulatrix with a completely exposed duct.

SHELL (FIGS. 1C, 9A-E).—The shell is conical-terete in shape. Young specimens are conical-ovate. Subsequent growth of the last two whorls is progressively lower in position, producing a terete shape. Large specimens with more than five whorls are about 1.67-1.82 times as long as

wide. The spire is relatively long, being about 1.56-1.67 times the length of the aperture. The shell is nearly transparent and thin, light grayish-brown in color, and has a silky luster when free of encrusting dirt. The umbilicus is narrowly perforate and is partially obscured by the reflected columellar peristome. There are about 5.2-5.8 whorls in mature specimens (5.4 in holotype). The first whorl protrudes above the next, and is about 0.25 mm in diameter perpendicular to the initial suture. The whorls are broadly arched and strongly shouldered with a deeply impressed suture. The lower whorls are sculptured with well-incised, irregularly-spaced incremental striations that are usually continuous from the shoulder to the base of the whorl. The aperture is irregularly ovate in shape, is about 0.82-0.90 times as wide as high, and the upper corner is bluntly rounded. The peristome extends completely across the parietal wall in shells with four or more whorls. The aperture lies at an angle of about 12-14° to the axis of the shell, and the outer lip is slightly arched forward in lateral profile.

Measurements in mm of specimens with 5.2 or more whorls are as follows (holotype measurements in parentheses): shell length 4.0-5.1 (4.4), shell width 2.4-2.8 (2.5), aperture height 1.6-1.8 (1.7), aperture width 1.4-1.7 (1.4).

OPERCULUM (FIG. 25C).—Ovate, paucispiral, consisting of about two complete whorls. The nucleus is located in the lower left third of the face. Thin, membranous, amber yellow in color, transparent. The outer face bears several relatively strong incremental striations.

FEMALE (FIG. 10A-B).—The lower female system contrasts with that of *M. lustrica* as follows. The oviduct loop is more convoluted and oppressed flat against the posterior pallial oviduct, as opposed to being open and transverse to it as in *lustrica*. The glandular wall is much thinner, and the seminal receptacle lacks a distinct duct. The bursa copulatrix is very large, being almost as large as the posterior pallial oviduct, and has the distal 3/4 overlapping the posterior pallial oviduct. The bursal duct is completely exposed on the mesad surface of the posterior pallial oviduct, almost to its junction with the oviduct II.

MALE (FIG. 11A-C).—The verge is stocky and bears a broad, squarish apical lobe along its distal left margin. The penis is short and blunt and projects from the end of the verge along the right side. The apical gland is small and is confined to the inner surface of the tip of the apical lobe. Other glands are absent.

The vas deferens I is strongly convoluted above the prostate. The latter is about twice as long as wide and is more or less kidney-shaped. The vas deferens II is only slightly convoluted within the coelomic wall. It is nearly straight inside the verge and closely parallels the right margin of the verge and penis.

TYPE LOCALITY.—Owen Springs, Sequatchie, Marion Co., Tennessee. **HOLOTYPE:** UF 22179; collected 8 September 1973 by Fred G. Thompson. **PARATYPES:** UF 22180 (± 1000); same data as holotype.

The spring flows from a large crevice in a limestone ledge. About 100 feet below its source it forms a narrow, clear, cold creek that broadens intermittently into deeper, quieter pools. *M. ogmorhaphé* was found only in quieter pools within about 100 yards of the spring source, primarily on ooze that was free of sand and vegetation. Colonies were sporadic and localized.

RANGE (FIG. 8).—This species is known only from the type locality.

ETYMOLOGY.—The specific epithet, *ogmorhaphé*, is derived from the Greek *ogmos*, a furrow, and *rhaphe*, a seam, and alludes to the deeply impressed suture between the whorls.

Marstonia pachyta new species

DIAGNOSIS.—This species of *Marstonia* is readily identified by characteristics of both its verge and shell. Like other *Marstonia* species, the verge is stocky and has a terminal penis along the right margin. It shares with *M. castor*, but not with any other species, a small raised gland on the ventral surface of the verge. It is unique within the genus in having two small glands along the left margin of the apical lobe. The shell is readily identified by its ovate-conical shape, its pronounced thickness, and its complete peristome. Other conical-shaped *Marstonia* have a much

thinner, almost transparent shell, and the peristome is seldom complete across the parietal margin of the aperture.

SHELL (Fig. 3A; 12A-E).—The shell is ovate-conical in shape, and is about 1.43-1.70 times as long as wide. The spire is conical in outline, and exceeds the height of the aperture. The height of the aperture is about 0.39-0.46 times the length of the shell. The shell is very thick and opaque. The periostracum is light yellowish-gray in color and has a dull luster. The shell is sculptured with a few very fine, irregularly-spaced, incremental striations, which become stronger on the base of the last whorl and occasionally form low wrinkles behind the baso-columellar margin of the peristome. The umbilicus is imperforate or only narrowly rimate. There are 4.9-5.2 whorls in mature shells (5.2 in holotype). The whorls have a moderately impressed suture and are moderately arched. There is no tendency for the whorls to be shouldered. The initial whorl protrudes above the succeeding whorl and is about 0.25 mm in diameter perpendicular to the initial suture. The peristome is complete across the parietal margin of the aperture and may be slightly solute from the body whorl in some specimens. The outer lip is nearly straight in lateral profile. The aperture is broadly elliptical in outline, is about 0.80-0.88 times as wide as high, and is angulate both above and below. The upper corner of the aperture is considerably thickened, as are the outer and basal walls, whereas the columellar and parietal margins are thinner and nearly uniform in thickness.

Measurements in mm of mature specimens are as follows (holotype measurements in parentheses): shell length 3.3-4.0 (3.9), shell width 2.2-2.5 (2.3), aperture height 1.5-1.7 (1.5), aperture width 1.2-1.4 (1.3).

OPERCULUM (FIG. 25D).—Relatively elongate, irregularly ovate; thin, transparent, membranous, light amber colored. Paucispiral, consisting of about two rapidly expanding whorls. The nucleus is located just to the left of midline and is in the lower third of the face. The outer surface is almost devoid of sculpture and bears only a few incremental striations.

VERGE (FIG. 13A-D).—The verge is moderately stocky and bears a stout penis that projects from the right distal margin. The region of the apical lobe is not as enlarged as in other *Marstonia*, and it usually bears two small apical glands along the left margin and facing toward the snail's body (Fig. 13, B); however, in one of six specimens examined only a single well developed apical gland is present, with the second gland being indicated only by a few glandular cells (Fig. 13, D). In addition, the ventral (inner) surface of the verge bears a small gland raised on a very low pedicel about a fourth of the distance from the base to the apex and to the right of the midline. The penis and adjacent parts of the verge are dark gray. The remainder of the verge is white.

TYPE LOCALITY.—Limestone Creek, 0.7 mi. E Mooresville, Limestone Co., Alabama. **HOLOTYPE**: UF 22222; collected 1 October 1969 by Fred G. Thompson. **PARATYPE**: UF 22228 (45); same data as the holotype.

The creek at the type locality is shallow and consists of alternating shallow, quiet pools and riffles over broken limestone. Snails were found on dead leaves and tree rootlets in still shallow water at the edge of a pool.

OTHER SPECIMENS EXAMINED.—Piney Creek, Mooresville, Limestone Co., Alabama (UMMZ 160735).

RANGE (FIG. 8).—This snail is known to occur only in Limestone Creek and Piney Creek, Limestone County, Alabama.

ETYMOLOGY.—The name *pachyta* is derived from the Greek *pachytes*, meaning thickness, and refers to the characteristically thick shell of this species.

Marstonia olivacea (PILSBRY)

Amnicola olivacea Pilsbry 1895:115. Walker 1918:135.

DIAGNOSIS.—A thin-shelled *Marstonia* of dubious systematic status. It is similar to *M. lustrica* in its elongate conical shape and its wide umbilicus. It differs by having a relatively inflated penultimate whorl, a broader operculum, and a darker periostracum.

SHELL (FIGS. 1D, 14A-D).—The shell is elongate-conical, or in some obese specimens ovate-conical, and is 1.43-1.81 times as long as wide. The periostracum is very thin and grayish-brown.

The shell is relatively thin and translucent. The umbilicus is open, moderately wide, and is never obscured by the peristome. The aperture is 0.41-0.46 times the height of the shell. The spire is slightly convex in outline. There are 5.0-5.4 whorls (5.4 in holotype), which regularly descend to the aperture. The apical whorl projects above the succeeding whorl and is 0.25 mm in diameter. The whorls are strongly arched with a moderately impressed suture but are sloped and not shouldered. The penultimate whorl is slightly rotund. The postembryonic sculpture consists of fine, close, irregular incremental striations. Occasionally the striations are intensified about the umbilicus or may be folded into weak thread-riblets, as in the lectotype (Fig. 1, D). The aperture is broadly ovate in outline, is weakly angulate at the posterior corner, and is about 0.83-0.90 times as wide as high. The plane of the aperture lies at an angle of about 15° to the axis of the shell. The peristome is usually incomplete across the parietal wall, except in very large individuals. The peristome is very thin, except at the baso-columellar angle, is weakly reflected along the columella, and is straight in lateral profile.

Measurements in mm of specimens with five or more whorls (holotype measurements in parentheses) are as follows: shell length 3.9-4.5 (4.35), shell width 2.6-3.0 (2.75), aperture height 1.7-2.0 (1.8), aperture width 1.5-1.7 (1.5).

OPERCULUM (FIG. 25F).—Thin, membranous, light yellow in color, and transparent; paucispiral, broadly ovate in outline, and consists of about 2.5 whorls. The nucleus is located in the lower quarter and slightly to the left of the midline. The outer surface bears a few fine incremental striations.

VERGE.—Aspects of the soft anatomy are unknown in this species.

TYPE LOCALITY.—[Big Spring Creek], Huntsville, Madison Co., Alabama. **LECTOTYPE** by present designation: ANSP 65466a, collected by H. E. Sargent, 1894. **PARATYPES**: ANSP 65466 (456 specimens); same data as lectotype. The lectotype is a specimen selected by Pilsbry as the type but apparently never designated as such in print.

RANGE (FIG. 15).—Apparently this species was confined to Big Spring Creek, which drains south into the Tennessee River. Goodrich (1944:7) stated that the species was common in streams and springs in and about Huntsville, but no specimens are available in museum collections other than from Big Spring Creek. Goodrich (1939:130, 1944:7) also recorded this snail from the Ogeechee River system in Georgia and the Coosa River system in Alabama, but his records from both drainages are misidentifications of other species.

This snail probably is extinct. The creek is badly polluted and has been channelized for most of its course. No specimens were found by the author during two visits to Big Spring Creek during 1973.

REMARKS.—The specific status of this entity is questionable. Its shell differs from *M. lustrica* in having a more inflated penultimate whorl in large specimens, a broader operculum, and a darker periostracum. If *M. olivacea* was from a more northern locality, I would be tempted to consider it a synonym of the highly variable *M. lustrica*. However, extenuating circumstances dissuade me from doing so.

The type locality of *M. olivacea* is disjunct to the south from the known geographic range of *M. lustrica* by nearly 400 miles. This geographic isolation may not be so great as available data suggest, since almost nothing is known about the hydrobiid fauna of Kentucky and western Tennessee. On the other hand, I have collected extensively in the Duck and Buffalo rivers, and in portions of the Cumberland River system in Tennessee without finding *Marstonia*. It remains to be demonstrated whether or not the genus occurs in lower courses of the Tennessee River and in western Kentucky and Tennessee.

Even though the shells of *M. olivacea* and *M. lustrica* are very similar, other distinguishing features, such as the soft anatomy, must be considered. There are no available preserved anatomical specimens of *M. olivacea*. I attempted to extract and relax dried bodies from paratypes (ANSP 65466) but had unsatisfactory results. Because other species (i.e., *M. pachyta*, *M. castor*) differ from *M. lustrica* in the structure of the verge, it cannot be assumed that *M. olivacea* does not.

There is a tendency to conclude that if two forms cannot be distinguished on the basis of available evidence, they must be identical. In the case of *M. olivacea*, I hesitate to draw this conclusion for the reasons mentioned above. This species' status remains uncertain.

Marstonia lustrica (PILSBRY)

Ammicola lustrica Pilsbry 1890:53.

Ammicola (*Marstonia*) *lustrica* Pilsbry; Baker 1926:195; Berry 1943:29-32.

Ammicola winkleyi Pilsbry 1912:1, pl. 1, figs. 9-10.

Ammicola oneida Pilsbry 1917:46; Baker 1928:111-113, pl. 6, figs. 24, 25, 28-31.

Ammicola lustrica gelida Baker 1921:22.

Ammicola gelida Baker 1928:110-111, pl. 6, figs. 19-23.

Ammicola lustrica decepta Baker 1928:108-109, text-fig. 45.

Ammicola lustrica perlustrica Baker 1928:109-110, pl. 6, fig. 15, text-fig. 45.

Marstonia decepta (Baker); Taylor 1960:51, pl. 2, fig. 9; Clarke 1974:244-247, pl. 21, fig. 16.

Marstonia gelida (Baker); Clarke 1974:247, pl. 21, figs. 7-8.

DIAGNOSIS.—The verge is relatively simple in structure and similar to that of *M. arga* and *M. ogmorhophe*. It has a single apical gland on the apical lobe and a relatively short and stocky penis. Anatomically the species is unique because of the following features: (1) prostate consolidated and ovate in shape, being only slightly longer than wide; (2) glandular wall of oviduct loop relatively thick; (3) seminal receptacle borne on a short duct; (4) bursa copulatrix relatively small, projecting beyond posterior pallial oviduct for about half its length; and (5) bursal duct completely imbedded in posterior pallial oviduct.

The shell of *M. lustrica* is distinguished from other *Marstonia* by the combination of a moderately open umbilicus, conical spire, striate sculpture, and complete peristome that is nearly straight in lateral profile. The inside of the aperture never bears a thick callus, such as occurs in *M. arga*.

SHELL (FIGS. 2A-D; 16A-N).—The shell is dull olivaceous-gray in color, moderately thin, and weakly translucent or opaque. Occasional specimens may be thick-shelled, but they do not have heavy calluses deposited inside the aperture. The shell is ovate-conical to elliptical-conical in shape and generally about 0.55-0.75 times as wide as high. Some extremely narrow specimens from marshy lakes along the southern edge of the range may be terete. The spire is straight-sided or weakly convex in outline. The aperture is about 0.30-0.45 times the height of the shell. The base is openly umbilicate. The surface of the shell is sculptured with fine, rather widely-spaced incremental striations that are nearly continuous across the whorls. The suture is deeply impressed. There are about 4.5-6.0 whorls in mature shells. Large terete specimens may have six or more whorls. The whorls are arched and moderately shouldered. The apical whorl protrudes and is about 0.25 mm in diameter perpendicular to the initial suture. The remaining whorls increase rather regularly in size. The aperture is broadly elliptical or ovate in shape and is higher than wide, the posterior corner is weakly angulate or rounded, and the plane of the aperture lies at an angle of about 15° to the axis of the shell. The peristome generally is complete at maturity. The columellar margin is thin and slightly reflected. The outer lip is nearly straight in lateral profile.

Measurements in mm for selected specimens representing riverine, lacustrine, and marsh habitats are shown in Table 1.

TABLE 1.—MEASUREMENTS (IN MM) AND WHORL COUNTS FOR SELECTED SPECIMENS OF *Marstonia lustrica*, REPRESENTING RIVERINE, LACUSTRINE, AND MARSH HABITATS.

	Riverine	Lacustrine	Marsh
Shell Length	3.3-3.8	3.2-4.3	4.3-4.9
Shell Width	2.2-2.6	2.0-2.4	2.0-2.6
Aperture Height	1.4-1.7	1.3-1.5	1.3-1.6
Aperture Width	1.3-1.5	1.1-1.3	1.1-1.3
Whorls	4.4-4.7	4.9-5.5	5.2-6.0
Shell Width/Length	0.66-0.76	0.53-0.64	0.46-0.56
Aper. H/Length	0.41-0.46	0.35-0.41	0.30-0.36
Aper. H/Aper. W	0.82-0.93	0.80-0.88	0.78-0.93

VARIATION.—Throughout its range *M. lacustrica* shows a remarkable degree of ecologically-associated variation, as is indicated by the lengthy synonymy for the species. Specimens from lacustrine populations, for which the name *lustrica* Pilsbry was proposed (Figs. 2C; 16A-B), are usually more slender than are specimens from riverine habitats, for which the name *decepta* Baker was proposed (Figs. 2A-B; 16G-J). I consider the lake form to be typical of the species, because it is the most widespread and common variant and is found in the most commonly occurring habitat throughout its range. Some specimens from marshy lakes along the southern edge of the snail's range are extremely elongate or terete (Figs. 2D; 16M-N); these elongate forms were named *oneida* Pilsbry and *gelida* Baker. Two other named forms, *winkleyi* Pilsbry and *perlustrica* Baker, are minor variations of the riverine form. All degrees of intermediate variation in the shell occur between the various forms, even within single ecological stations (Turkey Foot Lake, Summit Co., Ohio and Lake Maxinkuckee, Marshall County, Indiana). I find no other morphological evidence to support recognition of more than one taxonomic entity. However, I have examined only a limited amount of anatomical material, representing riverine and lacustrine populations from Ohio and Michigan.

M. lustrica cannot be segregated into distinct subspecies of obvious zoogeographic significance. Consequently, I think it unwise to recognize its ecologically segregated forms as subspecies until additional evidence is forthcoming. Two genetic explanations can account for the observed ecologically associated variation: (1) these forms are different genetic entities that segregate ecologically *due to selection for* different environmental factors, or (2) they are *genotypic responses to* different environmental factors, thus producing different phenotypes. If variation is due to the former (1), then our system of trinomial nomenclature is applicable. If variation results from the latter (2), then trinomial epithets should not be applied. The terms ecotype and ecophenotype have been used rather haphazardly in malacology to explain similar patterns of variation observed among other freshwater mollusks.

In most cases the use of the term is an indication of ignorance on the part of the user, for it does not explain the genetic basis of the observed variations.

OPERCULUM (FIG. 25A).—The operculum is simple, ovate, corneous, very light amber-colored, paucispiral, and consists of about 2.5 whorls. The nucleus is located in the lower right third of the face. The surface is sculptured with a few fine incremental striations.

FEMALE (FIGS. 5B-C).—The female reproductive system is described for the genus. Specific characteristics are given above in the diagnosis.

MALE (FIG. 5A).—The verge is relatively stocky. The left margin terminates with a short, blunt apical lobe that is covered by a relatively large apocrine gland; the right margin ends in a relatively short, stocky penis. The vas deferens is nearly straight within the verge and penis, having very little convolution.

TYPE LOCALITIES.—The holotype (ANSP 284061; collected by James Lewis) of *Amnicolustrica* Pilsbry is from Little Lakes, Wayne Co., New York. The holotype (ANSP 105877; collected by The Rev. Henry W. Winkley) of *A. winkleyi* Pilsbry is from Saco, York Co., Maine. The holotype (ANSP 283876; collected by Frank C. Baker, 1916) of *A. oneida* Pilsbry is from Lower South Bay, Oneida Lake, Madison Co., New York. The holotype (University of Illinois Natural History Museum, P 926) of *A. gelida* Baker is from a post-Wisconsin deposit at Morris, Grundy Co., Illinois. The holotype (University of Illinois Museum of Natural History Z22501) of *A. decepta* Baker is from Silver Lake, Waukesha Co., Wisconsin. The holotype (University of Illinois Museum of Natural History Z18365a) of *A. perlustrica* Baker is from the shore of Lake Michigan, E of Sturgeon Bay, Door Co., Wisconsin.

I have examined the holotypes of *lustrica*, *winkleyi*, and *oneida*; but not those of *gelida*, *decepta*, or *perlustrica*.

RANGE (FIG. 15).—*Marstonia lustrica* is widely distributed from Maine and New York west through northwestern Pennsylvania, Ohio, northern Indiana, and northern Illinois to Iowa and Minnesota. The northern limits of its known range are in southern Quebec and Ontario. Clark (1973:245) recorded it from the Moose, Albany, and Winnipeg river systems in Ontario. These records are included on my distribution map, though I have not examined the specimens. Two southern records, one each from Missouri and Virginia, need to be confirmed with new material.

SPECIMENS EXAMINED.—ILLINOIS. COOK CO.: Chicago, Lake Michigan (MCZ 2221); Berry Lake, nr. Chicago (CM 62.24230); DEKALB CO.: DeKalb (MCZ 46577); FULTON CO.: Canton (FMNH 19976, UMMZ 69847); LAKE CO.: Highland Park, beach at Lake Michigan (USNM 523790); MASON CO.: (FMNH 9851); Illinois River above Havana (FMNH 15687); MCHENRY CO.: Algonquin, Fox River (FMNH 71860); ROCK ISLAND CO.: Rock Island (USNM 476863); WILL CO.: Joliet (FMNH 58692); Joliet, DuPage Crossing (FMNH 65031); Joliet, Lillycace Creek (CM). INDIANA. KOSCIUSKO CO.: Turkey Lake (UMMZ 120595, FMNH 87888); LAKE CO.: Berry (FMNH 112724); Lake Michigan, Millers (CM); Millers, Calumet River (UMMZ 120605); LA PORTE CO.: Pine Lake (UMMZ 69846, UMMZ 120618, MCZ 167502); MARSHALL CO.: Maxinkuckee Lake (CM, UMMZ 69045, FMNH 87850, USNM 541981, MCZ 71291); PORTER CO.: Tremont Dunes Park, beach drift (FMNH 157441); Indiana Dunes State Park (FMNH 114682); STEUBEN CO.: Pleasant Lake (USNM 346866, UMMZ 27572); Turkey Lake (CM). IOWA. DICKINSON CO.: Canal, Upper Gar Lake (USNM 508447); Lake Okoboi (USNM, 30 lots); Orleans (USNM 478427); Spirit Lake (USNM 514552, FMNH 130405); Arnold's Park (UF 22218-22221); MUSCATINE CO.: (USNM 510611); SCOTT CO.: Davenport, Mississippi River (USNM 528018). MAINE. YORK CO.: Saco (ANSP 105877). MICHIGAN. ALLEGAN CO.: Green Lake (UMMZ 120657, USNM 508421); BARRY CO.: Long Lake, 1 mi. NE Cloverdale (UMMZ 197694, USNM 622765); BERRIEN CO.: Niles (CM); BENZIE CO.: Crystal Lake (UMMZ 120656); BRANCH CO.: St. Joseph River, Union City (UMMZ 197695, USNM 622754); Marble Lake, nr. Quincy (UMMZ 164280); CALHOUN CO.: Ackley Lake, 9 mi. N Marshall (UMMZ 197709); 7.5 mi. S Battle Creek, Graham Lake (USNM 622764); Battle Creek River, 4.5 mi. NE Battle Creek (UMMZ 197692); Outlet of Hall's Lake, 2.5 mi. E Battle Creek (UMMZ 197711); Battle Creek, Bailey Park, Battle Creek River (UMMZ 171790); CHARLEVOIX CO.: Deer Lake (UMMZ 29586); Barney

Lake, Beaver Island (UMMZ 142517); Lake Michigan, Beaver Island, High Island Harbor (MCZ 30719, CM, FMNH 87849); CHEBOYGAN Co.: Outlet, Carp Lake (CM); Emmet, Carp Lake (UMMZ 120659); Carp Lake, nr. Mackinaw City (CM); DICKINSON Co.: Brown Lake (UMMZ 7421); EATON Co.: Battle Creek River, W Bellevue (CM 62.2757); CRAWFORD Co.: Manistee River, 7 mi. N Lake Mararethe (UMMZ 132277); GENESEE Co.: Silver Lake, nr. Fenton (UMMZ 41928); GRAND TRAVERSE Co.: Traverse City, Pine Lake (UMMZ 120711); HURON Co.: Rush Lake (UMMZ 7417); IONIA Co.: Long Lake (UMMZ 164293); IRON Co.: Pickerel Lake (UMMZ 150145); JACKSON Co.: Sandstone Creek, 5 mi. W Jackson (UMMZ 197701, USNM 622766); Concord, Michigan Spring Branch (UMMZ 197690); KALAMAZOO Co.: Outlet of Gourdreck Lake, 3 mi. NW Vicksburg (UMMZ 197691); W side Gull Lake (UMMZ 197706); 1.5 mi. N-NW Climax, Blue Lake (USNM 622759); KEEWENAW Co.: Davis Creek (UMMZ 160672); Isle Royale, W end Rock Harbor (UMMZ 120706); KENT Co.: Perch Lake (CM); Grand Rapids (UMMZ 120650); Dewey's Mill (FMNH 87890, USNM 697029); Byer's Trout Pond (CM); Grand Rapids, Reed's Lake (FMNH 102341, USNM 254122a); Perch Lake (CM, UMMZ 120651); LAKE Co.: Marl Lake (UMMZ 160649); Kinney Creek (CM, FMNH 87893); Pere Marquette River (FMNH 87889); Lake Twp., Bass Lake (UMMZ 37619); LENAWEE Co.: Posey Lake Outlet (UMMZ 46659); LIVINGSTON Co.: Whitewood Lake (UMMZ 120703, UMMZ 27571); MANISTEE Co.: Onekama (FMNH 59991); Bear Lake (USNM 172303); MONROE Co.: La Pausance Bay (UMMZ 27548); MONTCALM Co.: outlet Mud Lake, Riverdale (UMMZ 120677); Cedar (UMMZ 120667); MUSKEGON Co.: Blue Lake (MCZ 166005); Muskegon Lake (UMMZ 120678); NEWAYGO Co.: Mono Lake (USNM 539420); Hess Lake (MCZ 166003, FMNH 122002); Brook's Lake (FMNH 105144, UMMZ 120675); Hog Lake (MCZ); Pickerel Lake (UMMZ 120668); OAKLAND Co.: Deer Lake nr. Clarkston (UMMZ 7568); Orchard Lake (CM, UMMZ 69849); Straits Lake (UMMZ 29591); Huron River, above Milford (UMMZ 29591); PRESQUE ISLE Co.: Orchard Lake (CM); Black Lake (FMNH 87853); OGEAN Co.: Edwards Lake (UMMZ 41927); WASHTEENAW Co.: Delhi Mills, Huron River (USNM 622758, UMMZ 197702); Black Lake (FMNH 59990); Ann Arbor (FMNH 122786); Halfmoon Lake (UMMZ 46646); Ann Arbor, Huron River (FMNH 87891); nr. Ann Arbor (USNM 444141). KANKAKEE River, English Lake (CM 42); MINNESOTA. BLUE EARTH Co.: Eagle Lake (USNM 123902); DOUGLAS Co.: Alexandria, Lake Mary (USNM 347707); HENNEPIN Co.: Mississippi River (CM 62.16279); nr. Minneapolis, Lake Harriet (FMNH 58691) nr. Minneapolis, Kegons Lake (MCZ 2225); nr. Minneapolis, Lake Harriet (UMMZ 120609); ITASCA Co.: (FMNH 59987); PINE Co.: St. Croix River e. of Rock Creek (USNM 514469, 514470); STEARNS Co.: Kimberly, Rice Lake (USNM 347727); Birch Lake (UMMZ 120622); WRIGHT Co.: Clearwater Lake (UMMZ 143680). MISSOURI. SHANNON Co.: Jacks Fork (MCZ 2224). NEW YORK. Hudson River drift (CM); Mohawk River (USNM 24777, USNM 97910); ALBANY Co. Albany, Normans Hill (MCZ); ERIE Co.: Grand Island (FMNH 114728); HERKIMER Co.: Little Lakes (USNM 28085, FMNH 102421, FMNH 32841); Mohawk (UMMZ 120590, MCZ 53879); Erie Canal (USNM 121320); MADISON Co.: Lower South Bay, Oneida Lake (type lot *Ammnicola oneida* Pilsbry); ORLEANS Co.: Cedar Lake, nr. Albion (USNM 572662, USNM 572665); OTSEGO Co.: Outlet Schuyler's Lake (USNM 27895); Schuyler's Lake (UMMZ 27554, MCZ 2107, USNM 514615); WAYNE Co.: nr. Blyde (USNM 251446); YATES Co.: Seneca Lake (MCZ 2108); RYE Co.: Little Lake (FMNH 121117); WAYNE Co.: Sodus Bay (USNM 536640); Little Lakes (ANSP 74564, ANSP 122196); Skaneateles Lake (ANSP 95480); OSWEGO Co.: Barge Canal, 0.5 mi. SE Hinonansville (ANSP 113115). NEW BRUNSWICK. Portland, Harrigan's Lake (FMNH 107179). OHIO. ASHLAND Co.: Outlet of Long Lake (CM 62.24923); CHAMPAIGNE Co.: Cedar Swamp, nr. Urbana (US 22223); CLARK Co.: Midway (UF 22227); ERIE Co.: Sandusky (CM); Cedar Point (CM 62.24730); LUCAS Co.: Maumee River, Hocking Valley Docks (UMMZ 27549); OTTAWA Co.: Sandusky Bay Point (UMMZ 27556); PORTAGE Co.: Cuyahoga River, nr. Hiram (CM 31); GARETSVILLE (CM); STARK Co.: Tuscarawas River, Navarre (CM); SUMMIT Co.: Mud Lake (CM 62.24922); HUDSON (UMMZ 69850); HUDSON, Tinkers Creek (MCZ 15129, CM 62.25396, FMNH 71861); Big Reservoir (CM 62.24924); Long Lake (CM 62.25209); Springfield Lake (CM); TUSCARAWAS Co.: Side-cut on Mill-Race, New Philadelphia (CM); ditch from small swamp on river, s.e. New Philadelphia (CM); Tuscarawas River, New Philadelphia (CM); swamp below Blakes Mills, nr. New Philadelphia (CM); mill race, Tuscarawas River, New Philadelphia (CM); small swamp s.e. New Philadelphia (CM); New Philadelphia (USNM 117749). ONTARIO. ADDINGTON & LENNOX Cos.: Ernestown, Wilton Creek (MCZ 244172); Camden, Varty Lake (MCZ 244183) Adolphustown Twp. Hay Bay (MCZ 234626); Camden, Camden Lake (MCZ 248086);

Richmond, Salmon River (MCZ 248075); Bay of Quinte, Adolphustown (ANSP 234653); BRUCE CO.: Pond nr. South Hampton (FMNH 130428); CANTWELL CO.: stream, Mono Mills (UMMZ 133232); HASTINGS CO.: Hungerford, Dry Lake (MCZ 248101); Huntingdon, Moira Lake (MCZ 248115); HAMILTON CO.: (ANSP 67569); Lake Simcoe (UMMZ 120625); Lake Huron, Cohome, Georgian Bay (ANSP 105668) Giants Tomb. Id., Georgian Bay (ANSP 105667); Cohome, Georgian Bay (ANSP 105744); Lake Huron, Gravelly Point, St. Joseph's Id., North Channel (ANSP 153108); LAMBTON CO.: Lake Huron, Kettle Point (UMMZ 133273); Manitou Island, s.e. side of Lake Mendemoa (UMMZ 52633); PRINCE EDWARD CO.: Lake Ontario (UMMZ 138771); Athol Twp., Lake Ontario, Athol Bay (MCZ 248034); Matheson, Black River (MCZ 248047). Rochester, Lake Ontario (CNHM 121181); TRONTENAC CO.: Kingston (MCZ 244222); Wellington, w. Lake, Ontario, Shore 300 yds. w. of Harbour Pier, Wellington (USNM 464527). PENNSYLVANIA. ERIE CO.: Presque Isle, Long Pond (CM 62.24729); Presque Isle, Middle Bend (CM 62.24731); Presque Isle, sand flats (CM 62.24728). VIRGINIA. Nr. Alexandria (CM). WISCONSIN. DANE CO.: Madison (FMNH 115418); Lake Mendota (CM 62.26283); DOOR CO.: Newport, Newport Beach (FMNH 157444); MARINETTE CO.: North Woque Bay (UMMZ 120612); MILWAUKEE CO.: Milwaukee (USNM 7 lots); VILAS CO.: Rest Lake (FMNH 25727).

REMARKS.—This snail has a wide geographic distribution within the cool temperate areas of North America's Great Lakes region. Within its range it occupies a wide variety of habitats, including lakes, ponds, marshes, rivers, and small streams. Most specimens that I examined came from habitats that were characterized by clear water with submerged aquatic plants. Though it is widely distributed, it is not known from geologic deposits older than the Wisconsin Glacial Period, nor from fossil localities outside its present range (Taylor 1960).

Marstonia lustrica appears to be a species that originated in the upper Mississippi River system during the Wisconsin Glacial Period as a cold-tolerant member of *Marstonia*. It apparently moved north with the receding glacier, where it came to be widely distributed throughout the Great Lakes region.

Marstonia halcyon: new species

DIAGNOSIS.—This species is distinguished by a small, broadly ovate shell with a deep suture producing strongly shouldered whorls, a flattened periphery on the whorls, a wide umbilicus, and complete peristome that is nearly uniformly thick. The suture descends to the aperture in lateral profile. *M. halcyon* is related to *M. castor* and *M. agarhecta*, based on its slender apical lobe on the verge with a small apical gland on the mesad surface of the tip and an enlarged penis. It also shares with *M. castor* a small raised tubercular gland on the mesad surface of the verge, but differs in this regard from *M. agarhecta*, which has only the apical gland.

In addition to the characteristics of the verge, this snail differs from *M. lustrica* and its allies in having a slender copulatory bursa that does not extend to the end of the posterior pallial oviduct and is nearly completely imbedded in glandular tissue.

SHELL (Figs. 3D, 17A-E).—The shell is small, usually less than 2.5 mm long, and is broadly ovate in shape, being about 0.70-0.80 times as wide as high. The spire is as long as, or longer than the aperture and is slightly convex in outline. The aperture is about 0.40-0.50 times the length of the shell. The shell wall is nearly of uniformly moderate thickness and is almost transparent. Specimens with a complete peristome usually develop a slight callused ridge within the peristome. The periostracum is a very delicate light gray in color. The umbilicus is rather broadly perforate. The whorls are densely sculptured, with fine irregular incremental striations that are crossed by much finer spiral striations. There are about 4.0-4.3 whorls at maturity (4.3 in holotype); large gerontic specimens may have as many as 5.0 whorls. The suture is deeply impressed, causing the whorls to be almost flat-topped and shouldered. The periphery of the whorls are distinctly flattened, with the apical whorl protruding above the succeeding whorls. The body whorl

becomes ventrad in position and is usually constricted at the aperture, where it descends rather noticeably (Fig. 17B, lateral profile). The aperture is oval in outline, broadly rounded at the posterior corner when mature, and about 0.80-0.93 times as wide as high. The aperture is adnate to the preceding whorl for a short distance along the parietal margin. The peristome is nearly straight in lateral profile and lies at about 35° to the shell axis.

Measurements in mm for specimens with a complete peristome are as follows (holotype measurements in parentheses): shell length 2.0-2.5 (2.3), shell width 1.6-1.9 (1.75), aperture height 1.0-1.1 (1.0), aperture width (0.8-1.0 (0.9)).

Occasional gerontic specimens reach a length of 3.3 mm and are proportionately more slender than smaller specimens because of the ventrad position of the body whorl. Occasional small males of about 1.8 mm long may develop a complete peristome.

OPERCULUM (FIG. 25G).—The operculum is paucispiral, ovate, thin, transparent, membranous, and light yellowish-white in color. It consists of about two whorls and is sculptured on the outer surface with fine irregular incremental striations.

FEMALE (FIGS. 18A-B).—The female reproductive system is similar to that of *M. lustrica* and related forms, except as follows: (1) the oviduct loop is vertical to the axis of the pallial oviduct; and (2) the bursa copulatrix does not overlap the posterior end of the pallial oviduct and is completely imbedded in the posterior pallial oviduct, except for its distal tip.

MALE (FIGS. 19A-C).—The vas deferens I is only moderately convoluted and is only slightly thickened in the region of the convolutions. The prostate is relatively elongate and rather distinctly lobed, in contrast to the more concentrated prostate in *M. lustrica*. The verge originates on the nape on the right of the middorsal line and is forked distally. The penis is considerably longer and more enlarged than the apical lobe. The latter is papilliform and bears a single, small apical gland on the ventral side of its tip. A second small, raised gland is present on the ventral surface of the verge about halfway between the base and the apical lobe.

DISTRIBUTION (FIG. 20).—*M. halcyon* is confined to the lower half of the Ogeechee River System in eastern Georgia, where it is found in quiet water over a silt or sand bottom. It has been collected only in the Ogeechee River and Buckhead Creek, though it probably occurs in other creeks along the middle and lower course of the Ogeechee River.

TYPE LOCALITY.—Buckhead Creek, 0.6 mi. W Miller, Jenkins Co., Georgia. **HOLOTYPE**: UF 22312; collected 6 October 1974 by Fred G. Thompson and Beverly E. Johnson. **PARATYPES**: UF 22313; same data as the holotype.

At the type locality, Buckhead Creek is about 3-5 ft deep, with a hard sand bottom and a slight current. Snails were collected in quiet, shallow water on silty sand and in clusters of filamentous algae.

SPECIMENS EXAMINED.—**GEORGIA**. **BRYAN CO.**: Ogeechee River, 1.1 mi. SE Blichton (UF 22318); **EFFINGHAM CO.**: 1.7 mi. SW Guyton (UF 22316, 22319); **JENKINS CO.**: Buckhead Creek, 0.6 mi. W Miller (UF 22311); **SCREVEN CO.**: Ogeechee River, 0.7 mi. SW Ogeechee (UF 22310, 22314); Ogeechee River, 1.6 mi. SW Halcyon Dale; Ogeechee River, 3.0 mi. SW Oliver (UF 22320).

REMARKS.—This snail was always collected in open water, primarily on silty sand. Only rarely was it found on filamentous algae. On no occasion was it found on dead submerged leaves, moss, or other detritus, although other hydrobiids (*Ammicola* sp. and *Lyogyrus* sp.) were abundant on such substrates.

Goodrich (1939:130) recorded four species of hydrobiids from the Ogeechee River. His material was not available to me for examination, as it is being studied by another investigator. I cannot state the name(s) under which Goodrich recorded *M. halcyon*.

ETYMOLOGY.—In the area where *M. halcyon* was found, the Ogeechee River is gentle and quiet, bordered with large cypress trees and hardwood forests. The species name is borrowed from the Greek *halcyon*, a mythological sea bird that brought peace and serenity wherever it alighted. The name is suggested by one of the places near where it was collected, Halcyon Dale.

Marstonia castor new species

DIAGNOSIS.—*Marstonia castor* is a minute snail, less than 2.5 mm long, ovate-conical in shape, relatively thick and solid, and has about 3.9-4.4 rounded whorls with a deeply impressed suture. The peristome is complete at maturity, and the umbilicus is narrowly perforate. The verge has a tubercular gland on the mesad surface in addition to the apical gland.

SHELL (FIGS. 3C, 21A-D).—The shell is minute, ovate-conical in shape, and about 0.66-0.73 times as wide as high. It is narrowly but distinctly umbilicate. The circum-umbilical area is almost obtusely angulate. The shell is moderately thick for its size, semi-transparent, and light gray in color. The spire is slightly convex in outline and slightly longer than the aperture, which is about 0.44-0.49 times the length of the shell. There are 3.9-4.4 whorls in mature shells. Females tend to be slightly larger than males and have about 0.3 more whorls. The apical whorl is raised and rounded with a well-impressed suture, and is about 0.23-0.24 mm in diameter perpendicular to the initial suture. Post-apical whorls have a deeply impressed suture, are strongly and evenly arched, and have numerous fine incremental striations. The aperture is ovate in shape and about 0.81-0.91 times as wide as high. In lateral profile the plane of the aperture lies at about 18-20° to the axis of the shell. The peristome is complete across the parietal margin at maturity and is neither advanced nor reeded in lateral profile. The outer lip is sharp, nearly rounded to the columella, and may develop a relatively thick internal callus. The parietal margin of the aperture is nearly straight.

Measurements in mm of six adult specimens selected to show the range of variation are as follows (holotype measurements in parentheses): shell length 1.94-2.70 (2.30), shell width 1.40-1.98 (1.51), aperture height 0.94-1.33 (1.05), aperture width 0.83-1.08 (0.86).

OPERCULUM (FIG. 25E).—Broadly ovate in shape, paucispiral, and consisting of about two whorls, with the nucleus located in the lower left quarter. Thin, membranous, transparent. The outer surface shows a few fine incremental striations.

VERGE (FIG. 22A-B).—The verge is relatively slender and has a relatively enlarged penis, which is about twice the length of the apical crest. The apical crest is nearly completely covered by an apical gland. On the ventral side near the middle of the verge is a small globular gland raised on a low pedicel.

TYPE LOCALITY.—Cedar Creek, 3.4 mi. S-SW Coney, Crisp Co., Georgia. **HOLOTYPE:** UF 22176; collected 19 November 1973 by Fred G. Thompson. **PARATYPES:** UF 22177 (51); same data as the holotype.

In addition to the type series, I have examined about 300 other specimens from the type locality (UF 22178).

The type locality is a small clear stream that flows through a cypress slough and drains into the east side of Lake Blackshear, a reservoir on the Flint River. Snails were generally distributed in the creek on *Najas* and to a lesser extent on clumps of *Chara* in shallow clear water that had only a slight current. They were not found on the substrate or debris. At no place was the snail abundant.

RANGE (FIG. 20).—This snail is known only from the type locality.

ETYMOLOGY.—The species epithet *castor* is taken from the generic name of the beaver, *Castor canadense*, with which it shares the type locality.

Marstonia agarhecta THOMPSON

Marstonia agarhecta Thompson 1969:243-247; fig. 1A-F.

DIAGNOSIS.—This is a minute snail most closely related to *M. castor* but the structure of the verge, which bears a single enlarged epidermal gland on the apical lobe but lacks other glands. The penis is relatively large and about twice the length of the apical lobe. The shell is minute (about 2.3-2.7 mm long), conical, and very fragile. It has an incomplete peristome and about 4.4-4.6 whorls that are separated by a deeply impressed suture.

SHELL (FIGS. 3B, 23A-D).—The shell is minute, very thin and fragile, transparent, conical,

and about 0.64-0.74 times as wide as high. It is dimorphic in shape. Females tend to be broader than males. The spire is about equal to the aperture in height and nearly straight-sided. The umbilicus is open but narrowly perforate. There are 4.4-4.6 whorls in adult shells. The apical whorl is 0.23-0.25 mm in diameter perpendicular to the initial suture; protrudes above the succeeding whorl; is strongly rounded with a deep suture; and has very fine, close microscopic striations. The following whorls are strongly rounded with a deeply impressed suture. The body whorl is weakly shouldered. The sculpture on the lower whorls consists of very fine, close incremental striations that are equal in intensity over the surface of the whorls. The aperture is ovate, about 0.77-0.83 times as wide as high, and about 0.45-0.52 times the height of the shell. The greatest diameter of the aperture lies at about 30° to the shell axis. The plane of the aperture is slightly oblique to the shell axis in lateral profile. The peristome is incomplete across the parietal wall. The parietal callus consists only of a very thin glaze. The columellar lip is concave, very thin, and weakly reflected. The outer lip is weakly arched forward above the periphery and slightly recessed near the base.

Measurements are given in mm for large specimens as follows (holotype measurements in parentheses): shell length 2.3-2.7 (2.65), shell width 1.6-1.95 (1.75), aperture height 1.1-1.3 (1.2), aperture width 0.9-1.05 (0.95).

OPERCULUM (FIG. 25H).—Broadly ovate in shape, with a slight indentation along the parietal margin. It is very thin, membranous, and colorless or only slightly tinged with yellow. It is paucispiral with about 2.5 whorls. The nucleus is large and located in the lower left third of the face. The outer surface is sculptured with a few fine incremental striations.

VERGE (FIG. 24A-B).—The verge is stout and slightly compressed dorso-ventrally. The distal left margin terminates in an apical lobe that bears an enlarged apical gland. The penis is relatively slender, long, and enlarged.

RADULA.—Minute, about 450 μ long and contains about 42-46 transverse rows of teeth (10 specimens examined). The central tooth is about 19 μ wide and bears an enlarged mesocone with 3-5 ectocones and a single basocone on each side. The lateral tooth bears 2-1.4 to 3-1.5 cusps.

TYPE LOCALITY.—Bluff Creek, 10.4 mi. S-SE Hawkinsville, Pulaski Co., Georgia. **HOLOTYPE**: UF 20528; collected 31 January 1969 by Fred C. Thompson. **PARATYPES**: UF 20529 (296); same data as the holotype.

Specimens were found in clear water with only a slight current, predominantly in diatomaceous ooze on top of old submerged logs. Occasionally individuals were also found in silt that contained large amounts of diatoms.

RANGE (FIG. 20).—This species is known only from the type locality.

REMARKS.—Though very different in shell structure, this snail is most closely related to *M. castor*. Both species are alike in having an enlarged, elongate penis and a relatively enlarged and protruding apical lobe. In these respects the two species differ remarkably from other *Marstonia*.

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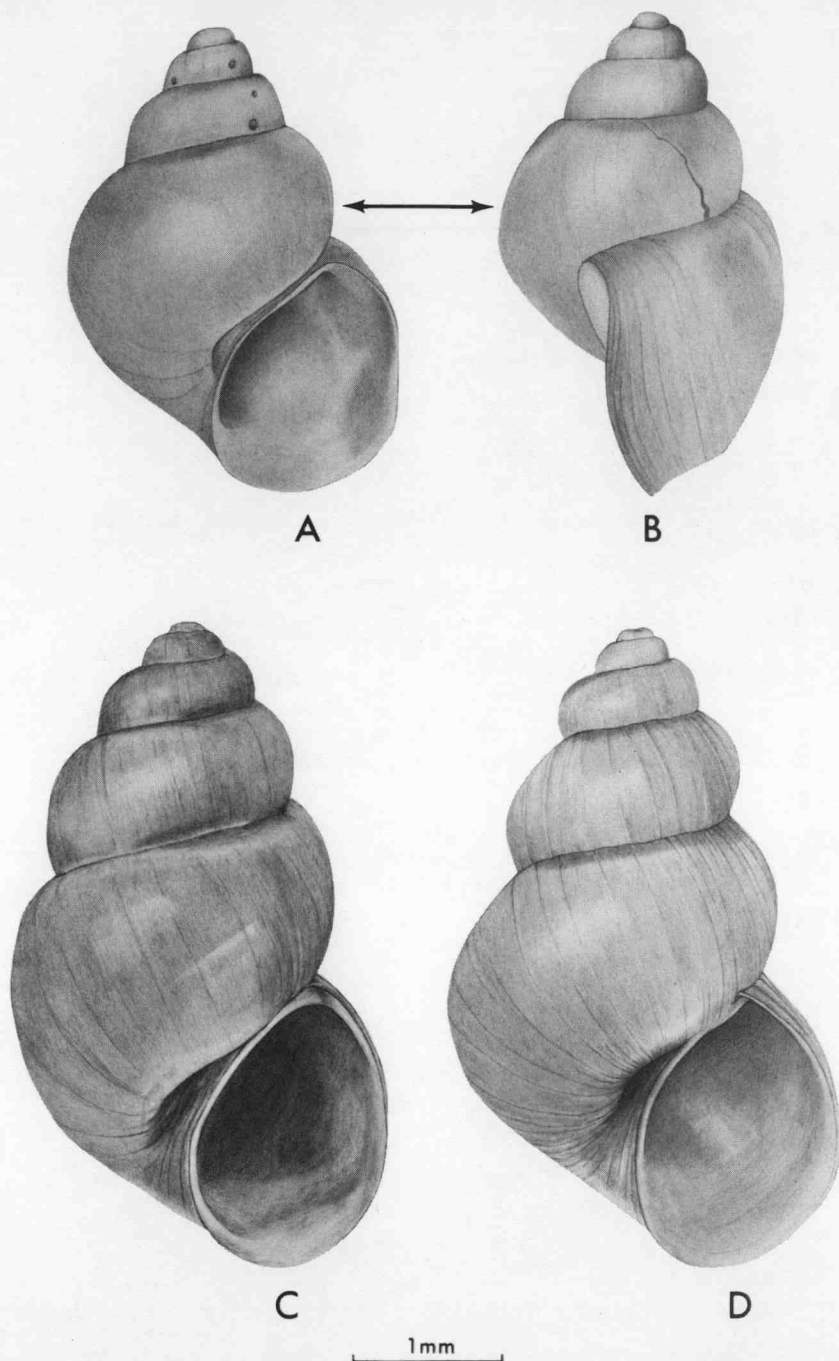


FIGURE 1.—(A, B) *Marstonia arga* new species, HOLOTYPE: UF 22286; (C) *Marstonia ogmorhapha* new species, HOLOTYPE: UF 22179; (D) *Marstonia olivacea* (Pilsbry), LECTOTYPE: ANSP 65460a.

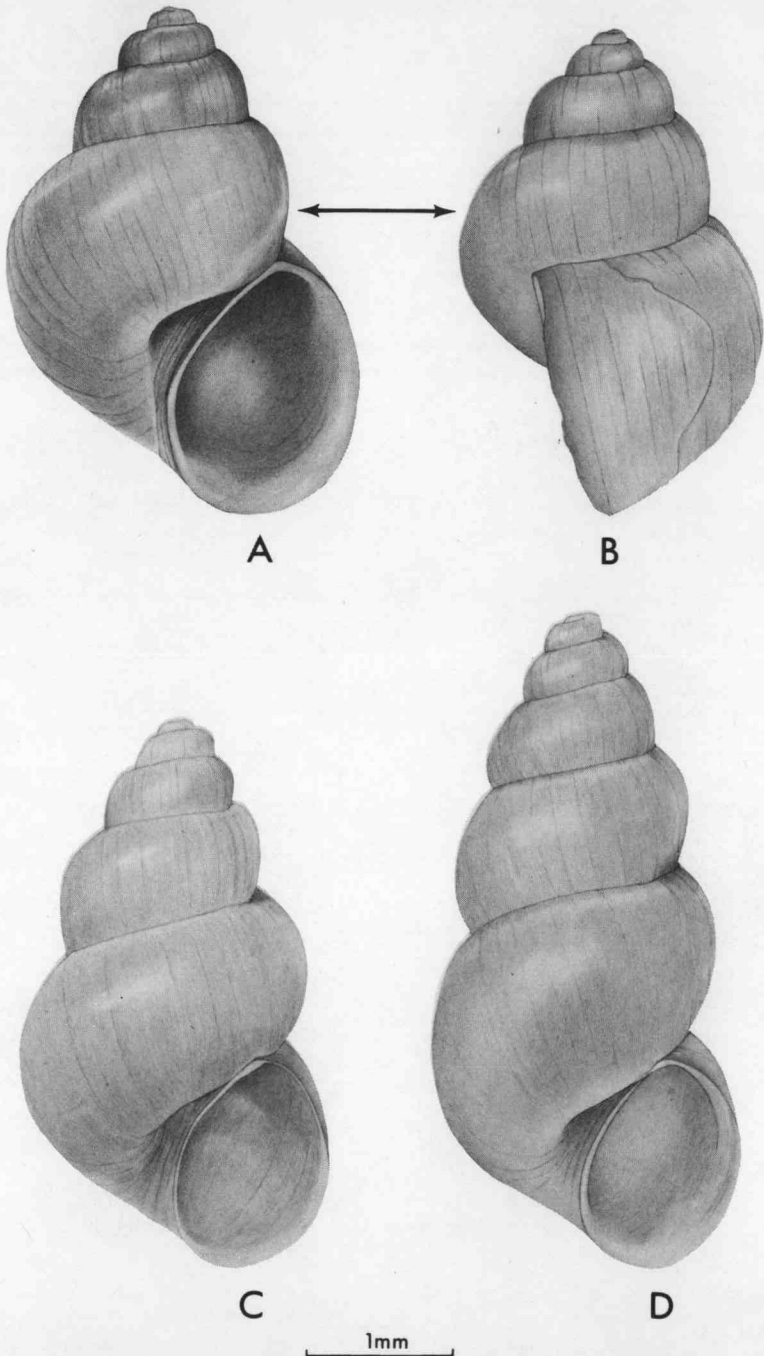


FIGURE 2.—*Marstonia lustrica* (Pilsbry): (A, B) Riverine form; Cedar Swamp, nr. Urbana, Champaign Co., Ohio (UF 22223); (C) Lacustrine form; Hess Lake, Newaygo Co., Michigan (UF 22190); (D) Extremely slender lacustrine form; Turkeyfoot Lake, Summit Co., Ohio (UF 22225).

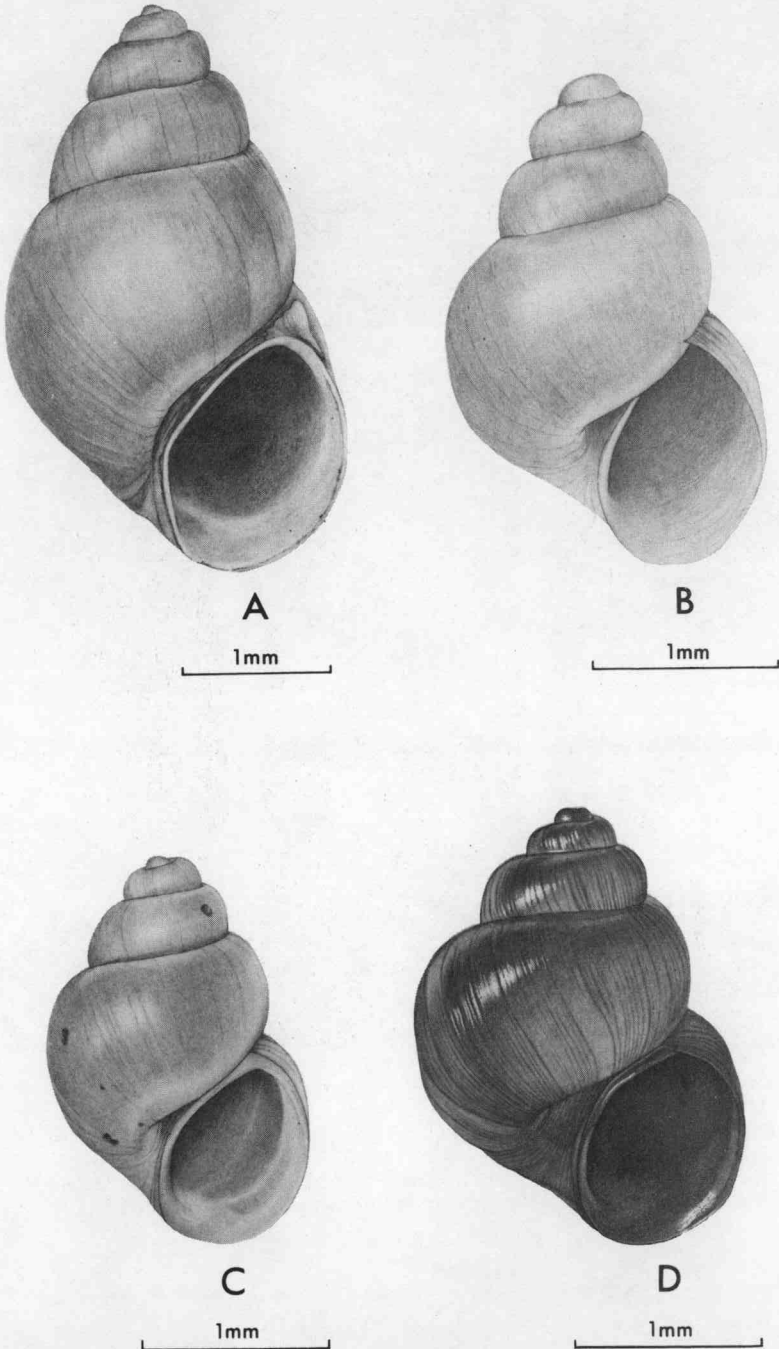


FIGURE 3.—(A) *Marstonia pachyta* new species, HOLOTYPE: UF 22222; (B) *Marstonia agarhcta* Thompson, HOLOTYPE: UF 20528; (C) *Marstonia castor* new species, HOLOTYPE: UF 22176; (D) *Marstonia halcyon* new species, HOLOTYPE: UF 22312.

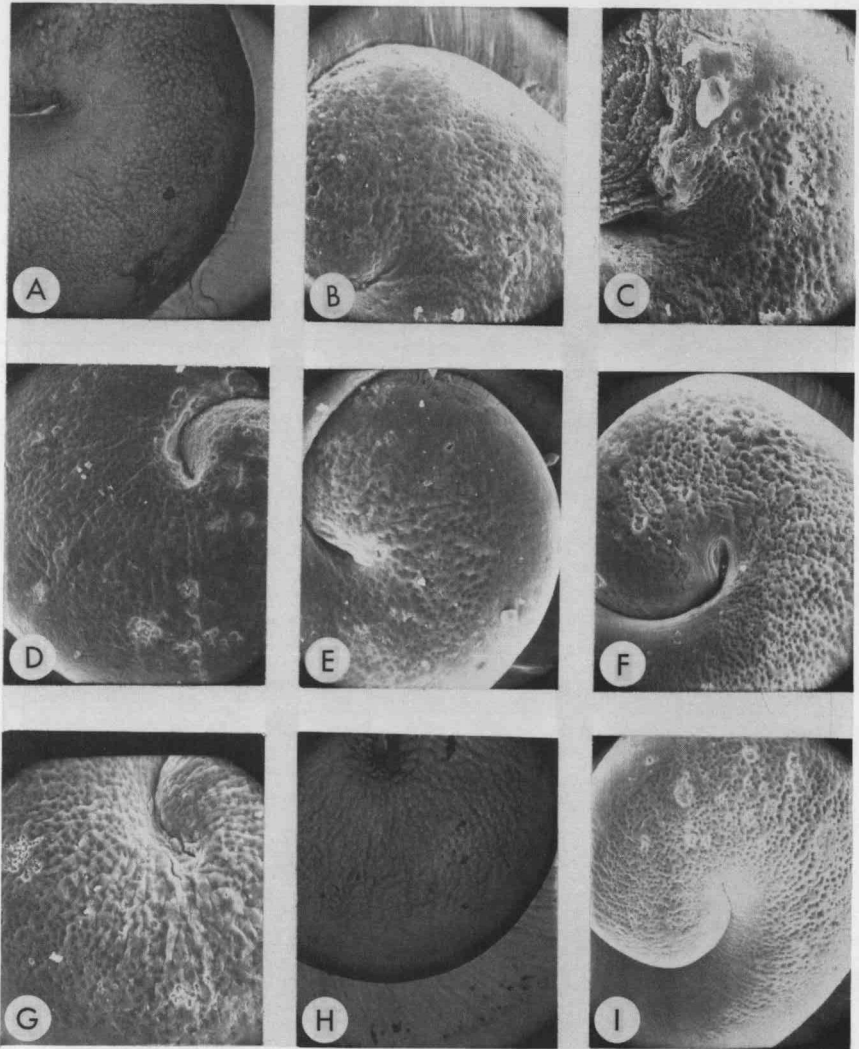


FIGURE 4.—Scanning Electron Micrographs of North American hydrobiid snail embryonic sculpture: (A) *Rhaphinema dacryon* Thompson (UF 22378) X196; (B) *Cincinnatia integra* (Say) (UF 22189) X224; (C) *Notogillia wetherbyi* (Dall) (UF 22191) X245; (D) *Marstonia lustrica* (Pilsbry) (UF 22190) X203; (E) *Marstonia ogmorhapha* new species (UF 22180) X214; (F) *Marstonia arga* new species (UF 22287) X210; (G) *Marstonia agarhcta* Thompson (UF 20529) X224; (H) *Marstonia castor* new species (UF 22177) X196; (I) *Marstonia halcyon* new species (UF 22313) X166.

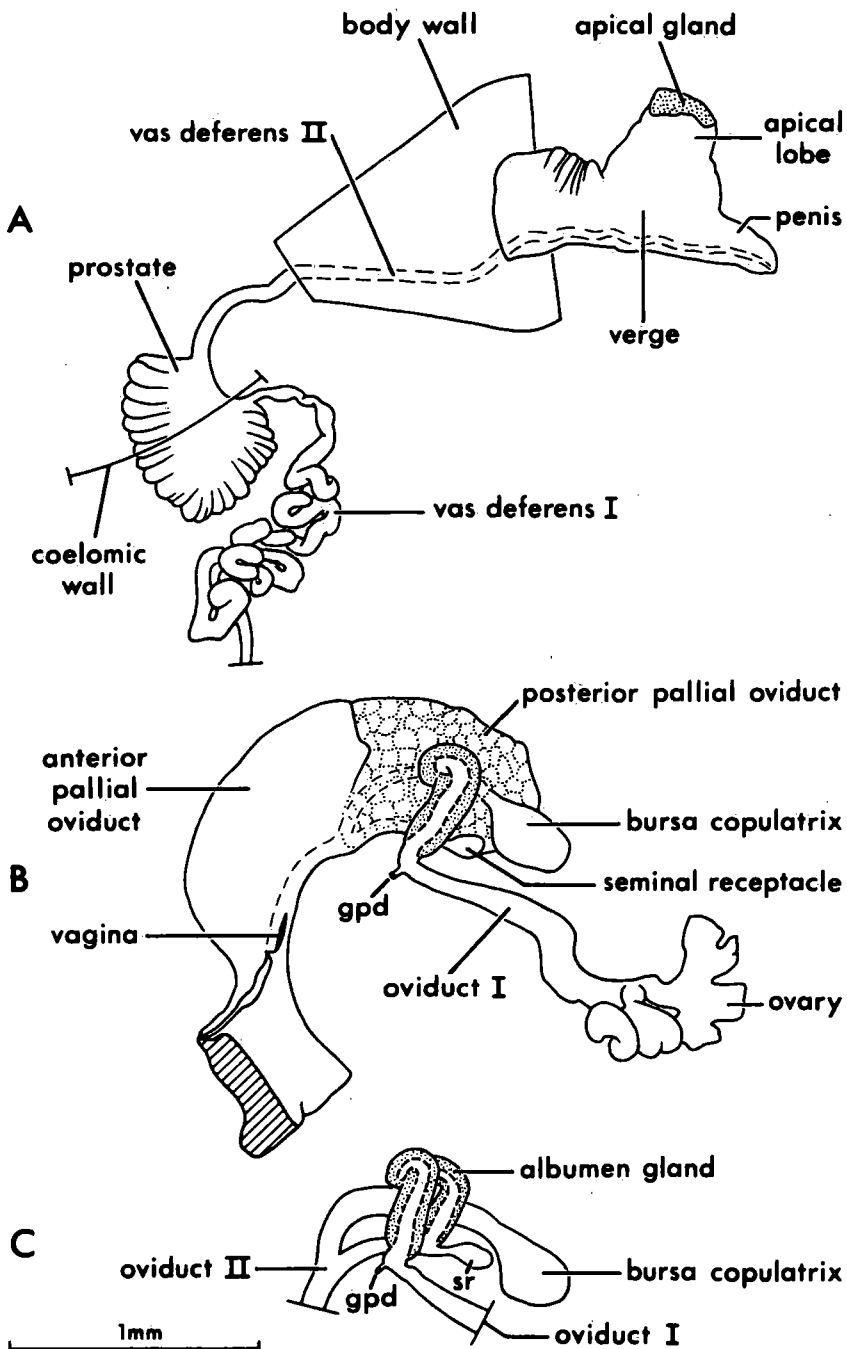


FIGURE 5.—*Marstonia lustrica* (Pilsbry); Midland, Clarke Co., Ohio (UF 22227). (A) male reproductive system; (B) female reproductive system; (C) oviduct and associated structures freed from the pallial oviduct; gpd = gonopercardial duct, sr = seminal receptacle.

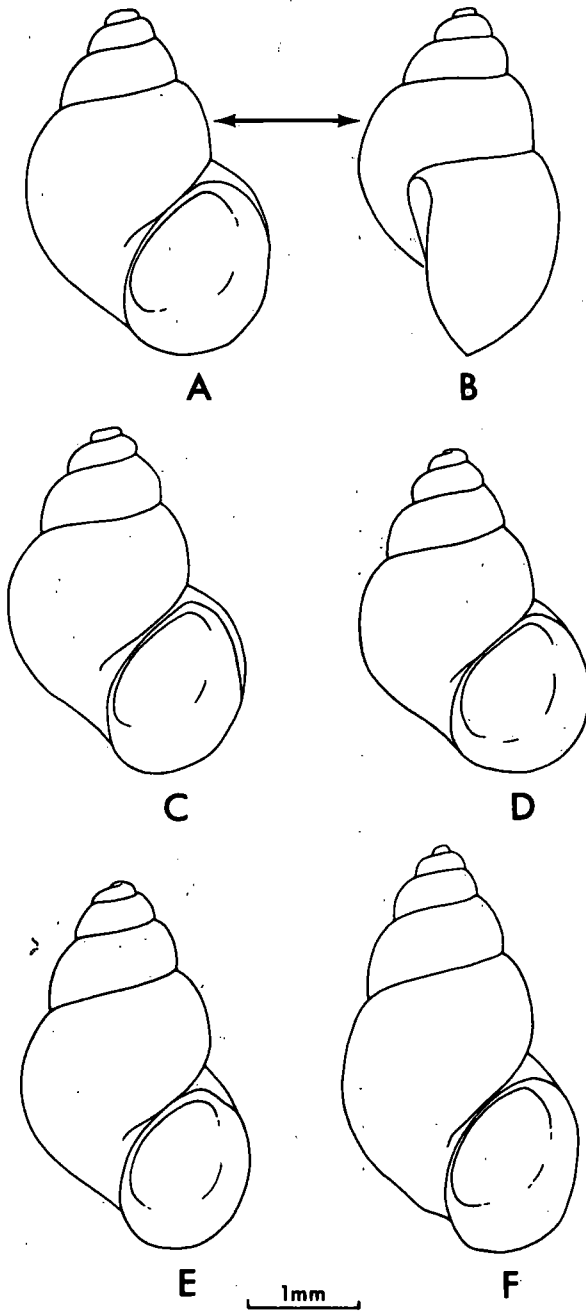


FIGURE 6.—*Marstonia arga* new species: (A, B) HOLOTYPE (UF 22286); (C-F) PARATYPES (UF 22287).

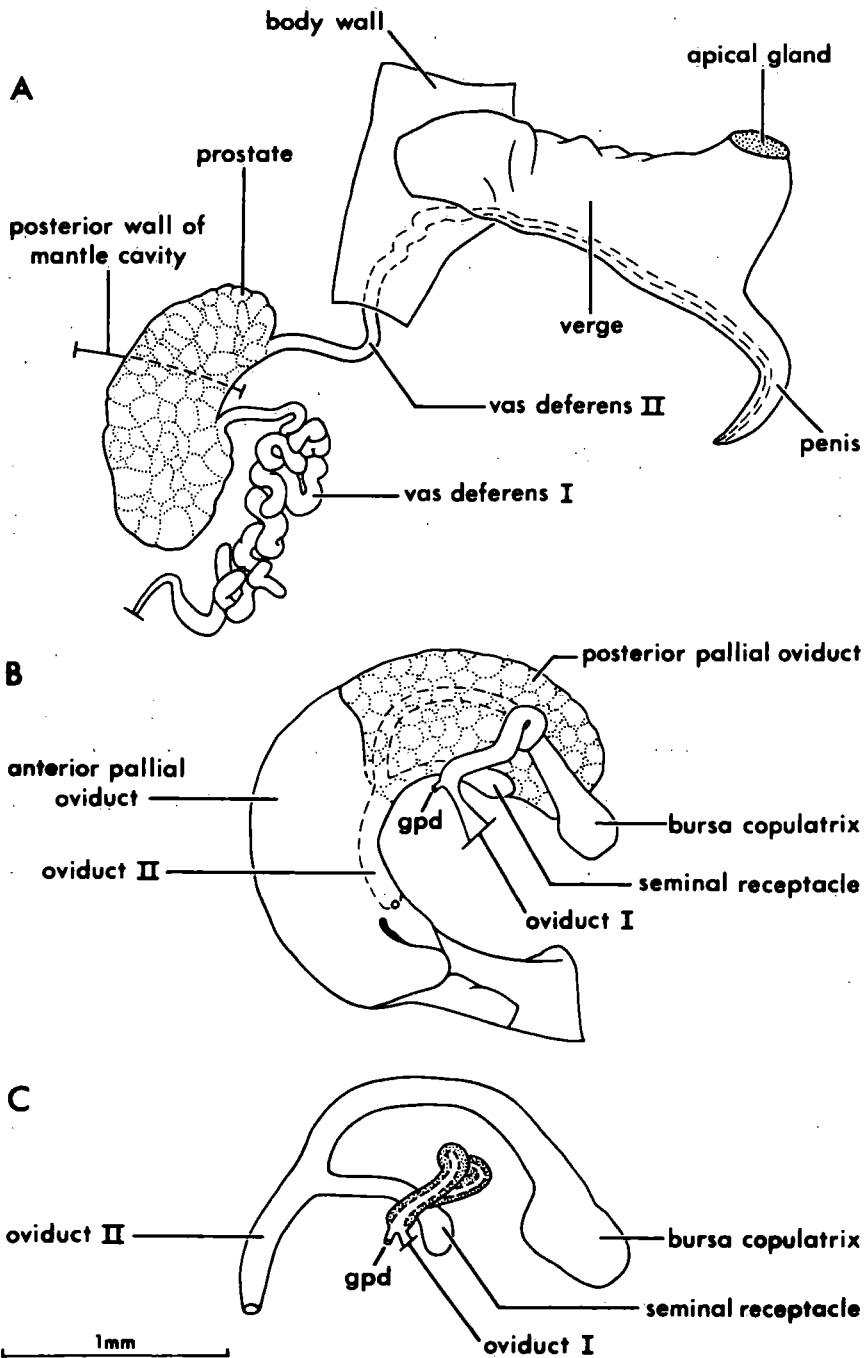
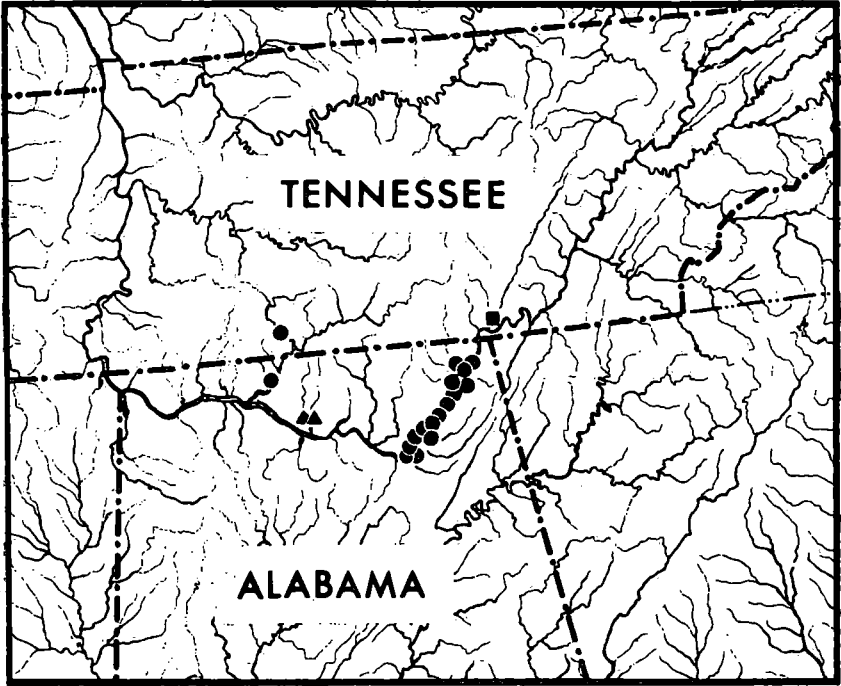


FIGURE 7.—*Marstonia arga* new species: (A) male reproductive system; (B) female reproductive system intact except for the ovary; (C) oviduct and associated structures freed from the pallial oviduct; gpd = gonopericardial duct.



▲ pachyta ● arga ■ ogmorhapse

FIGURE 8.—The geographic distribution of *Marstonia* in the Tennessee River System.

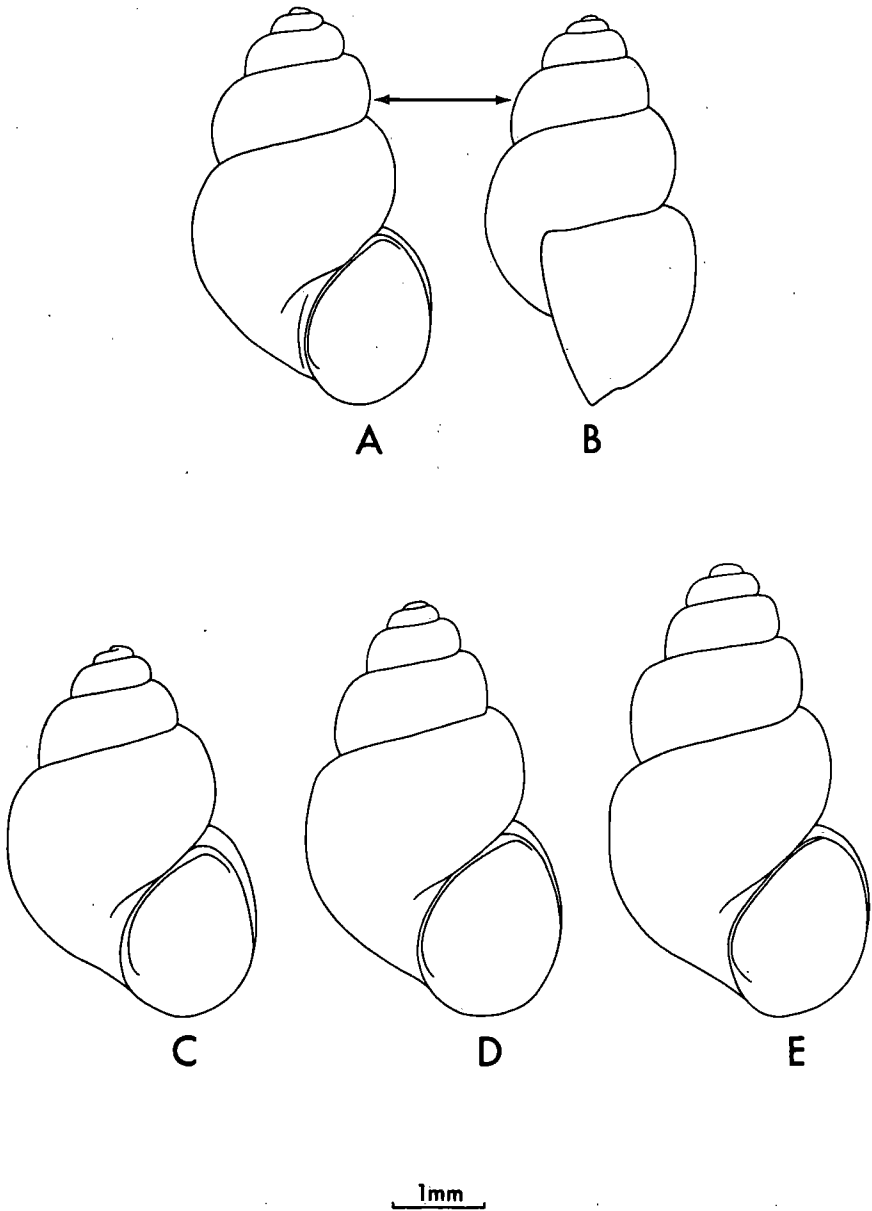


FIGURE 9.—*Marstonia ogmorhaphae* new species: (A, B) HOLOTYPE (UF 22179); (C-E) PARATYPE (UF 22180).

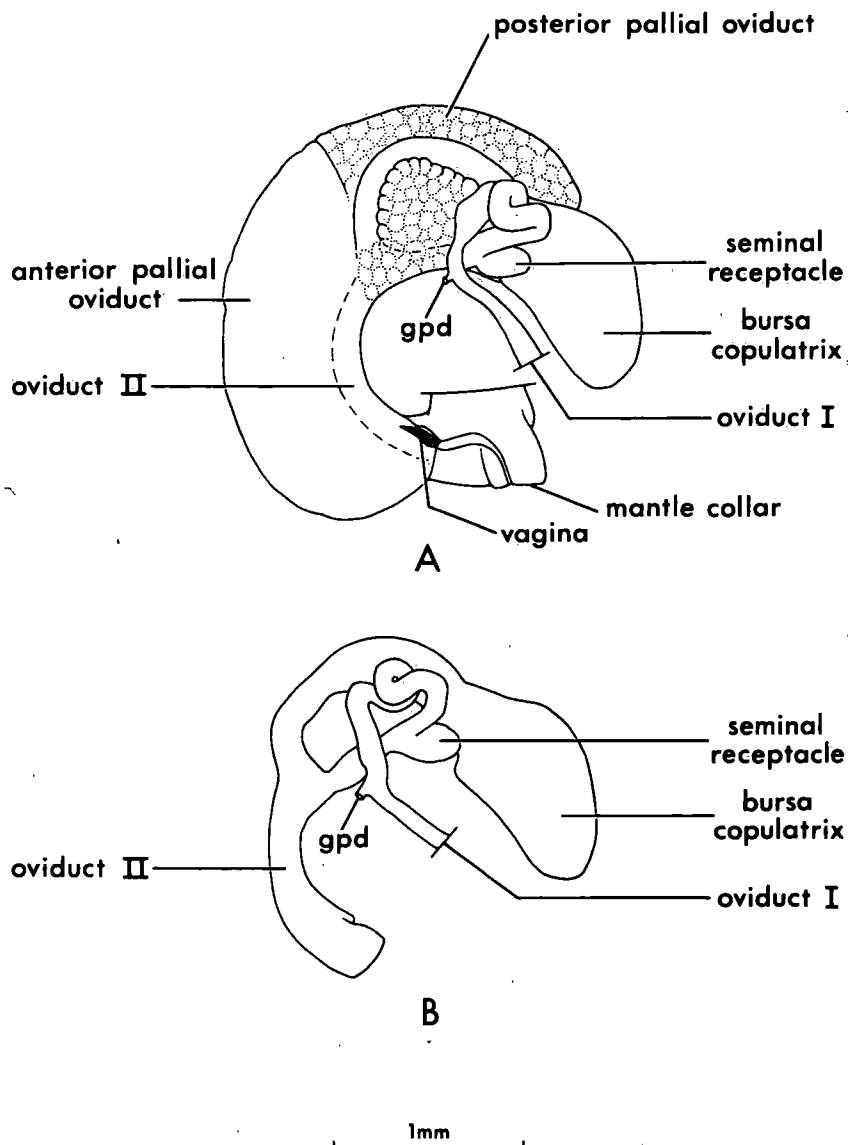


FIGURE 10.—*Marstonia ogmorhappe* new species: (A) female reproductive system; (B) oviduct and associated structures freed from the pallial oviduct; gpd = gonopericardial duct.

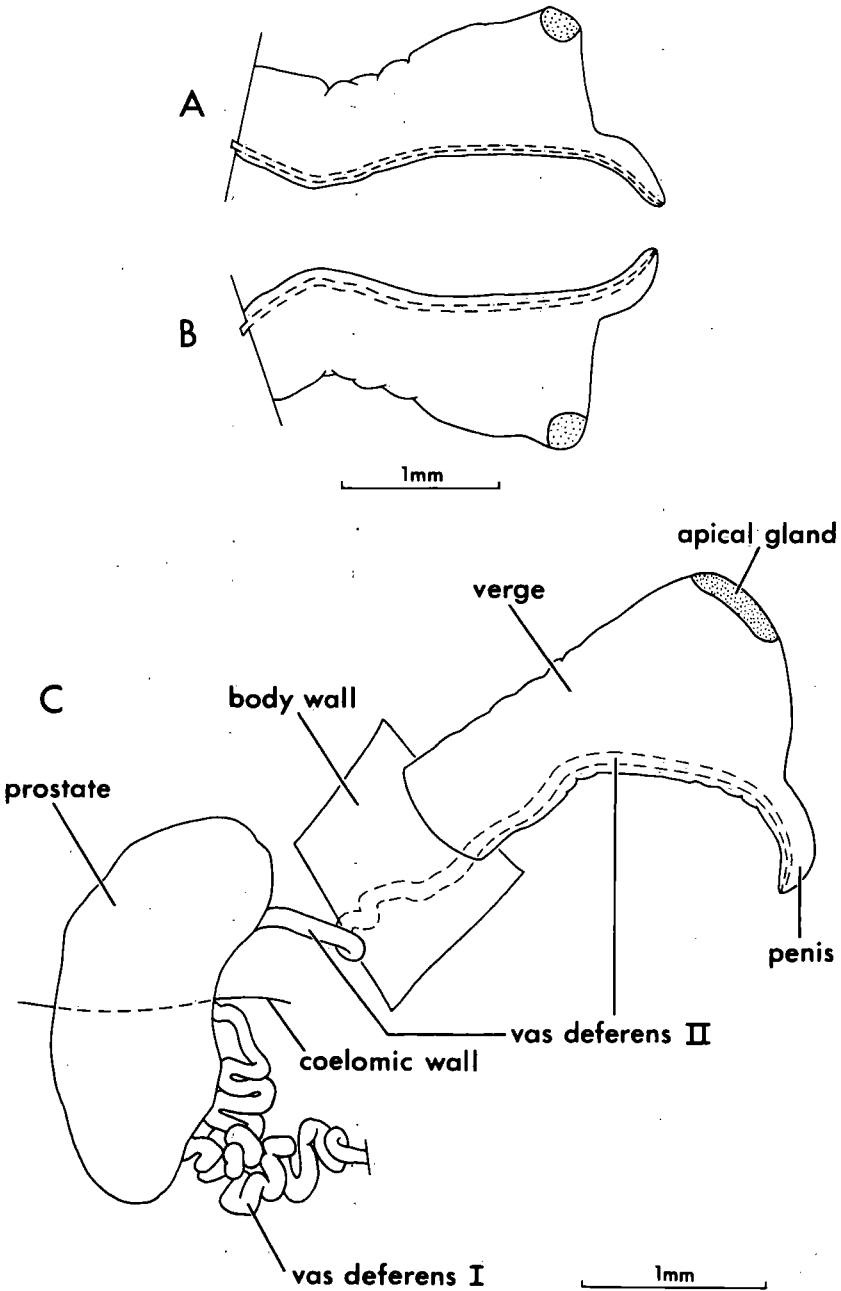


FIGURE 11.—*Marstonia ogmorhaphæ* new species: (A) verge, lateral surface; (B) verge, mesad surface; (C) male reproductive system.

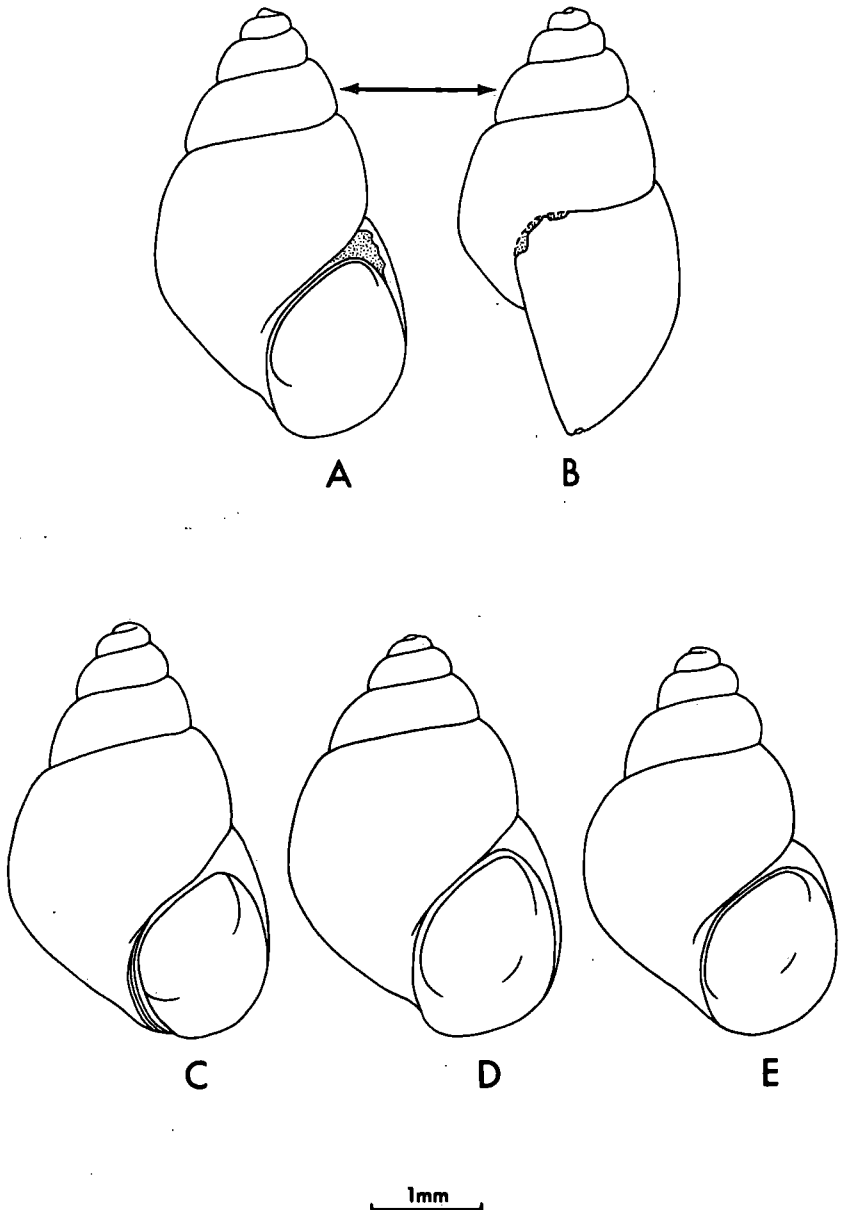


FIGURE 12.—*Marstonia pachyta* new species: (A, B) HOLOTYPE (UF 22222); (C-E) PARATYPES (UF 22228).

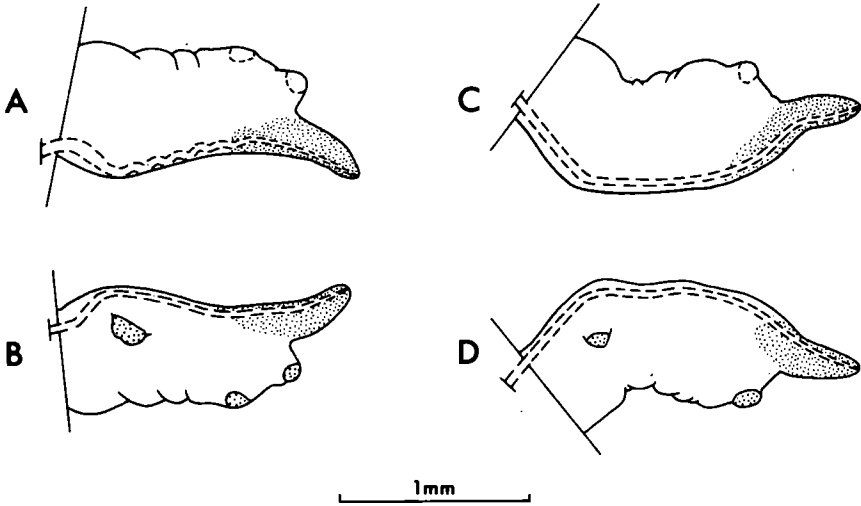


FIGURE 13.—*Marstonia pachyta* new species. Verges of two males from the type locality.

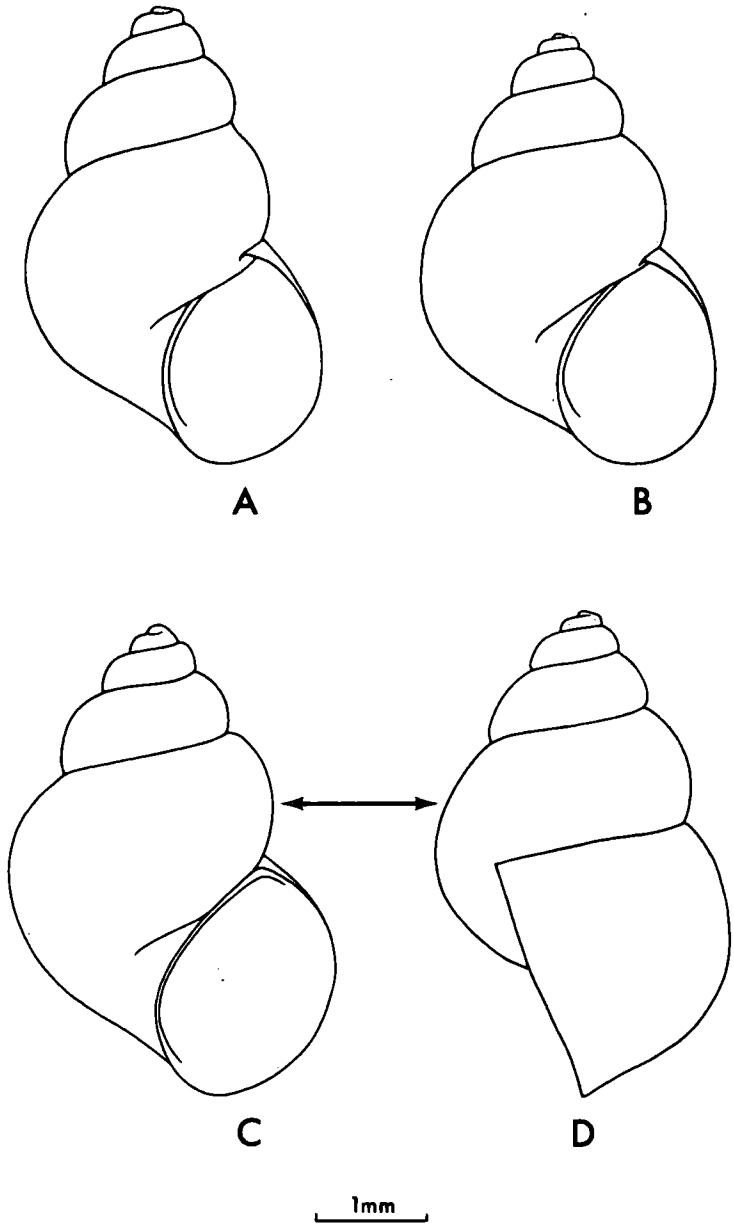


FIGURE 14.—*Marstonia olivacea* (Pilsbry): (A-D) PARATYPES (ANSP 65460).

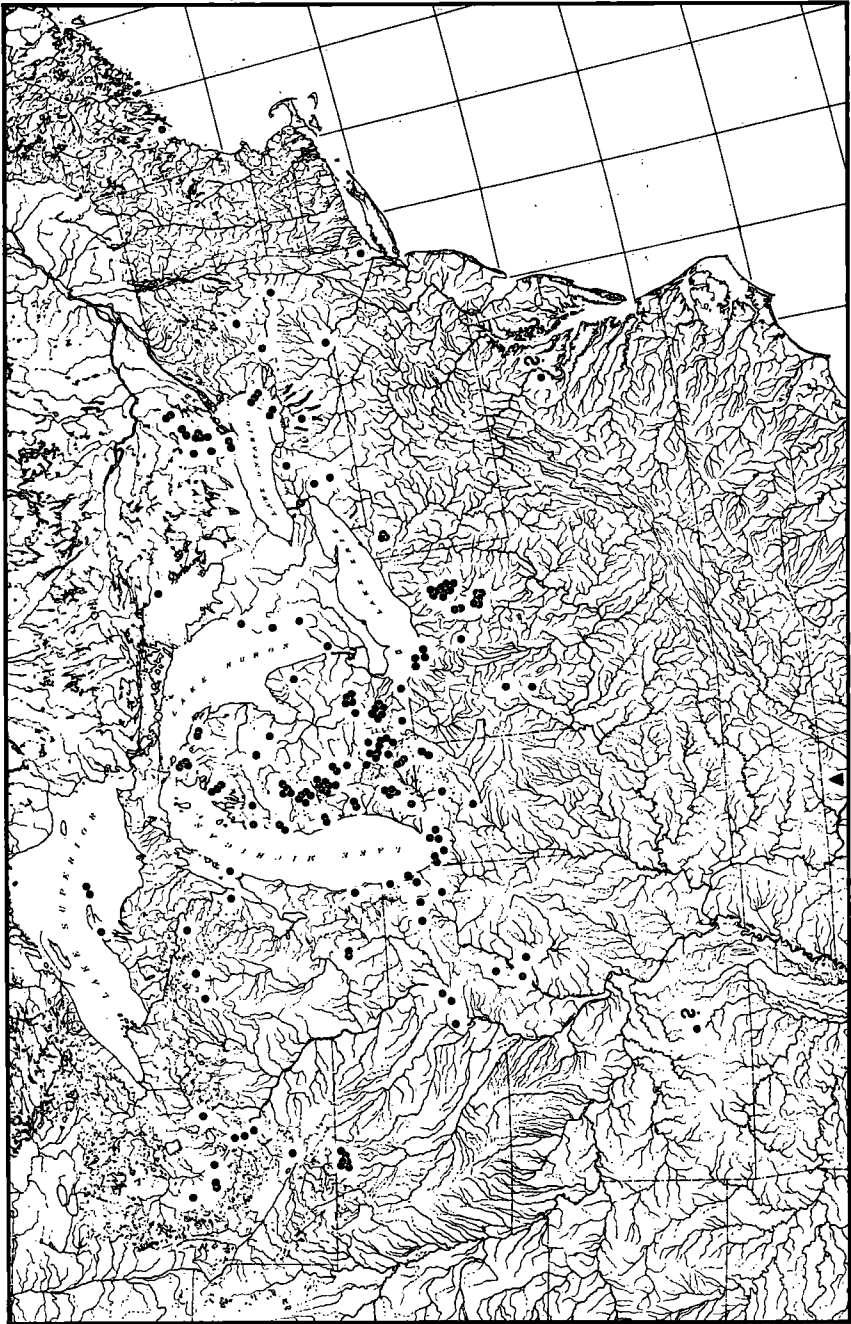


FIGURE 15.—The geographic distribution of *Marstonia lustrica* (Pilsbry) (circles) and *Marstonia olitacea* (Pilsbry) (triangle).

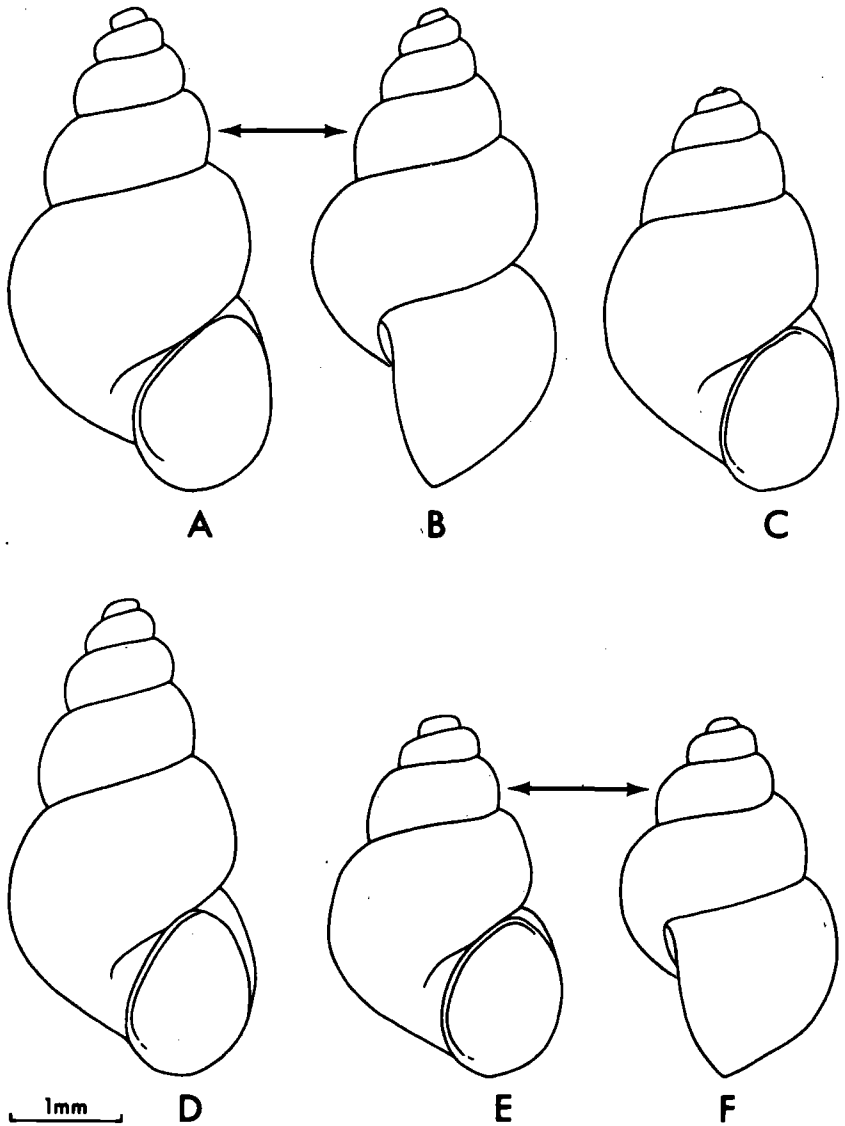
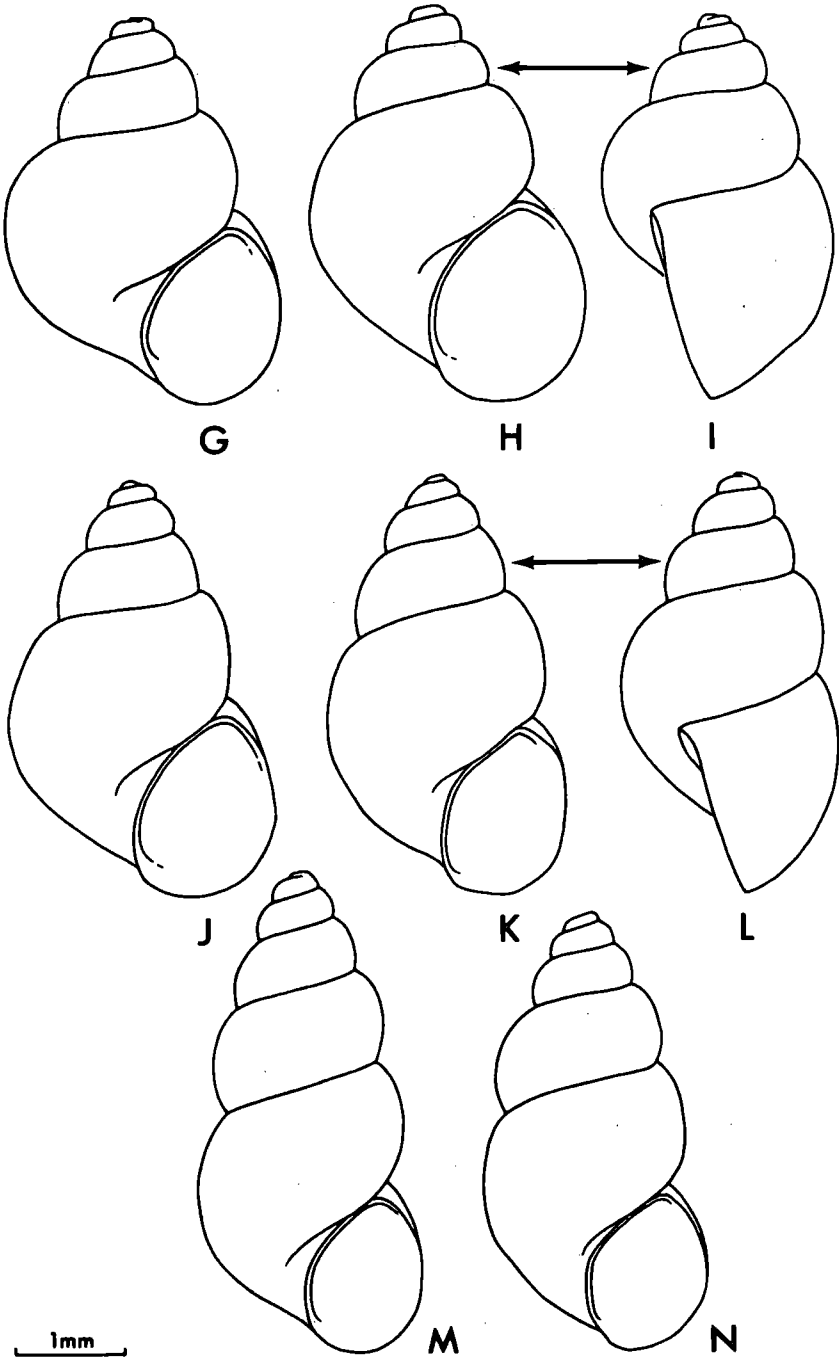


FIGURE 16.—*Marstonia lustrica* (Pilsbry): (A-F) lake, Newaygo Co., Michigan (UF 22190); (G-J) Cedar Swamp, Champaign Co., Ohio (UF 22223); (K-N) Turkeyfoot Lake, Summit Co., Ohio (UF 22225).



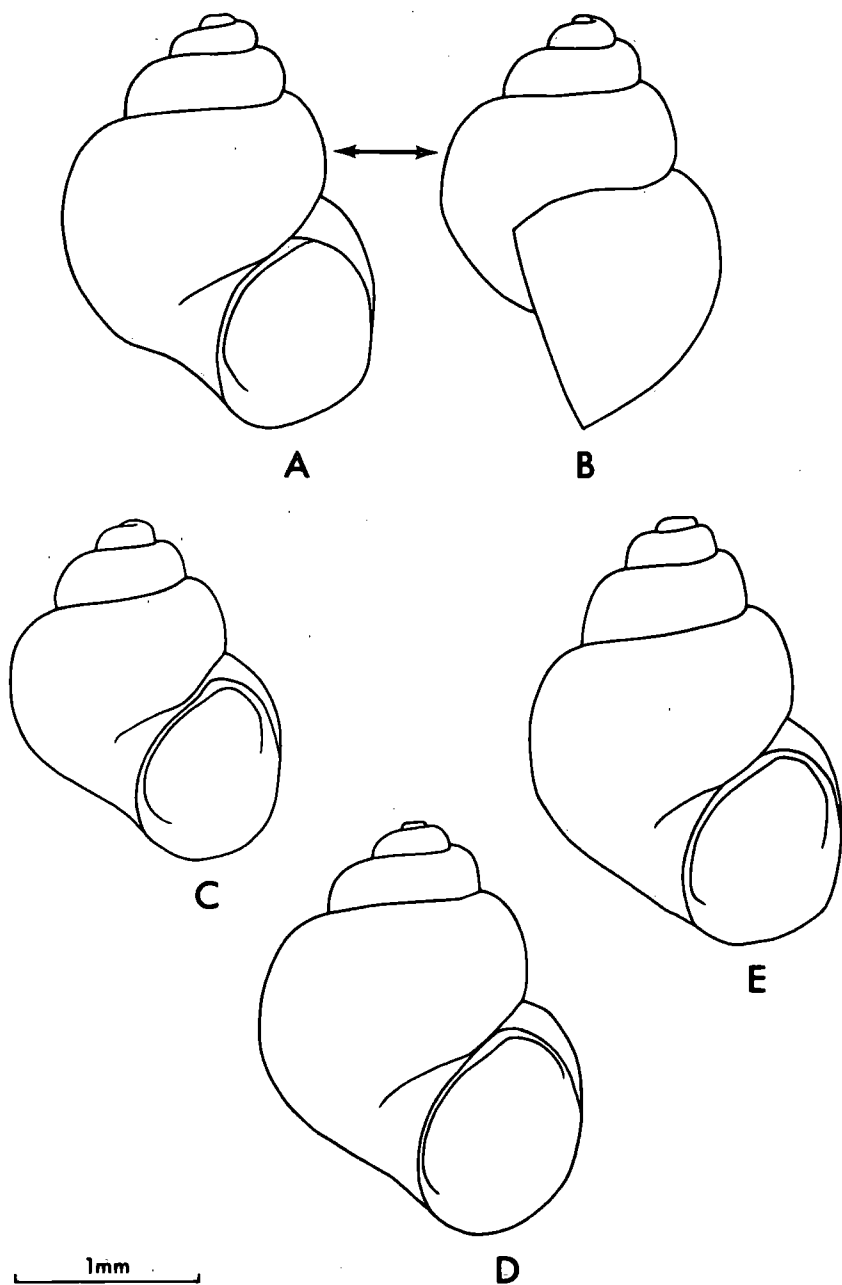


FIGURE 17.—*Marstonia halcyon* new species: (A, B) HOLOTYPE (UF 22312); (C-E) PARATYPES (UF 22311).

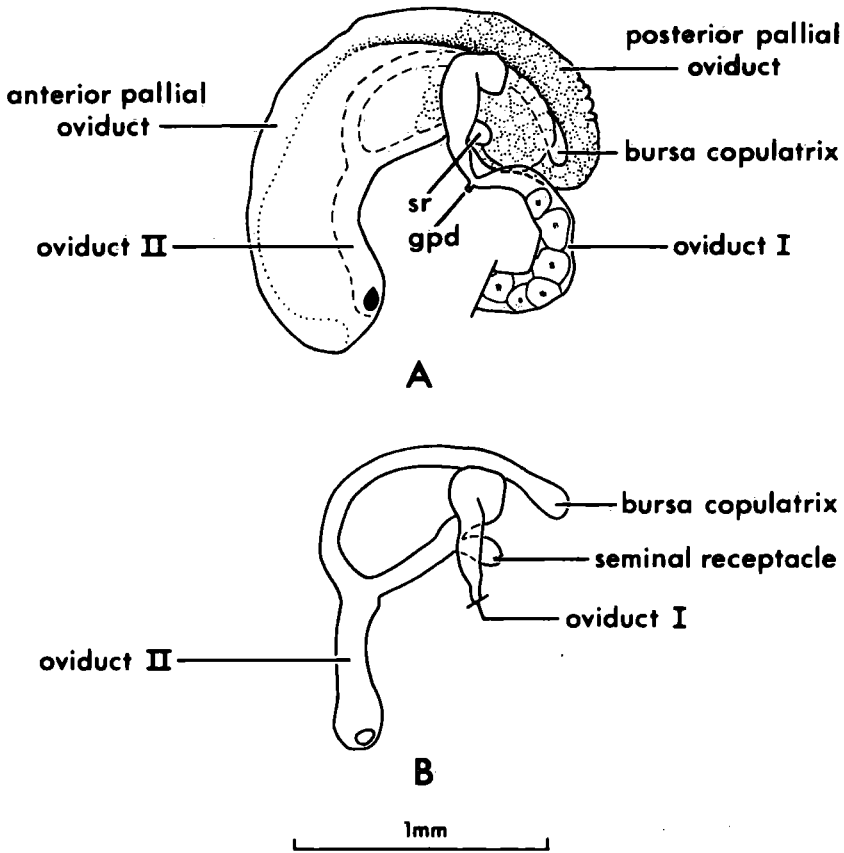


FIGURE 18.—*Marstonia halcyon* new species: (A) female reproductive system intact except for the ovary; gpd = gonopericardial duct, sr = seminal receptacle; (B) oviduct and associated structures freed from the pallial oviduct.

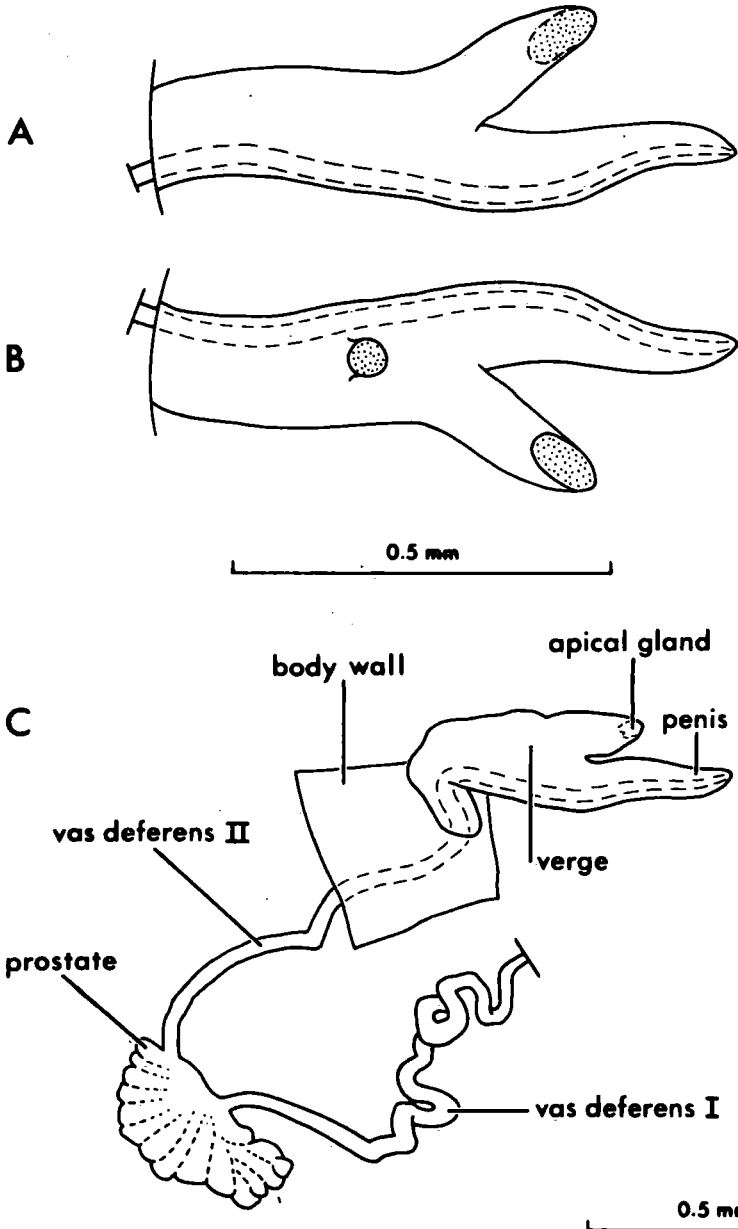
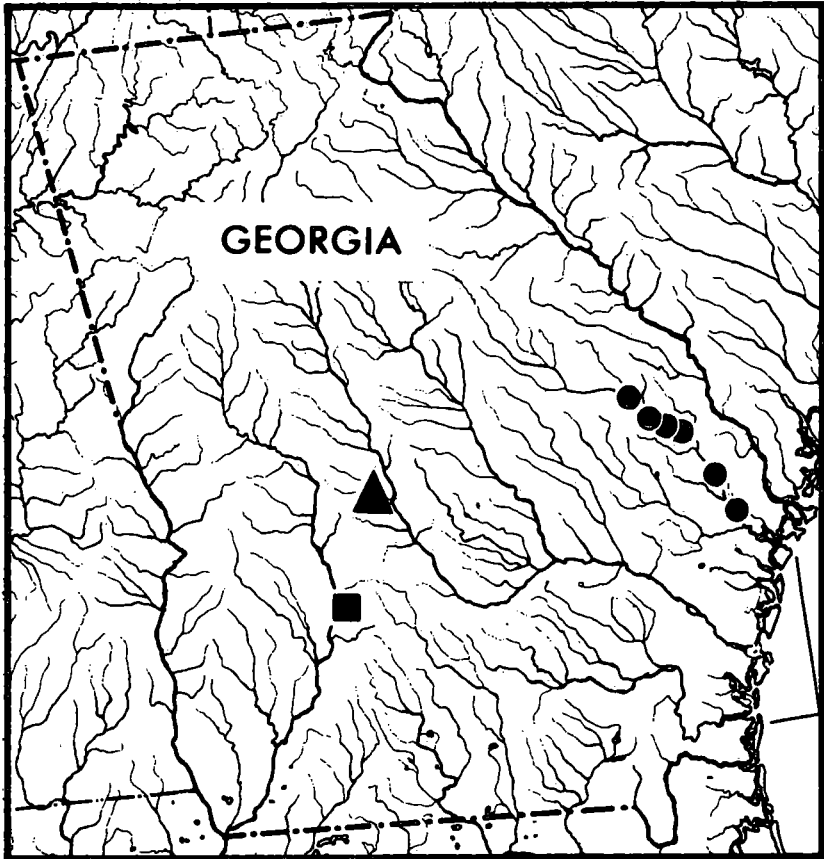


FIGURE 19.—*Marstonia halcyon* new species: (A) lateral view of verge; (B) mesad view of verge; (C) male reproductive system exclusive of the testis.



● halcyon

▲ agarhecta

■ castor

FIGURE 20.—The geographic distribution of *Marstonia* in the southeast coastal drainages.

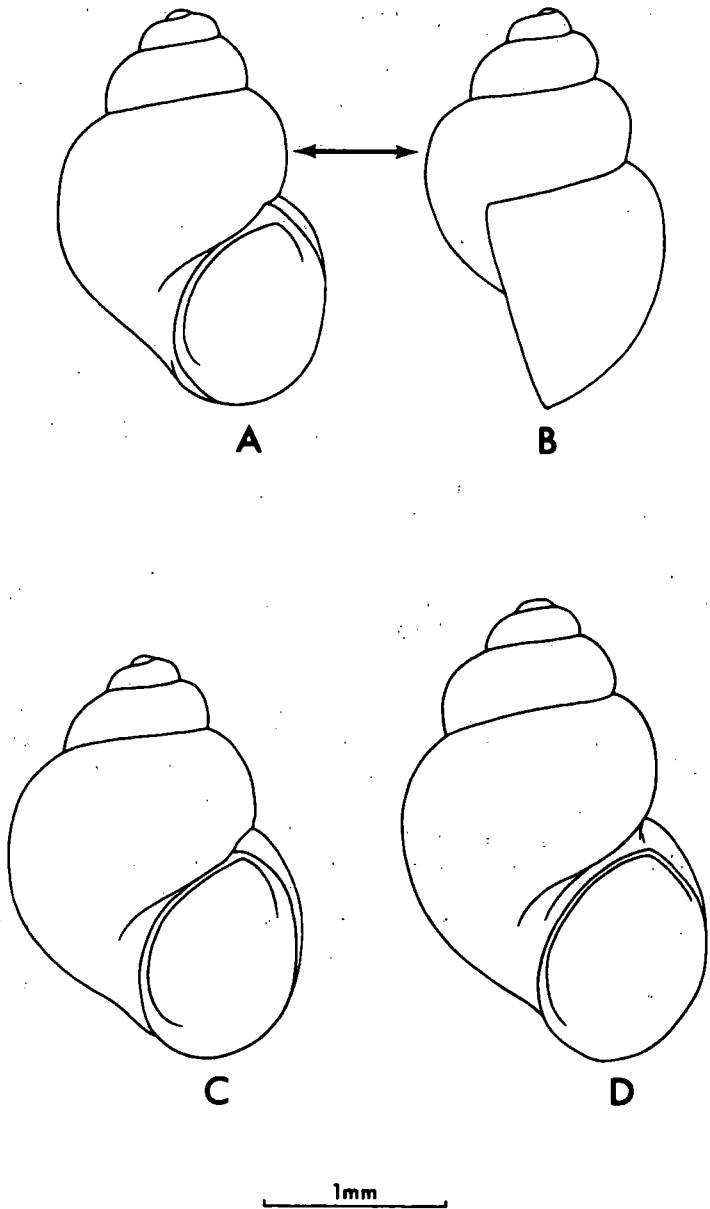


FIGURE 21.—*Marstonia castor* new species: (A, B) HOLOTYPE (UF 22176); (C, D) PARATYPES (UF 22177).

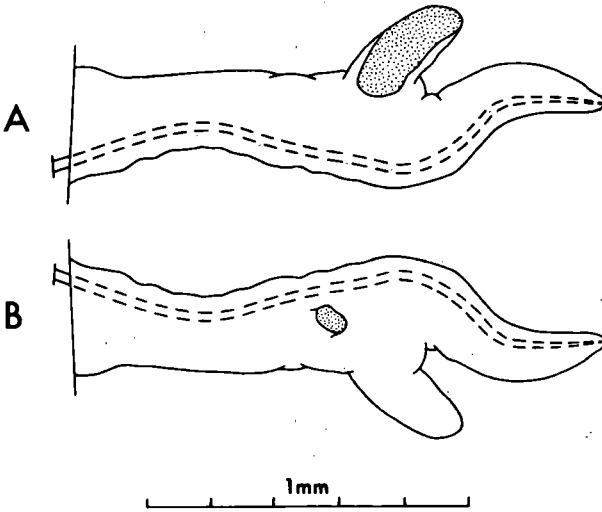


FIGURE 22.—*Marstonia castor* new species. Verge of male: (A) lateral surface; (B) mesad surface.

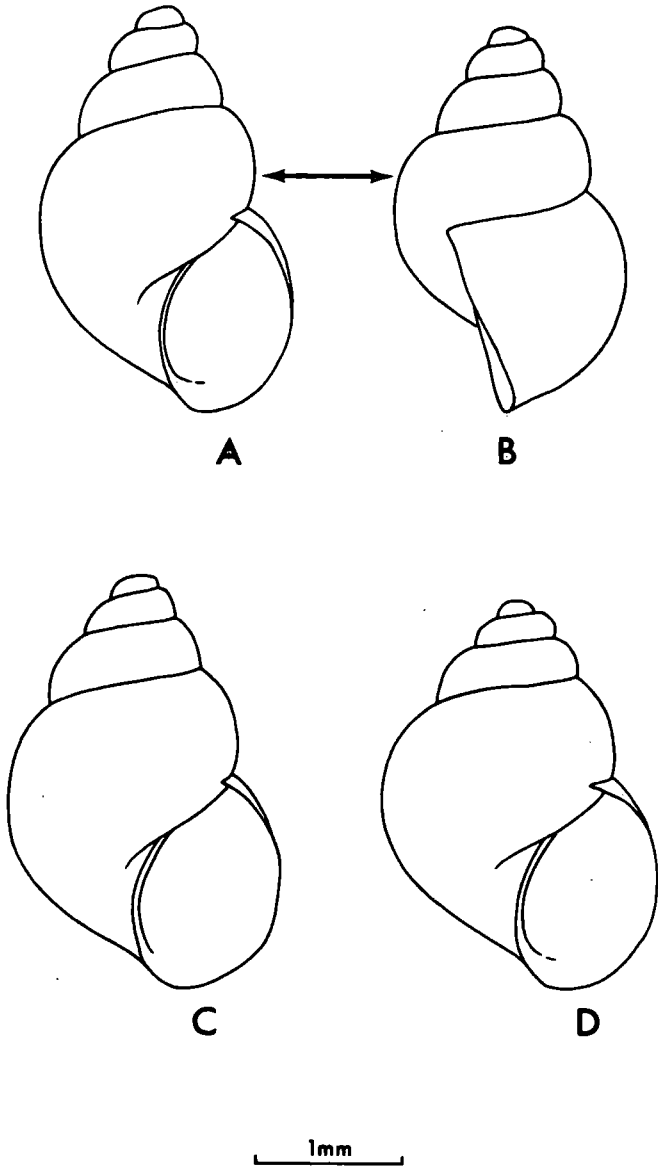


FIGURE 23.—*Marstonia agarhecta* Thompson: (A, B) HOLOTYPE (UF 20528); (C, D) PARATYPES (UF 20529).

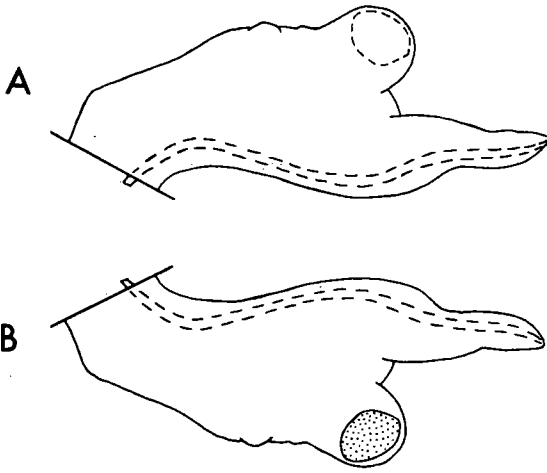


FIGURE 24.—*Marstonia agarhecta* Thompson. Verge of male: (A) lateral surface; (B) mesad surface.

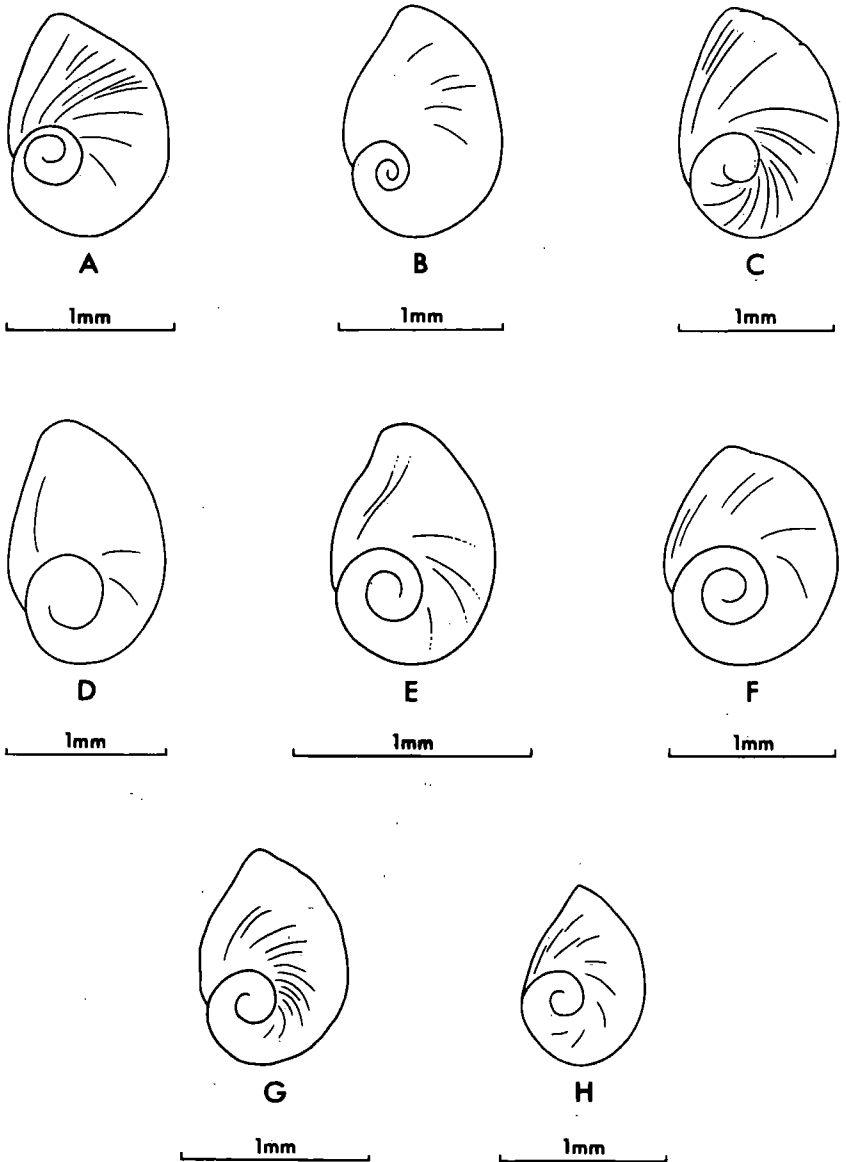


FIGURE 25.—*Marstonia opercula*: (A) *M. lustrica* (Pilsbry); (B) *M. argu* new species; (C) *M. ogmorhapse* new species; (D) *M. pachyta* new species; (E) *M. custor* new species; (F) *M. olivacea* (Pilsbry); (G) *M. halcyon* new species; (H) *M. agarhecta* Thompson.

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