

NORTH AMERICAN FRESHWATER SNAIL GENERA
OF THE HYDROBIID SUBFAMILY LITHOGLYPHINAE

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ABSTRACT

The classification of the North American genera of Lithoglyphinae is reviewed, based on anatomical and conchological characters. Five genera are recognized: *Gillia* Stimpson, 1865, *Fluminicola* Stimpson, 1865, *Somatogyrus* Gill, 1863, *Clappia* Walker, 1909, and *Lepyrium* Dall, 1896. The North American genera are conservative in their anatomies. Primary morphological differentiations involve radular and shell characters. The North American genera are demonstrated to have evolved through trophic specializations and microhabitat specializations.

Lepyrium Dall, 1896, formerly considered a monotypic family, is closely related to *Clappia* and *Somatogyrus*. *Birgella* Baker, 1926, is removed from the Lithoglyphinae, where it has been placed by authors, and is demonstrated to be in the Nymphophilinae. The following species are described in detail: *Lepyrium showalteri* (Lea, 1861), *Somatogyrus rheophilus* n. sp., *Gillia altilis* (Lea, 1841). A neotype is designated for the latter species.

Key words: Gastropoda, snails, Hydrobiidae, Lepyriidae, Lithoglyphinae, *Lepyrium*, *Clappia*, *Somatogyrus*, *Gillia*, *Fluminicola*, systematics, evolution.

INTRODUCTION

This paper discusses the systematic relationships between the North American lithoglyphine genera: *Lepyrium*, *Somatogyrus*, *Clappia*, *Gillia*, and *Fluminicola* (Class GASTROPODA, Subclass PROSOBRANCHIA, Order MESOGASTROPODA, Family HYDROBIIDAE, Subfamily LITHOGLYPHINAE). A sixth genus, *Antrobia* Hubricht, 1972, is placed by Burch & Tottenham (1980: 100) in the Lithoglyphinae. It is a monotypic genus from a cave in Missouri; the anatomy remains undescribed and *Antrobia* is omitted from further discussion in this paper. Another genus, *Cochliopina* Morrison, 1946, traditionally has been associated with the Lithoglyphinae. Hershler (in press) shows that it is a genus of the Littoridininae. *Birgella* Baker, 1926, is another genus that has been confused with this subfamily, even as recently as 1981 (Clarke). It is in the NYMPHOPHILINAE, as is discussed in Appendix B.

This study stems from two independent investigations. The first was an attempt to determine species-group characteristics within *Somatogyrus*, a genus containing many species (Burch & Tottenham, 1980: 104-106). The study was tabled temporarily because very little anatomical diversity was discovered among the species examined. Independently I examined the anatomy of *Lepyrium showalteri* (Lea), a snail previously

placed in a monotypic family of uncertain affinity within the MESOGASTROPODA (Pilsbry & Olsson, 1951). Its soft anatomy was found to be hardly distinguishable from that of *Somatogyrus*. These two genera have very dissimilar shells, but they have in common similar habitats. *Lepyrium* and most *Somatogyrus* live on rocks and boulders in high-energy rivers. The habitat deployments among these two genera focus on the adaptive radiation of the Lithoglyphinae in eastern North America. In order to clarify the limits of this basic radiation other relevant genera were examined. The results of these studies are presented herein.

MATERIAL AND METHODS

Anatomical descriptions and illustrations in this paper are based upon the following specimens:

Lepyrium showalteri (Lea). Two lots of about 100 specimens each, collected June 21, 1978 (UF 31343) and June 22, 1978 (UF 31342) in the Little Cahaba River, 2.4 km upstream from the Cahaba River, Bibb Co., Alabama by F.G.T. Relaxed with menthol crystals, fixed in Bouin's solution and preserved in 70% ethanol.

Somatogyrus rheophilus n. sp. (described below). One series of thousands of speci-

mens collected October 21, 1973, in the Flint River, 9.7 km SW of Lincoln Park, Upson Co., Georgia by F.G.T. (UF 40511). Relaxed with menthol crystals, fixed in Bouin's solution and preserved in 70% ethanol.

Gillia altilis (Lea). One series of about 400 specimens collected June 1, 1980 in Lake Waccamaw, Columbus Co., North Carolina by Hugh J. Porter (UF 27550). Fixed unrelaxed and preserved in 70% ethanol.

Fluminicola nuttalliana (Lea). One series of 23 specimen collected July 20, 1974 in the Satsop River at Satsop, Grays Harbour Co., Washington by Dennis R. Paulson (UF 34813). Fixed unrelaxed and preserved in 70% ethanol.

Dissections were made in 70% ethanol under a WILD M-2 dissecting microscope. Serial sections were made at 10 μ m and stained in 10% Harris' hematoxylin stain. Radulae were cleaned in a saturated solution of potassium hydroxide and examined with a HITACHI S-415A scanning electron microscope at the Department of Zoology, University of Florida.

Museum abbreviations are given in Appendix C.

ANATOMY OF THE GENERA

The genera *Lepyrium*, *Clappia*, *Somatogyrus*, *Gillia* and *Fluminicola* are placed in the subfamily LITHOGLYPHINAE. The conical, or depressed-conical, or globose-conical, or neritoid-shaped shells have in common spiral sculpture on the protoconch (Figs. 39–42). Other protoconch sculpture may also be present. Other aspects of the shell are not distinctive at the subfamily levels among North American hydrobiid genera, although the lithoglyphines tend to be stocky species with relatively heavy shells.

A high degree of anatomical uniformity exists among the North American LITHOGLYPHINAE. Principal morphological differences occur in trophic structures and in the shell. Minor diversity also occurs in the male and female reproductive systems. Because of this basic uniformity it is convenient to describe the anatomy of *Lepyrium* and compare other genera with it.

Lepyrium Dall, 1896

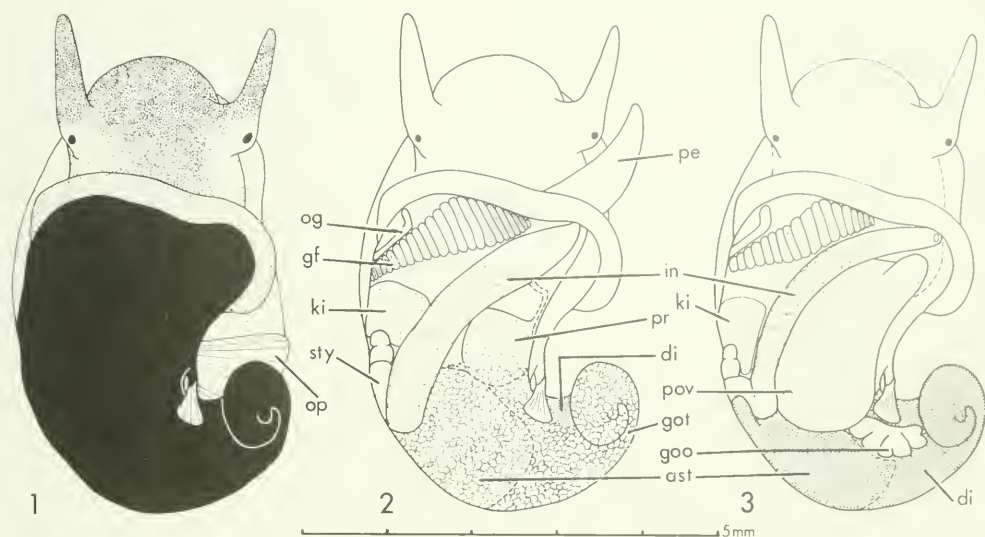
Lepyrium is a monotypic genus endemic to the Coosa and Cahaba Rivers in Alabama where it lives on boulders in high energy

shoals. *Lepyrium showalteri* (Lea) is described in detail because its systematic affinities have been in question since it was discovered. Its shell is described in Appendix A. The shell (Figs. 59–62) is peculiar because it has a depressed spire and an expanded, flattened body whorl, giving it a neritid appearance. The first whorl of the protoconch is smooth, except for a few short spiral furrows below the periphery (Fig. 39). The neomelanian type operculum (Fig. 7) is modified in shape to conform to the enlarged aperture. This is accomplished by rapid expansion of the last whorl from the paucispiral nucleus, a minor elaboration of the basic condition that also exists in *Somatogyrus* and *Gillia* (Fig. 52). Its radular teeth are modified for feeding on small-sized food particles. *Lepyrium* is the most divergent of the North American LITHOGLYPHINAE because of these specializations. Other aspects of its anatomy are conservative and indicate a close relationship to *Clappia* and *Somatogyrus*.

External morphology and color. Foot broad and rounded (Figs. 1–3). Operculigerous lobe overlaps on each side, and edge of operculum overlaps extended foot on left side and posteriorly. Mucous groove present along anterior edge of foot. Food grooves and epitaelial folds absent on body and snout. Columellar muscle extending into shell for about a quarter whorl. Columella muscle insertion short but wide, extending transversely nearly the complete width of body whorl (in other genera the insertion is narrower). Mantle collar complete around body, without tentacles or papillae. Mantle cavity of males semicircular in saggital section; triangular in females, bounded posteriorly by pallial gonoduct, pericardium and stomach. Gill (gf) consisting of 19–20 lamellae that are arranged in an oblique series on mantle wall. Lamellae triangular in shape (Fig. 8), with greatest height along intestine. Osphradium (og) long, narrow, L-shaped. Excurrent and incurrent siphons absent. Kidney small, broadly quadrangular, overlying posterior left corner of mantle cavity.

Tentacles long and slender in life, and actively beat substrate in alternate strokes as animal moves about. Snout highly extendable and constantly sampling substrate in moving animal.

Mantle jet black (Fig. 1) on all surfaces, completely opaque to all internal morphology. Snout and tentacles dark gray, fading posteriorly and laterally to light gray on sides of body



FIGS. 1-3. *Lepyrium showalteri* (Lea). Fig. 1. Specimen denuded of shell showing pigmentation of mantle. Fig. 2. Male with melanin removed showing internal anatomy. Fig. 3. Female with melanin removed showing internal anatomy. Legend: ast = anterior chambers of stomach; di = digestive gland; gf = gill filaments; goo = ovary; got = testis; in = intestine; ki = kidney; og = osphradium; op = operculum; pe = penis; pov = pallial oviduct; pr = prostate; sty = style sac.

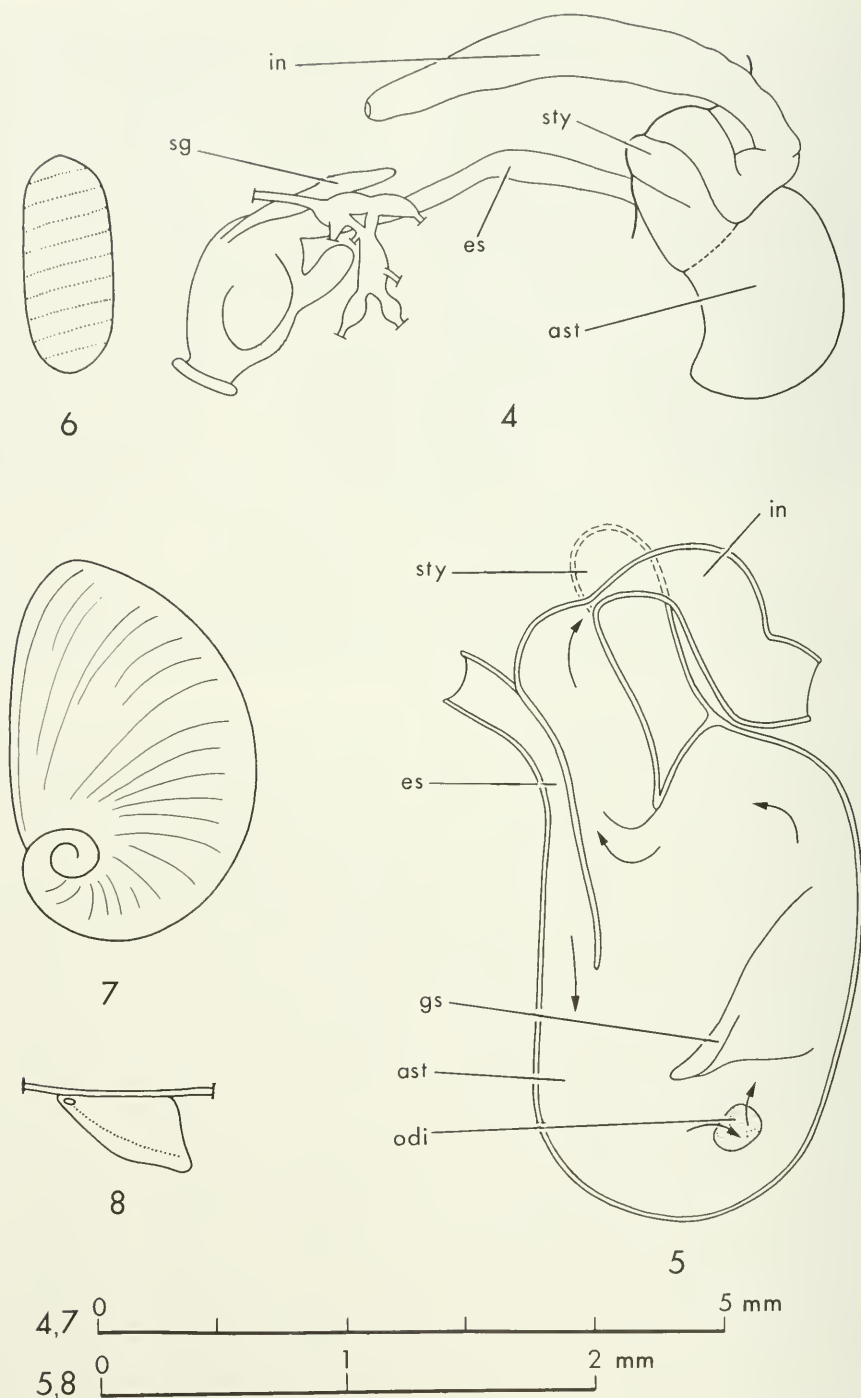
and nape. Tentacles also with diffuse, scattered xanthophores. Sole very light gray. Center of muzzle white. Penis white.

Digestive system. Typically hydrobioid in its configuration (Fig. 4). Two elongate claviform salivary glands (sg) enter posterior buccal mass along dorso-lateral edges, and extend posteriorly over top of nerve ring. Oesophagus (es) entering stomach on left side of posterior chamber (Fig. 5, ast). Stomach with a single opening into digestive gland (odi) posterior to gastric shield (gs). Style sac (sty) slender, at anterior end of stomach on left dorso-lateral surface. Caecae absent. Intestine (in) leaving anterior chamber on left side, passing beneath style sac and up to mantle where it continues diagonally forward to right corner of mantle collar. Anterior end of stomach abutting against kidney, pericardium and pallial gonoduct. In females it is covered by the digestive gland (di) on all sides except anterior end and anterior half of outer wall. In males digestive gland is more restricted due to distribution of testes.

Fecal pellets (Fig. 6) cylindrical, tapered at both ends, and spirally coiled with 4-10 whorls. Pellets about 0.40-0.57 mm long and 0.15-0.20 mm wide. Pellets oblique in intestine at about 45° to longitudinal axis of body.

Radula. Taenioglossate (Figs. 15-18, about 1.8 mm long, containing 140-149 transverse rows of teeth (7 specimens examined). Cusps rapidly worn, barely distinguishable on distal third of ribbon. Central tooth (Fig. 15) about 130 μ m wide, broadly trapezoidal in shape with a long mid-basal projection; lateral angles with a low ridge bearing 9-11 small, nearly uniform, acuminate basocones on each side (Fig. 16), in contrast to allied genera in which the basocones are enlarged toward the top of the series; dorsal margin weakly reflected with a slightly enlarged mesocone, and 22-24 ectocones on each side. Lateral tooth (Fig. 17) with a long, narrow, laterally projecting, flexed shaft and a strong slender cusp-like basal projection on face of tooth; laterals with 18-22 nearly uniform acuminate cusps. Inner marginals weakly sigmoid with about 50 small cusps. Outer marginals long, slender, with about 35 very small cusps (Fig. 18).

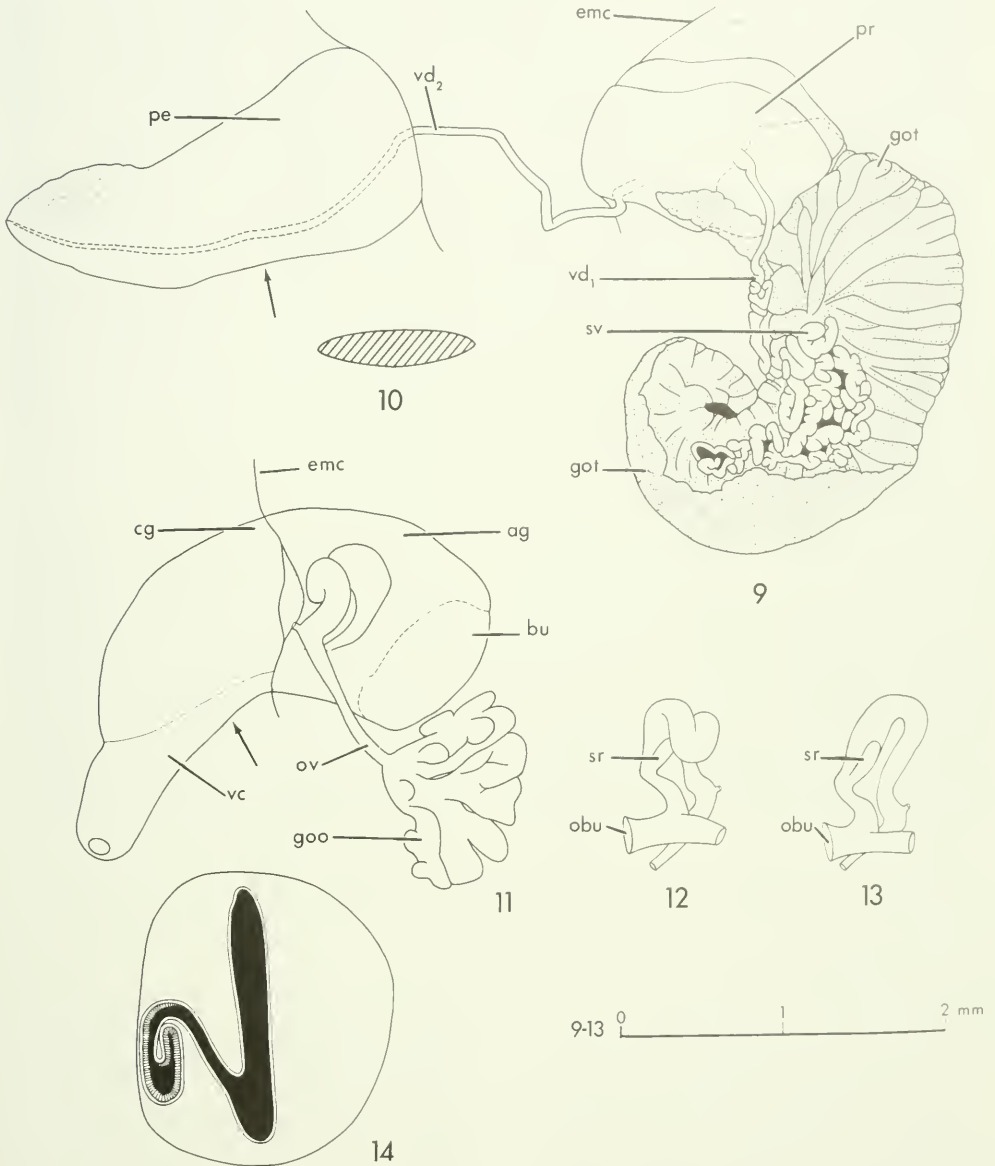
Female reproductive system. (Figs. 3, 11). Ovary (goo) consisting of 3-4 large subequal lobes, each of which is partially divided into smaller lobules. Ovary lying against posterior surface of pallial oviduct (bursa copulatrix) and along right side of stomach, but separated from latter by a thin zone of digestive gland tissue (di); ovary not occupying apical



FIGS. 4-8. *Lepyrium showalteri* (Lea). Fig. 4. Lateral view of digestive system excluding digestive gland. Fig. 5. Ventral view of stomach interior. Fig. 6. Fecal pellet. Fig. 7. Operculum. Fig. 8. Single lamella of gill. Legend: ast = anterior chamber of stomach; es = esophagus; gs = gastric shield; in = intestine; odi = opening to digestive gland; sg = salivary glands; sty = style sac.

whorl of digestive gland. Primary oviduct (ov) relatively stout, passing diagonally forward along ventral side of digestive gland, then mesad to right of oesophagus and style sac and along pericardium at junction of latter with

pallial oviduct. A very short gonopericardial duct is present. Primary oviduct enlarging and forming a loop along mesad side of albumen gland; top of loop folded down between rest of loop and albumen gland (Fig. 11). A short



FIGS. 9-14. *Lepyrium showalteri* (Lea). Fig. 9. Male reproductive system. Fig. 10. Diagrammatic cross-section of penis at arrow in 9. Fig. 11. Female reproductive system. Fig. 12. Right side of coil of primary oviduct. Fig. 13. Coil of primary oviduct unfolded to show seminal receptacle. Fig. 14. Cross-section of pallial oviduct at arrow in 11. Legend: ag = albumen gland; bu = bursa copulatrix; cg = capsule gland; emc = posterior wall of mantle cavity; goo = ovary; got = testis; obu = bursa copulatrix duct; ov = oviduct; pe = penis; pr = prostate; sr = seminal receptacle; sv = seminal vesicle; vc = ventral channel; vd₁ = proximal vas deferens; vd₂ = distal vas deferens.

narrow seminal receptacle (sr) projects upward on albumen gland side of descending limb of loop, and is partially covered by the loop so that it can be viewed only by serial section or by teasing the loop free from the albumen gland and unfolding the loop (Figs. 12–13). Seminal receptacle about 140 μm long. Descending segment of loop entering albumen gland (ag) where it forks to form ventral canal (vc) of pallial oviduct (pov) leading forward to vagina, and a short broad duct leading posteriorly to bursa copulatrix (bu). Bursa copulatrix large and saccate, lying against posterior end of albumen gland. Ventral canal spiral in cross-section (Fig. 14), and continuous with lumen of capsule gland (cg). Albumen gland and capsule gland intricately coalesced to ventral canal, and together form the pallial oviduct. Pallial oviduct confined postero-laterally by posterior wall of mantle cavity (emc); irregularly pyriform in shape when viewed from above; bounded along its left side by intestine. Pallial oviduct terminating within mantle cavity just posterior to mantle collar and anus. Capsule gland and albumen gland not clearly differentiated superficially. Albumen gland occupying posterior third of pallial oviduct and consisting of tightly coalesced large glandular cells. Capsule gland consisting of smaller, and more compact cells. Ventral canal extending about a fourth of its length beyond anterior end of capsule gland.

Eggs laid singly in capsules on hard surfaces. Capsules hemispherical and attached to substrate by a narrow hyaline collar. Width of hemispherical capsule about 0.7 mm; width of collar about 0.05 mm; total width of capsule and collar about 0.8 mm.

Male reproductive system (Figs. 2, 9). Testis (got) very large and completely covering posterior 1.5 whorls; overlying entire digestive gland, stomach and posterior third of prostate; testis consisting of numerous lobes that subdivide into small lobules that form a marbled pattern on outer surface. Lobes discharging into the primary sperm duct which forms a highly convoluted seminal vesicle (sv) on ventral surface of testis; this continues into posterior vas deferens (vd_1). The latter bearing 3–4 sigmoid coils near its middle. Posterior vas deferens passing mesad across ventral surface of body beneath junction of stomach and prostate, and then upward along right margin of pericardium, oesophagus and style sac to enter ventral side of prostate (pr) near its middle. Prostate with a relatively deep

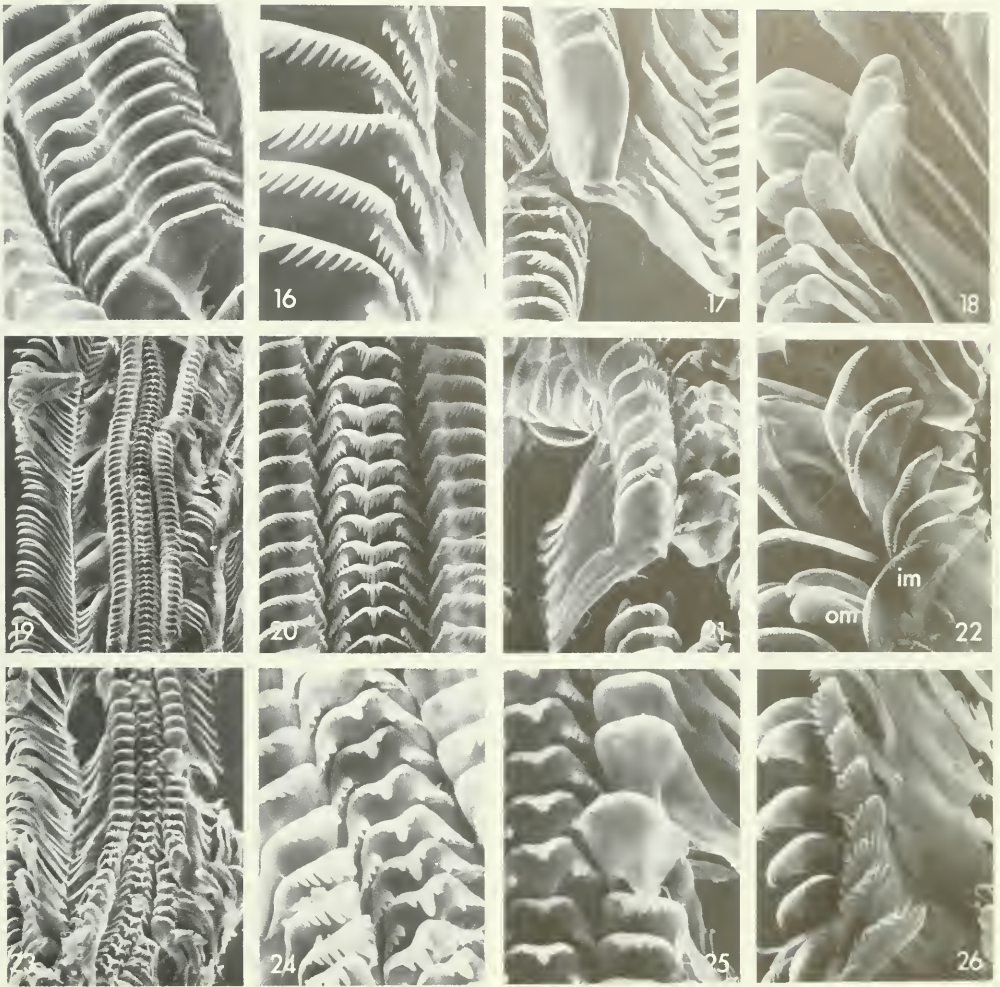
intestinal groove along its mesad curvature. Prostate completely posterior to transverse wall of mantle cavity (emc), but partially overlapping cavity. Anterior vas deferens (vd_2) leaving ventrocolumellar side of anterior edge of prostate, passing vertically down side of mantle cavity, and following an irregular sigmoid course across side of nape to base of penis (pe). Penis originating on right side of nape beneath mantle collar; long, flattened, blade-like, biconvex in cross section (Fig. 10) and unpigmented. When contracted, the penis is folded posteriorly and to the left within the mantle cavity. It bears a small patch of minute glands along its distal left margin on its ventral surface.

Clappia Walker, 1909

The genus was founded on a single species and was distinguished from *Somatogyrus* because of its open umbilicus (Fig. 68), its large opercular nucleus, and some characteristics of the radula. The sculpture of the protoconch remains unknown. The type-species, *C. clappi* Walker, 1909 (= *C. umbilicata* [Walker], 1904) from the Coosa River in Alabama apparently is extinct. A second species, *C. cahabensis* Clench, 1965, from the Cahaba River may also be extinct due to pollution from coal strip-mining in the area. Both species lived on high energy shoals.

External morphology and color. I have examined the dried bodies of 24 paratypes of *C. clappi* (ANSP 95037). The mantle is uniform black, similar to *Lepyrium* and most *Somatogyrus*. Walker (1909: 90) states that the animal is black. Presumably this refers to the foot, snout and nape, as well as the mantle. Dried males have a flattened, blade-like, unpigmented penis. Radulae were extracted from two specimens.

Radula. There are about 56–57 transverse tooth rows (Fig. 19). All teeth are characterized by having more numerous and smaller cusps than do those of *Somatogyrus*, but not to the extent that occurs in *Lepyrium*. Central tooth (Fig. 20) with moderately extended lateral angles; mesocone small, slender, acuminate, bordered on each side by 6–7 ectocones on a low ridge near outer edge of lateral angles; basocones subequal, gradually increasing in size dorsally. Lateral tooth (Fig. 21) with a strongly flexed, slender shaft; mesocone reduced in size, slender, bordered by 7–9 small entocones and 11–12 slender, subequal ectocones; basal projection long



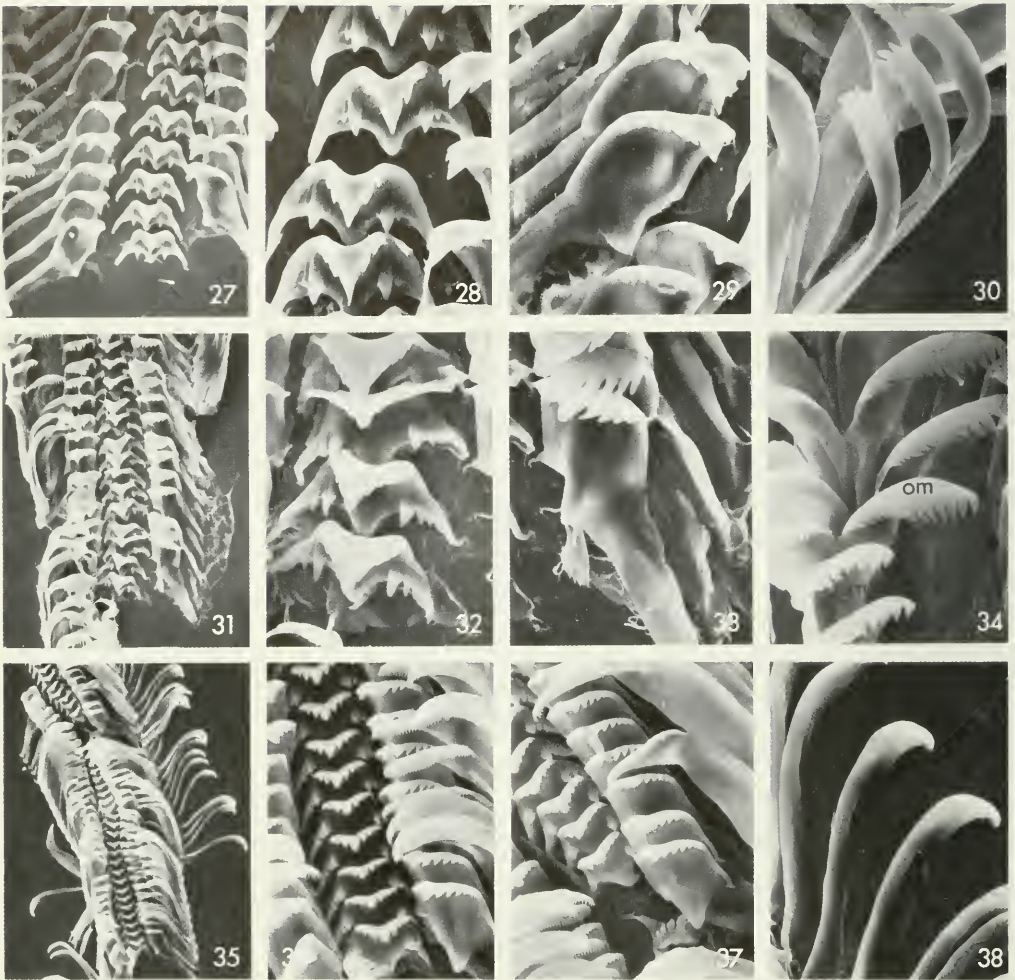
FIGS. 15–26. SEM photographs of radulae. Figs. 15–18. *Lepyrium showalteri* (Lea). Figs. 19–22. *Clappia umbilicata* (Walker). Figs. 23–26. *Somatogyrus depressus* (Tryon). Enlargements: Figs. 15, 17, 20, 21, 24, 25, 26 $\times 356$; Figs. 19, 23 $\times 95$; Figs. 18, 22 $\times 475$; Fig. 16 $\times 950$. Legends: im = inner marginal tooth; om = outer marginal tooth.

and slender. Inner marginal tooth (Fig. 22, im) with about 50 very small slender cusps. Outer marginal tooth (Fig. 22, om) with about 35 small slender cusps. Walker (1909: 89) stated that there are about 50, but the cusps are so small his count may have been only a rough approximation.

Somatogyrus Gill, 1863

The genus contains numerous species in eastern North America (Burch & Tottenham, 1980: 104–110). They have in common conical or ovate-conical shells 3–6 mm high. The

protoconch has numerous fine spiral threads. Punctate sculpture may occur in addition (Fig. 40). Walker (1915) stated that some species have pitted sculpture only. I have not been able to confirm this among the material I examined. The columella generally is thickened. The thickness and structure of the columella, and the nature of the umbilicus provide useful characteristics for grouping species. The soft anatomy of the type-species, *S. depressus* Tryon, remains undescribed. The only preserved specimens that I examined were infected with trematode sporocysts,



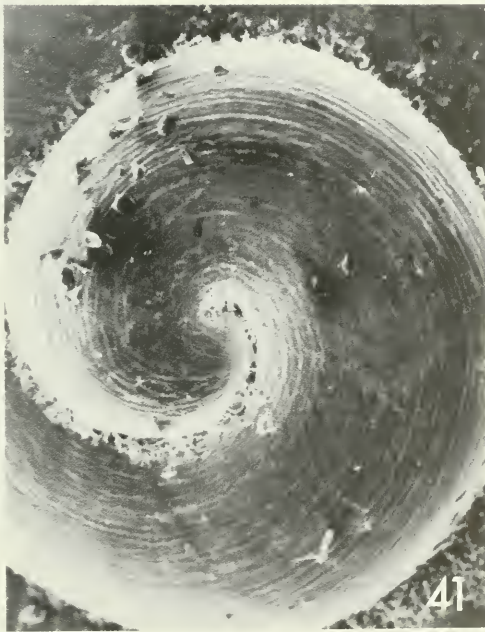
FIGS. 27–38. SEM photographs of radulae. Figs. 27–30. *Gillia altilis* (Lea). Figs. 31–34. *Fluminicola nuttalliana* (Lea). Figs. 35–38. *Somatogyrus rheophilus* n. sp. Enlargements: Fig. 27 $\times 143$; Figs. 31, 35 $\times 95$; Figs. 28–30, 32–34; 36–37 $\times 356$; Fig. 38 $\times 475$.

which grossly distorted the reproductive system. The radula of *S. depressus* was described by Stimpson (1865b: 21–22) who erred in reporting a perforation as occurring on the face of the lateral tooth. Walker (1909) used that as a characteristic to separate *Somatogyrus* from *Clappia*. Baker (1928: 148–149) correctly described and illustrated the radula of *S. depressus*. Its shell is illustrated in this paper (Figs. 65, 66) and its distribution is mapped (Fig. 71).

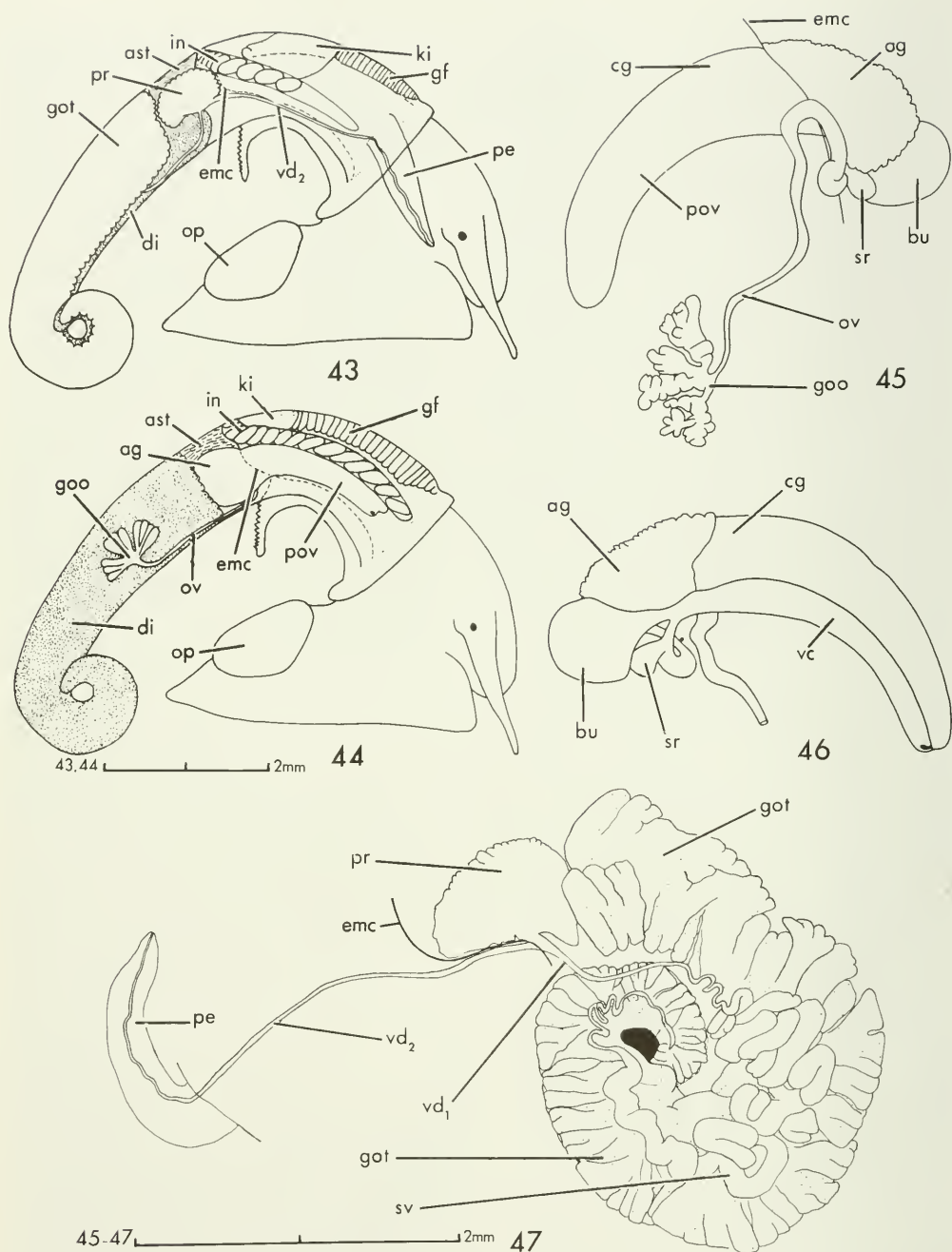
I have examined the anatomy of several species of *Somatogyrus* from Georgia, Alabama and Florida, and they are virtually identical in most features. I assume that *S. de-*

pressus is not significantly different. Because of similarities in the radula between *S. depressus* (Figs. 23–26) and other species, e.g. *S. rheophilus* n. sp. (Figs. 35–38), aspects of the anatomy of *S. rheophilus* are described as representative for *Somatogyrus*. Some data for other species also are provided. The shell of *S. rheophilus* is described in Appendix A.

External morphology. Body, top of snout, sides of foot and dorsal surface of tentacles grayish black. Slight grayish patch present on each side of posterior base of tentacles. Underside of tentacles, muzzle, and sole grayish white. Mantle collar golden-flecked. Penis unpigmented. Outer surface of mantle cavity



FIGS. 39–42. SEM photographs of protoconchs, showing embryonic sculpture. Fig. 39. *Lepyrium showalteri* (Lea), $\times 77$. Fig. 40. *Somatogyrus rheophilus* n. sp., $\times 116$. Fig. 41. *Gillia attilis* (Lea), $\times 116$. Fig. 42. *Fluminicola nuttalliana* (Lea), $\times 77$.



FIGS. 43-47. *Somatogyrus rheophilus* n. sp. Fig. 43. Male denuded of shell and partially uncoiled. Fig. 44. Female denuded of shell and partially uncoiled. Figs. 45-46. Female reproductive system. Figs. 47. Male reproductive system. Legend: ag = albumen gland; ast = anterior chamber of stomach; bu = bursa copulatrix; cg = capsule gland; di = digestive gland; emc = posterior wall of mantle cavity; gf = gill filaments; goo = ovary; got = testis; in = intestine; ki = kidney; op = operculum; ov = oviduct; pe = penis; pov = pallial oviduct; pr = prostate; sr = seminal receptacle; sv = seminal vesicle; vc = ventral channel; vd₁ = proximal vas deferens; vd₂ = distal vas deferens.

with a large dark gray patch that is bounded along right side of pallial oviduct and posteriorly by hypobranchial gland. Patch variable from light gray to nearly black. Most species of *Somatogyrus* that I examined are similarly colored; a few species (undescribed) have black blotches and spots on the mantle. Gill lamellae about 26–34. Osphradium elongate, nearly as long as gill. Operculum ovate, paucispiral, with a subcentral nucleus.

Radula. Data for *S. rheophilus* are taken from SEM photos comprising Figs. 35–38 and from prepared slides. Data for *S. depressus* are presented in Table 1. Radula with about 35–45 transverse rows of teeth. Central tooth trapezoidal in shape with a mid-basal projection; mesocone enlarged, blunt, bordered by 3–4 blunt ectocones on each side; 3–4 basocones in a low ridge in middle of lateral angles; basocones increasing in size dorsally. Lateral teeth (Figs. 35–37 with 4 entocones, an enlarged mesocone and 5–6 ectocones; shaft elongate, slender, and flexed, though not as much as in *Lepyrium* and *Clappia*; basal projection stout, pointed. Inner marginal teeth (Fig. 37) stocky, with about 30 fine, acuminate cusps. Outer marginal teeth more slender, with about 30 fine cusps (Fig. 38).

Female reproductive system (Figs. 44–46). Ovary (goo) confined to upper whorl of viscera along columellar wall and completely imbedded in digestive gland (di) (Fig. 44); consisting of 3–4 lobes, each of which is subdivided into several smaller lobules. Primary oviduct (ov) passing along ventral-mesad side of digestive gland almost to posterior wall of mantle cavity (emc), and then passing posteriorly to form an open loop along mesad side of albumen gland (ag) (Fig. 45). Gono-pericardial duct short but stout. *Seminal receptacle* (Figs. 45–46, sr) small,

saccate, located on descending arm of oviduct loop; appressed against ventral side of bursa copulatrix (bu), but visible externally. Bursa copulatrix large, saccate, overlapping posterior end of albumen gland. Duct from albumen gland joining primary oviduct at posterior partition of mantle cavity to form ventral canal (vc) of pallial oviduct (pov). Capsule gland (cg) extending to end of ventral canal. Pallial oviduct usually more slender than in other genera. Eggs deposited in single capsules on hard substrate. Egg capsule low, dome-shaped, 1.20–1.25 mm wide with a flat collar 0.20–0.25 mm wide.

Male reproductive system (Fig. 47). Similar in most aspects to *Lepyrium* except that the penis lacks small dermal glands and is relatively more slender and blade-like. Testis (got) very large, occupying upper two whorls of viscera, where it overlies dorsal surface of digestive gland, stomach, and posterior edge of prostate (pr, Fig. 43). Testes consisting of many large lobes that fork into 2–4 lobules each. Primary sperm duct lying along mid-ventral side of testis (Fig. 47). Its apical end very slender; in second visceral whorl primary sperm duct becomes greatly enlarged and convoluted forming a seminal vesicle (sv), and then narrowing to a thin delicate vas deferens (vd₁) above prostate. Prostate (pr) ovate in shape, imbedded in body wall just behind posterior wall of mantle cavity. Vas deferens (vd₂) imbedded in body wall for first half of its length, and then enters body cavity to base of penis (pe), where it courses through left side of penis and discharges at its tip. Penis originating on right side of nape behind right eye tentacle, sickle-shaped, dorso-ventrally flattened and recurved counterclockwise into the mantle cavity when contracted.

TABLE 1. Radular characteristics of some North American lithoglyphines and *Birgella*.

	Tooth rows	Central basocones	Central ectocones	Lateral cusps	Inner marginal cusps	Outer marginal cusps
<i>Gillia altilis</i> (7)	51–55	2	3–4	8–9	ca. 30	6–9
<i>Fluminicola nuttalliana</i> (5)*	—	2–3	4–5	7–8	ca. 16	12–13
<i>Somatogyrus depressus</i> (6)*	—	4	3–4	8–10	ca. 30	ca. 25
<i>Somatogyrus rheophilus</i> (7)	35–45	3–4	3–4	10–11	ca. 30	ca. 30
<i>Clappia clappi</i> (2)	56–59	6–7	6–7	18–21	ca. 50	ca. 35
<i>Lepyrium showalteri</i> (7)	140–149	9–11	22–24	18–22	ca. 50	ca. 50
<i>Birgella subglobosa</i> (2)	48–49	2	3–4	10–11	12	9

*SEM preparations; counts not taken.

Gillia Stimpson, 1865

Gillia is a monotypic genus found in streams along the Atlantic coast of eastern North America. Its shell is described and its distribution is discussed in Appendix A. The shell is characterized by its large size, ovate-conical shape, and fine spiral threads on the protoconch (Fig. 41).

External morphology. Similar to *Somatogyrus*. Mantle uniformly black or pigmentation may be reduced to a large fuscous blotch covering the mantle cavity and the stomach. Nape, top of snout, and top of tentacles black. Under side of tentacles white. Sides of foot and snout light gray. Operculum paucispiral, broadly ovate with a subcentral nucleus (Fig. 52). Baker (1918) described the eggs as laid singly or in small clusters at up to six on leaves and stems of aquatic plants. The capsules are hemispherical and 1.25 mm in diameter. An attachment collar is not mentioned or illustrated.

Radula (Figs. 27–30). The radula is specialized for feeding on coarser food particles than do the preceding genera. This is indicated by modifications of the central tooth (Figs. 27–28) and the lateral teeth (Fig. 29). The cusps on each tooth are modified and aligned to form a single large serrate blade. There is a corresponding loss of small cusps on the outer marginal tooth (Fig. 30) and among the basocones of the central tooth.

Central tooth (Figs. 27–28) broad and with greatly extended lateral angles; mesocone large, acuminate, bordered on each side by 3–4 ectocones that serve as serrations on the sides of the mesocone; basocones two on each side, the uppermost greatly enlarged and acuminate. Lateral tooth (Fig. 29) stout; shaft only slightly flexed, nearly aligned vertically with face of tooth; mesocone large, acuminate, bordered by 2 ectocones and 4–5 sharp ectocones; basal projection stout, pointed. Inner marginal tooth with about 30 cusps. Outer marginal tooth (Fig. 30) slender, with about 6 relatively stout cusps.

Female reproductive system. The female system (Figs. 48–50) is similar to that of *Somatogyrus* and *Fluminicola*, and differs from *Lepyrium* in the size and location of the seminal receptacle (sr) and the extent of the capsule gland (cg). The loop of the oviduct may or may not be folded along the side of the albumen gland (ag). The seminal receptacle originates at the base of the oviduct loop and lies along the lower edge of the bursa copula-

trix (bu), and like *Fluminicola* it is completely covered by albumen gland (ag) tissue. The capsule gland (cg) extends to the end of the ventral canal.

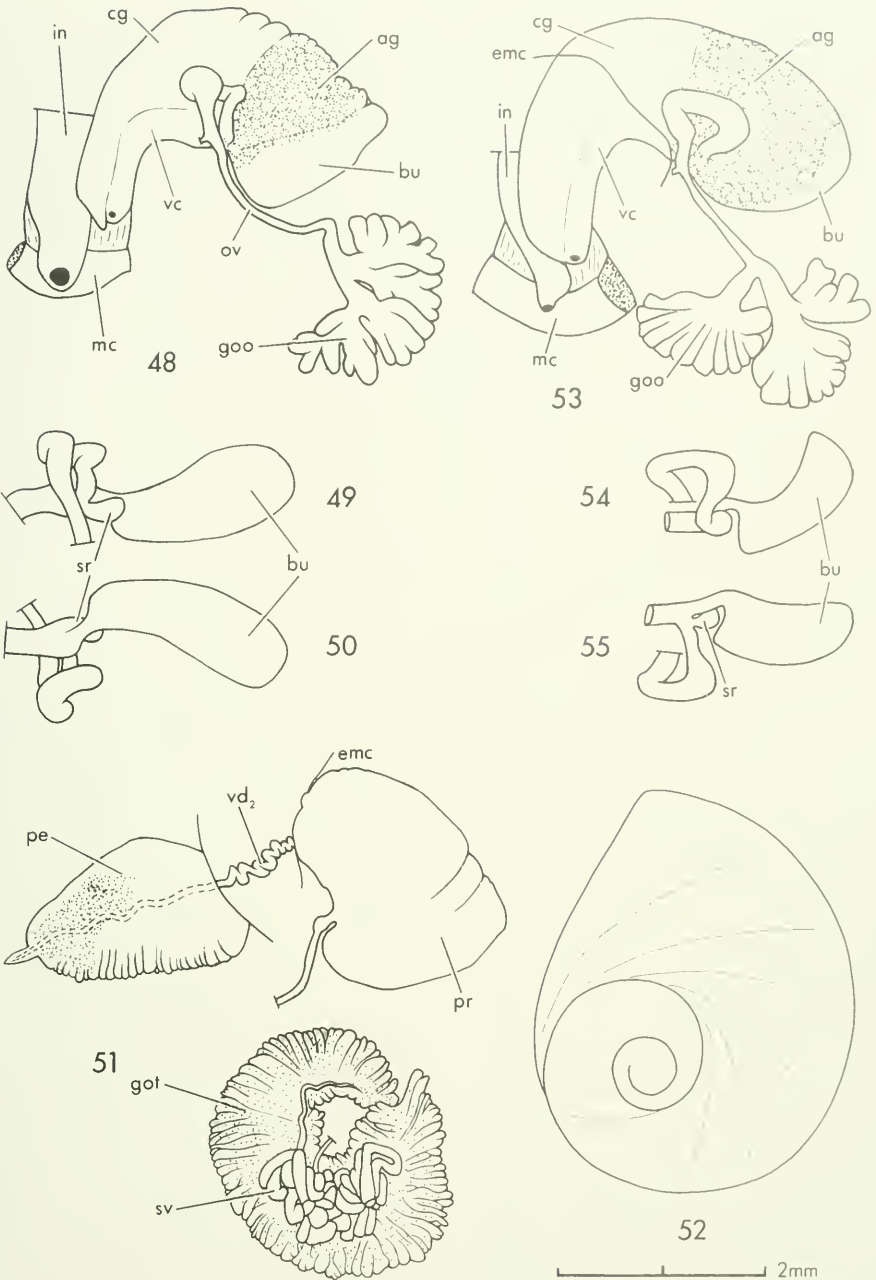
Male reproductive system. *Gillia* (Fig. 51) differs from *Lepyrium* and *Somatogyrus*, but is like *Fluminicola* in the extent of the testes and the pigmentation and shape of the penis (pe). The testis (got) extends forward only to the posterior half of the stomach and to the posterior edge of prostate (pr). Anterior vas deferens (vd₂) highly convoluted, passing along right side of body wall and then transversely across nape to base of penis. Penis flattened, blade-like (contracted in Fig. 51), and terminating in a slender fleshy papilla through which the vas deferens discharges; distal third of penis with an internal patch of melanophores along vas deferens.

Fluminicola Stimpson, 1865

The specimens I examined are tentatively identified as *F. nuttalliana* (Lea), the type-species of *Fluminicola*. They are typical in all aspects except that they are smaller than average. I have not seen sufficient material to review the systematics of *F. nuttalliana* nor to discuss its distribution. The shells of *Fluminicola* vary greatly in size, up to 12 mm. The shell varies from ovate-conical to globose. The protoconch of *F. nuttalliana* (Fig. 42) is similar to *Gillia* by having fine spiral sculpture.

External morphology. Animal like *Gillia*. Mantle uniformly black. Operculum like *Gillia*. Eggs laid on hard objects, single or in small clusters; hemispherical, 1.25 mm in diameter, with a narrow hyaline collar 0.12–0.15 mm wide.

Radula. The radula (Figs. 31–34) is similar to that of *Gillia* by having greatly enlarged cusps on the central and lateral teeth. It differs from *Gillia* primarily by the number of cusps on the marginal teeth. Central tooth with extended lateral angles; upper edge (Fig. 32) with an enlarged acuminate mesocone bordered on each side with 4–5 ectocones that combine to form a large, serrated, projecting blade; uppermost basocone greatly enlarged, followed by 1–2 much smaller basocones on each side. Lateral tooth (Fig. 33) with a weakly flexed, stout shaft, and an enlarged mesocone bordered by two smaller ectocones and four ectocones; basal projection long, slender, stout. Inner marginal tooth (Fig. 34) with about 16 acuminate cusps.



FIGS. 48-55. *Gillia altalis* (Lea). Fig. 48. Female reproductive system. Fig. 49. Coil of oviduct freed from albumen gland showing seminal receptacle. Fig. 50. Right side of oviduct coil showing relationship of bursa copulatrix to seminal receptacle. Fig. 51. Male reproductive system. Fig. 52. Operculum. Figs. 53-55. *Fluminicola nuttalliana* (Lea). Fig. 53. Female reproductive system. Fig. 54. Coil of oviduct freed from albumen gland. Fig. 55. Right side of oviduct coil showing relationships of seminal receptacle and bursa copulatrix. Legend: ag = albumen gland; bu = bursa copulatrix; cg = capsule gland; emc = posterior wall of mantle cavity; goo = ovary; got = testis; in = intestine; mc = mantle collar; ov = oviduct; pe = penis; pr = prostate; sr = seminal receptacle; sv = seminal vesicle; vc = ventral channel; vd₂ = vas deferens.

Outer marginal tooth (Fig. 34, om) with about 12–13 relatively stout cusps.

Female reproductive system. Similar to that of *Gillia altilis* except that the loop of the primary oviduct is not secondarily folded (Figs. 53–55). In contrast to other genera, the pallial oviduct lies lower along the right side and the intestine occupies a dorsal position over the pallial oviduct.

Male reproductive system (not figured). Most similar to *Gillia altilis*. The testis extends forward to overlap the posterior half of the stomach and the posterior margin of the prostate. Penis pigmented internally with two diffuse bands of melanophores along the distal third of the vas deferens, and tip of penis ending in a small fleshy papilla.

My observations on the penis differ from the description given by Stimpson (1865b: 24–26). He stated that the left base of the penis has a wing-like expansion. However, Stimpson's material came from an unspecified locality and was poorly preserved. Thus the identity of the species he examined is uncertain.

PHYLOGENETIC RELATIONSHIPS

The genera discussed above have been classified in two orders and three families within the Subclass PROSOBRANCHIA. *Lepyrium* was first considered to be in the Neritidae, a family in the Order ARCHAEOGASTROPODA, because of its neritid-shaped shell (Lea, 1861; Binney, 1865; Dall, 1896; Walker, 1918; Wenz, 1939). Pilsbry & Olsson (1951) established its affinities to the order MESOGASTROPODA on the basis of its taenioglossate radula. They proposed the monotypic Family Lepyriidae because the combination of its radular and opercular characters was dissimilar to other families of freshwater gastropods. The genera *Somatogyrus*, *Clappia*, *Gillia*, and *Fluminicola* traditionally have been grouped together in the mesogastropod family HYDROBIIDAE, Subfamily LITHOGLYPHINAE because of their thick, globose, lithoglyphine-type shells (Stimpson, 1865b; Walker, 1918; Burch & Tottenham, 1980). This relationship is correct but for the wrong reason.

The globose lithoglyphine-type shell is an adaptation for two very different habitats, and has evolved at least four times in unrelated hydrobioid subfamilies. It has evolved independently in the Pomatiopsidae (Triculiniae) and the Hydrobiidae (Lithoglyphinae) as

an adaptation for existence in high-energy streams. The globose shell accommodates an enlarged foot and muscle system for attachment to rocks in swift currents (Davis, 1979; Davis & da Silva, 1983; this paper). A similar type of shell has evolved twice again within the hydrobiid subfamily Nymphophilinae as an adaptation to a very different habitat. *Birgella* and *Notogillia*, two distantly related genera within the subfamily, live in quiet waters on fine-particle substrates (Thompson, 1968; this paper). A wide foot is required to support the snail's weight on a silt substrate, and the enlargement of the foot is accommodated by an enlarged globose shell. It is clear that the lithoglyphine-type shell is highly adaptive, and thus is convergent. Conclusions concerning suprageneric relationships based on this character-state must take convergence into account. During recent years, as knowledge about the anatomy of hydrobioid snails progressed, it has become increasingly difficult to define family units (families and subfamilies) (Taylor, 1966; Davis, 1966; Thompson, 1968; Radoman, 1973; Davis, 1979; Thompson, 1979; Hershler & Davis, 1980; Davis, *et al.*, 1982; Davis & Pons da Silva, 1983). With increasing knowledge about the anatomy of additional genera the distinctions between family units becomes less clear, and requires redefinition of established units or the designation of new units. The result is that family units are becoming separable by fewer and fewer characteristics, and frequently their definitions include words such as "except," "as in," and "shared with." Such instability is expected because fewer than 20% of the hydrobioid genera have been studied to the extent that the internal morphology is known for a single species. It is clear that the classification of the hydrobioids is in an embryonic state of knowledge. A great deal more must be learned before any stability in classification can be achieved. Such a classification will have to be based on consistent criteria of morphology, biochemistry, genetics, behavior, and ecology. At present the hydrobioids are classified only on morphological criteria that are proving not to be consistent. None-the-less the employment of such criteria is useful in deriving phylogenetic concepts.

Family relationships. On the basis of anatomical data it is clear that *Lepyrium*, *Clappia*, *Somatogyrus*, *Gillia* and *Fluminicola* constitute a compact monophyletic group within the Hydrobiidae as defined by Davis (1979).

The family relationship is established by seven morphological characters. The taenioglossate radula has a trapezoidal central tooth with pronounced lateral angles extending beyond the posterior margin. The central tooth has two or more pairs of ectocones on each side of the mesocone. Epitaenia and associated food grooves for filter feeding are absent. Sperm enters the female reproductive system through the genital pore at the anterior end of the pallial oviduct where it passes posteriorly *via* a ciliated ventral canal (except Littoridininae; Hershler, in press). The single seminal receptacle originates on the primary oviduct posterior to the bursa copulatrix. The eggs are deposited singly in tough hemispherical capsules and are not coated with sand. The prostate overlaps the posterior edge of the mantle cavity. Two other characters, though not unique to the Hydrobiidae, also serve to remove the group from other superfamilies. The simple, chitinous, paucispiral operculum lacks an internal peg. Sperm transmission from the male is accomplished through a penis that originates on the nape and is innervated by the pleuropedal connective.

Subfamily relationships. Within the Hydrobiidae six subfamilies presently are recognized in North America. Lithoglyphinae (this paper; Davis and Pons da Silva, 1983), Nymphophilinae (Thompson, 1979; Hershler, in press), Littoridininae (Davis *et al.*, 1982; Hershler, in press), Hydrobiinae (Davis, 1966; Hershler & Davis, 1980), Amnicolinae (Thompson, 1968), and Fontigentinae (Burch, 1982). The last two subfamilies are excluded from further discussion because of the presence of two (Amnicolinae) or three (Fontigentinae) ducts within the penis. They are considered remote in their relationships to the other subfamilies though their anatomies are poorly known. Eight character-states common to the *Lepyrium*-group of genera are useful for establishing relationships within the remaining subfamilies and for defining the subfamily Lithoglyphinae. (1) The shell is globose or conico-globose. (2) The protoconch is sculptured with spiral lirations; spirally arranged series of pits may occur in addition. (3) The mantle is uniform black or dark gray. (4) One or more pairs of basal cusps arise from the face of the radular central tooth, not the lateral angles. (5) The stomach lacks folds or protuberances on its posterior chamber. (6) The fecal pellets are cylindrical and are spiral in structure. (7) The penis is flattened and

blade-like, with a simple duct (vas deferens) internally. (8) The penis lacks lobes or complex glandular structures on the outer surface.

Within the Hydrobiidae characters 4, 5, 6, and 7 are exclusive to the Lithoglyphinae. Character 3 may also be. I am not aware of data to the contrary. The remaining character-states are shared with one or more subfamilies.

The globose or conico-globose lithoglyphine-type shell also occurs in some Nymphophilinae and Littoridininae. In those subfamilies, it is an uncommon character. All of the genera that have been shown to be Lithoglyphinae because of their soft anatomies have lithoglyphine-type shells. Two conclusions are suggested by this. The lithoglyphine-type shell in the Lithoglyphinae is fundamental, and thus is a primitive character-state. Also, the habitat deployment of the Lithoglyphinae in high-energy streams is a basic, and therefore primitive behavioral characteristic of the subfamily. Some species, *e.g.* *Somatogyrus depressus* (Tryon) and *Gillia altilis* (Lea) may inhabit quiet-water habitats as well as high-energy streams. This can be considered a secondary adaptation because it occurs seldom and sporadically with the subfamily, not among a cluster of closely related species, and it occurs among species that also inhabit fast streams.

The spiral sculpture of the protoconch is characteristic of the Lithoglyphinae. A secondary reduction may occur (*Lepyrium*) or secondary additions may occur (*Somatogyrus*). Spiral protoconch sculpture in *Birgella* (Figs. 79–80) is the only recorded occurrence in the Nymphophilinae. Spiral protoconch sculpture also occurs in some southeastern Amnicolinae, *e.g.* *Lyogyrus retromargo* (Thompson). This type of sculpture may be a primitive condition within the Hydrobiidae, with other types of sculpture representing derived states.

The absence of glandular ridges, raised glands, lobes or papillae on the penis is a character state that also occurs in some Littoridininae (Hershler, in press) and in some Hydrobiinae (Hershler & Davis, 1980). In those cases it may be a derived condition through the secondary loss of previously existing characters. The total absence of these structures in the Lithoglyphinae suggests that their absence is a generalized, primitive condition in the subfamily.

The Lithoglyphinae as presently understood includes seven genera. Five in

North America, *Potamolithus* in South America (Davis & Pons da Silva, 1983) and *Lithoglyphus* in Europe (Krause, 1949). In addition to the nine character-states listed above that differentiate North American lithoglyphines from other Hydrobiidae, the North American genera have in common five character-states that differentiate them from other Lithoglyphinae. In sequence with the character-states listed above these are as follows: (9) The testis is very large; it covers almost the entire dorsal surface of the digestive gland and partially overlaps the stomach and prostate. (10) The vas deferens is not modified into an enlarged ejaculatory duct at the base of the penis. (11) The penis may or may not have a terminal papilla; when present the papilla is non-retractable. (12) The penis lacks a preputium. (13) A nuchal node is absent.

The size of the testis separates the New World genera from *Lithoglyphus*. In *Lithoglyphus*, Krause (1949) describes the testis as overlying the digestive gland in the first and second whorl. The extent of its distribution in these two whorls is not clear. His illustration (p. 135, fig. 22) depicts a testis that is not larger than the prostate. If that is correct, the testis is very small compared to those in other genera. The remaining four character-states differentiate the North American genera from *Potamolithus* (see Davis & Pons da Silva, 1983).

THE NORTH AMERICAN LITHOGLYPHINE GENERA

The evolution of North American Lithoglyphinae centered about microhabitat selection and trophic specialization. Microhabitat selection produced variation in shell-form within the constraints imposed by a lentic environment. Trophic specialization is reflected in variations of the basic structure of the cusps on the radular teeth and the shaft of the lateral tooth. Character-trends are discernible in shell form and radular structures.

Shell form. A high degree of diversity exists in the shells of North American Lithoglyphinae. The species vary in size from small to large (2–12 mm) and may be obese with a short or depressed spire, ovate-conical with a pronounced spire, or flattened and limpet-like. They include the largest of the American Hydrobioidea. Most have a voluminous body whorl. Basically, most shells are imperforate or narrowly rimate. When viewed from the front, most have a noticeable spire protruding from the right side (Fig. 57). When the animal is active, the shell is raised and the eyes, tentacles, and muzzle extend considerably beyond the edge of the lip.

Two lines of specialization in shell form occur. *Clappia* diverges from the basic shell form by having a broadly perforate umbilicus (Fig. 68). The adaptive significance of this is

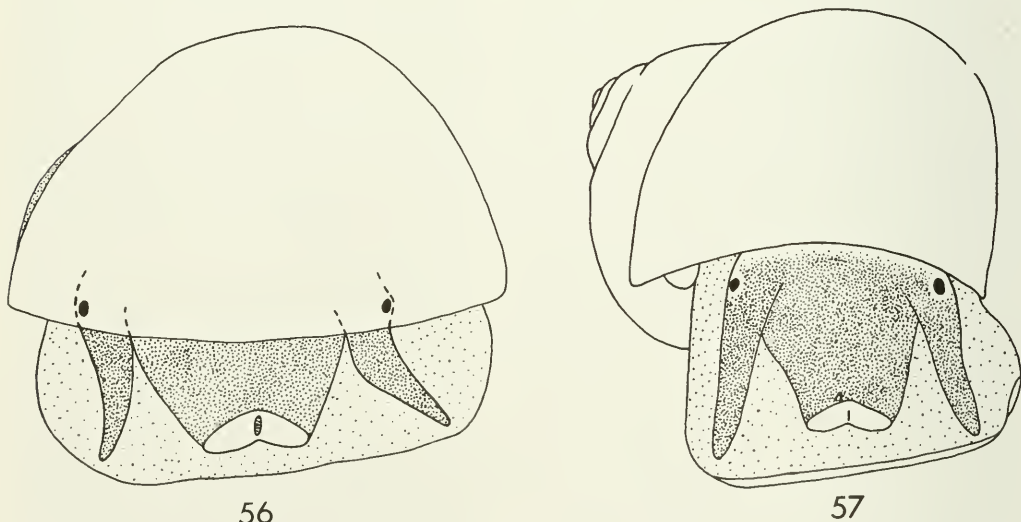


FIG. 56–57. Fig. 56. Anterior view of *Lepyrium showalteri* (Lea); note reduction of spire to produce a limpet-like shell. Fig. 57. Anterior view of *Somatogyrus rheophilus* n. sp., a lithoglyphine with a normal-spired shell.

not clear because little information is available on the ecology of *Clappia*. However, this is only a variation in degree from the perforate umbilicus of some *Somatogyrus* (Fig. 65). *Lepyrium* diverges from the basic shell form by being limpet-like, with a depressed spire and a greatly enlarged aperture. When the animal is viewed from the front, the shell covers the body like a low shield and the spire is barely evident (Fig. 56). The animal raises its shell only slightly as it moves, and the eyes, tentacles and snout barely protrude beyond the edge of the lip. The shell form of *Lepyrium* is a modification for reducing hydrostatic drag on an animal that lives in fast currents on smooth boulders, where characteristically it is found. The neomelanian type operculum of *Lepyrium* is a secondary specialization related to the enlarged aperture.

Other variations in shell morphology are significant as species-level criteria or species-group criteria. The large size of *Gillia altilis* readily distinguishes this monotypic genus from other eastern North American genera, but not from *Fluminicola*, which achieves an even larger size. However, it is not shell size by which *Gillia* is separated from other genera, but by trophic structures. Furthermore, some of the more globose species now placed in *Somatogyrus* may be found to belong in *Gillia* when their radulae are examined.

Radula. Three important character-trends occur in trophic structures. They are the primary modification through which adaptive radiation of the Lithoglyphinae has taken place in North America. Each genus is characterized more by its radular features than by other structures. These features indicate different feeding roles for the various genera. Radular data are summarized in Table 1. The trends are: (1) modifications in the number of transverse tooth rows, (2) modifications of size and numbers of cusps on the radular teeth, and (3) a corresponding modification in the size and orientation of the shaft of the lateral tooth.

Most species have a moderate number of transverse tooth rows, about 35–55 (Table 1, Fig. 23). In two groups, *Clappia* and *Lepyrium*, there is a significant increase in the number of rows. This increase is accommodated by a greater degree of overlap between successive rows, not by increasing the relative length of the ribbon (Figs. 15, 19).

Two trends can be recognized in mod-

ifications of size and numbers of radular cusps. In *Clappia* and *Lepyrium* there is a decrease in the relative size of the cusps accompanied by an increase in the number of cusps on each tooth, indicating that these genera are specialized for grazing on finer plant-food particles than does the related genus *Somatogyrus*. A second trend occurs in *Gillia* and *Fluminicola*. In these genera the basocones in the central tooth are decreased in number, but are greatly enlarged, as are other cusps on the central and lateral teeth. There is also a corresponding decrease in the number, but an increase in relative size of the cusps on the inner and outer marginal teeth. These are specializations for grazing on coarser food materials than do related genera.

The shaft of the lateral tooth is moderately stout and is flexed laterally at a slight angle to the tooth face in *Somatogyrus* (Figs. 23, 25). In genera with reduced cusp size (*Clappia* and *Lepyrium*) the shaft is slender and is flexed laterally at a greater angle (Figs. 21, 17). This accommodates an increase in transverse tooth rows without increasing the relative length of the ribbon. In genera with enlarged cusps (*Gillia* and *Fluminicola*) the shaft is stouter and is aligned almost vertically with the face of the tooth (Figs. 29, 33). These changes are related to trophic specializations. Those genera that feed on coarse foods require stout shafts with rectilinear vertical support for the lateral tooth. Those genera that feed on smaller food particles require less support and can function with slender, strongly flexed lateral tooth shafts.

Relationships. Ten character-states are useful for determining intergeneric relationships. These states are discussed at various points earlier in this paper and are summarized in Table 2. A phenogram based on these character-states is depicted in Fig. 58. *Gillia* and *Fluminicola* have eight character-states in common (1–8). They differ from each other in two character states (9–10). They differ exclusively from the other genera by six character-states (4–9). *Somatogyrus*, *Clappia*, and *Lepyrium* have three character-states in common (4, 5, 10). *Somatogyrus* differs from the *Clappia*-*Lepyrium* lineage by three character-states (7, 8, 9). *Clappia* and *Lepyrium* have three character-states in common (7, 8, 9). They differ from each other in four character-states (1, 2, 3, 6).

From the data presented in Table 2 it is apparent that modification of feeding struc-

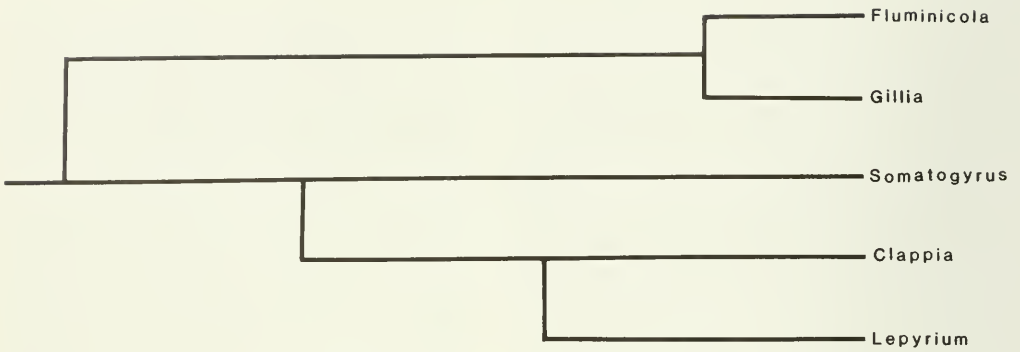


FIG. 58. Phenogram depicting intergeneric relationships of North American Lithoglyphinae based on characters listed in Table 2.

TABLE 2. Variation in ten character-states among North American lithoglyphine genera.

	<i>Somatogyrus</i>	<i>Clappia</i>	<i>Lepyrium</i>	<i>Gillia</i>	<i>Fluminicola</i>
Shell shape	0	0	1	0	0
ovate-conical (0)					
neritid (1)					
Umbilicus	0	1	0	0	0
imperforate-rimate (0)					
open (1)					
Operculum	0	0	1	0	0
subcentral (0)					
excentric (1)					
Size	1	1	1	0	0
large (<5 mm) (0)					
small (> mm) (1)					
Penis papilla	1	1	1	0	0
present (0)					
absent (1)					
Central tooth cusps	1	1	2	0	0
large (0)					
medium (1)					
small (2)					
Lateral cusps	1	2	2	0	0
large (0)					
medium (1)					
small (2)					
Lateral shaft	1	2	2	0	0
vertical (0)					
angular (1)					
flexed (2)					
Inner marginal cusps	1	2	2	1	0
large (16) (0)					
medium (30) (1)					
minute (50) (2)					
Outer marginal cusps	2	2	2	0	1
large (6-9) (0)					
medium (12) (1)					
small (25+) (2)					

tures (trophic specialization) is the fundamentally most important factor underlying the adaptive radiation of the Lithoglyphinae in North America. This is coupled with a minor degree of variation in the structure of the penis (reproductive specialization). It is also apparent that variation in the shell and operculum are significant at lower taxonomic levels, and that they are adaptations reflecting microhabitat specialization.

The North American lithoglyphine genera are redefined as follows. They have in common the characters discussed earlier in this paper, which differentiates them from European and South American genera.

Gillia Stimpson, 1865a

Type-species. *Melania attilis* Lea, 1841 (see Figs. 63, 64; Appendix A).

Definition. Shell medium to large (6–8 mm high). Imperforate or rimate. Conico-globose in shape. Protoconch sculptured with spiral striations. Operculum paucispiral. Penis with a small terminal papilla. Shaft of lateral tooth straight. Cusps of radular teeth enlarged; numbers of cusps given in Table 1. Outer marginal tooth with few (6–9) cusps.

Distribution. Atlantic drainage systems of eastern North America from South Carolina north to New York and Vermont.

Species. Monotypic.

Fluminicola Stimpson, 1965a

Type-species. *Paludina nuttalliana* Lea, 1839 (see Burch & Tottenham, 1980: 101, fig. 142, for an excellent illustration of the species).

Definition. Shell medium to large in size (up to 12 mm high). Imperforate or rimate. Conico-globose or globose in shape. Protoconch sculptured with spiral striations. Operculum paucispiral. Penis with a small terminal papilla. Shaft of lateral tooth straight. Cusps on radular teeth enlarged; numbers of cusps given in Table 1. Inner marginal tooth with few (16) cusps.

Distribution. Pacific drainage systems from California north to Washington and interior basin.

Species. Indeterminate. Burch & Tottenham (1980: 102) list 12 species. The radula and soft anatomy of only the type-species is known.

Note. Taylor (1966) synonymizes *Fluminicola* with *Lithoglyphus*. In light of the dif-

ferences in the prostate gland and the radular cusps, they are retained as separate genera pending additional anatomical data on other species of *Fluminicola*. Radoman (1966) figures the radula of *L. naticoides* (C. Pfeiffer) as having few cusps on the inner marginal tooth (8–9) and on the outer marginal tooth (7).

Somatogyrus Gill, 1863

Type-species. *Amnicola depressa* Tryon, 1862 (see Figs. 65, 66).

Definition. Shell small to medium in size (1–6 mm high). Imperforate, rimate or narrowly umbilicate. Conico-globose or globose in shape. Protoconch sculptured with spiral threads, and it may also have spirally arranged series of pits. Operculum paucispiral with a sub-lateral nucleus. Penis without distinct terminal papilla. Shaft of lateral tooth weakly angular. Cusps of radular teeth moderately large; numbers of cusps given in Table 1.

Distribution. Eastern North America throughout the Mississippi drainage system, and from the Potomac River south and west through the Gulf Coast systems. Panuco River system of Mexico.

Species. Numerous. Burch & Tottenham (1980) list 35 species in the United States. Pilsbry (1910) describes a species from the Rio Coy in Mexico. Another is described in this paper.

Remarks. Species may differ by the number and size of the cusps on the radular teeth and the number of tooth rows. Two subgenera have been recognized on the basis of cusp development: *Somatogyrus s. s.* and *Walkerilla* Thiele, 1928. The degree of cusp development does not seem to be an adequate feature for separating subgenera. Convergence in this characteristic among species of quite dissimilar shells (*S. coosaensis* and *S. tenax*; see Burch & Tottenham, 1980) suggests that *Walkerilla*, as used previously (Thompson, 1969: 260), is polyphyletic and artificial in concept.

Clappia Walker, 1909

Type-species. *Clappia clappi* Walker, 1909 (= *Somatogyrus umbilicatus* Walker, 1904) (Fig. 68).

Definition. Shell small (about 3 mm high). Broadly umbilicate. Conico-globose in shape. Protoconch sculpture unknown. Operculum

paucispiral with a large subcentral nucleus. Penis simple, apparently without a terminal papilla. Shaft of lateral tooth strongly flexed. Cusps of lateral and marginal teeth minute; numbers of cusps given in Table 1.

Distribution. Confined to the Coosa and Cahaba rivers in central Alabama.

Species. Two; both may be extinct.

Lepyrium Dall, 1896

Type-species. *Neritina showalteri* Lea, 1861 (see Figs. 59–62; Appendix A).

Definition. Shell medium in size (about 4 mm high). Imperforate. Flattened, neritid in shape, but with a complete internal spire; aperture greatly enlarged for a limpet-like mode of existence. Protoconch smooth with a few low, wide, spiral grooves. Operculum paucispiral with a very excentric nucleus (neomelanian, Fig. 7). Penis simple, without a terminal papilla. Shaft of lateral tooth strongly flexed. Cusps of all radular teeth minute, accompanied by a large proliferation of transverse tooth rows. Numbers of cusps given in Table 1.

Distribution. Coosa, Cahaba, and Little Cahaba rivers in central Alabama.

Species. Monotypic.

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APPENDIX A

The following Lithoglyphinae are described. Adequate descriptions of two are not available in contemporary literature. The third species is new, and its anatomy is discussed earlier in this paper.

Lepyrium showalteri (Lea)

Neritina showalteri Lea, 1861: 55.—Lea, 1863: 267, pl. 35, figs. 78, 78a.

Neritella showalteri (Lea), Binney, 1865: 106, fig. 212.

Lepyrium showalteri (Lea), Dall, 1896: 13–15.—Walker, 1918: 38, fig. 139.—Wenz, 1938: 432, fig. 1062.—Pilsbry & Olsson, 1951: 1–5, figs. 1–3, 3a.—Stein, 1976: 25.—Burch & Tottenham, 1980: 104, figs. 192–193.

Lepyrium showalteri cahawbensis Pilsbry, 1906: 51.—Goodrich, 1941: 7, 10.—Pilsbry & Olsson, 1951: figs. 4–6.—Stein, 1976: 25.

Shell (Figs. 59–62). Ovate in outline, adults 3.5–4.4 mm high and 4.0–5.0 mm wide,

about 0.81–0.94 times as high as wide. Strongly flattened with a strongly excentric apex and neritid-like in appearance; nearly uniformly dome-shaped with the apex hardly protruding when viewed from the rear (Fig. 61) or front (Fig. 56). Umbilical area imperforate. About 2.3–3.0 whorls, which rapidly expand. Apical whorls usually eroded to the level of the body whorl. Protoconch depressed, nearly smooth with a few low wrinkled depressions along outer surface (Fig. 39). Subsequent whorls rapidly expanding; sculptured with fine growth striations. Peristome greatly expanded, circular, but variable in shape, large specimens tend to have a proportionally higher aperture than do smaller specimens. Columellar callus deeply dished, about a third the width of the aperture area and with a wing-like extension on the upper left corner. Peristome 0.92–1.08 times as high as wide. Width of peristome about 0.79–0.95 time width of shell. Aperture flattened dorso-ventrally, continuing as a spire into upper whorls, not shelf-like as in Neritidae. Measurements in mm of three specimens selected to show variation are:

Cat. no.	Height	Width	Ap. H.	Ap.W.	Whorls
UMMZ 67445	3.84	4.46	3.91	3.60	2.5
UMMZ 67445	4.03	4.65	4.03	4.40	2.7
UMMZ 97448	4.40	4.96	4.40	4.65	3.0

Operculum (Fig. 7). Corneous; retractable into aperture for about $\frac{1}{4}$ whorl. Paucispiral with the nucleus located close to the lower left margin (neomelanian); $2\frac{1}{4}$ rapidly expanding whorls. Outer surface sculptured with distinct incremental striations, and finer, close spiral striations.

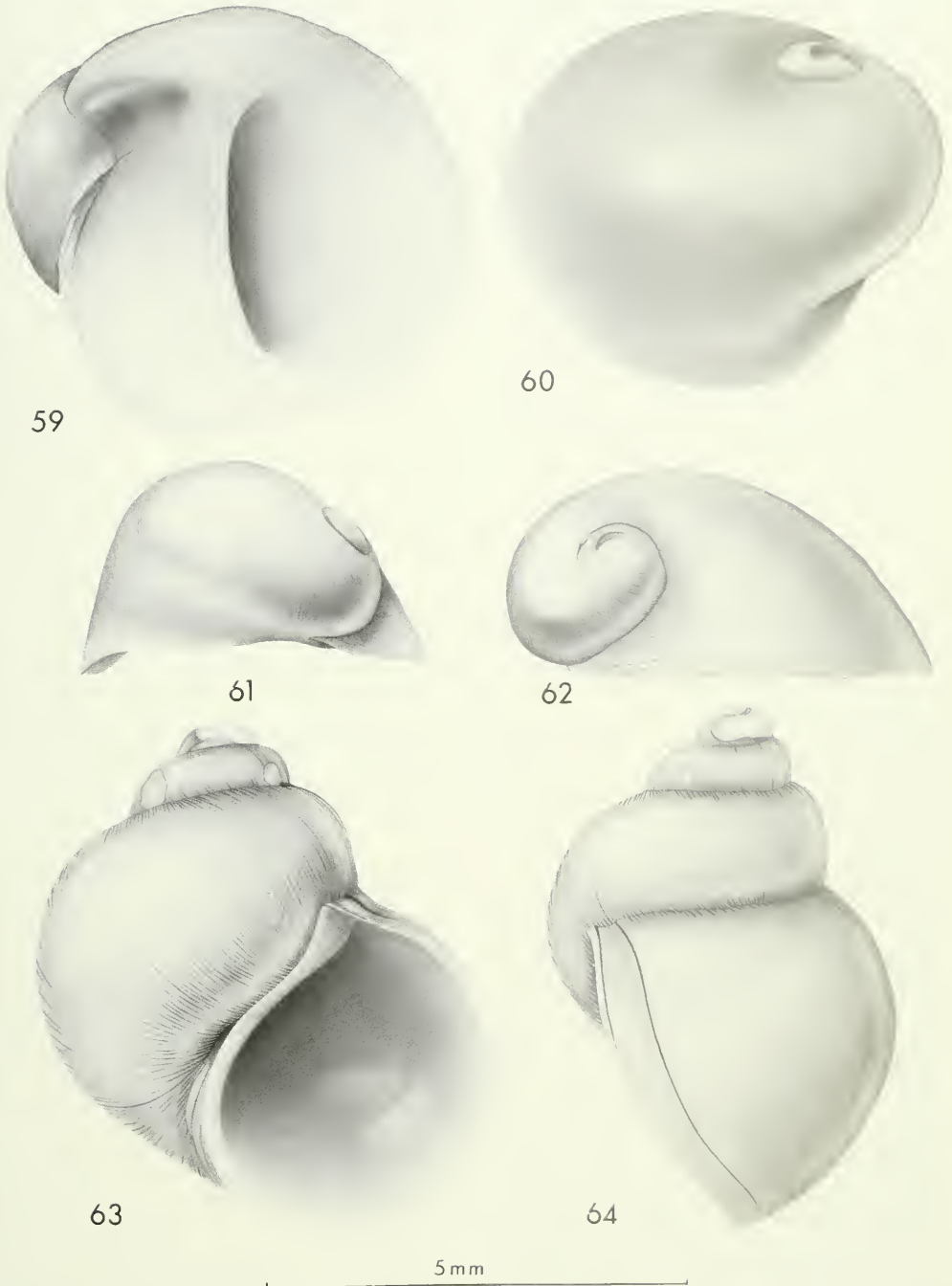
Distribution. Recorded from a short segment of the Cahaba River and the Little Cahaba River in Bibb County, and a short segment of the Coosa River in Shelby County, Alabama. Presumably it is extinct in the Coosa because of impoundment of the river. It still exists in the Cahaba and Little Cahaba rivers. Records of specimens examined are listed in Appendix C.

Remarks. Pilsbry (1906) recognized two subspecies, the typical subspecies from the Coosa River, and *L. s. cahawbensis* from the Cahaba River. The latter was based upon immature specimens which he characterized as being smaller, with a straight columellar

edge, and without a raised outer margin of the columellar area (causing the columella not to be dished). Later Pilsbry & Olsson (1951: 2) stated that the characteristics were inconsistent because they were based on juveniles, and they doubted the validity of *cahawbensis* as a distinct taxon. Unfortunately very little material is available from the Coosa River. However, specimens I have examined demonstrate that only one form is recognizable.

Somatogyrus Gill, 1863

The genus *Somatogyrus* includes 37 described species in North America. There are perhaps half again as many remaining to be described. Most of the described species are poorly known and inadequately illustrated, and must be restudied before meaningful specific comparisons can be made. Useful specific characteristics occur in the pro-



FIGS. 59-64. Figs. 59-62. *Lepyrium showalteri* (Lea), UMMZ 67445: Cahaba River, Guerney, Bibb Co., Alabama. Fig. 63. *Gillia altilis* (Lea), neotype: UF 40550. Fig. 64. *Gillia altilis* (Lea), UF 40551: Lake Waccamaw, Washington Co., North Carolina.

toconch sculpture, the radula, the pigmentation patterns of the mantle, tentacles and snout, the shape and structure of the columellar lip, other aspects of the aperture, size and obesity. Adults of most species are decollate due to erosion of the apical whorls. Thus, the last whorl and the aperture provide the only measurements of height that are useful for specific comparisons. Most species of *Somatogyrus* occur on rocks in high-energy rivers. Some occur in low gradient streams on sand and gravel. Most *Somatogyrus* are annual species. Ovipositing usually takes place in May and June, whereupon the adults die. Morphological maturity of the new progeny occurs in October and November. Most samples that are collected between June and September contain only immature specimens, which have not yet developed the definitive characteristics essential for correct species identifications.

Somatogyrus rheophilus Thompson,
new species

Diagnosis. A medium-sized species characterized by the tendency for its whorls to be weakly rounded above the periphery, its narrowly rimate umbilicus, its receded basal lip, its wide, rounded columellar lip, its advanced posterior corner of the aperture, its angular parietal-columellar corner, and its uniform black or grayish-black mantle. It is most similar to *S. alcoviensis* Kreiger from the Yellow River, Newton County, Georgia. The latter differs by having the columellar lip and parietal callus form a weak, oblique arch.

Shell (Fig. 67). Broadly conical or turbinate. Adults decollate with 2–3 whorls remaining. Medium sized for the genus; eroded adults 3.9–4.5 mm high (holotype 4.3 mm); body whorl about 3.5–4.0 mm high and 3.4–4.0 mm wide. Width about equal to height of last whorl (0.97–1.02). Penultimate whorl 0.48–0.54 times width of last whorl. Last whorl nearly flattened above periphery. Suture weakly impressed. Umbilicus narrowly rimate, or occasionally imperforate. Periostracum yellow-green with oblique, shallow growth striations. Protoconch (Fig. 40) with fine spiral threads at and below periphery; with dimples superimposed on spiral threads above periphery. Aperture broadly ovate, 0.83–0.95 times as high as wide, 0.66–0.73 times height of last whorl. Plane of aperture at 22–30° to axis of shell. Peristome complete across parietal area by a thick callus. Basal lip

slightly receded; base-columellar corner projecting forward. Posterior corner of aperture advanced forward and with a shallow angular groove internally. Columellar lip very wide; rounded in cross section; straight or weakly concave in lateral profile; vertical. Columellar lip forming a pronounced angle with parietal callus.

Measurements in mm for the holotype and ten paratypes selected to show variation follow (holotype in parenthesis).

Height, 3.5–4.0 (3.9); width, 3.4–4.0 (3.8); aperture height, 2.4–2.8 (2.8); aperture width, 2.0–2.5 (2.4).

Type-locality. Georgia, Upson County, Flint River at Spewrell Bluff, U.S. Army Corps of Engineers river mile 200. Holotype: UF 40500; collected 22 May 1981 by Fred G. Thompson. Paratypes: UF 31244 (246 specimens); 25 specimens each deposited in ANSP, FMNH, MCZ, UMMZ, USNM, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands, Senckenbergische Naturforschende Gesellschaft, Frankfurt-am-Main, Germany, and Herbert D. Athearn collection; same data as holotype.

Distribution. Endemic to the middle section of the Flint River in Georgia from Meriwether-Pike counties southeast to Taylor-Crawford counties. This species has been found only in shoals and rapids where it occurs on granite boulders and gravel in moderate currents. Locality records are given in Appendix C.

Gillia altilis (Lea)

Melania altilis Lea, 1841: 13.—Lea, 1843: pl. 5, figs. 23.

Leptoxis altilis (Lea), Haldeman, 1847: 6, pl. 5, fig. 152.

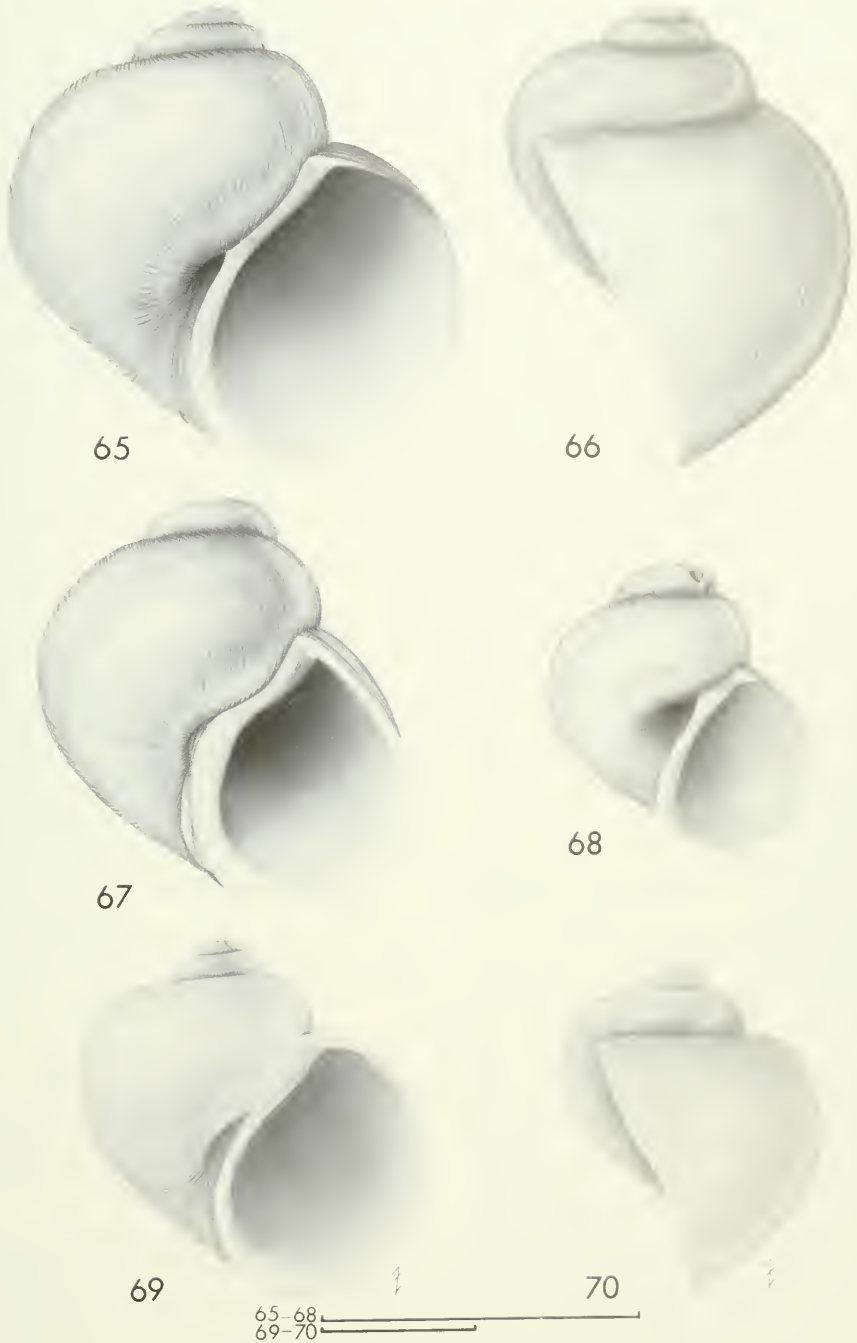
Gillia altilis (Lea), Stimpson, 1865a: 53.—Stimpson, 1865b: 51.—Binney, 1865: 74–75, fig. 146.—Walker, 1918: 32–33, figs. 115–116.—Burch & Tottenham, 1980: 104, fig. 191.—Burch, 1982: 23, fig. 191.

Somatogyrus altilis (Lea), Tryon, 1870: 60, pl. 17, fig. 9.

Leptoxis crenata Haldeman, 1847: 6, pl. 5, fig. 153.

Gillia crenata (Haldeman), Binney, 1865: 74–75, figs. 147–148.

Shell (Figs. 63, 64). Conico-globose. Light yellow-green. About 4.5 whorls, but apex usually eroded, leaving 2–4 whorls in adults. Moderately large, eroded adults usually 6–8 mm high (lectotype 6.6 mm). Body whorl



FIGS. 65-70. Figs. 65-66. *Somatogyrus depressus* (Tryon), UF 34969: Mississippi River, Davenport, Iowa. Fig. 67. *Somatogyrus rheophilus* n. sp.; holotype: UF 40500. Fig. 68a. *Clappia umbilicata* (Walker); ANSP 95037: Coosa River, Alabama. Figs. 69-70. *Birgella subglobosa* (Say); UF 35008: Ohio River at Five Mile Creek, Hamilton Co., Ohio.

conspicuously enlarged; adults tending to be shouldered or fluted below suture; height of body whorl 0.95–1.10 times width. Shell usually rimate; some specimens imperforate, or narrowly umbilicate. Apical whorl of protoconch elevated, 1.25 mm wide transverse to initial suture. Protoconch sculptured with fine spiral threads that are uniformly dispersed over surface of first whorl (Fig. 41). Subsequent whorls strongly rounded; sculptured with distinct, regularly spaced incremental striations; usually with 1–2 dark growth varices. Aperture broadly ovate-auriculate in shape. Plane of aperture lying at an angle of 18–20° to axis of shell. Height of aperture 0.70–0.78 times height of body whorl; about 0.78–0.90 times as wide as high. Peristome in mature specimens complete

across parietal wall by a thin callus; incomplete in sub-adults; peristome dark rimmed. Columellar lip moderately thickened, rounded. Outer lip and basal lip sharp-edged, evenly curved through columella. Outer lip conspicuously arched forward in lateral profile (Fig. 64).

Operculum (Fig. 52) oval in shape. Chitinous, yellowish-green. Paucispiral, consisting of three whorls. Nucleus located in the lower left third. Outer surface sculptured with fine incremental striations.

Measurements in mm based on 29 specimens selected to show variation are given below. UF 27500—Lake Waccamaw, North Carolina; UF 35027—Potomac River, District of Columbia; UF 35013—Erie Canal, New York.

Cat. no.	n	Total h.	Body wh. h.	Width	Apert. h.	Apert. w.
UF 27550	10	5.6–5.9	5.4–6.1	5.3–5.8	4.0–4.5	3.5–3.9
UF 35025	8	6.5–8.1	5.5–7.4	5.3–7.6	3.9–5.5	3.5–4.5
UF 35013	10	5.6–7.0	5.0–6.1	4.9–6.1	3.5–4.6	3.0–3.9
UF 40550	neotype	6.6	5.9	5.6	4.3	3.9

Type-locality. Lea (1841) stated that his specimens of *Melania altilis* came from the Santee Canal, South Carolina, and the Susquehanna River at Havre de Grace, Maryland. Haldeman (1847) stated that the type-specimen of *Leptoxis crenata* came from the Santee Canal, South Carolina. Type-specimens for neither *Melania altilis* Lea nor *Leptoxis crenata* Haldeman can be located. Presumably they are lost. It is clear that they are the same species, and a neotype must be designated. *Melania altilis* Lea: Neotype UF 40550 (Fig. 63). *Leptoxis crenata* Haldeman: Neotype UF 40550; same specimen as neotype for *Melania altilis* Lea. Neotype locality: Lake Waccamaw, Columbus County, North Carolina; neotype collected 12 September 1980 by Fred G. Thompson. Lake Waccamaw is selected as the neotype locality for the following three reasons. The species shows little variation throughout its range, and there is no basis to suspect that the Lake Waccamaw population is different from other populations in its taxonomic identity. On three occasions in 1980, 1981, and 1982, I was unsuccessful in finding the species in the Santee River. Apparently it no longer occurs there. The anatomical data given in this paper are based on Lake Waccamaw material.

Distribution (Fig. 71). The species is widely distributed in rivers draining into the Atlantic

Ocean from South Carolina north to New York and Vermont. It has entered the Lake Ontario system via the Erie Canal. The species is found in quiet lakes and rivers, as well as fast gradient streams. Locality records for this species are given in Appendix C.

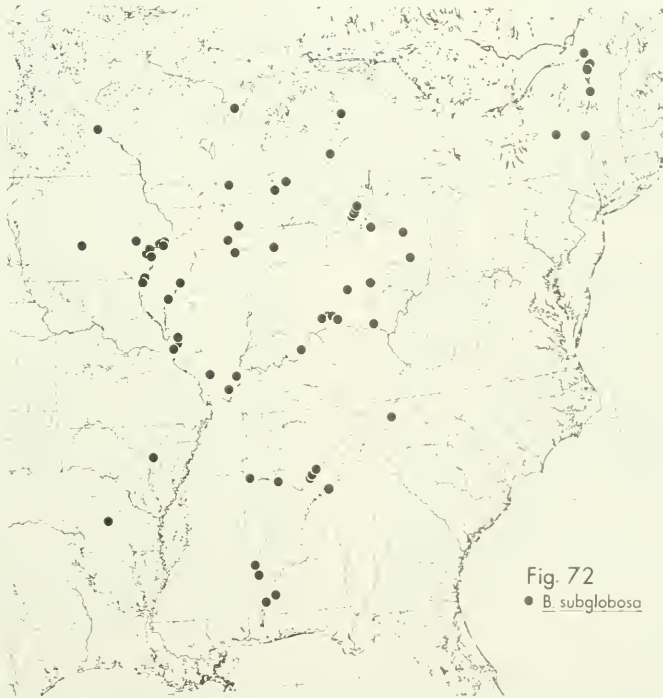
APPENDIX B

A North American snail incorrectly associated with the Lithoglyphinae:

Birgella Baker, 1926

Birgella Baker, 1926: 196.—Baker, 1928: 154–155.—Wenz, 1939: 575.—Thompson, 1979: 47.—Burch & Tottenham, 1980: 110. (Type-species: *Paludina subglobosa* Say, 1825).

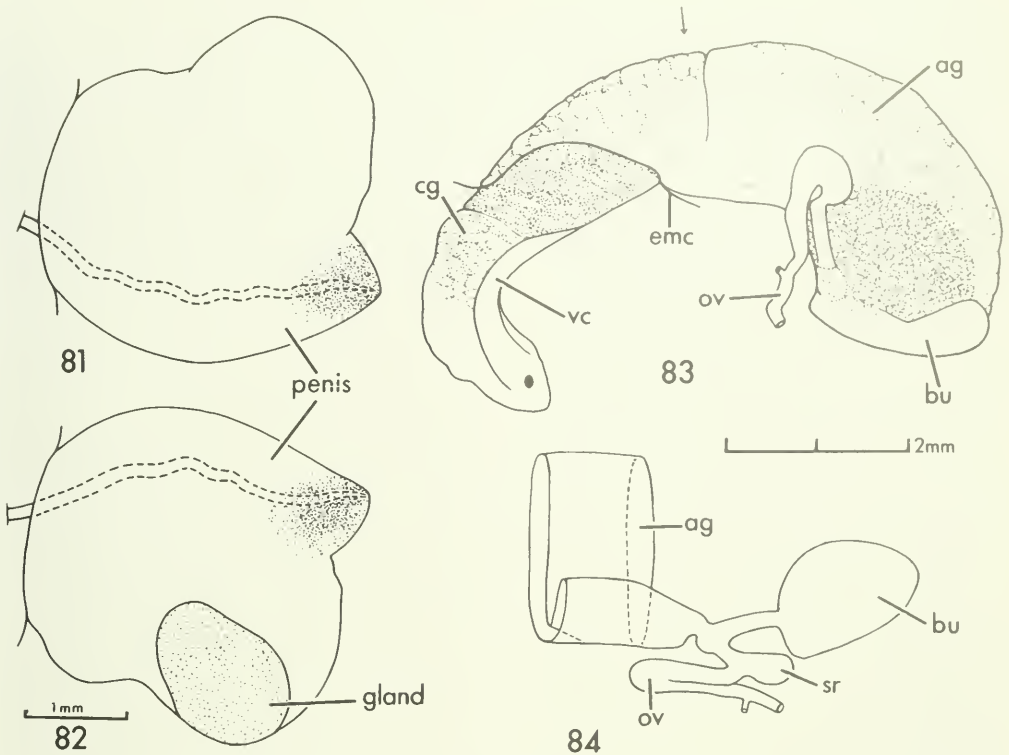
The shells of *B. subglobosa* (Say) (Figs. 69–70) are so similar to those of *Somatogyrus depressus* (Figs. 65–66), the type-species of *Somatogyrus*, that they were considered congeners for more than a century. Baker (1928) separated *Birgella* from *Somatogyrus* on the basis of differences in the verge and radula, but placed both genera in the Lithoglyphinae. Most subsequent authors failed to recognize *Birgella* as a distinct genus due to



FIGS. 71-72. Geographic distributions. Fig. 71. *Gillia altilis* (Lea) and *Somatogyrus depressus* (Tryon). Fig. 72. *Birgella subglobosa* (Say).



FIGS. 73–80. SEM photographs of radulae and protoconch sculpture. Figs. 73–75. *Nymphophilus minkleyi* Taylor, UF 34905: creek 10 km SW Cuatro Cienegas, Coahuila, Mexico. Figs. 76–78. *Birgella subglobosa* (Say), UF 35275, Alabama River, Choctaw Bluff, Clarke Co., Alabama. Figs. 79–80. *Birgella subglobosa* (Say), UF 35277: Ohio River at Five Mile Creek, Hamilton Co., Ohio. Enlargements: Figs. 73–75, 78 $\times 356$. Figs. 76, 77 $\times 238$. Figs. 78–80 $\times 48$.



FIGS. 81–84. *Birgella subglobosa* (Say). Figs. 81–82. Verge. Fig. 83. Female reproductive system without ovary. Fig. 84. Mid-segment of oviduct showing relationships between seminal receptacle, bursa copulatrix, and albumen gland. Legend: ag = albumen gland; bu = bursa copulatrix; cg = capsule gland; emc = posterior wall of mantle cavity; ov = ovary; sr = seminal receptacle.

the limited anatomical data available on the Hydrobiidae. Thompson (1979) placed *Birgella* in the Nymphophilinae, where it is clearly related because of features of the reproductive system and radula. Clarke (1981) continued to treat *Birgella* as a synonym of *Somatogyrus*. *Birgella* is differentiated from other nymphophilids because of its protoconch sculpture, its large globose shell and its ponderous penis. It is not closely related to other known genera. The protoconch sculpture is vaguely similar to that of *Nymphophilus* because of its coarse step-like wrinkles (see Thompson, 1979). The morphology of the penis has some similarities to that of *Marstonia*. Both have a single apocrine gland confined to the apical lobe (see Thompson, 1977, for a discussion of the morphology of *Marstonia*). The two genera have such dissimilarly shaped penises, the apocrine gland pattern must be considered convergent. *Birgella* is

characterized within the Nymphophilinae as follows.

Shell (Figs. 69–70). Large, about 6–9 mm high with about 4.3 whorls; globose, usually about 0.83–0.87 times as wide as high; some specimens as wide as high with a very ample aperture and a depressed spire. Protoconch sculptured with step-like, rugose wrinkles with superimposed spiral threads (Fig. 79–80). The spiral threads are a unique feature within the subfamily. Operculum paucispiral with about 2.5 whorls.

Penis (Figs. 81–82). With a large globose apical lobe on the left side and a short stocky tip on the right side. Tip pigmented with melanophores. Apical lobe with a large circular apocrine gland on the inner surface (incorrectly reported to be absent in an earlier report (Thompson, 1979)).

Female reproductive system (Figs. 83–84). Typical for subfamily Nymphophilinae (see

Thompson, 1979). A single seminal receptacle present and completely buried in albumen gland. Ventral canal of anterior pallial oviduct spirally offset. Lumen of canal continuous with capsule gland lumen (Fig. 84).

Radula (Figs. 76–78). With large acuminate cusps. Central tooth with 2–3 basocones on each side located on a reflected lateral ridge. Lateral teeth as in other Nymphophilinae, with a rounded basal lobe. Radular data for two specimens I examined (UF 35275, 35278) are given in Table 1. Baker (1928) and Berry (1943) gave slightly different cusp counts.

The radula of *Nymphophilus minkleyi* Taylor is figured for comparison (Figs. 73–75). *Birgella* contains a single species.

Birgella subglobosa (Say)

Paludina subglobosa Say, 1825: 125.—Haldeman, 1847: 10–11, pl. 10, fig. 7 (Type-locality: Northwestern Territory).

Somatogyrus subglobosus (Say), Tryon, 1870: 60–61, pl. 17, figs. 10–11.—Baker, 1902: 340–341, fig. 123.—Berry, 1943: 49–52, pl. 2, fig. 1 (shell), pl. 4, fig. 3 (radula), text-fig. 8 (penis).

Melania isogona Say, 1829: 277. (Type-locality: Bear Grass Creek, near Louisville, Kentucky).

Somatogyrus isogona (Say), Stimpson, 1865b: 22.—Binney, 1865: 77–78, fig. 151.

Birgella s. subglobosa (Say), Baker, 1928: 155–158.—Burch & Tottenham, 1980: 110, figs. 188, 198, 202.

Birgella subglobosa isogona (Say), Baker, 1928: 159–161, pl. 8, figs. 10–12.

Paludina pallida Lea, 1839: 22, pl. 23, fig. 104. (Type-locality: near Cincinnati, Ohio).

This is a well-known North American species. Detailed descriptions are given in Baker (1928) and Berry (1943). Some authors recognize two subspecies. The typical subspecies is said to be narrowly umbilicate or rimate and to have a thin parietal callus. The other subspecies is said to be imperforate and to have a thicker parietal callus (Baker, 1928). The material I have examined shows that these characters vary throughout the range of the species, and that they do not segregate with any geographic or ecological factor. Indeed, the differences seem to be consequences of growth. Old specimens have a thicker callus which tends to cover the umbilicus. Thus the two forms do not meet the accepted criteria for subspecies.

Birgella subglobosa is widely distributed in the central United States from Wisconsin, Michigan, and Ohio south to Arkansas and Alabama (Fig. 72). It also occurs in New York in the Mohawk and Hudson River systems. Usually it is found in large rivers and lakes. It is not confined to deep water, contrary to published statements. I have collected it in bays and sloughs at less than 1 meter depth. The snail is found most commonly in quiet water on a soft silt substrate. Specimens examined are listed in Appendix C.

APPENDIX C

Specimens of HYDROBIIDAE examined during this study are from the following museum collections, which are designated as indicated in parenthesis: Academy of Natural Sciences, Philadelphia (ANSP), Carnegie Museum, Pittsburgh (CM), Field Museum of Natural History (FMNH), Museum of Comparative Zoology, Harvard University (MCZ), Florida State Museum, University of Florida (UF), Museum of Zoology, University of Michigan (UMMZ), National Museum of Natural History (USNM).

Lepyrium showalteri (Lea)

ALABAMA.—*Bibb Co.*: Cahaba River (UMMZ 97447, UMMZ 97445, MCZ 133133); Cahaba River, near Anita (UMMZ 68301); Cahaba River, 1.6 km N. Centerville (USNM 672419, MCZ 252247); Cahaba River, Lilly Shoals (UMMZ 49272); Cahaba River, near Piper (MCZ 99174, UMMZ 69886, UMMZ 65996); Little Cahaba River (MCZ 99175, UMMZ 97444, UMMZ 97448); Little Cahaba River, 4.8 km E Piper (UMMZ 67444). *Dallas Co.*: Cahaba River Wildcat Island, near Cane Creek (UMMZ 87446). *Shelby Co.*: Coosa River (USNM 29016); Gurnee (MCZ 299176, USNM 321180, 321181); Coosa River, 16.1 km above Ft. Williams (USNM 102851, lectotype by present designation; USNM 102851a). Fort Williams was at the confluence of the Coosa River and Cedar Creek, W. of Fayetteville, Talladega Co., Alabama.

Clappia clappi Walker (= *Clappia umbilicata* Walker)

ALABAMA.—*Chilton Co.*: Coosa River, Duncans Riffle (ANSP 95307, paratypes).

Somatogyrus depressus (Tryon)

ILLINOIS.—*DeKalb Co.*: Kishwawkee Creek (MCZ 46592). *Fulton Co.*: Canton (UMMZ 116934, UF 34975). *Hardin Co.*: Elizabethtown, Ohio River (UMMZ 49781, UF 34976). *Rock Island Co.*: Rock Island (USNM 476878, USNM 512075). *Stephenson Co.*: 3.2 km S. Freeport (USNM 49781). *Washington Co.*: Okaw River, Covington (MCZ 68437).

IOWA.—*Cherokee Co.*: Cherokee (USNM 507933). *Clinton Co.*: Clinton (USNM 539849). *Dickinson Co.*: NE Okoboji (USNM 667011). *Dubuque Co.*: Dubuque (UMMZ 143740). *Emmet Co.*: Estherville (USNM 506130); Des Moines River near Estherville (USNM 526533). *Hardin Co.*: Eldora (USNM 506379, USNM 519429, USNM 514807); Iowa River, Eldora (FMNH 130351). *Humboldt Co.*: Dakota City (USNM 526532). *Johnson Co.*: Iowa City (USNM 506380, UMMZ 69940). *Muscatine Co.*: Muscatine (USNM 508369). *Scott Co.*: Davenport (USNM 121041, USNM 27904, USNM 38414—SEM radula, UF 34968–34970).

MISSOURI.—*Benton Co.*: Warsaw, Osage River (UMMZ 67435, UF 34980).

WISCONSIN.—*Brown Co.*: De Pere (FMNH 10649). *Jefferson Co.*: Pipersville Rapids, Bark River (UMMZ 116940, UF 34979); Watertown (UMMZ 143742, UF 34977). *Rock Co.*: Evansville (CM 62.24127). *Sauk Co.*: Wisconsin River (UMMZ 143743, UF 34981); Prairie du Sac (UF 34978).

Somatogyrus rheophilus Thompson

GEORGIA.—*Meriwether Co.*: Flint River, 2.7 km NE Gay (UF 40508); Flint River, 2.1 km E Gay (UF 40502); Flint River, 5.6 km SE Gay (UF 40503, 40506). *Talbot Co.*: Flint River, 5.1 km NW Carsonville (UF 40501); Flint River, 3.5 km NNW Fickling Mill (UF 40509). *Taylor Co.*: Flint River, 5.8 km NW Fickling Mill (UF 40507). *Upson Co.*: Flint River at Spewrell Bluff (type-series); Flin River, 11.9 km WSW Thomaston (UF 40504); Flint River at Yellowjacket Shoals, 9.7 km SW Thomaston (UF 31241); Flint River, 9.7 km SW Lincoln Park (UF 34902, SEM shell; UF 34903, SEM radula; UF 40511); Flint River, 11.3 km SSW Lincoln Park.

Gillia attilis (Lea)

DISTRICT OF COLUMBIA.—*Arlington Co.*: Analston (USNM 336089, USNM 252023);

Anacostia River, Buzzard's Point (USNM 697026); Popular Point (USNM 697025); Analston Id. (USNM 697015); between P.R.R. Bridge and Pa. Ave. Bridge (USNM 697021); C & O Canal (USNM 335872); near Asylum Wharf, East Branch (USNM 697023); Potomac River (CM 62.24224); above Long Bridge (CM 62.25465); Fox Ferry (USNM 251542, USNM 271700, USNM 465805, MCZ 2181, USNM 28918); E. Branch, Potomac River (UF 35025); Potomac River (UF 35024, UF 1002).

MARYLAND.—*Allegany Co.*: Cumberland (USNM 149952); Fall of the Potomac, Potomac State Forest (MCZ). *Cecil Co.*: near Charlestown (USNM 521817). *Hartford Co.*: Havre de Grace (USNM 121450). *Montgomery Co.*: Cabin John, C & O Canal (MCZ 2179); Sycamore Island (USNM 521974). *Prince Georges Co.*: Fort Washington (UMMZ 118414, UMMZ 364722); Fort Washington, Potomac River (USNM 227686); Fort Washington, Piscataway Creek (UF 35021).

NEW JERSEY.—*Burlington Co.*: Burlington (USNM 120468); Burlington, Delaware River (MCZ 57089). *Essex Co.*: Newark, Morris Canal (MCZ 186744). *Hunterson Co.*: Lambertville (USNM 536807). *Mercer Co.*: Raritan Canal, aqueduct near Princeton (CM 62.5699). *Sussex Co.*: Flatbrookville (MCZ 75217). *Warren Co.*: Phillipsburg, Delaware River (FMNH 87953).

NEW YORK.—*Albany Co.*: Albany (CM): Albany, Hudson River (USNM 465755, FMNH 59965, UF 35015). *Dutchess Co.*: Tivoli, Hudson River (MCZ). *Herkimer Co.*: Mohawk, Erie Canal (UMMZ 45998, UF 35013, USNM 697027, USNM 697028, UMMZ). *Monroe Co.*: Brighton (UMMZ 118415, UF 35014). *Niagara Co.*: Niagara Falls (USNM 473979). *Onondaga Co.*: Syracuse, Erie Canal (UMMZ 69880, UF 35019, FMNH 58688, UMMZ 69880). *Rensselaer Co.*: Troy (UMMZ 118412, UF 35012); Troy, Champlain Canal (MCZ 2178). *Ulster Co.*: Heath, Hudson River (MCZ 186739). *Wayne Co.*: Clyde (USNM 597809).

NORTH CAROLINA.—*Columbus Co.*: Lake Waccamaw (UF 28439, UF 29652, UF 28077, UF 29637, UF 29644, UF 27550, UF 35044, UF 34901—SEM shell, UF 34816—SEM radula). *Edgecombe Co.*: Swift Creek at NC Hwy. 97 (UF). *Nash Co.*: Tar River, S of Moccasin Creek (UMMZ 197725). *New Hanover Co.*: Wilmington, Greenfield Pond (UMMZ 69881). *Pitt Co.*: Little Continea River, 9.7 km SE Farmville (UMMZ 197724); S of Sandy Cross (UMMZ).

ONTARIO.—*Lincoln Co.*: Niagara-on-the-Lake (MCZ 104863).

PENNSYLVANIA.—*Bucks Co.*: Delaware River, New Hope (CM 62.5700). *Clinton Co.*: Flemington (USNM 28102). *Chester Co.*: Schuylkill River, Phoenixville (FMNH 87956). *Lancaster Co.*: Columbia (CM 62.16370, MCZ 2180, MCZ 186745). *Lycoming Co.*: Muncy, canal (MCZ). *Northampton Co.*: Delaware River, Easton (FMNH 15693, UF 35020). *Philadelphia Co.*: Philadelphia (FMNH 87950); Schuylkill Canal, Manayunk (CM 62.5701); Philadelphia (MCZ 186743).

SOUTH CAROLINA.—*Charleston Co.*: Charleston (MCZ). *Williamsburg Co.*: Lynche's Creek (USNM 63973).

VERMONT.—*Franklin Co.*: St. Albans Bay (CM 62.32653). *Grand Isle Co.*: Grand Isle, Lake Champlain (UMMZ 118422, UF 35018); Lake Champlain, Chimney Point (USNM 336443, USNM 336442, USNM 336445, USNM 336444, USNM 591730).

VIRGINIA.—*Alexandria Co.*: Potomac River (MCZ 186741, MCZ 70540). *Amherst Co.*: James River, Lynchburg (USNM 451904). *Cumberland Co.*: Cartersville, James River (MCZ 261289). *Fairfax Co.*: Dyke, near Mt. Vernon (USNM 420546); Mt. Vernon (UF 18435); near Great Falls (numerous lots, USNM, MCZ, UMMZ, UF). *Goochland Co.*: Columbia, James River (MCZ 261334). *Henrico Co.*: Richmond, James River (CM 62.24126). *Loudoun Co.*: Potomac River, 6.4 km N. Seneca, MD (USNM 697018). *Powhatan Co.*: James River across from Maidens (MCZ 261307). *Prince Co.*: Petersburg (FMNH 87949, USNM 121477).

WEST VIRGINIA.—*Jefferson Co.*: Harper's Ferry (MCZ 136500); Harper's Ferry, Potomac River (MCZ). *Morgan Co.*: Cherry Run, Potomac River (numerous lots UMMZ, MCZ, FMNH, UF).

Fluminicola nuttalliana (Lea)

OREGON.—*Lane Co.*: Willamette River, Eugene (UF 40521). *Linn Co.*: Willamette River, Albany (UF 40523, UF 40524, SEM shell).

Birgella subglobosa (Say)

ALABAMA.—*Choctaw Co.*: Tombigbee River, Ezell Fish Camp, E. of Lavaca (UF 35093). *Clarke Co.*: Alabama River, Choctaw Bluff (CM 65-57). *Colbert Co.*: Tennessee River, Mile 261.0, Union Carbide (UF 34998). *Limestone Co.*: Tennessee River, Mile

291.76. Brown's Ferry (UF 35001); Tennessee River, Mile 288.78, Brown's Ferry (UF 34999). *Monroe Co.*: Alabama River, Clairborne (UF 35099). *Sumter Co.*: Tombigbee River, Lock #3, ESE of Whitfield (UF 35095).

ARKANSAS.—*Dallas Co.*: Ouachita River, 3.9 km W. Sparkman (UF 35002). *Jackson Co.*: White River, Newport (MCZ 66659).

GEORGIA.—*Floyd Co.*: Silver Creek (UF 40639).

ILLINOIS.—*Cass Co.*: Beardstown, Illinois River (UMMZ 197758, FMNH 15694). *Cook Co.*: Chicago, Lake Michigan (FMNH 71888). *Fulton Co.*: Canton (FMNH 71890). *Gallatin Co.*: Shawneetown (FMNH 115352). *Kankakee Co.*: Kankakee Feeder (FMNH 58685). *Madison Co.*: Alton, Mississippi River (UMMZ 197760). *Mercer Co.*: Mississippi River (UMMZ 143748, MCZ 2202); Myers Slough (MCZ 2201). *Pope Co.*: Golconda, Ohio River (UMMZ 197755). *Rock Island Co.*: Moline, Mississippi River (USNM 465760). *Will Co.*: Dupage River, Joliet (FMNH 58686); Joliet (CM 62.25453). *Williamson Co.*: Blaireville, Big Muddy River (UMMZ 117191).

INDIANA.—*Dearborn Co.*: Ohio River, Lawrenceburg (FMNH 87928). *Floyd Co.*: (FMNH 58687). *Marshall Co.*: Lake Maxinkuckee (USNM 697009).

IOWA.—*Johnson Co.*: (FMNH 58701); Iowa City (UMMZ 143749). *Lee Co.*: Mississippi River, 4.7 km N Keokuk (UF 35009); Keokuk, pool above dam (MCZ 175918); Ft. Madison (UF 34997); Montrose (UF 35006). *Muscatine Co.*: Keokuk Lake (USNM 600748); Muscatine, Mississippi River (UF 31307). *Polk Co.*: Des Moines, Des Moines River (MCZ 2196); Des Moines, Bayou at N end Fort Dodge (UF 35011). *Scott Co.*: Le Clair, Mississippi River (MCZ 2197); Mississippi River, Davenport (UF 35003).

KENTUCKY.—*Campbell Co.*: mouth of Five-Mile Creek (UMMZ 70020). *Jefferson Co.*: Louisville, Falls of the Ohio (FMNH 87919).

MINNESOTA.—*Washington Co.*: Ft. Snelling, Minnesota River (MCZ 2200).

MISSOURI.—*St. Louis Co.*: Mississippi River near White House (UMMZ 177032); Jefferson Barracks (UMMZ 197756); Kirkwood, Meramec River (UMMZ 197759).

NEW YORK.—*Herkimer Co.*: Mohawk (FMNH 15520); Mohawk, Erie Canal (MCZ 62233); Mohawk, Mohawk River (CM 62.7056). *Schenectady Co.*: Schenectady (MCZ).

OHIO.—*Erie Co.*: Sandusky, Lake Erie

(CM 62.25454). *Franklin Co.*: Columbus (USNM 30139); Columbus, Ohio Canal (CM 62.7057). *Green Co.*: Clifton, Miami Canal (USNM 28515). *Hamilton Co.*: Cincinnati, (FMNH 115552); Cincinnati, Ohio River (CM 62.25457); Culloms Riffle, Ohio River (FMNH 87924); Five-Mile Creek, Ohio River (FMNH 87922); Mouth of Great Miami River (FMNH 87913); old canal bed near Harrison (FMNH 87912); 9.7 km W. Cincinnati (UMMZ 45448). *Scioto Co.*: Portsmouth, Ohio River (CM 62.8229). *Summit Co.*: (UF 35010). *Tuscarawas Co.*: Mill Race on Ohio Canal, New Philadelphia (CM 62.26560); Tuscarawas River, New Philadelphia (CM 62.25456).

QUEBEC.—*Rouville Co.*: Richelieu River, 3.2 km S. Iberville (MCZ).

TENNESSEE.—*Nolachucky River* (UF 35007).

VERMONT.—*Addison Co.*: Chimmey Point, Lake Champlain (MCZ 28232); Hospital Creek (USNM 336445). *St. Franklin Co.*: Lake Champlain, St. Albans Bay (MCZ 142046). *Grand Isle Co.*: Lake Champlain, Grand Isle, 3.2 km SE Hero (MCZ).

VIRGINIA.—*Fairfax Co.*: Great Falls (USNM 252381) (doubtful record).

WISCONSIN.—*Milwaukee Co.*: Milwaukee (MCZ).