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FRESHWATER SNAILS OF THE GENUS *ELIMIA* FROM THE COOSA RIVER SYSTEM, ALABAMA

Fred G. Thompson[1]

ABSTRACT

Four new species of *Elimia* are described from the Coosa River drainage. Nomeclatorial changes are proposed for other species. ***Elimia teretria* n. sp., *E. broccata* n. sp.** and ***E. mihalcikae* n. sp.** are endemic to Coldwater Spring, Calhoun County, Alabama. ***Elimia godwini* n. sp.** is found in streams and springs in Calhoun County and adjacent Talladega County, Alabama. It was formerly misidentified in the literature as *E. bentoniensis* (= *Goniobasis bentoniensis* Lea 1862). The names *Goniobasis bentoniensis* and *Melania sublirta* Conrad 1850 are subjective junior synonyms of *Elimia caelatura* (= *Melania caelatura* Conrad 1850), a species endemic to the Savannah River system. *Elimia caelatura* is re-described. Previously, *Elimia caelatura* had been misidentified as a species found in the Coosa River system. The Coosa River species is correctly known as *Elimia lecontiana* (= *Melania lecontiana* Lea 1841). It includes seven subspecies: *E. l. lecontiana* (Lea 1841)., *E. l. stearnsiana* (Call 1886), *E. l. excellens* (Goodrich 1935), *E. l. luteacella* (Lea 1868), *E. l. infuscata* (Lea 1862, *E. l. decorata* (Anthony 1860), and *E. l. georgiana* (Lea 1862). The species formerly known as *Elimia gerhardti* (*Goniobasis gerhardti* Lea 1862) is correctly named *E. modesta* (= *Melania modesta* Lea 1845). Systematic and taxonomic observations are provided also for *Elimia carinifera* (Lamark 1822), *E. modesta* (Lea 1845), *E. carinocostata* (Lea 1854) and *E. catenaria* (Say 1825).

Key words: Gastropoda, Prosobranchia, Pleuroceridae, *Elimia*, freshwater snails, Alabama, Georgia, Coosa River, Savannah River.

INTRODUCTION

This paper describes four new species of *Elimia* from Calhoun County, Alabama. Three are from Coldwater Spring, near Anniston. A fourth species is more widely distributed in Calhoun and Talladega Counties and had been misidentifies in the literature as *E. bentoniensis* (Lea 1862). Taxonomic changes of two other *Elimia* from the Coosa River system are also proposed. These are the species formerly known as *Elimia caelatura* (Conrad 1850) and *Elimia gerhardti* (Lea 1862)

A major problem in working with *Elimia* is the long list of species names associated with the genus (Graf, in press). Tryon (1865) lists approximately 500 species that have been proposed within *Elimia*. Additional species described since then increase the list to approximately 550. The numerous papers by Goodrich placed 136 names in synonymy among 109 spe-

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cies and subspecies that he recognized as valid. The remaining names are left without further mention.

Goodrich had little regard for nomenclatorial seniority. He provided little or no discussion regarding names that he synonymized, nor did he provide amended descriptions or illustrations of the species he recognized as valid. The result is that most of the species he recognized can be identified only with extraordinary difficulty and with a high degree of uncertainty. This leads one who attempts species identifications to despair and abandon the task, or to settle for questionable determinations.

Few species of *Elimia* have been described sufficiently to determine characteristics of the juvenile shell, ontogenetic changes, and features of the operculum. The internal anatomy remains virtually uninvestigated for comparative purposes. Thus, the status of most of these nominate taxa must be considered unresolved at this time. Resolution of their status requires extensive and intensive field surveys in order to determine reproductive cycles, ontogenetic changes in character-states, ecological deployment patterns, local geographic distribution patters, and local population variation. Field samples should be large enough to include all of the growth stages that are available at the time they are collected. This data is available for very few species. In most *Elimia* the apical whorls of the adult shells are strongly eroded, and important specific characteristics are lost from the shell, such as juvenile sculpture patters, total whorl development, suture development and spire shape. The adult shell may be very similar among species that have very different juvenile characteristics. Species with similar juvenile shells may have very different adult shells.

The allocation of species of *Elimia* into natural categories reflecting phylogenetic relationships is not possible on the basis of available data. This is due in part to the lack of (1) morphological data that would permit comparisons among diverse species and (2) the lack of genetic data that could determine these relationships. Goodrich (1940, 1941, 1942) recognizes 22 species-groups in the genus *Goniobasis* (= *Elimia*), but he did not characterize these groups other than as would be indicated by their content. Clearly, the groups are not monophyletic. Some of the groups, such as the *carinocostata*-group and the *catenaria*-group, appear to be unnatural assemblages in which the included species are alike only because of convergence in adult shell characters. Juvenile shell and opercular traits are inconsistent with these groupings. As an example, in the *carinocostata*-group Goodrich (1941), and Burch (1989) included five species: *Elimia carinocostata* (Lea 1845), *E. bentonensis* (Lea 1962), *E. curvicostata*

(Reeve 1861), *E. dickinsoni* (Clench & Turner 1956) and *E. induta* (Lea 1862). The first two occur in the Mobile drainage system. They have neomelanian opercula and two types of juvenile sculpture. The other three species are found in smaller Gulf Coastal rivers to the east. They have paleamelanian opercula and a common juvenile sculpture pattern that differs from the Mobile basin species (Mihalchik & Thompson, in press). This paper continues the use of the species-groups recognized by Goodrich, but only for the convenience of reference to earlier literature. Close phylogenetic relationships among the included species are not implied.

METHODS

The shell measurements given below apply to about 95% of the adult individuals in a given sample. Many specimen-samples contain a few individuals that are much larger than their cohorts. They are excluded from the range of variation for measurements of those particular samples. For example, a description may state that the adult shell is *about* 7-11 mm long, because this represents the vast majority of the specimens in a sample, but there may be a few adult specimens in that sample that are significantly longer or shorter. More precise meristic data are given in Tables 1-5.

The length of the shell is measured from the top of the apical plug to the base of the last whorl. Because of the extreme decollation of the apex and the variable point at which the apical plug develops in many species, the ratio of shell length to shell width has little comparative value other than as a general descriptor of the shell. This ratio varies considerably even between sub-adult and mature specimens (see *Elimia broccata*). The length of the last whorl is measured from the previous suture above the lip insertion to the base of the shell. It includes one full whorl. Because of the extreme decollation of the apex in many species the length of the last whorl is the only remaining longitudinal measurements that reflects the dimension of shell length relative to other growth parameters.

The width of the shell is standard, and is measured across the last whorl perpendicular to the axis of the shell. The aperture height is measured from the posterior (upper) corner to the base of the aperture parallel to the shell axis. The aperture width is measured from the outside of the outer peristome to the inside edge of the columellar callus and is perpendicular to the shell axis. The number of whorls is counted from the end of the apical plug to the base of the shell. Remnants of previous whorls above the apical plug may be present, but they are excluded from the data presented in this paper because of the variable number that may be retained and their condition. Some individuals may have two apical plugs, the uppermost of which encloses an unoccupied whorl. In such cases only measurements taken from whorls below the lower plug are included in the data. All photographs in a set are enlarged to the same extent, and the shell length of a given specimen is indicated in the caption.

The operculum contains useful characters for differentiating groups of species, and two types of opercula exist among the species discussed in this paper. A *paleomelanian operculum* has a relatively large and centrally positioned nucleus with slowly expanding whorls (Fig. 126). A *neomelanian operculum* has a nucleus located close the basal-columellar margin and has rapidly expanding whorls. Growth occurs through regularly expanding whorls so that the relative width of the operculum does not change (Fig. 118). Among species with a strong neomelanian structure, the operculum grows much like an opening fan (Figs. 117), and the relative width may increase with growth.

GENUS *Elimia* H. & A. ADAMS, 1854

***Elimia mihalcikae* new species**

Vernacular name: latticed elimia

Figs. 1-3, 8

Diagnosis. A small, slender, decollate species up to 11 mm in length and 0.41-0.55 times as wide as long. The sides of the spire diverge at about 14-20°. The adult shell retains 3-5 whorls. The color is uniform greenish yellow in adults. The whorls are scalariform and are flat above the peripheral cord-like keel. They are sculptured with strong, widely spaced ribs above the peripheral keel. The operculum is paleomelanian in form.

Shell. A small, slender, costate species of *Elimia* that reaches a length of about 7-11 mm and is about 4.2-5.5 mm wide. The shells are thin and translucent. Adult shells are uniformly light greenish-yellow. The whorls of juvenile shells and the early whorls of sub-adults are reddish brown. The shell is decollate and retains about 3-5 whorls in adults; rates of juvenile shell growth indicate that about 9 whorls are developed. The straight-sided scalariform spire diverges at an angle of about 14-20°. The width of the shell is about 0.41-0.51 times the standard length, and about 0.73-0.88 time the length of the last whorl. The whorls are flat-sided or weakly concave above a scalloped, strong peripheral keel. The apical plug is bluntly obtuse and nearly vertical. The protoconch consists of a single smooth whorl that is about 0.4 mm in diameter (Fig. 12). The following whorl of the teleoconch is about 0.5 mm wide and develops a weak peripheral angle which becomes the peripheral carina on subsequent whorls (Fig. 13).

A comparison of various stages of growth indicate that the shell has a total development of about twelve whorls throughout its life. During early growth stages the whorls are smooth above the peripheral keel. Subsequent whorls soon develop strong posteriorly arched axial ribs that are about half as wide as their interspaces (Figs. 1-3). The ribs extend from the suture to the periphery, and cause the peripheral carina to become weakly scalloped where the ribs intercept it. A weak sub-peripheral carina also may be present at the suture. Occasionally there are additional obsolete supra-peripheral spiral cord that form weak knobs where they cross the ribs. Adult shells have about 7-12 ribs on the last whorl. The ribs become obsolete and indistinguishable on the last whorl or two in old adults (Fig. 8). The microsculpture in the inter-spaces between the ribs consists of about 5-7 very weak axial threads, which in turn are crossed by very fine incised spiral striations. Decalcified shells have a thin, fragile periostracum.

The aperture is sub-ovate or rhomboidal in shape, and is about 0.72-0.94 times as wide as high. The base is rounded or bluntly angular in outline. The height of the aperture is 0.59-0.68 times the length of the last whorl, and 0.30-0.40 times the standard length. The columellar margin of the aperture is narrow and concave. The parietal callus is very thin. The aperture is vertical in lateral profile but is slightly recurved in outline between the suture and the base. Shell measurements are given in Table 1.

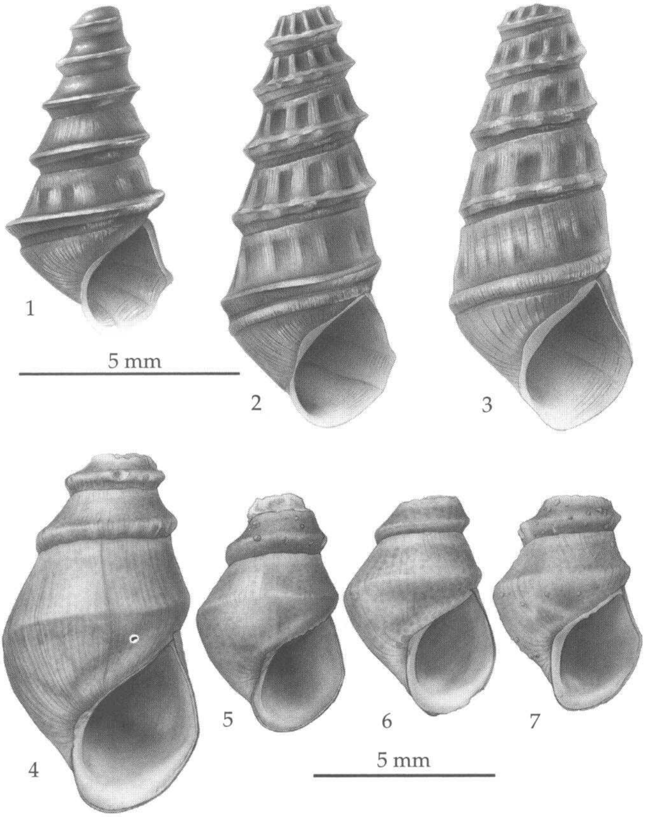
Operculum (Fig. 109-110). The paleomelanian operculum is thin and transparent; the outer surface with few incremental growth striations. Paucispiral, consisting of 2.5 whorls. Nucleus slightly impressed, located at about 0.35 of distance from base to apex, and about 0.35 of distance from left margin. Muscle attachment scar narrowly ovate-elliptical.

Type locality. Alabama, Calhoun Co., Coldwater Spring, 5.6 miles west of Oxford (33°36.1'N, 85°55.6'W). HOLOTYPE: UF 263213; collected 28 June, 1976, by Fred G. Thompson. PARATYPE: UF 230361, UF 263213, UF 263263, UF 267630, UF 267631, UF 267732, USNM 880392, UMMZ 266702, MCZ 317947, UA, ANSP 402012; same locality as the holotype.

Coldwater spring is located at the west base of Coldwater Mountain. It is about 6 miles west of the city of Oxford and serves as a municipal water source for the city of Anniston. The spring forms a large kidney-shaped pool that is enclosed by a cement retainer wall and discharges by a dam at its west end (Fig. 133). The shallow spring-run below the impoundment flows over a gravel substratum for about 200 yds and then enters Coldwater Creek, a tributary of Choccolocca Creek, which is tributary to the Coosa River. The spring flows from a brechiated zone in the Jacksonville Fault in the Weisner Formation. It has an average flow of about 22,000 gal./minute. The water has a total hardness of 100 ppm expressed as $CaCO_2$ and is nearly uniform in temperature throughout

TABLE 1. *Elimia mihalcikae* new species. Measurements in mm based on the holotype (UF 263213) and 14 paratypes (UF 267631) and. SL = standard length, LW = length of last whorl, SW = standard width, AH = aperture height, AW = aperture width, Wh = whorls remaining, std = standard deviation.

	SL	LW	SW	AH	AW	Wh	SW/SL	AH/SL	SW/LW	AH/LW	AW/AH
holotype	9.6	5.0	4.0	3.0	2.5	4.1	0.44	0.35	0.79	0.61	0.85
min.	7.4	4.2	3.6	2.8	2.1	3.0	0.41	0.30	0.73	0.59	0.72
max.	11.0	5.5	4.5	3.6	2.9	5.0	0.51	0.40	0.88	0.68	0.94
avg	8.3	4.7	3.7	3.0	2.4	4.1	0.46	0.37	0.80	0.64	0.81
S^2	1.50	0.79	0.54	0.47	0.37	0.55	0.03	0.03	0.05	0.03	0.06



FIGS. 1-7. New species of *Elimia*. FIGS. 1-3. *Elimia mihalcikae* new species. FIGS. 1-2. Paratypes (UF 267631). FIG. 3. Holotype (UF263213). FIGS. 4-7. *Elimia teretria* new species. FIG. 4. Holotype (UF 260982). FIGS. 5-7. Paratypes (UF 236650).

the year, varying between 16-18°C (Warman & Causey, 1961). The brook is clear and is less than 0.1 m deep. *Elimia mihalcikae* was found only on gravel and cobbles in the spring run where it was associated with *Stiobia nana* Thompson & McCaleb, 1976 and the species of *Elimia* listed below. We did not find it in Coldwater Creek, nor in quieter parts of the spring run. The snail occurs only in the upper half of the run where it is abundant on cobbles and gravel. It is not found on vegetation. Other snails found in the spring run in quieter waters are *Physella* sp., *Elimia carinocostata "liedyana"* (Lea 1862), *E. modesta* (Lea 1845) [= *E. gerhardti*, Lea, 1862] and two new species of *Elimia* described below.

Distribution. This species is endemic to Coldwater Springs Run (Fig. 132, arrow).

Conservation status. *Elimia mihalcikae* is abundant within its very limited range. Coldwater Springs and the spring run are protected by the city of Anniston. No additional protective measures are required.

Remarks. This species is compared to *Elimia cochliaris* (Lea 1868) and to a lesser extent to *E. taitiana* (Lea 1841). These three inhabit small spring-fed streams and spring brook within the Mobile Basin. They have in common small, slender, attenuate shells and similar paleomelanian opercula. *Elimia cochliaris* (Figs. 9-11) is readily recognized by it's strong lyrate spiral sculpture. It is found in small streams in the Cahaba and the Black Warrior drainages. *Elimia taitiana* has a smooth shell with a weak peripheral angle to the whorls. It is found in small streams in the lower Alabama and Escambia drainages. It is being redescribed and figures elsewhere (Mihalcik & Thompson, in press).

Etymology. This species is named for Elizabeth L. Mihalcik in recognition of her studies on pleurocerid systematics.

Elimia teretria, new species

Vernacular name: auger elimia

Figs. 4-7

Diagnosis. A very small species that is usually less than 7 mm long, and has a strongly pagodiform shell with a strongly eroded apex. Usually two or fewer whorls remain. The whorls have a strong peripheral angle and are weakly concave above the periphery. Juvenile shells may have an additional weak spiral ridge below the periphery and sub-obsolete riblets on the first postembryonic whorl. The operculum is paleomelanian in form.

Shell. A small-sized, strongly-scalariform species that reaches a maximum length of about 10 mm, but seldom exceeds 7 mm in length. Normally the shell is broadly conical and auger-shaped and is about 4-5 mm in diameter perpendicular to the shell axis. The width of the shell is about 0.76-0.87 times the length of the last whorl. The periostracum is thick and leathery and is uniformly light brown. The interior of the aperture is livid in color, and the shell is moderately thin and translucent.

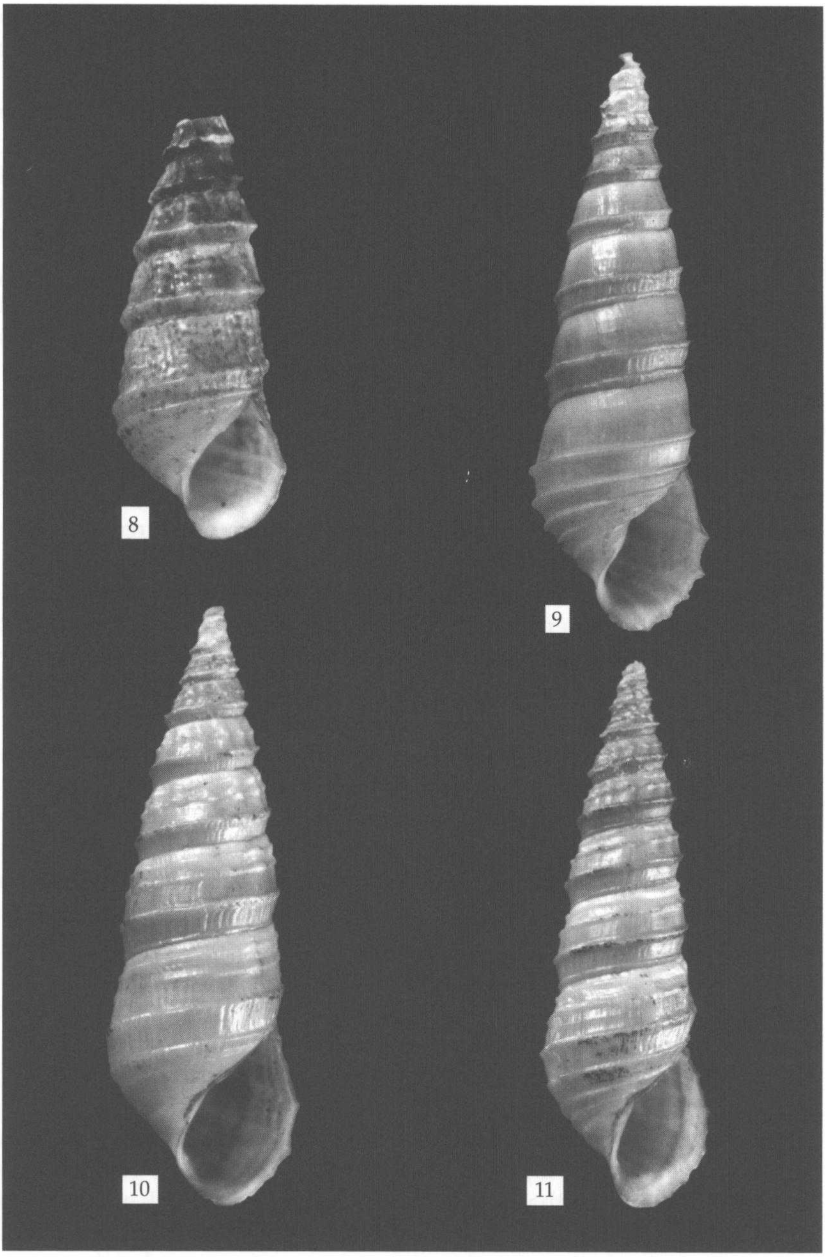
The shell is short and truncate due to erosion of the apex. Normally only about 2.3-3.0 whorls remain below the apical plug. Seldom are there more than 2.7 whorls except among juvenile shells. Only very rarely does an adult retain 4 whorls, as in the holotype. The first 3-4 whorls of the juvenile shell are slender and elongate, and then the whorls rapidly increase in relative width (Figs. 14-15). The rates of growth indicate that about 4-6 juvenile whorls are lost from above the truncate adult apex, yielding about 7-8 whorls in total development. In adult shells the sides of the spire diverge at an angle of about 32°-46°. They diverge strongest in young adult. Older specimens become more gradually tapered. The whorls are flat above the carina, and nearly flat below. The shoulder of the whorls slope at and angle of about 30°-35° to the axis of the shell. Juvenile shells have a single strongly compressed spiral keel at the periphery of the whorls (Fig. 14). Juvenile whorls 1.6 mm in diameter or smaller may have a second, weaker, sub-peripheral spiral carina or a turgid spiral swelling about midway between the periphery and the base of the body whorl. Both carina overlay internal grooves. The older adult shells have a single strong peripheral carina on the upper whorl. The carina becomes obtusely angulate on the body whorl and then obsolete and rounded on the last quarter whorl (Fig. 4). Ribs or folds are absent on all growth stages. The microsculpture consists of very fine incremental growth striations and finer segments of spiral striations.

The aperture is ovate-elliptical in shape. In younger specimens it is nearly quadrangular. The outer lip is straight above the periphery. The baso-columellar angle is evenly rounded and slightly canaliculate. The columella is weakly concave, and moderately and uniformly wide. The height of the aperture is 0.63-0.70 times the length of the last whorl, and is about 0.0.70-0.81 times as wide as high. Shell measurements are given in Table 2.

Operculum (Figs. 111-112). The paleomelanian operculum is broadly ovate in shape and is about 1.25 times as high as wide. Upper columellar margin straight or weakly indented. Thick, leathery, reddish-brown, with three rapidly expanding whorls. Nucleus weakly indented and forming a small rise on inner surface; nucleus located at about 0.3 of distance from base to apex, and at about 0.4 of distance from columellar margin.

TABLE 2. *Elimia teretria* new species. Measurements in mm based the holotype (UF 266982) and on 15 paratypes (UF 230650). The length of the shell includes the distance from the apical plug to the base of the peristome. Because of the extreme decollation of the apex, and the variable point at which the apical plug develops in this species, the ratio of standard shell length to shell width has little comparative value other than as a general descriptor of the shell. SL = standard length, LW = length of last whorl, SW = standard width, AH = aperture height, AW = aperture width, Wh = whorls, Sp = angle of spire.

	SL	LW	SW	AH	AW	Wh	Sp	SW/LW	AH/LW	AW/AH
holotype	10.6	7.8	6.1	5.3	3.7	3.0	33.0	0.77	0.67	0.70
min.	6.1	4.8	4.1	3.3	2.4	2.3	34.0	0.76	0.63	0.70
max.	7.8	6.6	5.0	4.2	3.2	3.0	46.0	0.87	0.70	0.81
avg	6.6	5.5	4.5	3.7	2.8	2.5	39.5	0.83	0.67	0.74
S^2	0.5	0.5	0.3	0.3	0.2	0.2	3.9	0.03	0.02	0.03



FIGS. 8-11. *Elimia* species. FIG. 8. *Elimia mihalcikae* new species (Paratype, UF 232107). FIGS. 9-11. *Elimia cochliaris* Lea 1868); Little Cahaba River, at road from Piper to Montivello, Bibb Co., Alabama (UF 74057). FIG. 8 = 10.3 mm.

Outer surface nearly smooth, with occasional fine incremental striations. Attachment scar on inner surface narrowly elliptical, minutely granular in texture.

Type locality. Alabama, Calhoun County, Coldwater Springs, 5.7 miles west of Oxford. HOLOTYPE: UF 260982; collected 28 July, 1978 by Fred G. Thompson. PARATYPES: UF 230650, UF 260980, UF 260981, UF 263206, UF 263210, UF 263214, UF 263254, UF 263259, UF 263265, UF 263256, UF 267733, USNM 880391, UMMZ 266701, MCZ 317946, ANSP 402011 (numerous specimens in each lot). *Elimia teretria* was found only on gravel and cobbles in the spring run below the impoundment where it was associated with *E. mihalcikae* n. sp. and *Stiobia nana* Thompson & McCaleb, 1978. We did not find it in Coldwater Creek.

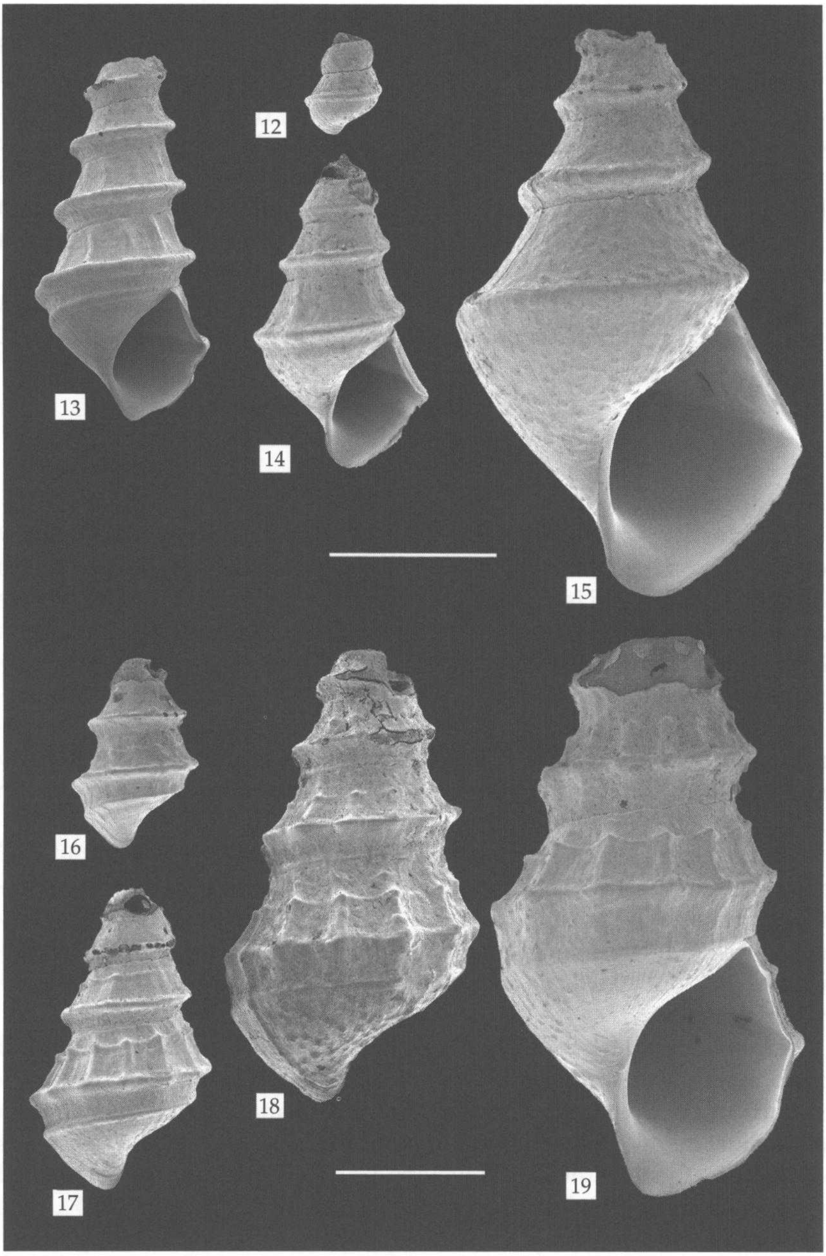
Distribution. This species is endemic to Coldwater Spring Run and immediately adjacent portions of Coldwater Creek.

Conservation status. The species is abundant within its range. Coldwater Springs and the spring run are protected by the city of Anniston, which uses the spring as a municipal water source. No additional protective measures are required.

Remarks. The periostracum of the shell is pocked with randomly distributed algal attachment scars which do not penetrate the periostracum (Figs. 15, 21). These are formed after shell formation. They are absent in zones of new growth immediately behind the peristome. Similar features occur on the shells of other *Elimia* at Coldwater Springs.

The shell of *E. teretria* is similar in sculpture and form to some smooth-shelled small-stream species that inhabit the Tennessee River system, such as those of the *Elimia simplex* species-group. A close phylogenetic relationship between *E. teretria* and *E. simplex* is not postulated other than that they are similar-appearing species and close relationships elsewhere are not apparent. Goodrich (1941) recognized three species in the group, and included 22 synonyms, but it is beyond the scope of this paper to resolve the systematics of the *E. simplex* species-group. None of the previously known forms of the *E. simplex* group have been reported from the Alabama River system. *Elimia teretria* differs from known forms of the *E. simplex* group by its small size and its very pronounced short pagodiform shell.

The shell of *Elimia teretria* has some superficial similarity to immature *E. carinocostata* (Lea 1845) and *E. modesta* (Lea 1845) (= *E. gerhardti*, see below). It differs from that of *E. carinocostata* by (1) its much smaller size, (2) its fewer whorls, (3) its scalariform shape with a strong peripheral keel, (4) its lack of other spiral sculpture except for a weak sub-peripheral cord in the juvenile stage of some shells, (5) its lack of ribs or longitu-



FIGS. 12-19. *Elimia* species. SEM micrographs of juvenile shells. FIGS. 12-13. *Elimia mihalcikae* new species (UF 267631). FIGS. 14-15. *Elimia teretria* new species (UF 230650). FIGS. 16-19. *Elimia broccata* new species (UF 271230). Scale bars 1.50 mm.

dinal folds at any stage of growth, and (6) its paleomelanian operculum. *Elimia carinocostata* is a large species about 15-20 mm in length with 5-7 whorls, the early whorls are slightly scalariform, but not to the exaggerated degree that occurs in *E. teretria*, nor do they have as strong a peripheral keel even among juveniles. The apical whorls have a single narrow raised spiral thread above the periphery, and one or more around the base of the body whorl, longitudinal folds are present on all but the first two whorls of the juvenile shell and the lower-most whorls of the adult shell. *Elimia carinocostata* has a neomelanian operculum.

Etymology. The species name *teretria* is from the Classical Greek τερετριον, a diminutive wood bore, and alludes to the shape of the shell.

Elimia broccata new species

Vernacular name: brooch elimia

Figs. 20-24

Diagnosis. A medium-sized, dark-reddish *Elimia* with an strongly eroded apex. The shell retains 4.2-5.1 whorls at maturity. It attains a length of up to17.5 mm and is about 0.41-0.47 times as wide as high. The whorls are strongly scalariform with a strong nodular peripheral keel. The whorls bear stout axial ribs that form sharp nodes where they intersect the peripheral keel and also where they are crossed above by one or two narrow spiral cords. The ribs are very reduced in size above the upper spiral cord. The base is smooth in adults. The sides of the spire are nearly straight. They diverge at about 20-28°. The operculum is paleomelanian in form.

Shell. Small to medium-sized, attaining a total length of about 17.7 mm in adults; narrow, last whorl about 6.1-7.7 mm wide; shell about 0.48-0.62 times as wide as long. Spire very slightly convex in outline, nearly straight sided; forming an angle of about 20-28°. Rate of growth indicates that about 10 whorls are developed; eroded adult shell with 4.2-5.1 whorls remaining.

Periostracum dark reddish-brown with a narrow grayish sub-sutural zone. Interior of aperture livid with a reddish tinge. Juvenile shell strongly scalariform with a strong nodose peripheral carina and a smaller smooth carina just below the periphery (Figs. 16-19). The lower carina becomes obsolete by the time the shell develops 4-5 whorls. Beginning on the third whorl bold radial ribs develop above the peripheral keel (Fig. 17). The ribs are crossed above by a narrow spiral cord that forms sharp nodes where it crosses the ribs (Figs. 17-21). An additional weaker nodose spiral cord may be present between the periphery and the upper cord (Fig.

18). The sculpture continues almost undiminished through the development of the adult shell.

The aperture is elliptical in shape, and is about 0.58-0.65 times as wide as high. The outer lip has an indented notch underlying the end of the peripheral carina. The canaliculate base of the aperture is broadly angular and projects downward slightly. The narrow columellar margin curves evenly into the parietal margin. Shell measurements are given in Table 3.

Operculum (Figs. 113-115). The paleomelanian operculum is broadly ovate in shape with a nearly straight parietal margin; about 1.4 times as high as wide with 2.5 rapidly expanding whorls. Light brown and leathery. Outer surface smooth with occasional incremental striations. Nucleus sunken, about 0.33 times distance from columellar margin and about 0.37 times distance from base to apex. Muscle attachment scar narrowly elliptical, smooth.

Type locality. Alabama, Calhoun Co., Coldwater Spring, 5.6 miles west of Oxford (33°36.1'N, 85°55.6'W). HOLOTYPE: UF 263204; collected 28 August, 1996 by Fred G. Thompson. PARATYPES, all topotypic: UF 245099, UF 263224, UF 263261, 263269, UF 271230, UF 267734, UMMZ 266703, USNM 880393, MCZ 317944, ANSP 402013; same data as the holotype; UF 263261; collected August 30, 1996 by Fred G. Thompson; UF 267734; collected 22 May, 1997 by James C. Godwin.

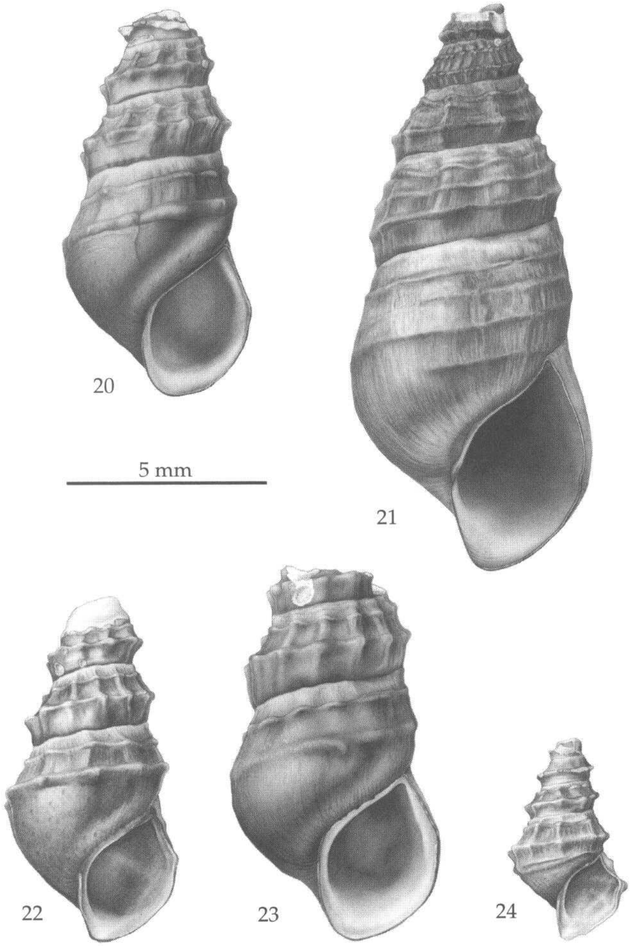
Elimia broccata inhabits a shallow, quiet marshy zone along the south side of the spring run where it is found primarily on aquatic angiosperms.

Distribution. This species is endemic to the type locality.

Conservation status. Coldwater Springs and the spring run are protected by the city of Anniston which uses the spring as a municipal water

TABLE 3. *Elimia broccata* new species. Measurements in mm based on two sets of paratypes and the holotype (UF 271280). The first set of measurements is based on eight large adult specimens (UF 263224). The second set, which includes only the average and the standard deviation, is based on fourteen sub-adults (UF 270231). The standard length of the shell includes the distance from the apical plug to the base of the peristome. SL = standard length, LW = length of last whorl, SW = standard width, AH = aperture height, AW = aperture width, Wh = whorls.

	SL	LW	SW	AH	AW	Wh	SW/SL	SW/LW	AH/LW	AW/AH	AH/SL
holotype	13.0	9.0	6.1	5.5	3.4	5.0	0.47	0.68	0.61	0.62	0.42
min.	14.5	9.1	6.2	6.2	3.7	4.2	0.41	0.74	0.61	0.58	0.37
max.	17.4	11.9	7.6	7.7	4.7	5.1	0.47	0.70	0.65	0.65	0.47
avg.	15.4	10.1	6.9	6.4	4.0	4.7	0.44	0.66	0.63	0.62	0.41
S^2	1.27	0.83	0.54	0.60	0.36	0.35	0.03	0.03	0.02	0.02	0.02
avg	9.9	7.0	5.2	4.5	3.2	3.4	0.53	0.75	0.65	0.71	0.46
S^2	1.01	0.54	0.34	0.34	0.28	0.25	0.03	0.02	0.04	0.05	0.04



FIGS. 20-24. *Elimia broccata* new species. FIG. 20. Holotype (UF 271280). FIGS. 21-24. Paratypes (UF 271230). FIG. 20 = 13.0 mm.

source. No additional protective measures are required.

Remarks. The sculpture of the shell is somewhat similar to that of *Elimia carinifera* (Lamarck 1822). The latter species is much larger, the whorls are rounded with a deep suture but (1) they are not scalariform, (2) they lack a strong peripheral crest, and (3) the adult shell typically has a straight-sided and complete spire with about nine whorls. The nodular sculpture of *E. broccata* contrasts with the simpler ornamentation found in *E. carinifera*.

Etymology. The name *broccata* is derived from the Latin *broccus*, a brooch or ornamental band. The name refers to the band of ornate spiral sculpture above the periphery.

Elimia carinifera (Lamarck 1822)
Vernacular name: sharp-crest elimia

Melania carinifera Lamarck, 1822. Histoire Naturelle des Animaux sans Vertèbres ... 6: 167. (Habite dans l'Amerique septentrionale, pay des Chérokées, dans un ruisseau qui se jette dans la rivière d'Estan-Alley).

The illustration given in Burch (1989: 129, fig. 331) is typical for *Elimia carinifera*. It depicts a species that has a shell with a complete spire containing about 8-9 whorls that are separated by a moderately impressed suture and bear a scalloped carina about half way between the periphery and the suture.

A great deal of confusion exists concerning the identity of this species. This is due in part to the large number of names that have been synonymized incorrectly with *Elimia carinifera*, and thereby attributed greater morphological variation and geographic deployment to the species than actually exists. Goodrich (1941) lists *Melanian perangulata* Conrad 1849, *M. percarinata* Conrad 1849, *M. nebulosa* Conrad 1849, *M. symmetrica* Conrad 1849, *M. conradi* Brot 1862, *Melania bella* Conrad 1834, *M. vittata* Anthony 1854, *M. imbricata* Anthony 1854, and *Goniobasis anthonyi* Lea 1862 as synonyms. The first five names are associated with the Savannah River fauna and belong in the *Elimia catenaria* species-group. Their taxonomic status remains undetermined (*see* APPENDIX).

Melania vittata is described from "Alabama." As pointed out by Tryon (1865: 159) its shell is similar to *Elimia taitiana* (Lea 1862). Nothing about its description suggests a close similarity to *E. carinifera*.

Melania imbricata is another species described from "Alabama." Tryon (1865: 233) states that the label accompanying the type specimens indicates that they came from Georgia. No population identifiable as this taxon has been recognized. It appears to belong in the *Elimia symmetrica* species-group, and bears little similarity to *E. carinifera*.

Goniobasis anthonyi must be considered a *nomen dubium*. It was described from an unspecified locality in Tennessee. Nothing about the shell suggests that it is closely related to *Elimia carinifera*. It has a smooth shell and a pronounced canaliculate aperture.

Melania bella was described from "stream in north Alabama." It has a slender attenuated shell with "a prominent crenulated line near the summit of each [whorl]." It is the only name that may be a synonym of *Elimia* *carinifera*.

Lamarck (1822: 6) stated that *Melania carinifera* came from a stream flowing into the East Alabama River in the Cherokee country of North America. Essentially, this is the Coosa River system. Goodrich (1941: 2) stated that *Elimia carinifera* was found "in springs, brooks, creeks and occasionally in rivers of the Alabama River system, north Georgia to Monroe Co., Alabama, and in parts of the Tennessee River system in the vicinity of Chattanooga, Hamilton Co., Tennessee." New studies are needed to verify this distribution. The taxonomic status of populations throughout this range needs to be re-examined.

***Elimia modesta* (Lea 1845)**

Vernacular name: coldwater elimia

Figs. 25-30

Melania modesta Lea 1845, *Proceedings of the American Philosophical Society*, 4: 166. (Chattahoochee River, Columbus, Georgia).

Goniobasis parva Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 14: 264; Lea, 1863, *Journal of the Academy of Natural Sciences of Philadelphia*, 5: 297, pl. 37, fig. 129. (Georgia).

Goniobasis whitei Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 14: 266; Lea, 1863, *Journal of the Academy of Natural Sciences of Philadelphia*, 5: 310, pl. 37, fig. 151. (Georgia).

Goniobasis gerhardti Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 14: 270; Lea, 1863, *Journal of the Academy of Natural Sciences of Philadelphia*, 5: 330, pl. 38, fig. 187; Goodrich, 1941, *Occasional Papers of the Museum of Zoology, University of Michigan*, (427): 3. (Chattanooga [Chattooga] River, Georgia).

Goniobasis etowahensis Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 14: 264; Lea, 1863, *Journal of the Academy of Natural Sciences of Philadelphia*, 5: 299, pl. 37, fig. 133. (Etowah River, Georgia; preoccupied by *Melania* [*Goniobasis*] *etowahensis* Reeve, 1861).

Goniobasis quadricincta Lea 1864 (in part), *Proceedings of the Academy of Natural Sciences of Philadelphia*, 16: 112; Lea, 1864, *Observations on the genus* Unio, *etc.*, 11: 87, pl. 23, fig. 33. (Coosa and Cahawba Rivers, Alabama).

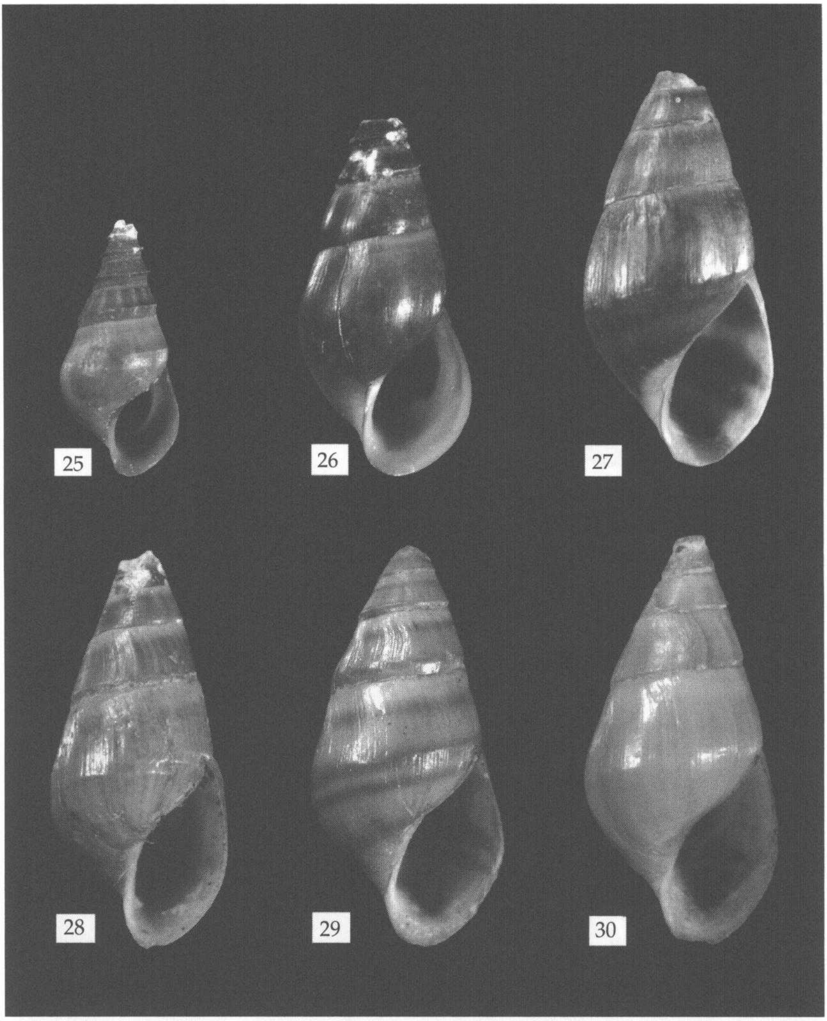
Goniobasis subrhombica Lea 1864, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 16: 3, 111; Lea, 1864, *Journal of the Academy of Natural Sciences of Philadelphia*, 6: 132, pl. 23, fig. 34. (Hog Creek, north Georgia).

Goniobasis murrayensis Lea 1868, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 20: 152; Lea, 1868, *Journal of the Academy of Natural Sciences of Philadelphia*, 6: 334, pl. 54, fig. 13. (Swamp Creek, Whitfield Co., Georgia).

Goniobasis venusta Lea 1868, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 20: 152; Lea 1868, *Journal of the Academy of Natural Sciences of Philadelphia*, 6: 336, pl. 54, fig. 17. (Coosa River, Alabama).

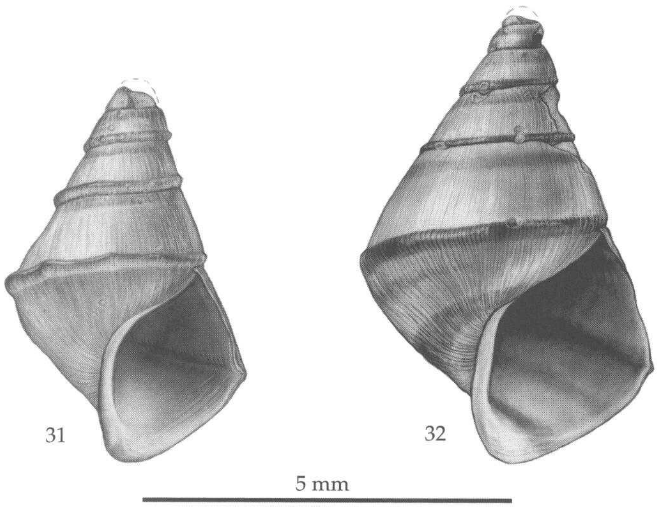
Goniobasis canbyi Tryon 1873, *Smithsonian Miscellaneous Collections*, (253): 260, fig. 500 (not *Goniobasis canbyi* Lea 1862).

Elimia gerhardti (Lea), Burch, 1987, *North American Freshwater Snails:* 136, figs. 361, 362, 373; Lydeard, *et al.*, 1998, *Malacologia*, 39: 185.

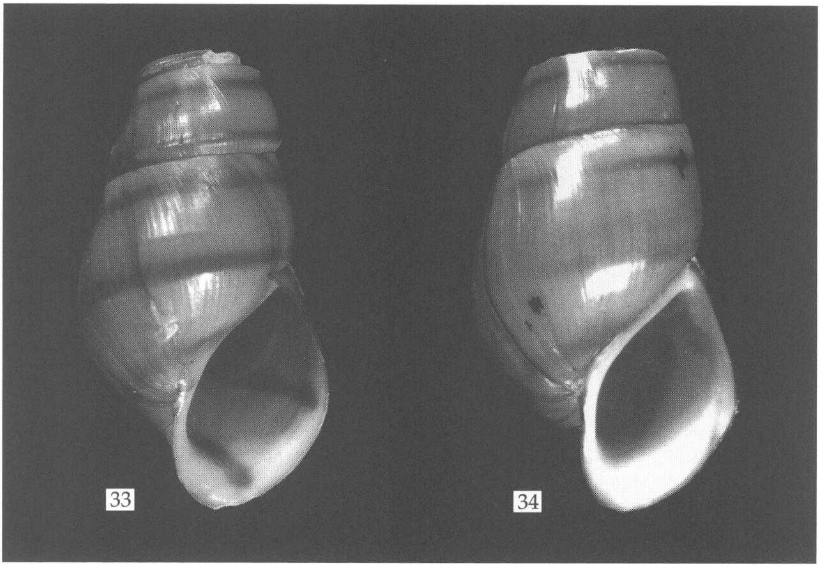


FIGS. 25-30. *Elimia modesta* (Lea 1845). FIGS. 25-26. Spring 2 miles E of Fayetteville, Cedar Creek drainage, Talladega Co., Alabama (UF 232181). FIG. 27. HOLOTYPE (USNM 119189). Locality unknown. FIGS. 28-30. Choccolocca Creek, White Plaines, Calhoun Co., Alabama (UF 74639). FIG. 27 = 15.0 mm.

Most of the synonymy is taken from Goodrich (1941). All of these names are junior subjective synonyms of *Melania modesta* Lea 1845. The name *modesta* must be adopted as the earliest available name for this species. The holotype of *Melania modesta* Lea 1845 (Fig. 27) is a typical specimen of the species formerly known as *Elimia gerhardti* (Lea 1862) . It is more



FIGS. 31-32. *Elimia flava* (Lea 1862). Tallapoosa River, 7.7 mi. SSW of Daviston, Tallapoosa Co., Alabama (UF 230679). Scale bar = 5 mm.



FIGS. 33-34. *Elimia flava* (Lea 1862). Tallapoosa River, Wadley, Randolf Co., Alabama (UF 74450). FIG. 33 = 17.6 mm shell length.

strongly banded and darker than usual, but not uniquely so (Fig. 26). The very weak peripheral angle is a frequent shell feature in this species, and most population samples have some such specimens. The species is widely distributed in tributaries and small streams within the Coosa River system of Alabama and Georgia (Goodrich, 1941; Bogan & Pierson, 1993). Undoubtedly, the type locality "Chattahoochee River, Columbus, Georgia" is incorrect. It does not occur in the Appalachicola River system. Extensive field surveys in the Chattahoochee River drainage, tributary to the Appalachicola, by the author between 1966 and 1999 and by previous investigators have not found this species there.

Elimia modesta has a short truncate shell that seldom reaches16 mm in length (Figs. 25-30). The juvenile shell has a strong peripheral carina, and a much weaker carina just below the suture (Figs. 25, 100-101). In addition there are strong vertical ribs that are about twice as wide as their intervals. The ribs tend to be confined between the two carina. The upper carina is lost in adults. Frequently they retain some indication of the ribs. Generally the adult shell also retains an obsolete peripheral angle. Otherwise the adult shell is smooth. The rate of growth indicates that the snail attains about 10 whorls in life, of which 4-5 remain in the adult. The spire of the juvenile shell is conspicuously concave in outline. The spire of the adult shell is straight-sided or very weakly convex in outline. The shell is grayish-brown with a light zone just below the suture. Occasional specimens have up to four rust-colored bands, which may be very broad and cause the shell to be very dark colored, as in the holotype.

The operculum is elongate-ovate in shape and consists of two rapidly expanding whorls (Figs. 115-116). The nucleus is located near the base and is weakly indented. The outer surface has coarse incremental striations. The muscle attachment scar is elongate and sub-elliptical. It is almost half the width of the operculum, and extends from the nucleus to the apex. Its surface bears numerous fine granules.

Elimia modesta is similar to *E. flava* (Lea 1862). The latter is endemic to the Tallapoosa River system, a tributary of the Coosa River. *Elimia modesta* does not occur in the Tallapoosa system. *Elimia flava* is a larger, more robust species reaching a length of 17-18 mm The growth rate indicates that about 10 whorls are formed (Figs. 32, 34), of which 2-3 usually remain in adult shells. Usually the shell has two bold rust-colored spiral bands on a light yellow background (Figs. 33-34). Occasional specimens lack bands. The sculpture of the juvenile shell differs from *E. modesta*. *Elimia flava* has a broadly conical juvenile shell with a pronounced spiral carina at the periphery. The suture usually lies on top of the ridge which causes the spire to be perfectly conical, or the suture may insert at the bottom of the ridge causing the spire to be weakly scalariform (Figs. 31-32).

The *Elimia carinocostata* species-group

***Elimia carinocostata* (Lea 1854)**

Vernacular name: fluted elimia

Figs. 35-39

Melania carinocostata Lea 1845, *Proceedings of the American Philosophical Society,* iv: 165; Lea, 1848, *Transactions of the American Philosophical Society,* 10: 62, pl. 9, fig. 40; Tryon, 1865, *American Journal of Conchology,* 1: 164, figs. 316-317; Goodrich, 1941, *Occasional Papers of the Museum of Zoology, University of Michigan,* (427): 4; Burch, 1989, *North American Freshwater Snails,* 1: 134. (Type locality: Alabama).

Melania scabrella Anthony *in* Reeve 1861, *Monograph of the Melania,* spec. 388. (Type locality: Georgia).

Goniobasis leidyana Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 14: 264; Lea, 1863; *Journal of the Academy of Natural Sciences of Philadelphia,* 5: 322, pl. 38, fig. 173. (Type locality: Benton County?, Alabama).

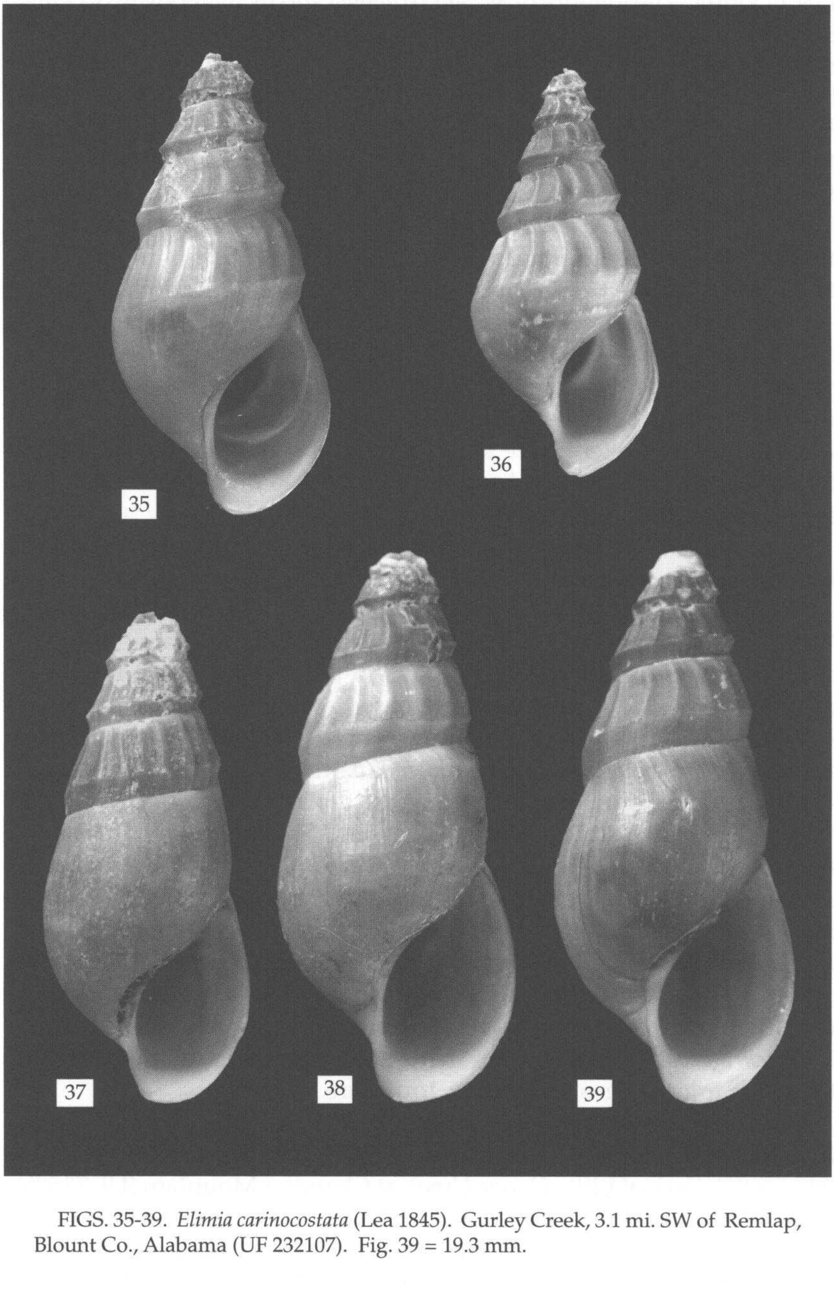
Goniobasis strenua Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 14: 267; Lea, 1863, *Journal of the Academy of Natural Sciences of Philadelphia,* 5: 316, pl. 37, fig. 161. (Type locality: Benton County, Alabama).

The synonymy given above is taken from Goodrich (1941). Tryon (1865) and Goodrich (1941) included three names they considered synonyms of *Elimia carinocostata*: *Melania scabrella* Anthony 1861, *Goniobasis strenua* Lea 1862 and *Goniobais leidyana* Lea 1862). The original description and illustration of *Goniobasis strenua* do not differ significantly from typical *carinocostata,* and there is no serious question concerning it's status as a synonym.

Three forms may warrant separate specific recognition on the basis of shell morphology and discrete geographic distributions. These are *carinocostata, scabrella* and *leidyana.* No taxonomic changes are proposed at this time due to the need for additional study. The three forms are illustrated for the purpose of discussion. The upper juvenile whorls of typical *Elimia carinocostata* have strong vertical ribs and a strongly carinate periphery (Figs. 36, 105). The ribbing usually continues onto the upper adult whorls (Figs. 35-39). Typical *Elimia carinocostata* is found in tributaries of the lower and middle Alabama-Coosa systems.

The juvenile shell of *leidyana* has weak vertical ribs and a weaker peripheral keel confined to the uppermost whorls (Figs. 40, 102). The ribs and keel do not extend onto the adult whorls (Figs. 40-45). It is found in the middle-upper part of the Coosa system.

The form that I identify tentatively as *scabrella* is a large, robust taxon (Figs. 46-49) in which the early juvenile whorls are attenuate and scalariform with vertical ribs (Figs. 103). The sculpture does not occur on the lower whorls of the adult shell. This form appears to be confined to some small headwater tributaries of the Coosa River in Polk and Floyd coun-



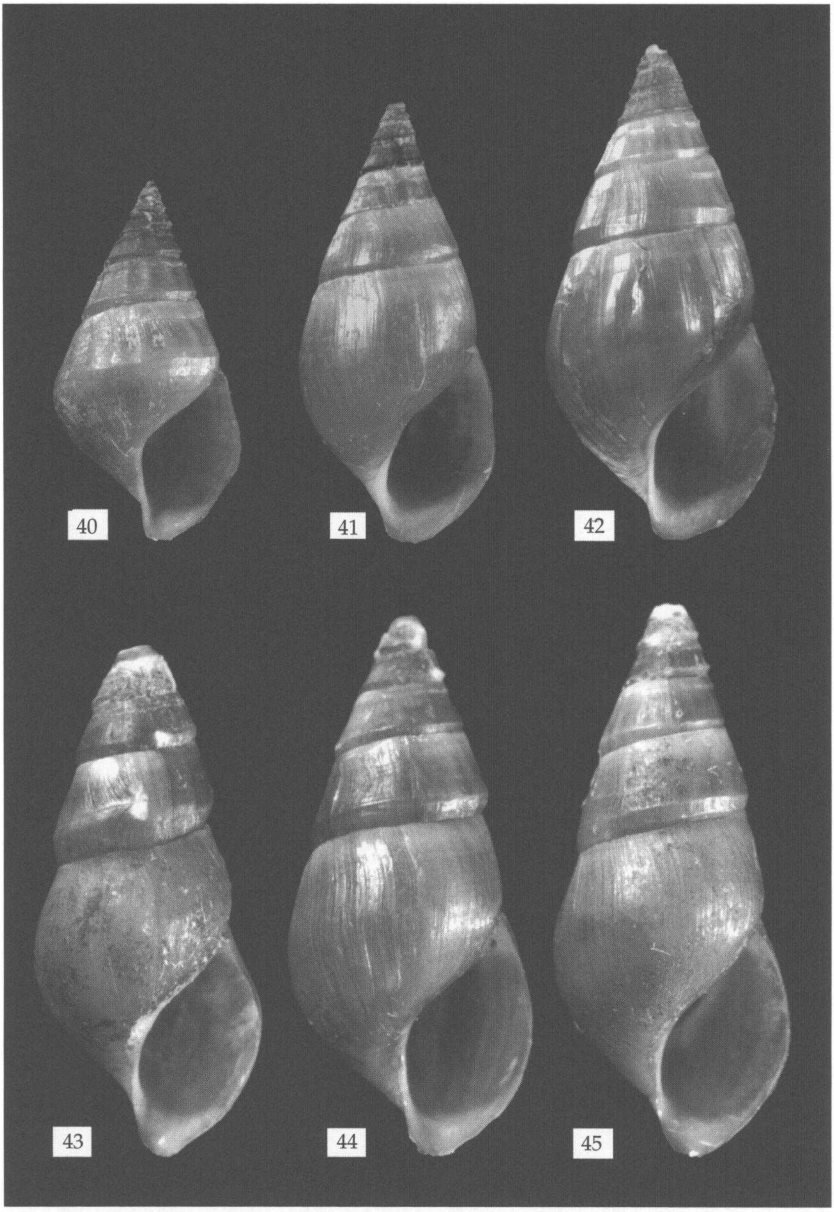
FIGS. 35-39. *Elimia carinocostata* (Lea 1845). Gurley Creek, 3.1 mi. SW of Remlap, Blount Co., Alabama (UF 232107). Fig. 39 = 19.3 mm.

ties, Georgia. The identity of *Melania scabrella* and its relationship to *Elimia carinocostata* leave much in doubt. The figure given by Reeve (1861: 388) shows a strongly ribbed shell with a canaliculate aperture. It appears to be a juvenile specimen. No locality is indicated other than Georgia. I have not examined any material from northwest Georgia that complies fully with the description or the figure. Thus, my identification of populations from Floyd and Polk counties as *scabrella* may not be correct. However, specimens from the collection of the Alabama Museum of Natural History, now in the Florida Museum of Natural History, identified by H. H. Smith and C. Goodrich comply with this identification.

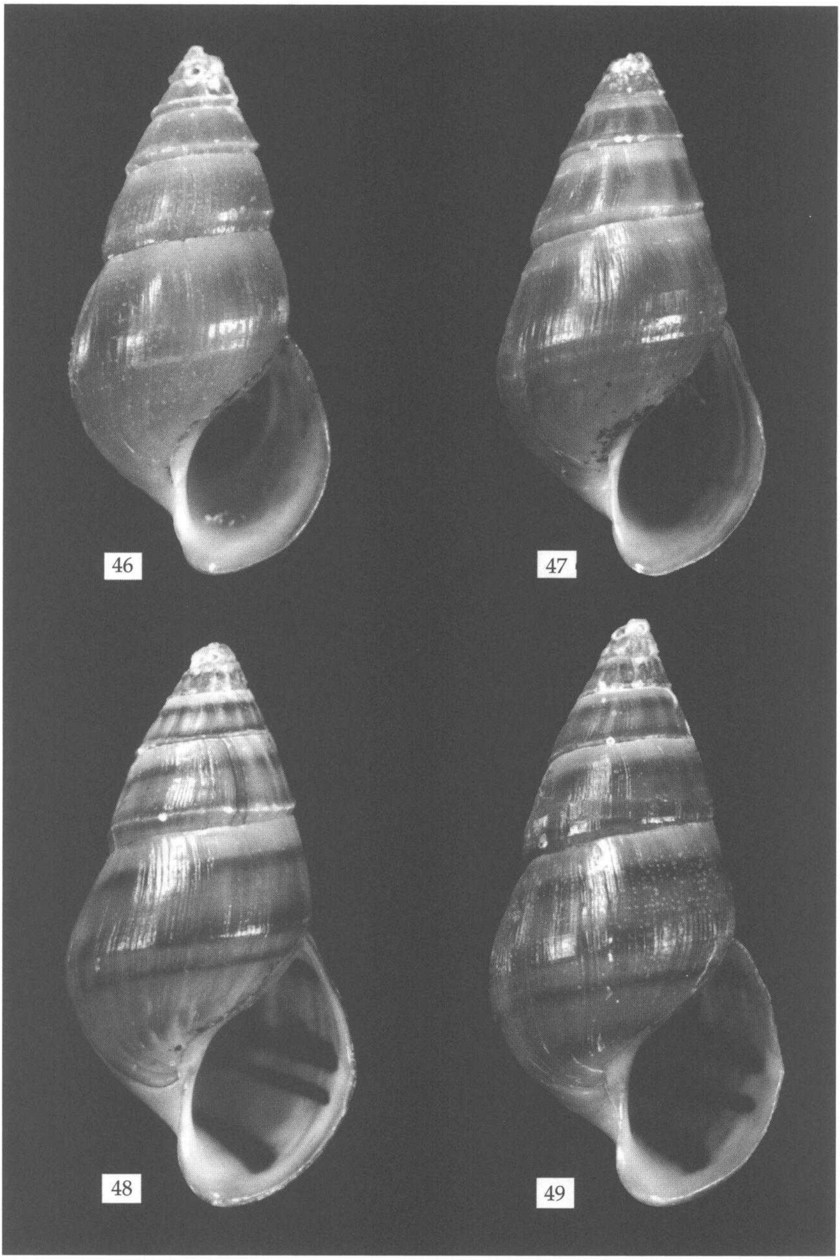
Most of the specimens in museum collections that are identified as *carinocostata* include only adult shells that lack juvenile whorls. They are of limited use for determining their taxonomic identities and for determining the distribution of each of the forms. Furthermore, other *Elimia* from the Coosa system have look-alike adult shells at terminal growth because their early whorls have been eroded so one cannot be certain about the correct identification of such specimens.

Separation of *Elimia carinocostata* into two or more species is supported by genetic data. Lydeard *et al.* (1997) reported on the genetic diversity of some *Elimia* from the Mobile Basin. They showed that *Elimia "carinocostata"* consists of at least two distinct and disparate clades that are recognizable as species on the basis of the mitochondrial 16S rDNA gene sequences. The samples were based on old adult specimens that lacked the earlier whorls of the spire. Samples from Camp Branch Creek and Waxahatchee Creek, Shelby Co., Alabama (5A-2, 11A-1, 11A-2, 11B-1, 11B-2) came from populations that are typical *carinocostata.* Samples from Beaver Creek, Little Canoe Creek and Shoal Creek, St. Clair Co., Alabama came from populations that are typical *leidyiana*. The material I examined for determining the identity of these populations is listed below. It includes citations only for those streams listed by Lydeard *et al.* and does not include the other streams from where either of these taxa occur. Lydeard *et al.*, did not examine specimens of *scabrella*. Genetic data for that taxon is lacking. I refrain from proposing taxonomic changes in *E. "carinocostata"* before the genetic and morphological identities and the geographic ranges of the three forms are resolved.

Specimens examined. ALABAMA. *St. Clair Co*.: Beaver Creek, Greensport (UF 73366, 73467); Little Canoe Creek, 1.5 mi. above Gallant (UF 73601); Fork of Little Canoe Creek at Chandler Mountain (UF 73575); Fork of Little Canoe Creek (UF 73430); Shoal Creek at junction with Coosa River (UF 73558). *Shelby Co*.: Camp Branch Creek, nr. Shelby Springs (UF 73476, UF 73549). Waxahatchee Creek (UF 73442, UF 73510, UF 73539);



FIGS. 40-45. *Elimia carinocostata "leidyana"* (Lea 1862). Cane Creek, Pelham Range, Ft. McClellen Military Reservation, Calhoun Co., Alabama (UF 264441). Fig. 42 = 17.5 mm.



FIGS. 46-49. *Elimia carinocostata "scabrella"* (Anthony 1861). Cedar Creek at Clyde Road, Cedartown, Polk Co., Alabama (UF 211380). Fig. 46 = 22.5 mm.

Waxahatchee Creek, 3 mi. SE of Shelby (UF 73381)Waxahatchee Creek, 4 mi. above mouth (UF 73437, UF 73494); Waxahatchee Creek, 8 mi. SW of Columbiana (UF 73548); Mill Creek, branch of Waxahatchee Creek, Shrader's Mill (UF 73525).

Remarks. The operculum of *Elimia carinocostata* (Fig. 120-121) is similar to that of *Elimia modesta* (Figs. 115-116). It is broadly elliptical in shape, and it's operculum is neomelanian in structure with about 2.3 rapidly expanding whorls. The nucleus is located near the lower columellar margin at about 0.20 of the distance from the base to the apex and about 0.25 of the distance from the columellar margin. The outer surface has numerous coarse incremental striations. The muscle attachment scar is about half as wide as the operculum, and it's surface is finely granular in texture. An operculum of each of the forms *leidyana* (Figs. 122-123), and of *scabrella* (Figs. 124-125), are illustrated for comparison.

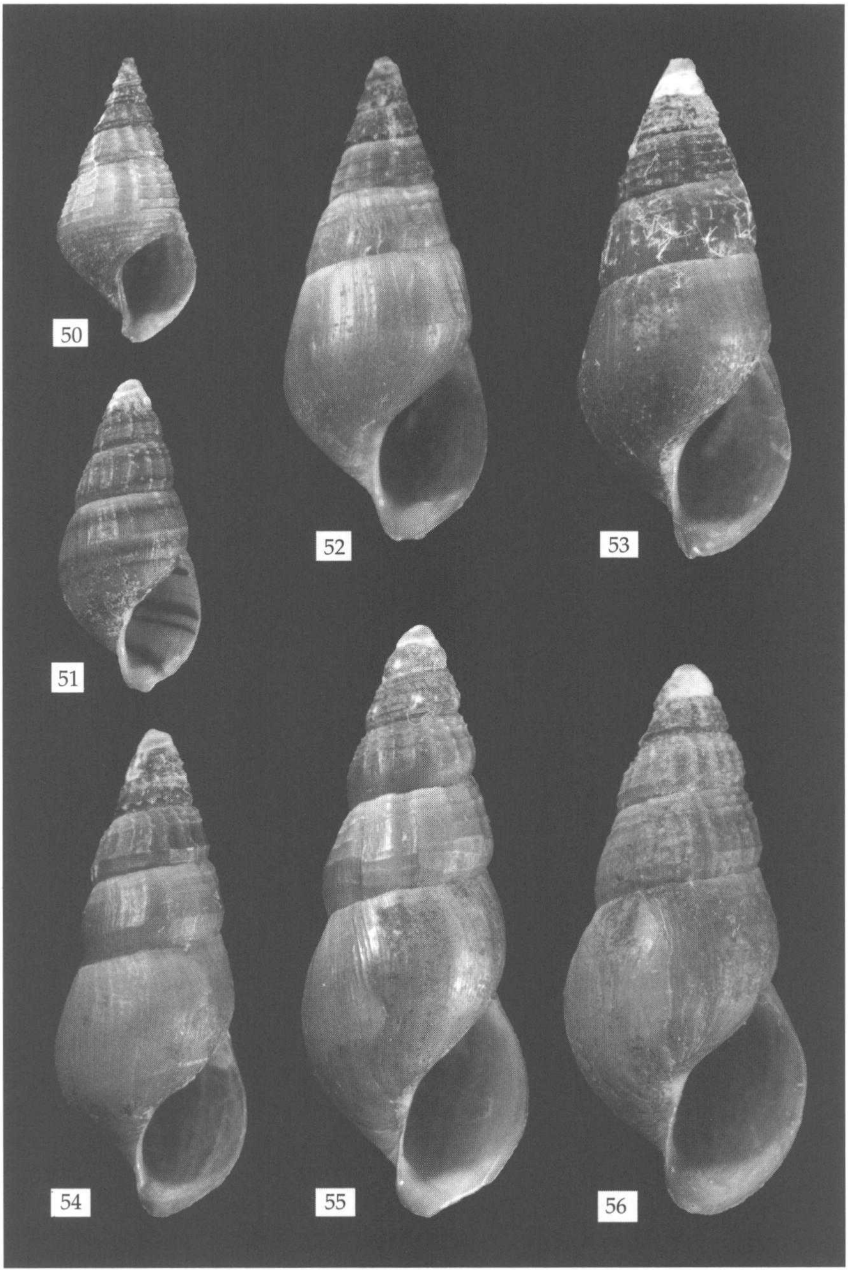
***Elimia godwini*, new species**

Vernacular name: rusty elimia

Figs. 50-56

Diagnosis. A large, slender species up to 26 mm long and 0.33-0.44 times as wide as high with a weakly convex spire. The upper whorls are cancellate with low, widely-spaced axial ribs and 2-5 spiral threads. The lower-most whorls of adult with coarse growth striations. Mature shells have about 5-7 whorls that are separated by a strongly impressed suture. Aperture narrow, with a thin vertical columellar lip. The operculum is neomelanian in form.

Shell. Color uniformly light brown; occasional specimens with four reddish bands (Fig. 51). This is a large-sized but slender species of up to 26 mm long. Adult shell about 0.33-0.44 times as wide as high. Spire straight-sided in juveniles (Figs. 50, 52, 104), but becoming slightly convex in outline at maturity (Figs. 53-56). Sides of spire diverging at an angle of about 34-40°. Last whorl 0.55-0.66 times as wide as high, consisting of about 0.59-0.65 of shell length. Mature shell with about 4.8-6.9 whorls remaining below apical plug. The rate of growth of juvenile shell indicating that about 2-3 whorls are lost above the apical plug. Suture moderately impressed, becoming strongly impressed on last two whorls of older shells. Sculpture of first six whorls of juvenile shell consisting of low, widely spaces ribs crossed by 2-5 thin spiral threads above periphery and about 5-6 finer spiral threads on the base (Fig. 104). The ribs and spiral sculpture become diminished and usually discontinue after the sixth or seventh whorl. The aperture is spindle-shaped and relatively narrow, 0.53-0.59 times as wide as high, about 0.37-0.43 time length of



FIGS. 50-56. *Elimia godwini* new species. Corn Creek, Pelham Range, Ft. McClellen Military Reservation, Calhoun Co, Alabama. FIGS. 50-55. Paratypes (UF 263201). Fig. 56: Holotype (UF 271284). Fig. 56 = 21.6 mm.

shell, and about 0.61-0.67 times length of last whorl. Columellar lip thin, straight and vertical. Outer lip uniformly rounded to base, thin and fragile, slightly retracted at the periphery. Basal lip projecting slightly downward and forward.

Measurements based on 25 adult shells are given in Table 4.

Operculum (Figs. 118-119). Ovate-elliptical in shape with a slightly concave parietal margin. Neomelanian, with about 2.5 rapidly expanding whorls. Nucleus relatively small, located at about 0.15 of the distance from the base to the apex, and at about 0.35 from the columellar margin. Outer surface sculptured with rugose incremental striations and wrinkles. Muscle attachment scar narrow, with a very fine granular texture. The operculum from a gerontic adult is illustrated (Fig. 117) to show how late growth stages may effect the shape.

Type locality. Alabama. Calhoun County, Ft. McClellen Military Reservation, Pelham Range, Cane Creek; 33°34.8' N, 85°54.7' W. HOLOTYPE: UF 271284. PARATYPES: UF 263201, UF 264440, USNM 880394, UMMZ 266704, MCZ 317945, ANSP 402014; same data as the holotype.

Distribution. This species is known only from northeastern Alabama in Calhoun County and Talladega County. Goodrich (1941) reported this species as *Goniobasis bentoniensis* from St. Clair County. I have seen no specimens from there.

Specimens examined. ALABAMA. *Calhoun Co*.: Ft. McClellen Military Reservation, Pelham Range, Willett Springs (UF 263200); Cane Creek, 3.5 mi. NW of Anniston (UF 263274); Spring Branch, a tributary of Cane Creek(UF 71661); Ohatchee Creek (UF 73576); Ohatchee Creek, at Reed's Mill (UF 263277); a spring run at Reed's Mill (UF 263279); Sulphur Springs, on Tallasseehatchee Creek, 7 mi. W of Jacksonville (UF 73405, UF 263242); Little Tallasseehatchee Creek, 5 mi. S of Jacksonville (UF 73582); small tributary to Tallasseehatchee Creek, 7 mi. W of Jacksonville (UF 263239); Tallassehatchee Creek, 1.6 mi. SW Jacksonville (UF 232026); Blow Nesbit's

TABLE 4. *Elimia godwini* new species. Measurements in mm based on 24 paratypes (UF 263201) and the holotype (UF 271284). The standard length of the shell includes the distance from the apical plug to the base of the peristome. SL = standard length, LW = length of last whorl, SW = standard width, AH = aperture height, AW = aperture width, Wh = whorls, Sp = angle of spire.

	SL	LW	SW	AH	AW	Wh	SW/SL	SW/LW	AH/LW	AW/AH	LW/SL
holotype	21.6	14.0	9.4	8.7	5.0	6.2	0.44	0.67	0.62	0.57	0.64
min.	18.9	10.9	6.8	7.3	4.0	4.8	0.33	0.55	0.61	0.53	0.59
max.	26.5	16.2	10.0	9.9	5.5	6.9	0.44	0.68	0.67	0.59	0.65
avg	21.3	13.1	8.05	8.44	4.69	6.06	0.38	0.61	0.65	0.55	0.62
S^2	1.42	1.20	0.91	0.59	0.34	0.71	0.04	0.04	0.03	0.03	0.85

Lake, nr. Jacksonville (UF 73392); Cedar Springs, 0.2 mi. N of Cedar Springs Village, 3.8 mi. W of Jacksonville (UF 236459, UF 263250); Rex Branch, Angel (UF 73516); Seven Springs, 6.5 mi. WNW Jacksonville (UF 232025); Maxwellborn Spring, 4.1 mi. ENE Jacksonville (UF 232027); Glass Springs, 3.2 mi. E of Alexandria (UF 232029); McCullars Springs, 3,8 mi. N of Alexandria. *Talladega Co.*: Talladega Springs, 3 mi. SW of Fayetteville (UF 232116).

Remarks. *Elimia godwini* is one of the most common species of freshwater snails within its range. It inhabits slow-moving streams where it is found on sand and on gravel substrates. Frequently it is associated with *E. carinocostata "liedyana."* It is remarkably consistent in it's characteristics. The principal variation is in the intensity of the sculpture on the upper whorls. The vertical ribs and spiral threads may be quite bold on some specimens, but these and other shell features show little variation between populations.

Goodrich (1941) related this species to *Elimia carinocostata* without providing a reason for doing so. The neomelanian opercula of the two species are quite similar. However, the juvenile shell traits of *E. carinocostata* are too different to indicate a close relationship between the two species. The shell of *Elimia godwini* is similar to that of *E. striatula* (Lea 1842) from the Tennessee system because of the cancellate sculpture on the upper whorls. However, *E. striatula* has a more slender shell with a straight-sided spire, and the spiral sculpture extends down the spire to the last whorl.

Goodrich identified this species as *Goniobasis bentoniensis* Lea 1862. The name *Goniobasis bentoniensis* is a junior subjective synonym of *Elimia caelatura* (Conrad 1850) from the Savannah River System (*see* APPENDIX).

Etymology. I take pleasure in naming this species after James C. Godwin of the Alabama Natural Heritage Program, in appreciation for the assistance he has given me on this project. The vernacular name, "rusty elimia," was applied to this species when it was formerly identified as *E. bentoninsis* (see Turgeon *et al.*, 1998: 65). The name "rusty elimia" is retained for *E. godwini* because vernacular names are not tied to former scientific names.

Elimia lecontiana (Lea 1841)

Vernacular name: rippled elimia

This species from the Coosa River system was formerly referred to by Goodrich (1935: 1) and subsequent authors as *Goniobasis* [*Elimia*] *caelatura* (Conrad, 1849). The name caelatura cannot be applied to any taxa found in the Coosa River system. *Melania caelatura* Conrad 1849 was described from the Savannah River. It is the common large-river species in the Savannah River near Augusta, Georgia, and its tributary, the Broad River.

Anthony *in* Reeve (1860) seems to have been the first to apply the name *caelatura* to a species from the Coosa River. Goodrich (1935: 2) stated that "Conrad assigned the species to the Savannah River, a mistake for which a southern correspondent of his appeared to have been responsible." Later Goodrich (1936: 29) stated "Conrad received his shells from J. Hamilton Couper, who lived in eastern Georgia. The Savannah River was given as the type locality. Five other melanian species, described at the same time, were also so assigned. Yet all are northwestern Georgian, distinctly different from coastal plain shells."

The fauna of the Savannah River was poorly known in 1936, and its molluscan fauna still remains understudied. Recent collections from the Savannah River confirm that the name *caelatura* is correctly associated with that river, and not with the Coosa River. *Elimia caelatura* is discussed below in the APPENDIX.

Not withstanding that the name *caelatura* had been incorrectly applied to a species of *Elimia* from the Coosa River, the name *Melania lecontiana* Lea 1841 is the senior name available for the Coosa River species under consideration. Its availability predates *caelatura* by eight years, and it should have been the name Goodrich used for the Coosa River species. *Elimia lecontiana* is in need of careful systematic study in order to determine the status of the subspecies recognized by Goodrich (1941). The subspecies Goodrich recognized as *caelatura* must bear the next available name, *Melania decorata* Anthony, 1860 which is now identified as *Elimia lecontiana decorata* (Anthony 1860). The following name changes are in order. Synonymies and distributions for the subspecies follow Goodrich (1941).

The vernacular name Rippled Elimia is retained for this species.

Elimia lecontiana lecontiana (Lea 1841)

Figs. 57-60

Melania lecontiana Lea 1841, *Proceedings of the American Philosophical Society,* 2: 11-15; Lea, 1841, *Transactions of the American Philosophical Society,* 8: 177, pl. 5, fig. 20; Tryon, 1865, *Smithsonian Miscellaneous Collections,* (201): 167-168. (Georgia)

Goniobasis caelatura lecontiana (Lea). Goodrich, 1941, *Occasional Papers of the Museum of Zoology, University of Michigan,* (427): 5.

Elimia caelatura lecontiana (Lea), Burch, 1989, *North American Freshwater Snails*: 144.

Goniobasis semigradata Reeve 1861, Monograph of the *Melania;* species 472. (Alabama).

Distribution. "Creeks of northwest Georgia and northeast Alabama."

Elimia lecontiana infuscata (Lea 1862)
Figs. 61-64

Goniobasis infuscata Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 14: 270; Lea, 1863, *Journal of the Academy of Natural Sciences of Philadelphia,* 5: 330, pl. 338, fig. 188. (Georgia and Coosa River, Alabama).
Goniobasis gerhardtii Lea; Tryon, 1865, *Smithsonian Miscellaneous Collections,* (201): 226-227 (in part).
Goniobasis caelatura infuscata (Lea); Goodrich,1941, *Occasional Papers of the Museum of Zoology, University of Michigan,* (427): 5.
Elimia caelatura infuscata (Lea); Burch, 1989, *North American Freshwater Snails,* p. 144, fig. 410; Lydeard, *et al.*, 1998, *Malacologia,* 39: 185.

Distribution. "Bartow, Floyde, Gordon, and Mussay counties, Georgia; Cherokee, Etowah and St. Clair counties, Alabama." Type locality: Coosa River, Alabama.

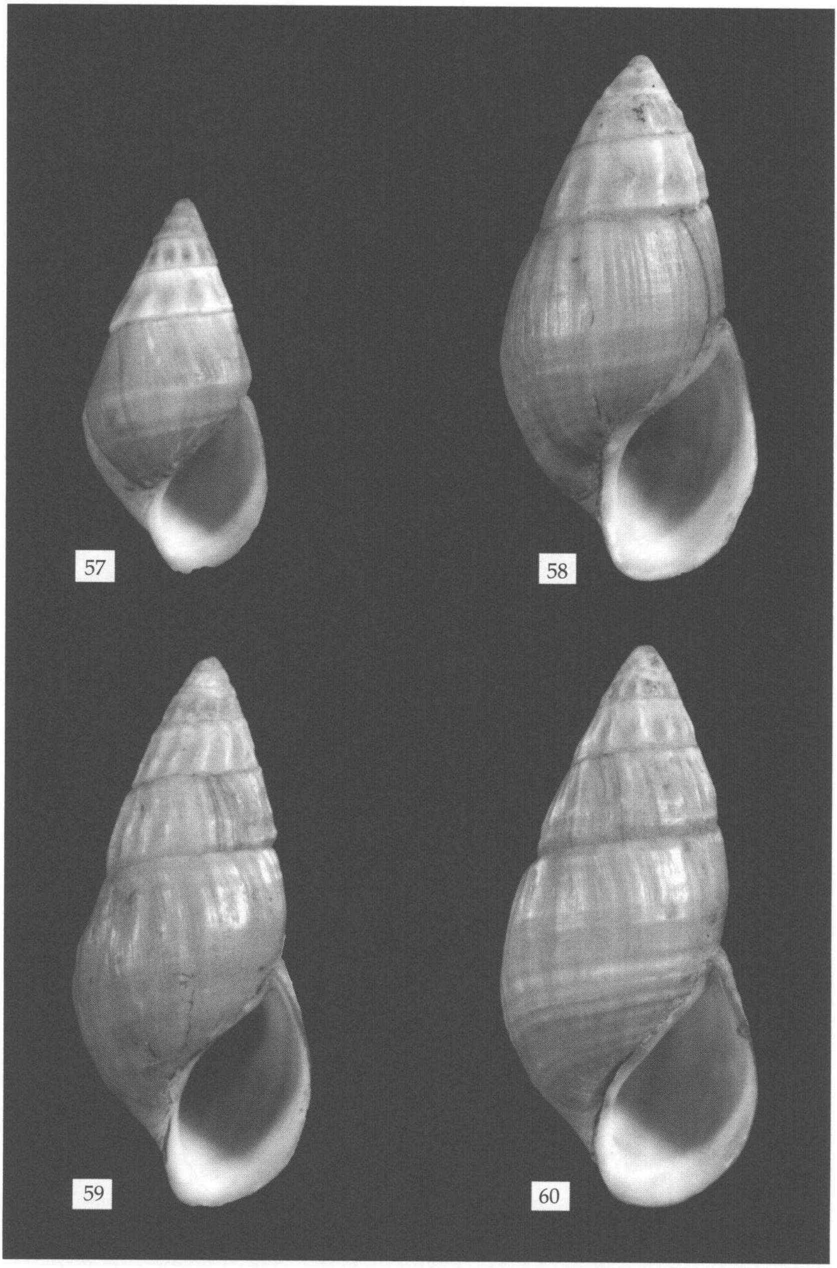
Remarks. A juvenile specimen is figure for comparison with other species (Fig. 106). The specimens was collected at Spring Creek, 3.6 miles west of Spring Cave, Floyd Co., Georgia (UF 271289). The early shell is broadly conical with a concave-sided spire. Initially the whorls are scalariform and bear a strong peripheral keel and two weaker spiral carinae below the periphery. Wide axial ribs lay above the peripheral keel. The first three whorls are soon lost and the remaining early spire is broadly conical in shape and the peripheral keel becomes progressively less evident.

I have examined juvenile specimens of the other subspecies. None that I examined retained the initial two or three juvenile whorls, but the subsequent whorls are broadly conical, much as they are in this subspecies.

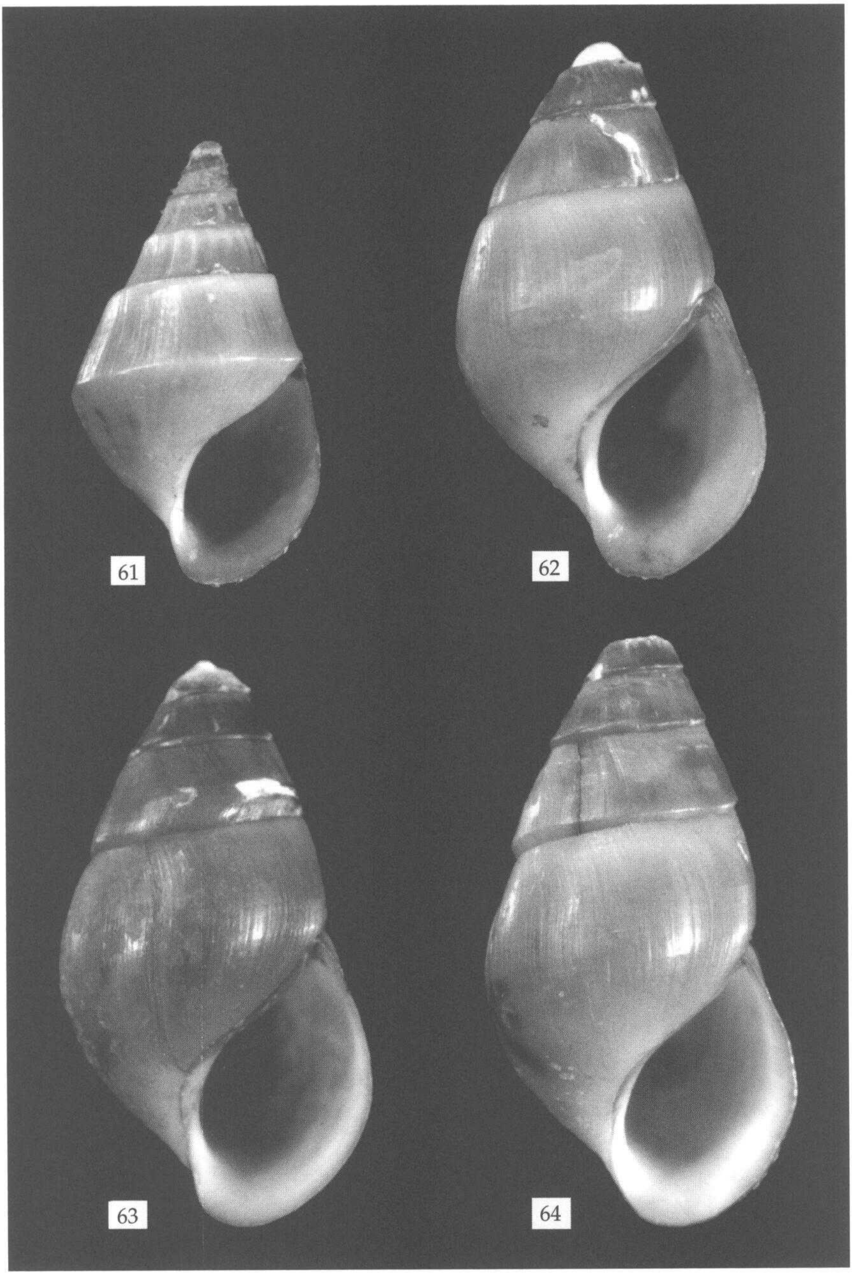
Elimia lecontiana excellens (Goodrich 1935)
Figs. 65-69

Goniobasis caelatura excellens Goodrich 1935, *Occasional Papers of the Museum of Zoology, University of Michigan,* (311): 2-3.
Elimia caelatura excellens (Goodrich 1935); Burch, 1989, *North American Freshwater Snails:* pp. 144, 145, fig. 408.

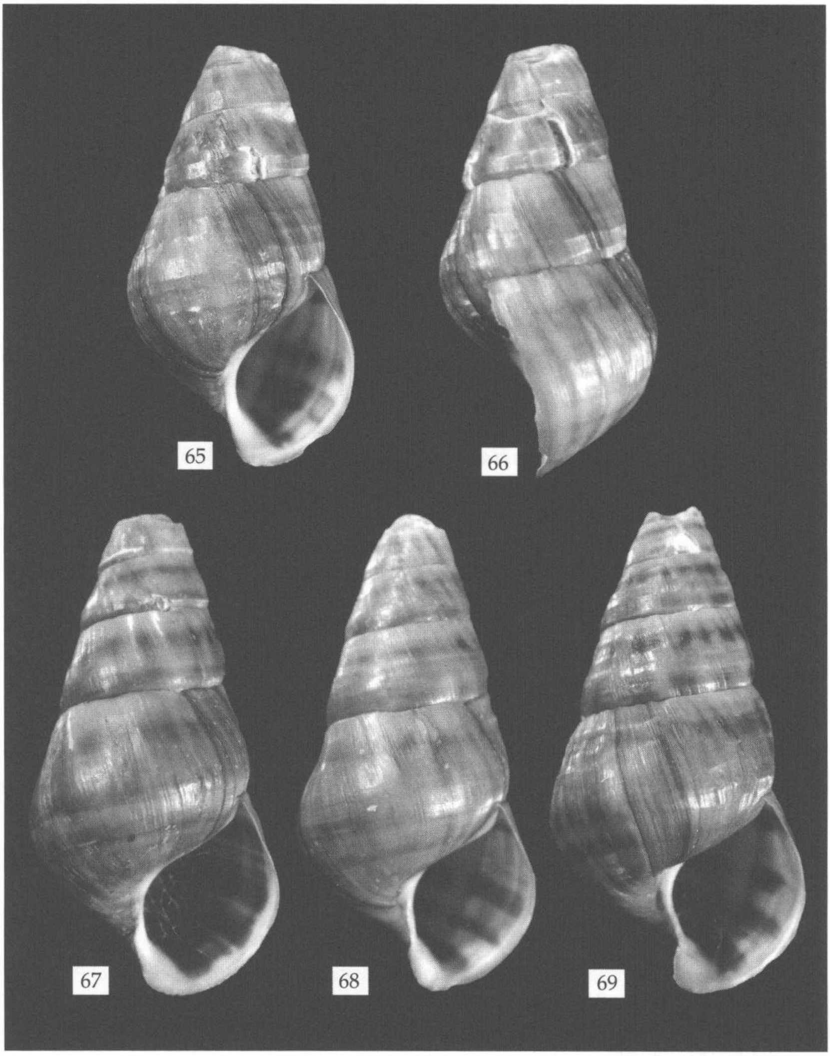
Distribution. "Known from three streams in northwest Georgia and northeast Alabama." Type locality: Little River, 5 miles north of Cedar Bluff, Cherokee County, Alabama. Holotype UF 86931; collected 1 October 1910 by H.H. Smith.



FIGS. 57-60. *Elimia lecontiana lecontiana* (Lea 1841) Silver Creek, near Rome, Floyd Co., Georgia (UF 72350). FIG. 57 = 20.8 mm.



FIGS. 61-64. *Elimia lecontiana infuscata* (Lea 1862). Young's Mill Creek, 6 mi. E, 0.5 m. N of Rome, Floyd Co., Georgia (UF 236374). FIG. 62 = 16.4 mm.



FIGS. 65-69. *Elimia lecontiana excellens* (Goodrich 1935): Little River, 5 miles N of Cedar Bluff, Cherokee County, Alabama. FIGS. 65-66. Holotype (UF 86931). FIGS. 67-69. Paratypes (UF 72402). Fig. 65 = 23.0 mm.

Elimia lecontiana luteocella **(Lea 1868)**
Figs. 70-73

Goniobasis tenebrosa Lea 1868, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 20: 151. (Name preoccupied, not *Melania tenebrosa* Lea 1841.)

Goniobasis luteocella Lea 1868, *Journal of the Academy of Natural Sciences of Philadelphia,* 6: 330, pl. 54, fig. 6. 151; Walker, 1918, *Miscellaneous Publications of the Museum of Zoology, University of Michigan,* (6): 159. (Connesauga Creek, Whitfield Co., Georgia and Oconee River).

Gonibasis whitfieldensis Lea 1868, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 20: 151; Walker, 1918, *Miscellaneous Publications of the Museum of Zoology, University of Michigan,* (6): 162. (Connesauga Creek, Whitfield Co., Georgia).

Goniobasis caelature luteocella (Lea); Goodrich, 1941, *Occasional Papers of the Museum of Zoology, University of Michigan,* (427): 5.

Elimia caelatura luteocella (Lea 1868); Burch, 1989, *North American Freshwater Snails,* p. 144, fig. 410.

Distribution. "Northwest Georgia, northeast Alabama, Talladega County, Alabama."

Elimia lecontiana stearnsiana (Call 1886)
Figs. 74-78

Goniobasis stearnsiana Call 1886. *Proceedings of the Davenport Academy of Natural Science,* 5: 6; Walker, 1918, *Miscellaneous Publications of the Museum of Zoology, University of Michigan,* (6): 161.

Goniobasis caelatura stearnsiana (Call); Goodrich, 1941, *Occasional Papers of the Museum of Zoology, University of Michigan,* (427): 5.

Elimia caelatura stearnsiana (Call 1886); Burch, 1989, *North American Freshwater Snails,* p. 144, figs. 411, 116.

Distribution. "Of irregular occurrence from north Georgia to Calhoun, Shelby and Talladega counties, Alabama." Type locality: Dyke's Creek, Floyd Co., Georgia.

Elimia lecontiana decorata (Anthony 1860)
Figs. 79-83

Melania decorata Anthony 1860, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 12: 55 (Oostenaula River, Georgia).

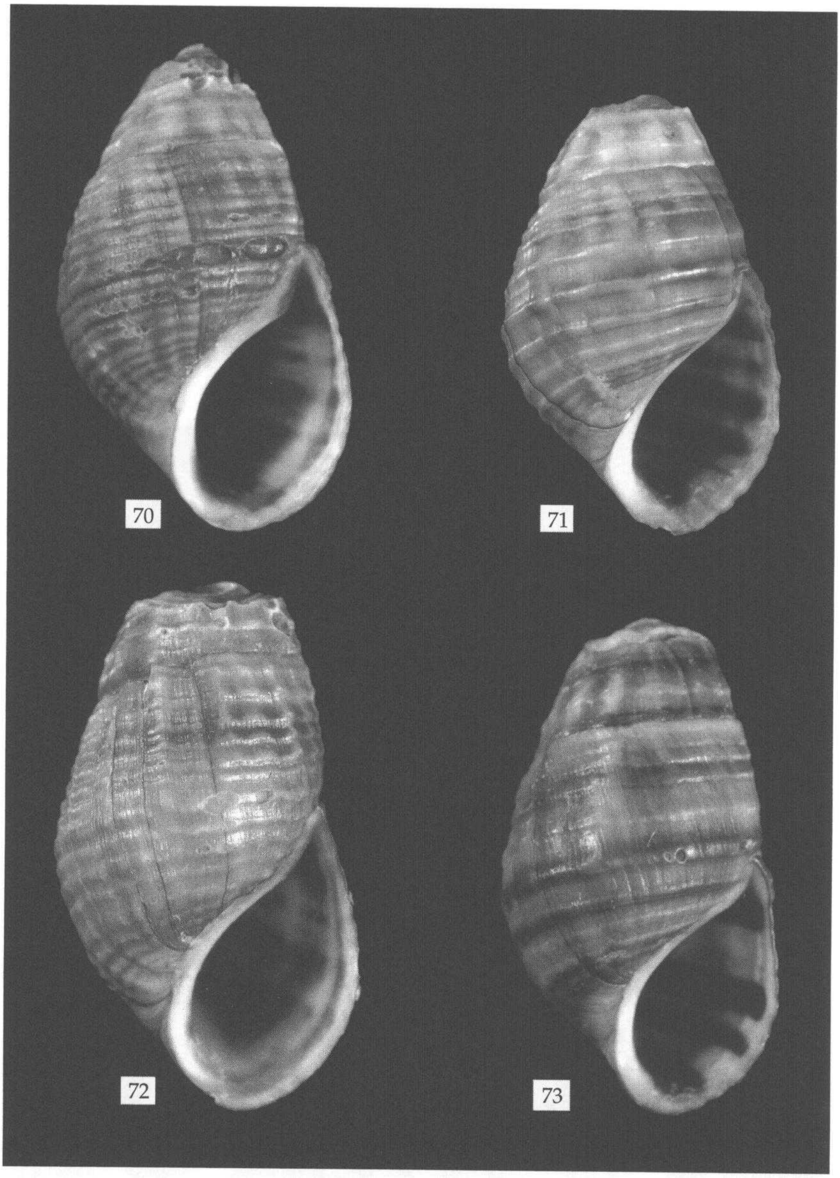
Goniobasis decorata (Anthony); Tryon, 1865, *Smithsonian Miscellaneous Collections,* (201): 141, fig. 262.

Goniobasis binneyana Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 14: 266 (Coosa River, Alabama); Lea, 1863, *Journal of the Academy of Natural Sciences of Philadelphia,* 5: 310, pl. 37, fig. 152.

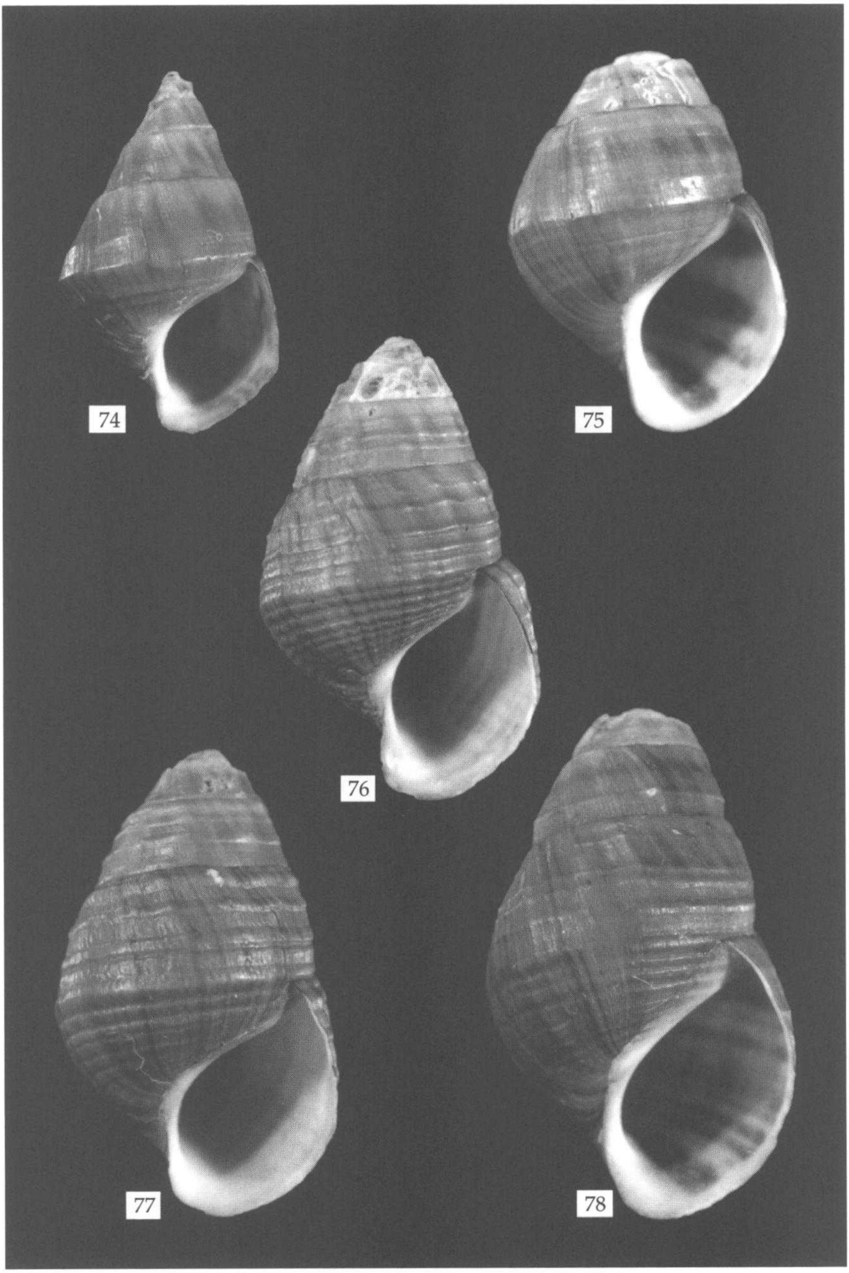
Goniobasis flavescens Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 14: 271; Lea, 1863, *Journal of the Academy of Natural Sciences of Philadelphia,* 5: 339, pl. 38, fig. 202. (Oconee and Tennessee Rivers, Tennessee).

Goniobasis cadus Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 14: 272; Lea, 1863, *Journal of the Academy of Natural Sciences of Philadelphia,* 5: 345, pl. 38, fig. 211. (Georgia).

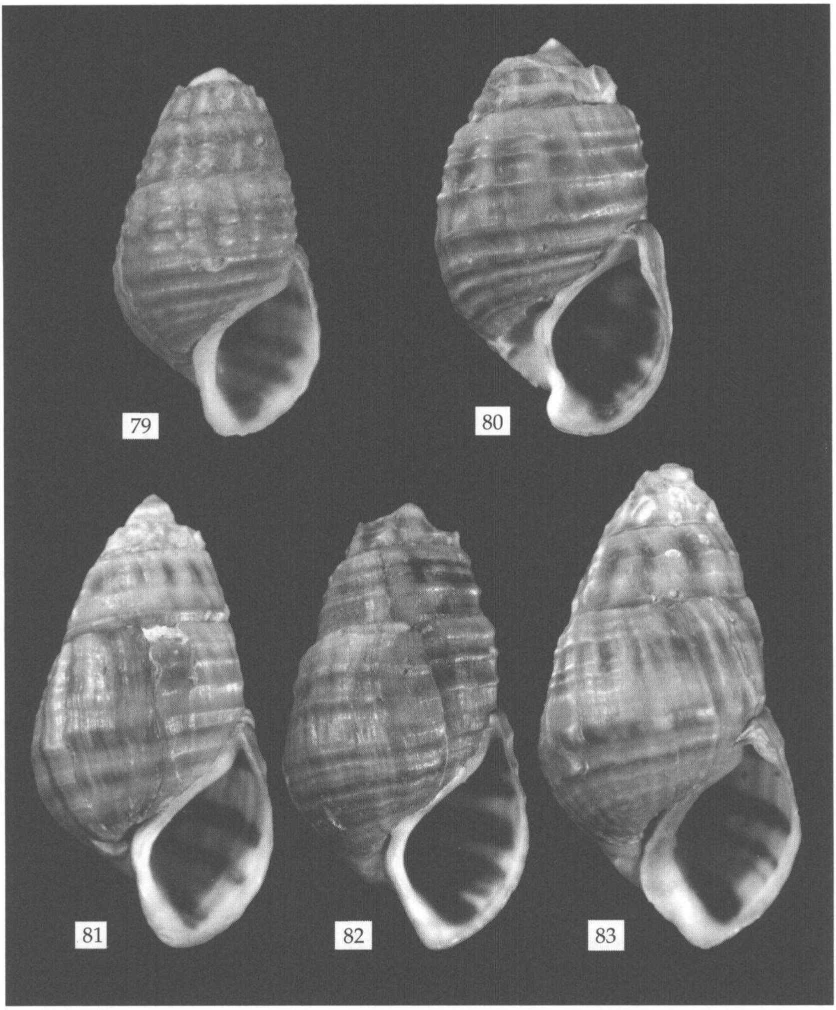
Goniobasis tryoniana Lea 1862, *Proceedings of the Academy of Natural Sciences of Phila-*



FIGS. 70-73. *Elimia lecontiana luteocella* (Lea 1868). Conasauga River, Mt. Tilton, Whitefield Co., Georgia (UF 72432). Fig. 70 = 15.3 mm.



FIGS. 74-78. *Elimia lecontiana stearnsiana* (Call 1886). Dykes Creek, Floyd Co., Georgia. (UF 72496). Fig. 74 = 16.1 mm.



FIGS. 79-83. *Elimia lecontiana decorata* (Anthony 1850). FIG. 79. Oostanaula River, near Rome, Floyd Co., Georgia (UF 72386). FIGS. 80-83. Chattooga River, near Cedar Bluff, Cherokee Co., Alabama (UF 72381). Fig. 79 = 18.6 mm.

delphia, 14: 272; Lea, 1863, *Journal of the Academy of Natural Sciences of Philadelphia,* 5: 342, pl. 38, fig. 207.

Goniobasis granata Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 14: 272; Lea, 1863, *Journal of the Academy of Natural Sciences of Philadelphia,* 5: 343, pl. 38, fig. 209. (Oostenaula River, Georgia).

Goniobasis similis Lea 1868, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 20: 151; Lea, 1868, *Journal of the Academy of Natural Sciences of Philadelphia,* 6:

328, pl. 54, fig. 2. (Connasauga Creek, Whitfield Co., Georgia).

Goniobasis connesaugaensis Lea 1868, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 20: 152; Lea, 1868, *Journal of the Academy of Natural Sciences of Philadelphia,* 6: 333, pl. 54, fig. 11. (Connasauga Creek, Whitfield Co., Georgia).

Goniobasis granitoides Lea 1868, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 20: 152; Lea, 1868, *Journal of the Academy of Natural Sciences of Philadelphia,* 6: 335, pl. 54, fig. 14. (Connasauga Creek, Whitfield Co., Georgia).

Goniobasis leai Tryon 1873, *Smithsonian Miscellaneous Collections,* (253): 163. (not *Goniobasis leai* Brot 1862)

Goniobasis caelatura caelatura (Conrad); Goodrich, 1935, *Occasional Papers of the Museum of Zoology, University of Michigan,* (311): 1; Goodrich, 1936, *Miscellaneous Publications of the Museum Zoology, University of Michigan,* 29-31, pl. 1, fig. 14; Goodrich, 1941, *Occasional Papers of the Museum of Zoology, Unversity of Michigan,* (427): 5.

Elimia caelatura caelatura (Reeve, 1850); Burch, 1989, *North American Freshwater Snails,* p. 142; fig.407.

Distribution. "Headwater of Coosa River in northern Georgia and downstream to Talladega County, Alabama."

Remarks. Goodrich (1941: 5) provisionally included *Melania casta* Anthony, 1854 in the synonymy of *Goniobasis caelatura* [*Elimia lecontiana decorata*]. The name *Melania casta* predates *Melania decorata*. However, *Melania casta* Anthony 1854 is a *nomen dubium,* and it cannot be used for this taxon. It is based on what appears to be a juvenile stage of some form of *E. lecontiana*. It is not identifiable with any particular subspecies and its provenance is unknown.

An operculum (Figs. 130-131) of *Elimia lecontiana decorata* is figured for comparison with *E. caelatura* (Figs. 126-127). It is neomelanian in structure and has rugose incremental striations on the outer surface.

Elimia lecontiana georgiana (Lea 1862)

Figs. 84-87

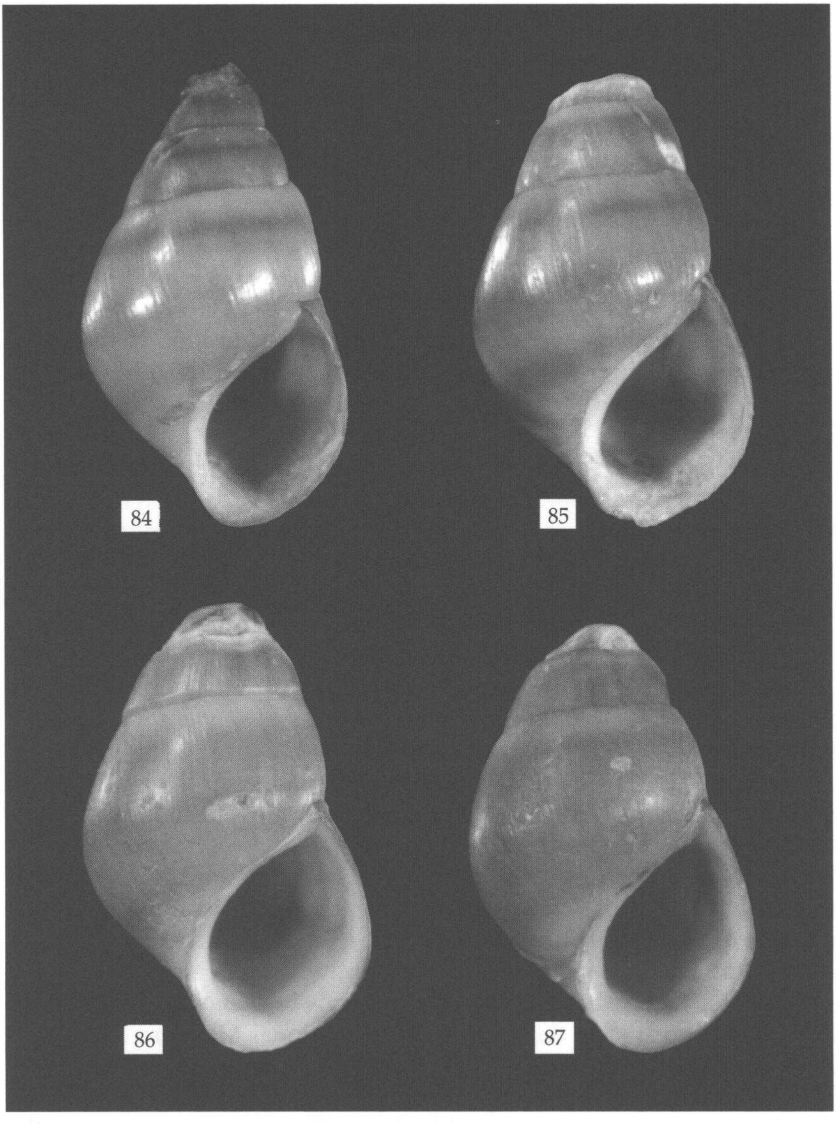
Goniobasis georgiana Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 14: 265; Lea, 1862, *Journal of the Academy of Natural Sciences of Philadelphia,* 5: 308, pl. 37, fig. 148; Goodrich, 1941, *Occasional Papers of the Museum of Zoology, University of Michigan,* (427): 6.

Goniobasis caelatura georgiana (Lea); Goodrich, 1941, *Occasional Papers of the Museum of Zoology, University of Michigan,* (427): 6.

Elimia caelatura georgiana (Lea, 1862); Burch, 1989; *North American Freshwater Snails,* p. 144; fig. 409.

Distribution. "Chattooga River, Georgia."

Remarks. Goodrich assigned *georgianus* to subspecific status within *caelatura* [*lecontiana*] on the basis of similarities of the opercula. The shell of *georgianus* is much smaller than other forms of *lecontiana*, it lacks spiral sculpture, the base of the aperture is thickened and broadly rounded,



FIGS. 84-87. *Elimia lecontiana georgiana* (Lea 1862). Chattooga River, Chattooga Co., Georgia (UF 72406). Fig. 84 = 9.6 mm.

and intermediate populations are not known. These differences are sufficient to recognize *Elimia georgiana* as a distinct species, pending a revision of the group.

APPENDIX
SOME *ELIMIA* FROM THE SAVANNAH RIVER SYSTEM

Goniobasis bentoniensis Lea 1862
Figs. 88-89 (shell of lectotype)

Goniobasis bentoniensis Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia* 4: 271; 1863; *Journal of the Academy of Natural Sciences of Philadelphia.*, 5: 336, pl. 38, fig. 198; 1863, *Observation on the genus* Unio, 9: 158; Tryon, 1865, *Smithsonian Miscellaneous Collections*, (201): 151, fig. 286.

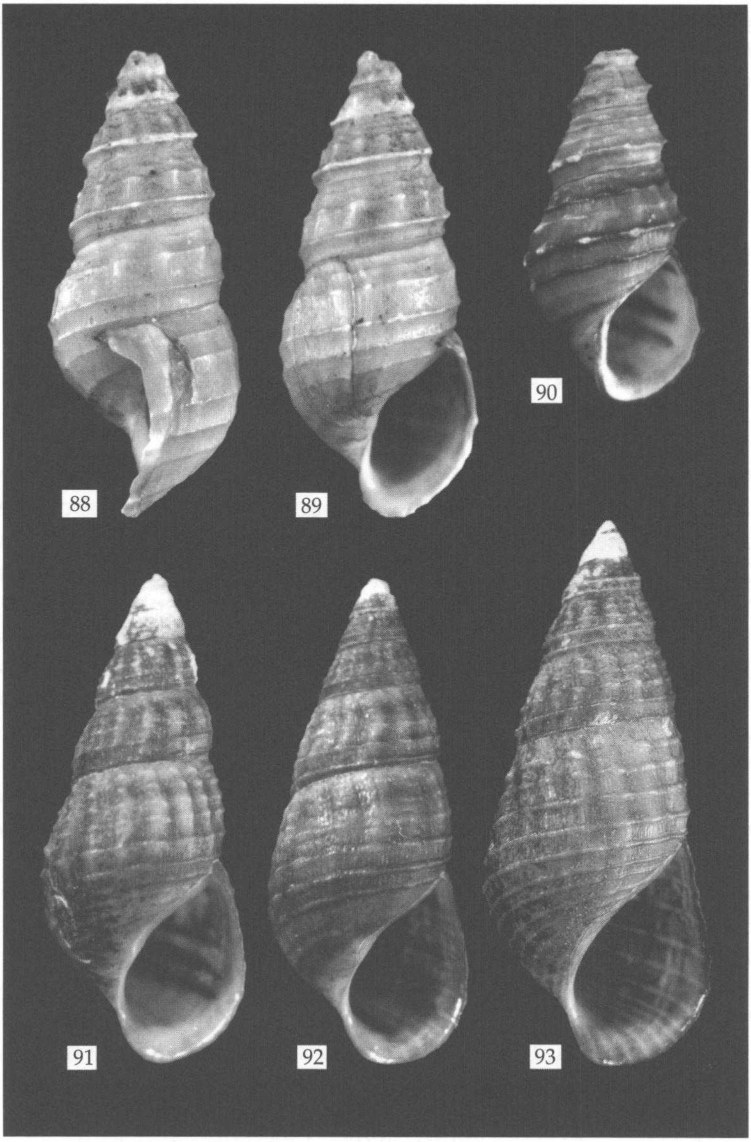
The name *Goniobasis bentoniensis* has been misidentified in the literature. It was briefly described and illustrated by Lea in 1862, and again in 1863 and 1865. His description and figure were reproduced by Tryon (1865). Lea's original description is quoted below.

"*Description.* Shell carinate, folded, striate, conical; greenish horn-colored, without bands; spire raised, conical; suture very much impressed; whorls seven, slightly convex; aperture rather small, ovately rhomboidal, whitish within; outer lip acute, scarcely sinuous; columella bent in, somewhat twisted."

Lea (1862: 271) described *Goniobasis bentoniensis* from "Benton County, Alabama." What was Benton County, Alabama is now Calhoun County. Benton County existed from ca. 1832 to 1857 or 1858, at which time the name was changed to Calhoun County (*personal communication*, James C. Godwin).

Goodrich (1941) stated that *Goniobasis bentoniensis* occurs in small streams and spring discharges in St. Clair, Calhoun and Talladega Counties, Alabama. He cites no specific locality, nor does he provide other information about the species. Pilsbry (1890) suggested that *G. bentoniensis* may be a synonym of *Elimia catenaria* (Say 1822), a species found in coastal streams of South Carolina and Georgia. Goodrich made no comment concerning Pilsbry's suggestion of its identity.

Lea states that he examined two specimens of *Goniobasis bentoniensis.* One was deposited in the United States National Museum of Natural History (USNM 118464, FIGS. 88-89), and the other was in the cabinet of Dr. Hallenbeck. The USNM specimen is herein designated the LECTOTYPE. It is the specimen figured by Lea. The label states that it is the "type," but some ambiguity could be read into whether this type specimen was one of the two "types" (cotypes, syntypes) or whether it was meant by Lea that the type (holotype) was the specimen in the USNM. Comparison of the lectotype of *bentoniensis* with specimens of *Elimia caelatura* (Conrad 1849) (Figs. 90, 94-99) from the Savannah River near



FIGS. 88-93. *Elimia* from the the Savannah River and the Santee River systems. FIGS. 88-90. *Elimia caelatura* (Conrad 1849). FIGS. 88-89. LECTOTYPE of *Goniobasis bentoniensis* Lea 1862, (USNM 118464). FIG. 90. *Elimia caelatura* (Conrad 1849); Savannah River, at lock and dam, Augusta, Georgia (UF 261840). FIGS. 91-93. *Elimia catenaria* (Say 1822). Eutaw Springs, Burke Co., South Carolina (MCZ 82511). Fig. 88 = 21.3 mm.

Augusta, Georgia demonstrate that they are the same species. The name *Goniobasis bentoniensis* Lea 1862 is a subjective junior synonym of *Melania caelatura* Conrad 1849.

Elimia caelatura (Conrad 1849)

Vernacular name: savannah elimia

Figs. 90, 94-99

Melania caelatura Conrad 1849, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 4: 154; Conrad, 1850, *Journal of the Academy of Natural Sciences of Philadelphia*, 1: 278, pl. 38, fig. 3. (Type locality: Savannah River).

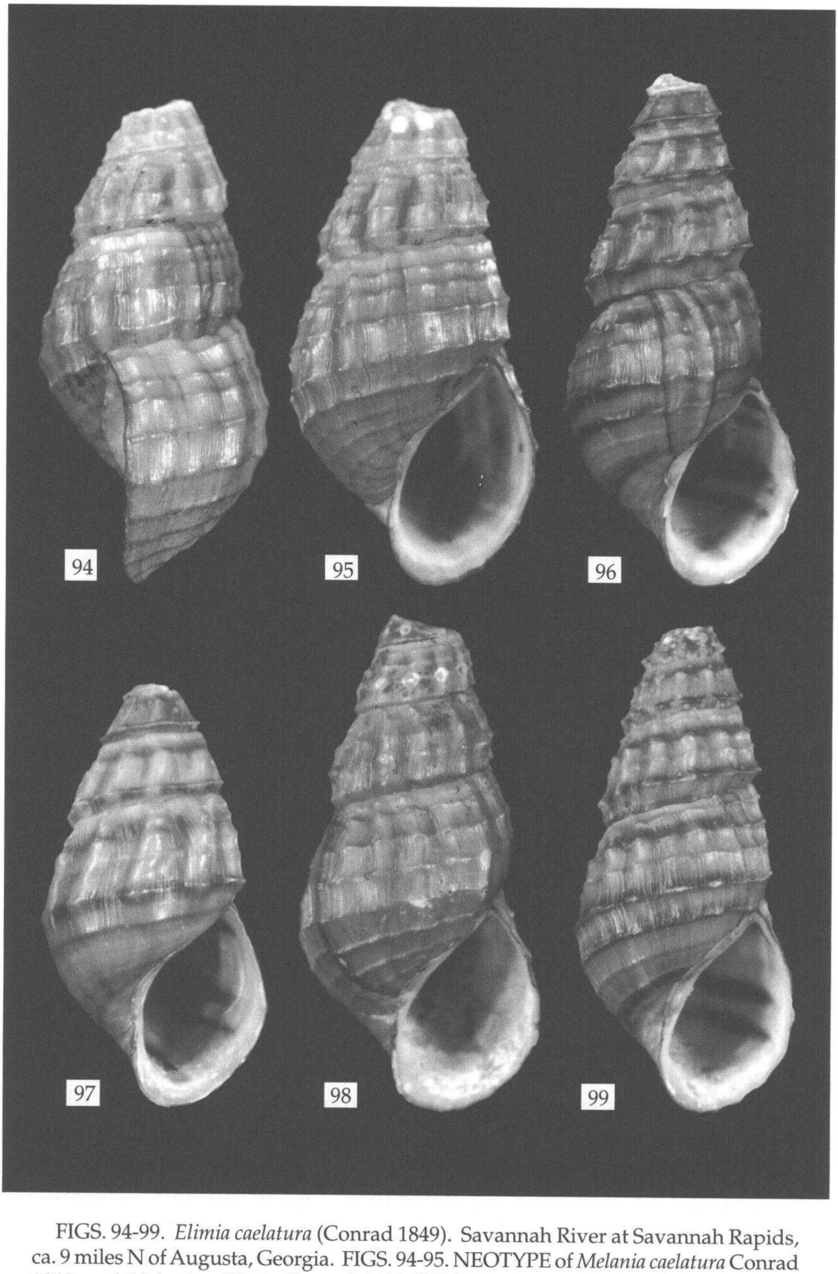
Melania sublirata Conrad 1850, *Journal of the Academy of Natural Sciences of Philadelphia*, 1: 277, pl. 38, fig. 1 (Type locality: Savannah River).

Goniobasis bentoniensis Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 4: 271; Lea, 1863, *Journal of the Academy of Natural Sciences of Philadelphia*, 5: 336, pl. 38, fig. 198. (Type locality: in error as Benton County, Alabama).

Diagnosis. A large robust snail in which the lower whorls become scalarifom and form a sulcus below the periphery. A total of about seven whorls are formed; 2.5-4.4 remain in the adult shell. The first four whorls of the juvenile shell have a strong peripheral carina. The vertical ribs form on the following whorl. The adult shell is sculptured with bold vertical ribs that extend from the suture to the periphery. These are crossed by a strong peripheral carina and 2-4 spiral threads that form nodes on the ribs. On the lower whorls the spiral threads become discontinuous between the ribs. The base of the adult shell has 2-4 fine spiral threads. The operculum is broadly paleomelanian with a large slowly expanding nucleus. The operculum is very similar to *Elimia catenaria*, a coastal plane species, and is very unlike the neomelanian operculum of *E. lecontiana* of the Coosa River system.

Shell (Figs. 94-99). Shell large, up to 22 mm in length; robust, about 0.66-0.72 times as wide as high. Juvenile shell broadly conical, forming an angle of about 40-52°; adult shell becoming more attenuate and slightly convex in outline; sides of spire in large adults diverging at about 34-40° with the last whorl or two tending to be scalariform and form a sulcus along the suture. Adult shell with 2.5-4.4 whorls; rate of growth indicating that a total of about seven whorls are developed. Periostracum light yellowish-green.

First three whorls of juvenile shell (Fig. 107) without vertical sculpture but with a strong peripheral carina just above the suture. On the following whorls, the carina becomes weakly nodular where it is crossed by broad but low vertical ribs that extend from the upper suture to the periphery. A second spiral ridge lies below the periphery and becomes overlaid by the advancing suture. In adult shells the ribs become more pro-



FIGS. 94-99. *Elimia caelatura* (Conrad 1849). Savannah River at Savannah Rapids, ca. 9 miles N of Augusta, Georgia. FIGS. 94-95. NEOTYPE of *Melania caelatura* Conrad 1849, and *Melania sublirata* Conrad 1849 (UF 271349). FIGS. 96-99. *Elimia caelatura* (Conrad 1849) (UF 271315). Fig. 94 = 21.0 mm.

TABLE 5. *Elimia caelatura* (Conrad, 1849). Measurements in mm based on the neotype (UF 271349)and 11 large adults (UF 271315). The standard length of the shell includes the distance from the apical plug to the base of the peristome. SL = standard length, LW = length of last whorl, SW = standard width, AH = aperture height, AW = aperture width, Wh = whorls, Sp = angle of spire.

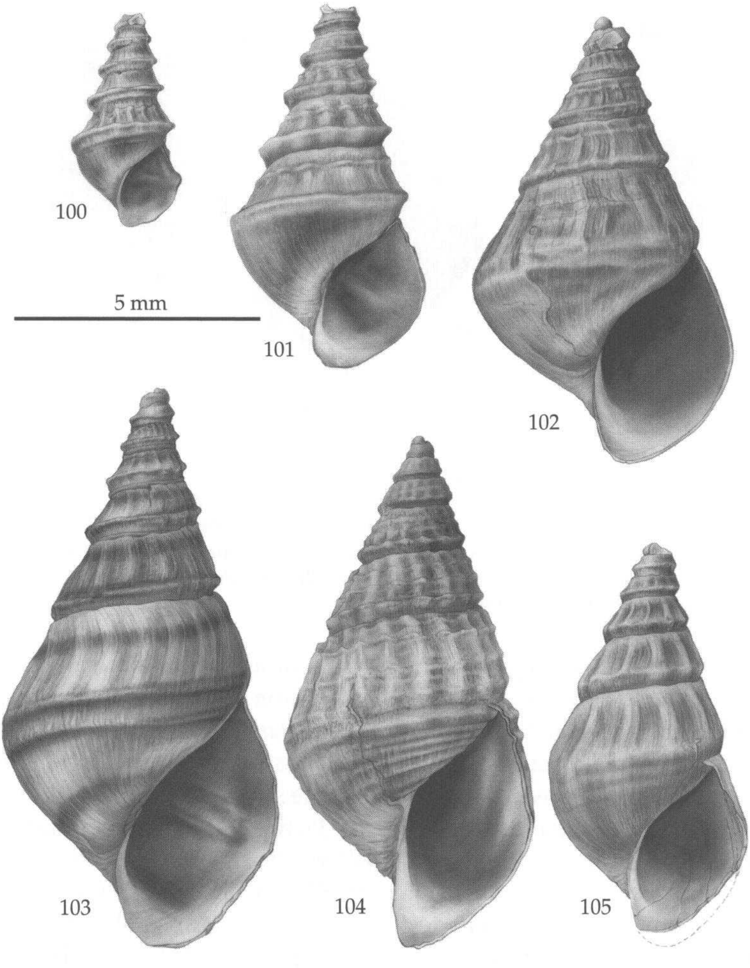
	SL	LW	SW	AH	AW	Wh	SW/SL	SW/LW	AH/LW	AW/AH	LW/SL
Neotype	21.0	15.0	10.8	9.5	6.1	3.5	0.51	0.72	0.63	0.62	0.71
Min.	19.0	14.4	10.0	9.1	5.9	2.5	0.48	0.66	0.58	0.59	0.71
Max.	21.9	17.0	11.2	10.0	6.7	4.4	0.53	0.72	0.69	0.71	0.83
Avg.	20.3	15.3	10.4	9.7	6.4	3.4	0.51	0.68	0.64	0.65	0.76
S^2	0.94	0.69	0.41	0.31	0.30	0.54	0.03	0.02	0.03	0.04	0.03

nounced and are crossed by 2-4 additional low spiral threads that form weak nodes where they cross the ribs. The spiral sculpture above the periphery becomes discontinuous between the nodes on the last whorl or two. The base of the shell after whorl 5 develops 2-4 smooth spiral threads.

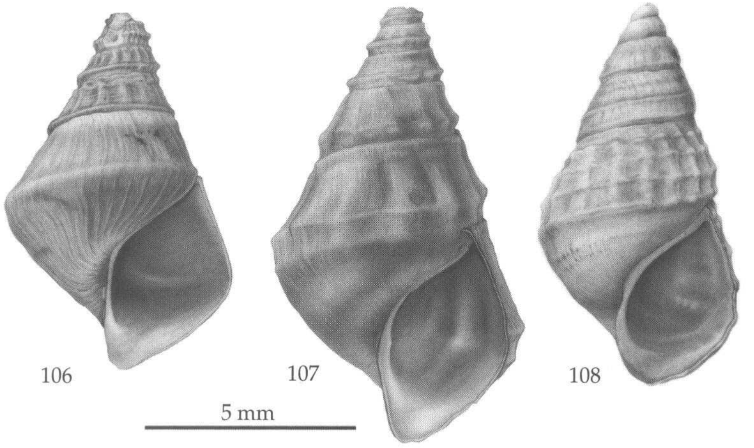
The aperture is elliptical in shape; about 0.59-0.71 times as wide as high; about 0.58-0.69 times the length of the last whorl. Outer lip weakly scalloped by spiral sculpture; basal margin rounded; columellar margin narrow and slightly concave in mature specimens. Shell measurments are given in Table 5.

Operculum (Figs. 127-128). Light brown, thin and hyaline. Broadly ovate, nearly round, with a large sub-central nucleus. Outer surface smooth with a few weak radial striations. Muscle attachment scar finely granular, and about half the width of the operculum. The operculum is very similar to that of *Elimia catenaria* (Say 1822). An operculum of *E. catenaria* from Eutaw Springs, Burke Co., South Carolina is figured for comparison (Figs. 128-129). An operculum of *Elimia lecontiana decorata* (Figs. 130-131) also is illustrated because this is the taxon with which *caelatura* had been confused by earlier authors.

Type locality. Conrad (1849, 1850) described six species of *Melania* [*Elimia*] from the Savannah River: *M. caelatura*, *M. symmetrica*, *M. perangulata*, *M. nebulosa*, *M. percarinata* and *M. sublirata*. The location of the type specimens of these species is unknown. Baker (1964) did not find type specimens of any of these species in the ANSP, nor are they in the National Museum of Natural History (Robert Hershler, personal communication). Conrad (1850: 70) states that "Of the following freshwater shells those from Georgia were kindly loaned to me for description by J. Hamilton Couper, Esq." Apparently the type specimens remained in Couper's collection, the present location of which is unknown. It must



FIGS. 100-105. *Elimia* species. Drawing of juvenile shells showing sculptural characteristics. FIGS. 100-101. *Elimia modesta* (Lea 1945) Coldwater Spring, Calhoun Co., Alabama (UF 270973). FIG. 102. *Elimia carinocostata "leidyana"* (Lea 1862); Cane Creek, Pelham Range, Ft. McClellan Military Reservation, Calhoun Co, Alabama(UF 263203). FIG. 103. *Elimia carinocostata "scabrella"* (Lea 1862); spring tributary to Cedar Creek, Philpot Rd. and Ellawood Rd., Cedartown, Polk Co., Georgia (UF 271376). FIG. 104. *Elimia godwini* new species (PARATYPE, UF 203201). FIG. 105. *Elimia carinocostata carinocostata* (Lea 1845), Clear Branch, 0.4 mi. W Argo, Little Cahaba R. drainage, Jefferson Co, Alabama (UF 23211). Scale bar = 5 mm.

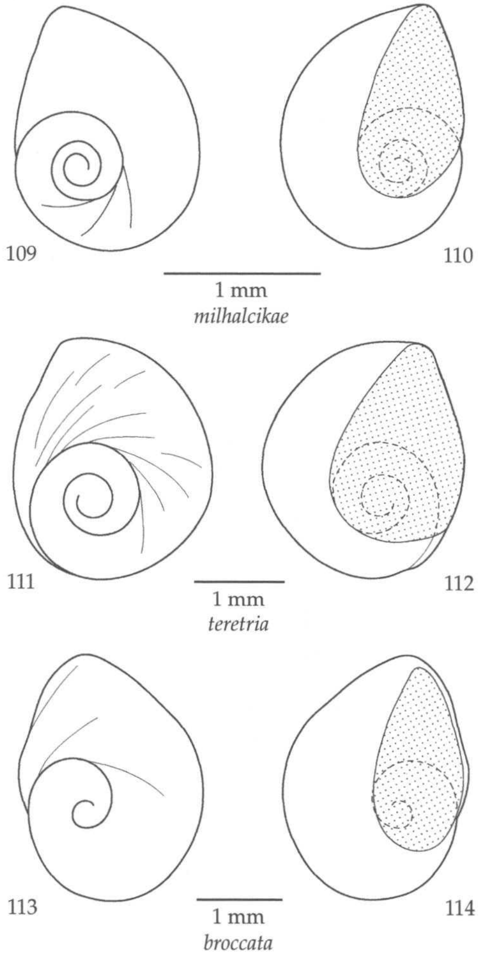


FIGS. 106-108. *Elimia* species. Drawing of juvenile shells showing sculptural characteristics. FIG. 106. *Elimia lecontiana infuscata* (Lea 1862); Cedar Creek, Cedartown, Polk Co., Georgia, (UF 271389). FIG. 107. *Elimia caelatura* (Conrad 1849); Savannah River, Savannah Rapids Dam, ca. 9.0 mi. N of Augusta, Georgia (UF 271315). FIG. 108. *Elimia catenaria* (Say 1822) Eutaw Springs in St. Johns & Berkeley Counties, South Carolina (UF 73909). Scale bar = 5 mm.

be concluded that the type specimens of Conrad's species are lost.

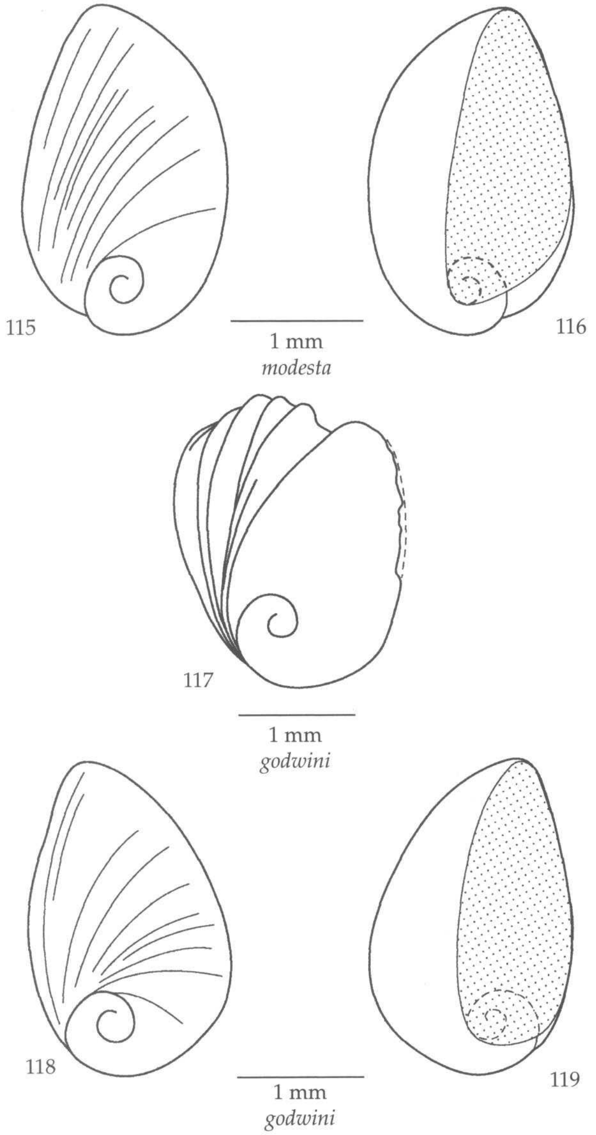
Melania caelatura is the senior available name applicable to *Elimia* described from the Savannah River system. *Melania caelatura* Conrad 1849, *Melania sublirata* Conrad 1850 and *Goniobasis bentoniensis* Lea 1862 are based on different growth stages of the same species. Conrad's figure of *caelatura* represents an old adult (1849: pl. 38, fig. 3). His figure of *sublirata* represents an immature specimen (1849: pl. 38, fig. 1). The lectotype of *bentoniensis* is a young adult (Figs. 88-89). A NEOTYPE for *Melania caelatura* Conrad 1849 is herein designated (UF 271346). A NEOTYPE for *Melania sublirata* Conrad 1849 is herein designated (UF 271346). They are the same specimen (Figs. 94-95) which has the following data: Georgia, Columbia Co., Savannah River below the Savannah Rapids Dam, *ca.* 9.0 miles north of Augusta; 33'32.0° N, 82'03.3° W; collected 20 March, 1999 by Fred G. Thompson.

Distribution. At present this species is known only from a short segment of the Savannah River above Augusta, Georgia, and from it's tributary the Broad River. Undoubtedly it had a wider distribution prior to when the Savannah River was impounded. The river had numerous shoals which are now covered by many feet of reservoir water, and which

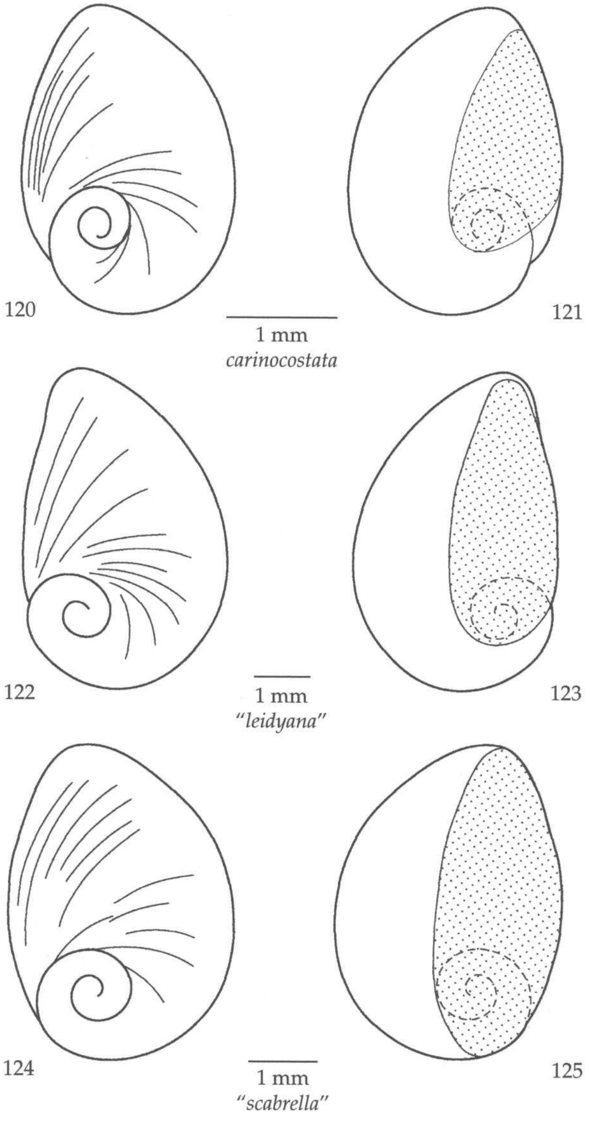


FIGS. 109-114. Opercula of *Elimia* species. FIGS. 109-110. *Elimia mihalcikae* new species. FIGS. 111-112. *Elimia teretria* new species. FIGS. 113-114. *Elimia broccata* new species.

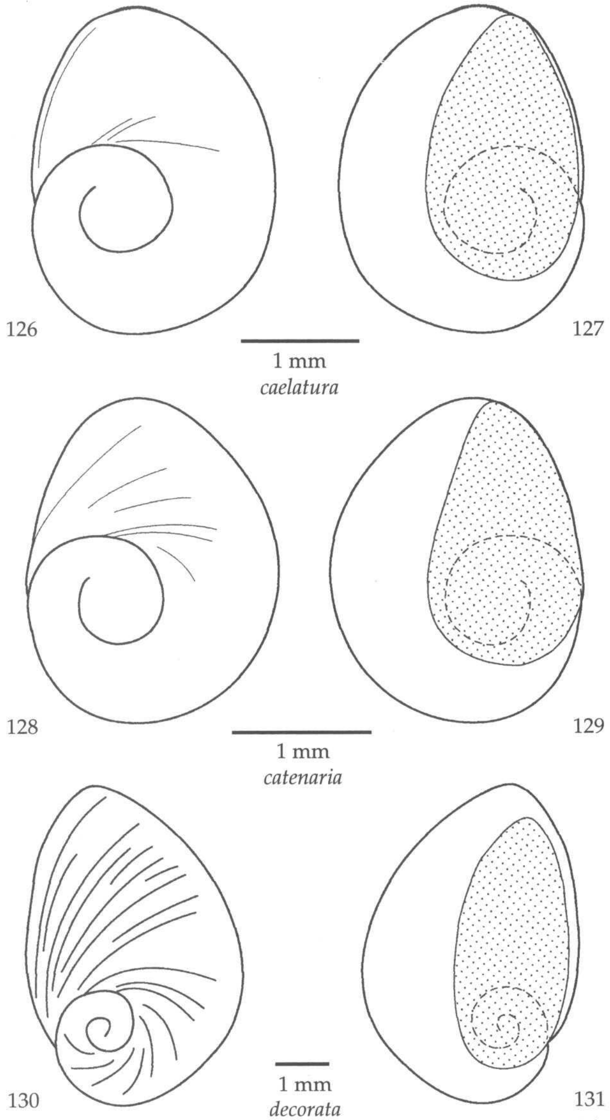
undoubtedly were suitable habitat for *Elimia*. I have examined specimens from the following localities. GEORGIA: Savanna River at New Savannah Lock and Dam, river mile 185 (UF 261840). *Columbia Co.*: Savannah River below the Savannah Rapids Dam, ca. 9.0 miles north of Augusta; 33'32.0° N, 82'03.3° W (UF 263330); Savannah River 0.8 mi. above Interstate Hwy. I-20 (UF 261841). *Elbert Co.*: Broad River at Georgia Hwy. 17 (UF 271156); Broad River, 5.1 mi. SW of Bowman (UF 231152, 231153,



FIGS. 115-119. Opercula of *Elimia* species. FIGS. 115-116. *Elimia modesta* (Lea 1845). FIGS. 117-119. *Elimia godwini* new species.



FIGS. 120-125. Opercula of *Elimia* species. FIGS. 120-121. *Elimia carinocostata* (Lea 1845). FIGS. 122-123. *Elimia carinocostata "leidyana"* (Lea 1862). FIGS. 124-125. *Elimia carinocostata "scabrella"* (Lea 1862).



FIGS. 126-131. Opercula of *Elimia* species. FIGS. 126-127. *Elimia caelatura* (Conrad 1849). FIGS. 128-129. *Elimia catenaria* (Say 1822). FIGS. 130-131. *Elimia lecontiana decorata* (Anthony 1860).

FIG. 132. Aerial photograph of Coldwater Spring, Calhoun Co., Alabama. Courtesy of the City of Anniston Water Board. The arrow indicates the zone in the spring run inhabited by *Elimia mihalcikae* new species, *E. teretria* new species and *Stiobia nana* Thompson & McCaleb, 1978.

271373); Broad River 8.6 mi. S of Elberton (UF 271367). *Madison Co.*: South Fork Broad River, shoals 2.0 mi. SE of Coleman (UF 271368).

Conservation status. There is no doubt that the present range of this species is significantly smaller than before, due to impoundment of major portions of the Savannah River and the lower part of most of its tributaries. Only a single short section of the Savannah River above Augusta, Georgia now contains this species. Numerous former shoals above there are now covered by deep reservoirs. These shoals would have been suitable habitats for this snail. The species is more widely distributed in the Broad River, but the upper and middle portion of that tributary are being impacted rather severely by organic pollution (personal observation, May, 1999). For conservation purposes *Elimia caelatura* should be considered a threatened species.

Remarks. *Elimia caelatura* is most similar to *E. catenaria* (Say 1822) (Figs. 91-93) with which it shares some shell and opercular characteristics, most notable of which are the superficially similar shell sculpture and the broadly spiral opercula (Figs. 128-129). I have examined two topotypic series of *E. catenaria* for comparison with *E. caelatura*. The type locality of *E. catenaria* is Eutaw Springs, Burke Co., South Carolina. The type locality is now covered by 60 feet of water in Lake Marion, a reservoir on the

Santee River. Fortunately, William Clench collected a fine series of specimens from there prior to the impoundment of the river. Specimens were distributed to several museums, including the Alabama Museum of Natural History. These are now deposited in the Florida Museum of Natural History (UF 73909). I also have examined another large series of specimens deposited in the Museum of Comparative Zoology (MCZ 82511).

The two species differ in some characteristics of the adult shell sculpture, the shell-shape and the juvenile shell. In adult *Elimia catenaria* (Figs. 91-93) (1) the spiral threads are finer than in *E. caelature*, (2) they are continuous over and between the vertical ribs, and (3) they do not form nodes on the ribs as they do in *E. caelatura*. The lower whorls do not become scalariform, and the adult shell is not as robust. The aperure of *E. caelatura* is irregularly elliptical in shape due to the nearly straight vertical columellar margin. In *E. catenaria* the columellar margin is strongly convex causing the aperture to be broadly elliptical in shape. The juvenile shell of *E. catenaria* (Fig. 108) is more narrowly conical, diverging at an angle of 45-50°, and it has comparatively smaller whorls than does *E. caelatura*. As with *E. caelatura*, the first four whorls are smooth, but the following whorls bear lower and narrower ribs which are cancellated by several raised spiral threads.

Turgeon *et al*. (1998) provide the vernacular name "rippled elimia," in allusion to the sculpture of the dominant form of *Elimia* from the Coosa River system formerly referred to *Elimia caelatura*. The name "rippled" is inappropriate because the Savannah River species has a very different type of sculpture, and the vernacular name is not tied to the scientific name. I propose that *Elimia caelatura* be known by the vernacular name "savannah elimia."

OTHER NAMES ASSOCIATED WITH *ELIMIA* FROM THE SAVANNAH RIVER SYSTEM.

The taxonomic status of the following nominate species remain unresolved.

Melania perangulata Conrad 1849, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 4: 154; Conrad, 1850, *Journal of the Academy of Natural Sciences of Philadelphia*, 1: 278; pl. 38, fig. 6. (Savannah River) (type lost).

Melania symmetrica Conrad 1849, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 4: 155; Conrad, 1850, *Journal of the Academy of Natural Sciences of Philadelphia*, 1: 278, pl. 38, fig. 5 (Savannah River) (type lost); (not *Melania symmetrica* Haldeman 1841).

Melania percarinata Conrad 1849, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 4: 155; Conrad, 1850, *Journal of the Academy of Natural Sciences of Phila-*

delphia, 1: 278, pl. 38, fig. 10 (Savannah River) (type lost).

Melania nebulosa Conrad 1849, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 4: 155; Conrad, 1850, *Journal of the Academy of Natural Sciences of Philadelphia,* 1: 278, pl. 38, fig. 9. (Savannah River) (type lost).

The four species appear to belong to the *Elimia catenaria* species-group. Two other species (below) described from the Savannah River drainage appear to belong to different species groups.

Goniobasis abbevillensis Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 4: 268; Lea, 1863, *Journal of the Academy of Natural Sciences of Philadelphia,* 5: 323, pl. 38,fig. 174. (Abbeville District, South Carolina); Goodrich (1942: 3) lists this name as a synonym of *Elimia catenaria dislocata* (Ravenel 1834).

Goniobasis barratti Lea 1862, *Proceedings of the Academy of Natural Sciences of Philadelphia,* 4: 271; Lea, 1863, *Journal of the Academy of Natural Sciences of Philadelphia,* 5: 325, pl. 38, fig. 196 (Abbeville District, South Carolina); Goodrich (1942: 3) lists this name as a synonym of *Elimia catenaria dislocata* (Ravenel 1834).

ACKNOWLEDGMENTS

I wish to thank James C. Godwin, Alabama Natural Heritage Program, Montgomery, Alabama for assistance in the field, and for help is tracing the history of Alabama county name changes. Robert Hershler (USNM), John B. Burch (UMMZ), Diarmid O'Foighil (UMMZ), Gary Rosenberg (ANSP and Kenneth J. Boss (MCZ) loaned me specimens from their respective collections. This paper greatly benefited from a review by Daniel L. Graf (UMMZ). Judith Johnson and Kristin Lenertz (Aubern University) provided me with juvenile specimens of *Elimia* from the Tallapoosa River system. This paper is made better by the exquisite drawing of *Elimia* shells rendered by Susan Trammell. Finally, I am especially grateful to Liath Appleton (UF) for her assistance with many aspects of the preparation of the manuscript.

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THREE NEW FRESHWATER SNAILS OF THE GENUS *CINCINNATIA* FROM PENINSULAR FLORIDA (PROSOBRANCHIA, HYDROBIIDAE)

Fred G. Thompson[1]

ABSTRACT

Three new species are described from the St. Johns River system in Central Florida, *Cincinnatia leptospira* n. sp., *C. alexander* n. sp. and *C. porterae* n. sp. Each is endemic to a single epigene spring system. The species are characterized by aspects of the male and female reproductive systems, as well as by shell characters. Biogeographic relationships are with other species from the St. Johns River system.

Key words: Gastropoda, Prosobranchia, Hydrobiidae, *Cincinnatia*, freshwater snails, Florida, St. Johns River System, Ocala National Forest.

INTRODUCTION

The freshwater molluscan fauna of the southeastern United States remains greatly understudied due to two factors. There are very few systematic malacologists in this country who are interested in freshwater mollusks, and few drainage systems in this region have been survey satisfactorily to reveal the taxonomic diversity of their faunas. Florida is one of the better known states in the southeast, but there remain numerous small springs and streams that have been overlooked in previous surveys. The three new species described below come from such habitats.

Cincinnatia is widely distributed in North America east of the Great Plains and south of the St. Lawrence drainage system. The largest number of species occurs in the Florida Peninsula. Most are endemic to isolated springs and small independent streams. Thompson (1968) recognized two species-groups of *Cincinnatia* in Florida, the *C. floridana* group, and the *C. vanhyningi* group. A third species-group consists of only the type species of the genus, *Cincinnatia integra* (Say 1821). It is widely distributed in the central part of the United States (Hershler & Thompson, 1996). *Cincinnatia integra* is unique among nymphophilines because of the presence of a posterior bursal duct connecting the common oviduct with the bursa copulatrix. This feature has not been found in other species of the genus.

The *Cincinnatia floridana* group consists of six previously known spe-

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cies. Five are confined to the Florida peninsula from the Suwannee River System south. A sixth species, *C. winkleyi* (Pilsbry 1912), occurs in the New England states (Davis *et al.*, 1982). A new species of questionable relationship to this group is described below from the Ocala National Forest. The group is characterized by having a relatively simple pattern of glands on the penis compared to members of the *C. vanhyningi* group. In the *C. floridana* group, the ventral surface of the penis lacks a glandular accessory crest and an inferior crest.

The *Cincinnatia vanhyningi* group consists of six previously known species and two new species described below. All are confined to the Florida peninsula. The *C. vanhyningi* group is confined to springs and small streams along the middle and lower course of the St. Johns River. It is characterized by having an accessory crest and an inferior crest on the ventral surface of the penis. Some species may lack one or more of these crests, and even some individuals of a given species also may lack either crest.

Family HYDROBIIDAE
Subfamily Nymphophilinae
Genus *Cincinnatia* Pilsbry 1911

In the Nymphophilinae, specific diagnostic features exist in the penis, the female reproductive system, the shell and, to lesser extents, the radula and the operculum. The new species described here differ from known congeners by shell and reproductive features. The penis of *Cincinnatia* has a complex configuration that is further complicated by the presence of various patterns of glands on its surface. The penis was referred to as a verge in some earlier literature (*e.g.*, Thompson, 1968). The terminology used in this paper follows Hershler & Thompson (1996). A generalized penis is illustrated in Figs. 36-39.

The penis originates on the nape at a distance behind the tentacles equal to the length of the snout. When contracted the penis is folded upon itself with the distal end directed forward and to the right. When erect the penis extends from beneath the mantle and along the right side of the animal. The penis is broad and dorso-ventrally flattened. A penis *filament* (Fi) originates on the distal half along the right side and is a small slender conical structure; the vas deferens discharges through its distal end. The filament is short and usually does not extend much beyond the end of the penis, in contrast to some other nymphophilid genera. A large number of *glandular crests* and *glandular tubercles* are scattered over the surface of the penis and the filament. They are named as follow. The secondary lobe of the verge terminates with a heavy glandular crest called the *apical crest* (ApC). A bulb-like protuberance, the *terminal lobe* (TL), extends dorso-laterally from the apical crest toward the penis, and a small patch of gland is usually present at the tip of the lobe. Scattered over the mid-region of the dorsal (outer) surface of the penis and the filament are a series of small glandular tubercles and crests, collectively called the *superior tubercles* (ST). They may occur as a few scattered tubercles or they may be fused into a series of long slender crests. On the ventral (inner) surface of the penis and slightly behind the apical lobe is a transverse glandular crest called the *parapical crest* (PC). This crest may be very heavy and raised on a fleshy pedicel. Slightly distal to the parapical crest is a small glandular crest, the *accessory crest* (AC). Lying across the penis about halfway between the base and the parapical crest is another glandular crest, the *inferior crest* (IC). The accessory crest and the inferior crest are absent in some *Cincinnatia*. All species possess the other glandular processes in some modified form. The combination of glands and the patterns they form on the verge are important species diagnostic features.

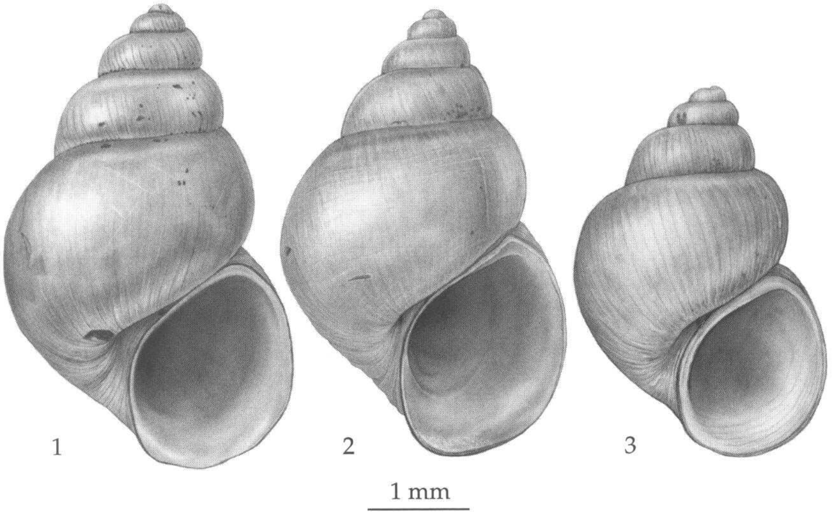
The *Cincinnatia floridana* species-group

***Cincinnatia leptospira*, new species**

Flatwood siltsnail

Diagnosis. This is a relatively slender, graceful species that lives in shallow pools along a woodland slough. It is unique within the genus because of the darkly pigmented mantle overlying all of the whorls. It is tentatively placed in the *Cincinnatia floridana* group because of the absence of an inferior crest and an accessory crest on the inner surface of the penis. It is distinguished from other species in the *floridana* group in that the penis has an invagination on the outer surface, the penis has a black band extending the length of the filament, and the filament extends slightly beyond the apical lobe. The saddle-shaped configuration of the coiled oviduct, and the presence of an anterior seminal receptacle are unique character-states within the genus. The shell is similar in size and whorl count to *Cincinnatia monroensis* (Dall 1885), except that it is thinner and lighter olivaceous in color, the spire is slenderer and slightly convex in outline and it has a more deeply impressed suture.

Shell (Figs. 1, 4-7). Moderately large, 4.3-5.5 mm in length (Table 1); moderately stocky, 1.43-1.61 times as long as wide. Elliptical in shape. Spire elongate, weakly convex in outline, slender, 0.89-1.23 times the height of the aperture. Aperture height 0.43-0.53 times length of shell.



FIGS. 1-3. Shells of *Cincinnatia*. FIG. 1. *C. leptospira* n. sp. Holotype (UF 244525). FIG. 2. *C. alexander* n. sp. Holotype (UF 150300). FIG. 3. *C. porterae* n. sp. Holotype (UF 150557).

Moderately thick-shelled; transparent in life. Periostracum light olivaceous in color, sculptured with occasional fine spiral striations and weak, but more numerous irregular incremental striations that become stronger around rim of umbilicus. Whorls 5.0-5.3; moderately arched; 0.96-1.19 whorls/mm. First embryonic whorl small, 0.28 mm wide transverse to the initial suture. Suture moderately impressed, uniformly descending to the aperture. Umbilicus narrow but not obstructed by columellar lip. Peristome continuous across parietal wall, and widely adnate to previous whorl. Aperture sub-rhomboidal in shape; columellar lip and parietal lip forming an angle; basal-columellar margin of aperture projecting downward slightly; outer lip and basal lip rounded. Aperture prosocline at 8-15° to columellar axis (Fig. 4); 0.76-0.86 times as

TABLE 1. Measurements in mm based on the holotype (UF 244525) and 13 paratypes (UF 267233).

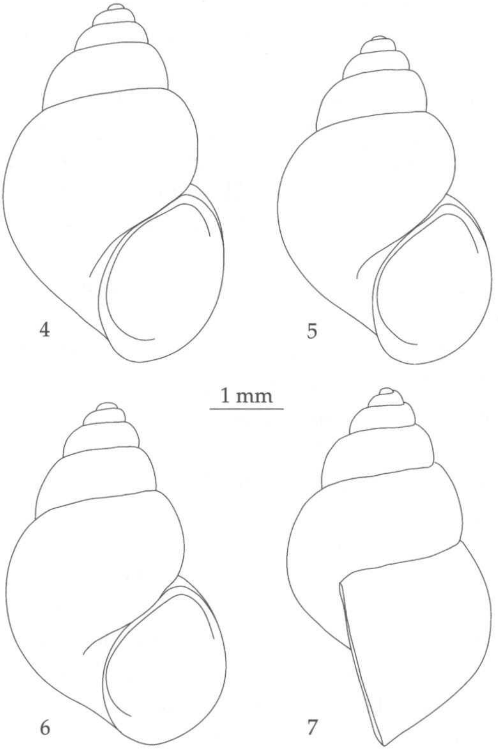
Specimen	Length	Width	AH	AW	whorls	L/W	AH/L	AH/AW	AW/W
holotype	4.7	2.9	2.1	1.7	5.2	1.61	0.45	1.26	0.57
min.	4.3	2.8	1.8	1.6	5.0	1.42	0.43	1.16	0.54
max.	5.5	3.3	2.5	1.9	5.3	1.68	0.53	1.43	0.59
avg.	4.72	3.11	2.24	1.75	5.16	1.52	0.66	1.27	0.57
std.	0.31	0.18	0.18	0.07	0.10	0.06	0.02	0.06	0.01

wide as high; width of aperture 0.54-0.59 times the width of the shell.

Operculum (Fig. 16). Thin, hyaline, light amber in color. Ovate-elliptical in shape; consisting of about 3 paucispiral whorls. Nucleus located in lower left third of face; inner edge straight. Muscle attachment scar weak, long and narrow; about 0.70 times length of operculum.

Mantle pigmentation (Fig.19). In contrast to other known *Cincinnatia*, the mantle of *C. leptospira* is densely pigmented with melanophores. Other species have a dark irregular band over the lower intestine and a similar dark band over the gill. These bands are also present in this species, but they are darker and are encompassed in a more diffuse field of pigmentation. The pigmentation extends along the outer and upper surface of the body to the apical whorl. The mantle collar and part of the mantle are unpigmented for a short distance behind the collar.

Reproductive anatomy. Eight females and six males were dissected (UF 244526). The ovary consists of a sequence of vertical branched lobes



FIGS. 4-7. *Cincinnatia leptospira* n. sp. Paratypes (UF 267663).

along the upper oviduct overlapping the apical end of the posterior stomach chamber and extending distally for one whorl. The posterior end of the albumen gland (Fig. 22) terminates opposite the septum separating the anterior and posterior stomach chambers. The coiled oviduct (Figs. 23-24) is unpigmented and is greatly enlarger. It forms a saddle-like loop and then undulates posteriorly and downward along the outer-mesad surface of the bursa copulatrix. Two seminal receptacles are present. One enters the oviduct at the bottom of the posterior end of the coiled oviduct, and the other enters the common oviduct a short distance posterior to the junction with the bursal copulatrix duct. The posterior seminal receptacle is large and elongate. It is impressed against the side of bursa copulatrix and extending nearly to the posterior end of the albumen gland. It entering the common oviduct distal to the saddle-like loop of the coiled oviduct. An anterior seminal receptacle is present on the dorsal side of the common oviduct at a short distance posterior to the bursal duct. It is small and ovate in shape, and is partially imbedded in the albumen gland beneath the ascending arm of the coiled oviduct. The bursa copulatrix branches from the common oviduct anterior to the pallial wall. The bursal duct is partially imbedded in the albumen gland. The bursa copulatrix is exposed and is very large and sacular and overlaps the distal end of the albumen gland. A posterior bursal duct is absent such as occurs in *Cincinnatia integra* (*e.g.*, Hershler & Thompson, 1996). The septum between the albumen gland and the capsule gland lies anterior to the pallial wall.

The testis consists of numerous vertical clusters of acini that are aligned along the inner curvature for two whorls above the pallial wall. It overlaps the posterior chamber of the stomach and extends to the distal end of the prostate (Fig. 31). The lower vas deferens is enlarged and tubular for about one whorl distal to the pallial wall. The prostate is bean-shaped and is about half the length of the stomach, and it slightly overlaps the transverse septum. The pallial vas deferens is sigmoid and forms a low ridge in the outer wall of the body cavity. It enters the penis at and passes anteriorly along the right margin. The penis (Figs. 28-30) is slightly constricted at its base, and bears a deep invagination on its outer surface (Figs. 28-29). The invagination is bordered by two or three elongate superior tubercles along its mesad edge and is bordered behind by a superior tubercle. The penis filament has an internal black band, and has two elongate narrow glandular crests on its outer surface. The crest along the mesad edge extends the length of the filament. A second crest may extend from the superior tubercle aligning the poster edge of the invagination and extend to the middle of the laterad edge of the filament, or is may consist of a short narrow crest along the outer edge of the penis and the base of the filament. The terminal lobe bears a strong apical crest along its distal edge. A strong parapical crest is present on the inner surface of the penis (Fig. 30). The penis lacks an accessory crest and an inferior crest.

Type locality. Florida, Lake Co., Ocala National Forest, Glen Branch, at Ocala National Forest Recreation Trail (29°02'18"N, 81°32'18"W). The type locality is reached where the hiking trail crosses a slough formed by the creek, Glen Branch, about 0.5 miles south of the national forest Road 539. The creek at the type locality is about 10-15 ft. wide and less than a foot deep. The substratum is a hard sand bottom with accumulations of silt and muck in quiet pools in the stream. HOLOTYPE: UF 244525; collected July 1, 1995 by Fred G. Thompson. PARATYPES: UF 267233 (50), USNM (15), UMMZ 266684 (15); same data as the holotype; UF 244522 (13), collected at type locality 26 June, 1995. ANATOMICAL SPECIMENS: UF 244523, collected 26 June, 1995; UF 244526, collected 1 July, 1995. Both lots are topotypic.

Distribution. This snail is known only from the headwater section of Glen Branch. The creek originates as seeps in a mixed hardwood-pine forest. It flows northeast for a distance of about three miles through a region of silica sand before it enters Alexander River. Snails were found only in the immediate vicinity of the type locality.

Distribution. *Cincinnatia leptospira* was found crawling on dead twigs, leaves and tree rootlets in quieter zones and pools along the stream edge. Specimens were very sparse and about three hours were required to collect the type series. Other mollusks found associated with this species are *Planorbella duryi* (Wetherby 1879), *Physella hendersoni arioma* (Clench 1925), *Laevapex diaphanus* (Haldeman 1841) and *Pisidium* sp.

Conservation status. The species is restricted to a protected area within the Ocala National Forest. No further protective measures are necessary as long as this part of the forest remains in its present use. A brass plaque should be erected along the hiking trail where it crosses the slough calling attention to the presence of this local endemic.

Remarks. The specific relationships of this species are not clear. The saddle-shaped configuration of the coiled oviduct distinguishes *Cincinnatia leptospira* from others of the genus in which the female anatomy is known. A secondary seminal receptacle is shared with the following two species. This structure has not been reported from other North American Nymphophilinae.

Etymology. The species name is derived from the Classical Greek leptoz, narrow, and σπειρα a spire.

The *Cincinnatia vanhyningi* species-group
***Cincinnatia alexander*, new species**
Alexander Spring Snail

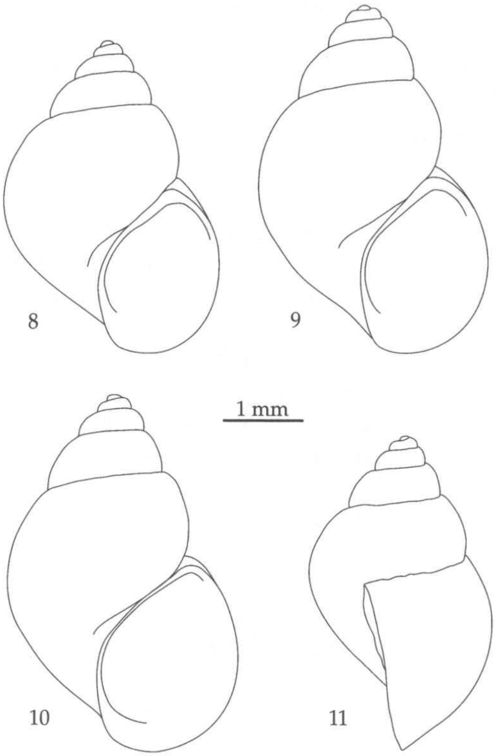
Diagnosis. A large robust species belonging to the *Cincinnatia vanhyningi* group by virtue of the presence of an inferior crest on the ventral surface of the penis but only in some specimens. An accessory crest is lacking. It differs from all species of the *vanhyningi* group by the reduced pattern of glands on the dorsal and ventral surface of the penis. The penis filament has a narrow black band internally. The coiled oviduct is simple. The bursa copulatrix is greatly enlarged and overlaps the posterior end of the albumen gland. The mantle is diffusely pigmented compared to most other *Cincinnatia*. The shell is very similar to *C. petrifons* Thompson, 1968, but it is more robust, the aperture is nearly quadrangular in outline and the columellar margin of the aperture tends to be canaliculate.

Shell (Figs. 2, 8-11). Large, about 3.8-4.3 mm long (Table 2). Moderately solid and translucent. Ovate-conical in shape with an elongate straight-sided spire; spire 0.91-1.17 times height of aperture. Shell 1.39-1.58 times as long as wide. Height of aperture 0.46-0.52 times length of shell. Whorls 4.8-5.3; 1.15-1.27 whorls/mm length; weakly arched compared to most other *Cincinnatia*. Suture moderately impressed. Umbilicus narrow, rimate. Periostracum grayish brown, sculptured with close weak incremental striations and occasional irregularly spaced spiral striae. Aperture height about 0.48-0.54 the length of shell; ovate-elliptical in shape, about 0.69-0.83 times as wide as long; posterior corner angulate. Peristome complete and tightly appressed against parietal wall, but thin; outer lip slightly arched forward in lateral profile (Fig. 8); slightly angulate along baso-columellar corner which tends to be canaliculate.

Operculum (Fig. 18). Thin and hyaline; consisting of about 3.0 paucispiral whorls; elongate-ovate in shape; nucleus located one third of distance from the columellar margin and from the base; columellar mar-

TABLE 2. Measurements in mm based on the holotype (UF 150300) and 11 paratypes (UF 150301).

Specimen	Length	Width	AH	AW	whorls	L/W	AH/L	AH/AW	AW/W
holotype	4.3	2.9	2.2	1.7	5.2	1.48	0.51	1.27	0.59
min.	4.1	2.8	2.1	1.6	4.8	1.32	0.48	1.20	0.56
max.	4.6	3.3	2.4	2.0	5.3	1.55	0.55	1.35	0.62
avg.	4.38	3.05	2.35	1.78	5.08	1.43	0.52	1.29	0.58
std.	0.16	0.14-	0.09	0.10	0.14	0.06	0.02	0.05	0.02



FIGS. 8-11. *Cincinnatia alexander* n. sp. Paratypes (UF 150300).

gin slightly concave. Outer surface with sparse, weak, incremental striations. Muscle attachment scar elongate, about three fourths of the length of operculum and nearly half its width. Muscle attachment scar very thin.

Mantle pigmentation (Fig. 20). The mantle has a narrow dark band that overlays the columellar side of the lower intestine. It extends distally from the mantle collar for about one fourth of a whorl. A diffuse field second band of melanophores overlays the gill and outlines most of the gill lamellae. The rest of the mantle and the mantle collar are unpigmented.

Reproductive anatomy. Female (Fig. 25-26): four specimens examined (UF 150309). The coil of the oviduct is enlarged, but otherwise simple. The seminal receptacle is elongate-elliptical in shape and opens directly into the oviduct. The common oviduct is simple. A very small secondary seminal receptacle is present on the mesad side of the oviduct just posterior to the bursal duct (not illustrated). The bursa copulatrix is impressed ito but exposed on the mesad side of the albumen gland. It is large and overlaps the posterior end of the albumen gland. The bursal duct is imbedded in the albumen gland and enters the common oviduct distal to the pallial wall.

Male (Figs. 32-35): numerous specimens examined (UF 150309). The penis filament is short and does not extend beyond the end of the apical bulb. It is black due to an internal narrow band of melanophores. The glandular pattern on the verge is highly simplified. The dorsal surface has a few scattered superior tubercles. Two usually are present near the left margin near the base of the apical bulb. Two others form elongate crests below and along the lower right margin of the penis. An additional glandular crest is present on the left dorsal surface of the penis. The transverse crest is relatively heavy and slightly raised on a pedicel. A moderately small inferior crest is present in about a fourth of the specimens examined. An accessory crest is absent.

Type locality. Alexander River at Florida Highway 445, Ocala National Forest, Lake County, Florida. HOLOTYPE: UF 150300; collected July 18, 1968 by Fred G. Thompson. PARATYPES: UF 150301 (200); USNM (150), UMMZ 266685 (100); same data as the holotype. ANATOMICAL SPECIMENS: UF 150309, collected 14 August, 1962; 150310, collected 18 July, 1968. Both lots are topotypic.

Distribution. Endemic to Alexander Springs and Alexander River in the Ocala National Forest. It occurs along Alexander River for a distance of about three miles below Alexander Springs. It is common, but is seldom numerous, on rooted and floating aquatic plants.

Conservation status. The species is endemic to a protected waterway in the Ocala National Forest. No additional protective measures are needed at present. A brass plaque should be placed along Alexander River at the Florida Highway 445 bridge to bring public attention to the presence of this locally endemic species.

Remarks. The systematic placement of this species is questionable. Its penis is intermediate in characteristics between the *floridana* group and the *vanhyningi* group because of the loss of glands on the dorsal and ventral surface. The simplified pattern of glands on the verge strongly resembles the pattern found in the *floridana* group. It would be placed there if it were not for the presence in some specimens of an inferior crest on the ventral surface. Within the *floridana* group the shell is comparable in size to *Cincinnatia monroensis*, which differs from *C. alexander* by having a broadly ovate aperture and by having the parietal wall of the aperture weakly in contact with or solute from the preceding whorl. Also, the spire of *C. monroensis* has more prominently arched whorls with a more deeply impressed suture (Thompson, 1968: 125-127, Figs. 66, A and B). Within the *vanhyningi* group the shell of *C. alexander* is most similar in size and appearance to that of *C. petrifons* Thompson 1968. The penis of *C. petrifons* has a complex circular pattern of numerous superior tubercles on the dorsal surface and a well developed inferior crest and an accessory crest on the ventral surface. None of the species of the *vanhyningi* group has a simplified glandular pattern approaching that of *C. alexander*, and none has a black penis filament. *Cincinnatia alexander* has a more slender spire and the aperture tends to be rhomboidal in outline, where as the spire of *C. petrifons* is more robust and the aperture is nearly ovate in shape.

Etymology. The species is named for the spring run in which it occurs. The name *alexander* is from the Latin and is a noun in the genitive case.

Cincinnatia porterae, new species
Green Cove Springsnail

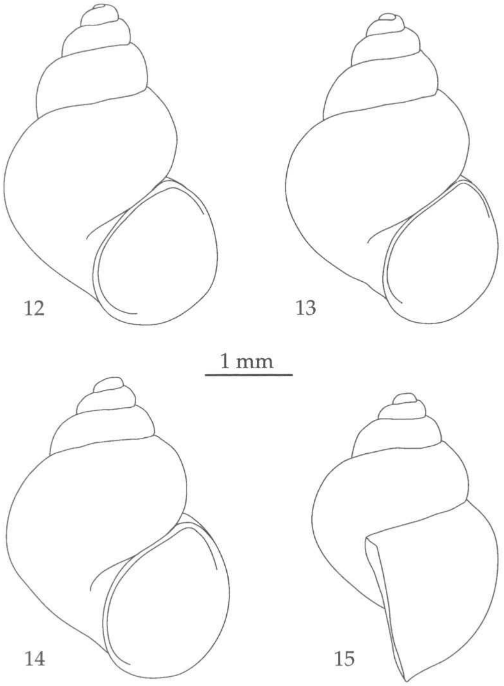
Diagnosis. A member of the *Cincinnatia vanhyningi* species-group because of the presence of an inferior glandular crest on the ventral surface of the penis. This is an elegant and graceful medium-sized species that is about 3.4-3.7 mm long and has an elongate spire, a deeply impressed suture and a broadly ovate aperture. The dorsal surface of the penis bears a few elongate superior tubercles that form a weakly defined U-shaped pattern around an invaginated pit. The ventral surface bears a large inferior crest that is raised on a pedicel. An accessory crest is absent. The penis filament has an internal black band, similar to that of *Cincinnatia alexander*. The coiled oviduct forms a simple loop.

Shell (Figs. 3, 12-15). Conical-ovate to elongate in shape; height of shell about 3.4-3.7 mm long (Table 3); about 1.35-1.61 times as heigh as wide. Spire elongate and straight sided; about 1.00-1.27 times the length of the aperture. Shell moderately thin, transparent in life; periostracum olivaceous in color with fine irregular incremental striations and occa-

TABLE 3. Measurements based on the holotype (UF 150557) and 14 paratypes (UF 150558).

Specimen	Length	Width	AH	AW	whorls	L/W	AH/L	AH/AW	AW/W
holotype	3.8	2.6	1.8	1.5	4.5	1.44	0.48	1.18	0.59
min.	3.3	2.2	1.6	1.4	4.5	1.35	0.43	1.14	0.53
max.	4.0	2.7	1.9	1.5	5.0	1.58	0.53	1.39	0.59
avg.	3.74	2.52	1.77	1.45	4.7	1.47	0.48	1.25	0.56
std.	0.19	0.11	0.08	0.05	0.15	0.07	0.02	0.06	0.02

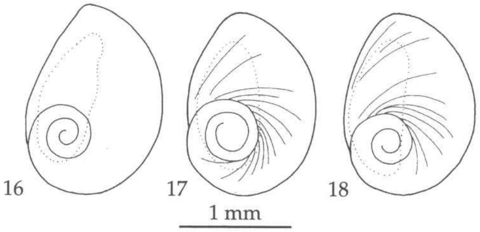
sional weak spiral striations. Whorls 4.6-4.9; 1.28-1.41 whorls/mm length;. The worls are strongly arched and have a deeply impressed suture which descends uniformly to the aperture. Umbilicus narrowly perforate. Aperture broadly ovate in shape with a rounded posterior corner; Height of aperture about 0.45-0.50 times length of shell. Aperture 0.71-0.82 times as wide as long. Aperture slightly prosocline in lateral profile (Fig. 12); lying at an angle of about 15° to axis of shell. The peristome is complete across the parietal margin and is only moderately or weakly attached to preceding whorl.



FIGS. 12-15. *Cincinnatia porterae* n. sp. Paratypes (UF 150558).

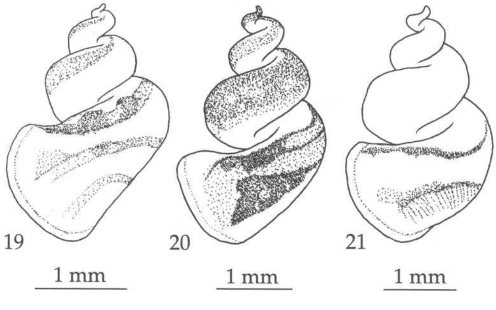
Operculum (Fig. 17). Thin, hyaline; amber colored; elongate-ovate in shape and consisting of about 3.0 rapidly expanding paucispiral whorls. Columellar margin weakly convex. Outer face with more numerous and distinct incremental striation. Nucleus located about one third of distance from inner margin and from base. The very thin muscle attachment scar is elliptical in shape and lies over and above the nucleus.

Mantle pigmentation (Fig. 21). The mantle bears three vaguely defined bands of melanophores. The uppermost band parallels the col-



FIGS. 16-18. Opercula of *Cincinnatia*. FIG. 16. *C. leptospira* n. sp. FIG. 17. *C. porterae* n. sp. FIG. 18. *C. alexander* n. sp.

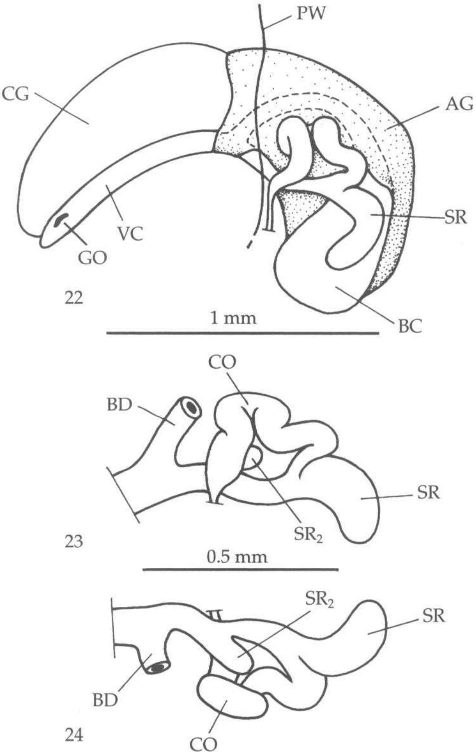
umellar side of the intestine, and then continues distally as a broad dark zone along the shoulders of the lower three whorls. The middle band passes obliquely along the periphery of the last whorl. It is diffuse behind the mantle collar, and then continues distally as a narrow stripe. The lower band is similar in intensity and overlays the gill, but it does not demarcate the individual gill lamellae. The mantle collar and the remainder of the mantle are unpigmented.



FIGS. 19-21. Mantle pigmentation patterns of *Cincinnatia*. FIG. 19. *C. leptospira* n. sp. FIG. 20. *C. alexander* n. sp. FIG. 21. *C. porterae* n. sp.

Reproductive anatomy. Female (Fig. 26): three specimens examined (UF 251900). The coiled oviduct consists of an enlarged simple loop with the ascending segment slightly flexed at its junction with the transverse segment. The seminal receptacle is elongate-ovate in shape and extends about half way to the distal end of the albumen gland. It is joined by the bursa copulatrix duct distal to the posterior pallial wall. The bursa copulatrix overlaps the distal end of the albumen gland, and is partially covered by the gland. A very small tuberular secondary seminal receptacle is present on the mesad side of the oviduct just posterior to the bursal duct (not illustrated).

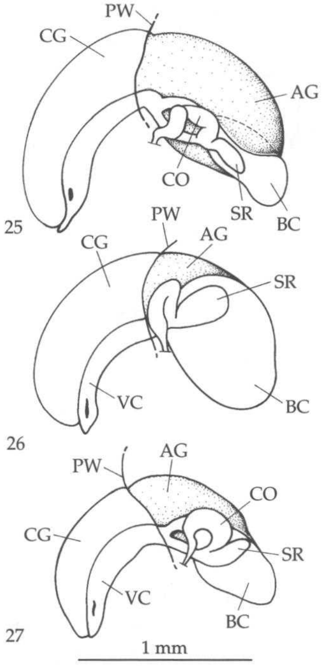
Male (Figs. 36-39): Numerous specimens examined (UF 251900). The



FIGS. 22-24. *Cincinnatia leptospira* new species. Pallial oviduct and associated organs. FIG. 22. Mesad view of pallial oviduct. FIG. 23. Coiled oviduct freed from albumen gland. FIG. 24. Opposite side of coiled oviduct showing anterior seminal receptacle (SR$_2$). AG – albumen gland, BC – bursa copulatrix, CG – capsule gland, CO – coiled oviduct, GO – genital opening, PW – pallial wall, SR$_1$ – posterior seminal receptacle, SR$_2$ – anterior seminal receptacle, VC – ventral canal.

penis filament is black due to a broad internal band of melanophores, and it expends slightly beyond the end of the terminal lobe of the penis. The dorsal surface of the penis bears a few scattered superior tubercles that tend to be arranged in a U-shaped pattern around an invaginated pit that extends longitudinally inward toward the base of the penis. The lateral margin of the penis filament bears a long slender superior tubercular crest. The crest may be continuous or broken into a few short disjunct crests along the outer margin of the filament. The ventral surface of the penis bears a large inferior crest and a smaller parapical crest. An accessory crest is lacking.

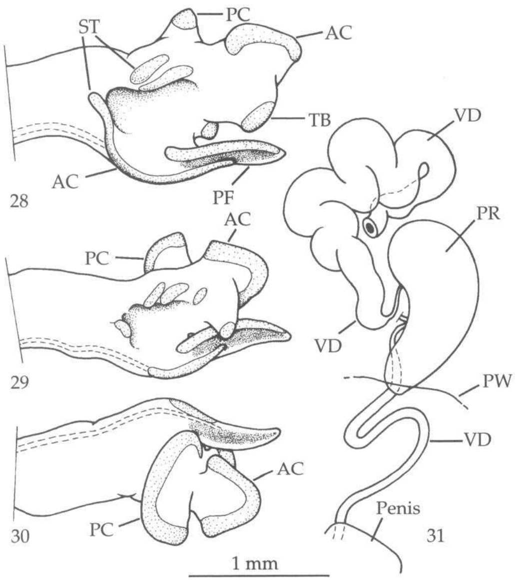
Type locality. Green Cove Spring Run, in the municipal park of the



FIGS. 25-27. Pallial oviduct and associated organs of *Cincinnatia*. FIG. 25. *C. porterae* n. sp. FIGS. 26-27. *C. alexander* n. sp. (See legend for Figs. 22-24).

City of Green Cove Springs, Clay County, Florida. The spring issues from a small depression below a municipal swimming pool. The run is about 1-2 meters wide, very shallow and flows about 100 meters to empty into the St. Johns River. The bottom of the run consists of fine sand. The snail occurs abundantly on rooted aquatic plants and occasional mats of algae in the spring run. HOLOTYPE: UF 150557; collected 21 March, 1963 by Fred G. Thompson. PARATYPES: UF 150558 (160), UMMZ 266686 (50), USNM (50); same data as the holotype. UF 150559, collected 12 January, 1975; UF 150560, collected 12 June, 1995; UF 29733, collected 17 January, 1981. ANATOMICAL SPECIMENS: UF 29733, collected 17 January, 1981; UF 150561, collected 21 March, 1963; UF 251900, collected 12 June, 1975.

Distribution. This species is endemic to Green Cove Spring Run, where it occurs with *Pomacea paludosa* (Say 1829) and *Planorbella duryi*. The species enters the St. Johns River immediately at the mouth of the spring run for a radius of a few meters where it is found on rooted aquatic plants (*Valasneria*) in clear water. The surrounding water is acid brown and has

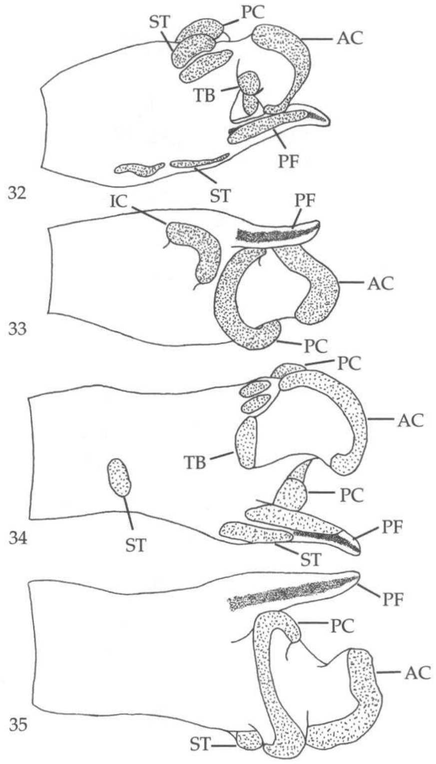


FIGS. 28-31. Male genital structures of *Cincinnatia leptospira* new species. FIGS. 28-30. Penes. FIG. 31. Prostate and associated ducts. AC – apical crest, AcC – accessory crest, IC – inferior crest, PC – parapical crest, PF – penial filament, PR – prostate, PW – pallial wall, PVD – pallial vas deferens, ST – superior tubercle, TB – terminal bulb, VD – vas deferens.

extensive beds of the same plant, where *Cincinnatia porterae* is replaced by *Littoridinops monroensis* (Frauenfeld 1863).

Conservation status. Green Cove Spring once formed a natural pool at the base of a slope where the municipal swimming pool is presently located. The spring now issues from the limestone substratum as a narrow spring run at the east side of the municipal pool. The spring run receives some protected because it is in a municipal park. Measures should be taken to assure that the run is not modified from its present natural state. A brass plaque should be erected along the stream to call attention to the presence of this locally endemic species.

Remarks. The geographically closest related congener is *Cincinnatia fraterna* Thompson 1968. *Cincinnatia fraterna* is common in small streams in adjacent areas along the St. Johns River. It differs from *C. porterae* by having a slenderer shell with a relatively shallow suture and a robust penis with a stout inferior crest. *Cincinnatia porterae* is strikingly similar in appearance and shell size to *C. wekiwae* Thompson 1968, a snail that is endemic to Wekiwa Springs, Orange Co., Florida. They are seperated geographically by a distance of about 75 miles. No consistent differences

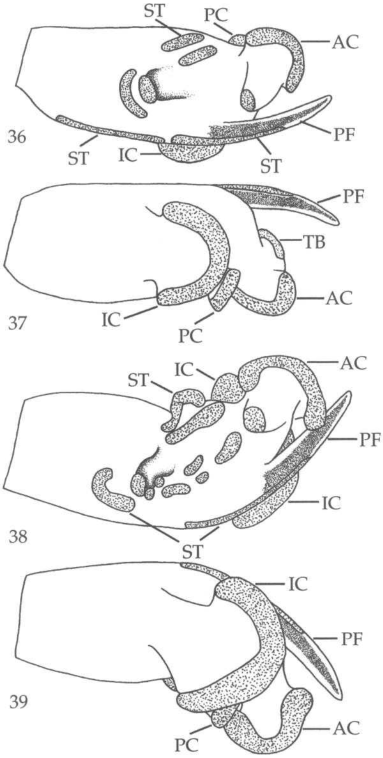


FIGS. 32-35. Penes of *Cincinnatia alexander* n. sp.

between the two species are apparent in the shell. They are distinguished by anatomical differences and by their isolated geographic separation. The penis of *C. wekiwae* differs by having a much denser pattern of superior tubercles and by having an accessory crest.

Like most Hydrobiidae this is an annual species. Samples collected from May through September consist mostly of immature specimens, where-as samples collected from November through early May usually are predominated by gerontic individuals that have significantly eroded shells and distorted growth of the last whorl. The specimens comprising the type series are mostly normal adults and some juveniles. Anatomical data is based on preserved specimens collected with the type series as well as a sample of gerontic specimens collected on January 18, 1981.

Etymology. This elegant little snail is named for Dr. Charlotte Michelle Porter, an historian of science at the University of Florida, in recognition for her extensive contributions about early naturalists of the southeast-



FIGS. 36-39. Penes of *Cincinnatia porterae* n. sp.

ern United States.

ACKNOWLEDGMENTS

Elizabeth L. Mihalcik, Zaidett Barrientos and Charlotte M. Porter assisted with collecting the species described in this paper. The skillfully rendered illustrations were made by Susan F. Trammell. I am grateful to Liath E. Appleton for assistance with the assembling the illustrations and for many other tasks that were necessary for the completion of the manuscript.

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ANALYSIS OF AQUATIC MOLLUSK DISTRIBUTIONS IN RELATION TO CHEMICAL PARAMETERS IN A SERIES OF NORTHERN U.S. LAKES

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Michael J.S. Tevesz[2]

ABSTRACT

This paper describes the relation of lacustrine mollusk taxa to ambient water chemistry of lakes in the eastern half of the northern United States. Tables of water chemistry variables for each lake were constructed, as well as matrices of presences or absences of all mollusk species across the lakes. Mollusk distributions among the sampled lakes are associated with discrete ranges of water chemistry variables. Analysis of these variables related to mollusk species distribution shows that the taxa are influenced by major ion concentrations, pH, and conductivity. Overall, the presence or absence of a given taxon is related to contrasts between pH and alkalinity on the one hand, and conductivity and concentration of the individual ions on the other.

Mollusk taxa form two broad groups, based on their association with particular sets of values of water chemistry variables. Most of the taxa are found within a relatively narrow range of "normal" water chemistries. A second, smaller group (various species of *Gyraulus, Planorbella, Fossaria, Lymnaea,* and *Pisidium*) are associated with high alkalinity lakes. This information is useful not only for better understanding the ecology of modern lacustrine mollusks, but also for enhancing their usefulness as indicators of hydrochemistry in Quaternary paleolake deposits where they occur as fossils.

Key words: aquatic mollusks, lake chemistry, canonical correspondence analysis.

INTRODUCTION

Shells of aquatic mollusks are often among the most common macroscopic animal remains in Quaternary non-marine sediments. They have been recovered from a variety of lacustrine environments that include marl lakes (Miller & Mullet, 1990), littoral and lagoonal deposits (Karrow *et al.*, 1975; Miller & Bajc, 1989) and deep, open water lake settings (Colman *et al.*, 1994a; 1994b; Tevesz *et al.*, 1997; 1998).

The shell carbonate of lacustrine mollusks has been used in stable isotope analyses to identify warming and cooling climate trends, fluctuations in water level, and the movement of water masses (Fritz *et al.*, 1975;

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Lewis & Anderson, 1992; Tevesz *et al.*, 1998). In addition, major, minor, and trace element analyses of shells have provided information on cation chemistry of ambient water (Imlay, 1982). Although these studies yield quantitative environmental data, most interpretations of fossil lacustrine mollusks are based on the assumptions that the fossils can be assigned to extant species; that the living and fossil members of the same species respond to environmental factors in a similar manner; and that the environmental factors controlling the occurrence of the extant taxa are known.

Unfortunately, the ecological variables controlling the occurrences of extant lacustrine mollusks are poorly known, although particular species have been reported as indicators for broad categories, such as eutrophication level (Clarke, 1979a; 1979b), and biogeographic or phytogeographic regimes (Clarke, 1973). As a consequence, analyses of fossil lacustrine mollusks are often limited to general and vague anecdotal interpretations (Taylor, 1960). There is a clear need for quantifiable physical and chemical data that deal with the factors controlling the occurrences of living lacustrine mollusks.

There have been several regional studies of North American aquatic mollusks that have focused on the acquisition of quantitative water chemistry data that could be used to explain the modern distribution of these species. These include Cvancara, 1983 (North Dakota), Jokinen, 1983 (Connecticut), Jokinen, 1992 (New York), and Pip, 1986 (eastern Saskatchewan, Manitoba, northwestern Ontario, northern North Dakota and Minnesota).

The purpose of this paper is to determine the extent to which the presence or absence of lacustrine mollusk species can be related to ambient water chemistry. The mollusk and water samples were collected from lakes in the northeastern, northcentral and midwestern United States (Table 1). This information is of potential value for not only better understanding the ecology of modern lacustrine mollusks , but also enhancing their usefulness as indicators of hydrochemistry in Quaternary paleolake deposits where they occur as fossils.

MATERIALS AND METHODS

Mollusk Samples: Geographic Location and Procedures

Aquatic mollusk and water samples were collected together in three different regions (Tables 1 and 2). The first sample set, which included mollusks, along with water and ostracode samples, was collected by Dr. Alison Smith, Kent State University, from the littoral and sublittoral zones of lakes in eastern North Dakota, South Dakota and western

TABLE 1. Names and locations of lakes used in this study.

Code	Lake Name	State	Latitude (°N)	Longitude (°W)
1	Moon Lake Wetlands	NY	44.26	75.73
2	Bond Lake	NY	43.18	78.92
3	Godfrey Pond	NY	43.03	78.12
4	Java Lake	NY	42.63	78.35
5	Findley Lake	NY	42.12	79.73
6	Gaylanta Lake	MI	45.97	84.30
7	Lake Fifteen	MI	44.98	84.18
8	Lake Ferdelman	MI	45.23	83.96
9	Lost Lake	MI	45.29	83.96
10	Silver Lake	MI	45.27	84.63
11	Ellis Lake	MI	44.66	85.75
12	Indian Lake	MI	44.80	84.93
13	Berry Lake	MI	44.22	85.36
14	Sunset Lake	MI	44.04	85.33
15	Lily Lake	MI	43.98	84.88
16	North Lake	MI	43.86	85.83
17	Pleiness Lake	MI	43.86	86.24
18	Reed Lake	MI	43.86	85.97
19	Jehnsen Lake	MI	43.70	85.27
20	Half Moon Lake	MI	43.25	85.06
21	Three Mile Lake	MI	42.19	85.96
22	Black Lake	MI	42.06	86.29
23	Shafer Lake	MI	42.19	86.11
24	Schoolsection Lake	MI	42.29	85.95
25	Clear Lake	MI	42.51	85.26
26	Bassett Lake	MI	42.66	85.48
27	Bassett Spring	MI	42.66	85.48
28	Fish Lake	MI	42.55	85.50
29	Virgin Run Lake	PA	40.04	79.73
30	High Point Lake	PA	39.78	79.21
31	Lime Lake	IN	41.71	85.12
32	Loon Lake	IN	41.65	85.05
33	McClure's Lake	IN	41.08	85.96
34	Loon Lake (II)	IN	41.08	85.97
35	Pleasant Lake	WI	42.79	88.55
36	Mukwonago Pond	WI	42.87	88.39
37	Lower Phantom Lake	WI	42.86	88.35
38	Rome Pond	WI	42.98	88.61
39	Hunter Lake	WI	43.00	88.46
40	Lake Five	WI	43.19	88.27
41	Crooked Lake	WI	43.62	88.16
42	Lake Seven	WI	43.61	88.14
43	Meilakee Lake	WI	44.03	89.30
44	Marl Lake	WI	44.11	89.38
45	Crystal Lake	WI	44.27	89.17

(Continued on the next page)

TABLE 1. Continued.

Code	Lake Name	State	Latitude (°N)	Longitude (°W)
46	Fountain Lake	WI	44.31	89.27
47	Coon Fork Lake	WI	44.70	91.02
48	Pepin Lake	MN	44.47	93.61
49	Reed's Lake	MN	44.18	93.62
50	Lake George	MN	44.23	93.87
51	Butterfield Lake	MN	43.96	94.81
52	Summit Lake	MN	43.86	95.07
53	Dead Coon Lake	MN	44.36	96.10
54	Dead Coon Spring	MN	44.35	96.10
55	Steep Bank Lake	MN	44.54	96.33
56	Indian Lake	MN	43.51	95.50
57	Elm Lake	IA	42.76	93.68
58	Beed's Lake	IA	42.23	93.24
59	Meyer Lake	IA	43.17	91.91
60	Pleasant Creek Lake	IA	42.12	91.81
61	Lee Lake	MI	41.78	85.37
62	New Germany Lake	MD	39.63	79.12
63	Lake Habeeb	MD	39.70	78.65
64	Indian Springs Lake	MD	39.70	77.94
65	Laurel Lake	PA	40.04	77.27
66	Card Pond	MA	42.33	73.37
67	Lily Lake	PA	41.14	76.08
68	Little Ball Club Lake	MN	47.42	93.98
69	Maple Lake	MN	45.78	95.37
70	Minnewaaka Lake	MN	45.60	95.45
71	Nokay Lake	MN	46.37	93.95
72	Sewell Lake	MN	46.15	95.82
73	Signallness Lake	MN	45.53	95.52
74	West Lost Lake	MN	46.38	95.87
75	Alkaline Lake	ND	46.67	99.85
76	Coon Lake	ND	47.97	98.38
77	Elbow Lake	ND	47.92	98.72
78	Horseshoe Lake	SD	44.98	97.32
79	Spring Lake	ND	47.95	98.82
80	Pickerel Lake	SD	45.52	97.27
81	Roslyn Lake	SD	45.48	97.50
82	Waubay Lake	SD	45.40	97.43
83	Crow Wing Lake	MN	46.23	94.35
84	Dead Coon Lake	MN	44.35	96.10
85	Elk Lake	MN	47.18	95.22
86	Elk Lake	MN	45.87	95.80
87	Fish Trap Lake	MN	46.22	94.60
88	George Lake	MN	47.20	94.98
89	Itasca Lake	MN	47.22	95.20
90	Hazeldon Lake	SD	45.52	97.47
91	Round Lake	ND	48.03	99.27

TABLE 2. Taxa studied, including abbreviations for each taxon used in Table 3 and Fig. 4.

Phylum Mollusca	
Class GASTROPODA	
Subclass PROSOBRANCHIA	
Order MESOGASTROPODA	
Family HYDROBIIDAE	
Amnicola integra	Am-int
Amnicola limosus	Am-lim
Amnicola walkeri	Am-wal
Marstonia decepta	Ma-dec
Family PLEUROCERIDAE	
Elimia (= *Goniobasis*) *livescens*	Go-liv
Family VALVATIDAE	
Valvata sincera	Va-sin
Valvata tricarinata	Va-tri
Valvata spp.	Va-spp
Family VIVIPARIDAE	
Campeloma decisum	Ca-dec
Campeloma spp.	Ca-spp
Cipangopaludina chinensis	Ci-chi
Viviparus georgianus	Vi-geo
Subclass PULMONATA	
Order BASOMMATAPHORA	
Family ANCYLIDAE	
Ferrissia fragilis	Fe-fra
Ferrissia parallela	Fe-par
Laevapex fuscus	La-fus
Family LYMNAEIDAE	
Acella haldemani	Ac-hal
Fossaria decampi	Fo-dec
Fossaria exigua	Fo-exi
Fossaria obrussa	Fo-obr
Lymnaea stagnalis	Ly-sta
Pseudosuccinia columella	Ps-col
Stagnicola elodes	St-elo
Stagnicola emarginata	St-ema
Stagnicola reflexa	St-ref

(Continued on the next page)

TABLE 2. Continued

Family PHYSIDAE	
Physa jennessi	Ph-gen
Physella ancillaria	Ph-anc
Physella gyrina	Ph-gyr
Physella heterostropha	Ph-het
Physella integra	Ph-int
Physella parkeri	Ph-par
Physella sayi	Ph-say
Physella spp.	Ph-spp
Family PLANORBIDAE	
Gyraulus deflectus	Gy-def
Gyraulus parvus	Gy-par
Helisoma anceps	He-anc
Menetus dilatatus	Me-dil
Planorbula armigera	Pl-arm
Planorbella campanulatum	He-cam
Planorbella corpulentum	He-cor
Planorbella trivolvus	He-tri
Planorbella spp.	He-spp
Promenetus exacuous	Pr-exa
Class BIVALVIA	
Order UNIONIDA	
Family UNIONIDAE	
Anodonta imbecillis	An-imb
Anodonta (Pyganodon) grandis	Py-gra
Fusconaia flava	Fu-fla
Lampsilis siliquoidea	La-sil
Order VENEROIDA	
Family SPHAERIIDAE	
Musculium lacustre	Mu-lac
Musculium partumeium	Mu-par
Musculium securis	Mu-sec
Pisidium casertanum	Pi-cas
Pisidium compressum	Pi-com
Pisidium equilaterale	Pi-equ
Pisidium ferrugineum	Pi-fer
Pisidium nitidum	Pi-nit
Pisidium rotundatum	Pi-rot
Pisidium variabile	Pi-var
Pisidium ventricosum	Pi-ven
Pisidium walkeri	Pi-wal
Pisidium spp.	Pi-spp
Sphaerium rhomboideum	Sp-rho
Sphaerium simile	Sp-Sim
Sphaerium striatinum	Sp-stri
Sphaerium spp.	Sp-spp

Minnesota as described in Smith (1993). All of the lakes sampled for this study, with three exceptions (Alkaline Lake, Minnesota; Horseshoe Lake, South Dakota; and Spring Lake, North Dakota) contained mollusks. The samples were collected during the first half of June (1988) and mid-September (1987, 1988). An average of four samples per lake were obtained. The mollusks were collected in a 5 cm diameter Hongve sediment sampler (Wright, 1980) with wet volume capacity of approximately 60 cc. The sediment samples were washed through a series of 20, 100, and 230 mesh sieves and dried by freeze-drying. The majority of the mollusks from these collections were found in the 20 mesh residues. Only shells retaining either the soft-parts, operculum, or periostracum were included in this study.

A second set of samples was collected from Michigan lakes by the senior author using the procedures described above. The mollusks were collected during May, 1995, from the littoral zone of the lakes using a 15 cm diameter by 17 cm high hollow cylinder. Hardware cloth, with 2 mm diameter openings, covered one end of the cylinder that was connected to a telescoping handle approximately 1.8 m in length. These collections were supplemented with materials collected in deeper water with the Hongve sediment sampler.

A third set of samples were taken from lakes in Indiana (June, 1995), Iowa (June, 1995), Maryland (July, 1995), Pennsylvania (July and August, 1994-July, 1995) New York (July, 1997- May-August, 1993), Massachusetts (August, 1994), and Wisconsin (June, 1995); all were collected by Drs. Alison Smith and Donald Palmer, Kent State University, with the Hongve sediment sampler in the sublittoral zone.

Water Chemistry Measurements

The water samples from lakes in eastern North Dakota, South Dakota and western Minnesota (set 1) were collected to determine major dissolved ion concentrations (Smith, 1993). Specific conductance was measured in the field, using a YSI Model 33 salinity-conductivity-temperature meter. A Markson Model 88 pH meter with combination electrode was used to obtain the pH data. The water samples were analysed at the University of Minnesota Limnological Research Center for magnesium, calcium, sodium, potassium, sulfate, chloride, and total organic carbon; all data are reported as meq L^{-1}. Alkalinity was calculated as the sum of carbonate and bicarbonate using the procedures in Mackereth *et al.* (1978). Total dissolved solids were calculated as the summed total of the major ions measured.

The water samples from all other lakes were collected and analysed for the same ions as the Minnesota and Dakota samples. The analyses for this group of water samples, however, were done at the Denver laboratories of United States Geological Survey (Forester, Smith, Palmer, and Curry, unpublished data).

Mollusk Sample Processing and Identification

Sieved residues were examined for mollusks, which were picked by hand under dissecting microscopes, as necessary. Specimens were separated according to putative species. After all samples were processed, species identifications were determined by the senior author and verified through the use of the following references: Burch (1975 a,b; 1989); Clarke (1973; 1981); and Burch & Jung (1992). Nomenclature follows Turgeon *et al.* (1988). Voucher specimens are deposited in the Cleveland Museum of Natural History.

Data Analysis

Matrix tables of water chemistry variables for each lake were constructed, as well as matrix tables of presences or absences of all mollusk species across the lakes. These two data matrices formed the basis of all subsequent analyses.

All statistical procedures were implemented using the S statistical package (S-PLUS Version 4, MathSoft, 1997) on a Pentium-based computer, except for canonical correspondence analysis, which used the CANOCO package (Version 4: ter Braak & Smilauer, 1998).

To assess the spectrum of chemical environments in which the sampled mollusks were found, Principal Components Analysis (PCA) was employed. This technique assesses the major axis of variation among all water chemistry variables simultaneously (Gauch, 1982). A similar PCA based on the allocation of mollusk species among lakes was conducted using the matrix of presence/absence data. In addition, similarities in the distribution of mollusk species were revealed using an agglomerative clustering technique based on the average linkage pair-group algorithm (Sneath & Sokal, 1973).

We have used Detrended Canonical Correspondence Analysis (DCCA: ter Braak & Smilauer, 1998) as the most appropriate procedure for simultaneously relating the distribution of mollusk species to the spectrum of water chemistries of the lakes in which they have been observed (Gauch, 1982).

RESULTS

Descriptive Analyses

Taxonomic distribution

Table 3 gives the total number of occurrences for each taxon. The most widely distributed mollusks in the lakes that we sampled are *Amnicola limosus* and *Gyraulus parvus;* each of these species occurred in over half of the lakes. Other commonly occurring species were *Valvata tricarinata, Physella gyrina, Gyraulus deflectus, Helisoma anceps, Promenetus exacuous, Lymnaea decepta* and *Pisidium nitidum.* The least common mollusks were the ancyclids (*Ferrissia* and *Laevapex*) and unionid bivalves.

Species ranges of water chemistry

Table 3 also lists the minimum and maximum values for each of the nine water chemistry variables for each of the taxa. Among species that were relatively common (arbitrarily defined as occurring in more than 20 lakes), *Amnicola limosus, Gyraulus parvus, Marstonia decepta* and *Valvata tricarinata* had the widest pH range. These were also the species that occurred in lakes with the widest ranges in conductivity and alkalinity. The only other species that occurred over a wide range of calcium concentrations were *Campeloma decisum, Gyraulus deflectus, Gyraulus parvus, Pisidium compressum,* and *Promenetus exacuous.* However, these latter species occurred in lakes having a smaller range in pH. The minimum calcium concentration for all 12 common species was 0.18 meq L^{-1}. The only other species that occur at comparably low calcium levels were *Physella heterostropha* (which only occurred in 2 lakes), *Sphaerium striatinum* (occurring in 14 lakes), and *Viviparus georgianus* (in 10 lakes).

Syncretic Analyses

PCA of water chemistry

Our initial Principal Components Analysis (PCA) was based on all nine water chemistry variables. Because two variables (pH and conductivity) are incommensurate in physical units with the other seven, this initial analysis had to be based on the correlation matrix. Fig. 1 shows the projections of the lake data onto the first two PCA axes, which accounted for 67.3% and 13.2% of the total variation in the data, respectively. The first principal component had similar and positive loadings for all nine variables, whereas the second principal component involved contrasts between pH and alkalinity, on the one hand, and conductivity and the concentration of the individual ions, on the other hand. As shown

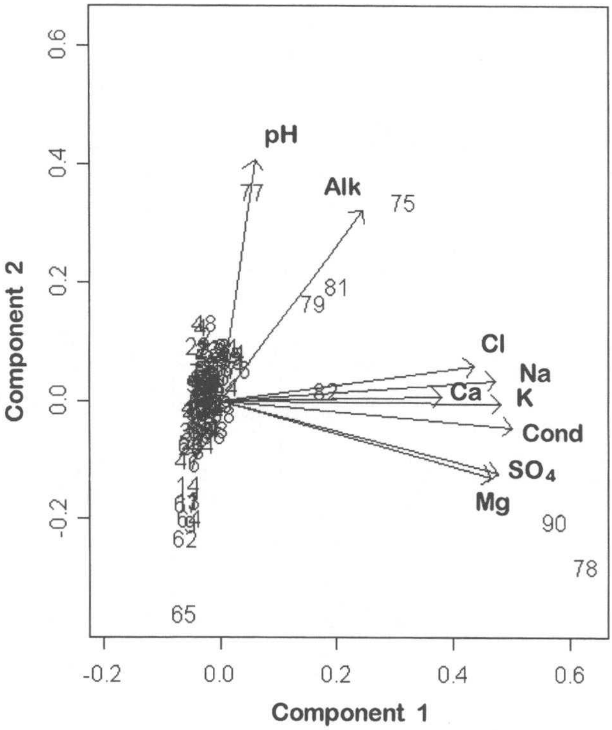

FIG. 1. Principal Components Analysis of water chemistry variables in sampled lakes. Numbers in figure correspond to lakes listed in Table 1. The composition of each component is indicated by the vectors labeled with the chemical variables.

TABLE 3. Maximum and minimum values for each of the nine water chemistry variables for each of the mollusk taxa (conductivity is measured in µS cm^{-1}, all other variables in meq L^{-1}); the number next to abbreviated names indicates number of occurrences in sampled lakes.

		Conductivity		pH		Calcium		Magnesium		Sodium		Potassium		Sulfate		Chloride		Alkalinity	
Species	#	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
Ac-hal	2	196	340	7.92	8.62	0.70	1.40	0.69	2.14	0.13	0.43	0.02	0.03	0.10	0.20	0.23	0.42	1.80	4.02
Am-int	1	355	355	8.04	8.04	2.05	2.05	1.56	1.56	0.30	0.30	0.04	0.04	0.50	0.50	0.39	0.39	4.64	4.64
Am-lim	49	34	12500	6.43	9.46	0.18	12.28	0.04	134.91	0.00	71.78	0.00	8.34	0.01	211.97	0.01	11.54	0.30	15.13
Am-wal	9	45	340	7.92	9.4	0.21	1.80	0.12	2.14	0.09	1.13	0.02	0.12	0.01	0.29	0.03	1.55	0.44	4.02
An-imb	1	230	230	8.42	8.42	1.57	1.57	0.89	0.89	0.28	0.28	0.05	0.05	0.07	0.07	0.10	0.10	2.48	2.48
Ar-cri	2	220	255	8.65	8.86	0.95	1.59	1.15	1.49	0.07	0.17	0.10	0.12	0.02	0.19	0.05	0.28	2.54	2.76
Ca-dec	21	40	12500	7.51	9.26	0.25	12.28	0.16	134.91	0.07	71.78	0.01	8.34	0.01	211.97	0.03	7.64	0.52	15.13
Ca-spp	1	690	690	8.66	8.66	2.74	2.74	2.30	2.30	1.78	1.78	0.05	0.05	1.40	1.40	2.20	2.20	6.45	6.45
Ci-chi	2	40	4850	7.76	8.65	0.21	3.24	0.09	54.70	0.04	15.75	0.02	3.73	0.17	65.10	0.04	3.43	0.30	7.28
Fe-fra	3	255	4850	8.65	8.91	1.59	6.49	1.49	54.70	0.07	24.06	0.12	3.73	0.02	65.10	0.05	11.54	2.76	7.69
Fe-par	3	256	340	8.18	8.57	1.45	2.79	1.15	2.13	0.17	0.26	0.01	0.08	0.01	0.21	0.03	0.14	2.62	5.97
Fo-dec	1	203	203	8.67	8.67	1.65	1.65	0.82	0.82	0.15	0.15	0.05	0.05	0.07	0.07	0.16	0.16	3.68	3.68
Fo-exi	6	40	4850	7.32	9.4	0.21	3.24	0.10	54.70	0.05	15.75	0.01	3.73	0.02	65.10	0.03	3.43	0.44	7.28
Fo-obr	9	40	870	7.94	9.02	0.25	4.04	0.16	5.82	0.04	1.78	0.01	0.20	0.01	14.17	0.01	2.20	0.52	6.45
Fu-fla	1	105	105	7.97	7.97	1.00	1.00	0.39	0.39	0.07	0.07	0.02	0.02	0.08	0.08	0.13	0.13	2.03	2.03
Go-liv	2	105	690	7.97	8.66	1.00	2.74	0.39	2.30	0.07	1.78	0.02	0.05	0.08	1.40	0.13	2.20	2.03	6.45
Gy-def	28	40	12500	7.34	9.09	0.21	12.28	0.12	134.91	0.04	71.78	0.01	8.34	0.01	211.97	0.01	7.64	0.44	7.28
Gy-par	57	34	12500	6.43	9.5	0.18	12.28	0.04	134.91	0.00	71.78	0.00	8.34	0.01	211.97	0.01	11.54	0.30	10.35
He-anc	28	40	1250	7.51	9.46	0.21	5.36	0.12	5.87	0.06	5.22	0.01	0.38	0.01	14.17	0.03	3.10	0.44	6.45
He-cam	17	100	3850	7.92	9.02	0.70	6.49	0.44	18.01	0.09	24.06	0.01	1.32	0.01	28.32	0.03	11.54	1.47	7.69
He-cor	1	265	265	8.98	8.98	1.90	1.90	1.15	1.15	0.29	0.29	0.04	0.04	0.25	0.25	0.34	0.34	4.31	4.31
He-tri	14	40	580	7.75	9.5	0.28	2.99	0.14	2.88	0.04	1.39	0.01	0.09	0.08	0.54	0.05	1.69	0.53	7.26
He-spp	2	265	355	8.04	8.55	1.35	2.05	1.15	1.56	0.22	0.30	0.04	0.07	0.29	0.50	0.20	0.39	3.25	4.64
La-fus	7	230	12500	8.28	9.17	1.45	12.28	0.89	134.91	0.07	71.78	0.05	8.34	0.02	211.97	0.05	7.64	2.48	6.07
La-sil	6	160	4850	8.45	8.88	1.60	4.04	0.72	54.70	0.04	15.75	0.02	3.73	0.01	65.10	0.03	3.43	2.60	7.28
Ly-sta	9	40	1250	7.32	8.8	0.21	5.36	0.10	5.87	0.05	5.22	0.01	0.38	0.08	4.71	0.03	0.42	0.44	6.07
Ma-dec	32	34	12500	6.43	9.46	0.18	12.28	0.09	134.91	0.04	71.78	0.01	8.34	0.01	211.97	0.03	7.64	0.40	7.28
Me-dil	3	420	1650	8.23	9.26	0.46	1.99	2.71	6.84	0.40	14.36	0.03	1.02	0.46	10.82	0.59	1.66	3.73	15.13
Mu-lac	2	203	405	8.04	8.67	1.65	2.00	0.82	1.15	0.15	0.96	0.05	0.06	0.07	0.44	0.16	0.90	3.68	4.37
Mu-par	17	120	1350	7.92	9.46	0.90	5.36	0.04	6.84	0.00	6.22	0.00	0.66	0.03	10.82	0.04	2.20	1.98	6.45
Mu-sec	8	100	3850	7.95	8.98	0.70	6.49	0.39	18.01	0.04	24.06	0.01	1.32	0.07	28.32	0.01	11.54	1.47	7.69
Ph-anc	1	235	235	8.33	8.33	2.08	2.08	0.85	0.85	0.12	0.12	0.02	0.02	0.10	0.10	0.05	0.05	2.44	2.44

TABLE 3. Continued.

Ph-gen	1	80	80	8.35	8.35	0.55	0.55	0.16	0.16	0.06	0.06	0.02	0.02	0.21	0.21	0.06	0.06	0.96	0.96
Ph-gyr	23	45	1350	7.7	9.17	0.21	4.04	0.12	6.84	0.04	6.22	0.01	0.66	0.03	14.17	0.04	1.33	0.44	6.94
Ph-het	2	34	40	6.43	7.76	0.18	0.21	0.09	0.09	0.04	0.08	0.02	0.02	0.06	0.17	0.04	0.06	0.30	0.40
Ph-int	9	45	4850	7.51	9.4	0.21	5.36	0.12	54.70	0.10	15.75	0.01	3.73	0.03	65.10	0.04	3.43	0.44	7.28
Ph-par	1	12500	12500	8.28	8.28	12.28	12.28	134.91	134.91	71.78	71.78	8.34	8.34	211.97	211.97	7.64	7.64	5.78	5.78
Ph-say	2	280	305	8.18	8.45	1.69	1.80	1.39	1.46	0.26	0.30	0.05	0.05	0.01	0.01	0.03	0.03	3.24	3.34
Ph-spp	23	34	730	6.43	9.5	0.18	4.94	0.04	3.62	0.00	3.39	0.00	0.12	0.06	5.42	0.05	3.10	0.40	7.97
Pi-cas	15	40	4850	7.47	9.02	0.21	6.49	0.09	54.70	0.04	24.06	0.01	3.73	0.03	65.10	0.04	11.54	0.30	7.97
Pi-com	22	34	12500	6.43	9.4	0.18	12.28	0.09	134.91	0.04	71.78	0.01	8.34	0.01	211.97	0.03	7.64	0.40	6.72
Pi-equ	1	319	319	8.75	8.75	1.15	1.15	1.97	1.97	0.24	0.24	0.02	0.02	0.25	0.25	0.39	0.39	3.48	3.48
Pi-fer	11	45	1250	7.7	9.09	0.21	5.36	0.12	5.87	0.06	5.22	0.01	0.38	0.06	4.71	0.06	0.48	0.44	6.72
Pi-nit	27	45	1650	7.7	9.46	0.21	4.94	0.04	5.15	0.00	14.36	0.00	1.02	0.01	5.42	0.03	3.10	0.44	15.13
Pi-rot	2	45	355	8.04	8.25	0.21	2.05	0.12	1.56	0.10	0.30	0.03	0.04	0.08	0.50	0.10	0.39	0.44	4.64
Pi-var	2	160	355	8.04	8.67	0.75	2.05	0.82	1.56	0.06	0.30	0.01	0.04	0.10	0.50	0.09	0.39	1.94	4.64
Pi-ven	2	355	395	8.04	8.74	1.70	2.05	1.56	2.22	0.30	0.32	0.04	0.07	0.42	0.50	0.39	0.51	4.47	4.64
Pi-wal	3	196	450	7.7	8.94	0.70	3.09	0.69	2.14	0.16	0.43	0.03	0.03	0.10	0.37	0.25	0.42	1.80	6.72
Pi-spp	17	34	12500	6.43	9.46	0.18	12.28	0.09	134.91	0.08	71.78	0.01	8.34	0.06	211.97	0.06	7.64	0.40	5.78
Pl-arm	3	210	1350	8.45	9.17	1.59	1.99	0.70	6.84	0.13	6.22	0.02	0.66	0.01	10.82	0.03	0.90	1.98	3.73
Pr-exa	26	40	12500	7.34	9.17	0.21	12.28	0.12	134.91	0.04	71.78	0.01	8.34	0.02	211.97	0.01	7.64	0.44	6.07
Ps-col	6	105	1350	7.97	9.17	1.00	5.36	0.39	6.84	0.07	6.22	0.01	0.66	0.01	10.82	0.03	0.90	2.03	6.07
Py-gra	10	210	4850	8.04	9.26	0.46	5.36	0.70	54.70	0.12	15.75	0.01	3.73	0.01	65.10	0.03	3.43	1.98	15.13
Sp-rho	5	100	1250	8.33	8.62	0.70	5.36	0.44	5.87	0.09	5.22	0.01	0.38	0.10	4.71	0.14	0.42	1.47	6.07
Sp-sim	6	100	340	7.97	8.62	0.70	1.69	0.39	2.13	0.07	0.43	0.02	0.11	0.01	0.14	0.03	0.42	1.47	3.58
Sp-stri	14	34	4850	6.43	9.02	0.18	5.36	0.09	54.70	0.04	15.75	0.01	3.73	0.03	65.10	0.04	3.43	0.30	7.28
Sp-spp	1	335	335	9.46	9.46	1.20	1.20	2.14	2.14	0.29	0.29	0.05	0.05	0.77	0.77	0.45	0.45	3.28	3.28
St-elo	7	180	405	8.02	9.42	1.00	2.84	0.38	1.89	0.12	0.96	0.01	0.06	0.21	0.54	0.05	0.90	1.69	6.45
St-ema	1	255	255	8.65	8.65	1.59	1.59	1.49	1.49	0.07	0.07	0.12	0.12	0.02	0.02	0.05	0.05	2.76	2.76
St-ref	1	203	203	8.67	8.67	1.65	1.65	0.82	0.82	0.15	0.15	0.05	0.05	0.07	0.07	0.16	0.16	3.68	3.68
Va-sin	6	80	355	7.34	8.82	0.70	2.05	0.30	1.73	0.04	0.43	0.01	0.04	0.06	0.50	0.01	0.42	1.47	4.64
Va-tri	37	34	12500	6.43	9.46	0.18	12.28	0.04	134.91	0.00	71.78	0.00	8.34	0.01	211.97	0.03	7.64	0.40	7.97
Va-spp	1	256	256	8.52	8.52	2.79	2.79	1.15	1.15	0.17	0.17	0.01	0.01	0.21	0.21	0.12	0.12	5.97	5.97
Vi-geo	10	34	12500	6.43	8.91	0.18	12.28	0.09	134.91	0.04	71.78	0.01	8.34	0.06	211.97	0.06	11.54	0.40	7.69

in the figure, a majority of the lakes formed a dense cluster, with seven lakes from the Dakotas (#s 75, 77, 78, 79, 81, 82, 90) separated from the general grouping. These seven lakes are characterized by high alkalinity.

To examine the chemistry of a more typical lake, the PCA procedure was repeated after these outliers (numbers listed above) were removed. Discriminatory ability was increased by using the covariance matrix based only on ionic concentrations. Again, the first component (accounting for 63% of the total variation in the data) loaded positively on all seven ions, while the second component (accounting for an additional 25% of the variation) was primarily a contrast between alkalinity and calcium, on the one hand, and sulfate and the other ions, on the other. Fig. 2 shows a dense clustering of the majority of the sampled lakes, with a few outliers: some of the Minnesota lakes and two additional North Dakota lakes.

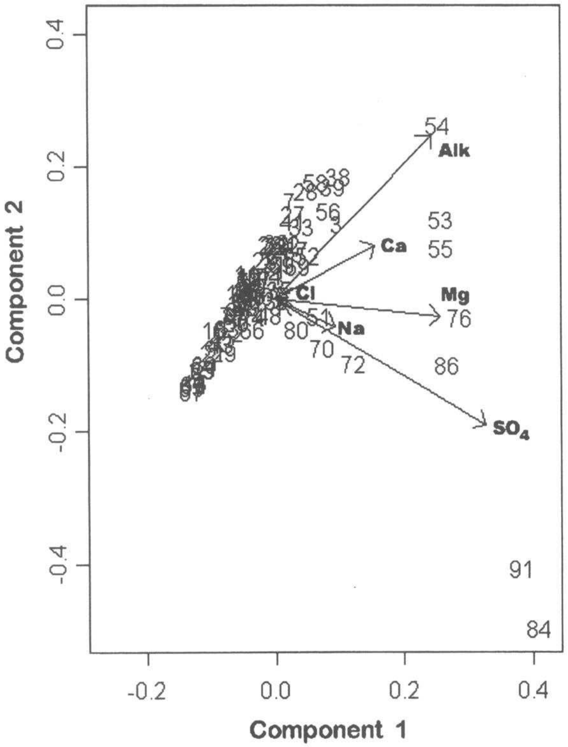

FIG. 2. Principal Components Analysis of ions only, with outliers removed. Numbers in figure correspond to lakes listed in Table 1. The composition of each component is indicated by the vectors labeled with the chemical variables.

PCA of taxa distribution

The ordination of taxa, based on PCA of the presence-absence matrix of distributions of taxa across the lakes, had relatively low resolving power, with only 26% of the variation explained by the first two principal axes. As shown in Fig. 3, species with the most distinct distribution among the lakes are *Amnicola limosus, Marstonia decepta, Gyraulus deflectus, Gyraulus parvus, Promenetus exacuous, Helisoma anceps, Valvata tricarinata, Campeloma decisum, Pisidium compressum,* and *Pisidium nitidium.*

Clustering analysis

Fig. 4 shows the results of clustering the taxa occurrence data, using the average linkage algorithm (Sneath & Sokal, 1973). This technique groups taxa that have similar patterns of co-occurrence among the lakes. Taxa that occur rarely are clustered at the lowest levels (*i.e.*, earliest stages of clustering), while the most common taxa join the dendrogram at the later stages of agglomeration. The two most widely distributed species, *Gyraulus parvus* and *Amnicola limosus,* form the highest clustering levels.

Detrended canonical correspondence analysis

Fig. 5 is the result of a detrended canonical correspondence analysis of the nine water chemistry variables and the mollusk taxa across the lakes. This figure presents the combined effects of water chemistry and taxa distribution simultaneously. The loadings of the chemical variables on the first canonical axes show, for the first axis, a contrast between alkalinity and individual ionic concentrations as well as conductivity, while the second canonical axis is determined significantly by pH and calcium concentrations. The distribution of the species across the two dimensional space determined by these chemical axes shows that all of the most widely distributed taxa (*i.e.*, those occurring in at least 20 lakes) are concentrated in the central region of the figure, while the taxa that are distinct from this general cluster, are those with the fewest occurrences. For example, *Amnicola limosus,* which occurred in 49 lakes, occurs near the center of the cluster, while *Amnicola integra* which occurred only in one lake occurs further out. *Physella gyrina,* which occurred in 23 lakes, is centrally located, while *Physella ancillaria* and *Physa jennessi* (each in one lake) are outliers. All of the extreme outliers, such as *Pisidium equilaterale, Fossaria decampi, Stagnicola reflexa,* and *Planorbella corpulentum,* occurred only in one lake, and two additional outliers, *Armiger crista* and

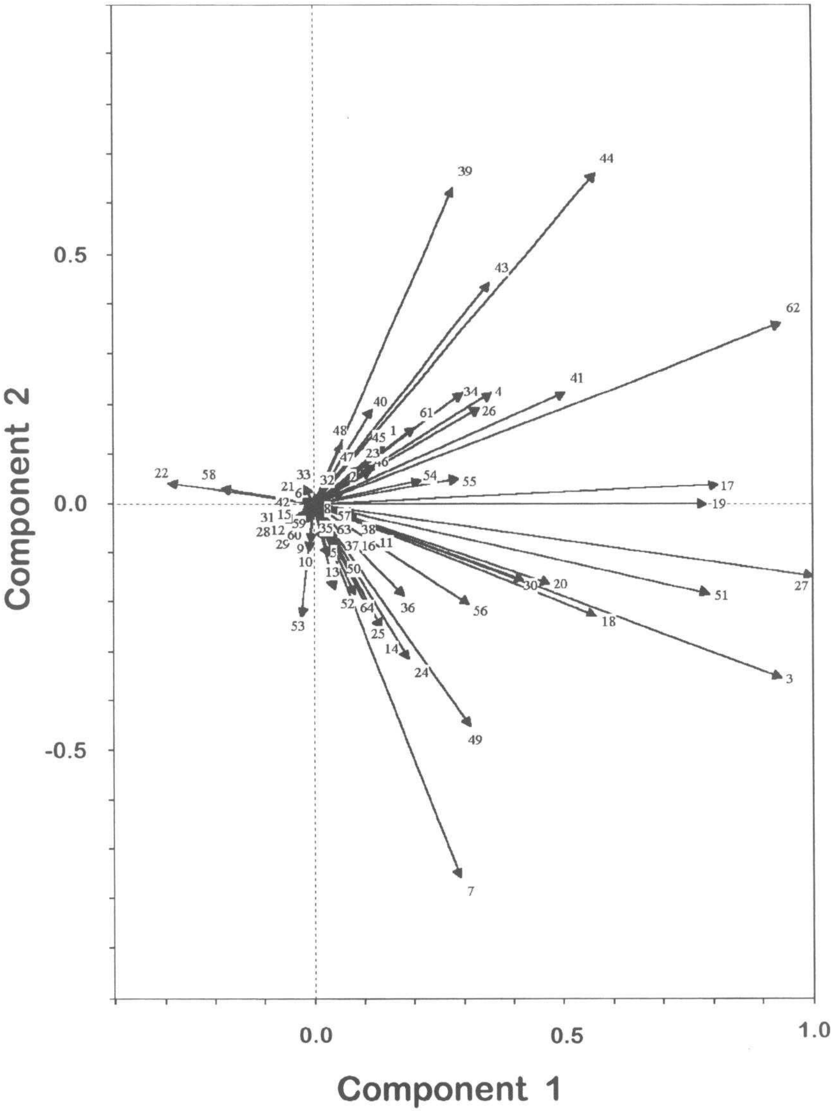

FIG. 3. Principal Components Analysis of mollusk taxa in lakes. The composition of each component is indicated by the vectors labeled with numerical labels for each taxon, as follows- 1, *Acella haldemani;* 2, *Amnicola integra;* 3, *Amnicola limosus;* 4, *Amnicola walkeri;* 5, *Anodonta imbecillis;* 6, *Armiger crista;* 7, *Campelama decisum;* 8, *Campeloma* spp.; 9, *Cipangopaludina chinensis;* 10, *Ferrissia fragilis;* 11, *Ferrissia parallela;* 12, *Fossaria decampi;* 13, *Fossaria exigua;* 14, *Fossaria obrussa;* 15, *Fusconaia flava;* 16, *Elimia* (*Goniobasis*) *livescens;* 17, *Gyraulus deflectus;* 18, *Gyraulus parvus;* [Legend continues at the bottom of the next page.]
]

Physella heterostropha, occurred only in two lakes each. The two commonest species, *Amnicola limosus* and *Gyraulus parvus*, are located near the center of the cluster.

DISCUSSION

The under-representation of unionids may be due to the 5 cm orifice of the Hongve sampler, as well as their patchy distribution within lakes. The underrepresentation of ancyclids may be a reflection of their preference for fluvial environments. Nevertheless, given the wide edaphic range of *Ferrissia fragilis*, its occurrence in only three of the lakes is surprising. While interpretation of details of individual species distributions is possible, this paper has concentrated on the general relationship between species distribution and lake chemistry. In addition to the vagaries of sampling, especially for patchily distributed species, the restricted biogeographic distributions of certain species provides another caveat to making firm conclusions about particular species.

The minimum calcium concentration for lakes in which mollusks were found is consistent with the known dynamics of shell chemistry (Hunter, 1964), and suggests that freshwater mollusks will not be found in any lakes with Ca ion concentration of < 0.18 meq L^{-1}. pH range may be more crucial in restricting mollusk distribution than calcium concentration *per se*, which has a comparatively broad range.

We have concentrated on multivariate techniques to discern the relationship between taxa distribution and water chemistry. The PCA that was based on the correlation matrix of all nine variables (Fig. 1) shows the distinctness of our sampled lakes from lakes from South and North Dakota. These lakes are characterized by high alkalinity and reflect the unusual conditions in these evaporative pan environments. Various spe-

FIG. 3 Legend continued. 19, *Helisoma anceps;* 20, *Planorbella campanulatum;* 21, *Planorbella corpulentum;* 22, *Planorbella trivolvis;* 23, *Planorbella* spp.; 24, *Laevapex fuscus;* 25, *Lampsilis siliquoidea;* 26, *Lymnaea stagnalis;* 27, *Marstonia decepta;* 28, *Menetus dilatatus;* 29, *Musculium lacustre;* 30, *Musculium partumeium;* 31, *Musculium securis;* 32, *Physella ancillaria;* 33, *Physa jennessi;* 34, *Physella gyrina;* 35, *Physella heterostropha;* 36, *Physella integra;* 37, *Physella parkeri;* 38, *Physella sayi;* 39, *Physella* spp.; 40, *Pisidium casertanum;* 41, *Pisidium compressum;* 42, *Pisidium equilaterale;* 43, *Pisidium ferrugineum;* 44, *Pisidium nitidum;* 45, *Pisidium rotundatum;* 46, *Pisidium variable;* 47, *Pisidium ventricosum;* 48, *Pisidium walkeri;* 49, *Pisidium* spp.; 50, *Planorbula armigera;* 51, *Promenetus exacuous;* 52, *Pseudosuccinea columella;* 53, *Anadonta* (*Pyganodon*) *grandis;* 54, *Sphaerium rhomboideum;* 55, *Sphaerium simile;* 56, *Sphaerium striatinum;* 57, *Sphaerium* spp.; 58, *Stagnicola elodes;* 59, *Stagnicola emarginata;* 60, *Stagnicola reflexa;* 61, *Valvata sincera;* 62, *Valvata tricarinata;* 63, *Valvata* spp.; 64, *Viviparus georgianus.*

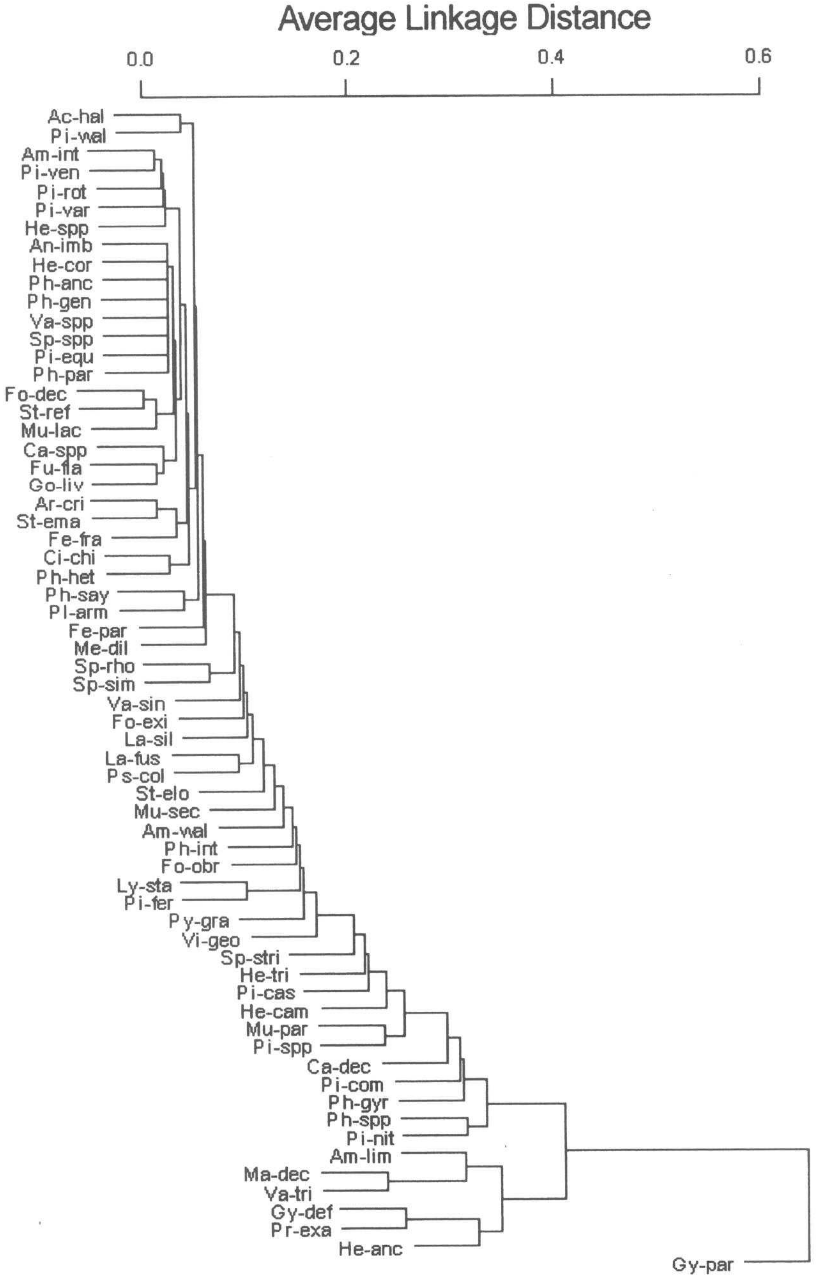

FIG. 4. Binary Average-Linkage Clustering of mollusk taxa.

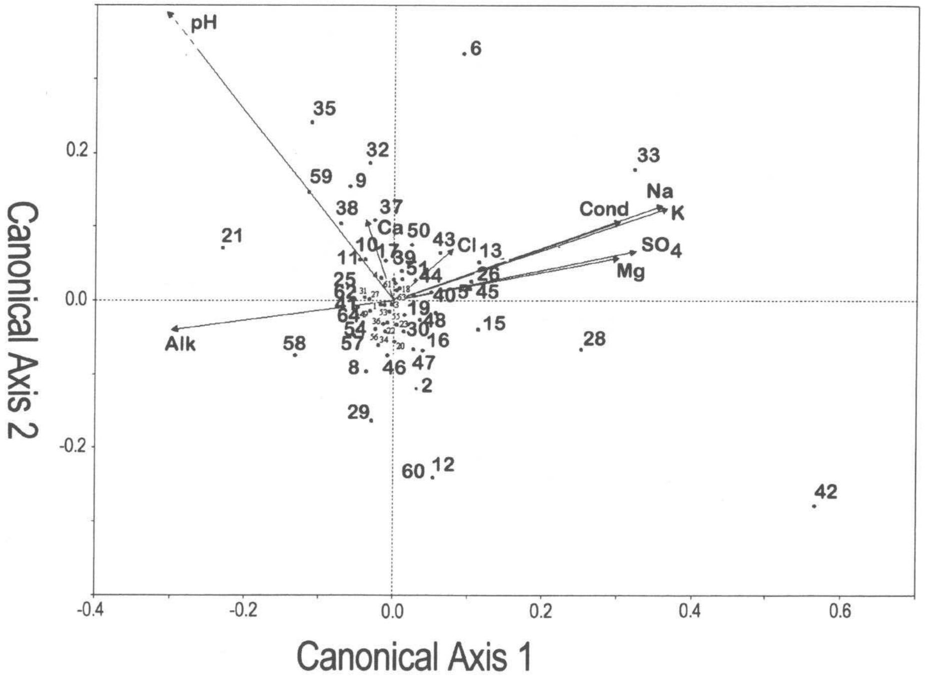

FIG. 5. Detrended Correspondence Analysis of mollusk taxa in lakes. Numbers correspond to mollusk taxa listed in the legend to Fig. 3. The composition of each factor is indicated by the vectors labeled with the chemical variables. The species represented by the enlarged numbers located away from the center of the diagram represent those living under progressively extreme conditions. The majority of species cluster around the center of the diagram and reflect a relatively narrow range of conditions. The identity of these latter species may be inferred from the key provided in the legend to Fig. 3.

cies of the genera *Gyraulus, Planorbella, Fossaria, Lymnaea,* and *Pisidium* were prevalent in these lakes. The PCA of the water chemistries using only ionic chemistries (Fig. 2) demonstrated that a few of the sampled lakes (primarily those from the Dakotas and Minnesota) have unusual chemical environments, while the majority of the lakes show no particularly distinct patterns based on the water chemistry measurements that we collected.

The PCA based on taxa occurrences (Fig. 3) confirms the major role that the most abundant taxa have in our analysis, because it is these taxa that dominate this PCA. Therefore, any patterns that might be discerned by other analytic techniques must be based on a joint consideration of species distributions against the background of water chemistry. The clustering analysis (Fig. 4) speaks with no greater authority than the PCA of the taxa occurrences- both analyses reflect the dominance of the most common taxa.

The detrended correspondence analysis (Figure 5) confirms the conclusions reached by the other analyses. In particular, the lakes sampled differed in their water chemistries by a fundamental contrast, between pH, on the one hand, and conductivity and ionic concentrations, on the other. Secondly, more widely distributed species of mollusks cluster together in the central, common region in this range of water chemistries, while the singleton species are outliers that occur under less usual conditions of water chemistry. Further analyses of the individual biotic and environmental constraints upon the rarer species are in order.

These analyses highlight the need for more focused studies on the rarer species of aquatic mollusks. Their rarity in our samples may reflect a narrower range of tolerance limits. One significant factor, not included in our analysis, but which may be of importance in restricting the distribution of uncommon, possibly even endangered, species, is temperature range. This study is an attempt to relate a number of aquatic mollusk taxa to environmental parameters that may be important in determining their distributions across the eastern half of the northern United States.

SUMMARY AND CONCLUSION

Mollusk distributions among the sampled lakes are associated with discrete ranges of water chemistry variables. Analysis of these variables related to mollusk taxa distribution shows that the taxa are influenced by major ion concentration, pH, and conductivity. Overall, the presence or absence of a given taxon is related to contrasts between pH and alkalinity on the one hand, and conductivity and concentration of the individual ions on the other.

Mollusk taxa form two broad groups, based on their association with particular sets of values of water chemistry variables. Most of the taxa are found within a relatively narrow range of water chemistries (those clustering around the "center" in Fig. 5; see also Table 3 for ranges). A second, smaller group (various species of *Gyraulus, Planorbella, Fossaria, Lymnaea,* and *Pisidium*) are associated with evaporative, high alkalinity lakes in North and South Dakota.

The mollusk taxa studied here are potentially useful for reconstructing the hydrochemistry of Quaternary lacustrine deposits, and the results presented may contribute to a better understanding of past climates and environments. This usefulness is limited, however, because most of the species reflect a rather narrow range of water chemistry values. Many of these species may be used to identify "normal" lacustrine conditions, while the remainder are indicative of conditions of high alkalinity. But overall, these mollusk species do not reflect a broad spectrum of possible hydrochemistries. Significant omissions include conditions of relatively low calcium ion concentration and pH.

The information presented in Fig. 4 is also of potential paleolimnological usefulness. The taxa that are most closely clustered together here represent modern life assemblages. Thus, knowledge of these associations could be used to help determine if fossil shells that occur together in sediments may have been part of the same living community as in Recent times. For example, Miller *et al.* (1998) used *Amnicola limosus* and *Valvata tricarinata* shells found together in the same sediment core as sources of oxygen isotope ratio data for reconstructing aspects of the history of the northern Lake Michigan basin. The fact that these two species cluster together in our modern samples suggest that the ones from the core samples also may have been part of the same living assemblage.

ACKNOWLEDGMENTS

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THE FRESHWATER MUSSELS OF THE TONAWANDA CREEK BASIN IN WESTERN NEW YORK

Paul J. Marangelo[1] and David L. Strayer[2]

ABSTRACT

We surveyed the unionid fauna of Tonawanda Creek basin in the Niagara River drainage in western New York in 1998, and found specimens of 19 species, of which sixteen were live. Our records of live or presumed live (found as recently spent shells) populations include two species that are rare in western New York and the eastern Lake Erie basin: *Lampsilis fasciola* and *Truncilla truncata*. We also found two old spent shells of *Epioblasma triquetra*. The basin's mussel diversity was primarily found in the lower mainstem, with tributaries being relatively species-poor. Despite some evidence of unionid decline and habitat degradation from the impacts of urbanization and agriculture (which is the predominant land-use in the basin), the mussel community of Tonawanda Creek is remarkably diverse. Moreover, it is regionally significant, given the decline of mussel communities elsewhere in the eastern Great Lakes basin.

Key words: Unionidae, Tonawanda Creek Basin, New York.

INTRODUCTION

We conducted a survey for freshwater mussels in Tonawanda Creek and its tributaries in western New York in August, 1998. Early historical records of the creek's mussel community (Robertson & Blakeslee, 1948; also see Strayer *et al.*, 1991 and Strayer & Jirka, 1997 for a treatment of earlier records) are sketchy. More recent records (Strayer *et al.*, 1991; Strayer, 1995) are limited in scope, but indicate that the creek contains one of the most diverse mussel communities in New York State, consisting of species typical of the Lake Erie basin. Our objective was to obtain more comprehensive data on the current status, species composition, distribution, and relative abundance of unionids in the Tonawanda Creek basin.

Tonawanda Creek (Fig. 1) originates on the northern edge of the Allegheny Plateau, running north and then west, emptying into the Niagara River in the vicinity of Grand Isle. The mainstem and tributaries from the headwaters to the Portage Escarpment (Fig. 1) are generally clear streams of moderate gradient with coarse, unconsolidated substrate,

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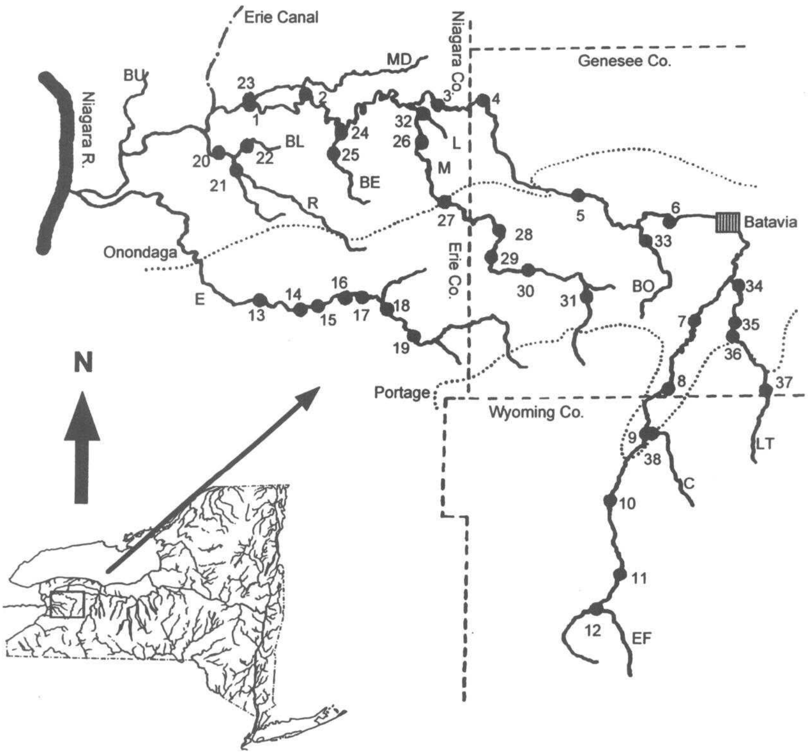

FIG. 1. Sampling stations in the Tonawanda Creek Basin. Numbers show sampling stations (See Table 1 for precise locations), and letters show tributaries, as follows: BE = Beeman Creek, BL = Black Creek, BO = Bowen Creek, BU = Bull Creek, C = Crow Creek, E = Ellicott Creek, EF = East Fork, L = Ledge Creek, LT = Little Tonawanda Creek, MD = Mud Creek, R = Ransom Creek. The interrupted line is the Erie Canal. Dashed lines show county boundaries, and dotted lines show the Onondaga and Portage Escarpments.

largely composed of loose glacial till material, and the catchment is a mix of forested and agricultural lands. Between the Portage and Onondaga Escarpments (Fig. 1), agriculture is the predominant land use. In this area, the water is fairly turbid and the gradient is moderate, with frequent riffles. Substrate is varied, ranging from coarse particles (cobble, boulder, and bedrock) to sand. Below the Onondaga Escarpment (at Indian Falls), the creek is a medium-sized river (15 - 40 m wide) and grades into a lowland/lake plain system: between the Onondaga Escarpment and site 3 (Fig. 1), riffles are still relatively frequent and the gradient is low to moderate, while below site 3, low-gradient pool habitats are abundant, bordered by infrequent riffle/runs of sand/gravel/cobble substrate. Here the water is typically extremely turbid.

Human activity has affected Tonawanda Creek substantially: the lower reach of the creek merges with the Erie Canal, for which the creek has been channelized. Between May and November, the entire flow of the creek is diverted northward into the canal towards Lockport rather than westward into the Niagara River. Also, point and non-point pollution from residential and commercial development in the metropolitan Buffalo area in the south-western most portions of the basin and from small cities and towns such as Batavia, Williamsville, and Akron have also impacted the river. In addition, much of the basin upstream of the Erie Canal supports agricultural activities, and the creek suffers from an array of associated habitat alterations.

METHODS

Thirty-eight sites (Table 1, Fig. 1) were visited in August 1998 during periods of low flow. Where water clarity allowed, timed visual searches were conducted with glass-bottomed buckets. Mussels were hand-picked, identified, recorded, and replaced in the substrate. Select spent shells were collected as voucher specimens, which will be deposited in the New York State Museum. We examined a variety of habitats, with an emphasis on riffles and runs. At sites with high water turbidity, substrate was manually probed for live animals and shore areas were searched for spent valves (sites 1, 2, 20, and 30). At sites with high turbidity and soft substrate, we pulled an upside down bow rake across the substrate to find mussels (sites 7, 34). A large number of additional sites (> 25) not listed in Tables 1 and 2 were quickly inspected and not sampled in accordance with judgments pertaining to poor accessibility, poor unionid habitat, and/or difficult sampling conditions. Two tributaries (Bull Creek, Mud Creek) are under-represented in this survey because of these factors. Mussel nomenclature follows Turgeon *et al.* (1988), except in the case of the taxonomic uncertainty surrounding *Lampsilis ovata* (= *cardium*), which is here referred to as *L. ovata* (Say), and *Pyganodon* (= *"Anodonta"*) *grandis* (Say) (Hoeh 1990).

RESULTS AND DISCUSSION

We observed 19 species, 16 of them as live specimens (Table 2). Two species were observed only as recently dead spent shells (*Lampsilis fasciola* (Rafinesque) and *Alasmidonta viridis* (Rafinesque)), and an additional species was observed only as old spent shells (*Epioblasma triquetra* (Rafinesque)). In addition, a live specimen of *Potamilus alatus* (Say) was observed at site 1 in 1987 (Strayer *et al.*, 1991). *Potamilus alatus* is often found in still-water, low gradient habitats (Strayer & Jirka, 1997), areas that we were unable to search due to deep water and extreme turbidity. Thus it is almost certain that *P. alatus* still exists in lower mainstem of Tonawanda Creek.

TABLE 1. List of sites. Numbers correspond to Table 2.

1. Tonawanda Creek, Transit Rd., Pendelton Twp., Niagara Co.; Amherst Twp., Erie Co.
2. Tonawanda Creek, Rapids, Lockport Twp., Niagara Co.; Clarence Twp., Erie Co.
3. Tonawanda Creek, Cedar Rd., Royalton Twp., Niagara Co.; Newstead Twp., Erie Co.
4. Tonawanda Creek, Meadville Rd., Alabama Twp., Genesee Co.
5. Tonawanda Creek, old bridge crossing near Christie Rd., Pembroke Twp., Genesee Co.
6. Tonawanda Creek, Route 5, Batavia Twp., Genesee Co.
7. Tonawanda Creek, Hunn Rd., Alexander Twp., Genesee Co.
8. Tonawanda Creek, Genesee St., Alexander Twp., Genesee Co.
9. Tonawanda Creek, Dunbar Rd., Attica Twp., Wyoming Co.
10. Tonawanda Creek, Eck Rd., Bennington Twp., Wyoming Co.
11. Tonawnada Creek, Centerline Rd., Orangeville Twp., Wyoming Co.
12. East Fork, Route 98, Sheldon Twp., Wyoming Co.
13. Ellicott Creek, Main St., Lancaster Twp., Erie Co.
14. Ellicott Creek, Stony Rd., Lancaster Twp., Erie Co.
15. Ellicott Creek, Pavement Rd., Lancaster Twp., Erie Co.
16. Ellicott Creek, Ransom Rd., Lancaster Twp., Erie Co.
17. Ellicott Creek, Town Line Rd., Lancaster Twp., Erie Co.
18. Ellicott Creek, Walden Ave., Alden Twp., Erie Co.
19. Ellicott Creek, North Rd., Alden Twp., Erie Co.
20. Ransom Creek, Millersport Hwy., Amherst Twp., Erie Co.
21. Ransom Creek, Dodge Rd., Amherst Twp., Erie Co.
22. Black Creek, Dann Rd., Amherst Twp., Erie Co.
23. Mud Creek, Transit Rd., Pendleton Twp., Niagara Co.
24. Beeman Creek, Rapids Rd., Clarence Twp., Erie Co.
25. Beeman Creek, Parker Rd., Clarence Twp., Erie Co.
26. Murder Creek, Swift Mills, Newstead Twp., Erie Co.
27. Murder Creek, Akron Falls Park, Newstead Twp., Erie Co.
28. Murder Creek, Lake Rd., Pembroke Twp., Genesee Co.
29. Murder Creek, Cohochton Rd., Pembroke Twp., Genesee Co.
30. Murder Creek, Route 77, Pembroke Twp., Genesee Co.
31. Murder Creek, Richley Rd., Darien Twp., Genesee Co.
32. Ledge Creek, Route 93, Newstead Twp., Erie Co.
33. Bowen Creek, Hopkins Rd., Batavia Twp., Genesee Co.
34. Little Tonawanda Creek, Old Creek Rd., Alexander Twp., Genesee Co.
35. Little Tonawanda Creek, West Bethany Rd., Alexander Twp., Genesee Co.
36. Little Tonawanda Creek, Gilhooly Rd., Alexander Twp., Genesee Co.,
37. Little Tonawanda Creek, Linden Mills, Bethany Twp., Genesee Co.
38. Crow Creek, Exchange St., Attica Twp., Wyoming Co.

Considering the unionid decline in the western Lake Erie basin in New York (Strayer *et al.*, 1991) and Canada (Metcalfe-Smith *et al.*, 1998) three of our records are notable for their regional or global rarity:

Epioblasma triquetra

We found two spent shells at two downstream mainstem sites (sites 1 and 3), the first records of this species from Tonawanda Creek, and the first specimens collected in New York since 1950. Both shells were old, though one (juvenile size) was considerably more recent than the other. While these specimens do not provide evidence that this species still exists in Tonawanda Creek, it may still be extant in the lower mainstem. With a few exceptions, *E. triquetra* is typically rare and can be difficult to detect. Historical records of this species in western New York are limited to the Niagara River, Lake Erie, and the Buffalo River (Strayer & Jirka, 1997), from all of which *E. triquetra* has probably been extirpated due to zebra mussel impacts (former two) and habitat degradation (latter, Strayer *et al.*, 1991). Moreover, *E. triquetra* has suffered serious declines in the lower Great Lakes basin in Canada, and may be extirpated from this area (Metcalfe-Smith *et al.*, 1998).

Lampsilis fasciola

Two recently dead spent shells were found at site 4 in the lower mainstem, in addition to a small number of old spent shells. There appears to be a small population of this species at this site. Also, an old spent shell was collected in 1996 at site 3 by Mike Wilkinson of the New York Department of Environmental Conservation, though we found no specimens of *L. fasciola* here. These are the first published records of this species from Tonawanda Creek, and the first collections of *L. fasciola* in the Erie/Ontario basin of New York since 1906. The habitat preference of this species (riffles in clear and hydrologically stable creeks and rivers (Strayer & Jirka, 1997)) may explain the limitation of its distribution to sites (sites 3 and 4) in the mainstem where turbidity was comparatively less than downstream areas (sites 1 and 2) and riffle/run habitats were most extensive.

Truncilla truncata (Rafinesque)

This species was observed at site 2 as three live specimens. This is the first live record of *T. truncata* in New York since Robertson & Blakeslee's (1948) record in Tonawanda Creek near Pendleton near our site 1. Also, an old shell was found at site 1 in 1994 (Strayer, 1995). This species appears to be sparsely distributed in the lower mainstem. Strayer & Jirka (1997) considered it likely that small populations of *T. truncata* lived in the Niagara River and Lake Erie, but these populations have probably been severely impacted by zebra mussels. Thus Tonawanda Creek may support the only population of *T. truncata* still extant in New York.

Species richness in the Tonawanda Creek basin was greatest in the lower portions of the mainstem (sites 1-4), which is a common pattern of

TABLE 2. Collection records of unionids from Tonawanda Creek. Site numbers correspond to Table 1. Numbers indicate the number of live specimens found at each site. D = recent spent shell; d = old spent shell. Search method key: V = visual searches; P = substrate manually probed, riverbanks searched for spent valves. PR = soft substrate probed with a rake.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Alasmidonta marginata			1	D			d								5			d	
Alasmidonta viridis			d																
Amblema plicata	13	26	>133	5															
Anodontoides ferussacianus							10							2	8	3		1	
Elliptio dilatata	1	2	d	D															
Epioblasma triquetra	d		d																
Fusconaia flava	d	4	6	D															
Lampsilis fasciola				D															
Lampsilis ovata	2	4	>57	6															
Lampsilis siliquoidea	2	41	6	4	1		20							2	17	4	8	39	5
Lasmigona compressa	D	3	1				1											1	
Lasmigona costata	11	18	7	11															
Leptodea fragilis	2	6	2																
Ligumia recta	d	4	22	1															
Ptychobranchus fasciolaris	1	d	2	d															
Pyganodon grandis	2	2	1		D	D									D			20	
Strophitus undulatus	D	1	1	D															
Truncilla truncata		3																	
Villosa iris	D	2	D	D															
Number of species	14	14	16	12	2	1	4	0	0	0	0	0	0	2	4	2	1	5	1
Search method	P	P	V/P	V	V	V	PR	V	V	V	V	V	V	V	V	V	V	V	V
Person-hours search time	2.7	3.2	5.2	3.9	0.5	0.6	1.4	0.5	1	0.5	0.5	0.5	1.2	0.6	2	0.7	0.5	1.3	0.5

TABLE 2: continued

Species	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Alasmidonta marginata							d												
Alasmidonta viridis		d				D	d								d				
Amblema plicata																			
Anodontoides ferussacianus				D		D	d			5		d			1	1			
Elliptio dilatata							d												
Epioblasma triquetra																			
Fusconaia flava							d												
Lampsilis fasciola																			
Lampsilis ovata																			
Lampsilis siliquoidea	18												1		4				
Lasmigona compressa						d													
Lasmigona costata																			
Leptodea fragilis																			
Ligumia recta																			
Ptychobranchus fasciolaris																			
Pyganodon grandis	89		45	D			1								9				
Strophitus undulatus																			
Truncilla truncata																			
Villosa iris						D	d												
Number of species	2	1	1	2	0	4	7	0	0	1	0	1	1	0	4	1	0	0	0
Search method	P	V	V	V	V	V	V	V	V	V	P	V	V	V	PR	V	V	V	V
Person-hours search time	0.5	0.5	0.3	0.5	0.3	0.6	1.2	0.4	0.5	0.6	0.5	0.5	0.3	0.4	0.7	0.4	0.5	0.5	0.3

unionid distribution in rivers (van der Schalie, 1938). Species richness patterns also corresponded to the physiographic divisions created by the Onondaga and Portage Escarpments (Fig. 1). Nineteen of the 20 species recently recorded from the creek were observed in the lower mainstem below the Onondaga escarpment (sites 1-4). The riffle/run habitats that we sampled in this reach were dominated by *Amblema plicata* (Say) (approximately 41% of the live specimens in sites 1-4), *Lampsilis ovata* (16%), *Lampsilis siliquoidea* (Barnes) (12%), and *Lasmigona costata* (Rafinesque) (11%). The water in this area was extremely turbid, and severely hindered the efficiency of our searches. This was especially so at sites 1 and 2, where visual searches could not be conducted. Also, Murder Creek yielded some evidence of a formerly diverse mussel community below the Onondaga escarpment at Akron Falls (site 26; Fig. 1; Table 2), with a species-poor community farther upstream (sites 27-31).

Between the Portage and Onondaga Escarpments (sites 5 - 8), mussels were locally dense in the mainstem, and habitats appeared suitable for many of the species found at sites 1-4. However, we observed only seven species in this area, suggesting that the Onondaga escarpment blocks upstream dispersal for many of the species below the escarpment. Species above this escarpment may have dispersed there early in the history of the basin, using either high-level postglacial lakes or postglacial drainage outlets.

Mussels were entirely absent from the mainstem and principal tributaries upstream of the Portage escarpment (sites 8-12), where the habitat is dominated by coarse unconsolidated substrate. It is unlikely that this area ever supported any unionids on account of poor habitat.

With the exception of the aforementioned Murder Creek, the principal tributaries were relatively species poor.

Unionids in Tonawanda creek have undoubtedly declined this century, given the anthropogenic habitat alterations noted earlier. Hints of unionid decline in the mainstem above the Onondaga escarpment can be gleaned from Robertson & Blakeslee (1948), who describe the presence of large specimens of *Lasmigona costata* and *Lampsilis siliquoidea* in the vicinity of our sites 5 and 6, as well as *Alasmidonta marginata* (Say) at site 6, while alluding that "rarer forms" could be found upstream to Batavia (below site 7) and downstream to North Pembroke (near site 5). We found a depauperate fauna in this area, consisting of only a few live specimens of *L. siliquoidea* and spent valves of *Pyganodon grandis*. Water pollution from the small city of Batavia has been undoubtedly responsible for much of this decline. We found a greater diversity of mussels upstream of Batavia at site 7 than at sites 5 and 6 (Table 2).

For the lower mainstem below the Onondaga Escarpment, we cannot determine whether the creek has retained its original mussel fauna despite the habitat alterations noted earlier, given the dearth of historical records available. The only reliable record of a species that we did not find is an old record of *Toxolasma parvum* (Barnes) from the Erie Canal at Buffalo (Strayer & Jirka, 1997). In the tributaries below the Onondaga Escarpment, mussel communities in both lower Murder Creek and lower Ellicott Creek (in the Buffalo metropolitan area between its confluence with Tonawanda Creek and site 14) have almost certainly been impacted by point source water pollution from industrial areas in upstream population centers.

There are a number of species that conceivably could have once lived (or may yet be found) in the lower mainstem of Tonawanda Creek for which no records exist, based on the historical unionid distribution in the Lake Erie basin in New York State and habitat preferences (gathered from Strayer & Jirka, 1997). It should be noted that these species (listed on Table 3) are all rare and of limited distribution in western New York, and are mostly represented by records that are over 50 years old. Thus the probability that any given species from Table 3 occurred in Tonawanda Creek is at best low, although small cryptic species (*Simpsonais ambigua* (Say)) or species that prefer habitats that we were unable to search (*Lasmigona complanata* (Barnes), *Ligumia nasuta* (Say), and *Toxolasma parvum*) are probably a bit more likely to be former (or present) residents of the creek than the others.

Despite the evidence of some decline, the lower mainstem of Tonawanda Creek is remarkable for its abundance and diversity of mus-

TABLE 3. Conjectural list of species that may have once occurred (or may yet persist) in Tonawanda Creek, based on reliable historical records and habitat preferences (see Strayer & Jirka, 1997). Locations in bold represent live specimens found since 1970.

Species	Range in the Lake Erie/Ontario basin in New York
Actinonaiais ligamentina	Niagara River, Oak Orchard Creek
Lasmigona complanata	Erie Canal (Monroe County)
Ligumia nasuta	Niagara River, Erie Canal, Lake Erie
Pleurobema cordatum	**Niagara River**
Potamilus capax	**Niagara River**, Twelvemile Creek
Quadrula pustulosa	Niagara River
Quadrula quadrula	Niagara River
Simpsonaiais ambigua	Lake Erie, Buffalo River, Cayuga Creek
Truncilla donaciformis	Lake Erie

sels. Moreover, Tonawanda Creek's unionid community in is regionally significant when viewed in the context of the decline of mussel communities in the eastern Lake Erie basin noted by Strayer *et al.* (1991), in the Lower Great Lakes basin in Canada (Metcalfe-Smith *et al.*, 1998), and the probable decline in the communities in the Niagara River and Lake Erie due to zebra mussel invasion. In this sense, Tonawanda Creek is clearly an outstanding remnant of the Great Lakes basin mussel fauna in New York and the eastern Lake Erie/Lake Ontario basin.

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A NEW SPECIES OF *PARABOYSIDIA* FROM THAILAND (PULMONATA: PUPILLIDAE)

Somsak Panha[1,2] and John B. Burch[2,3,4]

ABSTRACT

The gastrocoptine pupillid genus *Paraboysidia* Pilsbry is reported for the first time in Thailand, and a new species, *P. tamphathai*, is described from a limestone mountain at Tam Pha Thai National Park, Lampang Province. The shell of the new species is very small (4.1-3.7 mm in length), turbinate, and its surface is sculptured with close-set, raised, spiral striae and transverse growth lines. The shell has a slightly concave spire, and an aperture with three major teeth (parietal, columellar, and lower palatal) and up to seven other teeth ranging in size from prominent to nearly obsolete. The largest tooth in the aperture is the parietal lamella. The angular lamella and the upper palatal plica are at, or very near, the edge of the peristome.

Key words: *Paraboysidia tamphathai*, Pulmonata, Pupillidae, Thailand.

INTRODUCTION

Species of the *Boysidia*-related small gastrocoptine Pupillidae (*s. lat.*) are widely distributed in eastern Asia, occurring from India and China south to northern Australia. Pilsbry (1917) presented a taxonomic overview of this group and gave key characters for separating the taxa *Boysidia, Paraboysidia, Hypselostoma* and *Gyliauchen* [= *Gyliotrachela*]. Pilsbry pointed out the "interlacing" apertural characters of *Boysidia* and *Paraboysidia*, and included *Paraboysidia* as a subgenus of *Boysidia*, but believed that the two taxa would be eventually separated. He concluded that "no doubt a great many species remain to be discovered in southern China and Indo-China, and they will test the distinctions now drawn." Benthem Jutting (1949, 1961) re-presented Pilsbry's diagnostic apertural characters, and treated *Boysidia* and *Paraboysidia* as distinct genera, as did Thompson & Upatham (1997).

Pilsbry (*loc. cit.*) described his new subgenus as follows: "The shell has the shape and minutely granulose surface of *Boysidia*, but differs by having the angular and parietal lamellae separate, long and parallel (except in *B. robusta* and *B. kelantanensis*, where they are connected or concrescent). *The columellar lamella enters horizontally* (the inner end not turned

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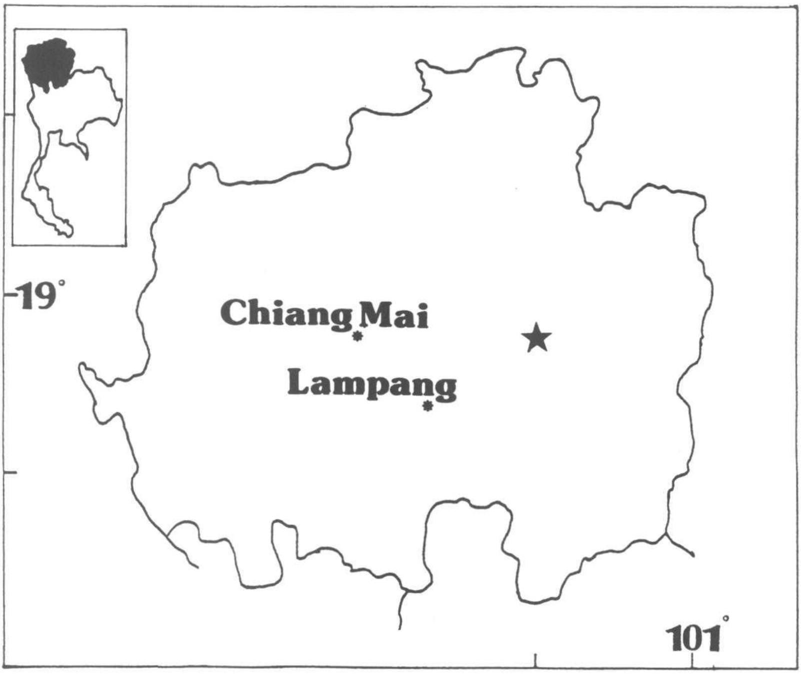

FIG. 1. Map showing location of Tam Pha National Park (star).

downward as it is in *Boysidia*); plicae situated as usual. Peristome is either continuous or interrupted above, expanded and thickened, a nodule on the inner margin limiting the sinulus. – Type *B. paviei* B. & D. – Distribution: India to Tonkin, south to Java."

For *Paraboysidia,* Pilsbry included the species *P. boettgeri* (Möllendorff), *P.* (?) *dayana* (Stoliczka), *P. hupeana* (Gredler), *P. kelantanensis* (Sykes) *P. lamothei* (Bavay & Dautzenberg), *P. landurensis* (Pilsbry), *P. paviei* (Bavay & Dautzenberg) [type species], *P. robusta* (Bavay & Dautzenberg), and *P. salwiniana* (Theobald). However, *P.* (?) *dayana, P. hupeana* and *P. salwiniana* were included only provisionally, and with uncertainty, because the original descriptions are poor and Pilsbry himself had not seen any authentic specimens.

Benthem Jutting included in *Paraboysidia* the species *P. frequens* Benthem Jutting, *P. kelantanensis tenuidentata* Benthem Jutting, *P. laidlawi* (Collinge), *P. neglecta* Benthem Jutting, *P. oreia* Benthem Jutting and *P. serpa* Benthem Jutting.

Our paper adds a Thai species to the genus, *Paraboysidia tamphathai,* found in the Tam Pha Thai National Park (Fig. 1).

Paraboysidia tamphathai new species

Description of holotype: The shell (Fig. 2) is small (4.1 x 2.6 mm; see Table 1), turbinate, umbilicate, with impressed sutures, and has 4 3/4 whorls. The spire is turreted and, in apertural view, slightly concave in outline. The last whorl is high (*i.e.*, elongate), about three times the height (length) of the visible part of the penultimate whorl. The last whorl is shouldered. The shell surface is marked with (1) fine growth lines, some of which are more prominent, becoming almost low, irregularly spaced, transverse riblets, and with (2) fine, close-set, raised, spiral striae. The aperture is rather widely adnate to the surface of the last whorl.

There are three major (*i.e.*, noticeably the largest) teeth in the shell aperture. The parietal and angular lamellae are well separated; the parietal lamella is the best developed of the apertural teeth; the angular lamella is developed but not complete, its outer end is near the edge of the peristome; the infraparietal lamella is a small tubercle. The columellar lamella is well developed, straight and horizontal; the subcolumellar lamella is a small, strong tubercle. The upper palatal plica is short, tubercle-like, and is located at the edge of the peristome; the two interpalatal plicae are a little deeper-set in the aperture; the upper interpalatal plica is about twice the size of the lower interpalatal plica; the lower palatal plica is the largest of the palatal plicae. The basal plica is a reduced, low, subobsolete tubercle.

Type locality: Tam Pha Thai National Park, Lampang Province, 18°36′20″ N, 99°53′49″ E, 490 meters elevation (Fig, 2).

Type material: The holotype (CUIZM, Ver 015), leg S. Panha, is deposited in the Chulalongkorn University Zoological Museum, together with five paratype specimens (CUIZM 016). Other paratypes, four specimens (CUIZM, Ver 017) will be deposited in the Museum of Zoology, University of Michigan, Ann Arbor, Michigan, U.S.A.

TABLE 1. Shell dimensions (in mm) of *Boysidia tamphathai* n. sp.

Types		Height	Width
Holotype		4.1	2.6
Paratype	1	3.8	2.3
	2	3.8	2.3
	3	3.7	2.3
	4	3.7	2.3
	5	3.7	2.3
	6	3.7	2.3
	7	3.7	2.3
	8	3.7	2.3
	9	3.7	2.3

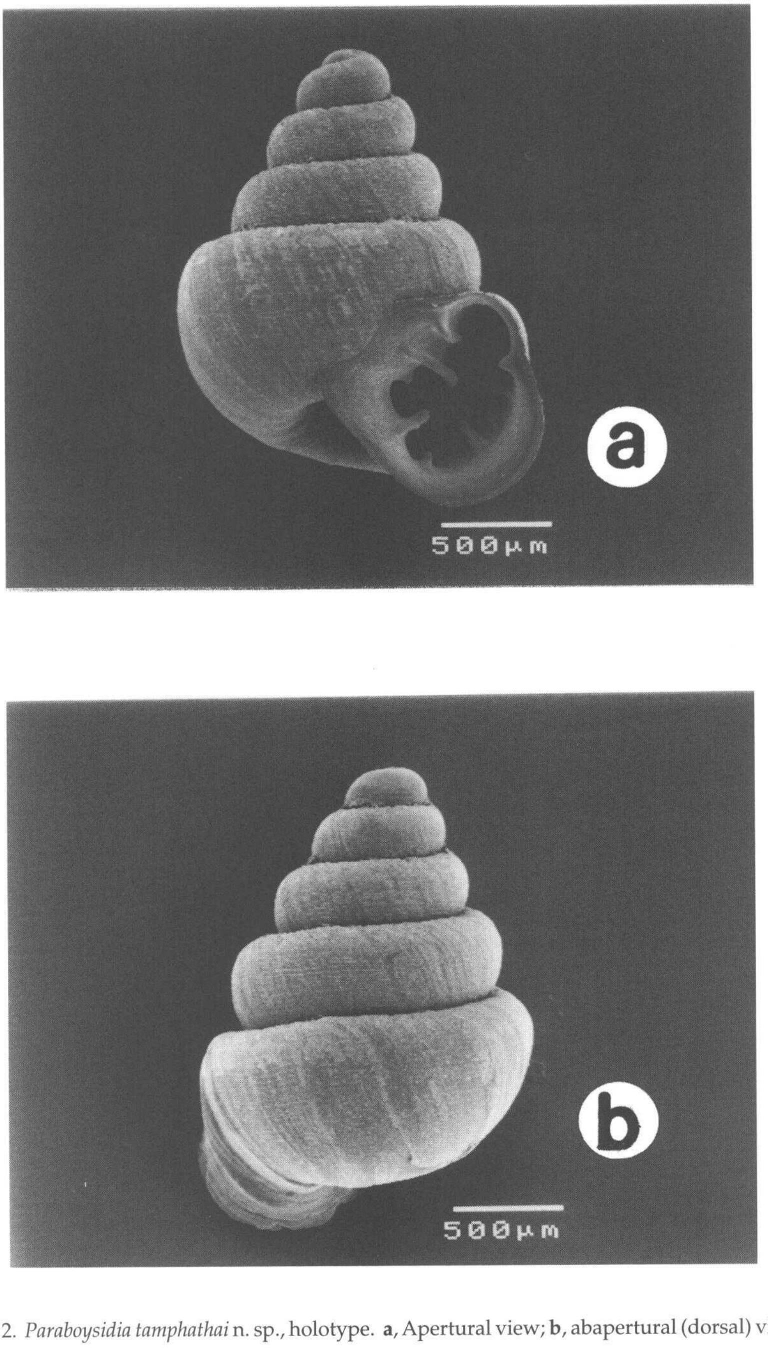

FIG. 2. *Paraboysidia tamphathai* n. sp., holotype. **a**, Apertural view; **b**, abapertural (dorsal) view.

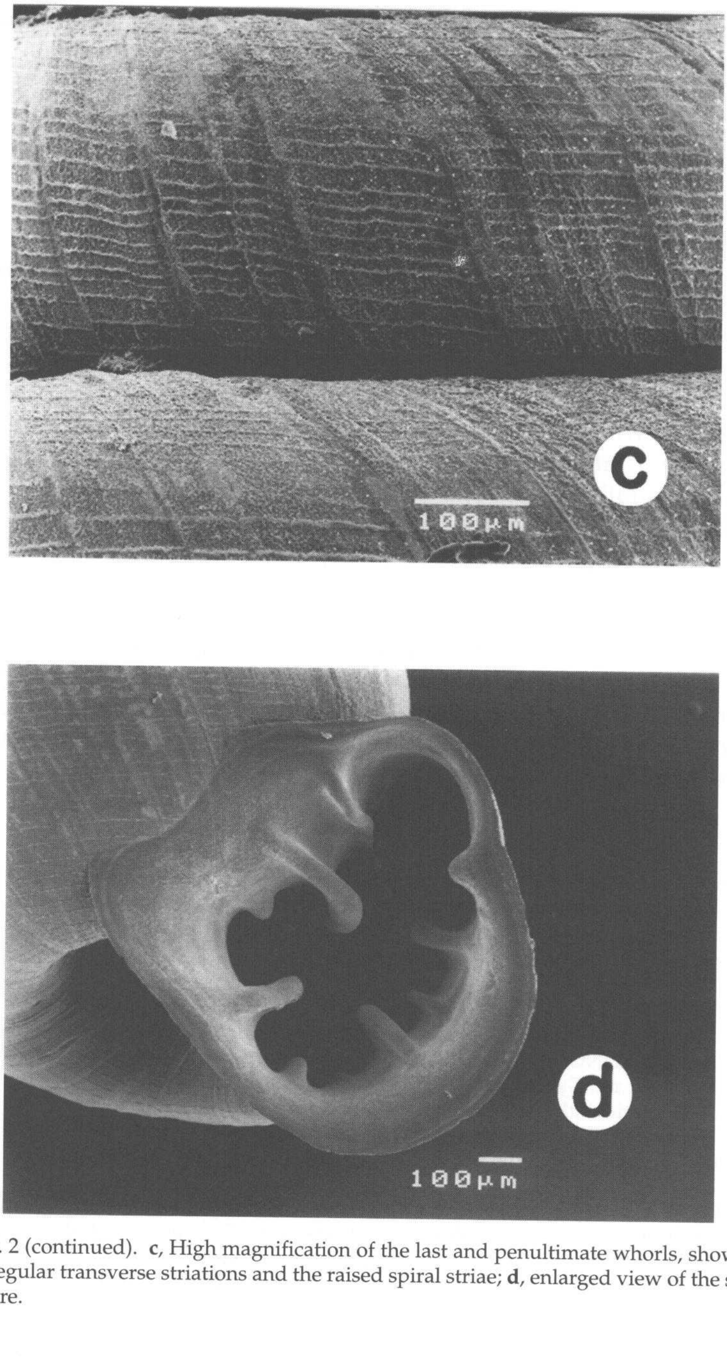

FIG. 2 (continued). **c**, High magnification of the last and penultimate whorls, showing the irregular transverse striations and the raised spiral striae; **d**, enlarged view of the shell aperture.

Etymology: The specific epithet *tamphathai* is from the name of the national park, Tam Pha Thai, in which the new species was found.

Diagnosis: Shell with surface sculpture of close-set, raised, spiral striae; a slightly concave spire; and an aperture with three major teeth (parietal, columellar, and lower palatal) and up to seven other teeth ranging in size from prominent to nearly obsolete. The largest tooth in the aperture is the parietal lamella. The angular lamella and the upper palatal plica are at, or very near, the peristome.

Remarks: Pilsbry describes the type species of *Paraboysidia, P. paviei* Bavay & Dautzenberg, as having a large apical whorl that "shows delicate spirals," and later whorls that are "minutely granulose, the granules indistinctly arranged in spiral lines." The shell surfaces of the other species that Pilsbry included in *Paraboysidia* are described as smooth, except for faint growth lines. Of the six species and subspecies of *Boysidia* named by Benthem Jutting, the shells of all are smooth except for *P. neglecta,* which is spirally striate. She describes the shell of *P. laidlawi* (Collinge) also as being spirally striate. Perhaps the spiral striae indicate that these spirally striate species, including *P. tamphathai,* are rather closely related – more so than to the species without spiral striae.

Thompson & Upatham (1997) described a new genus for Thailand, *Acinolaemus,* with five new species, all having raised spiral striae ("threads"). However, *Acinolaemus* is especially characterized by the enlarged angular lamella, the most conspicuous tooth in the aperture. In *Paraboysidia,* the angular lamella, while separate from the parietal lamella, is not the more prominent barrier in the aperture.

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