

OCCASIONAL PAPERS OF THE MUSEUM OF
ZOOLOGY

UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN

UNIVERSITY OF MICHIGAN PRESS

STUDIES OF THE GASTROPOD FAMILY
PLEUROCERIDAE—IV

BY CALVIN GOODRICH

AMONG the Pleuroceridae are groups of species or forms that are related to one another more or less closely. The species (or forms) may differ in shape, sculpture, ground color, and color banding. Yet certain characters persist through the entire complex—similar opercula, for example, or a peculiar habit of whorl coiling, or the presence or absence of a sinuous outer lip—that point to kinship. Almost invariably all members of a group of the kind occupy the same drainage system. More intimately sometimes, they inhabit merely a part of that basin. The present paper is concerned with such a group.

Goniobasis caelatura (Conrad) typically is a thick, somewhat cylindrical shell with a large aperture which is a little produced. The columella is usually poorly developed. The outer lip is straight. Sculpture consists of low, undulate, longitudinal plicae on the upper part of the spire followed in growth by heavy, closely-set, revolving striae or folds that extend to the base. Nearly smooth specimens that still retain the *caelatura* shape occur occasionally in colonies of normal mollusks. They are commoner in creeks than in rivers. The *granata* of Lea is a shell in which the folds are discon-

tinuous, being replaced by rows of pustules. Of 565 specimens of *caelatura* from the Oostanaula River at Rome, Floyd County, Georgia, 7.9 per cent are thus "granulated." Such individuals are perhaps instances of acceleration. They cannot be accepted as specifically distinct from the mollusks among which they have been found. The operculum of the species is of medium size, reddish brown to black; the spiral lines are open and occupy nearly half of the lower third of the structure. Twenty-three radulae have been examined without discovering characters differentiating typical *caelatura* either from related forms or from the radulae of *Goniobasis* in general. Conrad assigned the species to the Savannah River, a mistake for which a southern correspondent of his appears to have been responsible. Besides *G. granata*, *Melania decorata* Anthony, *G. tryoniana* Lea, and *G. flavescens* Lea are synonyms.

Stearnsiana Call.—Plicae in this mollusk are subdued or even entirely absent. The striae, present in most specimens although not in all, are finer than in the case of *caelatura*. Compared with *caelatura*, the sculpture of *stearnsiana* represents, therefore, a distinct obsolescence. In form the shell is robust, in almost all colonies short-spined. The presence of an angled, nearly keeled periphery is persistent among many of the adults.

Luteocella Lea.—Plicae in this shell are microscopic and sometimes obsolete. Typically the disk is covered with fine, crowded striae. Frequently they are microscopic or absent. The shape is much that of *Anculosa*, the shell having a short spire and a large body whorl. Most specimens are rather solid, with well-developed, white columellae. The outer lip is straight as in *caelatura* and *stearnsiana*. Synonyms are *G. whitfieldensis* Lea and *G. similis* Lea.

Excellens H. H. Smith.—This is a manuscript name for a somewhat difficult shell that sometimes suggests an elongate *stearnsiana* and has phases resembling *luteocella*. The following may be taken as its formal description:

Conic, somewhat elongate, subpublicate, striae often microscopic. Aperture widely ovate, produced; within are four discontinuous color bands. The columella is white, narrow, the outer lip straight, a little retrorse. The body whorl, instead of being flattened as in typical *caelatura*, is regularly rounded. Size of the type which is in the Alabama Museum of Natural History is: altitude 24 mm., diameter 12 mm. Aperture—altitude 9.5 mm., diameter 6 mm. Type locality, Little River, 5 miles north of Cedar Bluff, Cherokee County, Alabama.

Smith, on a label, says of the shell:

I found this only in one place, on rocks in swift water. Varies in being striate, especially below the periphery, or smooth. Rarely the bands are faint or obsolete. The large operculum and outer lip, straight in profile, seem to show the shell to be allied to *stearnsiana* Call.

Results of the study of the sculpture of 90 specimens from the type locality are:

	Number of shells	Percentages
Subpublicate	62	68.8
Lacking plicae	28	31.1
Striate above periphery	12	13.3
Striate only on base	41	45.5
Lacking striae	37	41.1

Some of the shells are nearly as large as specimens of *stearnsiana* from the type stream, and are thin and tend to be malleated. Others are small and have the well developed columella common to *luteocella*.

Lecontiana Lea.—As compared with *caelatura* and *stearnsiana*, *lecontiana* marks a distinctive alteration in shape from cylindrical to conic. The change is accompanied in all except one of the lots that have come to notice by a reduction of the striate sculpture. Certain colonies show a tendency toward

the elimination of the plicate sculpture as well, and a few specimens have been seen among individuals more normal that are without either striae or plicae.

Smithsoniana Lea.—This mollusk is more conic than any others of the complex. The outer lip is sometimes curving although oftenest it is straight. The aperture is large, and the operculum is of the familiar *caelatura* type. In *smithsoniana* the sculpture is confined to one or two of the post-embryonic whorls. As a rule, this ornamentation is plicate only, yet occasional specimens occur which suggest reversion to plicate-striate sculpture. Numbers of shells have the single striation at the top of the ornamented whorls which is mentioned in Lea's description. This is less persistent than it is in some colonies of *lecontiana*.

Smooth phases.—It has been shown that in this group sculpture varies from plicate-striate involving the whole shell surface except the nuclear whorls to simple plication that is confined to early whorls of the spire. In addition, there are forms in which plicae and striae have become obsolete. Entire colonies are made up of shells wherein the fine growth lines alone break the smoothness of the periostracum. These phases can derive, apparently, from three sources—*stearnsiana*, *lecontiana*, and *smithsoniana*. A depauperate pleurocerid which Lea described under the name of *Goniobasis georgiana* may be one of these developments. The types of *georgiana* consist of two specimens that are smooth, round-whorled, somewhat worn. They suggest *G. gerhardtii* Lea, also of the upper Alabama system, as much as they do the forms under consideration here. In the absence of opercula, it is scarcely possible to decide the question.

DISTRIBUTION

Caelatura.—The highest point in the Conasauga River where this shell is known to occur is at Lower King's Bridge, Murray County, Georgia. At Upper King's Bridge, a few miles above, the form is *luteocella*. Mixed forms inhabit the river as far downstream as Tilton, Whitfield County, Georgia.

From here on, into the Oostanaula River and the Coosa River to Talladega County, Alabama—the apparent limit of range of the group—the mollusk continues unaltered as to ornamentation although there are one or two local modifications of shape. In the Etowah River about five miles above Cartersville, Bartow County, Georgia, thousands of these shells occur in rapids. Among them have been taken a few specimens corresponding to *luteocella*. Near Kingston, lower down, the colonies are apparently all *caelatura*. The uppermost range of the form in the Chattooga River, so far as known, is Boiling Ford, Chattooga County, Georgia. A tributary of the Chattooga, Little River, Cherokee County, Alabama, has *caelatura* at its discharge, but not far above it. The shell has been taken in ten or twelve creeks of Georgia and Alabama, always where the rest of the molluscan fauna is of river rather than creek aspects. *Caelatura*, therefore, can be considered a large stream form.

Stearnsiana.—The type locality is Dyke's Creek, Floyd County, Georgia, a small, clear, rather fast moving tributary of the Etowah River. Locotypes are quite large for gonio-bases. Of 84 Dyke's Creek specimens, 73.8 per cent are striate from spire to base, 26.1 per cent striate only on the base. Lots nearly approaching the typical form are from Boiling Ford of Chattooga River and the mouth of Little River. Specimens from the Chattooga at Trion, Chattooga County, Georgia, show a tendency toward the obsolescence of all sculpture. This is even more noticeable in creeks of the upper Chattooga. Plicae are well marked in material from Silver Creek, Rome, Floyd County, Georgia; Armuchee River in the same county, and Stamp Creek, Bartow County, Georgia. The most southern occurrence is in the outlet of Coldwater Spring, discharging into Choccolocco Creek, eastern Alabama, wherein *caelatura* has been collected. The shape of the shell is more varied than in the other lots of *stearnsiana*. The plicae are microscopic. Of 39 mature specimens, 17 are striate from spire to base, 9 are striate on the base only, and 3 are without striae.

Luteocella.—Types of this shell came from Conasauga River, Whitfield County, Georgia. In this stream, it occurs at localities above typical *caelatura* and then for a stretch of the river mixes with it. Specimens taken in the Conasauga at Tilton are like those of the adjacent Swamp Creek rather than of the upper river form. The same thing is true of shells taken in the river just below the mouth of Coahulla Creek. The creek forms are less conspicuously sculptured than those of the main stream, more solid and conic. Similar feebly sculptured shells have been collected in Silver Creek, Rome, Floyd County, Georgia, in Alatoona Creek, near Cartersville, and in the Chattooga River at Cornwall, Cherokee County, Alabama. The Etowah River specimens have been mentioned under *caelatura*. Material at the mouth of Little River has characteristics alike of *luteocella* and *stearnsiana*. Three shells, nearly typical *luteocella*, have been seen that came from Choccolacco Creek, Talladega County, Alabama.

Excellens.—The bulk of individuals of this race that have been examined came from Little River of the Chattooga, five to eight miles above its mouth. They were taken by H. H. Smith "on rocks, in swift water." A few shells of the form have been collected at the mouth of Armuchee Creek of the Oostanaula River, and a single example in Big Cedar Creek, Floyd County, Georgia. The phase occurs in small numbers among *caelatura* in Terrapin Creek, Cherokee County, Alabama. Apparently, the Little River colony is the only "pure" race.

Lecontiana.—The types of this form, it is certain, came from Silver Creek, Rome, Floyd County, Georgia. Of 104 specimens taken in the creek, 58.6 per cent are striate only on the base; 39.4 per cent have one or two striae above the periphery of the body whorl; the rest are without striae. The plicae are well marked. Shells taken in Big Will's Creek at Attalla, Etowah County, Alabama, have well pronounced plicae, and occasional specimens are striate. Farther upstream, near Keener, the plicae of most specimens are reduced to microscopic proportions, and striae are absent. Excessively

striate individuals occur among examples of feebly sculptured *lecontiana* in Coahulla Creek, Cedar Ridge, Whitfield County, Georgia. At a higher locality in this stream, the shells were more nearly typical. Smooth shells among sculptured shells have been taken at the mouth of Armuchee Creek, a branch of the Oostanaula River. The range of the form is from tributaries of the Conasauga, Coosawattee, Oostanaula, and Etowah rivers in Georgia to creeks in Etowah County, Alabama. It is missing from the Chattooga drainage. *Lecontiana* is distinctly a small creek and brook mollusk.

Smithsoniana.—Specimens have been seen from two tributaries of the Coosawattee River and others from a small creek emptying into the Etowah River. The localities are high in the Alabama River drainage. A large colony occupies the stream flowing from Cave Spring, Floyd County, Georgia. Still other lots are known from Sandy Creek at Key, Cherokee County; Little Canoe Creek and a small branch of Big Canoe Creek, St. Clair County—all in Alabama. *Smithsoniana* of Big Will's Creek is associated with other forms of the *caelatura* complex. With the exception of this last taking, all the shells are from localities relatively remote from river influence. Variation in sculpture is small, and in the matter of shape it is toward the configuration of *lecontiana*.

Smooth phases.—Such shells have been collected in tributaries of the Etowah and Chattooga rivers as well as in one place in the Chattooga itself. They are found in a spring branch of Big Will's Creek, three creeks in St. Clair County, and three in Talladega County, Alabama. Higher parts of Terrapin Creek, previously mentioned, are occupied by the smooth phases. All the localities except one are little streams. The station in Chattooga River is Boiling Ford, Chattooga County, Georgia. Here, also, appear *caelatura* and *stearn-siana*.

DISCUSSION

These several forms, however unlike one another they sometimes appear, are nevertheless of the same genetic stock, and they constitute a single, fairly compact group of mollusks.

Certain morphological characters persist through the whole complex. Gradations and connecting forms exist. The same circumscribed area is occupied by all of them. At no place, geographically considered, are the extremes among the shells far apart. Five of the members of the group have been honored in the past with specific names, but whether in fact they are species or subspecies or merely "formae" the writer of this paper is unable to satisfy himself. Argument that must be respected can be presented for all three views pending experimentation under natural conditions.

The only one of these mollusks that inhabits the main Coosa River is *caelatura*, and that has the strongest plicate-striate sculpture of all of them. With a single known exception, the wholly smooth forms are occupants of head streams. Between the two highly contrasted shells are five forms which show various modifications of sculpture, and in a general sense—for there are confusing mixtures—the progression in an upstream direction is from stoutly sculptured to unsculptured. It should be made plain here that all the species of *Goniobasis* in the Coosa River are not excessively ornamented although two of them, *G. impressa* (Lea) and *capillaris* (Lea) are as striate as any other members of the genus, nor is it true that every headwaters species is unsculptured. The common *Goniobasis* of springs, brooks, and creeks of the drainage under consideration is *carinifera* (Lamarck) whose neanic whorls are persistently beaded.

Dealing with the Unionidae, Ortmann (1920) says:

A few shells which have, in the large rivers, a peculiar sculpture of large tubercles, lose these tubercles in the headwaters.

Adams (1915) has pointed out this phenomenon in the case of *Io*. Boycott (1929) experimented with *Hydrobia jenkinsi* Smith, ordinarily a smooth shell but in this instance keeled and spinose. Breeding was carried to F₄ in different strains. Spined mollusks, putting forth new growth in the laboratory, continued the ornamentation. Sculpture did not appear in young bred of spinose parents. Boycott decides that aculea-

tion is not a heritable character, and yet that it is "hardly legitimate to conclude that the character is purely environmental in origin." Miller (1922) declares that "number of ridges per unit area of the shell" of *Teredo navalis* has been "found to be definitely correlated with factors of the environment."

In the first paper of this series (Goodrich, 1934), I have made mention of a loss of nodulous sculpture in *Lithasia* of Duck River, Tennessee, the forms farthest upstream being entirely smooth. A reduction of sculpture as well as size is experienced by *G. arachnoidea* (Anthony) in certain springs and spring runs of eastern Tennessee. At the same time, other members of the group to which *arachnoidea* belongs, occupying large springs in South Carolina, Florida, and Alabama, have an excess of plicate-striate sculpture. *G. nigrina* (Lea) is a small, smooth, or microscopically sculptured shell belonging to the strongly ornamented *plicifera-silicula* group. It lives in headstreams of the Pacific slope. The smooth forms of the *caelatura* complex cannot, therefore, be considered isolated phenomena.

In typical *caelatura*, the shell passes quickly from an early conic shape to a cylindrical shape. *Lecontiana* and *smithsonianiana*, on the other hand, are conic throughout the shell growth, each new whorl being of noticeably larger diameter than the preceding whorl. Now while it is not proposed to argue that these three forms are specifically identical, attention is here called to the fact that such an alteration does occur in shells whose specific sameness is not disputed. An illustration is *Goniobasis hydei* (Conrad) of the Black Warrior River. It is manifest to the eye that specimens of this species from headwaters are more conic than specimens of the lower river. Further, it can be demonstrated statistically. The diameter of the shell immediately above the penultimate suture is divided by the diameter of the body whorl. This gives what may be termed an "index of cylindrization." Results of measurements follow:

	Number of specimens	Index and probable error
Locust Fork of B. Warrior R., near Warrior, Ala.	52	70.9 \pm .33
B. Warrior R., near "Mine," Jefferson Co., Ala.	41	73.7 \pm .32
Tuscaloosa, Tuscaloosa Co., Ala.	45	75.7 \pm .41

Dr. Lee R. Dice has been kind enough to examine the measurements and make this report upon them:

The average index of the lot from near Warrior is $2.2 \pm .5$ per cent less than the lot from near "Mine" in Jefferson County, a difference which is 4.8 times its probable error and therefore is statistically significant. The lot from near "Mine" has an index which is $2.9 \pm .5$ per cent less than the lot from Tuscaloosa, a difference which is 5.6 times its probable error and therefore significant. The lot from near Warrior has an average index $5.1 \pm .5$ per cent less than the lot from Tuscaloosa, and this difference is highly significant, being 9.6 times its probable error. "Cylindrization" increases, it will be seen, in a downstream direction.

The peculiarity of Coosa River goniobases which has impressed a number of writers on the mollusca lies a great deal in this tendency toward changing from an early conic shape into an adult cylindrical shape. Several of the species are confined to the river. Where they enter small streams they are shortly displaced by conic shells. The change of shape in the same stream direction has been observed in *G. livescens* (Menke) of the Tuscarawas River, Ohio. The *sordida* form of *Lithasia obovata* (Say) of Green River, Kentucky, is decidedly more conic than the form *undosa*. While *undosa* goes well down the river, *sordida* occurs only in upstream and tributary localities.

SUMMARY

The group of *Goniobasis caelatura* (Conrad) occupies a part of the Alabama River drainage system comprising streams that go to make the Coosa River and a section of the Coosa River itself.

The shells vary extremely in shape and in sculpture. Within the group are both conic and cylindrical members, both highly sculptured and entirely unsculptured forms.

In a general sense, the variation from conic to cylindrical shape is in a downstream direction. The same thing is true of variation from smoothness to sculpture.

The least variation within colonies as regards shape and ornamentation is in headstreams and near the downstream limits of geographical range. Mixtures of forms occur between the two types of environmental conditions.

With reference to the group it may be said that variations in shell shape and sculpture are associated with variations in ecological conditions. Whether the ecological conditions are the determining factors in the variations of the mollusks remains undetermined.

REFERENCES

ADAMS, C. C.

- 1915 The Variations and Ecological Distribution of the Snails of the Genus *Io*. Mem. Nat. Acad. Sciences, 12, Second memoir: 1-92, pl. 1-61.

BOYCOTT, A. E.

- 1929 The Inheritance of Ornamentation in var. *aculeata* of *Hydrobia jenkinsi*, Smith. Proc. Mal. Soc., 18: 230-234, pl. 14.

GOODRICH, C.

- 1934 Studies of the Gastropod Family Pleuroceridae—I. Occ. Pap. Mus. Zool., Univ. Mich., 286: 1-17, pl. 1.

MILLER, R. C.

- 1922 Variations in the Shell of *Teredo Navalis* in San Francisco Bay. Univ. Calif. Pub. in Zool., 22: 293-328, pl. 13-17.

ORTMANN, A. E.

- 1920 Correlation of Shape and Station in Fresh Water Mussels (*Naiades*). Proc. Amer. Phil. Soc., 19: 269-312.

