NUMBER 318 JULY 10, 1935

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY

UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN UNIVERSITY OF MICHIGAN PRESS

STUDIES OF THE GASTROPOD FAMILY PLEUROCERIDAE—V

BY CALVIN GOODRICH

THE original descriptions of a number of species of the Pleuroceridae lay emphasis on the striate sculpture of the shells.[1] They stress it further by the selection of such names as *capillaris, caelatura, pilula, striata,* and *microlineata.* Yet I can point to only three species, of all of the family, which show no variation in this regard. These three are *Goniobasis troostiana* (Lea), *G. crenatella* (Lea), and *Anculosa sulcata* H. H. Smith. The first species is confined to a small stream in East Tennessee and the third to a comparatively short stretch of Coosa River, Alabama, and so can be considered endemics with the narrow range of variation that endemism usually imposes. *G. crenatella,* on the other hand, inhabits the Coosa River in several localities and is known from three tributaries of that stream.

Goniobasis impressa (Lea) of the Coosa River may be taken as an example of a usually completely striate pleurocerid that is sometimes partly smooth. In a lot of nearly one hundred

[1] Plicate sculpture was discussed in the third paper of this series. The present paper deals with striate ornamentation. It is to be understood that "striate," "striae," "spirals," and "revolving lines" as herein used all have the same meaning.

specimens, about thirty lacked spirals on different areas of the body whorls. The variation occurs apparently in any colony. *G. vanuxemiana* (Lea) of the same drainage is typically striate. The shell known as *G. bullula* is a smooth form of the species. To judge by Mr. H. H. Smith's collections, the two forms occur together in several parts of the Coosa River, but not in the Alabama River where *vanuxemiana* ranges as far downstream as Claiborne, Monroe County. The association of striate and smooth forms occurs also in a few of the Coosa creeks. A mollusk that is closely related to *G. troostiana* is *G. striatula* (Lea). Several hundred specimens were collected by Mr. W. J. Clench in an artificial reservoir in Bradley County, Tennessee, and in its outlets and spring feeders. In all the localities, the young and nearly adult individuals are striate from neanic whorls to the base of the body whorls, but in gerontic shells the spirals tend to disappear on the body whorl above the periphery. No variation is noticeable as between the different kinds of habitat. This partial or complete elimination of spirals by individuals living in locations occupied by typically striate shells is observable in *Anculosa downei* Lea, *A. showalterii* Lea, and *A. flexuosa* H. H. Smith. *Pleurocera alveare* (Conrad) commonly bears striae on the base. They are sometimes absent, and their absence, so far as can be seen, carries no suggestion of a geographical bearing or environmental significance. Four species of *Gyrotoma* are usually heavily striate, but the spirals vary in number and prominence. In *G. alabamensis* (Lea), striation is at times entirely obsolete, smooth shells and striate shells occurring in association.

The spirals of certain striate pleurocerids vary in number and conspicuousness in different localities, the variation appearing to be racial and carrying no definite hint of environmental influence. *Goniobasis perstriata,* for instance, is stoutly striate in three springs of northern Alabama, much less striate in two other springs. In another spring, the spirals are confined to the neanic whorls. A creek on the south side of the Tennessee River has the strongly ornamented forms that Lea described as *crispa.* In a creek entering the river

from the north are shells that have striae on only one or two early whorls. There is uniformity in the sculpture of *G. pleurostriata* Wetherby at two localities of Little River, western Kentucky, and in two tributaries of that river. Differing decidedly in sculpture from these forms are specimens of the species from Ringgold Creek, Montgomery County, Tennessee. The molluscan fauna of this creek changes within five miles from a mixed river and creek association to a purely creek association. The *pleurostriata* of the two stations is the same so far as spiral sculpture is concerned. *G. clenchi* Goodrich is stoutly striate in Choctawhatchee River and branches, southeastern Alabama. The spirals are subdued in prominence and numbers in shells of tributaries of Chipola River, Florida. They are very nearly obsolete in specimens taken from a branch of Yellow River, Covington County, Alabama. Similar geographical variation characterizes the widely distributed *G. laqueata* (Say).

The genus *Pleurocera* is represented in the upper part of the Black Warrior River by the striate *P. annuliferum* (Conrad). Striation extends even to a narrow, elongate pleurocera of a headwaters stream and partly so to another which inhabits a creek entering the river about midway of its length. As the mouth of the Black Warrior is approached, *annuliferum* gives way to the smooth *P. prasinatum* (Conrad). Tryon (1873) distinguishes between *P. excuratum* (Conrad) and *P. moniliferum* (Lea), the one having spirals on the early whorls, the other lacking them. The two forms occur together in the Tennessee River, but in the Elk River, the smooth *moniliferum* is rare. Twenty to nearly thirty per cent of the shells of two Elk River colonies are striate over the whole surface. This is the *Melania rorata* of Reeve. *P. pyrenellum* (Conrad), *brumbyi* (Lea), and *planogyrum* (Anthony) may be taken tc constitute a group. The majority of the shells of the group at and near Huntsville, Madison County, Alabama, and in Limestone Creek, Limestone County, are completely striate. The majority in Piney Creek, Limestone County, and in Chickamauga Creek, near Chattanooga, Tennessee, together

with those of the big Crawfish Springs and their impounded waters, are only partially striate. The elongate *P. striatum* (Lea), so named because of its early spiral sculpture, occupies this same area.

Goniobasis boykiniana (Lea) of one form is distinctly more plicate than striate. The spirals although conspicuous are not numerous, and where they cross the longitudinal sculpture there is a tendency toward the development of nodulous ornamentation. In a second form, the plicae are not pronounced, the spirals are low and numerous, and they give a capillary appearance to the shell. The dimorphism is known to occur in only one locality, the Chattahoochee River at Columbus, Georgia; but in several places within the same drainage basin, the first or plicate form is present in "pure" colonies. It is sufficiently modified to justify the subspecific name *viennaensis* (Lea). The second or striate form, less ventricose than the shells at Columbus, less carinate and sometimes markedly elongate, is the subspecies *albanyensis* (Lea). This shell also has colonies wherein the other form does not occur. *G. carinocostata* (Lea) is normally only plicate. Occasionally, a single spiral appears on a neanic whorl. In certain streams flowing into the Coosa River from the left bank there are colonies of the species whose early whorls are ornamented with from three to eight or ten spirals. This sculpture has not been seen in *carinocostata* that occupies tributaries coming into the Coosa from the right.

Spirals appear more or less erratically on pleurocerids that in general are smooth or whose ornamentation is confined to the longitudinal plicae. Such spirals seldom exceed three or four in number, and usually there is only one. An example in *Goniobasis* is *curvicostata* (Anthony, Reeve), the *doolyensis* of Lea. Striae are absent in *curvicostata* of two creeks of central-west Georgia and a spring-fed tributary of Chipola River, Florida. Out of 279 specimens from a spring in Worth County, Georgia, only 0.7 per cent are striate, and they amount to 4.5 per cent of 111 shells of a millpond near Marianna, Florida. Specimens with spirals are fairly common

in Flint River, Albany, Georgia, and in Spring Creek, east of Marianna, Florida. Virtually all shells from Choctawhatchee River, Dale County, Alabama, and a spring tributary to this river are striate. Collections taken of *Lithasia obovata* (Say) in Green River, Kentucky, show spirals present or wanting in about the same number of locations. Of thirty-five lots from as many locations in tributaries of the river, only six have shells bearing striae. The form *microlineata* (Goodrich) of Rough River of this drainage has fewer spirals at a lower station of the stream than at an upper station, but the feature is more pronounced. Striation is common to all Ohio River material at hand and occurs in all lots from Big Blue River of southern Indiana, later to be discussed, except one lot which comes from a spring on its banks. The form *depygis* (Say) of the lower Wabash River is non-striate while the subspecies *biconica* Pilsbry, occurring higher in the river, is striate. Striation is rare in shells of *Lithasia pinguis* (Lea) from Caney Fork, Tennessee, and a constant in the shell living in the upper part of Duck River. When spirals appear on the surface of *Nitocris trilineata* (Say) and *N. virgata* (Lea) they usually cover the whole disk. Of eighty shells of *trilineata* from the Falls of the Ohio, less than eight per cent were found to be striate. Such shells amounted to about forty per cent in *virgata* taken near the mouth of the South Fork of the Holston River, Tennessee. In no other lot examined was the percentage so high.

The basal spirals of the young of *Pleurocera acuta* (Rafinesque) persist into the adult stage more often than do spirals of the upper parts of the whorls. The character is of irregular occurrence in the species, and this is true also of *P. canaliculatum* (Say) and its forms or subspecies. The related *P. prasinatum* (Conrad) of the Alabama River system is usually unstriate, yet any one colony in the Coosa River may have shells in which spirals occur.

It has been shown in the foregoing that variation in spiral sculpture sometimes occurs within colonies of striate Pleuroceridae no matter what position in a stream the colonies oc-

cupy, that a variation of the kind exists which may be termed geographical, and that the sculpture may make its appearance irregularly or sporadically. The study has further brought to light evidences of relationship between spiral ornamentation and environment. An example of this correlation, the goniobases of Big Blue River of Indiana, may properly be considered in some detail.

The Big Blue River is a short stream draining a district of cavernous limestone. It rises in Washington County and discharges into the Ohio River near the town of Leavenworth, Crawford County. In comparatively little distance, the molluscan fauna passes from a creek to a river phase. Collections have been made at six localities of the main stream, in the two main tributaries, in a spring and a spring brook. The spiral sculpture of upstream goniobases, where it occurs, is that common to *G. semicarinata* (Say). This includes branches of the river. The sculpture of most far downstream shells is of the multistriate *G. indianensis* Pilsbry. The table shows the distribution.

It will be seen by the table that the only shells wholly lacking in spirals are from the spring branch in Washington County and the spring at nearly the opposite end of the Big Blue River drainage. Goniobases having only a single spiral are commonest in Mill Creek, the upstream part of Marengo Creek, and the upper reaches of the river. Going downstream in the river, the forms with two spirals increase irregularly in numbers. The first multistriate specimens appear at Fredericksburg as a low percentage. They are definitely a part of the river fauna in the vicinity of Wyandotte Cave. The spring branch in Washington County is two to four feet wide, and at the time it was visited it was not more than eight or ten inches deep. The shells were collected within forty feet of where the water issues from a low bluff. A stream flowing from a cave contributes a good deal of water to Mill Creek within a mile of its mouth. Marengo Creek is a spring branch at its beginning, and collections were made in the stream a few hundred yards below the spring. The river is a fairly

	Number of shells	Without spirals in %	With 1 spiral in %	With 2 or more spirals in %	Multistriate in %
Spring br., 1¼ mi. e. of Beck's Mill, Washington Co.*	93	34.3	56.0	9.7	0.0
Mill Cr., Beck's Mill	85	0.0	98.8	1.2	0.0
Big Blue R., 1 mi. e. of Beck's Mill	15	0.0	86.6	13.2	0.0
" 5 mi. above Fredericksburg, Washington Co.	89	0.0	97.7	2.2	0.0
" Fredericksburg	81	0.0	87.6	11.1	1.2
" Milltown, Crawford Co.	112	0.0	84.9	15.1	0.0
" 5 mi. e. of Wyandotte Cave, Crawford Co.	23	0.0	39.1	4.3	56.5
" Wyandotte Cave	91	0.0	24.1	23.0	52.9
Marengo Cr., Marengo, Crawford Co.	100	0.0	93.0	7.0	0.0
" Milltown, "	100	0.0	86.0	14.0	0.0
Stark's Spg., Wyandotte Cave†	18	11.1	83.3	5.5	0.0

* More than 200 specimens were taken here, but in the majority the spire was eroded to a point below where early spiral lines occur.

† A badly eroded lot of forty-two specimens, only eighteen of which retained sufficient of the spire to reveal the sculpture.

rapid stream to within a short distance of Wyandotte Cave. It is there worn down nearly to grade, and, as the Unionidae and *Anculosa* indicate, the fauna of the locality, leaving out *Goniobasis,* is closely akin to that of the Ohio River.

Pilsbry (1906) found that non-striate forms of *Goniobasis comalensis* dominated in Comal Creek, New Braunfels, Texas, "but there were also some individuals with numerous spiral ridges." Dwarfed forms of the species lived in springs and spring discharges along Comal Creek. None of these shells bore spirals. Bartsch (1906) remarks on the differences between *G. virginica* (Gmelin) in the Potomac River at Mount Vernon and at other parts of the drainage basin. While the variations are not specifically named, they presumably relate to the existence or non-existence of striae. Specimens that the Museum of Zoology has from the Potomac at Mount Vernon and the nearby Hunting Creek are striate over the whole surface. Shells taken in the Cumberland Canal at Harper's Ferry, fed from the Potomac River, are multistriate to the amount of about twenty-five per cent, the rest of the shells being smooth or striate on a few early whorls. Something of the same contrast is observable in *virginica* taken at tidewater and near headwaters in the Raritan River of New Jersey. *G. edgariana* (Lea) of the Caney Fork drainage of Tennessee was found by the writer (1923) to increase in the matter of striation in a down-river direction. In the case of *G. caelatura* (Conrad), to which an earlier paper of this series is devoted, there is a loss of both plicate and striate sculpture within the group (species, subspecies, or formae) as collections are made upstream.

Goniobasis porrecta Lea of the big hillside spring at Cumberland Gap has one or two striae on the juvenile whorls. No multistriate specimens have been seen as from the locality, but such individuals amount to 32.4 per cent of seventy-seven shells taken from Gap Spring Creek, about four miles below the spring. A similar increase in striation has been observed in *G. arachnoidea* (Anthony) after the water of Cannon Spring, Monroe County, Tennessee, discharges into Sweet-

water Creek. *G. catenaria cancellata* (Say) is a common mollusk of springs, creeks, and rivers of northern and central Florida. Typically, it is plicate-striate, the sculpture being usually developed into connected nodes at the periphery of the whorls. Spirals continue to the base of the shell. In the subspecies (or form) *vanhyningiana* (Goodrich) the spirals are either obsolescent or entirely obsolete. Alexander Springs, Lake County, Florida, contains the common *cancellata.* The spring forms a creek, and here the shell is *vanhyningiana.* The creek discharges into Wekiva River, which is inhabited by *cancellata.* Strong spirals occur on the surface of *G. curreyana* (Lea) of Green River at Brownsville, Kentucky; but in the nearby Beaverdam Creek is a race of the species wherein the spirals are restricted to the neanic whorls, and in some specimens they are almost obsolete. A difference in prominence of spirals is noticeable in *G. interveniens* Lea in lower Shoals Creek, Lauderdale County, Alabama, as compared with material from an upper branch of the stream. Yet the numbers of spirals are about the same in the shells of the two localities. In the case of *G. capillaris* Lea, a strongly striate pleurocerid of the Coosa River, no tendency toward sculptural obsolescence is observable among colonies of the main stream, and this is true of shells taken in three tributaries; but in a fourth tributary, Choccolocco Creek, Talladega County, Alabama, there is a decided reduction in number and conspicuousness of spirals in the species. The *Goniobasis haysiana-alabamensis* Lea complex is striate in most specimens at Wetumpka and Ten-Island Shoals. In mid-river shoals between these two localities, the smooth forms are dominant.

Almost all individuals of *Gyrotoma excisum* (Lea) from the Coosa River at Wetumpka are striate. At the upper end of the range of the species, Three-Island Shoals, Talladega County, the shells are smooth. *G. pagodum* (Lea) is also striate at Wetumpka. At the Bar, Chilton County, there is a mixture of striate and smooth forms. This variation holds with *G. pumilum* (Lea) except that the change is in a fewer number of miles. Smooth forms of *Anculosa griffithiana* Lea

are comparatively rare in Wetumpka lots, but one shell in eight in lots from The Bar lacks spirals. *A. formosa* Lea occurs mostly in that area of the Coosa River which is inhabited by the smooth goniobases above mentioned. It is commonly striate at the upper end of its range and smooth at the lower.

There is an apparent increase in striation in a down-river direction in *Nitocris carinata* (Bruguière) of Roanoke River, Virginia. Some of the lots available for examination are too small to permit a definite statement on the subject. Of ninety shells of *N. dilatata* (Conrad) taken from quiet water of New River at Hinton, West Virginia, about one-third are striate and the rest smooth. The striate shells of seventy-three specimens taken in fast water are fifteen per cent.

Discussion

Von Linden (1895–6) summed up the studies which had been made to that time on the relationship of shell sculpture to the histology of the shell-secreting glands. In substance, these observations were that irregularities in the mantle, which bears the glands, impress themselves by irregularities in the surface of the shell. Von Linden herself found that there were ten or twelve folds in the mantle of *Trochus turbinatus* Born to match the ten or twelve revolving ridges on the disk of the mollusk. Archer (1933) reports that for "each of the three denticulations" in the aperture of *Polygyra inflecta* (Say) "there are corresponding pits in the soft parts just back of the edge of the mantle."

In the light of what is known of the control exercised by the mantle over the superficial sculpture of shells, it cannot be said that the spirals of the Pleuroceridae are invariably inherited, although possibly in most instances they are. For folds in the mantle to which these spirals are attributed might be of merely mechanical origin, due to crowding of the animal within the shell for one thing, that would affect some members of a colony and not other members. This could explain the sporadic occurrence of spirals in species that ordinarily have smooth shells. It has been pointed out above that striate

species of the family occupying certain springs of the southern states betray a tendency to sacrifice their sculpture. Now these shells are depauperate. This is shown by the marked dwarfing, the closely-set growth lines, and the loose coiling—all indicative of impoverishment. It seems reasonable to suppose that depauperization which involves the soft parts as well as the shells reduces folding of the mantle and that this, in turn, reduces or eliminates striation. Grabau (1907) considers that the spirals on the base of *Melania elevata* (Say)—apparently the *Pleurocera acuta* (Rafinesque) of modern designation—is a character "derived through progressive reduction of features inherited from specialized ancestors." It happens that in this species the spirals are as often absent as they are present. An explanation which carries less assumption than Grabau's is that the mantle of *acuta* is sometimes folded and sometimes not, and that there is a correspondence of basal spirals when it is folded.

Summary

Spirals, the revolving sculpture of shells, have the wide range of variation in the pleurocerids that might be expected of a secondary sculptural character. That variation serves in instances as a distinction between localized races of a species. It is sometimes plainly correlated with ecological conditions. More often, spirals appear to be transient or sporadic. In three cases only has this form of sculpture been found to be unvarying, and two out of these three species are endemics. Spiral sculpture must be considered, therefore, of far less value for specific diagnostic purposes than might be concluded by the accent which has been placed on the feature in original descriptions of species.

REFERENCES

Archer, A. F.

1933 A Study of *Polygyra Inflecta* (Say). Occ. Papers Mus. Zool., Univ. Mich., 276: 1–8.

Bartsch, P.

1906 Variation in the Shell of *Goniobasis Virginica*, with an Out-

line for Breeding Experiments. Science, n. s., 23: 465–466.

GOODRICH, C.

1923 Variations in Goniobasis Edgariana Lea. Nautilus, 36: 115–119.

1934 Studies of the Gastropod Family Pleuroceridae—III. Occ. Papers Mus. Zool., Univ. Mich., 300: 1–11.

GRABAU, A. W.

1907 Studies of Gastropoda. III. On Orthogenetic Variation in Gastropods. Amer. Naturalist, 41: 607–651, Pls. 1–3.

LINDEN, G. M. VON

1895–96 Die Entwicklung der Skulptur und der Zeichnung bei den Gehäuseschnecken des Meeres. Zeit. wiss. Zool., 61: 261–317, 1 pl.

PILSBRY, H. A., and FERRISS, J. H.

1906 Mollusca of the Southwestern States. II. Proc. Acad. Nat. Sci. Phila., 58: 123–176.

TRYON, A. W., JR.

1873 Land and Fresh-Water Shells of North America, Pt. IV. Strepomatidae. Smithson. Misc. Coll., 253: i–lv and 1–435.