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STUDIES OF THE GASTROPOD FAMILY PLEUROCERIDAE—III

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VON LINDEN (1895–96) makes the pronouncement that the first differentiation of the surface of gastropods—beginning in pre-Cambrian time as smooth shells—was the modification of the growth lines. Such a modification would be the development of longitudinal ribs technically spoken of as plicae. When plicae are present, they ordinarily appear early in shell growth, and frequently they persist after the disappearance of other sculpture. On these two counts, orthodox assumption would grant plicae the standing of a primitive character. Grabau (1907; 1912) has shown that sculpture in several groups of the Gastropoda begins after a smooth embryonic stage, and that where plicae and revolving spirals both occur on the same shell the plicae are in advance of the spirals. Further, the sculpture is plicate in instances of acceleration wherein sculpture has advanced into the nuclear whorls. Stearns (1893) undertakes to explain the sculptured forms of *Paludestrina protea* (Gould) as responses to high alkalinity in the water inhabited. The hypothesis is carried further by Dall (1896) who states that alkalinity causes a pleating of the glandular epithelium of the edge of the mantle, the folds influencing the form of the surface "as the teeth of a rake leave shallow furrows over the gravel of a garden walk."

The thesis of Beecher (1898) that elaborate sculpture is a manifestation of racial and specific senescence is supported by Pilsbry (1911) who considers that in the Amnicolidae and Viviparidae "shell sculpture is a phylogerontic character, showing the approach of senility of the race; strongly developed sculpture in a species signalizes its last incarnation." He holds it to be questionable that concentration of alkaline salts is correlated with the development of sculpture.

The sculpture of the Pleuroceridae is that which Grabau found widespread in the Gastropoda, namely, plicate, spiral, or striate, nodular to spinose. The marine and brackish-water analogue of this fresh-water family is the Cerithiidae. The sculpture of the two is basically identical. Wholly smooth species of the Cerithiidae are seemingly rare. They are fairly common in the Pleuroceridae. Nodular and spiral ornamentation has reached a high development in the one family, but not markedly so in the other.

In specific descriptions of pleurocerids, the neanic carinae are usually mentioned among the details regarding sculpture, but inasmuch as carinae, keels, or angulations are virtually constants in the family—perceivable even in tightly-coiled individuals by breaking the spires—they are passed over in these studies on variability. For the same reason, the more or less conspicuous wrinkling of the epidermis parallel with the suture is not discussed. The present paper deals with plicate sculpture although that is associated often with spiral sculpture and is sometimes modified into nodes and, in the case of *Io,* into spines.

Plicate Sculpture in *Pleurocera*

On the basis of ornamentation, four forms of *Pleurocera alveare* (Conrad) can be distinguished one from another. Each bears a specific name, given many years ago. More thorough knowledge of the species has shown that only one name is justified. The forms are:

Alveare typical. Strongly plicate on spire and body whorl, the plicae at the periphery often nodose or beaded. Striate

on the base. Lea's *Melania pernodosa* appears to correspond completely with the type.

Torquatum Lea. Spire smooth or slightly plicate, upper part of body whorl smooth, the periphery more or less nodose. Striate on the base.

Pumilum Lea. Plicae nearly microscopic and usually observable only on the very young. Striate on base. The form represents another step after *torquatum* in the sacrifice of sculpture.

Plicatum Tryon. Plicate on the upper part of the spire, smooth on body whorl, and lacking striae on the base. The shell was named for what was probably a partly grown specimen of *torquatum*. Yet certain full-grown individuals elsewhere than at the type locality, Nashville, Tennessee, have its characters.

In most of the sixty-five lots which have been examined the races run true, that is, the instances in which a lot will have more than one of the above forms are comparatively rare. Cases occur in which it has been difficult to decide whether the specimens belong, say, with *alveare* or *torquatum*. The line between *torquatum* and *pumilum* is also obscure, and I am inclined to think that usually these forms occur together, but have been separated by early collectors misled by differences in size. As regards almost all the examples of *plicatum*, they were received directly from the field and have not experienced "separation."

The geographical distribution of *P. alveare* is in the lower Ohio River and lower parts of the tributaries, Wabash, Green, and Saline rivers; the Cumberland River and main branches; the Tennessee River in the vicinity of Muscle Shoals together with four adjacent tributaries; the White River system of Arkansas and Missouri.

While typical *alveare* occupies a slow-moving and muddy part of the Ohio River, it occurs also among rapids of the Wabash River. It is found in the upper part of the Cumberland River below the falls and, after a gap in distribution, in a lower part. It is unmixed in the upper end of its range in Green River, but mixed with *torquatum* near the mouth of the stream. It is the form of four branches of the Cumberland, of two of the Tennessee, and two of the White rivers.

Torquatum in "pure" colonies is in the Saline River of the Ohio and in parts of the Cumberland from about Celina to Carthage, Tennessee, which may be considered a middle zone of the stream. The largest lot of shells from Muscle Shoals at hand is made up entirely of *torquatum,* but another consists partly of *alveare* and partly of *torquatum.* The shell of the main Obey River of the Cumberland is *alveare,* of its West Fork, *plicatum,* and of a second tributary, Wolf River, *alveare* and *plicatum.* Specimens from the Cumberland at Nashville are made up of forms *torquatum* and *pumilum.* The latter form occurs in Cypress Creek at the foot of Muscle Shoals as do also *alveare* and *torquatum.* In Shoals Creek, discharging into the Tennessee above Florence, Alabama, the forms are *alveare, torquatum,* and *plicatum.* An unmixed colony in Harpeth River of the Cumberland is *plicatum.* The lowermost known colony in White River, Arkansas, is of mixed *torquatum* and *plicatum.* At a locality several miles above it, the mixture is *alveare-plicatum.*

Plicate Sculpture in *Goniobasis*

An example of plicate ornamentation in *Goniobasis* is *G. carinocostata* (Lea). The species inhabits tributaries of the Coosa River, the upper part of the Cahaba River together with some of its creeks, and at least two affluents of the Black Warrior River—all within the drainage of the Alabama River. In nearly every individual the plicae are visible to the unaided eye. Striae occur only occasionally, and cannot be considered a racial character. Geographical differences in strength of plicae have not appeared in the large amount of material examined. Environmental differences, while inconclusive, are perhaps suggestive. For instance, the *carinocostata* of a spring-fed branch of Little Canoe Creek in St. Clair County, Alabama, is only feebly plicate whereas the shells of the adjacent creek itself are robustly plicate; yet specimens from two springs of the same region are as stoutly plicate as any common creek forms. H. H. Smith collected a very large form of the species in a millpond of Beaver Creek, Greensport, St.

Clair County, the plicae of which were almost obsolete. Normally plicate shells were taken in the creek both above and below the millpond. To see whether ponded situations have an influence on sculpture, all shells from such localities that were available were examined. In three instances, no modification was observable. In a fourth, non-plicate specimens of *G. arachnoidea* (Anthony) were found among normally plicate shells from the pond below Cannon Spring, near Sweetwater, Tennessee. Shells of the spring were not so modified, nor were those of Sweetwater Creek into which the waters of spring and pond were discharged.

G. ebenum (Lea), commonly a smooth species, occurs in the Cumberland River drainage basin. In the upper part of the drainage, material containing plicate shells has been taken. The only lot at hand that can be accepted as a "pure" race of these forms is from New River, Scott County, Tennessee. Of 46 shells from Straight Creek at Pineville, Bell County, Kentucky, 54.4 per cent are plicate. In the Cumberland River a few miles below Pineville, 18 per cent of 72 shells are so sculptured; 74 shells of *ebenum* taken just above the falls of the Cumberland are 14.8 per cent plicate. The only specimens from the river below the falls which have been seen, taken at Smith's Shoals near Burnside, Pulaski County, Kentucky, are all smooth; so also are shells of all lots of the species ranging as far to the west as streams of Dickson County, Tennessee.

Certain goniobases that are ordinarily unornamented have plicated phases which appear to be cases of reversion. Three species may be taken for illustration: *G. mutabilis* Lea, *gerhardtii* Lea, and *murrayensis* Lea. In each, plicae are crowded into the early whorls of the spire and are unassociated with spirals.

All shells of *mutabilis* from Rocky Creek, five miles southwest of Waynesville, Burke County, Georgia, making up a large lot, are plicate, but only 9.3 per cent of 75 individuals from Buckhead Creek, into which Rocky Creek drains, have plicae. Specimens from four localities of the Chocktawhatchee

River of southeastern Alabama, together with shells from two small tributaries of the stream, are smooth. Yet three lots from Pea River, belonging also to the Choctawhatchee, contain plicate shells among smooth ones. Mollusks from eight different tributaries of the Conecuh River of south central Alabama are smooth, and material from four other tributaries of the same river are of mixed smooth and plicate specimens.

G. gerhardtii is an inhabitant of streams in the extreme northwest corner of Georgia, ranging into creeks of Alabama on the southern and eastern side of the Coosa River. The plicate forms occur in the lower part of the range, that is, streams of Cherokee and Calhoun counties. Apparently, they are nowhere in "pure" colonies.

G. murrayensis, scarcely distinguishable from *gerhardtii,* belongs to streams of the upper Coosa River to the east of *gerhardtii* "territory." In the Conasauga River[1] there is an increase of plicate forms in a downstream direction to judge by the shells examined.

	numbers	smooth in %	plicate in %
Conasauga, Polk Co., Tenn. . .	400	100	0.0
Beaverdale, Whitfield Co., Ga.	113	88.5	11.5
Campbell's Mill, Whitfield Co., Ga.	26	88.4	11.6
Treadwell, Murray Co., Ga. . .	116	70.6	29.3
Tilton, Whitfield Co., to Resaca, Gordon Co., Ga. . . .	44	26.7	73.2

In Swamp Creek at Tilton, 88 per cent of 67 specimens were found to be smooth, contrasting with shells of the river a few hundred yards below. This percentage is about the same of 50 examples from the creek one and one half miles above Tilton. Plicate forms of *murrayensis* in "impure" lots appear in material from six other streams of the area.

[1] Conasauga River of the upper Alabama River basin should not be confused with Conasauga Creek, which belongs to the Tennessee River drainage.

G. interupta (Haldeman), a pleurocerid of upper Coosa River drainage aspects, has been taken in Hiwassee River and branches of the Tennessee River. Doubtless, it has been involved in the intricate stream piracies of the region. Both plicate and non-plicate specimens occur. While plicate shells run to 22.2 per cent among 36 specimens from the river at Murphy, North Carolina, they amount to only 2.6 per cent of 77 shells from Conasauga Creek, a tributary. Small lots from two localities of the river above Murphy consist of smooth shells.

The longitudinal ribs of goniobases of the Coosa River are so subdued that the character may best be described as subplicate. Commonly, the subplicae are crowded into the upper part of the spires of the shells, leaving off abruptly before the development of spirals where such sculpture obtains. They are sharply defined, relatively, in *G. alabamensis* Lea, *haysiana* (Lea), and *punicea* Lea, and tend to be microscopic in *bellula* Lea, *laeta* (Jay), and *pilsbryi* Goodrich. Similarly, the sculpture of *G. olivula* (Conrad) of the Alabama River is suggestive of atrophy. In *G. vanuxemiana* (Lea) and *bullula* (Lea), the latter an unstriate race or mutation of the other, the spire is subplicate or wholly unornamented. Usually the subplicae are microscopic, but sometimes they are strong enough to be seen with the unaided eyes. From the Coosa River and three of its tributaries, 330 specimens were examined. These were separated as to whether the spires were smooth, microscopically sculptured, or conspicuously sculptured. The results when reduced to percentages showed that smooth-spired shells are apparently absent at the top of the range in the river and comparatively rare at the end of it, but running as high as 20 and 22 per cent at localities in the middle river. As between microscopic sculpture and visible subplication, there was small difference in one part of the stream as distinguished from another part. In the creeks, smooth shells were relatively high in numbers. No smooth-spired shells were found among *vanuxemiana* taken in the Alabama River, about 200 shells in all. At the same time, strongly sculptured shells in these lots were very rare.

There are six subplicate species of *Goniobasis* in the Cahaba River: *ampla* (Anthony), *bridgesiana* Lea, *pupoidea* (Anthony), *varians* (Lea), *variata* (Lea), and one which appears to have escaped description. No plicate-striate species occurs, and the only striate pleurocerid, *G. sulcata* Lea, is under suspicion as an infrequent mutation of a smooth species. Shells of *variata* from three shoals of the middle Cahaba River, about twenty miles apart, have subplicate and smooth shells in about equal numbers. Lots from the Little Cahaba River of Jefferson County show a smaller percentage of plicate specimens than material from the Little Cahaba River of Bibb County, another stream entering the Cahaba lower down. Buck Creek and Bishop Creek have low percentages of plicate shells as compared with takings from the Cahaba, but *variata* from streams at Montevallo, Shelby County, Alabama, is invariably subplicate seemingly. Collections of *bridgesiana* that were made in Waxahatchee Creek, tributary to the Coosa River, by H. H. Smith, very definitely show increase in strength and definition of plication going downstream.

Plicate Sculpture in *Anculosa*

The only plicate species of the anculosae are confined to the basin of the Alabama River. It is difficult to decide in some instances whether the ornamentation is of plicae or of bosses, making it apparent that in these cases at least nodulous sculpture has developed out of plicate sculpture. Plicae as a rule are associated with spirals, but to judge from insufficient material there are areas of the Coosa River in which plicate-striate sculpture is more common than in other areas. There is a seeming increase in strength of plication in a downstream direction in the species *downei* Lea and *formosa* Lea, but as this is correlated with an increase in shell size it can scarcely, by itself, be taken as an ecological response. One species, *ligata* Anthony, is feebly plicate on an early whorl or two, but is never striate.

The common *Anculosa* of the Cahaba River is *ampla* Anthony. Out of 81 shells from Lily Shoals, Bibb County, Ala-

bama, 58 per cent are plicate, the rest unsculptured. Shells from near Centerville, farther downstream, amounting to 133 specimens, are 82.8 per cent plicate. Lots from two tributary streams of the Cahaba show a marked decrease in plication as compared with the river shells. In neither instance do the sculptured shells exceed 27 per cent. Samples of *A. plicata* Conrad of the Black Warrior River are too few in numbers of shells to serve for comparative purposes. They do suggest, however, that as in *ampla* the species experiences increased ornamentation upstream to downstream.

Plicate Sculpture in Other Genera

The three forms of *Io* from headwaters are usually spoken of as smooth, but they are not smooth in the sense of the word as applied to other pleurocerids. They have a well-marked plicate sculpture on the spire, extending from suture to periphery. It is the modification of the lower ends of the plicae which brings about the nodes and spines in downstream shells.

Most of the sculptured species of *Lithasia* classify as nodulous. There occurs, however, a ribbed form of *L. obovata* (Say) to which Wetherby attached the specific name of *plicata*. The types came from the Kentucky River, although assigned in the description to Green River. The Museum of Zoology has two lots of such shells, one supposedly of Wetherby's collecting. Both are of mixed plicate and smooth specimens. The same kind of plicate forms of *obovata* occur in small creeks of the Obey River of Tennessee. The sculptured forms occur in company with smooth forms.

Carinae ignored, the upper parts of the spires of *Gyrotoma* are ordinarily smooth. Occasional individuals, as in *excisum* (Lea) and *incisum* (Lea), show an early subplication which quickly becomes obsolete. A single specimen of *pyramidatum* Shuttleworth was found which had low plicae from post-embryonic whorls to the penultimate whorl. Plicate sculpture in the genus appears to have become submerged or suppressed through the development of the sutural fissure, the chief distinctive character of the genus.

The two species of *Eurycaelon* are nodulous. No plicate shells have been observed in *Nitocris*.

Summary

The sculpture of the Pleuroceridae, carinae and epidermal wrinkling excluded, is of plicae, spirals, nodes, and spines. Combinations of kinds of sculpture are of more or less frequency. Occurrence of plicae and spirals together is, for example, more common than the occurrence of either kind alone.

The present paper is devoted to plicate sculpture.

Only one species of the genus *Pleurocera* is plicate. Four forms of this species are distinguishable according to variations in sculpture. No indication is revealed by the study of these different forms that distribution has proceeded from any geographical center, nor is definite ecological influence, broadly applicable, suggested.

A plicate species of *Goniobasis* of relatively wide range, *carinocostata* (Lea), shows small variation in sculpture throughout that range. Two instances of seeming environmental response are recited. They are wanting in conclusiveness. A second species rather broadly distributed is smooth in the lower part of its range, and has a tendency toward plication in the upper part. The same phenomenon is true of the only species of *Lithasia* which has plicate forms. Cases of plication apparently through reversion are described. In one of them, plication is seen to increase in a downstream direction. Plicae occurring among the peculiar goniobases of the Coosa River are crowded into a few whorls of the spire, possibly representing examples of obsolescence. Smooth-spired shells in *G. vanuxemiana-bullula* are commoner in tributary streams of the Coosa River than in the river itself. An increase in prominence of plicae is observable in *G. bridgesiana* in the direction of downstream.

Plicate species of *Anculosa* occur only in the drainage of the Alabama River. Among shells of *A. ampla* Anthony taken from two shoals of the Cahaba River, there is a higher percentage of plicate shells from the lower shoals than from

the upper shoals. Specimens of *ampla* from two tributary streams of the Cahaba are less frequenty plicate than specimens from the river.

All forms of *Io* are plicate, but the plicae of headwaters forms do not become modified into nodes and spines as do plicae of *Io* in down-river situations.

Plicate sculpture of the endemic genus *Gyrotoma* of the Coosa River is more clearly atrophied than in the instance of the goniobases of the same stream.

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