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STUDIES OF THE GASTROPOD FAMILY
PLEUROCERIDAE—VIII

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THE sculpture of the Pleuroceridae, aside from axial lines marking arrests of growth and the adventitious wrinkling of the epidermal surface, consists of vertical ribs commonly spoken of as plicae; revolving ridges to which the terms striae, carinae, and spirals are variously applied, and nodes, nodules, or spines. The first of these phases of sculpture was discussed in the third paper of this series (Goodrich, 1934), and the second in the fifth paper (Goodrich, 1935). It is intended here to deal with sculpture distinctively nodulous or spinose, genus by genus.

IO

The steps in the development of sculpture in *Io* are plicate, to plicate-nodulous, to simply nodulous or spinose. Each step may represent a period in the life history of the complex or, in the case of a downstream inhabitant, in that of an individual mollusk. Plicae appear first on the sixth or seventh whorl. They extend at this stage from suture to periphery and are of uniform thickness. As growth proceeds, there is a gradual thickening of the peripheral end of the plicae until the sculpture is noticeably nodulous. On maturing and final whorls the upper part of the plication has become obsolete or nearly

so, the lower part magnified into bosses or pronounced spines. Occasional specimens are met with in which plicae of the juvenile stage of the mollusk are altogether absent, the sole sculpture being nodes or spinosities. Headwaters forms of *Io* are usually described as smooth, by which is meant that they are without the pronounced tubercles of downstream forms. Yet the great majority of headwaters shells are plicate, and in a given lot there are likely to be a few individuals which are slightly nodulous. Moreover, there are colonies below headwaters that, though made up mostly of nodulous examples, contain reversions to the smoother upstream aspect.

LITHASIA

Two phases of nodulous sculpture occur in this genus, one in which the "ornamentation" is restricted to the periphery of the shell or is there emphasized, and one in which nodules are developed on the shoulder of the whorl immediately below the suture.

Lithasia armigera (Say) may be taken as representative of the first of these modes of nodular secretion. Commonly in the species, rather low and inconspicuous plicae develop on the sixth or seventh whorl, and there is a thickening or enlargement of the peripheral ends of the plicae on the eighth or ninth. At maturity, the nodules are stout, triangular, and sometimes are joined together by weak ridges of shell material, but more often not. Of 117 mature specimens, 23.9 per cent had lost all sign of plicae. That is, in *armigera*, as in *Io*, a tendency toward the elimination of the primitive axial sculpture and focusing upon a later form of sculpture can be observed.

In certain tributaries of the Cumberland River, forms occur in which the nodulous sculpture is reduced to faint projections or is absent altogether. Thus is *L. armigera stygia* (Say), of which *L. downei* Lea and *angulata* Wetherby are synonyms. Wetherby took his material from Stone's River, Rutherford County, Tennessee. Of seven specimens at hand of the original lot, three have obscure tubercles. About 35 per cent of

sixty-four examples from the same stream, collected by others than Wetherby, are entirely without sign of nodulous sculpture, indicating that development toward a nonnodulous state is only partial.

A race known as *L. jayana* (Lea) has both peripheral and sutural nodules. This may be understood as an instance in which the thickening or swelling of the vertical plicae takes place at top and base. This double sculpture, if it can be called that, is observable more or less often in *L. duttoniana*. *L. lima* (Conrad), like *L. armigera*, has developed nodular sculpture strongly at the periphery, but has as many as four accompanying rows of nodules. In something like a third of 113 specimens, the plicate stage, from which the nodular sculpture has developed, has been passed over. There is evidence in shells of *lima* in Elk River, Tennessee and Alabama, that this obsolescence of plicate sculpture occurs in a downstream direction.

In *L. verrucosa* (Rafinesque), the tubercles are more frequently linear than strictly nodulous. The sculpture is made up of several revolving rows of such linear processes, usually set apart from one another at the periphery of the shell, frequently joined or connected above the periphery, or reduced to striae on the base. The number of rows of nodules is correlated with the size of the shell, and this, again, is correlated with the size of the stream occupied. Thus, specimens from the Tennessee River at Bridgeport, Jackson County, Alabama, are more tuberculate than the smaller shells from the Holston River above Knoxville, Tennessee. Young of *verrucosa* commonly are plicate, but this sculpture is occasionally absent. Specimens have been found in which the nodules are coalesced into continuous striae or carinae. To these aberrants or reversions, Anthony gave the specific name *Melania procissa*, Lea the designation *Goniobasis stewardsoniana*. *Lithasia curta* Lea is a race of low-spined, globose shells closely related to *L. verrucosa*. It is confined to Muscle Shoals and near-by tributaries of the Tennessee River. Seventy examples have been examined. In none could plicate sculpture be remarked.

The tubercles may be distinctly separated or connected by intermediate ridges. The rows of completely broken processes are usually the second and third below the suture. The Muscle Shoals lots are more stoutly sculptured than are those from the side streams, and this possibly bears correlation with the size of the shells and with the size of the waters occupied.

The study of the two species *L. verrucosa* and *curta* indicates that here nodular sculpture has developed from striate sculpture, not from the axial plicate tuberculations. The nodules are vestiges of once continuous revolving striae or carinae. Reversions occur.

Nodulous sculpture which has developed at the shoulder of the whorl—in contrast to that restricted to the periphery, or there most pronounced—is peculiar to two species, *L. geniculata* Haldeman and *salebrosa* (Conrad).

The nodules in *geniculata* reverse the position of those in *armigera*, that is, the broad part of the triangle is at the top, its obtuse point toward the aperture. They begin at whorl $6\frac{1}{2}$ –7, and are confined almost wholly to a single wide-spaced row. Only four specimens out of 160 have more than one row of the tubercles; 7.5 per cent of the 160 make it clear that in *geniculata* the nodules are a development from plicate sculpture, that is, the species has very nearly completed an alteration of plicae into sculpture solely nodulous.

The distinction between *geniculata* of the Cumberland River system and *salebrosa* of that of the Tennessee River is chiefly that the latter commonly has two or more rows of nodules. For example, in seventy-eight specimens, forty-seven, or 60.2 per cent, have rows of tubercles exceeding one. Inasmuch as only old and eroded shells are available as material for study, it is impossible to say positively that the sculpture of *salebrosa* is a development from plicae, but the fact may be assumed from the findings in the closely related *L. geniculata*. The mollusk called *L. subglobosa* Lea is apparently simply a depauperate form of *salebrosa*, occurring with it and having but few nodules and these all in a single row at the shoulder.

Lithasia geniculata and *salebrosa* each has upstream or side-

stream forms, distinguished by an elongation of the spire and an alteration of proportions of altitude to diameter, together with the curious characteristic of a development of nodulous sculpture, when that exists, at the periphery of the shell and not at the shoulder. Also, the axial plicae have been retained in most instances, not suppressed as in the riverine stock. Because of the feebleness of these ribs, they may best be spoken of as subplicae. Details of the findings are recited.

L. geniculata fuliginosa, belonging to the Duck River of Tennessee and its tributaries, shows a variation in sculpture with reference to position in the stream. In the following tabulation the localities read upstream to downstream:

	Number	Percentage
Bedford County		
Shells subplicate	20	58.8
Shells nodulous	0	0.0
Shells lacking sculpture	14	41.1
Marshall County		
Shells subplicate	32	58.1
Shells nodulous	11	20.0
Shells lacking sculpture	12	21.8
Maury County		
Shells subplicate	90	70.3
Shells nodulous	29	22.6
Shells lacking sculpture	9	7.0

Thus, as in *Io*, sculpture increases downstream. That this is also true in *L. salebrosa florentiana* is probable, though there are not series of specimens enough to furnish proof. In Harpeth River, a tributary of the Cumberland River, is a procession of forms similar to that in the Duck River—stoutly sculptured *fuliginosa* near the stream's mouth, slightly sculptured *fuliginosa* about midway the length of the river, and the completely nonnodulous form named *Melania venusta* by Lea in headwaters.

PLEUROCERA

Nodulous sculpture in this genus, wherever it occurs, is a development from plicate sculpture, as in most of the species of Pleuroceridae so far considered. It shows a tendency

toward becoming the dominant sculpture and even the only one.

Of eighty-five adolescent and adult specimens of *P. alveare* (Conrad) from the Cumberland River at Burnside, Pulaski County, Kentucky, 86.5 per cent are plicate-nodulous, the rest purely nodulous. This is the highest percentage of plicate-nodulous forms among several lots from the river. Below Burnside, the relative numbers of shells having only nodulous sculpture increase. Representatives of colonies of the Cumberland from Davidson and Montgomery counties, Tennessee, give no indication of having or of having had plicae. Cumberland tributary forms correspond in sculpture to those of the Burnside area rather than to shells of the main river. *P. alveare* of the Tennessee River is like that of the lower Cumberland. Yet plicate-nodulous examples amount to 40.6 per cent of thirty-two shells from Cypress Creek, a Tennessee River tributary, and are common in other side-stream lots. There is seemingly another step in the formation of sculpture. This is the replacement of the peripheral row of nodules with a smooth, unbroken, fairly heavy carina. It is absent in the Cumberland River headwaters and most frequently present in extreme down-river colonies.

A second plicate species, *P. foremanii* (Lea), belongs to the Alabama River system. The plicae are crossed by revolving striae, and nodules are formed at these conjunctions or intersections. The number of rows of nodules is from one to three, the largest number being in riverine individuals as a rule. With one exception, small-stream shells are lacking in plicae, and in one other instance both plicae and striae are wanting, the nodules occurring alone. This finding is in contrast with that in the case of *P. alveare*, observed above.

Three other species of *Pleurocera* have nodulous sculpture, but in none of them is evidence left of a previous plicate state. In all three, the nodulous sculpture is more or less replaced with one purely carinate, already remarked in down-river colonies of *P. alveare*. Of eighty specimens of *P. canaliculatum excuratum* (Conrad) from the Tennessee River at

Muscle Shoals, Alabama, 65.0 per cent are nodulous, 15.0 per cent nodulous-carinate, and the others strictly carinate. In the few instances in which the subspecies invades tributary streams, there is a tendency toward a reduction in the number of nodulous forms and an increase in the development of modified phases of this sculpture. *P. nobile* (Lea) of the main Tennessee River is either nodulous or carinate-nodulous, to judge from about fifty shells seen. Of thirty-six taken in the tributary Sequatchie River, 5.6 per cent have lost all sign of nodulous sculpture.

The typical form of *P. canaliculatum undulatum* (Say) occurs in the Kentucky River, the subspecific name having reference to nodulous sculpture on the periphery of adolescent and adult individuals. This sculpture is not a constant. Of one hundred specimens from the Kentucky from about mid-stream to near the mouth, 82 per cent are purely nodulous, 14 nodulous-carinate and 4 per cent carinate only. Elsewhere, the prevailing form of *undulatum* is a strictly carinate mollusk. Yet there are sporadic appearances of nodulous sculpture in the subspecies, in the Clinch River, Roane County, Tennessee, in the Ohio River, Hardin County, Illinois, and in the Green River of Kentucky near its discharge. The sculpture occurs also in that part of the Cumberland River where *undulatum* is being replaced by the subspecies *excuratum*.

To summarize: Purely nodulous sculpture increases in a downstream direction in *P. alveare* and is the characteristic sculpture in large-stream forms of *P. nobile* and *canaliculatum excuratum*. It is the small-stream forms of *P. foremanii*, on the other hand, which are most often purely nodulous. This sculpture, as it occurs in *P. canaliculatum undulatum*, is to be considered relict or a reversion. Although in *P. alveare* carinate sculpture is seemingly a successor of nodulous sculpture, it can be argued, on the same kind of evidence, that the reverse is true in *P. nobile*, *canaliculatum excuratum*, and *canaliculatum undulatum*.

GONIOBASIS

The shells of seven species and two subspecies were exam-

ined—about three thousand specimens in all. The nodulous sculpture of the nine forms is a development out of plicate sculpture.

In *G. carinifera*, beadlike nodules are a feature of adolescent life, appearing usually as plicae are becoming obsolete or have disappeared. The complete elimination of plicae, leaving nodules as the sole sculpture, is manifest mostly among inhabitants of springs. This amounts to as little as 1 per cent in one spring and reaches 32.1 per cent in another, with an average in eight springs of about 12 per cent. Little change from these findings was found in shells of four bodies of water, two of which were natural pools below springs and two artificial. Only two of four small-stream lots contained specimens in which plicate sculpture was lost. In two streams known as rivers, the percentage of loss was 1.9 of fifty-three specimens and 12 of seventy-five specimens, respectively. The nodulous sculpture of *G. bella-crenata* is distinguished from that of *carinifera* only in being restricted to fewer whorls.

Nodulous sculpture in *G. caelatura* appears first at the crossing of the axial plicae and the revolving striae. With growth, plicae disappear. Sometimes the striae also become obsolete. There is left then only the nodules. This restricted sculpture was found to be fairly common in material from Etowah River, Georgia, which is about midway in the range of the species, and rare in headwaters and down-river lots.

Three phases of nodulous sculpture were found in *G. boykiniana*: (1) the peripheral ends of plicae are thickened into bosses; (2) the centers of plicae are enlarged; (3) tubercles are formed at the conjunction of plicae and striae. This last is the most commonly occurring of the three phases. In the subspecies, *viennaensis*, both plicate and striate sculpture may be passed over, and nodulous sculpture remains alone. The second subspecies, *albanyensis*, is excessively striate, light nodules occurring where plicae and striae interjoin. Sometimes the nodules stand apart from one another, vertical and revolving sculpture being either nearly microscopic or absent. *G. boykiniana* is a mollusk of large streams and *viennaensis*

one of smaller streams; *albanyensis* occurs in still smaller streams and, at least in one instance, in a spring.

Nodulous forms are present among plicate forms of *G. interrupta*, but so far as material at hand indicates this is only among riverine inhabitants.

Nodulous sculpture in *G. hydei* (Conrad) has developed out of plicate sculpture the same as in other species so far considered. Nevertheless, the conspicuous "ornamentation" is striate-nodulous, that is, the tubercles are joined together by sharply defined internodal ridges. The material was studied with reference to the occurrence or nonoccurrence of this combination of two phases of sculpture. Of eighty-one specimens from a headstream of the Black Warrior River of Alabama, 65.4 per cent were found to be striate-nodulous, 34.5 per cent nodulous only. Forty-eight specimens from Tuscaloosa, a down-river locality, were made up of 22.0 per cent striate-nodulous forms and 78.0 per cent nodulous.

Some forms of *G. lachryma* are plicate-nodulous and others are nodulous only. The plicae are in course of disappearance. Tubercles, where they occur, are formed on the peripheral ends of the plicae, and are large, irregularly shaped, tearlike.

ANCULOSA

Some of the larger species of *Anculosa* inhabiting the Coosa River of Alabama have low bosses on the shoulder of the adult whorl, and these are frequently made conspicuous by deposits of coloring matter, darker than the ground pigment, in the depressions between them. In only an occasional individual is the earlier plicate stage indicated.

The development of nodulous sculpture from plicate sculpture can be followed in two species, *A. ampla* Anthony of the Cahaba River and *A. plicata* of the Black Warrior River, the two streams being parts of the Alabama River system. Upstream and in tributaries, *ampla* begins as a smooth, unsculptured shell. These smooth forms do not altogether disappear, but decrease in relative numbers downstream. Reading in a down-river direction, purely nodulous specimens constitute

68.4 per cent of thirty-eight adults from Nunley Ford, Shelby County. That percentage is closely held to below Piper, Bibb County. There is thereafter a drop until Centerville, Bibb County, is reached. Here the nodulous forms constitute 54.3 per cent of forty-six specimens. The shells are smooth in five branches of the Cahaba, in the majority in two other branches. In an eighth tributary, the Little Cahaba River of Bibb County, plicate and plicate-nodulous examples are more abundant than are those purely nodulous. The same more or less noticeable progression of forms from smooth to plicate to plicate-nodulous to nodulous sculpture is indicated in the case of *A. plicata*, though the material, amounting to only forty specimens, is insufficient to warrant a positive conclusion in the matter.

EURYCAELON

The nodules in *Eurycaelon*, wherever they exist, are bosses of anomalous shape and of varying prominence. In *E. anthonyi* (Redfield, Budd), belonging to the Tennessee River system, the nodules are more protuberant among shells from the vicinity of Knoxville, Tennessee, than in those taken at Muscle Shoals, Alabama, which is about the end of the range of the genus. Nodules are almost entirely absent in lots collected in Little Sequatchie River, the lower Clinch River, Battle Creek, and Piney Creek. In *E. crassa* (Haldeman) the bosses are highly developed, and apparently no individual mollusk is without them. The formation of this sculpture appears to be in this wise: The snail forms a heavy deposit of callus at the top of the aperture. This is not absorbed as growth proceeds after a rest period, but is an obstruction over which new shell material has, as it were, to climb, to a new rest stage during which callus is again secreted. The rest is a series of nodes. Shells lacking the heavy apertural callus lack also the nodules.

DISCUSSION AND SUMMARY

The nodulous sculpture of almost all members of the Pleuroceridae is derived from plicate sculpture. Only two exceptions have been observed. In the *Lithasia verrucosa-curta*,

group nodulous sculpture has been brought about by the breaking up or splitting of revolving striae which are at right angles to the axial or plicate sculpture. The nodules of the genus *Eurycaelon* are correlated with heavy depositions or secretions of apertural callus. Where these deposits are light or absent, there are no nodules. The process may be termed mechanical, casual, or random. Pleuroceridae of three genera inhabiting the Coosa River at Ten Island Shoals, St. Clair County, Alabama, are more or less distorted by irregular swellings which simulate plicae or nodules, or, in some instances, both. The occurrence is local and appears to involve hardly more than 20 to 25 per cent of the individuals of any one colony. This sculpture, as in *Eurycaelon*, can be considered fortuitous.

Nodulous sculpture for the most part develops by the enlargement or thickening of the peripheral ends of plicae. As growth proceeds, the upper part of the plicae becomes a vestige or disappears entirely. In the short-spined *L. geniculata* and *salebrosa* it is the sutural ends of the plicae which enlarge. Yet in subspecies of these mollusks, which are long-spined, nodules form at the peripheral terminations. It would appear from these differences that the formation of nodulous sculpture, either as peripheral or as sutural magnifications, is linked with manner of whorl coiling. The question is confused by the fact that in one species of *Goniobasis*, enlargement into nodules takes place, not at the ends of the plicae, but in the centers. This, however, may be adventitious, since it does not affect or involve all individuals of a colony.

No generalization regarding correlation of nodulous sculpture to place in stream, involving all the genera of the Pleuroceridae, can be drawn. This type of sculpture reaches its greatest development in *Io* and *Lithasia* at or near the downstream limits of their geographical range. This is the case also with the two species of *Anculosa* the details of which have been given above, but with not all the Anculosae. Downriver colonies of *Pleurocera canaliculatum excuratum* and of *nobile* have a larger number of purely nodulous forms than upriver or tributary colonies have. But in *P. canaliculatum undu-*

latum nodosity characterizes the majority of individuals of only one stream and is elsewhere of irregular or sporadic occurrence. *P. alveare* is stoutly nodulous in headwaters and middle-river situations; farther downstream the sculpture becomes weak and grades into purely carinate sculpture. Middle-river forms of four species of *Goniobasis* are conspicuously nodulous, and in two other species, possibly depauperate; this is a marked trait of occupants of springs and spring pools.

The first part of Hyatt's law of acceleration (1894) is to the effect that adult and adolescent characteristics of organisms tend to become characteristic of the juvenile stage, and finally the embryonic. Adams (1915), seemingly with the Hyatt law in mind, observed that "spinosity [in *Io*] may be said to be 'crowded back,' or acquired earlier and earlier, until it occupies the entire postembryonic development of the shell, as in *spinosa* and its allies." That is, the acquirement of nodes or spines takes place at a younger period in down-river shells than in upstream forms. Of the species examined in this study, acceleration is especially evident in *Pleurocera nobile*; it is less noticeable, though present, in *Goniobasis caelatura*. The Hyatt law possibly applies in those instances in other species of *Goniobasis* wherein sculpture is a pronounced adult feature among upstream shells, and an adolescent or juvenile characteristic of downstream inhabitants.

Hyatt further directs attention to the fact that "in many cases" the early characteristics which are impinged upon by later characteristics "are resorbed and disappear during this process." It is a process of the kind, obviously, which brings about a substitution of purely nodulous sculpture for sculpture that, to begin with, was plicate and then plicate-nodulous. The process may work gradually and affect a whole genus, as in *Io*, or be hastened by the factors of depauperization, such as those observed in *Goniobasis carinifera*.

REFERENCES

ADAMS, C. C.

- 1915 The Variations and Ecological Distribution of the Snails of the Genus *Io*. Mem. Nat. Acad. Sci., 12, 2: 1-92, Pls. 1-61.

GOODRICH, CALVIN

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

1935 Studies of the Gastropod Family Pleuroceridae. V. *Ibid.*,
318: 1-12.

HYATT, A.

1894 Phylogeny of an Acquired Characteristic. Proc. Amer. Phil.
Soc., 32, 143: 349-640.

