

OCCASIONAL PAPERS OF THE MUSEUM OF  
ZOOLOGY

---

UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN

UNIVERSITY OF MICHIGAN PRESS

---

STUDIES OF THE GASTROPOD FAMILY  
PLEUROCERIDAE—VII

BY CALVIN GOODRICH

THE light yellow to dark brown ground color of the periostracum of the Pleuroceridae is frequently relieved by spiral stripes of a darker hue. Customarily, these stripes are spoken of as bands, and that practice is followed in this paper. The bands are not always continuous, as implied by the word, but are sometimes broken into interrupted squares and rectangles as though the secretion of pigment by the animal was intermittent. In another phase the bands consist of many capillary lines which are crowded together—apparently a linear division of the ordinarily few and well-spaced stripes. Again, the bands may take the form of zigzag markings of a bizarre appearance. This is an exceedingly rare phenomenon in the family, and is to be considered as due to disease or abnormality of the pigmentation glands of the mantle. In the same category is hypersecretion in which the color material involves the whole of the periostracum and the porcelaneous layers, the shell being uniformly purple or black. The statement should be qualified by saying that in certain streams or areas all pleurocerids are melanistic and, in the circumstances, can scarcely be thought of as anomalies.

The bands, when they occur, are ordinarily in both the perio-

tracum and the crystalline shell substance. Yet occasionally the pigmentation is confined to one or the other. This may affect only certain individuals of a colony, all members of a colony, or all the colonies of a species of a given stream.

This paper is the result of studies of the banding in the Pleuroceridae in order to learn whether or not the character is correlated with the environment, conclusively, seemingly, or not at all. By reason of pollution, hydroelectric engineering, and navigation enterprises, the time is past for taking large series of specimens through the full length of those rivers which would have the most incontrovertible information to reveal. The facts set down vary, therefore, in value as the amounts of material available for study vary. Due allowance on the part of the reader is asked on that score.

#### PLEUROCERA

Forms or subspecies of *Pleurocera canaliculatum* (Say) range throughout the larger streams of the Ohio River system, usually occupying muddy situations. Banding in the genus is seldom likely to be pronounced or intense. It tends to fade early. The shell thickening of revolving ridges has the appearance of bands when seen through transmitted light. Hence, more than in other groups, care has to be employed in the examination of shells of *P. canaliculatum*. In a collection of 59 shells from the Wabash River at Lafayette, Tippecanoe County, Indiana, 37.3 per cent were found to be banded. The percentage was 44.7 among 38 that were taken in the same stream at New Harmony, Posey County, Indiana, which is much farther downstream. Of a lot of 300 from the tributary West Fork of the White River, Wheatland, Knox County, 9.5 per cent were banded. The typical subspecies, *undulatum* (Say), inhabits the Kentucky River. In this river at Monterey, Owen County, Kentucky, of 68 taken, 69.1 per cent were banded. By river, Boonesboro, Madison County, is about one hundred miles upstream. Here, 65.0 per cent of 42 specimens were with bands. Series from the Green River of Kentucky, reading upstream to downstream, make the following showing:

	Number of Specimens	Banded Specimens	Per Cent of Banded Specimens
Rio, Hart Co. ....	79	3	3.8
Rochester, Butler Co. ....	104	57	54.8
Calhoun, McLean Co. ....	72	34	47.2
Sebree, Webster Co. ....	42	38	90.5

The *Pleurocera* of the upper Cumberland River is *canaliculatum* form or subspecies *filum* Lea. Smith's Shoals, Pulaski County, Kentucky, is about three miles above the head of navigation; Horseshoe Bottom, Russell County, is about fifty miles farther downstream. A sharp difference in banding in *filum* is indicated by the following table:

	Number of Specimens	Banded Specimens	Per Cent of Banded Specimens
Smith's Shoals .....	259	41	15.8
Horseshoe Bottom .....	82	55	67.0

Mr. Leslie Hubricht has kindly compared for me the banding of 376 specimens of *P. acuta* (Rafinesque) taken in the Meramec River at Kirkwood, Saint Louis County, Missouri, with about five hundred from an artificial lake in Fairgrounds Park of the same county. Among the river shells, 42.3 per cent were banded; none of the lake specimens were banded. An opportunity for comparison between mainstream shells and those of two tributaries, one small and one large, is provided by *P. parvum* (Lea) of Little River, Blount County, Tennessee:

	Number of Specimens	Banded Specimens	Per Cent of Banded Specimens
Little River, near Kinzal Springs ..	283	241	85.5
Nale Creek .....	428	24	5.6
Pistol Creek .....	138	81	58.6

## NITOCERIS

A little more than 2 per cent of 521 specimens of *N. carinata* (Bruguère) from the South Branch of the Potomac River, near Upper Tract, Pendleton County, West Virginia, have bands. A lot of 731 shells of the same species from the Roanoke River, near Elliston, Montgomery County, Virginia, proved to be 28.3 per cent banded. The two situations can both be called headwaters stations, but in size the Roanoke at Elliston is a larger stream than the Potomac at Upper Tract. Collections of *N. dilatatus* (Conrad) in the Greenbrier River, West Virginia, and the New River immediately below the mouth of the Greenbrier, gave these findings:

	Number of Specimens	Banded Specimens	Per Cent of Banded Specimens
Greenbrier River			
Marlington, Pocahontas Co. . . . .	90	11	12.2
5 miles SE. of Lewisburg, Green- brier Co. . . . .	345	74	21.4
3 miles below Allerson, Summers Co. . . . .	364	64	17.7
10 miles below Allerson, Summers Co. . . . .	606	79	13.1
New River			
Hinton, Summers Co. . . . .	636	176	27.7

## LITHASIA

Material of *Lithasia* suitable for this study is scant, and scarcely of significance. It consists of 34 specimens of *L. verrucosa* (Rafinesque) from the Tennessee River at Knoxville, Knox County, Tennessee, and 47 of the same species from Muscle Shoals, Alabama, about two hundred miles by river farther downstream. In the upper locality the banded shells amounted to 29.4 per cent and in the lower to 73.5 per cent.

## ANCULOSA

*A. subglobosa* Say is the headstream representative of the genus in the Tennessee River system. It is replaced down-

stream by *A. praerosa* Say in the main river, and those forms of *Anculosa* which penetrate the lower tributaries are, with

	Number of Specimens	Banded Specimens	Per Cent of Banded Specimens
Clinch River			
Cedar Bluff, Tazewell Co., Va. . . . .	30	0	0.0
St. Paul, Wise Co., Va. . . . .	54	10	18.6
Clinchport, Va., to Clinch River Station, Tenn. . . . .	182	126	69.2
Agee, to Kingston, Tenn. . . . .	340	257	75.5
Tributary of Clinch River			
Indian Creek, Lee Co., Va. . . . .	68	1	1.4
Holston River			
Saltville, Va., to Kingsport, Tenn. . . . .	122	0	0.0
Rogersville, Hawkins Co., Tenn. . . . .	40	34	85.0
Hamblen Co., Tenn. (2 localities) . . . . .	95	81	85.2
Knox Co., Tenn. (3 localities) . . . . .	216	204	94.4
Tributary of Holston River			
Big Moccasin Creek, Scott Co., Va. . . . .	109	0	0.0
South Fork Holston River			
Near Damascus, Washington Co., Va. . . . .	95	0	0.0
Bluff City, Sullivan Co., Tenn. . . . .	135	29	21.5
French Broad River			
Near mouth, Nolichucky R., Hamblen Co., Tenn. . . . .	73	70	95.9
Tributaries of French Broad River			
L. Pigeon R., Sevierville, Sevier Co., Tenn. . . . .	29	13	44.9
Nolichucky R., mouth, Hamblen Co., Tenn. . . . .	55	52	94.5
Tennessee River			
Knoxville, Knox Co., Tenn. . . . .	420	313	74.5
Loudon, Loudon Co., Tenn. . . . .	89	69	76.6
Washington Ferry, Meigs Co., Tenn. . . . .	98	95	96.9
Bridgeport, Jackson Co., Ala. . . . .	47	46	98.0
Muscle Shoals, Lauderdale Co., Ala. . . . .	137	133	97.0
Tributaries of Tennessee River			
Little River, Blount Co., Tenn. . . . .	234	10	4.3
Sequatchie R., Dunlap, Sequatchie Co., Tenn. . . . .	64	18	28.1
Sequatchie R., 8 miles below Dunlap . . . . .	62	17	28.0
Sequatchie R., Jasper, Marion Co., Tenn. . . . .	30	30	100.0
Elk R., Elkton, Giles Co., Tenn. . . . .	118	108	91.5
Elk R., W. of Athens, Limestone Co., Ala. . . . .	491	480	97.7

only one or two exceptions, either this species or obvious offshoots of it. The group can be spoken of as the *subglobosa-praerosa* complex. The table is a count of banded and unbanded specimens of the complex from the Tennessee basin. The localities are listed in a downstream order:

*A. praerosa* is abundant in the Cumberland River from a point a few miles above the head of navigation to the vicinity of Nashville, Tennessee. An examination of available material from the river brought these results:

	Number of Specimens	Banded Specimens	Per Cent of Banded Specimens
Smith's Shoals, Pulaski Co., Ky. . .	949	120	12.5
Russell Co., Ky. (2 localities) . . . . .	60	52	86.6
Nashville, Davidson Co., Tenn. . . . .	39	36	92.3

The Museum of Zoology has 44 specimens of *A. plicata* (Conrad) from the Mulberry Fork of the Black Warrior River—Alabama River system—and 69 from the main Black Warrior at Tuscaloosa, Tuscaloosa County, Alabama. The banded individuals of the upper locality amount to 18.1 per cent; of the lower, 75.3 per cent. Species of the Anculosae of the Coosa River have been unsatisfactory for this study since, for the most part, they are localized. The river itself, until disturbed by man, was unlike almost all other streams of equal length and volume in that it had virtually no slack-water stage until within a few miles of its mouth. *A. ampla* Anthony of the Cahaba River has a comparatively short range, and the percentage of banded individuals at one end of that range is about the same as at the other. The same thing appears to be true of *A. taeniata* Conrad, which occurs in a lower section of the stream.

#### GONIOBASIS

The contrast sometimes obtaining between banding in large-stream pleurocerids and that of inhabitants of tributary small streams and springs is illustrated in sharp lines by the *Gonio-*

*basis semicarinata-indianensis* group of the Big Blue River of southern Indiana:

	Number of Specimens	Banded Specimens	Per Cent of Banded Specimens
Big Blue River			
1 mile E. of Beck's Mill, Washington Co. ....	15	0	0.0
5 miles above Fredericksburg, Washington Co. ....	85	2	2.3
Fredericksburg, Washington Co. . .	93	11	11.8
Milltown, Crawford Co. ....	112	15	13.4
5 miles E. of Wyandotte Cave, Crawford Co. ....	23	4	17.3
Wyandotte Cave, Crawford Co. . .	94	14	14.9
Tributaries			
Spring Branch, Washington Co. . .	232	0	0.0
Mill Creek, Washington Co. ....	85	0	0.0
Marengo Creek, Marengo, Crawford Co. ....	100	0	0.0
Marengo Creek, Milltown, Crawford Co. ....	100	0	0.0
Sharp's Spring, Wyandotte Cave, Crawford Co. ....	42	0	0.0

*G. livescens* (Menke) in the Sandusky River of northern Ohio shows an increase of more than 50 per cent in banding as between a headwaters colony and one about forty miles farther downstream. But between two localities of the Grand River of Michigan that are more than a hundred miles apart there is very slight difference in this respect. The Maumee River has its beginning in the junction of two fairly large streams. *G. livescens* taken in one of these, the Saint Joseph's River, is without bands. In the Maumee River itself, the showing is:

	Number of Specimens	Banded Specimens	Per Cent of Banded Specimens
Ft. Wayne, Allen Co., Ind. ....	91	17	18.7
Woodburn, Allen Co., Ind. ....	114	12	10.5
Maumee, Lucas Co., Ohio ....	76	48	63.1

Herbert H. Smith noted that 18 out of 173 specimens of *G. hydeii* (Conrad) from a small stream tributary to about the middle part of the Black Warrior River of Alabama were with bands. This is slightly more than 10 per cent of the whole. In 129 examples of the species from one of the two main forks of the river, farther upstream than the creek, the percentage of banded shells was 68.3. Shoals Creek is a small stream of southern Tennessee and northern Alabama. The characteristic *Goniobasis* is *interveniens* Lea. From a locality within eight miles of the source of the creek, 110 shells were taken which were all without bands. In 40 shells from a point four miles above the mouth of the creek, 25 were found to be banded. Findings similar to these have been made in *G. caelatura* (Conrad) and *G. carinocostata* (Lea) of the Coosa River basin.

Certain diversities in banding appear to be more conspicuous or more widespread in *Goniobasis* than in other genera of Pleuroceridae. One of these variants can be illustrated by *G. carinifera* (Lamarek) and *G. potosiensis* (Lea). *G. carinifera* is a common species of springs, brooks, and creeks of the Alabama River basin, and occasionally occurs in streams that are classified as rivers. Throughout northwestern Georgia the shell is without bands. In central and eastern Alabama banding is rather common to the species. *G. potosiensis* occupies a fairly restricted area of the Ozark region of Missouri. No specimen of several hundred examined has been found to be banded, yet the character is more or less common in *G. plebeius* (Anthony), to which *potosiensis* is very closely related if it is not actually a depauperate form of it.

An inhibition against the secretion of banding pigment which involves all members of a species of a locality does not always, it has been found, involve other species associated with it. As an example, we may take the case of the three goniobases of Campbell's Creek, near Clio, Barbour County, Alabama:

	Number of Shells	Banded Shells	Unbanded Shells
<i>G. curvicostata</i> .....	252	0	252
<i>G. mutabilis</i> .....	211	164	47
<i>G. clenchi</i> .....	11	0	11



The same kind of contrast is exhibited between genera. For instance, 85.5 per cent of the *Pleurocera* of Little River, Tennessee (see table, p. 3), is banded, whereas only 4.3 per cent of the *Anculosa* which occurs with it is banded.

Another variant is pigmentation penetration, if it can be called that. Baily, Pearl, and Winsor (1933) found that the bands of *G. virginica* (Gmelin) of Gunpowder River, Maryland, were confined to the periostracal layer. Several instances of this limitation of color secretion have been observed in the course of these studies. Shells so affected, as in the case cited, may be general to a stream, and the same species thus restricted may not be circumscribed in the same way elsewhere. Again, the limitation may apply to individuals. In the case of *G. capillaris* (Lea) of the middle part of the Coosa River, the bands are in the porcelaneous substance, but not in the periostracum. Associated species are banded after the common or normal habit. So also are specimens of *capillaris* from the Coosa tributary, Choccolocco Creek.

Hypersecretion wherein the banding pigment is diffused throughout the whole of a shell, giving the mollusk a dark brown, a purple, or a black appearance, occurs as an individual variation among colonies of goniobases. It is more common to some streams than to others, and in the Cahaba River of Alabama it is commoner to some species than to others. Not infrequently, bands of a darker hue may be seen in these melanistic specimens when the shells are held to the light. A pigmentation of the kind of a scope involving all shells of an area is known in a few cases. *G. semicarinata* (Say) of Ohio and Indiana streams is usually light brown in ground color, but in the bluegrass region of Kentucky virtually all shells of the species are very dark brown to dull black. *G. livescens* (Menke) of the western end of Lake Erie is commonly of a light straw color, of the eastern end decidedly darker. A like variation occurs in the species in the streams of Michigan, and shells from the northern part of the state can be recognized, usually, by a peculiarly light to dark bluish hue. The Museum of Zoology has specimens of *livescens* from forty-six different

localities of the Huron River basin of southern Michigan. Shells of all the upper creeks and brooks are dark. Most of the shells of the upper part of the river are also dark. In the lakes of the basin the species shows a marked tendency toward a light brown color. Shells of the middle part of the river are dark to light, and shells from one or two creeks of the section are lighter of hue near the mouths of the streams than they are in the upper parts. Specimens from the river at Flat Rock, which is within ten miles of the discharge, are light colored.

#### DISCUSSION

Pleurocerids of downstream colonies of ten streams or stream systems have a greater number of banded individuals than upstream colonies.

Pleurocerids of main-stream colonies of six rivers have more banded individuals than colonies of tributaries. The entire absence of banding, while common in colonies of small streams, is rare in river colonies.

In one instance, a species occupying a river is banded, whereas the same species in an artificial lake of the same drainage basin is not banded.

In several instances, no definite or significant difference in banding as regards position in stream is observable.

Differences in percentages of banded individuals of different species occupying the same locality have been noted.

As regards general pigmentation, that is, the dark coloration of periostracum and crystalline substance alike, differences occur as between species, as between parts of a river system, as between parts of a lake, and as between broad areas.

Bands, rays, and zonal demarcations are found from time to time in fossil mollusca and brachiopoda. D. K. Greger (1917) has brought together twenty-eight references to such preservations while reciting an example of his own discovery. Instances are known from Middle Devonian limestones of Alpena, Michigan. Bands occur in recent families and genera of Gastropoda whose range in habitat is from below the tidal levels of the ocean to the heights of mountains. This secretion

of pigment, widespread as it is in time and space, is to be understood, therefore, as a basic characteristic or endowment of the class. Under circumstances, the hereditary factor is recessive. The part that environment plays in conserving the character or in eliminating it is not clear, yet it does seem clear from the findings of this study that some environmental influence governs in the matter.

The phenomenon of pigmentation in aquatic mollusks has been studied by a few authors, some of whom have ventured to assign causes for it. Locard (1894), for example, found that shells in the Paris mains had undergone a marked decrease in coloration as compared with shells living under more natural conditions. He explained the decrease in pigmentation as due to the absence of light. After an examination of the epidermal color of naiads of the upper Ohio drainage and of corresponding species of Lake Erie, Grier (1920) came to three conclusions, namely, that "each drainage leaves its own imprint" in the "form of an associated or peculiar hue of epidermal color," that "the epidermis of most species shows clearly defined sex-correlative coloration," and that "a decided change of epidermal color is observed going downstream from the headwaters to the mouth." *Thaïas lapillus* of the Mount Desert section of Maine was found by Colton (1916) to be lightest in color where the shells occupied the least protected spots and darkest in the most sheltered localities. Baily, Pearl, and Winsor (1933) carried through an intensive study of two species of the Pleuroceridae of a stream of eastern Maryland. From their tables, it is plain that in the case of both forms the secretion of bands increased in a downstream direction. As regards *Goniobasis virginica* (Say) they were inclined to believe that an alkaline condition of the water inhibits the formation of bands, but in *Anculosa* [*Nitocris*] *carinata* (Brugière) they considered the bands "the expression of some genetic factor or factors, and that the populations at the different stations are differentiated in this respect." H. B. Moore (1936) has reported on experiments carried out with *T. lapillus*. Banded mollusks that were feeding on *Mytilus*

were transferred to localities having no *Mytilus*. As these shells continued their growth pigmentation was decidedly reduced. A retransfer to *Mytilus* beds was followed by a resumption of the normal pigmentation.

Pigment secretion in gastropods proceeds from the mantle edge. It is conceivable (1) that under certain environmental conditions the glands are inhibited from carrying on their function; (2) that the food necessary for the production of pigment is sometimes absent; (3) that individuals, races, and species vary in the matter of the activity of pigmentation glands.

## REFERENCES

- BAILY, J. H., R. PEARL, AND C. P. WINSOR  
 1932-33 Variations in *Goniobasis virginica* and *Anculosa carinata* under Natural Conditions. *Biologia Generalis*, 8: 607-30, Pls. 14-15; 9, 1 hälfte: 301-36, Pls. 7-9; 2 hälfte, 47-69.
- COLTON, H. S.  
 1916 On Some Varieties of *Thaias lapillus* in the Mount Desert Section. *Proc. Acad. Nat. Sci. Phila.*, 68: 440-54.
- GREGER, D. K.  
 1917 A Color-Marked *Euconospira* from the Pennsylvanian of Missouri, and a List of References to Coloration in Fossil Shells. *Nautilus*, 30: 114-17, Pl. 3.
- GRIER, N. M.  
 1920 Variation in Epidermal Color of Certain Species of *Najades* Inhabiting the Upper Ohio Drainage and Their Corresponding Ones in Lake Erie. *Amer. Midland Nat.*, 6: 247-85.
- LOCARD, A.  
 1894 Mollusca of the Paris Mains. [Quoted by *Nautilus*, 8: 59-69, without name and date of original article.]
- MOORE, H. B.  
 1936 The Biology of *Purpura lapillus*. I, Shell Variation in Relation to Environment. *Journ. Marine Biol. Assn. of United Kingdom*, 21: 61-89.