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STUDIES OF THE GASTROPOD FAMILY  
PLEUROCERIDAE—VI

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THREE fairly well-defined forms of the genus *Pleurocera* occur in the Alabama River system headwater streams in Georgia to the vicinity of Selma, Dallas County, Alabama. For the first of these, the name *attenuatum* (Lea) may be used because it is descriptive and the species is assigned to the drainage basin under consideration. It may, however, not have priority in the nomenclature. A second form, *showalterii* (Lea), is transitional in characters and in distribution between *attenuatum* and the third form, *prasinatum* (Conrad). The principal differences among these shells are differences of relative obesity. These are measurable. In this study the totals of the diameters of the specimens of each colony have been divided by the totals of the heights of the last two whorls, the use of the full heights being impracticable because the apices of nearly all shells are eroded. The indexes of obesity thus provided serve admirably for purposes of comparison. The following table covers *Pleurocera* of the Alabama River system with the exception of the Cahaba, Black Warrior, and Tombigbee rivers.

*P. attenuatum* of the Conasauga River shows a progressive increase in obesity from the uppermost station to the mouth.

	Number of Shells	Index in Per Cent
Conasauga River, Georgia:		
Upper Kings's Bridge, Murray Co. ....	38	73.8
Treadwell, Whitfield Co. ....	24	73.9
Tilton, Whitfield Co. ....	51	74.5
Near mouth, Murray Co. ....	21	78.1
Coahulla Cr., tributary of Conasauga River . . . . .	32	77.2
Oostanaula River, Georgia:		
Calhoun, Gordon Co. ....	50	82.8
Rome, Floyd Co. ....	65	81.1
Coosa River:		
Rome to Poole's Ferry, Floyd Co., Georgia . . . . .	33	79.9
Cedar Bluff to Slackland, Cherokee Co., Alabama	21	80.0
Gilbert's Ferry, to Riddle's Bend, Alabama . . . . .	62	84.9
Ten-Island Shoals area, St. Clair Co., Alabama . .	45	82.5
Clarence Shoals to Three-Island Shoals, Alabama	63	83.2
Ft. William Shoals to Weduska Shoals, Alabama	95	84.0
Chilton Co., Alabama . . . . .	68	85.1
Wetumpka, Elmore Co., Alabama . . . . .	44	84.1
Chattooga River:		
Trion, Chattooga Co., Georgia . . . . .	40	75.6
Cedar Bluff, Cherokee Co., Alabama . . . . .	41	80.1
Tributaries of Chattooga River:		
Duck Cr., Chattooga Co., Georgia . . . . .	55	72.7
Spring Cr., Chattooga Co., Georgia . . . . .	37	74.1
Little R., Cherokee Co., Alabama . . . . .	35	74.2
Tributaries of Coosa River in Alabama:		
Terrapin Cr., Cherokee Co. . . . .	54	76.9
Big Will's Cr., Etowah Co. . . . .	53	75.8
Sulphur Spring, Calhoun Co. . . . .	13	69.8
Tallaseehatchee Cr., Talladega Co. . . . .	72	75.6
Choccolocco Cr., Talladega Co. . . . .	16	81.1
Yellowleaf Cr., Shelby Co. . . . .	45	77.7
Alabama River, Alabama:		
Selma, Dallas Co. . . . .	58	83.0

The same increase is shown in the Chattooga River shells, and those of the Chattooga tributaries have a lower index than have pleuroceras in the main stream. In contrast to this is the relatively high index of specimens from Coahulla Creek of the Conasauga River. *P. showalterii* appears first in the Oostanaula River at Calhoun, Georgia, and continues downstream to the vicinity of Cedar Bluff, Cherokee County, Alabama. The species, if it can be called that, is of greater relative diameter than *attenuatum*, but obesity in the species is not correlated with position in stream in the way, for example, that *attenuatum* of the Conasauga and Chattooga rivers is.

*P. prasinatum* is marked by a greater proportional diameter than *attenuatum* or *showalterii*. It is the common *Pleurocera* of the middle and lower Coosa River and of the Alabama River. It seldom penetrates creeks for more than a short distance above their mouths. The shells of greatest relative obesity are not those farthest downstream, but occur at about the end of the middle part of the Coosa River, a section wherein species of *Goniobasis* of upstream characters are giving way to species more common to downstream habitats. *Pleurocera* of the Coosa River creeks, when above the river influence at the mouths, reverts to *attenuatum*. This is true even in Choccolocco Creek wherein the riverine molluscan fauna penetrates for several miles. It may be of significance that the shells of lowest relative diameter which have been seen are inhabitants of a spring.

There exists a fourth form of *Pleurocera* in the Alabama system, *foremanii* (Lea). It has not been included in the table because, while it appears distinct in the Coosa River, it is merely an individual variant in the neighboring Cahaba River.

About forty species of *Pleurocera* have been assigned exclusively or in part to the Tennessee River system. In addition there are certain other species whose type localities are given simply as "Tennessee" or "Alabama" and which obviously are of the Tennessee River fauna. The first species that appears in the Powell, Clinch, and Holston rivers, head

streams of the Tennessee, is *unciale* (Haldeman). In shell characters it is fairly uniform in each of the three rivers in the early sections of its range. The sharp definiteness of these characters is lost in the transition zones, and later in the course of the streams the species disappears. The findings for *unciale* are:

	Number of Shells	Index in Per Cent
Powell River:		
N. Fork, Big Stone Gap, Wise Co., Virginia . . . .	60	75.4
S. of Cumberland Gap, Claiborne Co., Tennessee	38	83.9
Clinch River, Virginia:		
Tazewell, Tazewell Co. . . . .	47	75.6
St. Paul, Wise Co. . . . .	48	78.1
Fairview, Lee Co. . . . .	34	75.1
South Fork, Holston River:		
Damascus, Washington Co., Virginia . . . . .	27	76.0
Bluff City, Sullivan Co., Tennessee . . . . .	35	81.4

The locality in Powell River south of Cumberland Gap is in a transition zone, as Adams (1915) found it to be also in the case of *Io*. Here and in the other two head rivers occurs *P. gradatum* (Anthony). Measurements have been taken of seven lots, numbering from fifteen to forty-nine individuals. There is indication of an increase in relative diameter in a downstream direction. Yet since the shell seems to be a transitional phase and is, at times, of greater width than the height of the last two whorls, it leaves the impression of being merely a variant of less importance taxonomically than an ecological race.

*P. canaliculatum undulatum* (Say) occurs in the Clinch and Holston rivers, but not in the Powell River. The results of measurements are given in the table at the top of page 5.

Possibly some of the shells from Rogersville should be placed with the wide-diameter *gradatum*, also occurring there, rather than with *undulatum*. The *Io* of the same locality is spoken of by Adams as "remarkably variable."

	Number of Shells	Index in Per Cent
Clinch River, Tennessee:		
Anderson Co. ....	34	86.3
Roane Co. ....	77	88.2
Holston River, Tennessee:		
Rogersville, Hawkins Co. ....	30	87.8
N. Morristown, Hamblen Co. ....	38	83.0
Strawberry Plains, Jefferson Co. ....	34	86.7
Armstrong's Mill, Knox Co. ....	45	86.0

The following table is of *undulatum* for the Tennessee River proper.

	Number of Shells	Index in Per Cent
Knoxville, Knox Co., Tennessee .....	50	87.8
Loudon, Loudon Co., Tennessee .....	39	87.6
Washington Ferry, Meigs Co., Tennessee .....	20	83.5
Bridgeport, Jackson Co., Alabama .....	22	79.2
Muscle Shoals, Lauderdale Co., Alabama .....	43	88.4

There is, it will be seen, small difference among the shells of the Clinch River of a previous table and those from Knoxville, Loudon, and Muscle Shoals of this last list. The uniformity is broken by the indexes of the specimens collected at Washington Ferry and Bridgeport, possibly due to admixture or hybridization with an elongate form, *excuratum* Conrad, not easily to be differentiated at these places from *undulatum*. A similar confusion in Cumberland River will be pointed out later. Curiously, the obscuration between these two shells does not occur at Muscle Shoals. Here, *excuratum* of Tennessee River has an index of 85.2, nearly exactly that of the subspecies living in Cumberland River, and of 80.3 in the Cypress Creek entering the river near the foot of the shoals.

Three forms or subspecies of *P. canaliculatum* occur in the Cumberland River of Kentucky and Tennessee. The one at

the highest station of the river is *filum* (Lea). It is succeeded downstream by *undulatum* (Say), and this shell is finally replaced by *excuratum* (Conrad). It is not difficult to separate the *filum* and *undulatum* of the first transition zone, which is in Russell County, Kentucky. It has proved impossible to separate *undulatum* from *excuratum* with certainty in the vicinity of Nashville, Tennessee, so much do the characters of the two forms merge. *Pleurocera* of the tributary Caney Fork is a *filum-undulatum* mixture at the mouth, but farther up the same stream *filum* occurs alone. Obey River, a higher branch of the Cumberland, contains a slender phase of *undulatum* that, in spite of appearances, has virtually the same proportions as more typical *undulatum* of Little River, a downstream tributary in Trigg County, Kentucky. There is a progressive increase in relative diameter of *filum* of the upper Cumberland River. With the incursion of *undulatum* in the river, the index of obesity falls and then near Nashville rises again. It drops once more in the lower river where *excuratum* is a "pure" race. Specimens from the three tributaries are all of a lower index than are the main river shells except far upstream where *filum* first appears. The shells measured numbered 375.

Of four separate lots of Ohio River *Pleurocera*, collected from Coraopolis, Pennsylvania, to Elizabethtown, Illinois, the shells of highest relative diameter are from the vicinity of Owensboro, Kentucky, the third station in a downstream direction. Material from four localities of the Wabash River of Indiana has low indexes of obesity at the highest and the lowest stations. There is a likeness between these two places to the extent that the water is fast flowing and, throughout most of the year, shallow. Gravelly bars are the feature of one habitat and rock reefs of the other.

*Pleurocera* of Duck River of central Tennessee can be separated as *filum* and *undulatum*, *filum* occurring in most of the river and *undulatum* supplanting it in a short stretch near the mouth of the stream. Reading downstream, the indexes of obesity are:

	Number of Shells	Index in Per Cent
Shelbyville, Bedford Co. ....	22	80.7
Wilhoite, Marshall Co. ....	46	84.1
12 miles N. of Lewisburg, Marshall Co. ....	37	87.0
Columbia, Maury Co. ....	30	88.5
Centerville, Hickman Co. ....	38	93.6
S. of Waverly, Humphries Co. ....	22	92.4
Tributaries:		
Buffalo R., Beardstown, Perry Co. ....	53	83.0
Buffalo R., 8 miles N. of Lobelville, Perry Co. ..	38	91.0
Cane Cr., near Beardstown ....	39	78.9
Hurricane Cr., Humphries Co. ....	14	89.3

The relative obesity of the shells of the main river undergoes an increase progressively until the last station is reached where there is a slight reversion. The downstream colony of Buffalo River is markedly of higher relative diameter than the upstream colony. The collection in Cane Creek was taken within a quarter mile of one in Buffalo River, and yet contrasts with it decidedly. The one from Hurricane Creek is from a locality within a mile or two of the discharge into Duck River. In form the shells correspond to the *undulatum* of the lowermost river reaches rather than to the upstream *filum*.

The Sequatchie River of Tennessee runs in the trough between Walden Ridge on the east and the steeper escarpment of the Cumberland Plateau on the west. There are few marked changes in the character of the stream from creeklike headwaters to deeper areas near the mouth where conditions appear to correspond with those of the Tennessee River into which the Sequatchie discharges. The variations of the *Pleurocera* of the stream, leaving out members of the section *Strephobasis*, are found noted in the table at the top of page 8.

The alterations in relative diameter are seen to be progressive in the river. The tributary streams contain shells that do not correspond in their proportions with those of the main river near-by, but instead with upstream forms.

	Number of Shells	Index in Per Cent
Pikeville, Bledsoe Co. ....	30	74.3
Dunlap, Sequatchie Co. ....	42	75.7
8 miles below Dunlap, Sequatchie Co. ....	50	77.1
E. of Jasper, Marion Co. ....	42	86.1
Tributaries:		
Little Sequatchie R., Sequatchie Co. ....	57	77.9
Spring Branch, Jasper, Marion Co. ....	16	74.5

So far, the information that has been gathered suggests or points to a natural law, namely, that *Pleurocera* increases in relative diameter in a downstream direction. As a "wet blanket" upon any such conclusion, these figures for shells of the Green River of Kentucky are to be taken into account.

	Number of Shells	Index in Per Cent
Rio, Hart Co. ....	62	93.8
Mammoth Cave, Edmonson Co. ....	42	91.2
Rochester, Butler Co. ....	51	89.6
Calhoun, McLean Co. ....	55	88.4
6 miles W. of Calhoun, McLean Co. ....	24	89.6
Sebree, Webster Co. ....	17	88.0

To all intents and purposes, this table reverses the findings for Sequatchie River wherein *Pleurocera* experiences a progressive increase in obesity in the downstream direction.

#### DISCUSSION

Tryon (1873) preserves ninety-seven species of *Pleurocera* from about one hundred and fifty that had been described up to 1865. He himself expresses doubt as to the specific value of some of the mollusks that he admits to the list. Of the ninety-seven, several are juveniles, and in this genus juveniles are so nearly alike that they can often be shifted about in the nomenclature at pleasure. Four have proved to belong to *Goniobasis*. There are probably others that are similarly out of place—



those accredited to North and South Carolina, for example. Six are gerontic or deformed, their descriptions defining individuals, not species. In addition there are ten or twelve that the section *Strephobasis* embraces. This section is reducible to three species and one subspecies (Goodrich, 1928).

After this, there remain a great number of species that are not so easily disposed of. On the basis of Tryon's monograph, it would seem possible to set up at least four natural groups from the residue under the names of *acuta* (Rafinesque), *canaliculatum* (Say), *pyrenellum* (Conrad), and *unciale* (Halde- man). Still, if they are natural groups, they are not invariably demarked one from another. Brooks (1931) has pointed out that *acuta* and *canaliculatum* merge into each other in headwaters of the Ohio River. The phenomenon has been observed by the writer in the Great and Little Miami rivers of Ohio and the Wabash River of Indiana. A member of the *pyrenellum* and one of the *canaliculatum* group do the same thing in North Alabama. In the transition zones of the upper Tennessee River are confusing blendings of the characters of *unciale* and *canaliculatum undulatum*. Now while such mergings or hybridizations do occur in certain places, the perplexing fact is that there are other localities, containing mixtures of groups, in which the distinctive group characters are retained among the individuals.

An examination of original descriptions of species of *Pleurocera* reveals the repeated statement that the shells are carinate, elongate, yellow-brown to blackish; that the apertures are rhomboidal or awl-shaped, that the columella is twisted, the outer lip sinuous and acute, and that folds or striae occur on the base. The describers, indeed, have had very little to go upon except characters that are widespread in the genus. Small help in the difficulty has come from studies of the internal anatomy although painstaking work upon it has been carried out by Van Cleave (1932) and Magruder (1935). Evidence is lacking that the so-called species of *Pleurocera* are distinct from one another in the matter of soft parts, and this is to say that whatever singularity an individual or species or

group may possess has been made manifest to the eye, as yet, only in the exo-skeleton.

A relationship between habitat and the proportion of altitude to diameter of shells of *Pleurocera* has been demonstrated. The relationship is not simple and must remain obscure until the underlying reasons for it have been discovered. In the Sequatchie River the relative obesity of the mollusks increases progressively from headwaters to mouth of stream. There are partial gradients of the kind in the Alabama River system, the Tennessee system, and the Cumberland, Duck, and Ohio rivers. In the case of the Green River, the relative obesity increases in an upstream direction, precisely opposite to the direction in the Sequatchie. Findings point to environmental influences or controls. These are localized, and not uniform in effect.

From the taxonomic standpoint, the indexes of obesity make out a case for close resemblances among the shells of *Pleurocera* of a given stream rather than for specific differences the describing naturalists thought they beheld. To a certain degree the indexes bring to light resemblances in shells of different river systems. To illustrate: 134 specimens of the Conasauga River, Upper King's Bridge to mouth, have a relative diameter of 75.5 per cent; 129 of the upper Clinch River, one of 76.6 per cent; 112 shells from the lower Coosa River have a relative diameter of 84.6 per cent; 111 of the lower Clinch River, one of 87.6 per cent. In short, there is a similarity in the proportions of shells of two river systems, first as between head streams and again as between lower sections. A detailed study of frequencies made the facts equally clear. Yet in another character there is this difference: The carinae of young Conasauga River *Pleurocera* are retained to the adult stage and usually become obsolete in the mature Coosa River shells; they are eliminated early in shells of the upper Clinch River and retained to maturity in individuals of the lower Clinch.

In each of the tables of the early part of this paper, the difference between the averaged index of shells of any one locality and that of the locality nearest to it is small and, taken by

itself, is without significance. Nowhere is there any very wide leap in the figures. Whether the figures are seen to proceed regularly or irregularly, they proceed by steps that do not suggest that one species has dropped out and another has entered. In this connection attention is directed to the approximation in indexes of shells of headwaters with indexes of shells of tributaries that may be at a distance away. *Pleuroceras* of the Conasauga and upper Chattooga rivers have virtually the same indexes of shells of Coosa River creeks, with the single exception of those of Choccolocco Creek. This stream is penetrated more deeply than usual by a river fauna. Shells of the small Sequatchie tributaries resemble in this matter the specimens from smaller parts of the river. Mollusks of the upper part of the Duck River have their counterpart in those of an upper part of the tributary Buffalo River. The kinship of headwaters forms with forms of distant tributaries is not direct, but derives through the intervening river forms. To believe that one form represents a relict colony of the other seems absurd in view of the repetition of the phenomenon observed.

#### SUMMARY

The relative obesity of shells of *Pleurocera* of several rivers has been found to increase in a downstream direction more or less regularly. In the case of shells of one river the increase is in the opposite direction.

Shells of headwaters of a river and those of the river's tributaries are alike in having ordinarily a low index of obesity. In one instance where a river has rapids near its mouth which resemble physical conditions far upstream, the shells of the two extreme localities have lower indexes of obesity than have those on the intervening reaches of the river.

Variations in relative obesity appear to represent environmental responses rather than genetic differences.

A revision of *Pleurocera* that was published in 1873 (Tryon) recognized the existence of ninety-seven species. Upon the basis of the present studies a large number of these species are

reducible to few species. This is to say that doubt is raised as to whether the word "species" is actually applicable to more than a small number of the described forms.

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