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THE NAIADES (FRESH-WATER MUSSELS) OF THE CAHABA RIVER IN NORTHERN ALABAMA

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Introduction

No thorough study of the mussel fauna of the Cahaba River has ever been made, although James Lewis, in his faunal lists of 1876 and 1877, catalogued some of the earlier collections available for reference. The present report is based upon the collections from two expeditions of which I was a member. The first, undertaken in 1933 with Mr. W. J. Clench of the Museum of Comparative Zoology, yielded a good series of mussels from the lower reaches of the river. Nine stations, which are indicated by small triangles on Map 1, were established. The second expedition, with Mr. Calvin Goodrich in 1935, added greatly to collections from the headwaters. At this time, also, a more detailed survey was made of the ecological conditions at Lily Shoals in Bibb County. The twenty-five stations established during this expedition are designated on Map 1 by small circles.

The Cahaba River is one of the main tributaries of the Alabama River. It flows, for about two hundred miles, through Jefferson, Shelby, Bibb, Perry, and Dallas counties. According to government reports, the navigable river, which lies in the coastal plain, is between Centerville and the Alabama River junction and is approximately one hundred miles in extent.

MAILED DEC 13 1938 Above Centerville, the drainage is divided geologically into two major zones: the plateau region and the valley region. Those tributaries entering the Cahaba from the east, including the Upper Little Cahaba, the Lower Little Cahaba, and Buck Creek, flow through the valley region; the main stream and the remaining tributaries are confined to the plateau region.

Our recent work in the Cahaba River has shown it to be unusually productive conchologically. In view, however, of the changes which have taken place in many of the streams, there are at present several potential dangers to the Cahaba fauna. Chief among these are (1) the possibility of pollution by acid-containing mine wastes from the Cahaba coal field area; (2) a likelihood of heavy concentrations of industrial wastes and sewage entering the river from Birmingham, situated close to the headwaters; and (3) a possible disturbance of the natural conditions now existing by the construction of dams in the

TABLE I

STATIONS AT WHICH COLLECTIONS WERE MADE IN THE CAHABA RIVER

CAHABA RIVER

Near Roper, Jefferson Co.
Henryellen, Jefferson Co.
Lovick, Jefferson Co.
Grant's Mill, Jefferson Co.
East of Merkel, Jefferson Co.
Acton, Jefferson Co.
Nunley Ford, Shelby Co.
Anita, Shelby Co.
*Lily Shoals, Bibb Co.
10 miles above Centerville, Bibb Co.
*7 miles above Centerville, Bibb Co.

1 mile above Centerville, Bibb Co.*Centerville, Bibb Co.7 miles below Centerville, Bibb Co.

*2 miles east of Harrisburg, Bibb Co.

8 miles north of Sprott, Perry Co. *5 miles northeast of Marion, Perry Co.

West of Sprott, Perry Co.

*½ mile west of Felix, Dallas Co.

*10 miles west of Selma, Dallas Co.

*Near Beloit, Dallas Co.

TRIBUTARIES

Little Cahaba River:

*2 miles north of Leeds, Jefferson Co.

1 mile south of Leeds, Jefferson Co.

4 miles south of Leeds, Jefferson Co.

6 miles south of Leeds, Jefferson Co.

Buck Creek, at Helena, Shelby Co.

Beaverdam Creek, 5 miles south of Helena, Shelby Co.

headwaters as well as in the lower section of the river. In view of these possible changes, studies of the fauna under natural conditions are highly desirable.

In Table I the localities from which mussels were taken are listed in order, beginning at the headwaters and progressing toward the mouth of the river. An asterisk indicates that the locality was visited in 1933.

FAUNAL STUDIES

The naiad fauna of the Cahaba River, as represented in our collections, consists of forty-eight species, comprising twenty-three genera. These are enumerated and discussed only in a general way. Because of the need for detailed study of many groups, it is considered advisable merely to mention the problems involved without theorizing as to their solution.

1. Fusconaia rubida (Lea)

This species is abundant in the Cahaba. It is confined to the main stream (Table II), and ranges from Nunley Ford, Shelby County, to the mouth of the river. Specimens from this drainage basin clearly show the species to be a southern representative of the Fusconaia undata group. A comparison of this species with F. undata from the Ohio River drainage basin shows such a degree of similarity as to make the two almost indistinguishable. F. undata is not represented in the Tennessee. The nearest related forms in the Tennessee are members of the F. cuneolus edgariana group. Some of the earlier collections made by H. H. Smith and sent to Bryant Walker contain specimens that were actually called F. undata. probable that later studies may show rubida to be at best a southern form of undata, and that it entered Alabama from the southwest at the time of the Mississippi embayment.

2. Fusconaia cerina (Conrad)

A situation parallel to that of F. rubida and undata occurs in the case of F. cerina which appears to be the southern representative of the F. flava group and probably entered the

Alabama drainage basin from the southwest, since it is not represented in the lower Tennessee drainage basin. In the Cahaba it is a relatively rare species (Table II).

3. Fusconaia ebenus (Lea)

Characteristically, this species is confined entirely to the lower reaches of the river (Table II). Although it does occur in the lower Tennessee, as far upstream as Savannah, Hardin County, Tennessee, no records are available to show that it has been found above this point. As there is no evidence that it entered the Cahaba from the north, it must have come by way of the Mississippi embayment. Its abundance in Arkansas and Mississippi gives evidence for this contention.

4. Amblema perplicata (Conrad)

This was one of the most common species in the headwaters of the Cahaba. Its distribution as shown in Table II is an unusually characteristic one. Specimens from the various stations show considerable variation in shape, but the definite quadrate outline which results from the development of the low wing is not obscured. The relation of perplicata to costata in the Tennessee drainage basin is somewhat problematical and needs careful study.

5. Megalonaias gigantea (Barnes)

This species is rare in the Cahaba and was found only at one station in the lower region of the river. It has been reported from the lower Tennessee and has been found upstream as far as Muscle Shoals, but is entirely absent in the upper Tennessee drainage. This is, unquestionably, a large-river species.

6. Quadrula pustulosa (Lea)

This is a common species in the Cahaba and is confined to medium-sized-river and large-river conditions (Table II).

Ortmann (1923: 76) has stated that forms from the Coosa and Cahaba designated as *Quadrula pustulosa pernodosa* should be known as *Q. asperatus* (Lea). In his diagnosis he called attention to the lack of the usual green color band on

TABLE II

SYNOPTIC TABLE SHOWING DISTRIBUTION OF NAIADES BY COLLECTING STATIONS IN THE CAHABA RIVER

				MAIN RIVER HEADWATERS TO MOUTH																							
			CRE	EKS				SM	ALL RI	VER		MEDIUM-SIZED RIVER				LARGE RIVER											
	2 miles north of Leeds	1 mile south of Leeds	4 miles south of Leeds	6 miles south of Leeds	Buck Creek, Helena	Beaverdam Creek, Helena	Near Roper	Henryellen	Lovick	Grants Mill	East of Merkel	Acton	Nunley Ford	Anita	Lily Shoals	10 miles above Centerville	7 miles above Centerville	1 mile above Centerville	At Centerville	7 miles below Centerville	2 miles east of Harrisburg	8 miles north of Sprott	5 miles northeast of Marion	West of Sprott	½ mile west of Felix	10 miles west of Selma	Near Beloit
Unioninae Fusconaia rubida Fusconaia cerina Fusconaia ebenus Amblema perplicata Megalonaias gigantea Quadrula pustulosa Quadrula vallata Quadrula aspera Quadrula rumphiana Quadrula rumphiana Quadrula metanevra Tritigonia verrucosa Pleurobema simulans Pleurobema rubellum Pleurobema instructum Pleurobema instructum Elliptio crassidens Elliptio arctatus Elliptio dilatatus Anodontinae					5 		1	30 1 15 2 1 137	20	40 	2 	10	5 31 33 3 3 10 10 6 1 1 62 41 1	23	103	15 17 17 21 6	26 1	1	1	7 	9 1 1 12 	18	6	2	1 	19	1
Lasmigona holstonia Lasmigona complanata Anodonta imbecillis Strophitus spillmanii Strophitus subvexus	2	33	2	20				2 5	2 1 6	 5	2		1		3 5					1		1					
Lampsilinae Ptychobranchus greeni Obliquaria reflexa Obovaria subrotunda Plagiola lineolata Leptodea fragilis Proptera purpurata Carunculina corvunculus Carunculina cromwelli Medionidus parvulus Medionidus acutissimus Micromya vanuxemensis Micromya vebulosa Micromya lienosa Micromya vibex Ligumia recta latissima Lampsilis clarkiana Lampsilis clarkiana Lampsilis anodontoides Lampsilis excavata Dysnomia metastriata Dysnomia othcaloogensis Truncilla donaciformis	4 1	1 5	1 2 9	1 17		1	1	5	3 3 3 3 18 31 2 14 24 35	7	4		23	20 1 2 22 5 4 3 2 111 23	9 1	1 2	2 1	1	1	1 2 40 1 3 1 7 8	1 18 18 18 18 18 18 18 18 18 18 18 18 18	4 53 7 1 2 8 3 20 8	10 80 1 3 1 2 2 10 60 1	3 31 1 	1 1 2 4 2	8 150 1 1 1 1 1	7 4

the disk of southern forms and to the supposedly different This color band is not present on the specimens in our collections, and it is my belief that color pattern in this species is not in itself a good specific characteristic. Specimens from the lower Tennessee River have patterns much like those found in the Coosa and the Cahaba. The Tennessee forms are not given a special taxonomic designation, and there is no good reason for assigning a special name to the Cahaba forms of this In the Ohio River drainage basin Q. pustulosa has a prominent green band which gradually disappears in specimens of drainages toward the south. Intergradation is more or less complete between specimens with bands in Kentucky and those with only the merest trace of bands in Alabama. know more about the significance of this variation, it is best to simply recognize this intergrading series as one species, Q. The marked similarity between specimens of this species in the Cahaba and Coosa rivers to specimens inhabitating the lower Tennessee River is believed to be good evidence that this species entered the Cahaba and Coosa from the Tennessee.

7. Quadrula cahabensis (Lea)

The specific status of this species is not clear. Its distribution is limited to the headwaters (Table II). Our collections clearly suggest that *cahabensis* is an ecological form of *pustulosa* in that it is merely a compressed headwater form of the latter. In a later paper statistical data will be presented to test the validity of this contention.

8. Quadrula vallata (Lea)

At present it is difficult to define the specific status of vallata. There appears to be a complete intergradation between forms of cahabensis and vallata. Consequently, this species is directly related to cahabensis and pustulosa. Either we may be forced to consider cahabensis and vallata as forms of pustulosa, or we may have to consider cahabensis (Lea, 1871) and vallata (Lea, 1868) as synonyms to be recognized as vallata (Lea). In distribution (Table II) this species is not common and may

occur in the headwaters along with *cahabensis*, as well as in the lower part of the river where *cahabensis* is not found.

9. Quadrula aspera (Lea)

This species is closely related to Quadrula quadrula of the Tennessee drainage basin and probably represents a southern race of that species. Its range in the Cahaba is similar to that of Q. pustulosa, with fewer specimens in the headwaters. Both Q. aspera (Lea, 1831) and Q. forsheyi (Lea, 1859) are reported from the Cahaba. These species so thoroughly intergrade that they are probably synonymous.

10. Quadrula rumphiana (Lea)

In the Cahaba this species was most common in mediumsized-river and large-river conditions (Table II). It is closely related to Q. aspera and also has evident relationships to Q. metanevra. Q. rumphiana is peculiar to this area. Its distribution is restricted to Alabama and Georgia.

11. Quadrula metanevra (Lea)

This species in the Cahaba is restricted to the region having large-river characteristics (Table II). It is of interest that the *metanevra* form from the Cahaba is identical with that of the Tennessee drainage. A local variant from *metanevra* in the Alabama drainage basin is Q. stapes, which has been recorded from the Coosa but never from the Cahaba.

12. Tritigonia verrucosa (Rafinesque)

This species has unusually wide distribution in the Cahaba. Generally, verrucosa is considered to be a large-river form, but here it is found more abundantly in small-river conditions (Table II). The forms of this species in the Cahaba are identical with those from the Tennessee drainage. However, the Cahaba specimens are unusual in that many have a purple nacre. It was particularly interesting to observe that a definite trend in nacreous coloration could be correlated with the distribution in the river (Table III).

Locality	Purple	\mathbf{White}	Mixed
At Lovick, Jefferson Co.*	20	14	0
Henryellen, Jefferson Co	7	7	1
Grant's Mill, Jefferson Co	0	3	3
Merkel, Jefferson Co	0	2	0
Acton, Jefferson Co	0	0	1
Nunley Ford, Shelby Co	· 4	6	0
Anita, Shelby Co	2	10	0
Lily Shoals, Bibb Co	9.	20	0
10 miles above Centerville, Bibb Co	2	4	0
7 miles above Centerville, Bibb Co	0	3	0
7 miles below Centerville, Bibb Co	1	2	0
8 miles above Sprott, Perry Co	. 0	7	0
mile west of Felix, Dallas Co	0	2	. 0
10 miles west of Selma, Dallas Co	0	7	-0
Near Beloit, Dallas Co	0	6	0

^{*} The stations are arranged in order from the headwaters toward the mouth of the river.

Colored nacre is more commonly found among specimens in the headwaters than among those inhabiting the lower regions of the river. This, of course, may be only a local characteristic.

The Alabama drainage has unquestionably produced more species of *Pleurobema* than any other. The Bryant Walker and Museum of Zoology collections contain some thirty-five species of *Pleurobema* which were collected in this river system. Of these approximately seventeen are credited to the Cahaba River. There are, no doubt, several species of this genus in the Cahaba, but the number listed is excessive. No careful attempt has been made to determine the systematic status of the species described for this area. However, a conservative list of those obtained by our expeditions is given.

13. Pleurobema simulans (Lea)

Members of this species are uniformly dark in color. They are clearly separable from the other species of this genus. Only

three specimens of *P. simulans* were collected. These were found at Lily Shoals, Bibb County. The following records were added from material made available at the Alabama Museum of Natural History. The collections show this species to live under small- and medium-sized-river conditions.

TABLE IV

CAHABA RIVER RECORDS OF PLEUROBEMA SIMULANS AVAILABLE IN THE

ALABAMA MUSEUM OF NATURAL HISTORY

Locality	Specimens
Cahaba River, near Henryellen, Jefferson Co	2
Cahaba River, near Helena, Shelby Co	5
Cahaba River, Lily Shoals, Bibb Co	68
Cahaba River, near Piper, Bibb Co	
Cahaba River, Pratt's Ferry, Bibb Co	
Buck Creek, near Helena, Shelby Co	5

14. Pleurobema nux (Lea)

Since specimens of *nux* occasionally approach *simulans* in appearance it is not always easy to separate the two. For the present, however, *nux* will be recognized because of its uniformly lighter color and more globose form. This species, although never abundant, is found throughout the entire course of the main river.

15. Pleurobema rubellum (Conrad)

Only one specimen, considered to be *rubellum*, was collected in 1933, at a station about one-half mile west of Felix, Dallas County. This form belongs to the *nux-simulans* complex.

16. Pleurobema decisum (Lea)

This is by far the most common species of *Pleurobema* in the Cahaba River. Specimens classified as *P. chattanoogense* and *P. interventum* are included in this category. Justification for this inclusion will be presented in a later paper on the taxonomy of this group. In the Cahaba, *P. decisum* ranges mainly through the central region of the main stream, occupying neither the extreme headwaters nor the lower reaches of the drainage (Table II).

17. Pleurobema instructum (Lea)

The center of distribution for this species is evidently the Cahaba River. Its specific characters appear to be good, although H. H. Smith¹ had difficulty separating some specimens of *instructum* from those designated as *interventum* by Bryant Walker. This species will be permitted to stand for the present, although a more careful study of the group may relegate *instructum* to other rank. Its distribution is similar to that given for *P. decisum* (Table II).

18. Pleurobema cordatum (Rafinesque) and varieties

This species has not previously been considered a part of the Cahaba fauna, and it is with some degree of hesitance that it is listed here. Three specimens, each taken at a different station in the river, have been classified as $P.\ cordatum$. These may well belong with $P.\ taitianum$ (Lea) and $P.\ tombigbeeanum$ Frierson, but a careful comparison of specimens in the Museum of Zoology collections has thrown considerable doubt on the systematic status of both taitianum and tombigbeeanum.

19. Elliptio crassidens (Lamarck)

In the Cahaba this species is confined mainly to large-river conditions. Its range is similar to that of Quadrula pustulosa, Fusconaia rubida, and Leptodea fragilis (Table II). E. crassidens is common in the Tennessee River in Alabama, and no differences have been found in specimens from the Tennessee and Cahaba drainage basins.

20. Elliptio arctatus (Conrad)

The distribution of *arctatus* in the Cahaba is very definite in that it is limited almost entirely to the headwaters, being confined to what may be called small-river conditions (Table II). Specimens are uniform in character, with but small variations in nacreous color, external texture, and general shape. This species represents a type peculiar to Alabama. It is not found in the Tennessee drainage basin, and there is no species closely related to it there.

1 Information taken from original labels in the Bryant Walker collection.

21. Elliptio dilatatus (Rafinesque)

Only one specimen, taken at Nunley Ford, Shelby County, was found in the Cahaba. It is much more common in the Coosa River, where a peculiar form referred to as "subgibbosus" occurs. It is difficult to define accurately just what the subgibbosus form represents, but probably it is a local form of dilatatus which has entered the Alabama drainage from the Tennessee. The scarcity of dilatatus in the Cahaba indicates that it is not an important representative of the fauna. In this respect it is like Pleurobema cordatum referred to above.

The scarcity of genera and species belonging to the Anodontinae in the Alabama drainage is striking. There are but five representatives of this major group, three of them clearly belonging to the Tennessee drainage and two being peculiar to the Alabama system.

22. Lasmigona holstonia (Lea)

This species is found in the tributaries of the Tennessee River, and also is in some of the creeks in the headwaters of the Cahaba (Table II) and Coosa rivers. Since *holstonia* is definitely restricted to creek environments, its entrance into the Alabama River drainage basin must have been brought about by the capture of small tributaries in the extreme headwaters of the Cahaba and Coosa rivers. That this capture must have taken place in geologically recent time is evident from the fact that no new forms of *holstonia* have developed in these streams.

23. Lasmigona complanata (Barnes)

In the Cahaba complanata is confined to medium-sized- and large-river conditions. It is by no means a common species here and is not found in the Tennessee River. Records of complanata from the Tombigbee and Pearl rivers in Mississippi indicate that it must have entered Alabama from the west.

24. Anodonta imbecillis Say

This species was found only in the headwaters, occurring most commonly at a station six miles below Leeds, where the stream was impounded (Table II). This clearly shows the ecological preference of this group. As there are no records to indicate that *imbecillis* is found in the Tennessee drainage basin in Alabama, it presumably entered the Alabama drainage from the southwest.

25. Strophitus spillmanii (Lea)

Only a single specimen of this species, taken at Lovick, was collected in the Cahaba, whereas twenty-four specimens of *subvexus* were obtained from the river at the same time. The well-developed pseudocardinals of *spillmanii* are characteristic of this species.

26. Strophitus subvexus (Conrad)

Conrad (1834: 341) described *subvexus* as an *Anodonta* and gave the Black Warrior River as the type locality. Our species from the Cahaba is in close agreement with his description and figure. A comparison of *subvexus* with specimens of *connasaugaensis* shows them to be identical.

Simpson (1914: 352) in discussing S. alabamensis writes:

I confess that this form and the *Margaritana connasaugaensis* and *M. gesnerii* Lea are quite puzzling. Unfortunately, I have been able to examine but little material belonging to the group, and I am not at all sure but what all three are forms of one and the same thing. . . .

Ortmann (1919: 206) in a discussion under *Strophitus* rugosus reports:

Records from the southern Atlantic and Gulf states are lacking, though Simpson cites Tyner, Tuscaloosa County, Alabama, and a number of allied forms, separated as species, are credited to Georgia, Alabama and Mississippi. I cannot judge of these; but I may mention, that specimens from the Alabama-drainage in the Carnegie Museum, partly collected by H. H. Smith, partly by myself, seem to differ, and to represent possibly two other species: S. connasaugaënsis (Lea) (= alabamensis Lea = gesneri Lea), and spillmanii (Lea). Both have the pseudocardinal teeth better developed than S. edentulus.

Since subvexus of Conrad is unquestionably the connasaugaensis of Lea, we should recognize Conrad's name, and include connasaugaensis, alabamensis, and gesneri as synonyms of subvexus. Ortmann (1923: 130) synonymized some of the above species under connasaugaensis, but he failed to consider subvexus of Conrad, which obviously had priority in this case. This species is confined to the headwaters in the Cahaba and definitely belongs to the group existing under small-river conditions (Table II).

27. Ptychobranchus greeni (Conrad)

Most of the specimens of this genus collected in the Cahaba in the past have been called *P. foremanianum* (Lea). Our collections permitted an examination of many specimens from this stream as well as a comparison with material which has authentically been called *P. greeni*. The intergradation is so complete that synonymizing seems the only recourse. As a consequence, foremanianum (Lea, 1842) becomes a synonym of greeni (Conrad, 1834). This species is primarily a small-river inhabitant (Table II). Although specifically distinct, greeni was probably derived from fasciolare of the Tennessee River.

28. Obliquaria reflexa Rafinesque

This species is mainly confined to large-river conditions in the Cahaba (Table II) and is of wide distribution. In its extensive range it exhibits a remarkably small degree of variation. Occasional specimens found in the Alabama drainage basin have a purple or pink nacre. Three individuals representing three different localities in the Cahaba were found to have such nacreous coloration. This is relatively rare and does not appear to show any relationship to stream distribution as was indicated for *Tritigonia verrucosa*.

29. Obovaria subrotunda (Rafinesque)

In the Cahaba, subrotunda was abundant and restricted entirely to the large-river zone (Table II). It is also common in the Tennessee River where specimens are very similar to those from the Cahaba. The faunal relationships of subrotunda in these two drainage basins are not well understood. Related forms occur in Mississippi and Louisiana. Later investigations may reveal whether or not these western forms are a secondary development from subrotunda of the Cahaba.

30. Plagiola lineolata Rafinesque

This species is confined to the large-river zone in the Cahaba and has a distribution pattern similar to that of *Obovaria subrotunda* (Table II). There are records of *P. lineolata* from streams in Mississippi, Louisiana, Arkansas, and Oklahoma, and it is also found in the Tennessee drainage. It probably entered Alabama from the west.

31. Leptodea fragilis (Rafinesque)

Leptodea fragilis is common in the medium-sized-river and large-river zones of the Cahaba, and is entirely absent in the headwaters (Table II). The number of specimens collected at any one locality was not large. Generally the shells were rather small and stunted. This species may have entered the Alabama drainage from the southwest.

32. Proptera purpurata (Lamarck)

P. purpurata in the Cahaba is identical in its distribution to Leptodea fragilis and is almost as abundant (Table II). It is represented in the Tennessee drainage basin by another species, Proptera alata. Since purpurata occurs in rivers of the Gulf drainage west of Alabama, it probably entered the Cahaba from that direction.

33. Carunculina corvunculus (Lea)

This species is relatively scarce in the Cahaba, being confined to the headwaters (Table II). Carunculina glans, a form hardly distinguishable from corvunculus, is found in tributaries of the Tennessee River in northern Alabama. Whether or not these two species are identical is an open question.

34. Carunculina cromwelli (Lea)

C. cromwelli has been found only at one locality in the headwaters of the Cahaba (Table II). It is difficult to separate cromwelli from corvunculus, which may occur with it. The characters of nacreous color and beak sculpture are used to distinguish them. Since the beaks of adults are often eroded, the color of the nacre alone remains as a diagnostic feature, and it is questionable in this species whether or not such a criterion is sufficient. A more detailed study based on larger series is needed.

35. Medionidus acutissimus (Lea)

Three species, acutissimus, parvulus, and conradicus, have been credited to the genus Medionidus from the Cahaba. Ortmann (1923:58) has shown that only acutissimus and parvulus occur in the Alabama drainage and has given characters to separate these species. His descriptions, however, fail to distinguish the intergrades. Our collections show acutissimus to be the more common species in the Cahaba. It was found throughout the entire course of the main stream (Table II).

36. Medionidus parvulus (Lea)

A large series of mussels taken from the Cahaba at Lily Shoals, Bibb County, by R. E. Call and H. H. Smith in the early part of this century contained many specimens of the parvulus form (Table II). Briefly, acutissimus is characterized by a strongly plicate shell having a prominent posterior ridge, whereas parvulus has a rounded posterior ridge and is less plicate. Within large series, however, there are usually many intergrades. From the material at hand it is clear that parvulus was far more abundant in the Cahaba formerly than at the present time.

37. Micromya vanuxemensis (Lea)

The distribution of this species in the Cahaba is rather irregular (Table II). The ecological conditions occurring at Lily Shoals, Bibb County, are evidently most ideal for it. Although it inhabits small creeks, it does not go as far into the headwaters as other species of *Micromya* described in this report. Specimens of *vanuxemensis* taken in the Cahaba are identical with those found in the Tennessee drainage.

38. Micromya nebulosa (Conrad)

This species is relatively rare in the Cahaba, confined almost exclusively to the headwaters (Table II). The presence of

nebulosa, normally a creek species, at Lily Shoals, Bibb County, indicates that the ecological conditions there are unusual. Evidently a creek environment is present on portions of these shoals which favor species not normally found in this zone of the river. Since specimens of nebulosa in the Cahaba and Tennessee drainage basins are identical, this species, like Lasmigona holstonia, probably entered the Cahaba from the north as a result of stream capture.

39. Micromya vibex (Conrad)

M. vibex was confined to the creek and small-river zones of the Cahaba (Table II). It is found in the Alabama drainage but not in the Tennessee. Some of the specimens taken in the extreme headwaters of the Cahaba had unusually thick shells. This may have been due either to ecological adjustment or to crossbreeding with the related nebulosa inhabiting the same region of the river.

40. Micromya lienosa (Conrad)

Although, as a rule, *lienosa* inhabits creeks and headwater areas it was common throughout the entire course of the Cahaba River (Table II). In general distribution *lienosa* is abundant in the Gulf drainage of Alabama and also west of it, as well as in the headwaters of the upper Tennessee. Curiously enough, it is not found in tributaries of the lower Tennessee in Alabama. The need for detailed studies of this and related species is obvious.

41. Ligumia recta latissima (Rafinesque)

This species was collected at only three localities in the largeriver zone of the Cahaba (Table II), and is also present in the Tennessee. Since there are records from both Arkansas and Oklahoma, recta latissima may have entered Alabama from the west, although it is still unreported from western Mississippi and Louisiana.

42. Lampsilis claibornensis (Lea)

L. claibornensis is not as abundant in the Cahaba as certain other species of this genus. It is, however, well established

throughout the river (Table II). It is not present in the Tennessee drainage, but a form, *Lampsilis virescens*, found there appears to be closely related.

43. Lampsilis clarkiana (Lea)

An examination of nine lots sent by the Alabama Museum, and a dozen lots collected by our expeditions, all from the Cahaba River, shows conclusively that clarkiana and doliaris are essentially alike. L. clarkiana (1852) has priority over doliaris (1865) and should stand. The habitat of clarkiana is the small-river zone (Table II). Specimens show wide variation: some are heavily rayed while others are rayless. The older females often have a distinct basal angulation accompanied by a blunt posterior end.

44. Lampsilis anodontoides (Lea)

This species was found mainly in the medium-sized-river and large-river zones, with but few specimens in the headwaters (Table II). It was one of the most abundant species in the Cahaba. Since *anodontoides* occurs in the lower Tennesse as well as in the Gulf drainage to the west of Alabama, it probably entered the Cahaba by way of the Mississippi embayment.

45. Lampsilis excavata (Lea)

This is a very widespread and abundant species in the Cahaba River (Table II). It is absent in the Tennessee drainage, where the related *Lampsilis ovata ventricosa* occurs. *L. excavata* is found in Mississippi and may have reached Alabama from the west.

46. Dysnomia metastriata (Conrad)

D. metastriata is usually associated with small- and mediumsized-river conditions. It is found sparingly in the large-river zone (Table II). This species is not present in the Tennessee but is represented there by the Dysnomia brevidens group.

47. Dysnomia othcaloogensis (Lea)

Two specimens of this doubtful species were collected in the Cahaba at Lily Shoals, Bibb County. It is difficult to deter-

mine the specific status of *othcaloogensis*, but it is probably the young male form of *D. metastriata*.

48. Truncilla donaciformis (Lea)

The distribution of this species is puzzling, since it does not seem to have a restricted distribution pattern. It is more abundant, however, in the lower reaches of the river (Table II). *Truncilla truncata*, which is associated with *donaciformis* in the Tennessee drainage, is absent in the Cahaba.

(Uniomerus tetralasmus Say)

This species was not found by our expeditions, but single specimens from the Cahaba at Helena, Shelby County, and Marion, Perry County, were collected by H. H. Smith.

ECOLOGICAL ZONES FOR THE NAIADES IN THE CAHABA DRAINAGE BASIN

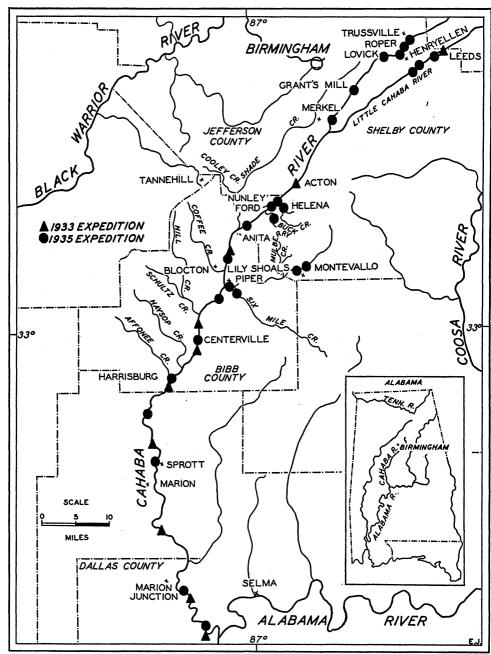
Ecologically the mussels in the Cahaba are distributed into three major zones, each zone being clearly delimited faunistically, geologically, and physiographically. Each of these zones is defined in terms of the stations which belong to it, the species constituting its fauna, and certain of its major physical features. Information on the geological zones and on the distribution of the soils was kindly submitted to me by Dr. Walter B. Jones, State Geologist of Alabama.

- Zone 1. This is an anticlinal valley located to the east of the main stream and harboring the upper and lower Little Cahaba rivers, together with Buck and Beaverdam creeks.
- Zone 2. The main stream from the headwaters to the marginal fault below Piper forms this zone. Faunistically, the region is subdivided into two sections: (1) small river and (2) medium-sized river.
- Zone 3. That portion of the river flowing through the coastal plain between Centerville and the mouth is included in this zone.

ZONE 1

Creeks (Table II)

In the streams of this category the water is frequently turbid. The bottom types include sand, gravel, and mud, and the rate



MAP 1. Cahaba River.

of flow was approximately one-third meter per second. Mussels were found only where the bottom was relatively firm, which in most instances occurred along the banks of the creek near shore or in the more stable shoal areas. Streams of this type are limited to about twenty-five feet or less in width. Specimens were found at depths varying from a few inches to three feet.

Three streams are represented in this zone, from which collections were made at the stations listed:

Little Cahaba River, two miles north of Leeds, Jefferson Co. Little Cahaba River, one mile south of Leeds, Jefferson Co. Little Cahaba River, four miles south of Leeds, Jefferson Co. Little Cahaba River, six miles south of Leeds, Jefferson Co. Buck Creek, at Helena, Shelby Co.

Beaverdam Creek, south of Helena, Shelby Co.

The five species associated with these creeks are:

Lasmigona holstonia

Micromya lienosa

Anodonta imbecillis

Micromya vibex

Micromya nebulosa

ZONE 2

Small River (Table II)

The water is mostly clear in the portion of the main stream considered in this zone. Bottom types include slabs of lime-stone, shale, boulders, gravel, sand patches, and small accumulations of mud and silt. The rate of flow is approximately one-third meter per second. The width ranges from about twenty-five to seventy-five feet. The surrounding country is mountainous and wooded, and the river lies in a deep trough. Naiades were collected at depths varying from one inch to two feet.

The stations in the headwaters of the Cahaba River are as follows:

Near Roper, Jefferson Co. Henryellen, Jefferson Co. Grants Mill, Jefferson Co. East of Merkel, Jefferson Co.

There are sixteen species common to this region:

Amblema perplicata Quadrula cahabensis Tritigonia verrucosa Carunculina corvunculus Medionidus acutissimus Micromya lienosa Elliptio arctatus Anodonta imbecillis Strophitus spillmanii Strophitus subvexus Ptychobranchus greeni Micromya vibex Lampsilis claibornensis Lampsilis clarkiana Lampsilis excavata Dysnomia metastriata

Medium-sized River (Table II)

The ecological conditions in this part of the zone are similar to those mentioned for the small-river section. In approaching Centerville there is a sharp transition towards coastal plain topography. The Cahaba enters low rolling country in an ever-widening valley, and varies in width from approximately seventy-five feet at Nunley Ford to about one hundred and fifty feet in the region of Centerville. The stations of this zone are as follows:

Nunley Ford, Shelby Co.
Anita, Shelby Co.
Lily Shoals, Bibb Co.
Ten miles above Centerville, Bibb Co.
One mile above Centerville, Bibb Co.

The thirty-one species characteristic of this zone are:

Fusconaia rubida
Amblema perplicata
Quadrula pustulosa
Quadrula aspera
Quadrula rumphiana
Tritigonia verrucosa
Pleurobema simulans
Pleurobema decisum
Pleurobema instructum
Elliptio crassidens
Elliptio arctatus
Lasmigona complanata
Strophitus subvexus
Ptychobranchus greeni
Obliquaria reflexa

Leptodea fragilis
Proptera purpurata
Carunculina corvunculus
Carunculina cromwelli
Medionidus parvulus
Medionidus acutissimus
Micromya lienosa
Micromya vibex
Ligumia recta latissima
Lampsilis claibornensis
Lampsilis clarkiana
Lampsilis anodontoides
Lampsilis excavata
Dysnomia metastriata
Dysnomia othcaloogensis

Truncilla donaciformis

ZONE 3

Large River (Table II)

In this zone the water is clear, and the bottom types include loose sand, gravel, and patches of mud and clay. The rate of flow is approximately one-third meter per second, and the width varies from one hundred and fifty to three hundred feet. The surrounding area has the physiographic features of the Gulf Coastal plain, with the river meandering across its much-widened valley. Mussels were most abundant on the gravel bars and in mud alongshore at depths varying from a few inches to four feet.

The stations in this zone are:

Seven miles below Centerville, Bibb Co. Two miles east of Harrisburg, Bibb Co. Eight miles north of Sprott, Perry Co. Five miles northeast of Marion, Perry Co. West of Sprott, Perry Co. One-half mile west of Felix, Dallas Co. Ten miles west of Selma, Dallas Co. Near Beloit, Dallas Co.

Four species were found to be restricted to this zone:

Fusconaia ebenus Quadrula metanevra Obovaria subrotunda Plagiola lineolata

Twenty others are common to this area:

Fusconaia rubida
Megalonaias gigantea
Quadrula pustulosa
Quadrula aspera
Quadrula rumphiana
Tritigonia verrucosa
Pleurobema nux
Pleurobema rubellum
Pleurobema instructum
Elliptio crassidens

Obliquaria reflexa
Leptodea fragilis
Proptera purpurata
Micromya lienosa
Ligumia recta latissima
Lampsilis claibornensis
Lampsilis anodontoides
Lampsilis excavata
Dysnomia metastriata
Truncilla donaciformis

In order to determine the relative abundance of carbonates available in the Cahaba River, certain water analyses were taken at the time the collections were made. The results of these tests are given in Table V.

These divisions or faunistic zones based upon the distribution of mussels are also characterized by geological differences, according to Dr. Walter B. Jones of the Alabama Geological Survey. In answer to a personal inquiry concerning agreement

TABLE V

CHEMICAL ANALYSES AT A SERIES OF STATIONS IN THE CAHABA RIVER,

SEPTEMBER 3 TO 10, 1935

	Carbonates or M.O. alkalinity in p.p.M.	p.H.
Little Cahaba River, 1 mile south of Leeds	131	7.8
Cahaba River, at Trussville	88	7.9
Cahaba River, Lovick	88	8.2
Cahaba River, near Merkel	78	8.0
Cahaba River, at Helena		8.2
Cahaba River, Nunley Ford		8.1
Cahaba River, Lily Shoals		8.2
Cahaba River, west of Sprott		8.0
Cahaba River, near Beloit		8.0

between the proposed faunistic zones and those recognized by geologists, he writes:

The Upper Little Cahaba flows past Leeds and occupies a sharp, anticlinal valley during most of its existence. The same is true of the Lower Little Cahaba River and Cahaba Valley Creek. If I were suggesting a geological reason for faunal difference, I would put these three streams in one zone. The soil in this area would be red cherty clays, and the streams would carry a rather frequent succession of gravel bars and no rock. The chert is angular and the sand is likewise angular. I happen to know that these three streams are frequently muddy.

The Cahaba River from its head waters southwestward to the marginal fault below Piper belongs in a second zone. The river proper, in this area of the Cahaba Coal field, flows along a trough of a rather prominent syncline, as contrasted with the sharp, anticlinal folding of the valley zone. In the synclinal plateau zone you will find shallow, sandy soil, and the river bed frequently shows scoured rock exposures of both shale and sandstone, frequent sand bars, and very occasional gravel bars, most of which occur within a short distance below the mouths of the several creeks which enter from one side or the other.

The third zone, below the fall line, has a variety of soil ranging from loose sand and gravel to red clay, and the bed in the stream is pretty heavily charged with well worn, rounded sand and gravel.

Whether you put your faunal limits at Centerville or at the junction below the Lower Little Cahaba with the Cahaba, does not make a great deal of difference. The coal measures are sharply faulted out and we have about twelve miles of folded Paleozoics from that point down to Centerville. There is a remarkable agreement between the zones given above by the geologist and those found to exist from this study of the ecology and distribution of the Naiades. It is my belief that this correlation of data can also be projected into conditions of the past so that we can perhaps substantiate the history of the drainage from the present distribution of the fauna.

FAUNAL RELATIONS BETWEEN THE NAIADES OF THE CAHABA AND TENNESSEE DRAINAGE BASINS

- D. W. Johnson (1905a) has given geological evidence to prove that "the Tennessee River has held its present course throughout Tertiary and more recent times." He also claims that the biological evidences previously given to show that a connection must have formerly existed between the Tennessee and Alabama systems are for the most part "to be explained just as readily and satisfactory entirely independent of that theory." This survey of the distribution and ecology of the Naiades of the Cahaba River reveals that there are biological data which indicate that there were former connections between these two major drainage basins.
- C. C. Adams (1901: 844) attempted to show the significance of "base-leveling" and the "migration of divides" on the Pleurocerid fauna of the Tennessee and Alabama drainages. He placed special emphasis on the connections which Hayes and Campbell (1894) reported to have formerly existed between these two drainage basins. Among other groups whose relationships were cited by Adams as giving evidence for such a connection were certain members of the gastropod family Viviparidae and a few species of crayfish.
- C. T. Simpson (1900) also tried to show faunal relations between some of the Naiades of the two drainages. He pointed out that there is a preponderance of species of *Pleurobema* in the Alabama River system. He then called attention to the fact that the species belonging to this genus in the Alabama drainage are not the same as those in the Tennessee, although they are closely related. Simpson merely scratched the surface

of this problem and concluded with a very general statement (p. 135):

In this brief sketch I have not gone exhaustively into the evidence presented by the Unionidae. There are many other species found in the Alabama River system which are evidently identical or nearly related to Tennessee River forms, but which have no very close relationships with the species of any other region and which are, most likely, descendents of Tennessee forms. In fact it is probable that nearly all the Unionidae of the Alabama River system have been derived from the Tennessee.

Johnson (1905a: 212–17) was quick to see the glaring loopholes left by Simpson's meager and conflicting evidence, and thoroughly refuted his claims. It is obvious, however, from Johnson's refutation that, although his arguments were logical, he showed no knowledge of the biological factors involved in considering the matters pertaining to the distribution and ecology of this group. Careful studies, such as those of the late Dr. A. E. Ortmann, have shown that such biological data should not be brushed aside as irrelevant in geological and physiographical studies. Simpson had some facts to support his theory, but he lacked the evidence necessary to prove his contentions. In the following discussion some support is given to the idea that connections existed between the Tennessee and Alabama drainages at two different times.

The Tennessee River is reported to contain about fifty-nine species, or groups of species and their forms, of Naiades. Of these, about twenty-eight, or nearly one-half, have never been found in the Alabama drainage basin:

Cumberlandia monodonta*
Fusconaia barnesiana
Quadrula cylindrica
Cyclonaias tuberculata*
Plethobasus cooperianus*
Lexingtonia dolabelloides*
Pleurobema cordatum
Lastena lata*
Amblema costata
Alasmidonta minor*
Alasmidonta marginata*
Pegias fabula*

Dromus dromas*
Obovaria olivaria
Actinonaias carinata gibba*
Actinonaias pectorosa*
Leptodea leptodon
Conradilla caelata*
Micromya fabalis
Micromya trabalis
Lampsilis orbiculata
Dysnomia triquetra
Dysnomia stewardsoni
Dysnomia propinqua

Ptychobranchus subtentus Cyprogenia irrorata* Dysnomia biemarginata Dysnomia capsaeformis

*The genera of these species have never been found in the Alabama drainage.

The Cahaba River has about forty-eight species, or groups of species and their forms, of Naiades. Of these seven are absent from the Tennessee drainage:

Megalonaias gigantea

Lasmigona complanata Carunculina cromwelli

Elliptio dilatatus

Micromya vibex

 $Uniomerus\ tetralasmus$

Lampsilis anodontoides

Megalonaias and Uniomerus are the only genera absent in the Tennessee drainage, and neither is an Alabama type. The following species are the only types peculiar to Alabama: (1) Fusconaia rubida, which, as a group, has close relationships with Fusconaia undata of the interior basin. It is abundantly represented in the Cahaba River, but has not been found in the Coosa River. (2) Elliptio dilatatus subgibbosus, which is fairly common in the Coosa, is extremely rare in the Cahaba. (3) Elliptio arctatus is found exclusively in the Alabama River and on the Atlantic coastal plain, as is also (4) Micromya It is obvious, therefore, that the Coosa and Cahaba rivers have no clearly defined indigenous forms or groups. Although there are peculiar Cahaba and Coosa forms, they all have generalized relations. Furthermore, these areas do not appear to represent an important center of development, but only a secondary one, having received and partially modified elements from various directions. There has developed in the Tennessee-Cumberland drainage basins a large number of peculiar forms, some of which have spread to Alabama, the Ohio, and the interior basin drainages. The Alabama drainage has no indigenous forms, and, consequently, there is no spreading into other drainages.

The following list contains eleven species which are common to both the Tennessee and Alabama drainage basins:

Tritigonia verrucosa Elliptio crassidens Lasmigona holstonia Plagiola lineolata Leptodea fragilis Micromya nebulosa Anodonta imbecillis Obliquaria reflexa Micromya vanuxemensis Ligumia recta latissima

Truncilla donaciformis

Three of this series are restricted to the Tennessee-Cumberland drainage: (1) Lasmigona holstonia, (2) Micromya nebulosa, and (3) Micromya vanuxemensis. These are creek species ecologically, and the only likely way they could have entered the Cahaba and Coosa drainages is by way of stream capture of small streams. The fact that the forms of both drainages are identical gives evidence that this capture apparently took place at a geologically recent time. The remaining eight species are of wide distribution, and there is evidence to show they entered the Alabama drainage from the west. Practically all inhabit large rivers.

There are seven related and representative groups in both the Cahaba and Coosa rivers which could not have entered Alabama from the west, and which, according to our best judgment, probably came from the north:

- 1) Quadrula pustulosa is found in the Tennessee while Q. pustulosa (asperata, kieneriana, cahabensis) is found in the Alabama drainage. Except in the color pattern there is little difference between the Q. pustulosa of the two drainages. Forms in the southwest (Mississippi, Louisiana, Texas) appear which differ from those in the Cahaba and Coosa rivers. The Alabama forms probably originated from those in the Tennessee.
- 2) Pleurobema oviforme-clava is found in the Tennessee, and P. decisum-georgiana is found in the Alabama, drainage. Although the taxonomy of the Pleurobema group in Alabama is confusing, it is probable that these forms were derived from one main type which represents the Pleurobema group in the Tennessee River. This type, P. oviforme and its varieties, changes to clava, which has a wide distribution in the Tennessee, Cumberland, and Ohio drainage basins, but is entirely missing in the Mississippi embayment region. Consequently, the Alabama forms of Pleurobema probably came from the north or from forms of the Tennessee.

- 3) Ptychobranchus fasciolare is found in the Tennessee, whereas P. greeni is found in the Alabama drainage. P. fasciolare is widely distributed in the Tennessee, Cumberland, and Ohio drainage basins. In the Ozark region it is replaced by P. clintonensis, but fasciolare is missing in the Mississippi embayment region. Consequently, P. greeni presumably entered the Alabama drainage from the Tennessee system.
- 4) Carunculina glans is found in the Tennessee, and C. corvunculus is found in the Alabama drainage. These two are hardly distinguishable. C. glans is abundant in tributaries of the Tennessee in northern Alabama; corvunculus does not have the characters of the western and southwestern glans, but is like the Tennessee form. In all probability it entered the Alabama drainage from the Tennessee.
- 5) Medionidus conradicus is found in the Tennessee, and M. acutissimus-parvulus is found in the Alabama drainage. Northward the genus Medionidus is not found outside of the Tennessee-Cumberland region. Southward the genus is only in Alabama, Georgia, and northwestern Florida. Thus these forms presumably did not come from the west or southwest where the group is not represented, but from the Tennessee drainage.
- 6) The *Dysnomia brevidens* group is in the Tennessee, and the *metastriata* group occupies the Alabama drainage. The *brevidens* group is restricted to the Tennessee and Cumberland drainages. In the Cahaba and Coosa rivers it is replaced by *D. metastriata* and related forms. The Alabama forms are all found in the Alabama drainage and are not reported either to the east or west. Thus, the forms in the Alabama probably came from the Tennessee River.
- 7) Lampsilis fasciola is found in the Tennessee, and the L. clarkiana group is confined to the Alabama drainage. L. fasciola is common in the Tennessee, Cumberland, and Ohio drainage basins, and has not been found west of the Mississippi River. The L. clarkiana group is related to L. fasciola but is not found anywhere except in the Alabama drainage. Pre-

sumably, the only way clarkiana forms could have reached the headwaters of the Alabama River is from the Tennessee drainage.

It seems necessary to conclude that in geologically recent time tributaries of the headwaters of the Alabama drainage were connected with tributaries of the Tennessee drainage. This confluence permitted the three creek species known to belong to the Tennessee drainage to enter the headwaters of the Alabama drainage.

The seven representative species which entered the Alabama River system from the north by way of the Tennessee drainage indicate that streams somewhat larger than creeks were connected. Since these forms are at present more or less differentiated in the two river systems, sufficient time must have elapsed to permit differentiating evolutionary tendencies. Thus, the connection of the larger streams must have preceded that of the creeks.

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