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FURTHER STUDIES IN CORRELATION OF SHAPE AND STATION IN FRESH WATER MUSSELS*

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Various students of the Naiad shells have commented upon the fact that the same species may assume different forms in response to different environments. Ortmann,[13] with Ball,[2] lists 22 species groups of mussels, in each of which the flatter and less inflated form is found in the tributaries and the upper part of the stream, while the more swollen shells are in the lower stretches of the river. Where these upstream forms had previously been considered distinct species, Ortmann's researches showed them to intergrade with the downstream shells and they were reduced to the rank of varieties. These observations of Ortmann's for many of the species are confirmed by those of Utterback,[17] Danglade,[4] Wilson and Clark,[19] and Meek and Clark.[11]

Ortmann further found that a loss in diameter in the headwaters was compensated for by a gain in size and circumference (as best expressed by the total length of the shell), but he makes it clear that in 12 species at least he could detect no evidence of a compressed form peculiar to the tributaries and an inflated form found further downstream. This paper will present two exceptions to his findings. Isely [9, 10] observed that peculiarities of distribution are very probably to be traced back to the young shells which are mostly carried about by fish and are thus subjected to varied conditions which are potent in determining the character of the adults. This point was taken in account by Ortmann, who mentions the possibility that compressed and inflated forms of the same species are the consequence of reaction to local environmental conditions. Where, however, the larval stages are carried by more stationary, rather than migratory, fishes, he believes that the development of local races, in consequence of reaction to local environmental conditions, is favored. In the cases where migratory fishes are the hosts, he thought no such local development was possible, any tendency toward it being promptly obliterated by the mixing of different stocks. This may account for the behavior of certain species which do not react in the manner described.

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The preceding comprises a summary of the literature immediately pertinent. For the benefit of those who are further interested in the variation of fresh water mussels, it is remarked that most of this literature, including that of European investigators, has been reviewed by Grier[6] and Ball.[2]

While engaged in mussel survey and appraisal work for the U. S. Bureau of Fisheries on the Upper Mississippi River region, we had the opportunity of observing the variations of fresh water mussels in what will be seen to represent four sharply differing types of environments. The headings under which they will be discussed are the Mississippi River above Lake Pepin (upper river), Lake Pepin, the Mississippi River below Lake Pepin (lower river), and the sloughs adjacent to these bodies of water. The underlying physiographic conditions may be summarized briefly, following Galtsoff:[5]

"Between St. Anthony Falls and the mouth of the Ohio the Mississippi flows in the narrow flood plain between steeps and bluffs forming its gorge. The river winds from one side of the flood plain to the other, numerous islands dividing the channel and forming many sloughs and bogs which are often transformed by the sandbars into pools of stagnant water. In the northern part, about 52 miles below St. Paul, the river fills out its gorge, covering the whole flood plain from bluff to bluff, forming the so-called Lake Pepin, which covers an area of 38½ square miles and has a depth of about 35 feet. Lake Pepin owes its origin to the Chippewa River, a small tributary entering the Mississippi from the east; the delta of the Chippewa extending into the main stream lies at the south end of the lake, and is now covered with modern flood plain deposits. It has dammed the Mississippi, leaving a narrow outflow opposite Read's Landing, and the river above the delta has overflowed its banks and filled out the whole gorge. At the northern end of Lake Pepin the Mississippi has built its own delta, which is still growing. It has reduced the inlet of the lake to a narrow stream less than 1,000 feet in width, while the outlet above the mouth of the Chippewa is 1,400 feet in width. The northern part of the lake is now very shallow and is almost entirely filled with sand and silt. Bluffs and terraces form the shores of the lake on the low shore lines while, especially on the Minnesota side, the waves and currents have deposited sand and have formed spits. The fall of the river from Red Wing, about five miles above the head of the lake, to Read's Landing, on the outlet 28 miles below, is only .02 feet per mile. In the middle part of the lake there is no fall of water at all. At the foot of the lake above the mouth of the Chippewa the slope is 0.25 foot per three miles, while just below Read's Landing it is 1.65 feet per three miles."

Lake Pepin is seen to represent what is more accurately termed a *river lake:* lake-like in that it represents a body of relatively still water, but yet intimately connected with the river. Says Coker,[3] "With the opportunity for the internal circulation, plankton conditions and community life corresponding in some degree to typical lakes, there are combined in a measure the features of circulation and regular renewal of water corresponding more nearly to usual river conditions."

Now, as is well known, lake and river forms of the same mussel

are frequently quite different in character, as pointed out by Walker.[18] Lake forms in general are shorter, have a higher degree of inflation, more regular lines of growth, a polished epidermis, and somewhat of a depauperate aspect. It is rare also for a lake to produce shells of such thickness and form as to be useful for button making, but Coker states, in the instance mentioned (Lake Pepin), "We find, however, characteristic river mussels and, what is more striking, we find that a species such as the fat mucket (*Lampsilis siliquoidea* Barnes), which is generally abundant and worthless in true lakes, is in river lakes abundant and valuable. Are its good qualities attributable to the unusual combination of river and lake conditions, or are they characteristic of a geographic region?" A paper by Baker,[1] portions of which are now cited, is of interest in this connection:

"Lake Winnebago is . . . really a widened out portion of the Fox River. . . . One of the most interesting features brought out by the study of the molluscan fauna of the Lake Winnebago region is the difference in size and shape between the *Unionidæ* (Naiades) of the Fox River and those of the lake, a difference which seems comparable to that noted by Grier (1920), between the Naiads of Lake Erie and the upper drainage of the Ohio River. Grier states, 'if we put a shell into the lake environment we may expect it will change its morphological features, not at random, but in a distinct, determinate or orthogenetic direction.' This change in the morphology of shells which have migrated from a river to a lake is strikingly shown in the Lake Winnebago fauna and study of the two areas by the methods of Grier would produce the same results as attained by the study of Lake Erie shells. It is to be noted as a significant fact that the same varietal forms inhabit both Lake Winnebago and Lake Erie, indicating that the law holds good under similar conditions in widely separated areas." After pointing out the effects of the lake environment on other types of molluscan life Baker finally states, "the entire molluscan fauna is affected by the same law of variation produced by river and lake environment, clearly indicating that ecological station plays a large part in the evolution of species. . . . Just what factors have been potent in producing these changes does not seem to be definitely known. It is probable that variation in food supply, in the chemical character of the fluid medium in which they live as well as in the general physical environment, plays a large part in these changes of form." It is of interest to the authors that while they had collected the data forming the basis of this article four years before Baker published his article, the latter anticipated to a large extent their conclusions, as may hereafter appear. In fact, they were ignorant of his work until their own manuscript had been drafted.

Limnological data obtained from Galtsoff's paper permit us to qualify our preceding statement as to the distinction in the environments of the Upper River, Lake Pepin, Lower River, and the Sloughs. Observations made by him indicate that the following physical conditions are characteristic of each:

UPPER RIVER

Depth.—5–37 feet, but usually varying from 9–15 feet.
Temperature of Water.—Warmer than in lake.
Velocity of Current.—1.38 feet per second one mile above Lake Pepin.
Units of Discharge.—2000 cubic feet per second.
Transparency of Water.—80 cm. Becomes more opaque downstream (sediment).
Bottom Conditions.—Gravel, sand, snags.
Plankton.—21.5 cc. per cubic meter of water.

LAKE PEPIN

Depth.—35–56 feet, the latter depth occurring only in a small area.
Temperature of Water.—Cooler than in sloughs, upper and lower river.
Velocity of Current.—.9 to .83 foot per second.
Units of Discharge.—8000–127000 cubic feet per second.
Transparency of Water.—19 to 102 cm. (at outlet).
Bottom Conditions.—Smaller gravel, sand, mud; very rocky near outlet.
Plankton.—21.5–33 cc. per cubic meter of water. Greater production at low water stages. Richer in Crustacea and Rotifera. Has additionally all the organisms found in the river plankton.

LOWER RIVER

Depth.—5–37 feet, but usually varying from 9–15 feet.
Temperature of Water.—Warmer than in lake.
Velocity of Current.—2.05 feet per second at Read's Landing immediately below the lake, 2.42 between Winona and Homer.
Units of Discharge.—16000–177000 cubic feet per second.
Transparency of Water.—22–79 cm.
Bottom Conditions.—Principally mud and sand, due to construction of wing-dams.
Plankton.—18.5–21.5 cc. per cubic meter of water.

SLOUGHS

Depth.—Shallower for the most part than any of the preceding.
Temperature of Water.—Higher than in main channel.
Velocity of Current.—Varying between .32 and 1 foot per second.
Units of Discharge.—Less than other habitats.
Transparency of Water.—.27 cm.
Bottom Conditions.—Sand, smaller gravel.
Plankton.—10–18 cc. per cubic meter of water, but under certain conditions richer qualitatively and quantitatively than the main channel.

So far as these different types of environment are concerned, the greatest resemblances between them are seen to lie on the one hand between the upper and lower rivers, and on the other, between the (river) lake and the slough. One difference between the upper and lower river seems to be expressed in the velocity of currents and units of discharge, while the resemblance between the river lake and the slough consists of a somewhat similar velocity of current, transparency of water, bottom conditions and possibly plankton.

The general differences between lake and river mussels of the same species being known, it will be one object of this paper to point out the more commonly observable morphological differences which we have found to exist between the river and river lake forms of the same species of mussel in possible response to the described environments, as well as to ascertain in this peculiarly interesting case the effect on the mussel shells of the interpolated river lake environment between that of the upper and lower river regions. There will also be an attempt to follow the line of attack of previous investigators in an effort to correlate the shape of the mussel with its geographical location in the river as well as to indicate the more prominent shell characters of the same species when found in sloughs where conditions are largely lake or pond-like, except during the normal high water period of May and June, when a great deal of the drainage passes through them.

METHOD

The conditions under which we worked in the field permitted us to make but three measurements of each mussel specimen—the length (L); the dorso-ventral diameter, or height (DVD), and the dextro-sinistral diameter (DSD). These measurements were made in centimeters and later resolved to factors for comparison by division into the length. Thus $\frac{\text{DVD}}{\text{L}}$ expresses the value of the height in terms of the length and $\frac{\text{DSD}}{\text{L}}$ gives the value of the convexity obesity or degree of inflation of the shell. Such computations were made for the greatest number of shells available from the types of environment already mentioned, and from these results the conclusions are derived. For the fullest information of those who are particularly interested in a study such as this, it is remarked that the shells from the upper river were collected over a distance of 10 miles; from Lake Pepin throughout its length of 28 miles, while those from the lower river were taken over varying distances over 42 miles. In the case of the sloughs most of the material came from those below Lake Pepin and over a distance roughly estimated at 15 miles. The physical conditions make it improbable that the shells found in these sloughs have their origin in Lake Pepin, rather their presence there is to be explained mostly by the fact that they are dropped from the fish in these their spawning and feeding grounds, and have continued to develop there. It is true that some shells may be carried into the sloughs by high water, but this would mostly affect only certain lighter species, such as the paper shells and floaters. Ordinarily, the mussels are pretty well entrenched on the bottom of their habitat.

RESULTS

These are presented in connection with the more modern system of nomenclature of the species studied and with each species is also given its common name. Under the heading of each species will be found the number studied from each type of environment, and the maximum, minimum, and mean values for L, $\frac{\text{DSD}}{\text{L}}$ and $\frac{\text{DVD}}{\text{L}}$. From the mean values are plotted the accompanying graphs, which will illustrate more clearly to some the variation in each species in response to the particular environment, and where those environments tend to converge, as in the case of the sloughs and Lake Pepin, the somewhat parallel effect to be observed on certain species. It is unfortunate that in some instances the comparisons have had to be made on an unequal number of specimens, and that the differences resulting in certain conclusions have not been greater. In these cases, however, the conclusions taken are fully supported by further study of the maxima of the measurements.

SUB-FAMILY UNIONINÆ

QUADRULA VERRUCOSA (Raf.). Buckhorn

Locality	DSD/L				DVD/L			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	7	.44	.33	.36	.76	.29	.56	9.6	7.7	8.6
Below Lake Pepin	13	.38	.31	.34	.64	.54	.58	11.9	7.4	10.3

AMBLEMA PERUVIANA (Lam.). Three ridge

Locality	DSD/L				DVD/L			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	50	.71	.25	.53	.75	.56	.69	12.2	6.2	8.6
Lake Pepin	50	.70	.49	.57	1.00	.58	.73	11.	3.8	7.4
Below Lake Pepin	50	.69	.43	.56	.81	.63	.74	10.2	3.6	6.7
Sloughs	50	.72	.40	.55	.85	.58	.72	11.9	3.8	6.6

FUSCONAIA EBENUS (Lea). Niggerhead

Locality	DSD/L				DVD/L			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	9	.80	.66	.71	.84	.74	.79	7.9	6.0	6.78
Lake Pepin	..	..	..	..	..	..	..	..	..	..
Below Lake Pepin	11	.74	.55	.64	.84	.67	.77	10.3	7.4	9.8
Sloughs	12	.66	.58	.63	.88	.77	.84	8.8	4.9	6.6

FUSCONAIA FLAVA UNDATA (Barnes). Pigtoe

Locality	DSD/L				DVD/L			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	20	.93	.75	.86	.83	.56	.74	7.9	5.8	6.95
Lake Pepin	50	1.4	.57	.72	1.3	.73	.97	6.6	1.6	4.52
Below Lake Pepin	50	.79	.55	.69	.99	.79	.86	7.3	2.7	4.76
Sloughs	50	.89	.58	.69	1.09	.68	.87	7.0	2.5	4.93

PLETHOBASUS CYPHYUS (Raf.). Bullhead

Locality	DSD/L				DVD/L			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	..	..	..	..	..	..	..	..	..	..
Lake Pepin	..	..	..	..	..	..	..	..	..	..
Below Lake Pepin	13	.64	.33	.53	.75	.49	.69	11.6	6.2	8.7
Sloughs	13	.78	.50	.56	.72	.65	.69	9.7	4.1	6.8

ELLIPTIO DILATATUS (Raf.). Spike

Locality	DSD/L				DVD/L			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	3	.39	.31	.34	.48	.46	.47	12.9	9.9	11.25
Lake Pepin	23	.39	.22	.33	.54	.45	.51	9.4	6.1	7.7
Below Lake Pepin	24	.40	.27	.33	.62	.44	.49	11.9	7.2	9.35
Sloughs	6	.45	.32	.38	.54	.46	.50	11.4	5.9	9.56

SUB-FAMILY ANODONTINÆ

LASMIGONA COMPLANATA (Barnes). White Heel Splitter

Locality	DSD/L				DVD/L			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	9	.26	.15	.21	.69	.56	.59	17.0	9.2	14.0
Lake Pepin	23	.37	.19	.26	.73	.55	.64	15.4	7.05	10.7
Below Lake Pepin	6	.28	.20	.24	.72	.60	.65	14.9	8.9	11.63
Sloughs	5	.31	.25	.29	.73	.62	.68	15.9	12.5	13.6

ANODONTA CORPULENTA (Cooper). Floater

Locality	DSD/L				DVD/L			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	..	..	..	..	..	..	..	..	..	..
Lake Pepin	32	.62	.35	.42	.85	.60	.71	12.9	6.9	9.5
Below Lake Pepin	32	.54	.32	.43	.72	.56	.64	13.2	7.5	10.5
Sloughs	32	.48	.37	.42	.70	.58	.63	14.1	6.2	10.2

STROPHITUS EDENTULUS (Say). Squaw Foot

Locality	DSD/L				DVD/L			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	4	.44	.38	.40	.60	.57	.58	9.4	7.9	8.6
Lake Pepin	15	.47	.17	.42	.74	.56	.62	7.11	4.7	5.75
Below Lake Pepin	15	.48	.26	.34	.69	.48	.52	11.17	4.6	8.0
Sloughs	12	.48	.35	.44	.62	.52	.58	11.2	4.7	7.7

SUB-FAMILY LAMPSILINÆ

OBLIQUARIA REFLEXA (Raf.). Three-horn warty back

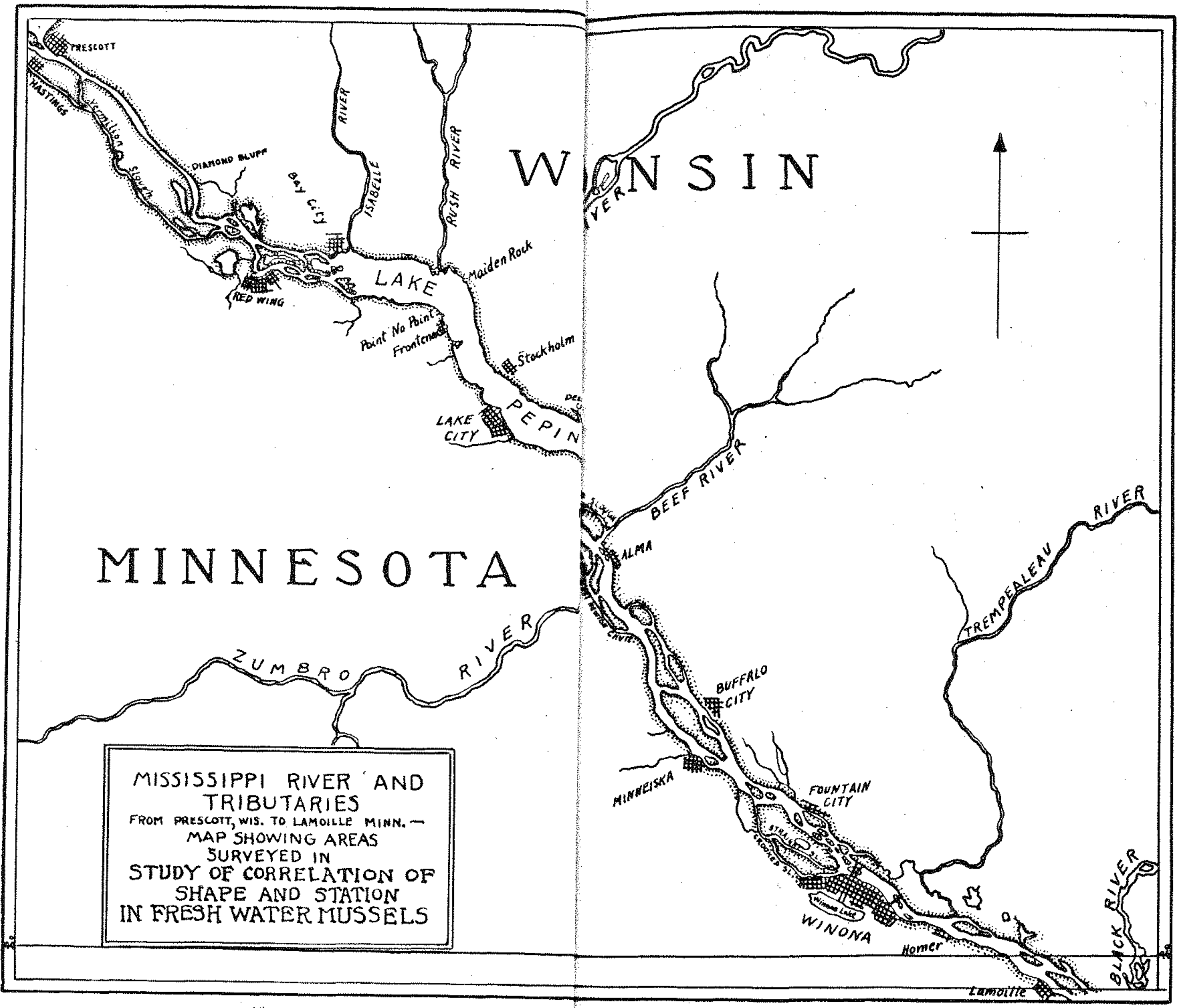
Locality	DSD/L				DVD/L			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	..	..	..	..	..	..	..	..	..	..
Lake Pepin	14	.76	.42	.59	.80	.50	.70	5.09	3.3	4.2
Below Lake Pepin	14	.67	.26	.57	.84	.64	.78	7.8	3.8	4.9
Sloughs	3	.65	.60	.63	.84	.83	.82	5.4	4.8	5.2

TRUNCILLA TRUNCATA (Raf.). Sugar spoon

Locality	DSD/L				DVD/L			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	..	..	..	..	..	..	..	..	..	..
Lake Pepin	13	.60	.44	.58	.83	.66	.74	4.9	3.7	4.5
Below Lake Pepin	13	.67	.47	.56	.84	.67	.76	6.5	4.05	5.11
Sloughs	3	.61	.57	.60	.85	.77	.81	5.97	4.1	5.01

LEPTODEA FRAGILIS (Barnes). Paper shell

Locality	DSD/L				DVD/L			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	..	..	..	..	..	..	..	..	..	..
Lake Pepin	19	.39	.27	.31	.64	.47	.53	10.7	7.04	8.7
Below Lake Pepin	19	.40	.23	.31	.62	.50	.54	12.8	5.5	8.47
Sloughs	19	.45	.26	.32	.63	.48	.54	12.8	7.04	9.32



MISSISSIPPI RIVER AND TRIBUTARIES
FROM PRESCOTT, WIS. TO LAMOILLE MINN. —
MAP SHOWING AREAS SURVEYED IN
STUDY OF CORRELATION OF SHAPE AND STATION IN FRESH WATER MUSSELS

PROPTERA ALATA (Say). Pink heel splitter

Locality	$\frac{DSD}{L}$				$\frac{DVD}{L}$			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	..	..	..	..	..	..	..	..	..	..
Lake Pepin	50	.37	.23	.30	.65	.43	.56	13.5	8.6	12.5
Below Lake Pepin	17	.39	.25	.30	.68	.54	.59	15.11	7.3	12.5
Sloughs	12	.38	.26	.30	.64	.52	.58	12.32	6.4	10.12

OBOVARIA OLIVARIA (Raf.). Hickory Nut

Locality	$\frac{DSD}{L}$				$\frac{DVD}{L}$			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	50	.79	.40	.67	.90	.64	.73	7.7	5.4	6.9
Lake Pepin	2	.62	.51	.56	.75	.70	.73	5.2	5.1	5.1
Below Lake Pepin	50	.67	.54	.60	.79	.51	.71	8.6	3.1	5.6
Sloughs	34	.63	.53	.59	.94	.66	.73	8.4	3.1	5.9

LIGUMIA RECTA LATISSIMA (Raf.). Long John

Locality	$\frac{DSD}{L}$				$\frac{DVD}{L}$			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	23	.37	.21	.28	.46	.36	.41	15.4	8.9	11.4
Lake Pepin	24	.38	.24	.30	.68	.20	.42	13.3	9.8	12.1
Below Lake Pepin	24	.37	.24	.29	.45	.39	.41	15.1	9.1	12.3
Sloughs	8	.31	.26	.29	.42	.38	.40	13.6	6.6	10.6

LAMPSILIS ANODONTOIDES FALLACIOSA (Smith). Yellow Sand Shell

Locality	$\frac{DSD}{L}$				$\frac{DVD}{L}$			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	7	.41	.33	.35	.56	.47	.48	14.0	11.8	13.2
Lake Pepin	11	.43	.31	.36	.47	.36	.44	9.6	8.05	8.85
Below Lake Pepin	13	.41	.34	.38	.51	.46	.49	13.5	7.7	10.8
Sloughs	3	.50	.34	.39	.49	.43	.47	13.4	7.3	11.34

LAMPSILIS SILIQUOIDEA (Barnes). Lake Pepin Mucket

Locality	$\frac{DSD}{L}$				$\frac{DVD}{L}$			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	50	.54	.31	.41	.66	.50	.56	11.9	6.8	9.7
Lake Pepin	50	.64	.32	.46	.76	.53	.62	9.7	6.2	8.1
Below Lake Pepin	33	.56	.39	.46	.65	.49	.56	12.1	5.5	8.7
Sloughs	50	.54	.31	.43	.79	.48	.54	12.1	4.5	8.7

LAMPSILIS OVATA VENTRICOSA (Barnes). Pocketbook

Locality	$\frac{DSD}{L}$				$\frac{DVD}{L}$			L		
	No.	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Above Lake Pepin	50	.70	.45	.53	.96	.64	.70	12.8	9.4	10.5
Lake Pepin	50	.72	.47	.55	.83	.62	.72	12.4	5.7	9.0
Below Lake Pepin	50	.73	.49	.53	.91	.63	.72	11.5	6.8	9.7
Sloughs	50	.68	.42	.54	.91	.60	.69	13.9	7.6	10.6

The *Unioninæ* are regarded as the most primitive of these subfamilies, and the only member of it represented in our material which we found to conform to the general law of becoming more convex in outline, passing downstream (upper river compared with lower river) is *Amblema*. This confirms Wilson and Clark's observation.[19] Possibly by way of compensatory growth it is longer in the upstream stretches, but on the other hand it is proportionately higher in the lower parts of the stream.

Species of *Unioninæ* which do not conform are *Fusconaia flava undata*, *Elliptio*, *Fusconaia ebenus*, and *Quadrula verrucosa*. Ortmann's observation for *Elliptio* is thus confirmed. The first two of these species are longer upstream and have a less proportionate height there; the latter two are shorter upstream, while only *Quadrula* has less height there. *Fusconaia* is the most primitive of these species.

The exception we note for *Fusconaia* is not at all in harmony with the observations on other members of this primitive genus. Ortmann[14] reports no less than six species groups belonging to this genus including this species that respond to the law as stated. Differences in the amount of material studied may explain the results in *ebenus* but hardly in *flava undata*. Perhaps in the latter a high compressed race of shells has developed in response to the conditions of the Mississippi below Lake Pepin.* There seems little probability of a confusion of identity in the material studied. However, as will be seen later, this species responds to the river lake environment in an expected and typical manner.

Among the *Anodontinæ* we see that *Lasmigona complanata* conforms to the law and this appears to be the first case noted as occurring in this sub-family. The longest shells were found in the upper river, but there is also a compensatory increase in height going downstream. *Strophitus* does not become inflated in the lower river, confirming Ortmann's earlier observation, but shows, however, a shortening of the shell and a decrease in height.

The sub-family *Lampsilinæ* has many characters intermediate between those of the *Anodontinæ* and the *Unioninæ*, and includes the most advanced types of the Naiades, as shown in part by the expression of sexual differentiation in the shell. The genus *Lampsilis* is among those most highly differentiated. Members of this subfamily which follow the law are *L. siliquoidea*, *Ligumia* and *L. anodontoides*. Ortmann could not detect any such response in his material for the first two species named. A possible explanation for this variance from Ortmann's results in *L. siliquoidea* is that the shells may have been carried downstream from Lake Pepin, where the environment is known to be exceptionally favorable for this species of shell,† where it is being continually propagated by the

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* Ortmann studied typical *flava* (Raf.) and *F. flava trigona* (Lea). The relation of these forms to var. *undata* Barnes is open to further investigation, although Utterback (loc. cit.) considers that *undata* passes into *trigona*.

† *L. siliquoidea*, in the upper Ohio drainage, distinctly prefers quiet reaches of the streams. Ortmann further states in correspondence that this divergence from his results may be explained by the fact that he had hardly any material from a river as *large* as the Mississippi.

Bureau of Fisheries, and where, as will be seen, the shells are generally more inflated than in the lower river. It is possible also that the same factors may affect our results from other species to some extent. No change in proportionate height in the lower river is noted for either of these two species, but *L. siliquoidea*, *L. anodontoides* become shorter and *Ligumia* longer in the lower stretches of the river. *L. anodontoides* becomes higher in the lower stretches of the river but no such change is noted for *L. siliquoidea* or *Ligumia*.

The species of this sub-family which do not conform are *Lampsilis ventricosa*,* which averages the same degree of inflation in both the upper and lower river, and *Obovaria olivaria*. The latter is also a primitive genus within the *Lampsilinæ*, but the related species *subrotunda* Raf., is known very definitely to become inflated in the lower stretches of streams. We had no material from the upper river for the remaining species of *Lampsilinæ* listed, but our results in the case of *Obliquaria reflexa*, another primitive form, confirm Danglade's observation[4] that it does not become inflated in the lower stretches of streams, but instead is longer and higher. These conclusions are essentially those reached by Ball,[2] viz., that shells of the same species often change in shape according to the size of the stream in which they occur; that shells of a smaller stream are less swollen than those of larger streams; that certain groups show this correlation much more strongly than others, and that in some cases there is apparently no relation between the size of stream and the degree of obesity. To these may be added the statement that changes in one dimension of a shell are usually accompanied by compensatory changes in other dimensions, possibly to be correlated with the environment.

THE (RIVER) LAKE ENVIRONMENT AND THE UPPER AND LOWER RIVER ENVIRONMENTS

Most of the shells from Lake Pepin have the regular growth lines and polished epidermis characterizing lake shells, and possibly less disturbed water, but none of the shells we collected there were depauperate in appearance, although certain species appear to avoid the lake. The tables permit us to observe other effects of the river lake environment in the following species, which attain at least a slightly greater obesity in Lake Pepin than either the upper or lower river, viz., *Ligumia*, *Amblema*, *Lasmigona*, *Lampsilis ventricosa*, and *Strophitus edentulus*. Of these, *Amblema* and *Lasmigona* were observed to be more inflated in the lower river than the upper river. *Lampsilis ventricosa* and *Strophitus* attain a higher degree of inflation in Lake Pepin than in either the upper or lower river. *Lampsilis siliquoidea* averages the same in both lake and lower river, possibly for reasons already given. Correlated also with the river lake environment is a greater proportionate height in *Lampsilis siliquoidea*, *Strophitus*, *Ligumia* and possibly *Lampsilis ventricosa*, while *L. complanata* has a greater proportionate height in the lower river

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* Ortmann writes to one of us under date of Feb. 5, 1926, that *L. ventricosa* of the Mississippi, lower Ohio and Illinois River is a peculiar swollen race, not exactly identical with the *ventricosa* of the head waters of the Ohio.

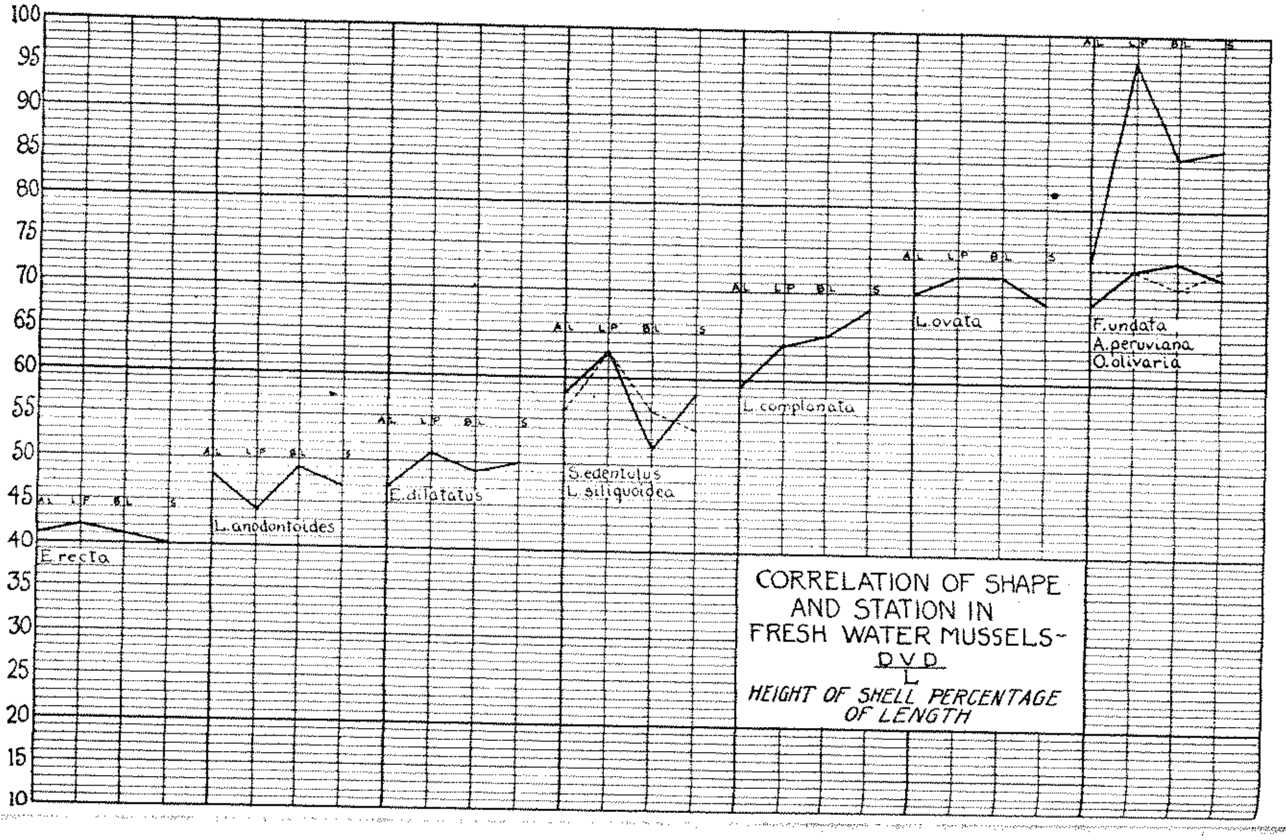
only. This characteristic of the latter shell may be a direct response to the swifter current and sand and mud bars on which it is found burrowing there. In this connection, its common name of "hell splitter" becomes significant. Common in the same habitats are *Fusconaia flava undata*, *Leptodea*, *Amblema* and *Proptera alata* which in these circumstances all attain a greater proportionate height. The external resemblance between *Lasmigona* and *Proptera* is unusually close, and they may be distinguished superficially only by their beak sculptures, hinge and color of nacre. Generally speaking, they also parallel one another in their habitats. Shall we say that their shell architecture is an effect of their common environment?

While *Elliptio* and *Fusconaia flava undata* attain their greatest inflation elsewhere, it was noted that specimens of these shells collected from the (river) lake, Lake Pepin, agree in general resemblance and dimensions to the variety *sterkii* of the former and the variety *F. flava parvula* related to the latter, described by Grier from Lake Erie.[7] The degree of inflation of *F. flava undata* is greater in Lake Pepin shells than in the Lake Erie variety mentioned, although it is less than those from upstream. Baker records var. *sterkii* from Lake Winnebago.[1] Further comparison of all applicable dimensions given by Ortmann of shells from Lake Erie[12] with the maxima, minima, and mean of the shells we collected from Lake Pepin indicate the close similarity in morphological characters of the following species in Lake Pepin, with the corresponding species or variety in Lake Erie, viz., *Amblema peruviana* (*Amblema plicata* Say); *Leptodea fragilis* (*Paraptera fragilis* Raf); *Proptera alata* Say, *Ligumia recta latissima* Raf. (*Eurynia recta* Lam.); *Lampsilis siliquoidea*, Barnes (*Lampsilis luteola rosacea* DeKay); *Lampsilis ovata ventricosa* Barnes (*Lampsilis ovata canadensis* Lea). This fact offers some confirmation of the statement of Baker,[1] earlier cited in this paper, to the effect that the morphological characters of shells which have migrated from a river to a lake are highly predictable ones.

Lasmigona, *Strophitus*, *L. ventricosa* and *L. siliquoidea* are shorter in Lake Pepin than the other environments. *Ligumia*, however, is longer in Lake Pepin than in the upper river, but approximately the same in the lower river. *Amblema* is longer in Lake Pepin than in the lower river, but shorter there than in the upper.

THE RIVER LAKE ENVIRONMENT AND THE SLOUGHS

Most of the shells from the sloughs had the same general appearance as those collected in Lake Pepin. Comparing these shells with those from the upper and lower river alone, a greater obesity is noted in the slough forms of *Plethobasus*, *L. ventricosa*, *Lampsilis anodontoides*, *Lasmigona*, *Fusconaia flava undata* (as compared with lower river), *Elliptio* and *Strophitus*. Correlated with the environment is a greater height in *Lasmigona*, *Elliptio* and *Fusconaia*. There is no change in the proportion in our material for *Plethobasus*, while *L. ventricosa* apparently attains a greater height in both upper and lower rivers and Lake Pepin than in the sloughs. *L. anodontoides* is higher in both upper and lower rivers than in the sloughs. *Strophitus* is higher in Lake Pepin and possibly the upper river, but lower in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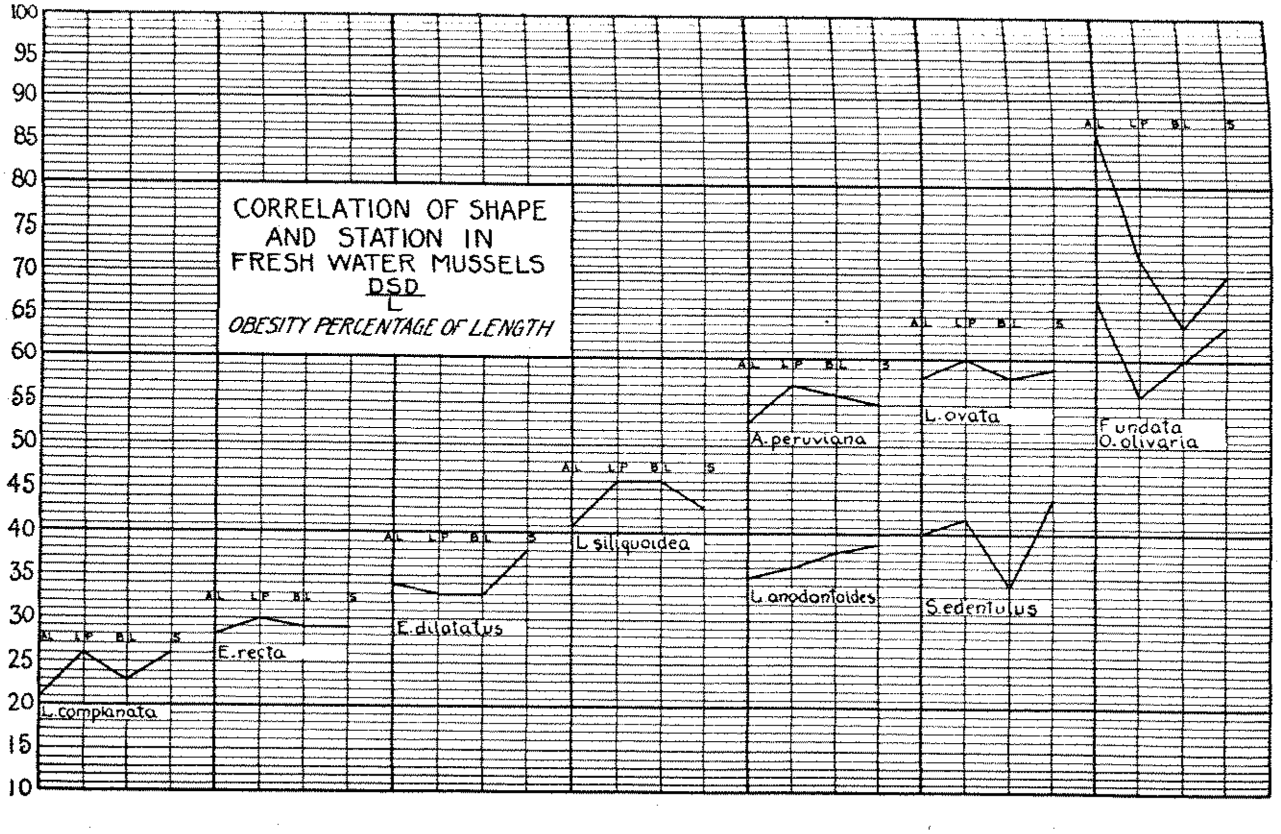
L. anodontoides
E. dilatatus
S. edentulus
L. siliquoidea
L. complanata
L. ovata
F. undata
A. peruviana
O. olivaria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E. recta
E. dilatatus
L. siliquoidea
L. anodontoides
A. peruviana
S. edentulus
L. ovata
F. undata
O. olivaria

the lower river than in the sloughs. *L. ventricosa* and *Lasmigona* attain their greatest length in the sloughs; *L. anodontoides*, *F. flava* and *Elliptio*, a greater length than in any other place except the upper river. *Strophitus* is shorter in the sloughs than in any other habitat except Lake Pepin.

Of the species attaining their greatest inflation in the sloughs as compared with the upper or lower river, the following are also more inflated in Lake Pepin than either the upper or lower river; viz. *Lasmigona*, *L. ventricosa* and *Strophitus*. These three species are shorter here than elsewhere, and their other correlations have been previously dealt with. The behavior of these three shells may possibly indicate some parallelism of effect on these species of the more greatly similar lake environment. No appreciable effect is noted for *Anodonta* in either the slough or lake environment beyond the fact that it is higher in Lake Pepin, where it also possibly attains a maximum inflation. However, other observers have previously commented on the greater size it attains in lakes and sloughs although longer specimens were found outside of them.

If we compare the sloughs with all other types of environments, we find that *Lasmigona* and *Elliptio* attain a higher degree of inflation there than anywhere else. Such a statement can hardly be made for *Leptodea* and *Plethobasus* on account of the scarcity of proper material. Correlated with this habitat is a greater proportionate height in *Lasmigona* and possibly *Elliptio*. *Lasmigona* undoubtedly attains its greatest height here, while *Elliptio* is higher in the sloughs than in the upper or lower river. *Obliquaria* is more inflated in the sloughs than elsewhere for the material we had, and is also higher and longer there. The most satisfactory results from the slough shells would, of course, have been obtained from mussels which had unquestionably passed their entire life there.

CONCLUSIONS

1. Under the conditions of this study and within the limits of the material used, three species of Naiades in addition to those previously known show evidence of becoming more convex in the lower stretches of streams. They are *Lasmigona complanata*, *Ligumia recta*, *Lampsilis anodontoides*, and possibly *Lampsilis siliquoidea*. Correlated with the increase in degree of inflation is the fact that three of these species (*Lasmigona*, *L. anodontoides* and *L. siliquoidea*) become shorter, while two (*Lasmigona* and *L. anodontoides*) proportionately higher.

2. The effect of the interpolated (river) lake environment between the upper and lower rivers is to increase the convexity of certain species, viz., *Ligumia*, *Lasmigona*, *Amblema*, *Lampsilis ventricosa*, and *Strophitus edentulus*. While some of these are also shown to become more inflated in the lower stretches of the river, yet their convexity is greatest in the (river) lake environment. Correlated with the latter is a greater proportionate height in three of these species, *L. siliquoidea*, *Strophitus* and *Ligumia*, and a diminution in the length of four of them—*Lasmigona*, *Strophitus*, *L. ventricosa* and *L. siliquoidea*. The foregoing indicate some of the differences between the river and the river lake forms of the same species of mussel.

3. The tendency of the slough environment is to parallel that of the lake in inflating the shells of certain species. In some species this is accompanied by a proportionately greater height, as in *Lasmigona*, *Elliptio* and *Fusconaia flava undata;* in others by less height, as in *Lampsilis ventricosa* and *anodontoides;* in still others by a greater length, as in *L. anodontoides*, *F. flava undata*, *Elliptio*, *L. ventricosa* and *Lasmigona;* and by less length in *Strophitus*.

Little can be said to account for the facts brought out. It is conceivable that some of the changes in shell architecture shown to take place are advantageous to the mussels; for instance, the flatter and larger forms of shells found in the upper river might enable the animal to orientate itself to the current much more easily than a swollen form, such as that found in Lake Pepin. Ball[2] observed in most of the species studied by him that young shells were more swollen than older ones. Perhaps a partial explanation to some of the more inflated shells of some species downstream or in Lake Pepin lies in the possibility the more highly inflated young shells being carried there by the current and dropped; but according to inferences to be taken from a recent paper by Ortmann,[14] such a process does not explain the presence of the inflated varieties of shells in Lake Erie. Much of course may depend on the habits of the species. But Ortmann[16] gives us an interesting clue in his observation on *Fusconaia cuneolos* Lea which "possibly indicates that not so much the size of the stream, as the character of bottom and current, determines the development of the big-river-type." To the authors the statement of Haas and Schwarz[8] has peculiar pertinence in connection with the results of the investigation.

"The same types under the same biological (ecological) conditions produce the same variants; different types under like conditions produce convergent (parallel), local variants. In the case of sufficiently lengthy isolation the local variants subject to biologically similar conditions may become constant or fixed local forms." (Free translation.)

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