

CLINES IN THREE SPECIES OF *LAMPSILIS*
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ABSTRACT

In relating the latitudinal position of three species of fresh-water mussels to shell measurements, an attempt is made to demonstrate a geographic north-south cline. Specimens used for this study range from northern Michigan southward to southern Alabama. Three shell measurement ratios: height/total length, width/total length and posterior length/total length, are plotted against the latitudinal position of specimens for each of the three species: *Lampsilis ventricosa* (Barnes) (121 specimens), *L. ovata* (Say) (79 specimens) and *L. excavata* (Lea) (60 specimens). Scatter plot diagrams indicate a trend of gradual shifting of points to one side or other of the diagram depending on the shell measurement ratio used. Diagrams of the shell ratios height/total length and width/total length show an increase in the ratio number as lower latitudes are approached. The posterior length/total length plot shows a decrease in the ratio number with lower latitudes. Some support for a cline is given in that the ranges of the three species overlap. The more northerly species, *L. ventricosa* and *L. ovata*, overlap in their respective ranges, and the range of *L. ovata* merges with that of the southern species, *L. excavata*. A statistical analysis of the data offers little to prove or disprove a cline. The concept of a cline, as suggested, raises the implication of a change in the taxonomy of the three species considered here. It is suggested that these nominal species are probably subspecies. A definite judgment must depend on confirmative studies based on soft part morphology and cross-fertility experiments.

INTRODUCTION

A gradual change in some character over large areas has been noted in many animal groups. This character gradient or cline has even led some workers to formulate "rules", which, in a general way, can be applied to express gradual geographic variation (for summary of rules, see Mayr, 1942: 88-94). The purpose of this paper is to demonstrate a regional cline in fresh-water mussels (family Unionidae), which, as far as the writer is aware, has not been done previously.

Clines in mollusks, in general, are rather well-known (examples in Clench, 1954: 122-125 and van der Schalie, 1948: p. 26-30 and p. 57-60). However, clines reported in naiads are few, and these may be termed ecoclines (Huxley, 1938, p. 219). Ortmann (1920: 269-312) found that in certain mussels of the upper Ohio drainage, obesity (length of shell divided by diameter or width) increases gradually in a downstream direction. Stated in an-

other way, shells are more obese (swollen) downstream in the larger rivers and less obese (compressed) in the headwaters. Ball (1922) statistically analyzed obesity and size of stream and arrived at the same conclusions as Ortmann.

This study is an analysis of a cline of regional extent and is based on shell measurements of river naiads which range from northern Michigan southward to southern Alabama. The specimens used are from an area bordered approximately on the east by the Appalachian Mountains and extending west to eastern Kansas. Three species of *Lampsilis* (subfamily Lampsilinae) were chosen for the study because they are suspected of forming a closely related group: *L. ventricosa* (Barnes), *L. ovata* (Say) and *L. excavata* (Lea) (Fig. 1). They are typically developed, as follows:

Lampsilis ventricosa (Barnes); shell subovate to subelliptical; beaks high and sculptured with few coarse irregular

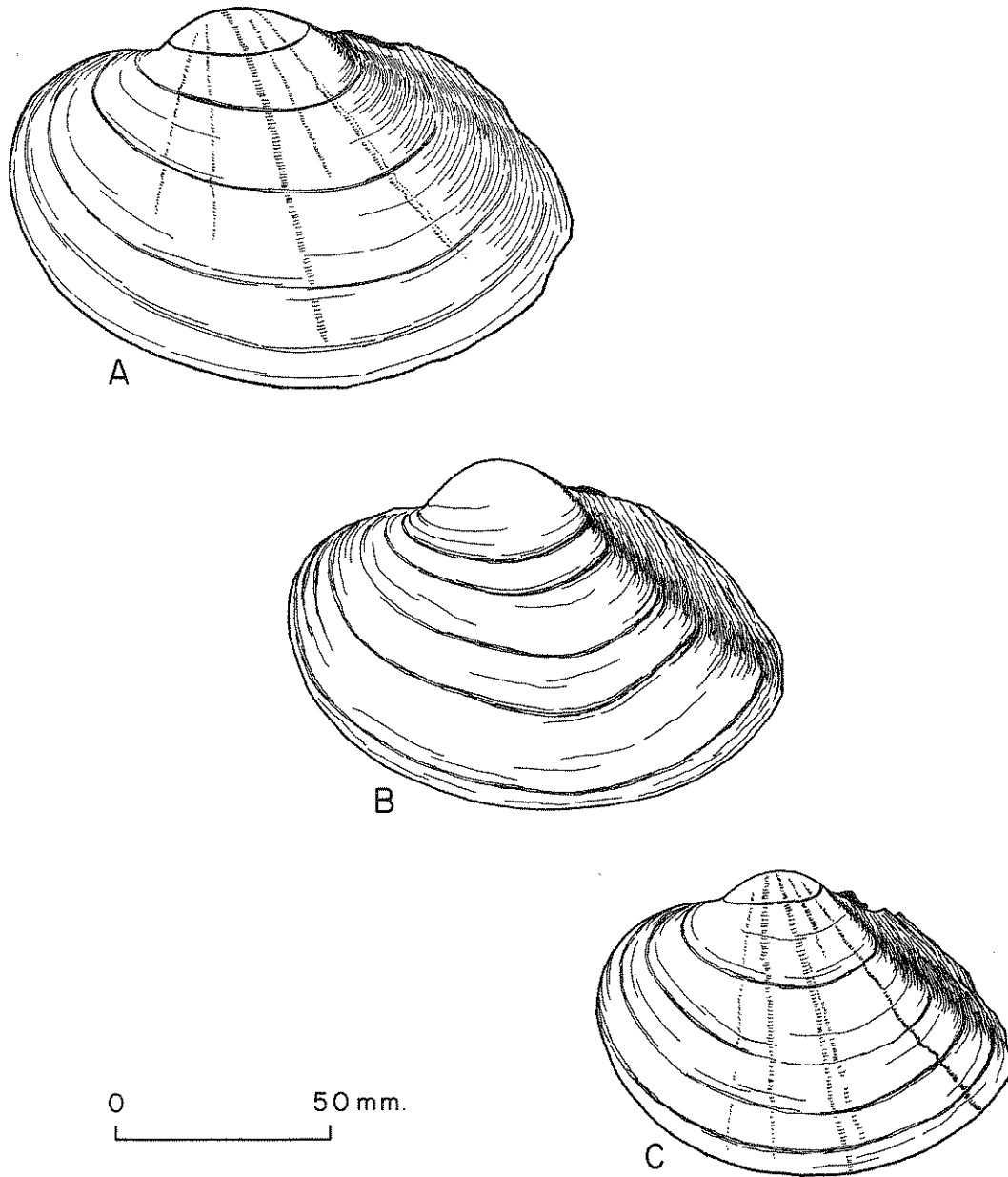


FIG. 1. Comparison of the left valves of three species of fresh-water mussels: *Lampsilis ventricosa* (Barnes), A (UMMZ 165196), Grand River, Michigan; *L. ovata* (Say), B (UMMZ 86356), Wabash River, Indiana; *L. excavata* (Lea), C (UMMZ 65656), Cahaba River, Alabama. All specimens are of approximately the same age, each having 5+ annulae.

ridges; posterior ridge low or wanting (upper Mississippi drainage; in latitudinal extent from about northern Michigan to northern Illinois).

Lampsilis ovata (Say); like *L. ventricosa* but with strong, well-developed posterior ridge (Kentucky and Tennessee).

Lampsilis excavata (Lea); with well-developed posterior ridge but smaller than *L. ventricosa* and *L. ovata* (Alabama River system).

MATERIAL AND METHODS

Shell measurements used in the present study are (Fig. 2):

Total length - greatest length measured parallel to the hinge line.

Posterior length - distance from posterior end of shell to point of beak, parallel to hinge line and measured on interior of left valve.

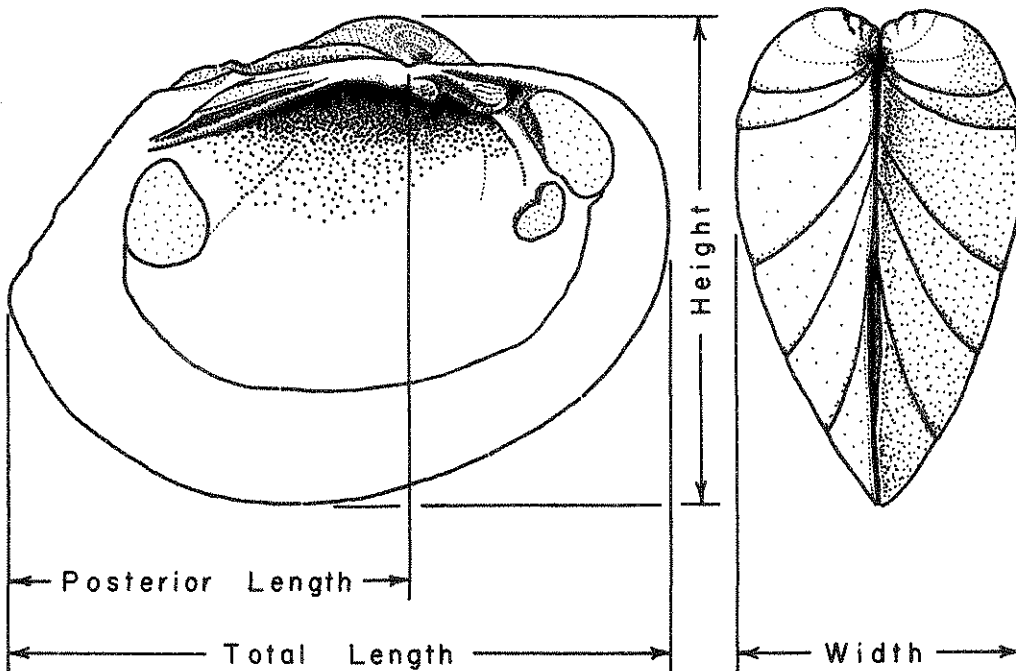


FIG. 2. Left interior (left) and anterior (right) views of *Lampsilis ventricosa* (Barnes) showing where shell measurements were taken.

Height - distance at right angles to hinge line at highest part of umbo.

Width - distance across both valves, measured at same relative position as height.

Another measurement, the distance between the outer edges of the adductor muscle scars (DAS) measured parallel to the hinge line, was also made on all specimens. However, this measurement does not appear significant, as is mentioned again in the Discussion. All measurements were made with vernier calipers. Measurements from the shell interior were obtained by fixing the shell to the back of a framed plate glass by stiff rubber bands. Desired distances were transferred through the glass on paper with triangle and T-square and then measured with calipers.

Since all three species involved here are sexually dimorphic, care was taken to measure specimens of the same sex, i.e., males. Male shells have a somewhat pointed posterior end, whereas the posterior end in females is bluntly truncated and the postero-ventral part is more inflated. To maintain relative size within and between all three species, only river forms were measured; lake forms are often typically stunted. Also, in this study are included only those specimens which have four annulae or more. All specimens measured are in the collections of the Mollusk Division, Museum of Zoology, University of Michigan.

From the measurements of the 260 specimens (*Lampsilis ventricosa*, 121, *L. ovata*, 79, *L. excavata*, 60), various shell ratios were computed: height/total length, width/total length, posterior length/total length, distance between outer edges of adductor muscle scars (DAS)/total length, and width/height (these data are on file in the Mollusk Division, Museum of Zoology, University of Michigan). These ratios were then plotted against the latitudinal position of each specimen. Of five ratio plots constructed, three are presented here: height/total length, width/total length and pos-

terior length/total length (Figs. 3, 4, 5). Each point on the three grades represents a single specimen. In some localities the spread of several points on a given latitude gives some idea of station variation.

DISCUSSION

It can be seen that points on the scatter plot diagrams (Figs. 3, 4, 5) show a trend of gradual shift to one side or the other with a change in latitude, depending on the measurement ratio used. The gradual shift seems to indicate quite clearly a gradual change in a measurable character, i.e., a cline. Additional support for the concept is given in that the three species overlap in their geographic ranges. The range of the northerly species, *Lampsilis ventricosa* and *L. ovata* overlap, and the range of *L. ovata* merges with that of the southern species, *L. excavata*. The clinal situation also seems to be reflected in certain physical factors of the shell. As pointed out earlier, *L. ovata*, as well as *L. excavata*, typically differ from *L. ventricosa* in the possession of a well-developed posterior ridge, which is low or completely lacking in the latter species. However, the development of this ridge in *L. ventricosa* and *L. ovata* is gradual and intermediate in strength in certain areas where the two species occur together. Another gradational character appears to be size. Although no statistical proof has yet been compiled, there seems to be a gradual decrease in size within the three species from north to south.

In a way, it seems rather surprising that a gradual trend is indicated by shell measurements of specimens over an area of regional extent. One might expect local environmental effects to "mask", more or less, any regional trend which might be present. Some idea as to the effect of habitat on size, shape and other characters on mussel shells is given by Ball (1922: 93-97, summary of observations by earlier workers).

The shell ratio height/total length (Fig. 3) seems to show the most uniform shift of points, with an increase in the ratio number as lower latitudes are approached.

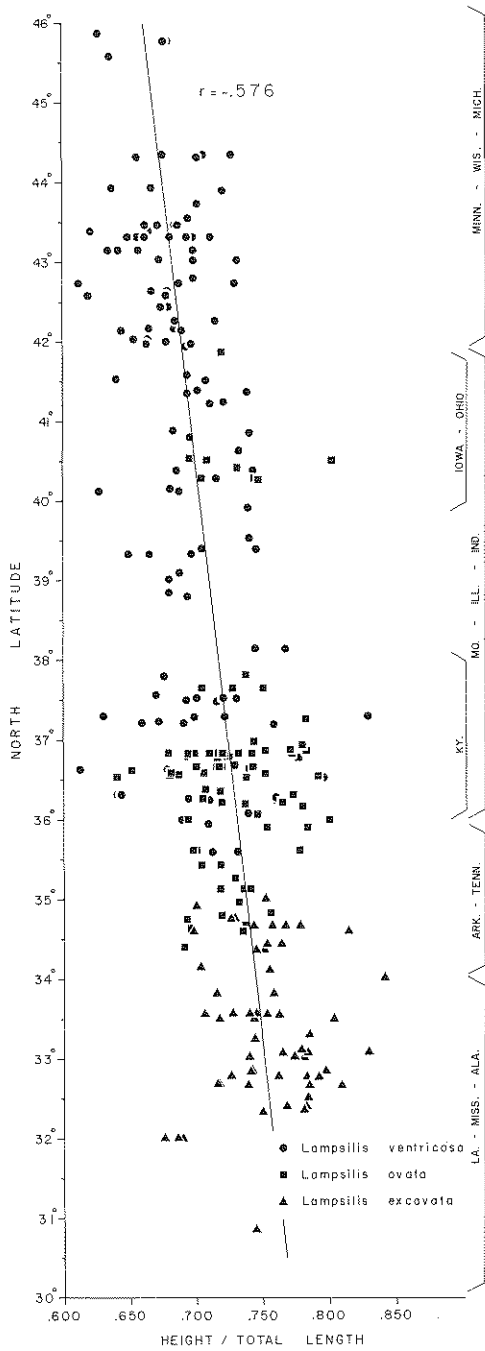


FIG. 3

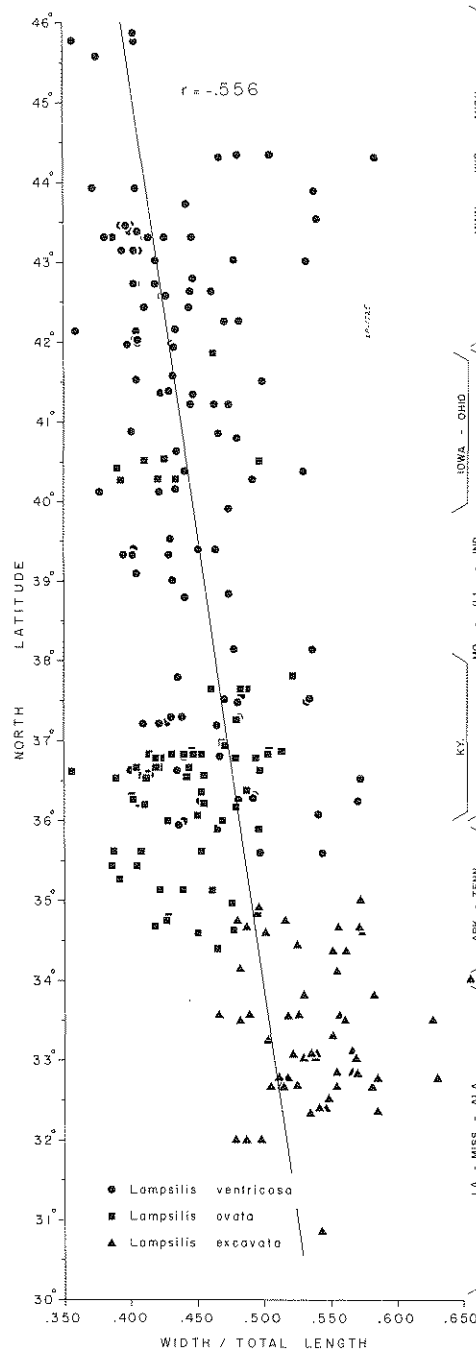


FIG. 4

FIG. 3. Scatter plot of height/total length of shell to latitude in three species of fresh water mussels. Latitudinal limits of various states are given only for orientation; shells from states other than those given are also included in the plot.

FIG. 4. Scatter plot of width/total length of shell to latitude in three species of fresh-water mussels. Latitudinal limits of various states are given only for orientation; shells from states other than those given are also included in the plot.

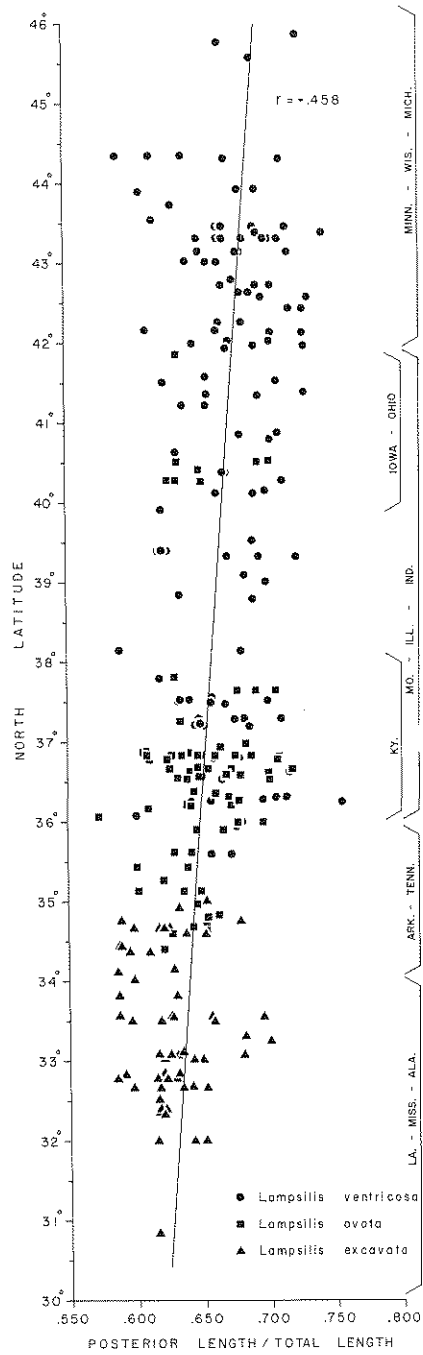


FIG. 5

FIG. 5. Scatter plot of posterior length/total length of shell to latitude in three species of fresh-water mussels. Latitudinal limits of various states are given only for orientation; shells from states other than those given are also included in the plot.

This would indicate a decrease in total length of shell relative to height with more southerly forms. The shell ratio width/total length (Fig. 4) gives a similar increase in ratio number with the approach of lower latitudes, indicating a gradual decrease in total length relative to width. The points on this plot, however, appear more widely scattered, indicating that width is a more variable measurement than height (Fig. 3).

Part of this apparent variability may be due to using shells of rather variable age. Ball (1922: 118) pointed out that younger shells are more obese (swollen) than older ones in the species he considered. However, this does not seem to be the case with the three species considered here, at least as can be determined from those localities where several specimens were measured. The width/total length plot also differs from the preceding one in that the points representing *Lampsilis excavata* are rather markedly "skewed" toward the side of higher ratio numbers, and show a break from the general trend. The reason for this difference, at present, is unknown.

Figure 5 shows a plot of the ratio posterior length/total length which gives a general trend of lower ratio numbers with lower latitudes. These measurements reflect a change in the position of the beak, and they indicate that a more centrally located beak occurs in the more southerly specimens. This plot also appears to show that the points for *Lampsilis excavata* are slightly skewed, in this case toward lower ratio numbers.

Two other shell measurement ratios were analyzed, but they are not shown here in graphic form; these were width/height and DAS/total length. The width/height plot was very similar to the width/total length plot (Fig. 4) with points for *L. excavata* skewed somewhat more markedly toward higher ratio numbers. A plot of DAS/total length showed no apparent trend, a condition taken to mean that the position of the adductor muscle scars is not significant and is probably a mechanical factor. A long shell would require adductor

muscles to be spaced farther apart for effectively closing the two valves, with the reverse being true in shorter shells.

STATISTICAL ANALYSIS OF DATA

Regressions were computed for three shell measurement ratios on latitude, for each species separately, and also for all three species taken together (Table 1). For the height/total length and width/total length ratios of *Lampsilis ventricosa* there is a significant correlation at the 95 percent significance level, indicating a change of ratio number with latitude. For the posterior length/total length ratio of *L. ventricosa* there is little, if any, correlation. *Lampsilis ovata* and *L. excavata* show, from the correlation coefficients, essentially no correlation, for each of the ratios analyzed. Two interpretations can be given for the data of the latter two species: (1) there is actually no change in any of the ratio numbers with a change in latitude; (2) the latitudinal distribution in each of the two species is too limited to indicate a change, although one may be present.

Regressions computed for the three species taken together produce relatively high correlation coefficients for all three shell measurement ratios, indicating a rather significantly high correlation or change with latitude.

However, these data should be treated with some reservation. A high correlation coefficient could be obtained for three populations widely separated latitudinally and in some specific measured character. That is, there could be plots of three clusters of points, separated along one axis by a difference in latitudinal range and along the other axis by a difference in some measurable character. If these clusters were more or less offset, *en echelon*, there would result a relatively high correlation coefficient and a regression line would pass through the three separated clusters of points. If there is a valid correlation for all species taken together, it would point out that sufficient latitudinal range is needed for the corre-

TABLE 1. Statistical data of three shell measurement ratios for *Lampsilis ventricosa*, *L. ovata*, and *L. excavata*. Numbers written as exponents and subscripts to the correlation coefficient (r) indicate the 95 percent confidence interval on r .

Species and shell measurement ratios (X)	Correlation coefficient (r)	Number	Arithmetic Mean (\bar{x})	Standard Deviation (s_x)
<i>Lampsilis ventricosa</i>				
Height/total length	-.346 ^{-.179} _{-.494}	121	.6912	.03736
Width/total length	-.379 ^{-.179} _{-.522}	"	.4453	.04731
Posterior length/total length	+.088 ^{-.092} _{+.262}	"	.6732	.03384
<i>Lampsilis ovata</i>				
Height/total length	+.050 ^{-.173} _{+.268}	79	.7291	.03316
Width/total length	-.014 ^{+.208} _{-.234}	"	.4416	.01553
Posterior length/total length	+.139 ^{-.085} _{+.350}	"	.6508	.02922
<i>Lampsilis excavata</i>				
Height/total length	+.007 ^{-.247} _{+.260}	60	.7533	.03501
Width/total length	-.013 ^{+.208} _{-.266}	"	.5371	.03782
Posterior length/total length	-.067 ^{+.190} _{-.315}	"	.6268	.02730
All 3 species of <i>Lampsilis</i> combined				
Height/total length	-.576 ^{-.488} _{-.652}	260	.7170	.04380
Width/total length	-.556 ^{-.466} _{-.635}	"	.4653	.05735
Posterior length/total length	+.458 ^{+.359} _{+.549}	"	.6557	.03609

lation to appear. It would then follow that the significant correlation of *Lampsilis ventricosa* for the height/total length and width/total length ratios is merely additive to the more extensive trend. It is concluded that the statistical analysis offers but little proof or disproof of the thesis presented here.

CONCLUSIONS

The attempt to analyze the clinal possibilities as they relate to three nominal species of fresh-water mussels, *Lampsilis ventricosa* (Barnes), *L. ovata* (Say) and *L. excavata* (Lea), stems from the practical problem one faces when names

are to be applied to this group. It has been a common experience to label northern forms *L. ventricosa*; that is, those forms found in the upper Mississippi River drainage (in latitudes encompassing New York, northern Ohio, Michigan, Wisconsin, and northern Illinois). On the other hand, specimens from Kentucky and Tennessee would be considered "southern" and with their more centrally placed beaks and their high and well-developed posterior ridges, these forms are identified as *L. ovata*. But in such intermediate areas as southern Ohio and Illinois intergrades are common and they have usually been named *L. ovata ventricosa*. As for *L. excavata*, it seems to have most of the characteristics of *L.*

ovata with respect to the more central position of the beaks and the prominent high posterior ridge; it varies essentially in being consistently smaller in size than *L. ovata*. In distribution *L. excavata* is part of the fauna of the Alabama River system; its differences probably reflect a change brought about since the time the Alabama and Tennessee drainages may have been connected.

Indication that a cline exists among *Lampsilis ventricosa*, *L. ovata* and *L. excavata*, based on shell measurement ratios, raises some doubt regarding the taxonomic status of these three species. One would naturally suggest that these species could be represented by sub-specific taxa. If so, various possibilities come to mind; for example, the three groups could be treated as separate subspecies of a single species complex. On the other hand, the *L. ovata ventricosa* complex is already recognized as quite intimately related so that it could be separated subspecifically from the southern form, *L. excavata*. It is also possible to use taxa of lesser rank, but this approach does not seem warranted here. It must be emphasized that the taxonomic characters used are only those of shell measurement ratios and that only the shells of these animals were examined. Much work remains on the anatomy of the animals and the cross-fertility among these three species has not been studied. The recognition of the possibility that a cline exists

may be helpful in future studies designed to understand better the interrelationships in this complex.

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ZUSAMMENFASSUNG

GEFÄLLE IN DER MUSCHELGATTUNG *LAMPSILIS* (PELECYPODA: UNIONIDAE)

Es wurde versucht ein geographisches Nord-Süd Gefälle in der Süßwassermuschel *Lampsilis* dadurch nachzuweisen, dass Schalenmessungen an 3 Arten dieser Gattung auf deren Vorkommen in verschiedenen Breitengraden bezogen und graphisch dargestellt wurden. Die 260 Exemplare auf denen diese Studie beruht stammen aus einem Gebiet, dass sich vom nördlichen Michigan bis ins südliche Alabama erstreckt; es handelt sich um *L. ventricosa* (Barnes) (121 Exemplare), *L. ovata* (Say) (79 Exemplare) und *L. excavata* (Lea) (60 Exemplare). Die angewandten Verhältniszahlen betreffen folgende Masse der Schale: Höhe/Gesamtlänge, Breite/Gesamtlänge und Hintere Länge/Gesamtlänge. Die eingetragenen zerstreuten Punkte neigen zur Verdichtung auf der einen oder anderen Seite des Diagrammes, je nachdem um welche Messungen es sich handelt. Die Werte der Verhältniszahlen von Höhe und Breite zur Gesamtlänge steigen, je südlicher die Fundorte der Muscheln gelegen sind, während sie für diejenigen der hinteren Länge

zur Gesamtlänge nach dem Süden hin fallen. Für das Bestehen eines Gefälles spricht, dass die Verbreitungsgebiete der 3 Arten sich überschneiden; dies trifft für die beiden nördlichen Arten *L. ventricosa* und *L. ovata* zu, und auch für die südliche Art *L. excavata*, deren Verbreitungsgebiet in dasjenige von *L. ovata* übergeht. Ob ein solches Gefälle nun besteht oder nicht, liess sich mittels der statistischen Analyse nicht eindeutig beweisen. Dennoch liegt es nahe, dass diese 3 nominellen Arten nur Unterarten sind. Ein endgültiges Urteil wird jedoch nur auf Grund weiterer Studien über die Anatomie der Weichteile und die wechselseitige Fruchtbarkeit gefällt werden können.

RÉSUMÉ

"CLINE" DE TROIS ESPECES DE *LAMPSILIS* (PELECYPODA: UNIONIDAE)

Nous avons essayé de mettre en évidence un "cline" géographique nord-sud pour 3 espèces de *Lampsilis*, en mettant en rapport les latitudes de leurs lieux de provenance et les proportions de leurs coquilles. Ces rapports ont été représentés graphiquement. Les 260 spécimens utilisés dans cette étude appartiennent aux espèces *L. ventricosa* (Barnes) (121 spécimens), *L. ovata* (Say) (79 spécimens) et *L. excavata* (Lea) (60 spécimens) et proviennent d'un territoire allant du Nord du Michigan jusqu'au sud de l'Alabama. Les rapports hauteur/longueur totale, largeur/hauteur totale et longueur postérieure/longueur totale furent mis en face des positions latitudinales. La dispersion des points des diagrammes, montre une tendance graduelle vers un côté ou l'autre, selon les mesures considérées: pour ceux qui concernent les rapports de la hauteur et de la largeur à la longueur totale, l'on distingue une augmentation des valeurs en allant vers le sud, tandis que pour les rapports de la longueur postérieure à la longueur totale, les valeurs calculées diminuent en allant vers le sud. Le fait que les aires de répartition de ces 3 espèces se chevauchent donne prise à la supposition de l'existence de ce "cline": c'est le cas pour les 2 espèces septentrionales, *L. ventricosa* et *L. ovata* et également pour l'espèce méridionale *L. excavata* dont l'aire se confond avec celle de *L. ovata*. Quoique l'analyse statistique ne nous ait pas permis de décider définitivement pour ou contre l'existence de ce "cline", il existe probablement et il se pourrait bien que ces 3 espèces ne soient que des sous-espèces. Un jugement définitif ne sera possible qu'après confirmation par des études supplémentaires sur la morphologie des parties molles et sur l'interfertilité de ces espèces.

RESUMEN

CLINO EN TRES ESPECIES DE *LAMPSILIS* (PELECYPODA: UNIONIDAE)

Se utilizaron en este estudio 121 ejemplares de *Lampsilis ventricosa* (Barnes), 79 de *L. ovata* (Say) y 60 de *L. excavata* (Lea). Esas tres especies se distribuyen desde el norte de Michigan hasta el sur de Alabama. Se señalaron, en diagramas de correlación, tres medidas proporcionales de la concha - las razones entre altura/longitud total, diámetro/longitud total y longitud posterior/longitud total - en oposición a la situación latitudinal de los ejemplares de cada especie. Se observó una tendencia a la dislocación gradual de los puntos para un u otro lado del diagrama, de conformidad con la razón utilizada. Así, en la dirección de las bajas latitudes aumenta la frecuencia de las razones altura/longitud total y diámetro/longitud total, y disminuye la frecuencia de la razón longitud posterior/longitud total. Las especies de más al norte, *L. ventricosa* y *L. ovata*, se sobrepone en sus respectivas distribuciones, y la distribución de *L. ovata* se continúa con aquella de la especie del sur, *L. excavata*. Estas relaciones espaciales entre las tres especies favorecen la hipótesis de un clino geográfico de norte a sur. Sin embargo, el análisis estadístico de los datos ofrece poco para probar o negar esa hipótesis. El concepto de clino implicará en un cambio en la taxonomía de las tres especies nominales consideradas. Se sugiere que ellas son probablemente subespecies. Un juicio definitivo depende de estudios confirmatorios basados en la morfología de las partes blandas y en experimentos sobre la fertilidad de los cruzamientos.

АБСТРАКТ

КЛИНАЛИ В ТРЕХ ВИДАХ РОДА *LAMPSILIS* (BIVALVIA, UNIONIDAE)

Алан Кванкара

Сравнивая широтный ареал трех пресноводных перловиц с измерениями их раковин, попытка сделана показать их клиналы с севера на юг. Экземпляры были взяты для изучения их ареала от северного края озера Мичиган и на юг до южной Алабамы. Три измерения раковины в пропорции: высота ко всей длине; ширина ко всей длине и задняя часть раковины ко всей длине ее были занесены на графу в соответствии с широтным ареалом каждого из трех видов: *Lampsilis ventricosa* (Barnes) - (121 экземпляр), *L. ovata* (Say) - (79 экземпляров) и *L. excavata* (Lea) - (60 экземпляров). Разбросанность точек диаграммы показывает тенденцию постепенного их сползания то в одну сторону, то в другую, в зависимости от того, какой пропорцией мы пользовались. Диаграммы пропорции раковины - высота ко всей длине и ширина ко всей длине - показывают увеличение, когда измерения относятся к экземплярам нижних широт. Пропорции же задней части раковины ко всей длине уменьшаются в экземплярах с нижних широт. Некоторое подтверждение клиналы дает то обстоятельство, что ареалы всех трех видов перекрываются и почти совпадают. Более северные виды *L. ventricosa* и *L. ovata* сливаются своими ареалами и *L. ovata* в своих южных границах совпадает с ареалом *L. excavata*. Статистический анализ имеющихся данных не достаточен для подтверждения или отрицания наличия клиналей. Указание на возможность наличия клиналы заставляет поднять вопрос таксономического характера трех указанных видов: возможно, что это только подвиды. Окончательное заключение об этом зависит от изучения их анатомии и экспериментов скрещивания.

