A TAXONOMIC STUDY OF TWO FORMS OF THE
*LAMPSILIS OVATA* COMPLEX IN THE OHIO
RIVER DRAINAGE SYSTEM. (MOLLUSCA:
BIVALVIA: NAIADOIDA)

A Thesis
Presented in Partial Fulfillment of the Requirements
for the Degree Master of Science
by
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The Ohio State University
1971

Approved by

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Adviser
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INTRODUCTION

In the life sciences, the origin of species has long interested some researchers. This interest in evolution at the species level has largely developed since Linnaeus (1758) and especially since Darwin's work in 1859. In some cases, the processes of evolution have seemed simple. In others, the precise nature of these processes has eluded investigators to this day. This study is concerned with the relationship of two forms of pearly, freshwater mussels, or naiads.

*Lampsilis ovata* form *ovata* (Say, 1817) and *Lampsilis ovata* form *ventricosa* (Barnes, 1823) are part of a large group of very similar naiads called the *Lampsilis ovata* complex. It is called a complex because the relationship of some seven "species" remains uncertain despite the fact that all were described over a century ago. They range from the rivers of the East Coast to the Gulf Coast, including the Mississippi River drainage system. Their distributions seem to be either adjacent or intermixed. *Lampsilis ovata* form *ovata* is found exclusively in the Ohio River drainage system (Call, 1885, 1900; Ortman, 1918, 1919; Simpson, 1914), while *Lampsilis ovata* form *ventricosa* is distributed throughout most, if not all, of the Mississippi River and lower Great Lakes systems (Baker, 1928; Call, 1885; Walker, 1913; Simpson, 1914; Ortman, 1919; Utterback, 1916). These two forms are found together at some locales.

There are also some specimens which have some shell characters of both the *ovata* and *ventricosa* forms, but cannot be placed satisfactorily in either category on this basis. These specimens could represent morphological intermediates of one highly variable species, while the *ovata* and *ventricosa* forms could be the morphological extremes of that
species. Another possibility is that the ovata and ventricosa forms could be two closely related species, and the morphological intermediates could be genetic intergrades between them. Or, the ovata and ventricosa forms could be two unrelated species where the intermediate specimens are variants which overlap in shell characters without interbreeding.

These considerations led to the realization that a statistical analysis of the shell characters and a careful examination of the soft parts might offer a clue to a better understanding of the relationship between the two recognized forms. This investigation is primarily concerned with a comparative statistical analysis of seven measurements taken from the shells of the two identifiable forms and such intermediate specimens as were available. A variety of collections have been utilized both from The Ohio State University Museum of Zoology and from The University of Michigan Museum of Zoology. The primary objective of this analysis was to determine if there were significant differences between the two forms. A secondary objective was a descriptive comparison of the anatomy of the soft parts of both forms. The beak sculpture was also studied because it is thought to be a major taxonomic character by at least one worker (Modell, 1942). Measurements of a few glochidia were also taken and an attempt was made to determine the chromosome number of the two forms.
HISTORICAL REVIEW

_Lampeilis ovata_ form _ovata_ was first described and figured as _Unio ovatus_ by Thomas Say in 1817. _Lampeilis ovata_ form _ventricosa_ has had a questionable taxonomic status in relation to the _ovata_ form since the time of its description as _Unio ventricosus_ by D. W. Barnes in 1823. These first papers dealing with the study of freshwater naiads in North America were of a purely descriptive nature. The authors either described shells that were brought to them, or those they collected themselves. Almost without exception, the soft parts of the animals were absent or ignored. Some of the early investigators were aware of their shortcomings in this respect (Say, 1817; Barnes, 1823), but most of these early students were less aware of their lack of knowledge. The descriptions of Rafinesque (1820) have caused problems because they have been difficult to interpret. The descriptions of Lea (1831) also caused problems. Conrad (1836) may have been the first to realize that many of Lea's names were synonyms of earlier descriptions by Rafinesque and others. Some of Lea's species were synonymous with each other as well as with previously described species. In Lea's final synopsis (1870) he recognizes only _Unio ovatus, Unio ventricosus_, and two species of his own, _Unio occidentis_, and _Unio subovatus_, which all recent workers consider to be synonyms of the _ventricosa_ form.

Say (1834) appears to be the first to deal with the relationship of _U. ovatus_ to _U. ventricosus_ to _Unio cardium_ (Rafinesque, 1820). In his synonymy, he lists _U. ovatus_ and _U. cardium_ as separate species with _U. ventricosus, U. occidentis, U. subovatus_, and _Unio capax_ (Green, 1832) as synonyms of _U. cardium_. Conrad (1836), in his monograph, agrees with Say (1834) in recognizing _U. cardium_ as separate from _U. ovatus_, and
considers *U. ventricosus* as a synonym of *U. cardium*. Conrad never published a figure of *U. cardium*, and in fact, his monograph stops in the middle of a quote in the discussion of the species. The complete quote may be found in Say's American Conchology (1832).

Call (1885), on the other hand, seems to consider *U. occidens* and *U. subovatus* to be synonyms of *U. ventricosus*, while treating *U. ovatus* as a separate species. W. A. Marsh (1887) seems to have been the first to realize that two of these names, *U. occidens*, and *U. subovatus* were actually the female and male of the same species. It was not until Sterki (1907) that these names from Lea were accepted as being the male, (*U. subovatus*), and female, (*U. occidens*), of the *ventricosa* form.

Call (1900) gives an idea why this confusion surrounds the *ventricosa* form. He says quite simply that it is a variable shell "and this may be the reason why it has had so many names given it by descriptive naturalists." (Call, 1900:480). It seems even his work was plagued with error. He describes and figures a *Unio subovatus* Say. Since Say never described a species by that name, I am assuming it is the *ovata* form due to the likeness of his description and figure to the original by Thomas Say (1817).

A new system of the naiads was initiated with the publication of Simpson's synopsis of the naiads (1900a). This classification was based on the recognition of apparent phylogenetic relationships confined to the genera *Anodonta*, *Alasmidonta*, and *Unio*. It was an attempt to arrange the genera and species in a better evolutionary order.

Arnold E. Ortmann (1919) was one of the few naturalists who actually went to the rivers and studied the biology of the naiads. He found that in the larger rivers the *ovata* and *ventricosa* forms are practically
always associated. The transition from a very sharp to an almost entirely effaced posterior ridge with the corresponding intermediate condition of the posterior slope was frequently found. This transition of characters is shown in Plate I. "I have quite a number of specimens which are so completely intermediate that I am unable to assign them to either form." (Ortmann, 1919:298).

He states he found a transition from a mixture of the ovata and ventricosa forms to the pure ventricosa form as he went upstream into the tributaries of the Ohio drainage. He states, "both are forms of the same species connected by numerous intergrades, but locally they may be pure." (Ortmann, 1919:303). From my observations and records, it seems that he had an unusual insight into this problem.

Ortmann seems to be a rare investigator in the field insofar as he observed the organisms in their habitat, then drew inferences supported by his data and observations, rather than exclusively on what someone previously said.

The only paper I have been able to find which deals primarily with members of the Lampsis ovata complex is that of Cvancara (1965). He attempted to show the occurrence of a cline, in the most general sense, between the ovata and ventricosa forms, and a related species, Lampsis excavata. He used a sample of 260 specimens for his study and does not note the distributional pattern of the ovata and ventricosa forms cited by Ortmann (1919). From his data, he inferred that all three taxa should be considered distinct species.

To assist in the study of these forms, I have compiled a synonomy of names. It consists of those works I have studied in detail, and often those having a written description of the shell and/or soft parts
Plate I: Comparison of the Posterior Ridge of *Lampsilis ovata* form *ovata* (Say, 1817), an Intermediate Specimen, and *Lampsilis ovata* form *ventricosa* (Barnes, 1823).

OSUM 18551.3, *Lampsilis ovata* form *ovata* with prominent posterior ridge, 4/5 actual size. Clinch River at Swan Island, 5.7 miles SW of Sneedville, Hancock Co., Tennessee.

OSUM 24403, *Lampsilis ovata*, an intermediate specimen with a moderate posterior ridge, slightly smaller than actual size. Clinch River at Kyles Ford, 10 miles NE of Sneedville, Hancock Co., Tennessee.

as well as a figure or plate of the shell. This synonymy is placed in Appendix I for the use of future students of this complex.

EXPERIMENTATION

Methods and Materials

The study is composed of two parts, a quantitative statistical analysis of measured shell characters, and a descriptive study of the beak sculpture and soft parts.

Seven measurements were taken of each specimen. Four of these were taken by using a board upon which the shells were placed. The lower left corner of the board had sides about two inches high and one inch thick. The top of each side was marked in millimeters so it corresponded precisely to the millimeter grid on the board. A transparent hair-line T square was used to eliminate parallax error. This is the same clam board that was used by Stansbery (1961) and is shown in figure 3. The measurements taken in this study are defined below. Those taken on the clam board are listed first.

The total LENGTH was taken to be the maximum anterior-to-posterior dimension of the shell. This was found to be roughly parallel to the hinge line. This was taken by the same method as Stansbery (1961) and is illustrated in Figure 1a.

The ANTERIOR LENGTH is a distance extending from a line at the umbone perpendicular to the total LENGTH, to the most anterior part of the shell. This measurement was also found to be parallel to the hinge line and is shown in Figure 1a.

The HEIGHT is the maximum dorso-ventral dimension of the shell taken at a right angle to the LENGTH. This measurement does not include the ligament or umbones because these structures, more often than
Figure 1: Interior view of left valve (a.), and dorsal aspect (b.) of *Lampsilis ovata* form *ventricosa* showing where shell measurements were taken.
not, are eroded, broken, or both. This measurement was also taken by the same method as Stansbery (1961) and is shown in Figure 1a.

The **DEPTH OF THE CURVE OF THE POSTERIOR RIDGE** is an exterior measurement taken as the maximum difference between a straight line drawn from the most dorsal part of the ridge to the posterior-most point of the shell, and the arc the ridge describes. This is illustrated in Figure 3. On some specimens there was no curve. This was typical of the *ventricosa* form. In other cases, the ridge itself was effaced.

The **WIDTH** is the maximum transverse dimension of the shell when both valves are fit together. Either dividers or a vernier caliper was used to determine this measurement. This was taken by the same method as Stansbery (1961) and is shown in Figure 1b.

The **DISTANCE FROM THE UMBONE TO THE LIGAMENTAL INDENTATION** was taken by determining the very beak of the umbone and measuring in a straight line from that point to the dark indentation on the interior edge of the shell just above the posterior part of the hinge teeth. This is illustrated in Figure 2. In most cases, the umbone was so badly eroded that it was necessary to carefully estimate the exact position of the beak. This seemed to be the only objective means of expressing the length of the ligament. Usually the ligament was broken off the shells and some more permanent measurement had to be substituted.

The above measurements from each shell were divided by the total length of that shell to eliminate as nearly as possible the variation due to age and growth rate. Since these two parameters seem to vary a great deal from one stream to another (Chamberlain, 1931, Isely, 1914), their exclusion introduces a uniformity into the samples which serves to point out any variation due to the measured characters, and reduce
Figure 2: Method of taking the measurement of the distance from the umbone to the ligamental indentation. The umbone is at the left point of the dividers and the indentation is at the right point of the dividers.

Figure 3: Method of determining the depth of the curve of the posterior ridge. The hairline transparent T square has a rule attached upon which the depth is read in millimeters.
the variation caused by these factors. This process resulted in a
series of indices: the WIDTH index, HEIGHT index, ANTERIOR LENGTH
index, DISTANCE FROM THE UMBONE TO THE LIGAMENTAL INDENTATION index, and
DEPTH OF CURVE OF THE POSTERIOR RIDGE index.

The last measurement, the ANGLE OF THE POSTERIOR RIDGE, was taken
with a goniometer specially modified for this purpose. The measurement
was taken at a distance of 4 centimeters from the beak of the umbone to
introduce uniformity in the taking of this measurement. This measure-
ment is shown in Figure 4.

The measurements were taken from many populations throughout the
Ohio River drainage system as shown in Figure 5. This map should not
be confused with a distribution map, but merely shows those sites which
were chosen for the statistical analyses. If more than one form was
present at a given site, or if there were some intermediate specimens,
univariate F-tests were applied to each type of measurement to determine
which was most significantly different at each of 45 different sites.
Those intermediate specimens which could not be placed in either form
were lumped into a group of their own for any given site.

Comparative univariate F-tests were applied to chosen lots of the
*ovata* and *ventricosa* forms. The selected lots of each form were treat-
ed separately. The lots were chosen on the basis of possible likeness
of characters within a given form. This was done to determine if there
were significant differences within a given form throughout its range
in the Ohio River drainage system.

The univariate F-tests, or one-way analyses of variance were pro-
grammed on the computer, and the data were manipulated by a technician
at the Statistics Lab at The Ohio State University. In the analyses,
Figure 4: Method of measuring the angle of the posterior ridge. The instrument is a goniometer.
Figure 5: Map of collection sites where more than 10 specimens were taken of *Lampsilis ovata* f. *ovata* and/or *Lampsilis ovata* f. *ventricosa*. The statistical analyses were performed on data from these sites only.
the null hypothesis, that the means of all the groups were equal, was tested against the alternate hypothesis that at least one pair of means was not equal. Since this test was used in an exploratory manner rather than in a decision-making situation, no particular level of significance was chosen.

The procedure for testing the hypotheses may be found in any introductory statistics text. I found Li (1964) and Hoel (1962) to be helpful. The test of the hypotheses is usually presented in an analysis of variance table as in Figure 6, found in the Results section. The analysis of variance table shows each index with its mean square of SSB and SSE, the F-statistic, and the level of significance as "P less than".

A problem that arises often in science is that of discriminating between two groups of individuals on the basis of several properties of those individuals. If two species were similar with respect to some measurement taken from them, it might not be possible to classify them by means of a single measurement because of a fair amount of overlap in the distributions of this measurement between the two species. However, it might be possible to find a combination of the various measurements whose distributions would not overlap. The linear combination could then be used to yield a type of discriminant score by means of which members of the two species could be differentiated.

Applying this concept to the analysis of the ovata and ventricosa forms, three groups were set up: one of the ventricosa form, one of the ovata form, and one of intermediate specimens.

Given a vector of observations \( Y_{ij} (= Y_{ij}^1, Y_{ij}^2, Y_{ij}^3, Y_{ij}^4, Y_{ij}^5, Y_{ij}^6) \) for the six observations of the jth individual of the ith group, we consider the linear combination \( X_{ij} = a' Y_{ij} \). We could compare the
three groups using the F-statistic,

\[
F = \frac{\sum_i \sum_j (\bar{X}_{ij} - \overline{X}_i)^2 / 2}{\sum_i \sum_j (X_{ij} - \bar{X}_i)^2 / n-3}
\]

Now the vector \( \mathbf{a} = (a_1, a_2, a_3, a_4, a_5, a_6) \) is chosen so that the F-statistic is as large as possible, or discriminates best between the groups. Then for any \( Y_{ij} \), \( X_{ij} \) is computed as \( \mathbf{a}^T \mathbf{Y}_{ij} \) or,

\[
X_{ij} = \mathbf{a}^T \mathbf{Y}_{ij} = (a_1 Y_{ij}^1 + a_2 Y_{ij}^2 + a_3 Y_{ij}^3 + a_4 Y_{ij}^4 + a_5 Y_{ij}^5 + a_6 Y_{ij}^6)
\]

This function is called the linear discriminant score for that vector of observations. The components of \( \mathbf{a} \) have been computed in the same program as the univariate F-tests on the computer at the Statistics Lab at The Ohio State University, and are given in the Results section, as discriminant coefficients. Any six indices from any member of the two forms under study may be multiplied by these coefficients and plotted on a graph (Anderson, 1971). The first taxonomic study to be treated in this manner was that of Fisher (1936), who studied three species of iris. This method has often been used in taxonomic studies (Li, 1964, Hoel, 1962).

A study of the beak sculpture was confined by necessity to very young specimens. The youngest usually have the sculpturing less eroded. Older specimens are often more eroded and no sculpturing can be found. A study of the soft parts was made by carefully dissecting the animal from its shell, and examining the gross anatomy. A total of 250 specimens was studied.

A few measurements of glochidia dimensions were made by using a
compound microscope equipped with an ocular micrometer. An attempt was made to determine the chromosome number of both forms. The squash method using aceto-orcein for a stain was used (LaCour, 1941).

Results

The means, standard deviations, museum numbers, number of specimens per lot, locales, and the level of significance for each index are given for the ovata and ventricosa forms and intermediate specimens in Appendix II. The summary table from the analyses of variance for these forms from the Ohio River drainage system are given in Figure 6. Those indices of a 5% level of significance or less are given in Figures 7, 8, and 9.

A histogram of the linear discriminant scores of the ovata and ventricosa forms, and intermediate specimens is shown in Figure 10. The discriminant coefficients used to calculate the linear discriminant scores are as follows: HEIGHT index = 0.116, WIDTH index = 0.196, DEPTH OF CURVE OF POSTERIOR RIDGE index = 0.781, ANTERIOR LENGTH index = -0.438, DISTANCE FROM THE UMBONE TO THE LIGAMENTAL INDENTATION index = -0.437, and the ANGLE OF THE POSTERIOR RIDGE = -0.247. The graph in Figure 10 clearly shows two peaks. A check back through the museum collections reveals that the peak scores for the ovata form correspond to shells which look very similar. However, those for the ventricosa form show a variety of shell shapes from very obese and swollen to a flatter shell with a moderate posterior ridge.

The gross anatomy of the soft parts of both forms was so similar that after an extensive search, only two differences were found. One is the pigmentation pattern of the mantle flap. The other is the
<table>
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<td>13115.711</td>
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Figure 6: Summary Table From the Overall Analyses of Variance. The data for this table was taken as a whole: 590 observations for the ventricosa form, 230 observations for the evoluta form, and 47 observations for the intermediate specimens.
Figure 7: The most significant ratios determined from the one-way analyses of variance for the comparison of the ventricosa form to the ovala form, to intermediate specimens.

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<td>.042</td>
<td>.001</td>
<td>.010</td>
<td>.001</td>
<td>.001</td>
</tr>
<tr>
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<td>.001</td>
<td></td>
<td>.001</td>
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</table>
Figure 8: The most significant ratios determined from the one-way analyses of variance for the comparison of different populations of the ventricosa form throughout the Ohio River drainage system.

<table>
<thead>
<tr>
<th>RIVERS</th>
<th>HEIGHT LENGTH</th>
<th>WIDTH LENGTH</th>
<th>DEPTH OF CURVE OF THE POSTERIOR RIDGE LENGTH</th>
<th>DISTANCE FROM THE VENTRAL TUBE TO THE LEGAMENTAL INDENTATION LENGTH</th>
<th>ANTERIOR LENGTH</th>
<th>DEGREES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Walhonding, Licking, and East Fork Little Miami</td>
<td>.002</td>
<td></td>
<td></td>
<td></td>
<td>.001</td>
<td>.028</td>
</tr>
<tr>
<td>Green, Red, and Greenbrier</td>
<td>.002</td>
<td>.001</td>
<td></td>
<td>.012</td>
<td>.003</td>
<td></td>
</tr>
<tr>
<td>Kanawha, lower Greenbrier, and upper Greenbrier</td>
<td></td>
<td></td>
<td></td>
<td>.022</td>
<td></td>
<td>.039</td>
</tr>
<tr>
<td>Scioto, Muskingum, Green, Rockcastle, and Clinch</td>
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<td></td>
<td></td>
<td>.006</td>
<td>.003</td>
<td>.001</td>
</tr>
<tr>
<td>Olentangy upper and lower</td>
<td>.023</td>
<td>.010</td>
<td>.001</td>
<td></td>
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</tr>
<tr>
<td>Rockcastle, Green, and Muskingum</td>
<td></td>
<td></td>
<td></td>
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<td>.001</td>
<td></td>
</tr>
<tr>
<td>Little Darby Creek, Big Walnut</td>
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<td></td>
<td></td>
<td>.001</td>
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<td>.027</td>
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<td>-</td>
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<td>-</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>Olentangy</td>
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<td>-</td>
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<tr>
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<td>-</td>
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<tr>
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<tr>
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</table>
Figure 9: The most significant ratios determined from the one-way analyses of variance for the comparison of different populations of the *ovina* form throughout the Ohio River drainage system.

<table>
<thead>
<tr>
<th>RIVERS</th>
<th>HEIGHT LENGTH</th>
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<th>DEPTH OF CURVE OF THE POSTERIOR RIDGE LENGTH</th>
<th>DISTANCE FROM THE UNION TO THE LIGAMENTAL INDENTATION LENGTH</th>
<th>ANTERIOR LENGTH LENGTH</th>
<th>DEGREES</th>
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<td></td>
<td>.001</td>
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<tr>
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<td>.043</td>
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<tr>
<td>Clinoh, and Rockcastle</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Rockcastle, Green, and Muskingum</td>
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<td>.003</td>
<td></td>
<td>.037</td>
<td>.039</td>
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</tr>
</tbody>
</table>
Figure 10: Histogram of the linear discriminant scores of *Lampsilis ovata* f. *ventricosa*, *Lampsilis ovata* f. *ovata*, and intermediate specimens. Each square represents one individual.
pigmentation or lack of pigmentation extending the length of the entire inner mantle margin.

The mantle flap is a posterior enlargement of the inner mantle margin peculiar to members of the subfamily Lampsilinae. It is longer than wide and free at the anterior end. The flap is fully developed in the mature gravid females. It is present in the males, but is reduced in size. The same color pattern is present in both males and females of a given form. The density of pigment varies from one river to another, and in some cases with the individual. Of the 250 specimens studied, about five could not be placed in either form due to a complete lack of pigment. This was probably due to some physical state of the specimen when preserved, or to the preservative itself especially if formalin was used in some stage of preservation. All specimens have been changed to a mixture of alcohol, glycerine and water (AGW). Those originally preserved in AGW seem to hold their color fairly well. All specimens available were preserved for only 15 years or less.

The pigmentation pattern of the mantle flap in the ventricosa form is shown in Figure 11. It has been discussed and figured by Ortmann (1912). I have illustrated those parts which show the differences between the forms. In the females of the ventricosa form, there is a band of dark pigment in the middle of the flap which begins at the papilli of the incumbent aperture and extends to the free end of the flap. Above the band is a lighter area, orange, dark red, or a flesh color. At the outside edge is a line of gray pigment which is on the outer side of the flap, too, and over the free end. The outer side of the flap is uniformly gray becoming darker at the base of the flap.

The pigmentation of the males is the same, only less pronounced. The
Figure 11: Illustration of Lampelia ovata f, ventricosa showing the interior (a.) and exterior (b.) of the female mantle flap, and interior (c.) and exterior (d.) of the male mantle margin.
ventricosa form usually has pigment extending the length of the inner mantle margin.

The ovata form is distinctly different in its pigmentation pattern. The margin of the mantle flap has no color except for the area of the flap. The edge of the flap is very dark or black as in Figure 12. In the female there is a dark spot on the mantle between the inner and outer margins at the base of the free end of the flap. The free part often has a reddish color on the inner side which radiates out to the gray edges, and a mottled light-dark outer side which may take on a striped appearance. The males of the ovata form lack the dark spot and prominent free end of the flap.

The overall body color of the ovata form is pale to white, but that of the ventricosa form is darker, sometimes beige to brown. I have used these color patterns to distinguish between the forms. All intermediate specimens whose soft parts were preserved were found to be of the ventricosa form.

The beak sculpture shows some variation in the ventricosa form. The most common sculpturing is of a double-looped type. Next are the heavily sculptured bars across the beaks, and the least common are the trapezoidal lines. The ovata form invariably had a double-looped sculpturing that was fine, closely set, and usually eroded even in young specimens. Figure 13 shows a contrast in the beak sculpture between the two forms. 191 specimens were studied, 25 of which were the ovata form. The small numbers of the ovata form may be considered an indication of how easily the beak sculpture had been eroded.

The measurements of glochidia did not vary significantly from those of Ortmann (1919). The ventricosa form had an average length of 0.25 mm,
Figure 12: Illustration of *Lampsilis ovata* f. *ovata* showing the interior (a.) and exterior (b.) of the female mantle flap, and the interior (c.) and exterior (d.) of the male mantle margin.
Figure 13: An illustration of the variety of beak sculpture of *Lampsilis ovata*

form ovata, 8 specimens. OSUM 20377. Clinch River between Brooks Island and Possumtrot Run, Hancock Co., Tennessee.

form ovata, 9 specimens. OSUM 16769, 23283, 19312. Clinch River at Kyles Ford, Hancock Co., Tennessee. Clinch River, 0.8 mi. above Sneedville Bridge, Hancock Co., Tennessee.

form ovata, 3 specimens. OSUM 24557. Clinch River at Webb Island, below Kyles Ford, Hancock Co., Tennessee.

form ventricosa, 5 specimens. OSUM 23263. Clinch River just below Kyles Ford, Hancock Co., Tennessee.

form ventricosa, 1 specimen. OSUM 17515. Green River at Manfordville, Hart Co., Kentucky.

form ventricosa, 5 specimens. OSUM 8480. Licking River at Butler, Pendleton Co., Kentucky.

form ventricosa, 4 specimens. OSUM 21826. Big Darby Creek at the Circleville Waterworks, Pickaway Co., Ohio.

form ventricosa, 1 specimen. OSUM 8002. Little Darby Creek at U.S. Rt. 42 bridge, Madison Co., Ohio.

form ventricosa, 1 specimen. OSUM 21756. East Fork Little Miami River, near Batavia, Batavia Twp., Clermont Co., Ohio.

and a height of 0.27 mm. The ovata form had a length of 0.24 mm, and a height of 0.28 mm. These measurements are too close to be considered significantly different.

The chromosome number could not be determined on specimens preserved in alcohol. The alcohol seems to change the solubility of the chromosome material. The cells of naiads are very small, and only those from the ovary or from young embryos in cleavage are large enough to see individual chromosomes by the squash technique. An intensive study of the chromosomes could not be included here as it would be a long-term project in itself.

A distribution map of the two forms is shown in Figure 14. It shows the present known distribution of these naiads. All available sources indicate that the distributions have been greatly reduced. Many early investigators state the ventricosa form was common throughout the Ohio River system even up into the smaller tributaries. This form presently has a spotty distribution in the large rivers, and into most tributary streams. Ortmann (1919:300) states the ovata form is a big river form and "occurs in very few of the tributaries" of the Ohio system. The present distribution shows the ovata form occurs primarily in tributaries, and few of them. Where it has been found in the lower Tennessee River, the breeding population seems to be dying out (Williams, 1969).

Discussion

The data from the one-way analyses of variance indicate differences between the two recognized forms. At least two measurements were highly significant. In all but two cases, they were the DEPTH OF THE CURVE OF THE POSTERIOR RIDGE index, and the measurement of the ANGLE OF THE
Figure 14: Recent distribution of *Lampsilis ovata* f. *ovata* and *Lampsilis ovata* f. *ventricosa* in the Ohio River drainage system. This map was compiled from records at The Ohio State University Museum of Zoology dating from 1956 to 1971.
POSTERIOR RIDGE. The two exceptions are from the lower Muskingum River, and the Tennessee River. Both samples are widespread and relatively small. Unfortunately, the \textit{ovata} form at these sites is today either very rare or absent. However, the statistical information collected here indicates that the \textit{ovata} and \textit{ventricosa} forms are significantly different from each other with regard to the two above measurements throughout their distributions in the Ohio River drainage system.

Significant differences have been found within a given form when comparisons of many populations of that form are made. For the \textit{ventricosa} form, there were five comparisons in which no significant differences were found. They were all of closely related drainages such as the comparison of sites in the Mohican, Kokosing and Walhonding Rivers. In the remaining comparisons, the \textit{WIDTH} index and/or \textit{ANTERIOR LENGTH} index were significant. The \textit{WIDTH} index has been found to change from an upstream to a downstream direction in many species of naiads (Ball, 1922, Ortmann, 1920). We might assume that the significant variations of that index in the populations studied here are due to that phenomenon. No direct correlation was found between the two significant measurements, the \textit{ANTERIOR LENGTH} index seemed to vary indiscriminantly. However, it is possible that a similar phenomenon to that of the \textit{WIDTH} index is in operation here. We may infer from these investigations that the \textit{ventricosa} form is fairly uniform within a tributary system, but may vary widely from one population in one tributary to another in a non-adjacent tributary of the Ohio system.

In the \textit{ovata} form, the \textit{ANTERIOR LENGTH} index and the \textit{DISTANCE FROM THE UMBONE TO THE LIGAMENTAL INDENTATION} index were significantly different in all cases where different populations were compared. I've casual-
ly observed that the DISTANCE FROM THE UMBONE TO THE LIGAMENTAL INDEN-
TATION index is large in northern rivers, such as the Wabash and Wal-
honding, is intermediate in the Green River, and is small in the Clinch
and Powell Rivers for both forms. This does not seem to be related to
stream size. In the ovata form only, as that index gets smaller the
ANTERIOR LENGTH index seems to get larger. This correlation may indicate
a certain uniformity of characters not apparent in the ventricosa form.
These changes may be due to climate, or to physical properties of the
rivers such as gradient or pH which may induce different expressions of
given genetic traits. Mayr, Lindsley, and Usinger (1953) state that no
two populations of a given species will be exactly alike. It is also
possible that these differences may be due to natural selection.

In the overall analysis shown in Figure 6 comparing the ventricosa
form to the ovata form to intermediate specimens, all indices except
the WIDTH index were significantly different. This index is highly
significant within the ventricosa form from population to population,
but not so in the ovata form. When an overall analysis is done, the
variability of the ventricosa form may exceed that of the ovata form
causing the analysis to show the WIDTH index as a non-significant mea-
surement.

The histogram, Figure 10, indicates several features. Most appa-
rent is that the ventricosa form is more numerous than the ovata form.
An effort was made to get a representative sample from the Ohio River
drainage system, not necessarily equal numbers. The allocation of
certain shells to certain groups is based, for the most part, on iden-
tifications made by Dr. D. H. Stansbery. Since the discovery of the two
distinct pigmentation patterns in the soft parts, this histogram could
be changed. The evidence from the study of soft parts indicates that many of the 47 intermediate specimens could have been grouped with the ventricosa form if their soft parts had been preserved. This would cause the two peaks to become taller, but would probably not cause a better separation of the peaks. From this graph, the two forms appear to be closely related but nearly always distinguishable according to the measurements taken from them.

The two peaks may not necessarily represent two forms. More than one form could be represented by a series of discriminant scores within one peak. Therefore, a cross-check was performed to see if there were any scores which corresponded exclusively to any collection site, or tributary drainage system so much so that they might represent a minor peak. No correlation could be found. The peaks may be considered to be representative of shells coming from the entire Ohio River drainage.

The anatomical studies show two differences between the forms. One is the pigmentation pattern of the mantle flap, and the other is the pigment or lack of pigment on the entire inner mantle margin. Some variation is found within the forms, the ventricosa form showing the greatest amount. Those characters illustrated in Figure 11 and 12 have been used to distinguish between the forms.

The beak sculpture indicates some difference between the forms. In the ventricosa form, a wide variety of sculpturing is found. Most of it is rather heavy and double-looped. In the ovata form, it is always double-looped, very fine and closely set. Considering the fact that the beak sculpturing is eroded more often than not, and that the variability found in this study is a fairly subjective matter, this may not be a good taxonomic character with which to distinguish naiads at
the species level.

When present distribution records are compared with those in the early literature, it becomes apparent that the present distributions are but a remnant of what they were over one hundred years ago. This seems to be somewhat a result of the methods of flood control and sewage disposal employed in the United States. Previous authors state that the ovata form inhabited all the larger rivers of the Ohio system, and the ventricosa form was found everywhere and extended far into all the tributaries. The present distribution is radically different. The ventricosa form is found in the larger rivers and most of the tributaries. It is not abundant. Where the ovata form is found, the ventricosa form is found above and below it. Although I have not been able to investigate most of these sites, the collections taken from them indicate that the ventricosa form is not discontinuous, but extends through the area inhabited by the ovata form. The ventricosa form seems to have a more or less continuous distribution, as man will permit, in the Ohio River drainage system. The ovata form, on the other hand, has a spotty distribution indicating a low tolerance level for the variety of stream situations presently available.

On the basis of the data presented here, I consider the ventricosa and ovata forms of the Lampsis ovata complex to be distinct, but closely related species. Another possible explanation of the data is that these forms are extremes of a single species. If this were so, intermediate specimens should be found at each site where the distributions overlapped. This is not the case. In the Powell and Clinch Rivers I have found virtually no intermediate-looking specimens.

Possibly the differences we see are due to different allelic
states of linked genes responsible for these phenotypes. To get these combinations, the genes would have to be tightly linked, and no crossing-over could occur. Otherwise, we would find ventricosa characteristics combined in the same specimen with ovata characteristics. Out of nearly one thousand shells, and 250 soft parts examined, this has never been observed. The possibility of genetic linkage occurring with the genes responsible for the pigmentation of the mantle flap, inner mantle margin, beak sculpture, and seven different shell dimensions is unlikely. However, until actual breeding studies are carried out, the relationship of these two forms is a matter of conjecture as is the relationship between nearly all closely related species. Possibly we may be at a point in the evolution of these forms where they cannot be said to be one species or two, but rather in between these two extremes. Such a situation is difficult to express taxonomically.

If we were to call the forms subspecies, then some intergrading specimens would have to be present. Also, an area would exist between the two subspecies wherein the intergrades would lie. The distributions of the ovata and ventricosa forms overlap with apparently no intergrading specimens. If we were to designate subspecies on the basis of characters related to geographical and ecological factors alone, at least four or five subspecies could probably emerge from the Ohio River drainage system. Specimens of both forms in the Mohican-Walhonding-Muskkingua system are different from their counterparts in the Clinch and Powell Rivers. The designation of subspecies seems to be premature at this stage of study of the Lampsilis ovata complex.

If the distributions of these forms are studied in relation to the changing environment through time, we find the Ohio River drainage
system may have been at one time drained by six different systems (Flint, 1957, Thornbury, 1968, Leverett, 1921, Coffey, 1961, Simpson, 1900b). By the process of glaciation the drainages were modified to the present system. Since these forms were, in historic times, distributed throughout the Ohio system, they must have spread, at least in the northern tributaries, during or after the time of the glaciers. Distinct ovata and ventricosa subfossils have been found in deposits which may be pre-glacial or interglacial (Stansbery, 1971). We might infer that the initial evolution of these forms took place sometime before the last glaciation, and that they had evolved into the forms as we know them before the time of the last glacier. Similar evolutionary trends between the ovata form, and Lampsilis saxatilis may have occurred as far back as the late Tertiary Age (Simpson, 1900b). Since the distributions of these latter two species are discontinuous, they do not have the opportunity of interbreeding as the ovata and ventricosa forms do.

Both the ovata and ventricosa forms may be found at the same collecting site. I have observed in the Elk River in West Virginia that although they are found together, they are seldom found on the same type of substrate or in the same riffle conditions. Since the ventricosa form is the most variable of the two, it might be more readily adaptable to a variety of habitats. If environmental factors favor the ovata form, the ventricosa form may assume characters similar to the ovata form causing us to suspect that they interbreed. The soft parts and glochidia suggest a close genetic relationship. The likeness of some of the shell characters may be attributed to environmentally related phenomena, natural selection, or to previous interbreeding which has been interrupted. More research on these forms is necessary to determine
if they do interbreed, and if so, to what extent this type of relationship occurs in the *Lampsilis ovata* complex. In the meantime, the bulk of the evidence indicates that we are dealing with two similar, closely related, but separate species.

CONCLUSIONS

The *ventricosa* and *ovata* forms of the *Lampsilis ovata* complex are significantly different from each other with regard to all but one measurement studied here throughout their distributions in the Ohio River drainage system. The one exception is the WIDTH index. The *ventricosa* form is fairly uniform within a tributary system, but may vary widely from one population to another in non-adjacent tributary systems of the Ohio system. The correlation of proportional changes of certain indices in the *ovata* form from one population to another indicates a certain uniformity of characters not apparent in the *ventricosa* form.

The histogram, Figure 10, suggests the two forms are closely related, but nearly always distinguishable according to the measurements taken from them. The two peaks on the graph represent the two forms from the entire Ohio River drainage.

The anatomical studies of the soft parts show two differences in pigmentation. All the other characters of the soft parts appear to be alike for both forms. The studies of the beak sculpture show some differentiation between the forms, again the *ventricosa* form showing the greatest variability. The measurements of glochidia show a likeness in size and shape for both forms.

The distributions of the two forms overlap, but they do not seem
to compete for the same habitat niche, at least not in the same habitat area. The subfossil and recent record indicates these forms may have evolved in preglacial times, and spread throughout their distributional range during or after the glacial ages.

The evidence indicates that these two forms are closely related species. Actual breeding studies should be carried out to determine if they are distinct species, or only one highly variable species.

SUMMARY

The purpose of this study has been to determine the relationship between *Lampeilis ovata* form *ovata*, and *Lampeilis ovata* form *ventricosa* on the basis of shell measurements and anatomical studies of the soft parts. A one-way analysis of variance was applied to each of five indices and one measurement taken from the shells of both forms in such a way that an index was not necessary. Also, a linear discriminant analysis was used to determine the overall relationship of the two forms based on these measurements. The analyses indicated significant differences between the two forms. An anatomical investigation of the soft parts and beak sculpture indicated additional differences. The observations of glochidia indicated a close relationship between the two forms. The geographic distributions of both forms overlap, but they do not seem to compete for a habitat niche at the same site in at least one river. Based on these data, the two forms should, at present, be considered two distinct, but closely related species.
APPENDIX I

A synonymy of names for *Lampsilis ovata* (Say, 1817) and *Lampsilis ventricosa* (Barnes, 1823) is compiled in order to help the reader obtain a better understanding of my concept of these two species. Under each species is a list of synonyms and following each name is its author's name, then the author, date and page of the publication where the name was found.

*Lampsilis ovata* (Say, 1817)

*Unio ovatus* Say, 1817. Say, 1817: pl.2, fig. 7 no pagination.


*Unio ovatus* Say, 1817. Conrad, 1836: 4, pl. 2.

*Unio subovatus* Say.

*Lampsilis ovata* (Say, 1817). Ortmann, 1919: 297-301, pl. 17, figs. 8,9 and pl. 18, figs. 1, 2, and 3.

*Lampsilis ovatus* (Say, 1817). Simpson, 1900: 530.

*Lampsilis ovata* (Say, 1817). Cvancara, 1963: 217, fig. 1b.

*Lampsilis ventricosa* (Barnes, 1823)


*Unio occidenta* Lee, 1829. Lea, 1829: 409,411,420,435, pl. 10, fig. 16.

*Unio subovatus* Lea, 1831. Lea, 1831: 188, pl. 18, fig. 46.

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**Unio canadensis** Lea, 1860.

**Unio cardium** Raf., 1820.

**Unio ventricosus** Barnes, 1823.

**Lampsilis ventricosus**
(Barnes, 1823).

**Unio ventricosus** Barnes, 1823.

**Lampsilis ventricosus**
(Barnes, 1823).

**Lampsilis ventricosa**
(Barnes, 1823).

**Lampsilis ventricosa** var.

**lurida** Simpson, 1914.

**Lampsilis ovata ventricosa**
(Barnes, 1823).

**Lampsilis ovata canadensis**
(Lea, 1860).

**Lampsilis ventricosa perglobosa**
Baker, 1928.

**Lampsilis ventricosa occidens**
Baker, 1928.

**Lampsilis ventricosa**
(Barnes, 1823).

**Lampsilis ventricosa lurida**
Simpson, 1914.

Lea, 1860: 268, pl. 44, fig., 148.

Conrad, 1836: 117-118.

Say, 1832: p1.32, no pagination.

Baker, 1898: 94, pl. 12, figs. 3, 4, and 5.

Call, 1900: 480, pl. 38.

Simpson, 1900: 526.

Simpson, 1914: 38.

Simpson, 1914: 41.

Ortmann, 1919: 301-307, pl. 18, figs. 4, pl. 19, figs. 1, 2, and 3.

Ortmann, 1919: 307-309, pl. 19, figs. 4 and 5.


Baker, 1928: 281-285, pl. 48, fig. 7.

Baker, 1928: 289-291, pl. 93, fig. 5, pl. 94, figs. 5 and 6.
Lampsilis ventricosa
vinnebagoensis Baker, 1928.

Lampsilis ventricosa
(Barnes, 1823).


Cvancara, 1963: 216-217, fig. 1a.
APPENDIX II

This section consists of a series of tables of data. The series is arranged so that the one-way analyses of variance applied to the two forms and intermediate specimens at a given site are first. Second are the analyses of variance applied to chosen lots within the ventricosa form, and third are those applied to the chosen lots of the ovata form. The tables are in alphabetical order according to the locale given in the upper left corner.

Each table is constructed in the following manner. The locale is at the extreme left. Next right is the particular form, or intermediate specimens that were studied at that locale. Under the designated form are the museum numbers. OSUM refers to The Ohio State University Museum of Zoology. UMMZ refers to The University of Michigan Museum of Zoology. The numbers of specimens are associated with their museum numbers. Across the top of the sheets are the indices and measurements. The means (M) and standard deviations (SD) are listed under the specific indices or measurements. The level of significance for each index is also listed as P LESS THAN. No more than two different analyses are listed on any one page. In some cases it was necessary to indicate two pages for a given analysis.
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P LESS THAN

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intermediate specimens

<p>| GSUM | 16770 - 1 M | 0.998 | 0.200 | 0.001 | 0.697 | 0.001 | 0.001 |</p>
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intermediate specimens

<p>| OSHU                                          | 11941 - 2      | .737         | .582        | .038                                    | .293                                              | .250                 | 142.500                |
|                                               | 13605 - 1      | .022         | .060        | .029                                    | .041                                              | .043                 | 2.032                  |
|                                               | 16611 - 1      |              |             |                                         |                                                   |                     |                        |
|                                               |                |              |             |                                         |                                                   |                     |                        |
|                                               | P LESS THAN    | .038         | .063        | .001                                    | .004                                              | .113                 | .001                   |</p>
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