The Tribe Alasmidontini (Unionidae: Anodontinae), Part I: *Pegias*, *Alasmidonta*, and *Arcidens*

ARTHUR H. CLARKE

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ABSTRACT

Clarke, Arthur H. The Tribe Alasmidontini (Unionidae: Anodontinae), Part 1: *Pegias*, *Alasmidonta*, and *Arcidens*. *Smithsonian Contributions to Zoology*, number 326, 101 pages, 32 figures, 24 tables, 1981.—The taxonomy, morphology, life history, and distribution of fourteen species, comprising four traditional genera, are described. Discussions of morphology include descriptions of the shell, anatomy, and glochidium (where possible) of each species and of character variation, together with statistical tables, illustrations, and scanning electron microscope photographs. Distributional data include organized lists of all museum material, with distribution maps, and with special reference to recently collected specimens that are likely to represent living populations. Also discussed are some quantitative effects of water hardness and temperature on shell weight and on characters linked with shell weight, new glochidial characters as observed with the scanning electron microscope, the indirect determination of sex in non-gravid specimens by examination of the demibranchs (Ortmann's method), and taxonomic relationships of the Tribe Alasmidontini. Species recognized are: *Pegias fabula* (Lea), *Alasmidonta* (*Pressodonta*) *viridis* (Rafinesque), *A.* (*P.*) *heterodon* (Lea), *A.* (*Alasmidens*) *mccordi* Athearn, *A.* (*Alasmidonta*) *undulata* (Say), *A.* (*A.*) *arcula* (Lea), *A.* (*A.*) *wrightiana* (Walker), *A.* (*Decurambis*) *marginata* Say, *A.* (*D.*) *atropurpurea* (Rafinesque), *A.* (*D.*) *raveneliana* (Lea), *A.* (*D.*) *varicosa* (Lamarck), *A.* (*D.*) *robusta* (new species), *Arcidens* (*Arkansia*) *wheeleri* (Ortmann and Walker), and *A.* (*Arcidens*) *confragosus* (Say). A new subgenus, *Alasmidens*, is described.

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Contents

The Tribe Alasmidontini (Unionidae: Anodontinae), Part 1: *Pegias*, *Alasmidonta*, and *Arcidens*

Arthur H. Clarke

Introduction

SCOPE.—This is a taxonomic revision of the *Alasmidonta* complex, a related assemblage of 14 species of freshwater mussels traditionally comprising the nominal genera *Alasmidonta* Say (1818), *Pegias* Simpson (1900), *Arcidens* Simpson (1900), and *Arkansia* Ortmann and Walker (1912). All of them live in rivers and several are found only near riffles or rapids where the water is well oxygenated. Nine of the species, at best, are either uncommon, rare, or very rare; in fact, three of these appear to have become extinct in this century. In general ecology and in status of endangerment they resemble another group of unionids in another subfamily (Lampsilinae), variously recognized under the names *Dysnomia* Agassiz (1852), *Epioblasma* Rafinesque (1820), and *Plagiola* Rafinesque (1820), and recently thoroughly monographed by Johnson (1978).

This paper has two parts, a general introductory section and a systematics section. The first part contains discussions of some effects of water quality on established taxonomic characters, some new taxonomic characters of glochidia, the indirect determination of sex in non-gravid specimens, and the taxonomic placement of the *Alasmidonta* complex. The systematics section contains accounts of the taxonomy, morphology (descriptions of shells, anatomy, and glochidia, and analyses of their variation), life history, and geographical distribution of each species, distribution maps, illustrations and SEM photographs. The sections on geographical distribution consist of organized lists, arranged by river systems, of all of the documented site records available from the writer's field work, from museum collections, and from the primary literature. Collections made since 1950 are identified by collector and date because those are most likely to reflect the present occurrence of living populations.

The specimen records listed are principally those from the collections of the Academy of Natural Sciences of Philadelphia (ANSP); the Museum of Comparative Zoology, Harvard University (MCZ); the National Museum of Natural Sciences, National Museums of Canada (NMC); the National Museum of Natural History, Smithsonian Institution (USNM); the Ohio State University Museum of Zoology (OSUM). Those collections produced so many records that the geographical distributions of most species were clearly defined. To save space, records from the

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large and important collection at the University of Michigan Museum of Zoology (UMMZ), and other sources, have been cited only in cases where they further extend the ranges of the species concerned.

For identification of species treated in this paper one should first make a tentative identification by using the illustrations and the distribution maps and then confirm that identification by reading the text. Characters are described in the same sequence under each species and detailed comparisons of species are therefore convenient. Parallelism among subgeneric and generic descriptions also facilitates comparisons at those levels.

SHELL CHARACTERS AND WATER QUALITY.—Correct taxonomic decisions about mollusk populations depend on our ability to discriminate between genetic and ecophenotypic effects. The proper taxonomic placement of the nominate species *Alasmidonta triangulata* (Lea) (Figure 12*e*), which differs in shell characters from typical *Alasmidonta undulata* (Say) (Figure 12*b–d*, *g*), presents such a problem. I believe that a solution to that problem, even if it is only approximate, may have application to similar problems in other species groups.

Alasmidonta "*triangulata*" occurs in coastal drainages south of Virginia and differs from *A. undulata*, which lives in coastal drainages in Virginia and northward, by two sorts of shell characters: those that clearly relate to shell thickness and those that are apparently unrelated to thickness. In individuals of the southern populations the shell is relatively thinner (i.e. more fragile), the hinge plate is narrower, there is no pronounced anterior-ventral thickening, the nacre tends to be pinkish, the beak sculpturing is coarser, the posterior slope tends to be more conspicuously sculptured, the umbones are more centrally located, and the shell is proportionately higher. The first three characters listed above are linked and are discussed here. The other characters are discussed elsewhere under *A. undulata.*

I approached this problem by assembling specimens from the whole geographical range of the group (the St. Lawrence River System in Ontario and Quebec to the Chattahoochee River System in Florida), by examining and measuring these specimens for all characters that appear to be revealing or have been used by other investigators to define taxa, and by comparing these results with the parameters of water quality about which data are available and which appear to be significant.

The specimens used in the investigation are in the Museum of Comparative Zoology, the National Museums of Canada, and the Smithsonian Institution. For most river systems it was necessary to combine measurements from several collection lots so that sufficient data were available for statistical analyses (see discussion below). These data are listed in Table 1.

The shell characters measured were length (L), height (H), maximum width with both valves appressed (W), distance from beak (umbone) to the anterior margin (distance designated BA) measured parallel to the long axis of the shell, strength and extent of sculpturing on the posterior slope (PSS), nacre color, hinge plate thickness measured at the pseudocardinal tooth of the right valve (Hp), and total shell weight (Wt). Linear quantities were measured in mm, weight in grams, and qualitative characters (sculpturing and nacre color) using arbitrary scales from 1 (absence) to 9 (maximal development). The results of linear and weight measurements only are discussed here; other results are given under *A. undulata.*

The water quality information was provided by the United States Geological Survey (Briggs and Ficke, 1977) and J. C. Briggs, (pers. comm.) for rivers of the United States and by the Canadian National Research Council for the Ottawa River in Ontario. The USGS data for each river reported here (Table 2) are from the recording station located farthest downstream but still above the influence of marine water. The Ottawa River data are from measurements taken near Ottawa, Ontario. All hardness and temperature data presented are averages of the most recent 3 years data (taken at approximately 2 week inter-

TABLE 1.—Analysis of the *Alasmidonta undulata* complex: Sample origins, quantities, and lengths

Arbitrary drainage code	*River system*	*Number of specimens (N)*	*Number of lots*	*Length (mm) minimum (mean) maximum*
370	Ottawa River	15	6	39.60 (58.90) 68.20
390	St. Lawrence River	5	1	28.84 (38.93) 47.13
410	St. John River	6	2	35.54 (39.88) 44.47
420	Maine Coastal	4	2	30.58 (49.37) 59.75
430	Merrimac River	29	4	27.16 (44.29) 69.43
440	Massachusetts Coastal	30	2	32.55 (48.06) 62.95
450	Connecticut River	21	4	22.79 (45.02) 72.87
460	Hudson River	31	14	21.28 (44.82) 66.55
461	Passaic River	3	2	29.27 (45.65) 67.25
470	Delaware River	16	3	9.80 (26.44) 46.43
480	Susquehanna River	43	8	22.29 (48.80) 67.34
510	Patuxent River	4	2	48.13 (56.67) 71.18
520	Potomac River	23	9	24.16 (37.71) 56.17
540	James River	22	7	23.73 (43.00) 56.63
550	Tar River	11	6	25.88 (50.36) 70.33
555	Neuse River	21	7	29.07 (52.30) 72.22
565	Wateree-Santee Rivers	4	1	21.20 (30.02) 43.40
620	Ocklokonee River	2	1	39.90, 44.50
625	Flint-Apalachicola Rivers	44	14	24.47 (52.31) 84.40
		334	95	

vals) except for drainages 461 (2 years) and 370, 410, 420, and 440 (1 year).

In order to use the existing data for comparative purposes, it was necessary to make assumptions. These assumptions are, that within acceptable limits, a genetically uniform population has existed within each river system during the period within which the museum specimens were collected, i.e., the past 150 years; that overall trends in annual, average, downstream values for water temperature and water hardness also have not significantly changed; and that, in the rivers under investigation, values measured far downstream are approximately representative of ambient conditions throughout each river system in the regions occupied by the *Alasmidonta undulata* group. These assumptions have not been rigorously tested and they probably cannot be tested. Museum collection lots cannot always be confidently used as unbiased natural population samples but, for some species in some river systems that are now polluted, they probably represent all of the recent historical material that will ever be available. This exercise, then, can only be used to produce "likely" generalities, but if such generalities indicate that particular taxonomic characters are probably ecophenotypic rather than genetic. I consider it imprudent to utilize them for taxonomic discrimination. It is incumbent on a systematist to make taxonomic decisions and to base them on the best information that is available.

The data (Table 2) indicate that high values of the quantity $(Wt \times 10^3) \div (L \times H \times W)$ appear to correspond with moderate hardness and low temperature and that low values of these ratios seem to be related to low hardness and moderate temperature. I am aware from previous experi-

TABLE 2.—Analysis of the *Alasmidonta undulata* complex: Statistical summary of shell measurements (mean and standard error of the mean) and of water quality measurements (mean)

Arbitrary drainage code	*H/L*	*W/L*	*Hp/L*	*Wt* × 10^3/*L* × *H* × *W*	*Hardness (ppm $CaCO_3$)*	*Av. temp. °C*	*No. days > 4.4°C*	*Av. temp on days > 4.4°C*
370	.605 ± .014	.504 ± .017	.098 ± .005	.395 ± .018	100	6.5	170	13.0
390	.645 ± .010	.515 ± .004	.118 ± .004	.358 ± .011	129	9.1	221	14.9
410	.636 ± .009	.501 ± .009	.086 ± .003	.230 ± .009	31	6.7	164	13.8
420	.620 ± .016	.464 ± .017	.088 ± .005	.213 ± .013	15	7.0	197	14.2
430	.636 ± .006	.469 ± .006	.080 ± .002	.213 ± .005	17	12.1	251	16.4
440	.636 ± .005	.446 ± .004	.083 ± .002	.229 ± .003	22	11.0	261	14.6
450	.632 ± .007	.456 ± .006	.097 ± .002	.247 ± .008	35	11.3	244	16.9
460	.613 ± .006	.444 ± .006	.082 ± .002	.253 ± .009	70	11.1	238	15.6
461	.635 ± .040	.467 ± .017	.096 ± .009	.244 ± .018	92	–	250	16.4
470	.673 ± .007	.505 ± .011	.082 ± .003	.226 ± .011	57	13.5	271	16.4
480	.611 ± .004	.407 ± .003	.090 ± .001	.265 ± .005	116	13.8	279	16.6
510	.624 ± .017	.483 ± .012	.072 ± .004	.224 ± .018	–	–	302	–
520	.621 ± .005	.449 ± .007	.088 ± .002	.245 ± .008	106	15.0	293	17.7
540	.635 ± .007	.432 ± .006	.079 ± .002	.234 ± .007	61	15.2	313	17.9
550	.665 ± .010	.477 ± .008	.050 ± .002	.134 ± .013	23	17.0	347	17.7
555	.667 ± .010	.491 ± .010	.062 ± .001	.159 ± .010	21	17.3	365	17.3
565	.666 ± .005	.497 ± .022	.067 ± .003	.161 ± .015	19	19.1	360	19.5
620	.698 ± .006	.566 ± .014	.062 ± .005	.212 ± .003	21	21.2	365	21.2
625	.682 ± .004	.561 ± .006	.064 ± .001	.190 ± .006	30	20.5	365	20.5

ence (Clarke, 1973 and included references) that hard water appears to favor the production of thick shells and that soft water is inimical to that development, but I am not aware that any quantitative relationships have been demonstrated. The effects of temperature on growth have been investigated by Howard (1922:71) who showed that in the Mississippi River at Fairport, Iowa, the rate of growth of several species of freshwater mussels taken together increases rapidly with rising temperatures in excess of about 45° F. Accumulated growth (as measured by increase in volume) within a single water body appears to be directly related to an appropriate summation of average temperature excesses above a critical minimum. Relative shell weight is therefore likely to be inversely related to that summation because, of course, the mantle edges of a more rapidly growing specimen will remain for a shorter time at each shell growth increment, and may be expected to deposit less shell material there, than a slower growing specimen. Furthermore in a rapidly-growing specimen that has attained a length of (say) 50 mm, the outer surface of the mantle has had a shorter period of time to cause additional thickening of the shell than in a slower-growing specimen that has also attained a length of 50 mm.

As a first approximation, the following coefficient (Q_{ht}) is proposed for combining aspects of water temperature and water hardness in a manner that reflects the effect of those two variables on relative shell weight in freshwater mussels:

$$Q_{ht} = \frac{Hd}{D_f \times T_f}$$

Hd = mean total hardness (in ppm $CaCO_3$ + $MgCO_3$), D_f = mean number of days per year when mean water temperature exceeds a threshold amount at which growth begins to occur (that threshold is dependent on the species), and T_f = mean excess of temperature in degrees Celsius on days when that threshold was exceeded.

Figure 1 demonstrates the relationship that

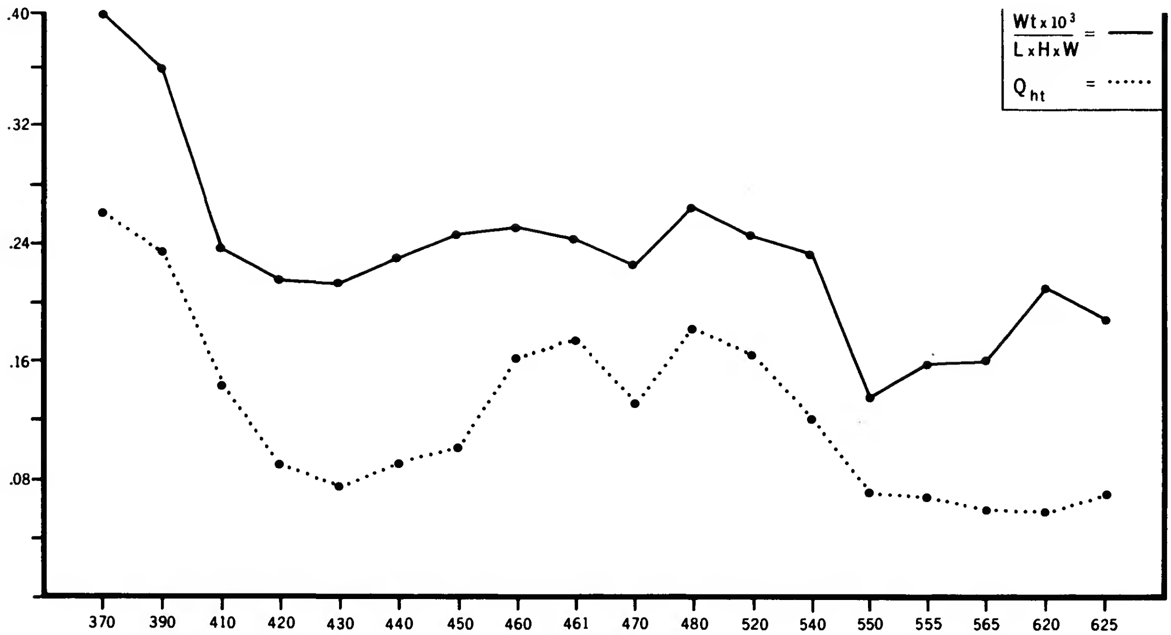

FIGURE 1.—The relationship between aspects of water quality and relative shell weight in *Alasmidonta undulata*.

exists between Q_{ht} and relative shell weight (Wt $\times$ 10^3) $\div$ (L $\times$ H $\times$ W). An arbitrary (but, I hope, reasonable) threshold temperature of 4.4° C (= 40° F) has been used. It has been assumed that *Alasmidonta undulata*, which occurs as far north as the Bousquet River in the cold boreal forest region of northern Ontario, has a growth threshold temperature of less than 7.2° C (45° F), so 4.4° C (40° F) was selected as a working approximation. Selection of a different threshold temperature between 0° C and 7.2° C would have produced a Q_{ht} contour line of similar shape, but located above or below the line shown here. The parallelism of Q_{ht} and relative weight would have remained, however.

The extent of numerical agreement between relative weight and Q_{ht} may also be estimated by use of the Spearman rank coefficient following the method given by Siegel (1956:212). A correlation with $p < 0.01$ results. This indicates a probability of correlation exceeding 99%.

Based on the above discussion I believe that, at least in this species group, intrapopulation differences in relative weight are so well correlated with aspects of water hardness and temperature that one may conclude that they are probably not genetically based and are therefore not useful for discriminating taxa. The characters of relative hinge plate thickness and anterior-ventral thickening are linked to relative weight and intrapopulation differences in those characters must be considered ecophenotypic for the same reasons.

GLOCHIDIAL CHARACTERS.—Surber (1912) provided, for his time, an excellent identification key for glochidia of mussels associated with the button industry. The diagnostic characters he used are size, relative dimensions, shape, general surface sculpturing, and presence or absence of "hooks." Other workers (e.g. Ortmann, 1911; Lefevre and Curtis, 1908, 1912; Baker, 1928; Inaba, 1941; Johnson, 1946) have studied the glochidia of many additional species but no important new, comparative taxonomic characters have been defined. Recently Giusti (1973), Wood (1974), and

Giusti, et al. (1975), have discussed the glochidial morphology of *Anodonta cygnea* L. They, and Calloway and Turner (1979), have shown that scanning electron microscope (SEM) studies of glochidia reveal much more detail than that which could be observed by previous techniques. That method has been used here in the search for additional taxonomic characters.

Unfortunately, most of the species of alasmidontine mussels are uncommon or rare. In addition, glochidia undergo progressive development while they are in the marsupium and only adult females collected that are well along in the breeding cycle contain mature glochidia. In most species that period occurs in the spring during a time of high water. Suitable specimens of some species have been obtained as the result of field work for this study and other studies, however, and a search of museum collections brought forth (especially from the magnificent collection at the Ohio State Museum) additional preserved adult female specimens in an advanced gravid condition. Mature glochidia were therefore available for seven of the fourteen species treated in this paper.

Internal characteristics of glochidial shells are best observed in specimens from which the soft parts have been removed. This is possible with fresh specimens (Calloway and Turner, 1979) but no practical method for completely removing soft parts from preserved glochidia has been described. I have found that useful preparations can be achieved by soaking the preserved glochidia in water for several days, then soaking in a 0.5 N solution of NaOH in water for 12 hours, washing in distilled water, and finally critical-point drying using amyl acetate. When many mature glochidia were treated together in this manner some were always gaped open and suitable for mounting and subsequent examination. Similar results were also obtained in some cases by omitting treatment with NaOH and by simply air drying the washed glochidia. Softening of the tissue with NaOH is often desirable, however; it does not cause distortion in shell characters but it may leave chemical residues that are difficult to wash away. The internal tissues are not removed by either method and the preparations are not "clean," but if the valves are open most internal shell characters are clearly visible.

Using the SEM, several new shell characters now appear to be available and useful for taxonomic studies. These are details of the shape and size of the valves, the fine structure of the "spines" or "hooks," the nature of surface microsculpture, and details of the ligament and hinge. Some aspects of valve shape and of the fine structure of the "hooks" are of special interest.

The valves of alasmidontine glochidia, like those of the European species *Anodonta cygnea* (see Wood, 1974), are not symmetrical as previously believed but exhibit clearly defined anterior and posterior areas. This asymmetry is particularly prominent in *Arcidens confragosus* but it is apparent to some significant extent in all of the species examined.

Each "spine" or "hook" of an anodontine or alasmidontine is a complex hinged structure especially adapted for piercing the skin, fin or scale of a host (a fish in most cases) and ensuring a successful period of attachment. It is much more complex than the generalized terms "spine," "hook," or "spiny hook" imply. The term "stylet," widely used in entomology for another complex structure, also finely adapted for piercing tissue, is therefore introduced here. SEM examination shows that most of the outer surface of each stylet is covered with tiny "microhooks," here termed microstylets. In some species these are flattened and bladelike and have two to six sharp cutting edges and in other species they are pyramidal and round in cross-section. As previously reported by Arey (1924) and others, and independently observed here, these microstylets are inclined forward, toward the point of the stylet, and in the opposite direction to what would be expected if they functioned as barbs on a hook. It is apparent that the sharp, blade-like point of the stylet is adapted to cause the initial piercing and wounding of the fishes fin or scale and that further closing of the valves is accompanied by inward folding of the stylets. This causes the numerous microstylets to pierce the fishes tissue, to anchor the glochidium much more firmly, and to produce enhanced irritation of the fishes flesh thus promoting the formation of a cyst. It also pulls the soft body of the glochidium into more intimate contact with the fishes blood and facilitates subsequent interaction. The size and shape of the stylet and the number, arrangement, shape, and size of the microstylets show clear differences when species are compared with each other. These and other glochidial features provide additional useful characters for the analysis of the interspecific relationships proposed and the taxonomic arrangement used in this paper.

INDIRECT DETERMINATION OF SEX.—In most species of Unionidae, including most of the alasmidontines, sexual differences in the mantle or shell are either obscure or do not exist. Unless a specimen is adult and gravid, prompt assignment of sex therefore presents a problem.

Ortmann (1911:291) demonstrated that males and non-gravid females can be differentiated, even as quite young specimens, by the unaided eye. His method appears to have been overlooked by most subsequent workers. He showed that the number of longitudinal connections (septa) that join the outer and inner laminal tissue (i.e. the outer and inner faces) of each demibranch are much greater in those demibranches that are potentially marsupial than in those that are not. Demibranches that may later become marsupial have more interlamellar connections because more connections are necessary to maintain the integrity of the organ when it becomes distended with eggs or glochidia. Ortmann states that: "the difference is very striking, and may be detected by the naked eye on holding up the gill [= demibranch] toward the light. When I was hunting for sterile females among my material I always used this method in discovering the sex, and the much more crowded septa in the gill examined always indicated the female sex. I never made a mistake, and a specimen selected as a sterile female according to this test always proved to belong to this sex, when a closer microscopical examination was made."

During the present study the number of primary water tubes (i.e. the spaces between the septa) was determined by placing an excised portion of the outer demibranch on a microscope slide, by slicing it transversely in an oblique plane with a razor blade so that the cut edges of the septa were exposed, and by counting the water tubes under a dissecting microscope while using an ocular micrometer scale. The results of these examinations and the tentative sex determinations are given under the species concerned.

I am conducting an evaluation of this convenient sexing method by comparing its results with the presence of sperm or ova, and/or spermatocytes or oocytes, in the sex glands as determined by histological sectioning. Preliminary results indicate that the method is reliable for distinguishing males from non-gravid females. Hermaphrodites have not yet been examined. See van der Schalie (1970) for extensive results of sexing by direct histological methods. I will continue to test the reliability of this indirect technique of sexing as more material becomes available.

TAXONOMIC RELATIONSHIPS OF THE *Alasmidonta* COMPLEX.—Several systems of classification have been proposed for demonstrating evolutionary relationships in freshwater mussels by grouping the genera into higher categories. These systems have recently been reviewed by Heard and Guckert (1970). I follow Ortmann (1910) in the opinion that the Subfamily Anodontinae is one of three major natural groups within the Family Unionidae, and I include in it the nominate genera *Anodonta* Say (1818), *Anodontoides* Simpson (1898), *Strophitus* Rafinesque (1820), *Alasmidonta* Say (1818), *Pegias* Simpson (1900), *Arcidens* Simpson (1900), *Arkansia* Ortmann and Walker (1912), *Lasmigona* Rafinesque (1831), and *Simpsoniconcha* Frierson (1914).

The features that unite these genera are as follows: the shells are thin or somewhat thickened but not massive (e.g. not thick enough for use in the pearl button industry); the hinge teeth are either lacking entirely or are incompletely developed; the microstructure of the marsupial demibranch is unique (all possess secondary water tubes and in all, except species of *Strophitus*, the marsupial water tubes are continuous and not divided by transverse septa); the glochidia are held in the whole of the outer demibranches and they are retained in the demibranches for many months (for example from early fall until late spring) before they are released; the glochidia of all the species that have been studied have stylets (all other species lack stylets except those of *Proptera* Rafinesque (1820), which are anomalous); and the glochidia, in general, attach to the scales, fins or tails of the fish host rather than to the gill filaments.

Morrison (1956) and Clarke and Berg (1959) recognize two related but distinct groups of genera within Anodontinae or its equivalent. We follow the latter authors and consider those groups as tribes. Tribe Anodontini contains *Anodonta*, *Anodontoides*, and *Strophitus* and is characterized by predominantly thin, unsculptured shells; absence or near absence of hinge teeth; and Holarctic distribution. (The placement of *Strophitus* is questionable.) Tribe Alasmidontini contains the remaining genera and is characterized by shells that are somewhat thickened and may or may not be sculptured; by the presence of pseudocardinal hinge teeth in all species; by the presence of an interdental projection and of unique, partly developed lateral teeth in most species; and by Nearctic distribution.

The present monograph is concerned with one of the three groups within the Alasmidontini, the *Alasmidonta* complex, which consists of the genera *Alasmidonta*, *Pegias*, and *Arcidens*. (*Arcidens*, as recognized herein, contains the nominate genera *Arcidens* and *Arkansia*.) The *Lasmigona* complex (containing only *Lasmigona*) and the *Simpsoniconcha* complex (containing *Simpsonconcha*) are the other members of the Tribe. *Simpsonconcha*, with its unusual, small, smooth shell; poorly developed hinge teeth; and unique glochidial host (an amphibian, *Necturus*, instead of fish) is aberrant and its relationship to other species is uncertain. The *Alasmidonta* complex may be distinguished from the *Lasmigona* complex by the beak sculpturing (principally single-looped or nodulous in the alasmidontids, fundamentally double-looped in the lasmigonids), shell morphology (the alasmidontids tend to be subquadrate, inflated, to have the distal end of the posterior ridge located posteroventrally, and not to be alate; the lasmigonids tend to be subovate and relatively longer, compressed, to have the distal end of the posterior ridge located higher, and to be alate), and zoogeography (the alasmidontids are more widely distributed and appear to have had more southern historical affinities than lasmigonids).

In the taxonomic treatment that follows, the conventional generic and subgeneric groupings have principally been used. The exceptions are that, to show presumed relationships, the nominal genera *Arcidens* and *Arkansia* are reduced to subgenera of a single genus (*Arcidens*), the nominal subgenus *Prolasmidonta* has been made a subjective synonym of the subgenus *Pressodonta* (Genus *Alasmidonta*), and a new subgenus of *Alasmidonta*, viz. *Alasmidens*, has been proposed for *A. mccordi*. The bases for these changes are explained in the text where they occur.

A thorough phylogenetic (or phenetic) evaluation of interspecific relationships is not justified at this time because the soft parts of three of the species, and the glochidia of seven, are still unknown. It is hoped that such an evaluation can properly be made in the near future when more complete material of all species of the Tribe Alasmidontini are available.

Acknowledgments.—Special thanks are extended to Ms. Carolyn Cox for meticulously preparing all of the art work, to Dr. Suzanne Hamilton for much expert laboratory work and for reading parts of the manuscript, and to Dr. D. H. Stansbery for generous access to the unparalled collection of dry and alcohol-preserved freshwater mollusks at the Ohio State University. I also thank Dr. Lee Ann Hayek and Dr. Charles Roberts for advice and assistance on statistical and numerical applications, Ms. Cathy Lamb, Ms. Nancy Helm, and Ms. Linda Cullen for other laboratory assistance, Ms. Susann Braden and Ms. Mary Jacque Mann for making the scanning electron microscope photographs, Dr. Eugene

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Genus *Pegias* Simpson, 1900

Pegias Simpson, 1900:660. [Type-species: *Margaritana fabula* Lea, by original designation.]

The glochidium of *P. fabula* (Figure 3) is unique: it is subovate, longer than high, with smooth, unpitted surfaces and two narrow stylets that each bears markedly fewer longitudinal rows (2 rows) of major microstylets on its distal half than on its proximal half.

Comparative features of adults are: shells small (up to about 35 mm long), of medium relative height (H/L about 0.56–0.70), with prominent sexual dimorphism (central posterior point much more acute and extended in males than in females), absence of strong sculpturing (except beak sculpturing) on the disc and on the posterior slope, dehiscent periostracum, and hinge teeth that consist only of one large pseudocardinal tooth in each valve. The anterior-ventral mantle margin is lobate and mantle fusion between the anal and supra-anal openings is absent.

Pegias fabula (Lea, 1838)

FIGURES 2–4

Margaritana fabula Lea, 1838:44, pl. 13:39. [Type-locality: "Cumberland River, Ten[nessee]." The lectotype, herein selected, is Lea's figured specimen and is in the Smithsonian Institution collection of mollusks (USNM 86325); it is labelled "Cumberland R., Tenn. Troost."]

Margaritana curreyiana Lea, 1840:288 [Latin description and localities only]; 1842:233, pl. 18: fig. 40 [same as 1840, with English description and discussion, figure labelled *Margaritana curreyana.*] [Type-locality: "Stone's river, Tenn[essee]." The lectotype, herein selected, is probably Lea's figured specimen and is in the Smithsonian Institution collection of mollusks (USNM 86227); it is labelled "Stone's River, Tenn., Currey."]

THE SHELL

FIGURE 2*a–c*

DESCRIPTION.—Shell small, subquadrate, unusual (resembling large specimens of the marine species *Hiatella arctica* (L)), up to 35 mm long, 22 mm high, and 13 mm wide, thickened anterior-ventrally (up to 3 mm thick) and relatively thin (1 mm thick) posteriorly. Anterior margin semicircular and evenly rounded; ventral margin flatly curved anteriorly and straight or somewhat concave posteriorly; posterior margin bluntly pointed above the midline, obliquely truncated below, and angular or bluntly pointed again at its junction with the ventral margin; dorsal margin long, openly curved, and bent ventrally near its posterior end. In some specimens, presumed to be females because of crowded septa in the outer demibranchs, the upper and lower posterior points are similar; in others (presumably males) the upper point is much more acute and extended. Maximum inflation on the posterior ridge near or above the long axis of the shell. Beaks of moderate width, bluntly pointed, located about 1/3 the distance from anterior to posterior or a little less, and projecting a little above the hinge line. Posterior ridge broad, rounded, quite prominent, and extending to the lower posterior point. A broad, shallow, radial groove in front of this ridge is also present. Posterior slope variable; in

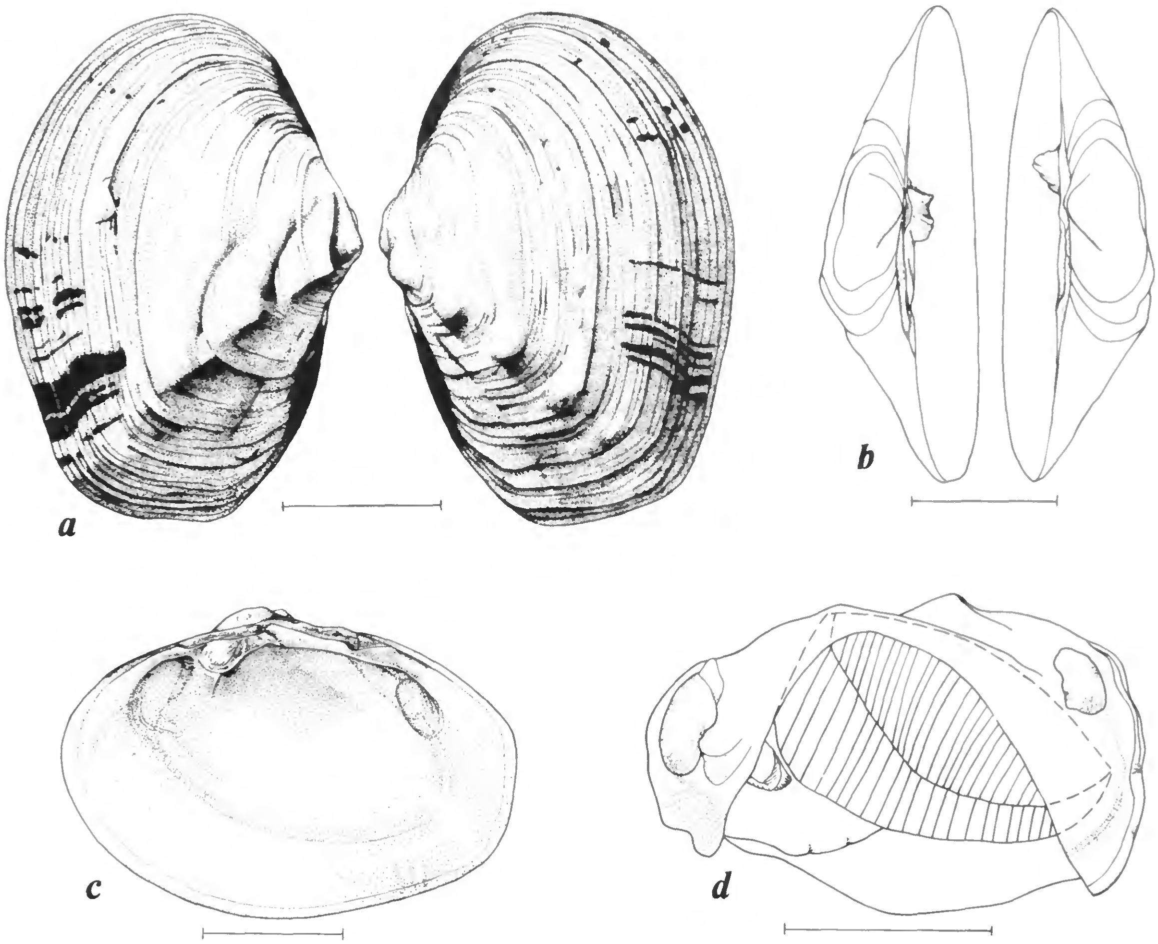

FIGURE 2.—*Pegias fabula*: *a-c*, USNM 86227, Red River, Tennessee; *d*, OSUM 33310, North Fork of Holston River, Nebo, Virginia. (Scale = 1 cm.)

specimens (males?) with a long upper posterior point, the posterior slope is traversed by a prominent, rounded, radial ridge, bounded by broad radial grooves, which extends into that point; in specimens without such a rostrum (females?) the posterior slope bears only an indistinct upper radial ridge. Growth rests apparent as unusually strong, widely-spread grooves, but not prominent. Additional post-juvenile sculpturing consisting only of thread-like, concentric lines of growth. Periostracum worn away from much or most of the shell surface, even in young individuals, and adherent principally posteriorly and in the central radial groove and in beak sculpture grooves (see below). In such specimens the surface is principally chalky or ashy white. Periostracum, where visible, seen to be yellowish brown with indistinct, broad and narrow, brown rays. Ligament rather short and narrow, principally dark brown, and located immediately behind the umbones.

Hinge teeth well-developed but incomplete. Right valve with one erect, irregularly pyramidal pseudocardinal tooth buttressed by a broad rib below. Left valve with one triangular pseudocardinal tooth (without a buttress) that is confluent with the interdental projection and forms with it one strong bifid tooth. A deep socket is present in each valve opposite each pseudocardinal. Lateral teeth short, and vestigial or entirely absent but where discernible numbering 2 in the right valve and 1 in the left. Beak cavity rather narrow and deep. Anterior muscle scars deeply sunken, pallial line impressed and prominent, and scars within beak cavity consisting of a few tiny, short, oval depressions, particularly in the left valve, and placed on the back of the pseudocardinal tooth. Nacre whitish, with a dull gloss, and with bluish or salmon-pink suffusions covering part or all of its surface.

Beak sculpture heavy and composed of about six bars, the first 1 or 2 narrow, semicircular and oblique; the following bars broadly double-looped and expanded on the posterior ridge. The distal bars become obsolete except on the posterior ridge and extend about 12 mm beyond the umbonal apex. Early bars obliterated in most mature specimens but later bars clearly visible in adults.

Variation.—According to Ortmann (1914:65–66) strong sexual dimorphism occurs in this species. Except for his comment that the radial depression in front of the posterior ridge is very faint, and indicated only in the female, no other information appears to have been published about the nature of this dimorphism. Our material is insufficient to establish a relationship with certainty, but of the eight alcohol-preserved specimens (soft parts only) that we have had available (see Table 4), seven were assessed as females either because they were gravid (4 specimens) or because there were about 3 water tubes per mm in the outer demibranch (3 specimens). (One of the presumed females was sectioned and had clearly discernible oocytes in the gonadal tissue.) One other specimen had only 2 water tubes per mm and this was considered as a probable male. The posterior edge of the mantle was also broadly rounded or roundly truncated in the females and the presumed females but centrally pointed in the presumed male. Shells in the Smithsonian Institution collection are also dimorphic in that most are broadly truncated posteriorly but in some the upper posterior ridge is much more pronounced and extended than the lower, giving the shell an acutely pointed posterior.

Aside from this presumed sexual dimorphism, the principal shell variation concerns the relative dimensions (some specimens are noticeably higher than others), size, and the extent to which the periostracum is worn away.

Table 3.—*Pegias fabula:* Shell measurements

Feature	*N*	*Range*	*Mean* ($\bar{x}$)	*S*
	Wallen's Creek, Lee County, Virginia			
Length (m)	13	16.85 -35.45	24.34	5.518
H/L	13	0.565 - 0.642	0.604	0.0217
W/L	13	0.373 - 0.502	0.411	0.0101
B-A/L	13	0.287 - 0.376	0.321	0.0282
Hp/L	13	0.0912- 0.1172	0.1020	0.0130
	Red River, Tennessee			
Length (m)	7	16.03 -35.00	28.09	7.29
H/L	7	0.608 - 0.706	0.660	0.0367
W/L	4	0.388 - 0.454	0.426	0.0307
B-A/L	7	0.310 - 0.400	0.356	0.0348
Hp/L	6	0.0776- 0.1080	0.0931	0.0100

Topographic Anatomy

Figure 2*d*

Specimen Described.—From North Fork, Holston River at Nebo, state route 619 bridge, 9.5 mi (15.2 km) NE of Marion, Rich Valley District, Smyth Co., Va. (OSUM 33310.5, D. H. Stansbery and W. J. Clench!); apparently not relaxed, preserved in 70% ethyl alcohol; shell removed, body length 23.5 mm; sex presumed male.

Description.—Mantle grayish white, patterned centrally with irregular, complex, whitish muscle strands and near the margin by densely packed, silvery white, radial muscle strands; mantle transparent with demibranchs and labial palps showing through. Adductor muscles orange-brown. Mantle outer margin smooth except anterior-ventrally where it is expanded into an abrupt, incurved point and a little posterior to that site where a rounded, low lobe is present; it

TABLE 4.—*Pegias fabula:* Variation in topographic anatomy (abbreviations: Extent = anterior extent of posterior pigmentation (0 = none, Inc. Op. = confined to area of incurrent opening, 1 = beginning at posterior ventral margin, 2 = beginning at mid-ventral margin, 3 = beginning at anterior margin); Strength (A = absent, H = heavy, M = moderate, W = weak); Inc = incurrent opening; Anal = anal opening; A-SA = distance between anal and supra-anal opening; SA = supra-anal opening; Posit. = position of distal end relative to inner demibranchs (NT = not touching, T = touching, OV = overlapping); (F) = female (inferred); GF = gravid female; (M) = male (inferred) (sexes inferred from number of water tubes per mm); Nemb. relax = relaxed with nembutal; Form. fixed = fixed with formalin)

		Mantel pigmentation		*Relative lengths of mantle features (as % of L)*				*Incurrent papillae*		*Labial palps*		*Water tubes*		*Pre-preserv. treatment*	
Spec. No.	*Length (mm)*	*Extent*	*Strength*	*Inc.*	*Anal*	*A-SA*	*SA*	*Ranks*	*Max. Ht. (mm)*	*Posit.*	*Grooves per mm*	*N/ mm**	*Sex*	*Nemb. relax.*	*Form. fixed*
		North Fork, Holston River, Nebo, Virginia (OSUM 33310)													
1	26.4	Inc. Op.	M	15	22	0	19	1	0.4	OV	10	3	(F)	-	-
2	24.3	1	H	17	22	0	21	1	0.4	T	19	-	GF	-	-
3	23.6	1	H	17	22	0	21	1	0.5	OV	12	3	(F)	-	-
4	23.5	1	H	21	21	0	20	2	0.8	OV	14	2	(M)	-	-
5	21.6	1	H	16	22	0	23	2	0.8	OV	11	-	GF	-	-
6	20.0	1	H	16	16	0	26	1	0.5	T	11	3	(F)	-	-
7	20.0	Inc. Op.	M	14	20	0	24	1	0.6	OV	12	-	GF	-	-
8	17.0	1	H	19	21	0	18	1	0.6	OV	16	-	GF	-	-

* Refers to outer demibranchs of non-gravid specimens.

also has a broken band of dense brown pigment running at the edge from the posterior ventral region posteriorly and dorsally to the dorsal end of the supra-anal opening. A band of dark purple-brown pigment is also present along the inner margin of the mantle in the same area; it is particularly wide in the region of the incurrent and anal mantle openings. The incurrent opening is 4 mm long and has a single (partially double) row of tiny rounded papillae just within the edge. The largest of these are about 0.4 mm long and 0.1 mm wide. The separation of the incurrent and anal openings appears to be achieved entirely by the diaphram. Further, the anal opening (3.5 mm long) is not separated from the supra-anal opening (7 mm long) by any permanent mantle connection, although appression of mantle edges for separation of the openings may occur during life. The anal and supra-anal openings are without papillae but a narrow, laminate, internal lip projects from the inner side of the anal opening below the edge.

The demibranchs of preserved specimens are gray-brown. The outer demibranch is 14.5 mm long, 5.5 mm high, with an irregular, openly-curved ventral margin that sweeps anteriorly (interrupted by a rather large marginal indentation) and posteriorly to acute junctions with the attachment line. The outer tissue of the outer demibranch has about 12 double radial filaments per mm and about 5 cross filaments; there are about 1½ underlying water tubes per mm. The inner demibranch is about 17 mm long and 9 mm high, truncated anteriorly, flatly curved ventrally, sharply rounded posteriorly, and projects far beyond the outer demibranch, especially in the anterior-ventral region (5 mm beyond). The outer surface of the inner demibranch also has about 12 double radial filaments per mm and 5 cross filaments, but the specimen is poorly preserved and water tubes are obscure. The inner lamina of the inner demibranch is not attached to the visceral mass. The diaphragm is therefore incomplete and opens into the interlaminar space of the inner demibranchs and also into the mantle cavity posterior to the foot, because the inner laminae of the two inner demibranchs are not fused together in that region.

The labial palps are short and triangular and overlap the inner demibranchs. The lower margin is bent in an open sigmoid curve, the upper margin is short, straight, and rolled outward, and the distal junction of these margins is round, not pointed. The outer surfaces are smooth and the inner surfaces are deeply furrowed and ridged (about 7 furrows per mm); the inner furrows are also visible through the outer surface. The outer member is attached to the mantle, and subdorsally attached to its inner member, for about 60% of its length.

VARIATION.—The material available (Table 4) shows little variation in most characters. Mantle pigmentation is continuous or broken into square spots; it is confined to the posterior region in all specimens. The anal and supra-anal openings are approximately equal in length and tend to be slightly longer than the incurrent opening. No mantle fusion is seen between the anal and supra-anal opening, an observation in agreement with Simpson (1900:661) but in disagreement with Ortmann (1914:66). The incurrent papillae are small and the labial palps touch or overlap the inner demibranchs in all specimens. The labial palps are more finely ridged and grooved than in other species, but substantial variation occurs.

Other characters examined were the extent of fusion of the inner laminae of the inner demibranchs with the visceral mass (free in all specimens) and the shape of the mantle margin. The single (presumed) male specimen, as described above, has an abruptly and acutely pointed protuberance in both mantle edges in the anterior-ventral region and a rounded lobe posterior to it. In the females (See Fig. 2*d*) and presumed females the mantle edge in that region is irregular and locally thickened but no acute point is present.

Relative dimensions of the demibranchs, expressed as percentage of body length, are: outer demibranch, length 55% to 69%, height 24% to 29% (two specimens were anomalous, i.e. height 19% and 39%); inner demibranch, length 60% to 76%, height 35% to 41%. The presumed male had intermediate values for these measurements.

GLOCHIDIUM

FIGURE 3

DESCRIPTION.—Glochidium oval, with hinge flattened, apex acentric and slightly protuberant, and valves flatly convex. Shell 0.309 mm high, 0.354 mm long, and about 0.100 mm in single valve convexity. The posterior margin is more broadly rounded than the anterior and the apex is located about 33% of the distance from anterior to posterior (measured parallel to the hinge axis). Except for a few curved concentric lines that are approximately parallel with the shell margin and located near the apex, the surface is smooth, i.e. not malleated and pitted as in other species. The hinge is slightly convex centrally and about 0.150 mm in length.

Each apical stylet is flatly folded inward, about 0.130 mm long, about 0.050 mm wide at the base, tapering rapidly in the proximal third of its length to about 0.022 mm wide, and tapering more gradually in the distal portion to about 0.019 mm wide near the tip and to a spatulate extremity. A wide membrane connects the stylet on both sides and for about two-thirds its length with the valve margins. The exposed surface of each stylet is covered with microstylets, the largest about 17 μm long and 8 μm wide, arranged in two parallel rows on the distal two-thirds of the stylet, and distally directed. These microstylets are lanceolate, with sharp, pointed apices and longitudinal ridges. The microstylets become much more numerous and gradually smaller near and on the base of the stylet and extend onto the membrane near the base of the stylet and along the ventral edge of the valve, for about one-third of its length, as micropoints <0.2 μm long.

The glochidium described is from an adult collected from the North Fork Holston River at Nebo, Smyth Co., Va. on 27 September 1971 by D. H. Stansbery and W. J. Clench (OSUM

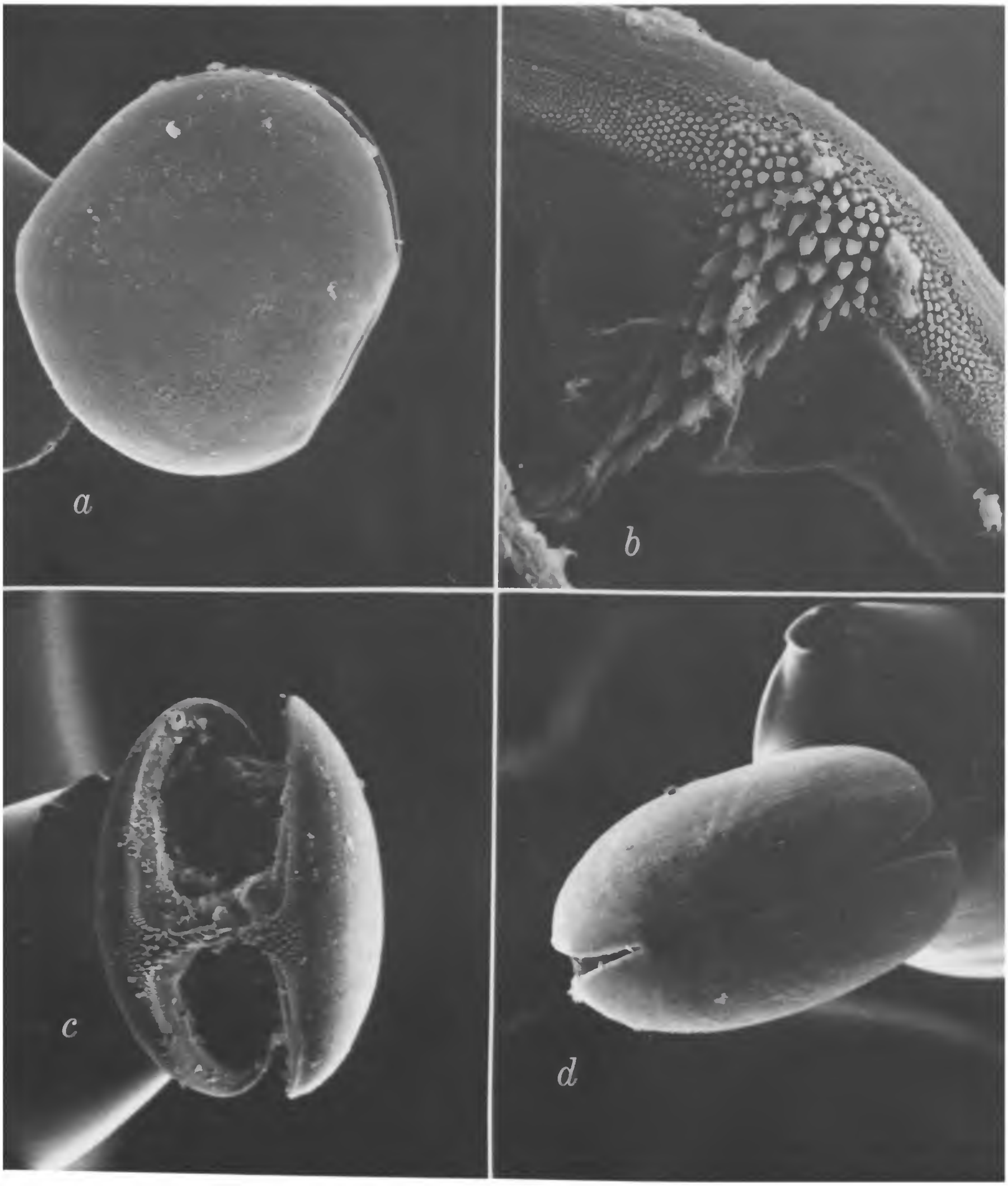

FIGURE 3.—Glochidia of *Pegias fabula*: *a–d*, OSUM 33310 (location same as 2*d*). (*a*, *c*, *d*, × 190; *b* × 475.)

33310). Another glochidium from the same adult is 0.310 mm high and 0.380 mm long. Still another glochidium from the same adult has irregularly arranged distal microstylets. Many of the glochidia were still enclosed in a vitteline membrane and appeared to be in various advanced stages of development.

It should be noted that the measurements of these, and all other glochidia described in this paper, have been taken from SEM photographs. During operation the SEM provides a digital read-out of the degree of magnification shown in the photographs. This read-out may be up to 5% inaccurate, however, so the glochidial dimensions given should be considered reliably accurate only to within 5%.

Life History

Breeding Dates.—Specimens have been reported to be gravid when collected in the North Fork Holston River on 17 September 1912 (Ortmann, 1914:65) and on 27 September 1971 (this study). The specimens reported herein were in various advanced stages of development but were not fully mature. It is probable that the breeding season extends from September to the following spring.

Natural Host.—Unknown.

Habitat.—Blankenship (1971:61) reported *P. fabula* from a creek (Horse Lick Creek, tributary to the Rockcastle River) and stated that "Not one specimen was found to be 'dug in,' but all were free to be moved by the churning water causing additional wear." No additional published data are available but all specimens have been taken from rivers or creeks. The species is now very rare.

Geographic Records

Figure 4

Cumberland River System.—*Rockcastle River Drainage, Kentucky*: Rockcastle River at Livingston, Rockcastle Co. (MCZ; USNM; 1963-64, D. H. Stansbery! (OSUM); and 1967, R. A. Tubb! (OSUM)) and Laurel Co. (MCZ).

Cumberland River Drainage: Little South Fork Cumberland River at Freedom Church Ford, 2 mi (3.2 km) ENE of Ritner, Wayne Co., Ky. (1977, W. and L. Starnes! (OSUM)). Caney Fork, Sweetgum, 4.6 mi (7.4 km) NE of Spencer, Van Buren Co., Tenn. (OSUM). Stones River at Murfreesboro, Rutherford Co., Tenn. (ANSP) and 2.0 mi (3.2 km) W of Murfreesboro at Tenn. Hwy. 96, Tenn. (ANSP and 1966, D. H. Stansbery! (OSUM)).

Red River Drainage, Kentucky: Watts Cove in West Fork Red River, 3.5 mi (5.6 km) W of Trenton, Todd Co. (D. H. Stansbery! (OSUM)).

Tennessee River System.—*Holston River Drainage*: North Fork Holston River at Nebo, 9.5 mi (15.2 km) NE of Marion, Smyth Co., Va.; 1.5 mi (2.4 km) SW of Chatham Hill, Smyth Co., Va.; Rt. 91 bridge at Saltville, Smyth Co., Va (all 1971, D. H. Stansbery and W. J. Clench! (OSUM)); Saltville, Va.; Mendota, Washington Co., Va. (both Ortmann, 1918). Middle Fork Holston River at Chilhowie, 9.5 mi (15.2 km) WSW of Marion, Smyth Co., Va. (1968, D. H. Stansbery and W. J. Clench! (OSUM)). South Fork Holston River at Wright Bridge, 1.9 mi (3.0 km) NW of Damascus, Washington Co., Va. (1974, D. H. Stansbery and W. J. Clench! (OSUM)) and Pactolus, Sullivan Co., Tenn. (Ortmann, 1918).

French Broad River Drainage, Tennessee: French Broad River (MCZ).

Powell River Drainage, Virginia: Flag Pond, Jonesville, Lee Co. (ANSP). Wallen's Creek, Lee Co. (MCZ, ANSP; Ortmann, 1918). Powell River, Dryden, Lee Co. (Ortmann, 1918). Big Mocassin Gap, Scott Co. (Ortmann, 1918).

Clinch River Drainage, Virginia: Clench River, 6 mi (9.6 km) of Cedar Bluff, Tazewell Co. (1965, D. H. Stansbery and J. J. Jenkinson! (OSUM)), 0.2 mi (0.3 km) E of Cliffield, Tazewell Co. (1970, J. M. Condit and M. B. Trautman! (OSUM)), and Jonesville, Lee Co. (USNM). Copper Creek, 1.6 mi (2.6 km) SW of Nickelsville, Scott Co. (1970, D. H. Stansbery and W. J. Clench! (OSUM)).

Hiawassee River Drainage, North Carolina: Valley Creek, Cherokee Co. (ANSP)

Elk River Drainage: Elk River at Estill Springs, Franklin Co., Tenn. (MCZ, USNM, and ANSP) and "in Ala" (MCZ).

Blue Water Creek Drainage, Alabama: Blue Water Creek, Lauderdale Co. (USNM).

Duck River Drainage, Tennessee: Duck River (USNM).

Genus *Alasmidonta* Say, 1818

Monodonta Say, 1817, no pagination. [Type-species: *Unio undulata* Say, 1817, by original designation. Not *Monodonta* Lamarck, 1799; 74 (Gastropoda).]

Alasmidonta Say, 1818:459. [Replacement name for *Monodonta* Say, 1817 (not Lamarck, 1799).]

Alasmodonta Say, 1819, no pagination. [Error for *Alasmidonta* Say, 1818.]

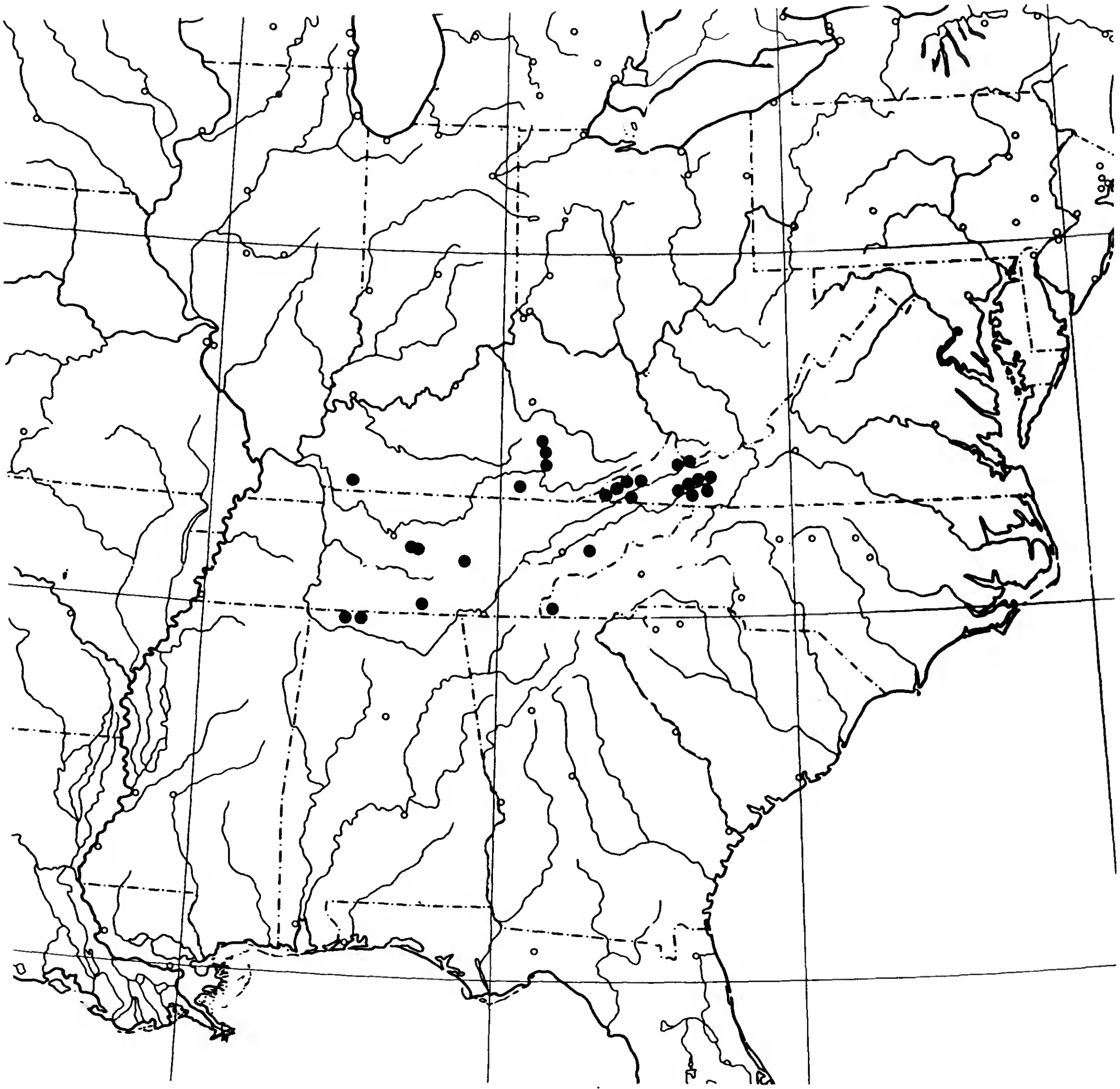

FIGURE 4.—Geographical distribution of *Pegias fabula*.

Alasmodon Thompson, 1820:110. [Unjustified emendation for *Alasmodonta* Say, 1819.]

Alasmisodonta Blainville, 1825:639. [Error for *Alasmidonta* Say, 1818.]

Alasmadonta Jay, 1835:18. [Error for *Alasmidonta* Say, 1818.]

Uniopsis Swainson, 1840:289, 382. [Species included are *Uniopsis radiata* Swainson, 1840 and *Uniopsis mytiloides* Swainson, 1840, both based on the same figure (Swainson's figure 62, which is of *Unio undulata* Say).]

Hemiodon Swainson, 1840:288, 381. [Species included are: "*H. undulatus* [Say?], *An. rugosus*, *purpurascens*, *areolata*" (all *nomena nuda*).]

Anelasmodonta Herrmannsen, 1846:54. [An unjustified emendation of *Alasmodon* Thompson (1820) and *Alasmodonta* Say (1819).

Alasmedonta Gray, 1847:196. [Error for *Alasmidonta* Say, 1818.]

Alasmesondonta Gray 1847:196. [Error for *Alasmidonta* Say, 1818.]

Bullella Simpson, 1900:672. [Type-species: "*Margaritana arcula* Lea" (=*Margarita* (*Margaritana*) *arcula* Lea, 1838), by original designation.]

Jugosus Simpson, 1914:357. [Type-species: *Strophitus wrightianus* Walker, 1901, by original designation.]

The glochidia of five species of *Alasmidonta* are known (*A. viridis*, *A. heterodon*, *A. undulata*, *A. arcula*, and *A. marginata*). All are pyriform, somewhat asymmetrical, with malleated and pitted surfaces and with stylets that are acuminate (wide at the base and rapidly narrowing distally) or somewhat lingulate and that bear fewer longitudinal rows (2–6 rows) of microstylets on their distal halves than on their proximal halves.

Comparative features of adults are: shell small to medium-sized (about 30 to 90 mm long), of low or moderate relative height (H/L about 0.44–0.70 except 0.73–0.83 in *A. arcula*) with mild sexual dimorphism (posterior lateral swelling in females but not in males) in some species but none in most, with sculpturing consisting of corrugations on the posterior slope of most species but none (except beak sculpturing) anterior to the posterior ridge, with nondehiscent periostracum, and with hinge teeth incompletely developed in most species (but not as in *Pegias*) and complete, but aberrant, in some. The anterior-ventral margin is non-lobate and the mantle edges between the anal and supra-anal openings are fused together.

Subgenus *Pressodonta* Simpson, 1900

Calceola Swainson, 1840:282. [Type-species, by monotypy, *Calceola angulata* Swainson, 1840 (=*Unio calceolus* Lea, 1827). Not *Calceola* Lamarck, 1799:89, a coral.]

Pressodonta Simpson, 1900:667. [Type-species *Unio calceolus* Lea (=*Alasmidonta viridis* (Rafinesque)) by original designation.]

Prolasmidonta Ortmann, 1914:44. [Type-species *Alasmidonta heterodon* (Lea) by original designation.]

The glochidia of both species in the subgenus *Pressodonta* are small (about 0.232 mm high in *A. viridis* and 0.255 mm high in *A. heterodon*), depressed pyriform, longer than high, and with narrow, acuminate stylets that bear about 2 longitudinal rows of major microstylets on their distal halves. Among the other alasmidonts, for which the glochidium is known, none has a glochidium less than 0.300 mm in height and none is depressed pyriform.

Comparative features of the adults are: the shells are small (up to about 56 mm long), are of medium relative height (H/L about 0.55–0.71), have low and uninflated umbones, lack sculpturing on the posterior ridge, exhibit discernible sexual dimorphism (the females tend to be posteriorly more inflated than the males), the hinge teeth are composed of pseudocardinal teeth, and (in *A. heterodon* and in many *A. viridis*) well-developed lateral teeth. The anal mantle opening is papillate or crenulate and the inner lamina of the inner demibranchs is variably attached to the visceral mass (i.e. some specimens show complete attachment, other show partial attachment, and in still others there is no attachment).

Alasmidonta (*Pressodonta*) *viridis* (Rafinesque, 1820)

Figures 5–7

Unio viridis Rafinesque, 1820:293. [Type-locality: Ohio River, Kentucky River, and small rivers adjacent to the Kentucky River. Original material lost; neotype selected herein. See remarks.]

Unio calceolus Lea, 1830:265, pl. 3: fig. 1. [Type-Locality: "Ohio." The lectotype (Lea's figured specimen), herein selected, is in the Smithsonian Institution collection of mollusks (USNM 86261) and is labelled "Ohio."]

Alasmidonta truncata Conrad, 1835:73. [A nomen nudum credited by Conrad to Say, with *Unio calceolus* Lea declared as a synonym. Say never published the name, however, so Conrad is its author and it is an objective synonym of *Unio calceolus* Lea.]

Margaritana deltoidea Lea, 1838:43, pl. 13: fig. 38. [Type-locality: "Ohio River, near Cincinnati [and] Scioto [River]." The lectotype, herein selected, is Lea's figured specimen and is in the Smithsonian Institution collection of mollusks (USNM 86215); it is labelled "Scioto River, Ohio. Dr. Kirtland."]

Calceola angulata Swainson, 1840:382. [Based on Lea's original figure of *Unio calceolus* and therefore an objective synonym of *Unio calceolus* Lea, 1827.]

Margaritana minor Lea, 1845:163 [Latin description and localities only]; 1848:82, pl. 8: fig. 26 [the same, with English description, remarks, and illustrations added]. Type-locality: "Tennessee [and] North Carolina." The lectotype, herein selected, is Lea's figured specimen and is in the Smithsonian Institution collection of mollusks (USNM 86224); it is labelled "N.C. Budd."]

Alasmidonta calceolus danielsi Baker, 1928:187, pl. 69: fig. 2; pl. 72: fig. 7–11. [Type-locality: "Moots Creek, White Co[unty], Ind[iana]." Holotype in the Museum of Natural History of the University of Illinois, catalog number Z-14301a (Franzen, 1956:27).]

Alasmidonta calceolus magnalacustris Baker, 1928:188; pl. 69: fig. 3; pl. 72: fig. 12–16. [Type-locality: "Sturgeon Bay, [Lake Michigan], Door Co[unty], Wis[consin]." Holotype in the Museum of The Wisconsin Geological and Natural History Survey, University of Wisconsin, catalog number 933A (Franzen, 1957:33).]

The Shell

FIGURE 5*a,b,d,e*

DESCRIPTION.—Shell variable, ovate, subquadrate or subtriangular; up to 56 mm long, 36 mm high, and 23 mm wide (most specimens are much smaller); slightly thickened anteriorly (up to 3 mm thick) and slightly thinner posteriorly, but not fragile. Anterior margin semicircular and evenly rounded; ventral margin flatly curved, nearly straight, or somewhat concave posterior of center; posterior margin sharply rounded or bluntly pointed below and obliquely flattened (or slightly concave in some specimens) above; junction of posterior margin and dorsal margin angular; and dorsal margin rather short and broadly convex throughout or, in some specimens, concave anteriorly. Maximum inflation above the midline and at center of shell or at posterior ridge. Beaks not inflated, located about 28% to 33% of the distance from anterior to posterior, and projecting only a little above the hinge line in most specimens. Posterior ridge rounded (almost angular above in some specimens), quite prominent, somewhat inflated (especially above), and extending to the posterior point. Posterior slope rather narrow and flattened or concave near the margin. Growth increments marked by concentric low wrinkles and grooves and by clearly apparent lines of growth. Additional postjuvenile sculpturing consisting of an obscure radial ridge dorsal to the posterior ridge and, on some specimens, a few short, raised threads on the posterior slope perpendicular to the lines of growth. Periostracum somewhat glossy and yellowish brown with broad and narrow, wavy green rays. In some specimens the greenish rays are very wide leaving only narrow yellowish rays between them. Rays visible in adults as well as in juveniles. Ligament rather short, of moderate thickness, and brown to blackish.

Hinge teeth well-developed but quite small and incomplete. Pseudo-cardinal teeth stumpy or pyramidal, erect, serrated, irregular, buttressed below, and numbering 1 in the right valve and (in most specimens) 1 in the left, although in some specimens only a socket occurs in the left valve. Interdental projection in the left valve prominent, elevated, irregular, and confluent with the pseudocardinal tooth or even enveloping it and forming a single structure. Lateral teeth absent in most specimens, vestigial or moderately developed in others, and therein numbering 1 or 2 in the right valve and 2 in the left. Beak cavity hollowed out but shallow. Anterior muscle scars well impressed and prominent, pallial line lightly or strongly impressed, posterior muscle scars shallow but clearly defined and scars within beak cavity consisting of a few short, irregular, variable grooves on the back of the hinge plate and two shallow radial grooves extending anterior-ventrally and posterior-ventrally. Nacre shiny, whitish, with a bluish tinge posteriorly, and iridescent posteriorly. In some specimens a creamy suffusion extends over the central part of the shell.

Beak sculpture variable, moderately strong and composed of about 6 irregular, broad curved ridges that are gently convex or sinuate centrally (i.e. double-looped), sharply angled on the posterior ridge, and narrow, straight and crowded on the posterior slope and directed thereon back toward the umbonal apex. Beak sculpture may be seen even on most adult specimens.

VARIATION.—*Alasmidonta viridis* is morphologically more responsive to special habitat characteristics than any other species of its genus. Baker (1928:185–189) has shown that in Wisconsin the species attains its maximum size and thickness in

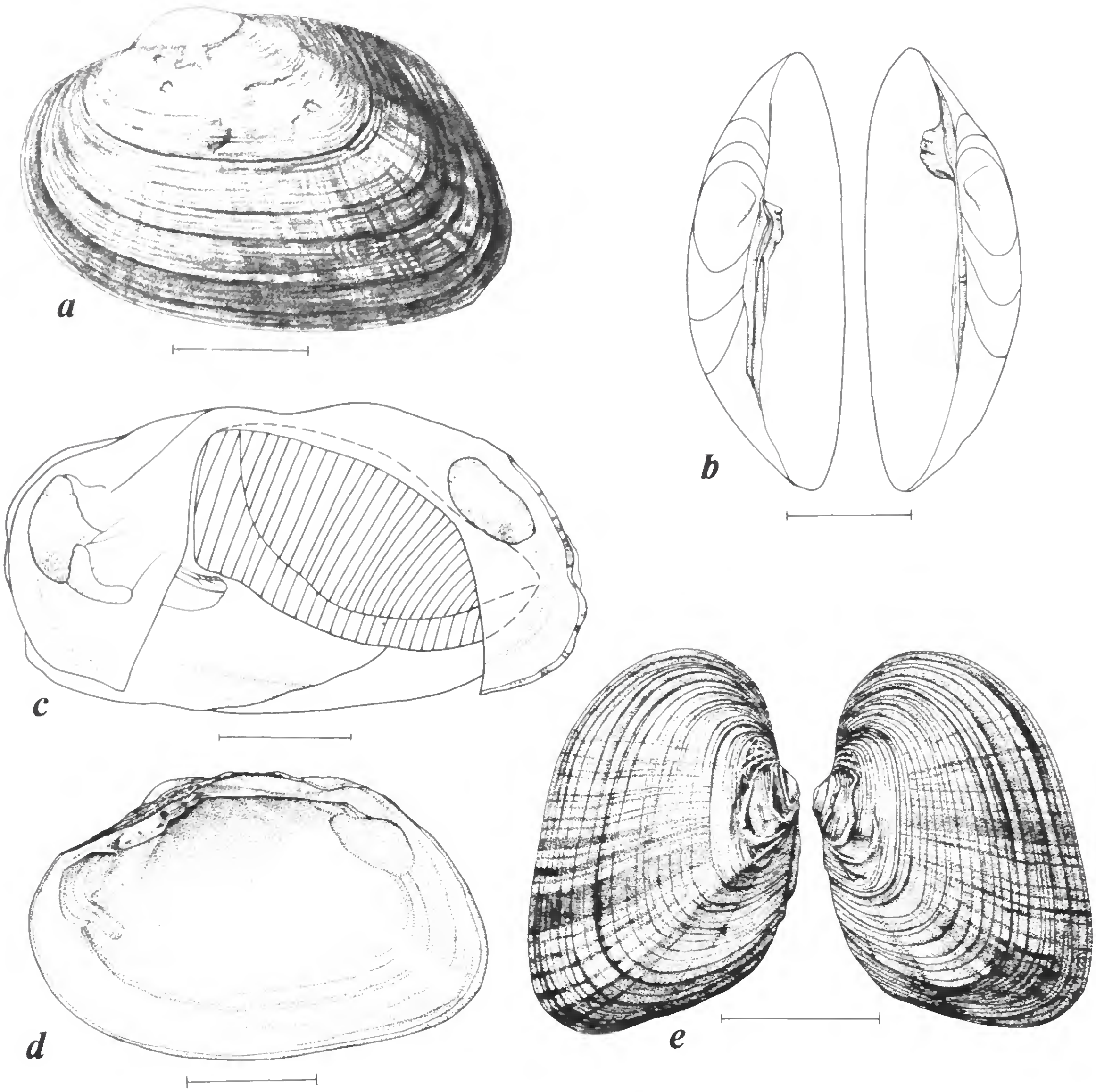

FIGURE 5.—*Alasmidonta viridis*: *a,b,d*, USNM 30085, Scioto River, Columbus, Ohio; *c*, OSUM 9656, Clear Fork, Mohican River, Ohio; *e*, details of umbonal area, USNM 505943, Rockford, Illinois. (Scale = 1 cm.)

large and medium-sized rivers. That is the morph described by Lea as *Unio calceolus*. In small creeks the species is much smaller, with a more obliquely truncated posterior. This is the morph that I believe was described in 1820 by Rafinesque as *Unio viridis* (see Remarks) and by Baker (1928: 187) as *Alasmidonta calceolus danielsi*. Population samples representing the large stream morph and the small stream morph are shown in Table 5 from Little Miami River, Ohio and Mad Creek,

TABLE 5.—*Alasmidonta viridis:* Shell measurements

Feature	*N*	*Range*	*Mean* ($\bar{x}$)	*S*
	Little Miami River, Cincinnati, Ohio (USNM 86214)			
Length (mm)	11	27.55 56.00	39.86	11.31
H/L	11	0.545 - 0.665	0.604	0.031
W/L	11	0.335 - 0.531	0.395	0.055
B-A/L	11	0.234 - 0.317	0.272	0.030
Hp/L	11	0.0571- 0.872	0.0666	0.0089
	Joliet, Illinois (USNM 504529)			
Length (mm)	11	23.52 -40.63	33.06	6.13
H/L	11	0.576 - 0.665	0.613	0.032
W/L	10	0.404 - 0.479	0.435	0.022
B-A/L	11	0.317 - 0.369	0.336	0.017
Hp/L	11	0.0482- 0.0747	0.0571	0.0078
	Mad Creek, Muscatine, Iowa (USNM 504528, 504864)			
Length (mm)	12	24.10 -37.93	30.67	3.26
H/L	12	0.628 - 0.714	0.669	0.030
W/L	12	0.376 - 0.518	0.437	0.046
B-A/L	12	0.253 - 0.350	0.301	0.030
Hp/L	12	0.0563- 0.0761	0.0682	0.0057

Iowa respectively. Intermediate specimens occur in ecologically transitional localities (Baker, 1928: 188). Another ecophenotype (from large lakes) was described as such by Baker (1928:188) under the name *Alasmidonta calceolus magnalacustris.* This morph is more compressed and smaller than the small stream morph.

Baker has also asserted that the female is more inflated at the posterior ridge than the male in the large river morph and shorter than the male in the lake morph. This could not be confirmed from available material.

TOPOGRAPHIC ANATOMY

FIGURE 5*c*

SPECIMEN DESCRIBED.—From Clear Fork, Mohican River, route 3 bridge, Hanover Township Ashland Co., Ohio, collected 25 May 1959 (OSUM 9656, D. H. Stansbery station 1959:57); preserved in 70% ethyl alcohol; shell length 31.9 mm, sex female (gravid).

DESCRIPTION—Mantle grayish white and covered with a fine reticulate pattern of small, pale, orange-white patches separated by grayish lines. Pallial muscles forming a grayish band and adductor muscles orange. A broken band of dark pigment runs along the edge of the mantle from the posterior ventral region to the dorsal end of the supra-anal opening. Incurrent opening 7 mm long and surrounded within the edge (and separated from the edge by a narrow lip) by densely-packed, small, round papillae; those on the inner row the longer (about 1.0 mm long and 0.2 mm wide at the base). Separation of incurrent and anal openings apparently achieved entirely by the diaphragm, although this cannot be fully determined from preserved specimens. Anal opening about 4 mm long, separated from the mantle edge by a lip, and surrounded at the edge by a single row of tiny papillae (about 0.2 mm long and 0.1 mm in diameter at the base). Mantle connection short (1.5 mm) between anal and supra-anal opening. Supra-anal opening narrow, long (7.5 mm), and without papillae.

Outer gravid demibranch of preserved specimen pale brown and inner demibranch pale yellowish brown. Outer demibranch 20 mm long, 8 mm high, 2 mm thick, pad-like, truncated posteriorly, gradually and irregularly curved ventrally, and with margin rising in a flattened curve to an acutely rounded anterior-dorsal apex. The outer tissue has about 10 radial double filaments per mm and 5 cross filaments and the underlying water tubes number 3.0 per mm. Inner demibranch 21 mm long, 9 mm high, irregularly truncated posteriorly, ventral margin flattened, anterior margin diagonally truncated, and projecting beyond the outer demibranch, especially so (4 mm) anterior-ventrally. Outer tissue with about 10 radial double filaments per mm and 5 cross filaments; water tubes about 3 per mm and every fourth water tube is wider than the rest. The inner lamina of the inner demibranch is not attached to the visceral mass. The diaphragm is open posterior to the visceral mass because the inner laminae of the inner demibranchs are not fused there; it is also sharply ridged and perforated by the ends of the water tubes.

Labial palps long-triangular; barely touching

TABLE 6.—*Alasmidonta viridis:* Variation in topographic anatomy; specimens from Clear Fork, Mohican River, Ohio (OSUM 9656) (abbreviations same as Table 4)

Spec. No.	Length (mm)	Mantle pigmentation: Extent	Mantle pigmentation: Strength	Relative length of mantle features (as % of L): Inc.	Anal	A-SA	SA	Incurrent papillae: Ranks	Max. Ht. (mm)	Labial palps: Posit.	Grooves per mm	Water tubes N/mm*	Sex	Pre-preserv. treatment: Nemb. relax.	Form. fixed
1	43.4	1	H	18	10	13	10	4	1.4	T	6	3.0	(F)	–	–
2	42.0	1	H	20	11	12	10	3	1.4	OV	8	3.0	(F)	–	–
3	41.0	1	M	21	10	12	11	4	1.6	NT	10	1.5	(M)	–	–
4	40.0	3	H	19	12	6	20	3	1.2	OV	7	–	GF	–	–
5	38.2	1	H	16	12	10	16	3	1.1	NT	10	–	GF	–	–
6	36.4	1	H	28	12	13	10	3	1.2	T	9	–	GF	–	–
7	36.1	1	H	18	14	14	13	3	1.0	T	9	–	GF	–	–
8	35.4	1	H	18	12	8	17	3+	0.9	T	11	–	GF	–	–
9	35.2	1	H	18	11	12	14	4	1.2	T	8	–	GF	–	–
10	35.1	1	H	23	13	10	17	4	1.4	T	10	–	GF	–	–
11	35.0	2	H	19	12	3	23	4	1.3	OV	9	–	GF	–	–
12	34.0	1	M	17	10	7	19	4	1.1	T	9	–	GF	–	–
13	32.3	3	H	17	11	7	18	4	0.8	T	8	–	GF	–	–
14	31.9	1	H	22	13	5	24	3	1.5	T	6	–	GF	–	–
15	30.5	Inc. Op.	W	19	12	10	13	3	1.0	T	8	–	GF	–	–
16	30.5	1	W	17	10	5	21	3+	0.8	T	7	–	GF	–	–

* Refers to outer demibranchs of non-gravid specimens.

the inner demibranchs; with flatly-sigmoid ventral margin; short, straight dorsal margin; and rounded, centrally located, distal point. The outer surfaces are smooth and the inner appressed surfaces are deeply furrowed (about 6 furrows per mm at the margin). The outer palpus is attached to the mantle for about 5/6 of its length and the free ends of the palpi are subdorsally attached to each other for only 1/4 of their lengths.

The demibranchs in the gravid female specimens from the Mohican River vary in length from 55% to 63% and in width from 25% to 33% of the shell length (13 specimens). The non-gravid specimens that are presumed to be females have outer demibranchs that measure: length, 56% (both) and height 22% and 24% shell length. The presumed male has outer demibranchs that measure: length 61% and height 21% of shell length. Inner demibranchs gave the following measurements in terms of shell length: length 61% to 69%, height 28% to 35% for gravid females; length 60% and 63%, height 27% and 29% for non-gravid females; and length 64%, height 26% of shell length for the single male.

It is of interest that the population sample from Mohican River contained 15 females and only 1 male. Although hermaphroditism might be expected in a headwater species such as *Alasmidonta viridis*, no hermaphrodites were found among 86 sectioned specimens of it reported by van der Schalie (1970). Of course population differences in sexuality may occur.

VARIATION.—Table 6 shows that in the available material most of the observed anatomical features are variable. According to Ortmann (1912:295–6), who then had only two specimens, the mantle connection between the anal and supra-anal openings (A-SA) is almost as long as the anal opening (A), the supra-anal (SA) is only slightly longer than A-SA, the anal opening is crenulate, and the labial palps do not touch the inner demibranch. Table 6 indicates that the relative lengths of A, A-SA, and SA are variable in the Mohican River specimens and that the labial palps overlap the inner demibranchs, or touch them, in many specimens. The anal opening in this species is finely papillate with a single row of short papillae from 0.1 to 0.6 mm long.

Ortmann (1912, 1914) has also shown that the extent to which the inner lamina of the inner demibranch is connected to the visceral mass is variable. Holston River specimens that he examined had the inner lamina completely connected to the visceral mass; in some Clinch River specimens it was almost entirely connected and in others it was only partly connected; and in two Cumberland River specimens it was entirely unconnected. The Mohican River specimens recorded in Table 6 all exhibited the entirely unconnected condition.

Glochidium

Figure 6

Description.—Glochidium short pyriform, 0.232 mm high, 0.286 mm long (parallel to hinge axis), and 0.086 valve convexity (each valve). The posterior margin is more fully rounded and more protuberant than the anterior and the apices are located slightly anteriorly of center (about 47% of the distance from anterior to posterior). The surface is finely malleated (depressions subcircular and about 3 to 8 μm wide) and even more finely pitted. A narrow area near the apex and the ventral margin is without malleations or pits and is sculptured with fine, concentric lines. The hinge is markedly concave and about 0.205 mm long. Ligament narrow and hidden at both ends by the expanded edges of the shell.

Each apical stylet is flatly recurved and bent inward, and is apparently about 70 μm long, 25 μm wide at the base, and very gradually narrowing to the apex (obscure in our partially open material). The stylets are supported on each side, for what appears to be about half its length, by a broad membrane, an expanded portion of the membrane that projects inward from the entire edge of each valve. Each stylet is covered in its exposed surface by parallel radial rows (about 4 rows near the base narrowing to about 2 rows toward the apex) of large microstylets, each about 10–12 μm long. The microstylets are principally subcircular in cross-section but with low, radial angulations. (The angulations are not acute as in *A. undulata* or *A. marginata*). On the base of the stylet the microstylets become gradually smaller and on the outer surface of the apex, and on the supporting membrane near the stylet, they are very small (<0.5 μm) and numerous.

The above description is of a glochidium (specimen B) from an adult mussel collected on 25 April 1959 from Clear Fork Mohican River, Hanover Township, Ashland Co., Ohio by D. H. Stansbery (OSUM 9656). Two other glochidia from the same adult have the following measurements: (specimen A) length 0.286 mm, height 0.235 mm, single valve convexity 0.089 mm; (specimen C) length 0.292 mm and width 0.232 mm. The hinge line of specimen A is approximately straight and that of specimen C is slightly concave (but not as concave as specimen B). The glochidia valves could not be opened completely so details of stylet morphology are still obscure.

The material available does not, of course, indicate the extent of morphological variation in the glochidia of *A. viridis.* Distinctive features are the relatively small size (length about 0.286 to 0.292 μm), height substantially less than length (about 80% of length), a tendency for the hinge to be concave, and a narrow stylet that has only a few (about 4 narrowing to 2) longitudinal rows of major microstylets.

Life History

Gravid Period.—Baker (1928:186) gives "Probably bradytictic, with mature glochidia in the fall (September)." The gravid specimen from Mohican River described above was collected on 25 April 1959 by D. H. Stansbery. A gravid period at least from September to late April is indicated but more data are surely desirable.

Natural Hosts.—J.P.E. Morrison (in Clarke and Berg, 1959) has reported that *Etheostoma nigrum* Rafinesque (johnny darter) and *Cottus bairdi*

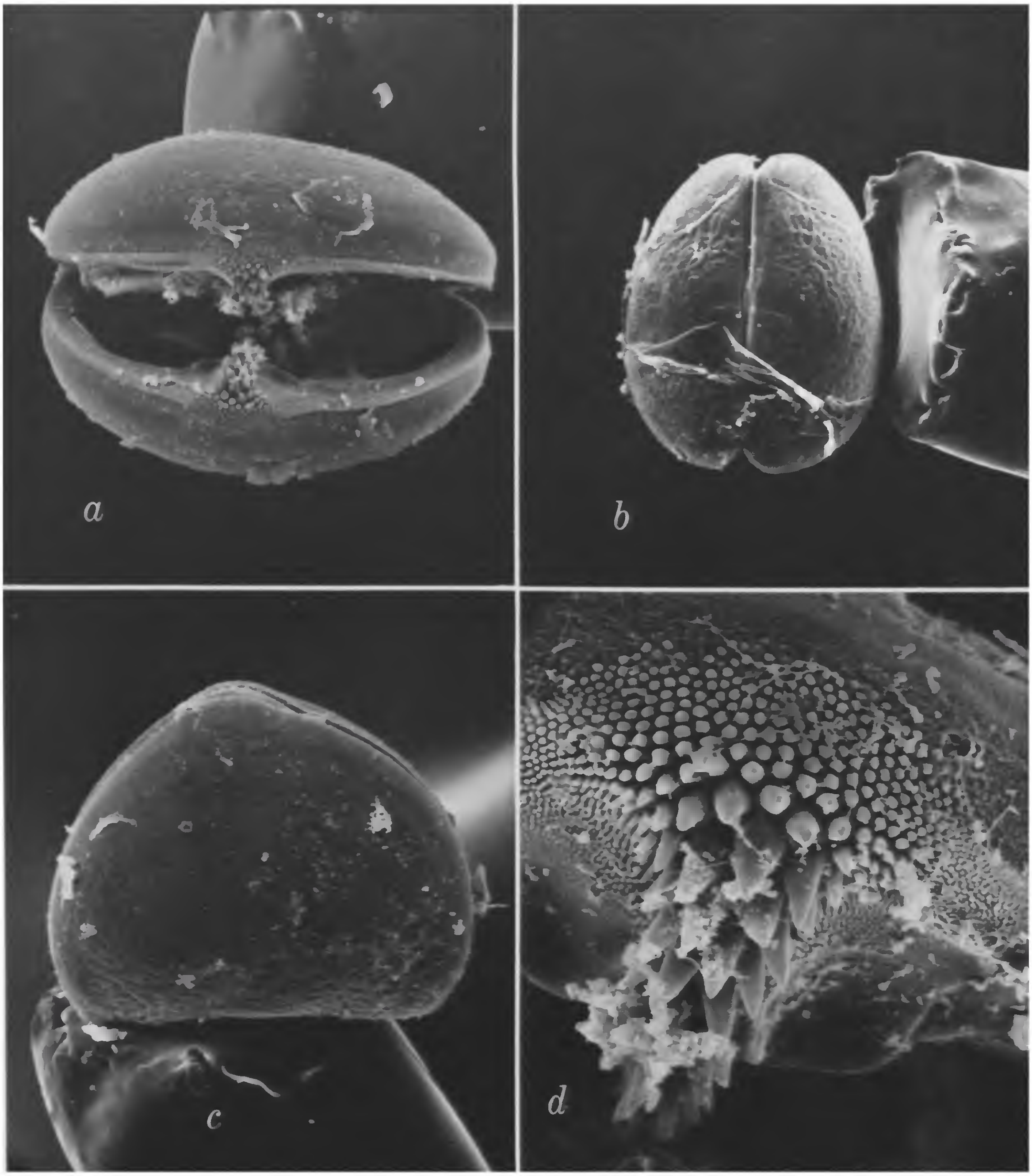

FIGURE 6.—Glochidia of *Alasmidonta viridis*: *a–d*, OSUM 9656 (location same as 5*c*). (*a* × 250; *b* ×180; *c* × 235; *d* ×1115.)

Girard (mottled sculpin) are natural hosts for *A. viridis*.

HABITAT —"In creeks, the usual habitat of this species, *calceolus* [=*viridis*] burrows down into the sand or gravel, locating itself either in the riffles or in the pools. Occasionally, it occurs in mud along the banks. In the larger parts of the [Huron] river it occurs sparsely on sand and gravel. A few abnormally large specimens were taken from a sandy mud substratum in [a] ponded area . . . It is evident that . . . this species follows Ortmann's law—a law to the effect that certain species tend to become more obese as the size of the stream in which they live increases" (van der Schalie, 1938: 58–59).

Baker (1928:186), describing the habitat of the typical morph, writes: "Usually borrowing in streams on a sand bottom in shallow water. Also on lake shores on a sand bottom. In Sturgeon Bay [Wisconsin] on a sandy-clay bottom in 1–1.1 m of water." For the small stream morph he gives (1928:188) the substrate as pebbles, gravel, or sand and the depth as 0.2 to 0.7 m or "shallow water," and adds: "The usual habitat is in sand buried from sight."

GEOGRAPHICAL RECORDS

FIGURE 7

GREAT LAKES–ST. LAWRENCE SYSTEM.—*Lake Michigan Drainage*: Pensaukee River, Abrams, Oconto Co., Wisc. (ANSP, USNM, MCZ). Crystal River, Waupara Co., Wisc. (MCZ). Lake Michigan shore near Milwaukee, Milwaukee Co., Wisc. (ANSP, USNM). Augusta Creek, 2 mi (3.2 km) NE of Midland Park, Kalamazoo Co., Mich., (1960, F. W. Grimm! (NMC)). Grand River, 6 mi (9.6 km) S of Jackson, Jackson Co., Mich. (NMC). Mud Creek, Phillips Road, 2 mi (3.2 km) N of Mason, Ingham Co., Mich. (1960, F. W. Grimm! (NMC)). Grand River, Lansing, Ingham Co., Mich. (ANSP). Bear Creek, Kent Co., Mich. (MCZ). Grand Rapids, Kent Co., Mich, (ANSP, USNM). Bear Lake, Muskegon Co., Mich. (USNM). Clam River, Lake Township, Missaukee Co., Mich. (OSUM). Crockery Creek, Ottawa Co., Mich. (USNM).

Lake Huron Drainage: Maitland River, Auburn, Huron Co., Ont. (NMC). Schoolcraft Lake, Grayling, Crawford Co., Mich. (ANSP). Lake Graylings, Crawford Co., Mich. (ANSP). South Branch, Tobacco River, at bridge just S of Farwell, Clare Co., Mich. North Branch, Chippewa River, Isabella Co., Mich. Prairie Creek, Hwy. 21 bridge, 1 mi (1.6 km) E of Ionia, Saginaw Co., Mich., (all 1966, C. B. Stein! (OSUM)). Saginaw River, Mich. (ANSP). Black River near Lexington, Sanilac Co., Mich. (USNM).

Lake St. Clair Drainage: Medway Creek, 5 mi (8.0 km) N of Arva, Middlesex Co., Ont. (NMC). Sydenham River, 0.5 mi (0.8 km) NNE of Coldstream, Middlesex Co., Ont. (1971, A. H. Clarke and L. R. Clarke! (NMC), empty shells). Thames River, Mitchell, Perth Co., Ont. (ANSP, MCZ).

Lake Erie Drainage: Union Lake, near Pontiac, Oakland Co., Mich. (USNM). Honey Creek, W of Ann Arbor, Washtenaw Co., Mich. (NMC). Huron River, Ann Arbor, Mich. (MCZ). Fleming Creek, Parker's Mill Station, about 5 mi (8.0 km) E of Ann Arbor, Mich. (1965, H. B. Herrington! (NMC)). Stony Creek, Monroe Co., Mich. (OSUM). St. Joe River, Hudson, Lenawee Co., Mich. (USNM). Ten Mile Creek, Sylvania, Lucas Co., Ohio (MCZ). Cedar Creek, Hwy. 6, E edge of Waterloo, De Kalb Co., Ind. (1969, D. H. Stansbery, C. B. Stein! (OSUM), empty valves). Tymochtee Creek, Hwy. 37, 0.1 mi (0.2 km) SW of Marseilles Township, Wyandot Co., Ohio (1971, R. E. Bowers! (OSUM)). Tymochtee Creek near Brownstone, Wyandot Co., Ohio (1971, R. E. Bowers! (OSUM)). Little Sandusky River near Upper Sandusky, Wyandot Co., Ohio (OSUM). West Branch Huron River near Willard, Huron Co., Ohio (1969, R. E. Bowers! (OSUM)). Grand River, 2.6 mi (4.2 km) NE of Dundalk, Dufferin Co., Ont. (1971, B. T. Kidd! (NMC); also 20 other lots from various localities in Grand River system collected by B. T. Kidd in 1971). Cox Creek, 0.6 mi (1.0 km) SE of Bethany Church, Wellington Co., Ont. (1971, B. T. Kidd! (NMC)). Irvine Creek, 3 mi (4.8 km) N of Fergus, Nichol Township, Wellington Co., Ont. and 3 other Irvine Creek localities (1971, B. T. Kidd! (NMC)). Eramosa Branch, Speed River, Guelph, Wellington Co., Ont. (1965, C. B. Stein! (OSUM); 1966, J. G. Oughton! (NMC); also 7 other Speed River lots (NMC)). Conagagique Creek tributary, 0.2 mi (0.3 km) N of Floradale, Waterloo Co., Ont. (1971, B. T. Kidd! (NMC)). Nith River, 100 yds (91 m) upstream from CNRR bridge, Blenheim Township, Oxford Co., Ont. (1971, B. T. Kidd! (NMC)).

Lake Ontario Drainage: West Branch, upper Niagara River, W of Beaver Island State Park, [Niagara Co.], N.Y. (MCZ). Dufferin Island, Niagara River, Ont. (USNM, worn valve). Old Erie Canal, Monroe Co., N.Y. (Robertson and Blakeslee, 1948). Beaver Creek, Warren, Herkimer Co., N.Y. (MCZ). Tonawanda Creek, N.Y. (MCZ). Oriskany Creek, Oriskany Falls, Oneida Co., (Clarke and Berg, 1959).

OHIO RIVER SYSTEM.—*Muskingum River Drainage, Ohio*: Lake Fork, Licking River, Hwy. 661, 2.2 mi (3.5 km) S of Homer, Licking Co. (1975, R. Jezerinac! (OSUM)).

Scioto River Drainage, Ohio: Whetstone Creek above McKibben Road, Gilead Township, Morrow Co. (1962, D. H. Stansbery and C. B. Stein! (OSUM)). Big River at Hwy. 36

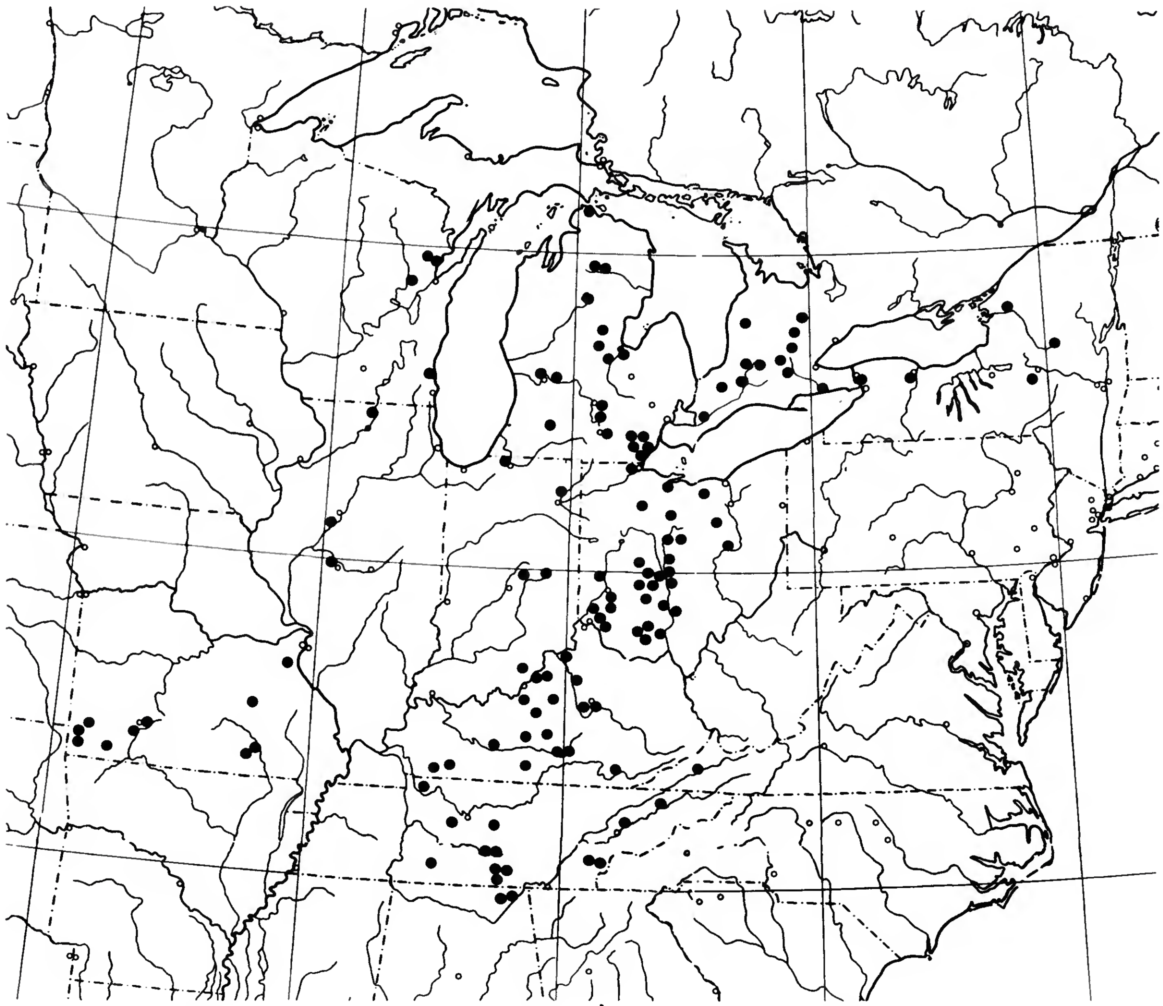

FIGURE 7.—Geographical distribution of *Alasmidonta viridis*.

and 37 bridge, 5 mi (8.0 km) ESE of Delaware, Delaware Co. (1969, D. H. Stansbery! (OSUM)). Shaw Creek, Canaan Township, Morrow Co. (1962, D. H. Stansbery and C. B. Stein! (OSUM)). Alum Creek near Columbus, Frankin Co. (MCZ). Scioto River, Columbus (ANSP), and Chillicothe, Ross Co. (USNM). Yellowbud Creek near Circleville, Pickaway Co. (OSUM). Big Darby Creek, Hwy. 40 bridge, Prairie Township, Franklin Co. (1957, D. H. Stansbery! (OSUM)). Little Darby Creek: just S of Union Co., Pike Township, Madison Co. (1965, C. B. Stein!); above Hwy. 40 bridge, West Jefferson, 11.0 mi (17.6 km) ENE of London, Madison Co. (1976, D. H. Stansbery!); and 3 other 1978 Little Darby Creek localities (all OSUM). North Fork, 6 mi (9.6 km) SE of Midway, Madison Co. (1967, K. A. Jennings and R. L. Hughes, Jr.! (OSUM)). Cloudy Creek, headwaters of River Styx, Hwy. 118, NW of Wadsworth, Medina Co. (1957, D. Myer! (OSUM)). Paint Creek, Rt. 165 bridge, 3 mi (4.8 km) SSW of Good Hope, Fayette Co. (1967, K. A. Jennings and R. L. Hughes, Jr.! (OSUM)). Sugar Creek, Concord/Union Townships, Fayette Co. (OSUM).

Licking River Drainage, Kentucky: [Licking River], Falmouth, Pendleton Co. (1969, D. H. Stansbery! (OSUM); also MCZ).

Little Miami River Drainage, Ohio: Todd Fork Little Miami River between Clarksville and Morrow, Warren Co. (1977, E. Secora! (OSUM), one valve only but huge, 58.2 mm long, 38.2 mm high). East Fork Little Miami River, Blue Sky Park

Road, 4.4 mi (7.0 km) NNE of Williamsburg, Clermont Co. (1973, J. M. Sears! (OSUM)). Cloverlick Creek just above mouth of Poplar Creek, 4 mi (6.4 km) SW of Williamsburg (1969, M. Trautman! (OSUM), very large, 53.0 mm long, 33.0 mm high, 23.8 mm wide). Little Miami River, Corwin, Telegraph Mill Bridge, Wayne Township, Warren Co. (1976, D. H. Stansbery! (OSUM)). Massie's Creek below falls, Cedarville Township, Green Co. (1958, G. Acker! (OSUM)).

Miami River Drainage, Ohio: Spring Creek, 4 mi (6.4 km) E of Piqua, Shelby Co. (1967, C. B. Stein! (OSUM)).

Kentucky River Drainage, Kentucky: Hanging Fork Creek, Lytle, Lincoln Co. (MCZ). Dix River, 5 mi (8.0 km) E of Stanford, Lincoln Co. (MCZ). Elkhorn Creek near Swallowfield, Franklin Co. (1950, H. D. Athearn! (MCZ)). Eagle Creek, Owen Co. (MCZ).

Harrods Creek Drainage, Kentucky: Harrods Creek at Hwy. 329 bridge, E of Prospect, Oldham Co. (1965, D. Bickel! (OSUM)) and at Rt. 1694 bridge just below mouth of Darby Creek, Oldham Co. (1966, C. B. Stein! (OSUM)).

Salt River Drainage, Kentucky: Salt Creek, Anderson Co. (1968, R. Jezerinac! (OSUM), empty shells). Rolling Fork Salt River, 1 mi (1.6 km) SW of Lebanon, Marion Co. (1958, W. J. Clench and J. Rosewater! (MCZ)). Floyds Fork Salt River, Hwy. 50 and 150 bridge, 3 mi (4.8 km) NNW of Mount Washington, Jefferson Co. (1965, D. Bickel! (OSUM), empty shells).

Green River Drainage, Kentucky: Russell Creek, Green Co. (USNM). Green River, 8 mi (12.8 km) S of Campbellsville, Taylor Co. (1958, W. J. Clench and J. Rosewater! (MCZ)) and Mumfordville, Hart Co. (1964, 1965, 1966, D. H. Stansbery! (OSUM)). Barren River (USNM) and Barren River, Hwy. 626 bridge, 9.5 mi (15.2 km) WNW of Bowling Green, Warren Co. (1969, D. H. Stansbery! (OSUM)). Nolin River, White Mills, 15 mi (24.0 km) ENE of Leitchfield, Hardin Co., (1964, C. B. Stein! (OSUM)).

Blue River Drainage, Indiana: Blue River near Fredericksburg, Washington Co. (1950, H. D. Athearn! (MCZ)).

Wabash River Drainage, Indiana: Wildcat Creek, Gray's Mill Burlington, Carroll Co. (USNM). Honey Creek, Russiaville, Howard Co. (USNM). Sixmile Creek, Blue River Township, Hancock Co. (1975, E. Secora! (OSUM)). Tippecanoe River, Delong, Fulton Co. (USNM). White River (USNM). Duck Creek, about 1 mi (1.6 km) N of Greensboro, Henry Co. (1975, E. Secora! (OSUM), empty shell). Wabash River (USNM).

CUMBERLAND RIVER SYSTEM.—*Cumberland River Drainage:* Cumberland River, Pineville, Bell Co., Ky. (Ortmann, 1914). Lynn Camp Creek of Laurel River, Corbin, Whitley Co., Ky. (MCZ). Stones River, Murfreesboro, Rutherford Co., Tenn. (MCZ). Harpeth River, 6 mi (9.6 km) S of Bellevue [*sic*, probably Bellsburg, Dixon/Cheatham Co.], Tenn. (ANSP). West Fork Red River at Bakers Mill, 7.6 mi (12.2 km) S of Pembroke, Christian Co., Ky. and 6.6 mi (10.6 km) WSW of Elkton, Todd Co., Ky. (both 1971, D. H. Stansbery! (OSUM)). Red River, Hwy. 161 bridge, 4 mi (6.4 km) NW of Barren Plain, Robertson Co., Tenn. (1969, D. H. Stansbery! (OSUM)).

TENNESSEE RIVER SYSTEM.—*Powell River Drainage:* Sheep Shank, Wallen Creek, Lee Co., Va. (MCZ).

Clinch River Drainage, Virginia: Clinch River, 1 mi (1.6 km) N of Tazewell, Tazewell Co. (USNM). Clinch River at Richland and at Cedar Bluff, both Tazewell Co. (Ortmann, 1914).

Holston River Drainage: Big Creek, Rogersville, Hawkins Co., Tenn. (MCZ). North Fork Holston River, Saltville, Smyth Co., Va. (Ortmann, 1914). Holston River, Tenn. (ANSP).

French Broad River Drainage, Tennessee: Big Pigeon River and French Broad River (both USNM).

Hiwassee River Drainage: Conasauga Creek, Monroe Co., Tenn. (ANSP, MCZ, OSUM).

Paint Rock River Drainage, Alabama: Larkin Fork, Paint Rock River, below county Rt. 27 bridge, 4.6 mi (7.4 km) SE of Francisco, Jackson Co. (1973, C. B. Stein and J. Frederick! (OSUM) and 1.5 mi (2.4 km) above its mouth, Jackson Co. (1966, D. H. Stansbery! (OSUM)). Estill Fork, Paint Rock River at ford, 2.9 mi (4.6 km) NNE of Estill Fork, Jackson Co. (1974, D. H. Stansbery and K. Borror! (OSUM)).

Elk River Drainage, Tennessee: Boiling Fork Creek, Cowan, Franklin Co. (ANSP, MCZ). Elk River, Estill Springs, Franklin Co. (USNM). Elk River, Hwy. 50, Marion Co., and 3 mi (4.8 km) W of Pelham, Grundy Co., Tenn. (both 1953, A. H. Clarke and L. R. Clarke! (NMC)).

Buffalo River Drainage: Buffalo River, Natchez Trace bridge, near Lapier, Lewis Co., Tenn. (1968, D. H. Stansbery and C. B. Stein! (OSUM), empty shell).

Duck River Drainage, Tennessee: Duck River below Dement Bridge, 1.8 mi (2.9 km) SE of Haley, Bedford Co. and near Tullahoma, Bedford Co. (both 1965, B. Isom and P. Yokley! (OSUM)); Shelbeyville, Bedford Co. (MCZ); and near Shelbeyville (1967, W. J. Clench and D. H. Stansbery! (OSUM)). East Rock Creek, 1.8 mi (2.9 km) NNE of Verona, Marshall Co. (1976, C. B. Stein! (OSUM)).

Main Tennessee River: Tennessee River, Jackson Co., Ala. (ANSP).

UPPER MISSISSIPPI RIVER SYSTEM.—*Rock River Drainage, Illinois:* Kents Creek, Winnebago Co. (MCZ). [Rock River], Rockford, Winnebago Co. (USNM).

Illinois River Drainage: Buelah Lake, near Mukwonago, Waukesha Co., Wisc. (USNM). [Kankakee River], South Bend, St. Joseph Co., Ind. (USNM). Tributary of Illinois River, Canton, Fulton Co., Ill. (ANSP). [Sangamon River], Athens, Menard Co., Ill.

Missouri River Drainage: Big Piney River, 7 mi (11.2 km) W of Licking at Hwy. 32 bridge, Texas Co., Mo. (1965, D. H. Stansbery! (OSUM)).

Meramec River Drainage: Old Mines Creek, Hwy. 21 bridge, 3.5 mi (5.6 km) W of Fertile, Washington Co., Mo. (1975, F. Schilling and H. Kemper! (OSUM)).

LOWER MISSISSIPPI RIVER SYSTEM.—*White River Drainage, Missouri:* Current River, Shannon Co. (MCZ) Jack's Fork, Shannon Co. (MCZ, USNM). Flat Creek near Flat Creek, Barry Co. (1974, W. H. Dieffenbach! OSUM)). James River, southern Green Co. (ANSP), 7 mi (11.2 km) NW of Ozark, Christian Co. (OSUM), Finley Creek, Linden, Christian Co. (1965, D. H. Stansbery! (OSUM)), and Galena, Stone Co. (MCZ).

Arkansas River Drainage, Missouri: Spring Creek, Lawrence Co.; Center Creek, Sarooxie, Jasper Co. (both 1964, W. H. Dieffenbach! (OSUM)). Shoal Creek, Lawrence Co. (1965, W. H. Dieffenbach! (OSUM)).

REMARKS

After much consideration I have become convinced that the well-known name *Alasmidonta calceola* (Lea, 1827) should be replaced by *Alasmidonta viridis* (Rafinesque, 1820), so I am following Morrison (1969) and Stansbery and Clench (1974), who recommended this change but who do not discuss the reasons for it.

Rafinesque's description is quite explicit. He calls attention to the small size, the obliquely truncate posterior, the heavy beak sculpturing, the buttressed pseudocardinal teeth ("dent ... decurrente"), and aspects of distribution and ecology (Rare dans l'Ohio, plus commune dans le Kentucky et les petites riviers adjacentes") which, taken together, appear to be characteristic of no other species. The phrases "de la longueur d'un pouce et demi au plus" [=the length is 1 1/2 pouce (about 38 mm) at the most] and "longueur 5/9, diameter 7/16, axe 1/3 de la largeur" [= length 5/9, diameter 7/16, and axis 1/3 of the width] are confusing, but in the early 19th century "length" was used to mean the distance from the umbone to the opposite margin, and was approximately equivalent to what is now called height. "Width" was equivalent to what is now called length.

The largest specimens of *Alasmidonta "calceola"* that I have seen are each 38 mm high and agree perfectly with the maximum height given by Rafinesque. One is labelled "Cincinnati, Ohio" (OSUM 8626a) and one is from Todd Fork, Little Miami River, between Clarksville and Morrow, Warren County, Ohio (OSUM 41257). Measurements of specimens from Little Miami River, Ohio (see Table 5) give ratios of H/L = 0.545–0.665 and W/L = 0.335–0.531. These are also in agreement with decimal equivalents of the ratios given Rafinesque (H/L = 0.56, W/L = 0.44). The meaning of "axe" (axis) is not clear, but it may refer to the length of the ligament and, if so, that measurement is also correct.

The identity of *Unio viridis* Rafinesque has been the subject of controversy for many years and I regret that the issue must be resurrected. Vanatta (1915) and Frierson (1915) both discussed a specimen in the Academy of Natural Sciences of Philadelphia (ANSP 20219), said to be from the Kentucky River, which was identified by Rafinesque in 1831 as the species he had described in 1820 as *Unio viridis*. Debate in the second and third decades of the twentieth century (see also Ortmann and Walker, 1922 and Frierson, 1927) centered on whether the ANSP specimen, on the one hand, and Rafinesque's original description, on the other, was referable to *Lasmigona compressa* (Lea, 1829) or *Lasmigona subviridis* (Conrad, 1834). Ortmann and Walker (1922) identified the ANSP specimen as *L. subviridis* but decided that Rafinesque's description did not fit either *L. subviridis* or *L. compressa* and that *Unio viridis* was therefore unidentifiable. Johnson and Baker (1973) confirmed the identification of the specimen seen by Rafinesque in 1831, illustrated it, and restricted the type locality to Yellow Creek, near Cincinnati, which is the type locality of *Symphynota* [=*Lasmigona*] *compressa* Lea (1829).

Based on a conversation with Dr. David H. Stansbery, and further consideration, it seems certain that Rafinesque made a mistake in 1831 when he identified the (now ANSP) specimen as his *Unio viridis*. "Kentucky River," the locality given for that specimen, must also have been added later; it is incorrect because *L. subviridis* does not occur there. (*L. compressa* does not occur there either.) The type locality restriction by Johnson and Baker is also inappropriate because it does not lie within the area of distribution of *Unio viridis* originally given by Rafinesque.

In order to stabilize the nomenclature of this species, selection of a neotype is necessary. None of Rafinesque's original material of *Unio viridis* is available (Johnson and Baker, 1973) so another specimen, from one of Rafinesque's localities (the Ohio River), is here designated. It is catalog number 8626a in the mollusk collection of the Smithsonian Institution. It is labelled "Cincinnati, Ohio."

The specimen was previously in the Isaac Lea Collection and was originally collected by Mr. J. Clark at an unspecified date, but certainly in the nineteenth century. Its measurements are: length 58.45 mm height (excluding the ligament) 37.70 mm, width of both valves appressed 23.73 mm, distance from umbonal apex to anterior (B-A) 16.58, and hinge plate thickness (Hp) 3.85 mm.

Alasmidonta (Pressodonta) heterodon (Lea, 1830)

FIGURES 8–10

Unio heterodon Lea, 1830:428, pl. 8:fig. 11 [Type-locality: "Schuylkill [River] and Derby [sic] Creek, P[ennsylvani]a." Figured specimen and other original material not in Smithsonian Institution. Syntypes in mollusk collection of Academy of Natural Sciences of Philadelphia, catalog numbers 41004 and 41005 (Johnson, 1970:347; Johnson and Baker 1973:157).]

THE SHELL

FIGURE 8*a,b,d,e*

DESCRIPTION.—Shell small, subtrapezoidal or "hump backed," with unusual hinge teeth, up to 56 1/2 mm long, 31 mm high, and 18 1/2 mm wide, slightly thickened anteriorly (up to about 2 mm thick) and thinner, but not fragile, posteriorly. Anterior margin sharply curved; ventral margin broadly and flatly curved, predominantly straight, or slightly concave centrally; posterior margin roundly pointed near the base and broadly and obliquely truncated above; and dorsal margin of medium length and slightly curved. Maximum inflation a little above the center of the shell. Beaks low, rounded, located slightly more than 1/4 the distance from anterior to posterior, and projecting only a little above the hinge line. Posterior ridge rounded, somewhat inflated, and rather prominent. Posterior slope of medium width, concave above, and in some specimens traversed below by a low, rounded, radial ridge above the posterior ridge. Growth increments marked by concentric wrinkles and lines, especially in northern specimens. Except for lines of growth, additional post-juvenile sculpturing is lacking. Periostracum yellowish, olive brown, or blackish brown and, in some specimens, with narrow and wide reddish brown rays.

Hinge teeth small but well developed and unusual. Pseudocardinal teeth elevated, compressed, serrated, and numbering 1 or 2 in the right valve and 2 in the left. Interdental projection in left valve well-marked and articulating with a corresponding depression in the right valve. Lateral teeth narrow but strong, extending posteriorly to the end of the ligament or a little beyond, and characteristically 2 in the right valve and 1 in the left, *the reverse* of all other North American species having lateral teeth. Beak cavity rather narrow and not very deep. Anterior muscle scars impressed, pallial line well marked anteriorly but becoming somewhat obscure posteriorly, posterior muscle scars shallow but clearly marked, and scars within beak cavity consisting of a small ovate, elongate pit on the back of the hinge plate. Nacre bluish or silvery white, iridescent posteriorly, and with pinkish or salmon suffusions near the beak cavity.

Beak sculpture strong and composed of about 4 or 5 moderately heavy, blunt bars, the first 2 concentric and simple, the following ones broadly double-looped and forming sharp angles on the posterior ridge. Ridges visible only in well-preserved young specimens.

VARIATION.—Ortmann (1919:174) observed sexual differences in the shell, i.e.: "The male as a rule has a more compressed, and more ovate and elongate shell, with the lower margin gently and uniformly curved, the posterior ridge less

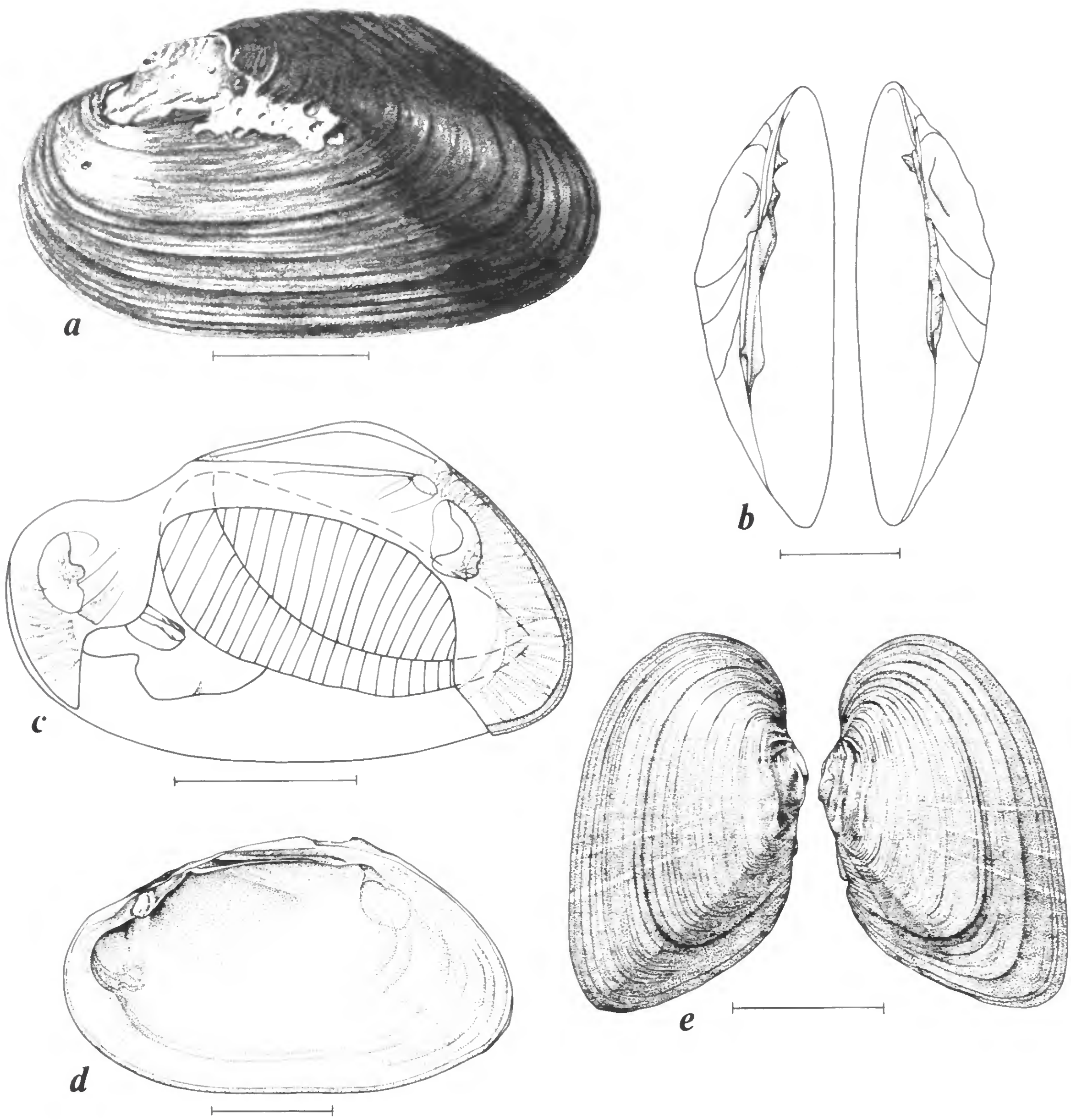

FIGURE 8.—*Alasmidonta heterodon*: *a,b,d*, USNM 201393, Granby, Connecticut; *c*, OSUM 46074, Petitcodiac River, New Brunswick, Canada; *e*, details of umbonal area, USNM 84468, "source of Connecticut River." (Scale = 1 mm.)

sharp, and the posterior slope not truncated; while in the female the shell is more swollen in the region of the posterior ridge and just in front of it; has a more distinct posterior ridge, which renders the posterior slope more truncate, and makes the whole outline of the shell shorter and more trapezoidal. Furthermore in the female the lower posterior angle is more produced downward, so that the lower margin of the shell becomes rather straight, in some cases even concave." Sexual differences in the shells of young specimens are not apparent.

Aside from this somewhat obscure sexual dimorphism the species is rather uniform in shell features (Table 7). There is some variation in the development of the hinge teeth. Specimens from some canals also tend to become larger and paler than those from other localities. The largest specimen seen, 56.5 mm long, is from a medium-sized river (Ashuelot River) near Keene, New Hampshire. Some of the largest specimens are also more conspicuously rayed than small, dark-colored specimens. The latter appear to be more characteristic of fine substrates containing organic material. This condition often occurs near river banks and coincides in part with the general trend seen in other unionids: that at a given river site small, dark-colored specimens tend to occur in mud near river banks whereas larger, paler specimens of the same species tend to occur in sandy substrates farther from the river banks when the current is more rapid.

Topographic Anatomy

Figure 8c

Specimen Described.—From Petitcodiac River, Riverglade, 19 mi (30.4 km) WSW of Moncton, N.B., collected 22 June 1960 (NMC 46074, A. H. Clarke station C50); preserved directly in 70% ethyl alcohol; shell length 31.6 mm, presumed sex male.

Table 7.—*Alasmidonta heterodon:* Shell measurements

Feature	*N*	*Range*	*Mean ($\bar{x}$)*	*S*
	Petitcodiac River, 19 mi WSW of Moncton, New Brunswick			
Length (mm)	7	26.92 -33.02	29.72	2.470
H/L	7	0.577 - 0.640	0.605	0.0189
W/L	7	0.325 - 0.410	0.365	0.0264
B-A/L	7	0.221 - 0.291	0.268	0.0238
Hp/L	7	0.0516- 0.0690	0.0582	0.00717
	Connecticut River, Hartland, Vermont			
Length (mm)	20	24.90 -37.95	29.93	3.275
H/L	20	0.569 - 0.681	0.611	0.0289
W/L	18	0.319 - 0.373	0.354	0.0153
B-A/L	20	0.220 - 0.287	0.254	0.0194
Hp/L	19	0.0508- 0.0776	0.0613	0.00753

Description.—Mantle pale brown but covered in the central portion with a network of fine, short, white, filamentous muscle fibers coalesced into spots and strands and in the posterior region by beautiful silvery radial muscle strands. Adductor muscles orange and contrasting with the mantle. A brown pigmented band runs just within the edge of the mantle from the posterior part of the ventral region to the posterior region and dorsally (touching the mantle edge) to a point above the posterior adductor. The incurrent opening is 5 mm long and surrounded just within the edge by about 3 ranks of small, narrow, reddish brown, pyramidal papillae, the inner papillae the longer (about 1.0 mm). Separation of incurrent and anal openings achieved by the diaphragm and by a narrow (0.5 mm) zone on each mantle edge that is held in contact with its opposite member during life. Anal opening 4 mm long and with crenulate edges and with a dark, reddish brown color band just within the opening. Mantle connection between anal and supra-anal opening of medium length (3.5 mm). Supra-anal opening narrow, slit-like, bordered within by a brown band, and 3 mm in length.

Demibranchs pale brown in preserved specimen. Outer demibranch 19.7 mm long, 5.9 mm high, with tapering ends and convex, ventral edge and with wavy radial wrinkles. Surface tissue with about 12 double radial filaments per mm and about 4 cross filaments; water tubes about 2.0 per mm. Inner demibranch about 26 mm long, 13 mm high, also with rounded ends and convex ventral edge, and extending well beyond the outer demibranch anteriorly and ventrally but only slightly overlapping it posteriorly. Surface tissue as in outer demibranch but cross filaments more obscure; water tubes also about 2.0 per mm. Inner lamina of inner demibranch not attached to visceral mass. Diaphragm split near the anal opening and perforated by the ends of the water tubes.

Labial palps narrow; slightly overlapping the inner demibranch; with long convex ventral edge; shorter, flatly sigmoid dorsal edge; sharp, centrally located posterior point; and with dorsal edges rolled outward. The outer surfaces are smooth and the inner opposing surfaces of each member are radially furrowed (about 7 furrows per mm at the margin); the furrows are also visible through the outer palp surfaces. The outer palpus is fused to the mantle and, for about 2/3 of its length, to the inner palpus.

Ortmann (1912:295) states: "Color of soft parts whitish; charged marsupium brown." In live specimens collected from Ashuelot River near Keene, New Hampshire, the foot was orange.

VARIATION.—Table 8 shows the extent of variation of most of the features observed in available material. Mantle pigmentation is in a continuous band and is restricted to the posterior region in all specimens, although it differs in intensity between individuals. The incurrent opening is slightly longer than the anal or supra-anal openings (which are about equal in length) and the mantle connection between the anal and supra-anal openings varies from being approximately equal to them in length (6 specimens) to being much shorter (2 specimens). The labial palps overlap or touch the inner demibranch in 7 of the 8 specimens examined. These observations are in only partial agreement with those of Ortmann (1912:295) who reported that in about 30 specimens seen from Pennsylvania, A-SA is shorter than A in all of them, and the labial palps do not touch the inner demibranch.

Other features examined were the presence or absence of crenulation at the margin of the anal opening and relative dimensions of the demibranchs. The Petitcodiac River specimens are all finely crenulated and the Tar River specimen is strongly crenulated. The length and height of the demibranchs were measured and are given below expressed as a percentage of the shell length. Petitcodiac River specimens: outer demibranch, length 57%–63%, height 16%–19% (females) and 23% (male); inner demibranch: length 62%–70%, height 26%–30% (females) and 31% (male). Tar River specimen (gravid): outer demibranch, length 62%, height 34%, inner demibranch, length 68%, height 34%. The inner lamina of the inner demibranch was free from the visceral mass in all specimens.

GLOCHIDIUM

FIGURE 9

DESCRIPTION.—Glochidium depressed pyriform, with hinge straight, apex protuberant, and valves convex and rounded. Shell 0.255 mm high, 0.325 mm long, and about 0.100 mm in single valve convexity. The posterior margin is longer and more convex than the anterior and the apex is located about 42% of the distance from anterior to posterior (measured parallel to the hinge axis). Except for a band near the margin and near the apex the shell is pockmarked with shallow depressions (about 5–10 μm wide) and tiny pits (1–2 μm wide) within many of the depressions. The hinge is about 0.267 mm in length.

Each apical stylet is flatly recurved, about 0.080 mm long, about 0.028 mm wide at the base, tapering rapidly in the proximal third of its length to about half that width, and tapering gradually in the distal portion. Each stylet is connected on each side, and for most of its length, by a wide membrane which is attached to the valve margin. The exposed surface of each stylet is covered with major microstylets, each about 10 μm long and 5 μm wide, and bluntly pyramidal in shape. On the distal two-thirds of the stylet they are arranged alternately in transverse rows of 2 or 1 microstylets, or in alternate positions in successive rows each with 2 microstylets. The microstylets become more numerous and smaller on the base of the stylet and extend as small micropoints (<0.5 μm) onto the shell surface near the apex and onto the supporting membrane.

The glochidium described is from an adult collected from Canoe River, 2.45 mi (3.9 km) NNE of Norton, Bristol Co., Massachusetts by H. D. Athearn on 2 June 1969 (OSUM 25106). Other glochidia from the same adult were similar

TABLE 8.—*Alasmidonta heterodon:* Variation in topographic anatomy (abbreviations same as Table 4)

		Mantle pigmentation		Relative lengths of mantle features (as % of L)				Incurrent papillae		Labial palps		Water tubes		Pre-preserv. treatment	
Spec. No.	Length (mm)	Extent	Strength	Inc.	Anal	A-AS	SA	Ranks	Max. Ht. (mm)	Posit.	Grooves per mm	N/mm*	Sex	Nemb. relax.	Form. fixed
		Petitcodiac River, 19 mi WSW of Moncton, New Brunswick (NMC 46074)													
1	32.8	1	H	13	13	10	13	2	0.9	OV	7	3	(F)	-	-
2	32.1	Inc. Op.	H	16	13	15	13	2	0.8	T	8	3	(F)	-	-
3	31.6	1	M	16	13	11	10	2	1.0	OV	7	3	(F)	-	-
4	28.6	1	H	16	13	10	12	2	0.9	OV	8	2.3	(M)	-	-
5	28.5	1	H	17	16	14	14	3	1.0	T	7	3	(F)	-	-
6	27.6	1	H	14	14	4	17	2	0.9	T	8.5	3	(F)	-	-
7	27.5	1	H	17	15	4	14	2	1.0	NT	7	3	(F)	-	-
		Tar River, 5 mi N of Creedmore, North Carolina (USNM 658679)													
8	24.0	Inc. Op.	W	14	10	12	11	2	1.0	OV	?	-	GF	+	+

* Refers to outer demibranchs of non-gravid specimens.

although minor variations in valve shape and convexity were apparent.

Life History

GRAVID PERIOD.—Ortmann (1919:174) gives the month of February and 24 April as gravid dates for *A. heterodon.* Additional dates provided now are 2 June 1969 for a specimen from Canoe River near Norton, Massachusetts (mature glochidia) and 27 August 1977 for a specimen from Tar River near Creedmore, North Carolina (immature glochidia). In the species as a whole the gravid period therefore spans at least the period from late August to the following early part of June.

NATURAL HOST.—Not recorded.

HABITAT.—"This is a rather rare and inconspicuous species ... [It] occurs in medium or rather slow-flowing rivers of varying size on gravel, sand, or muddy sand bottoms and sometimes among submersed aquatic plants" (Clarke and Berg, 1959:25). In the Ashuelot River 4 mi (6.4 km) west of Keene, New Hampshire, on 8 August 1978, I found *A. heterodon* in muddy sand in 12 to 18 inches of water depth near the river bank under overhanging tree limbs. It shows markedly clumped distribution there and in the Petitcodiac River, the only localities from which I have collected it in abundance. Ortmann (1919: 173) has also reported it as abundant in a canal. Its usual associate is *Elliptio complanata* and, occasionally, *Strophitus undulatus* or other riverine species.

Geographical Records

FIGURE 10

PETITCODIAC RIVER SYSTEM, NEW BRUNSWICK.—North River, 5 mi (8.0 km) NW of Salisbury, Westmoreland Co. (Athearn, 1953). Petitcodiac River at River Glade, 19 mi (30.0 km) WSW of Moncton, Westmoreland Co., (1960, A. H., A. R., and Louise R. Clarke! (NMC)).

MERRIMAC RIVER SYSTEM, MASSACHUSETTS.—Merrimac River, Andover, Essex Co. (MCZ).

TAUNTON RIVER SYSTEM, MASSACHUSETTS.—Canoe River, 2.45 mi (3.9 km) NNE of Norton, Bristol Co. (1969, H. D. Athearn! (OSUM)).

AGAWAM RIVER SYSTEM, MASSACHUSETTS.—Agawam River (MCZ).

CONNECTICUT RIVER SYSTEM.—Connecticut River at Bloomfield, Essex Co., Vt. (MCZ); Northumberland, Coos Co., N.H. (ANSP and MCZ); Ryegate, Caledonia Co., Vt. (MCZ); 2 mi (3.2 km) N of Monroe, Grafton Co., N.H.; Hanover, Grafton Co.; Northfield, Franklin Co., Mass. (all MCZ); Canal, Westfield, Hampden Co., Mass. (ANSP, MCZ, USNM); Springfield, Hampden Co.; and Granby,

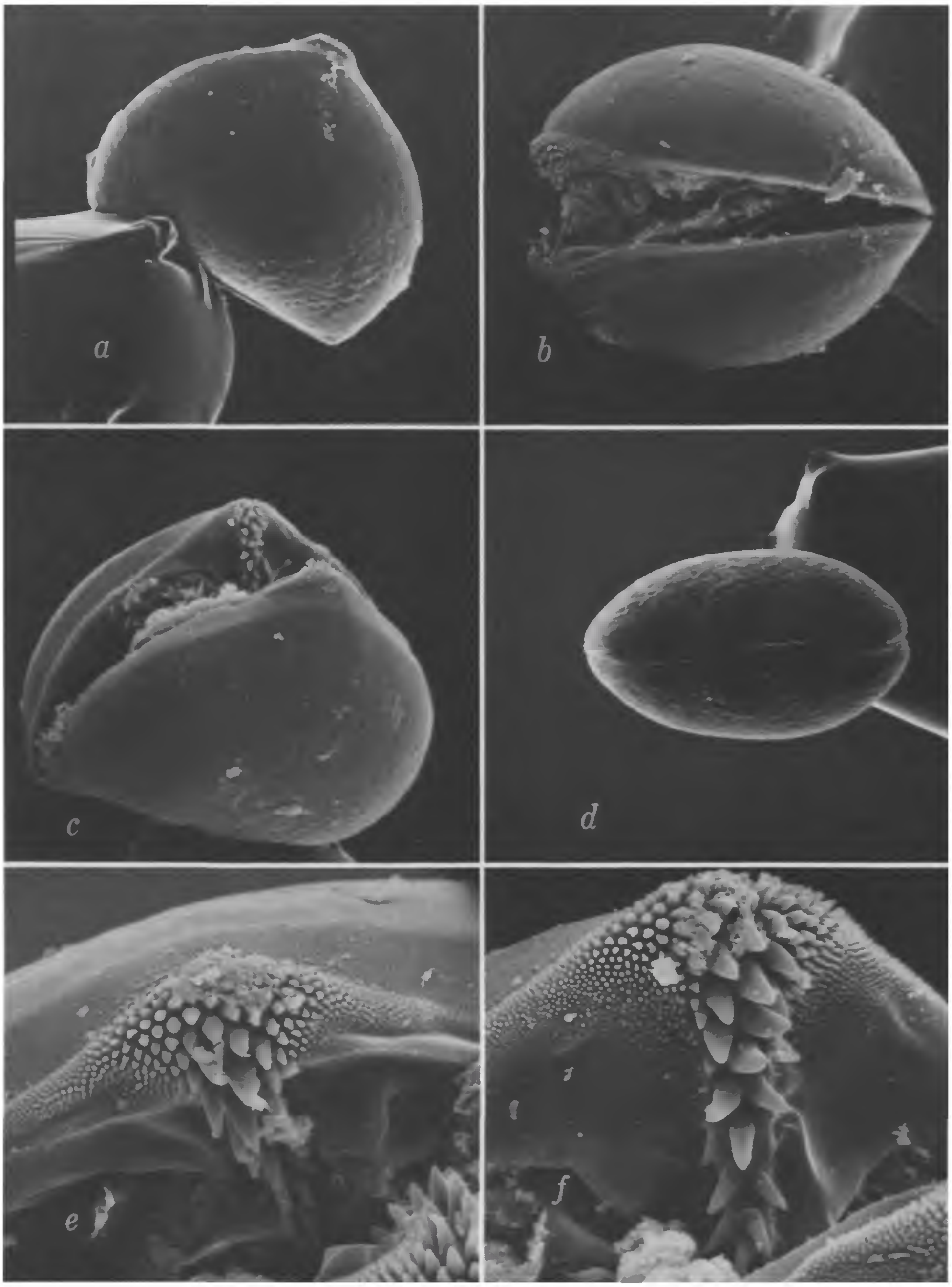

FIGURE 9.—Glochidia of *Alasmidonta heterodon*: *a–f*, OSUM 25106, Canoe River near Norton, Massachusetts. (*a,d* × 150; *b* × 215; *c* × 175; *e* × 620; *f* × 730.)

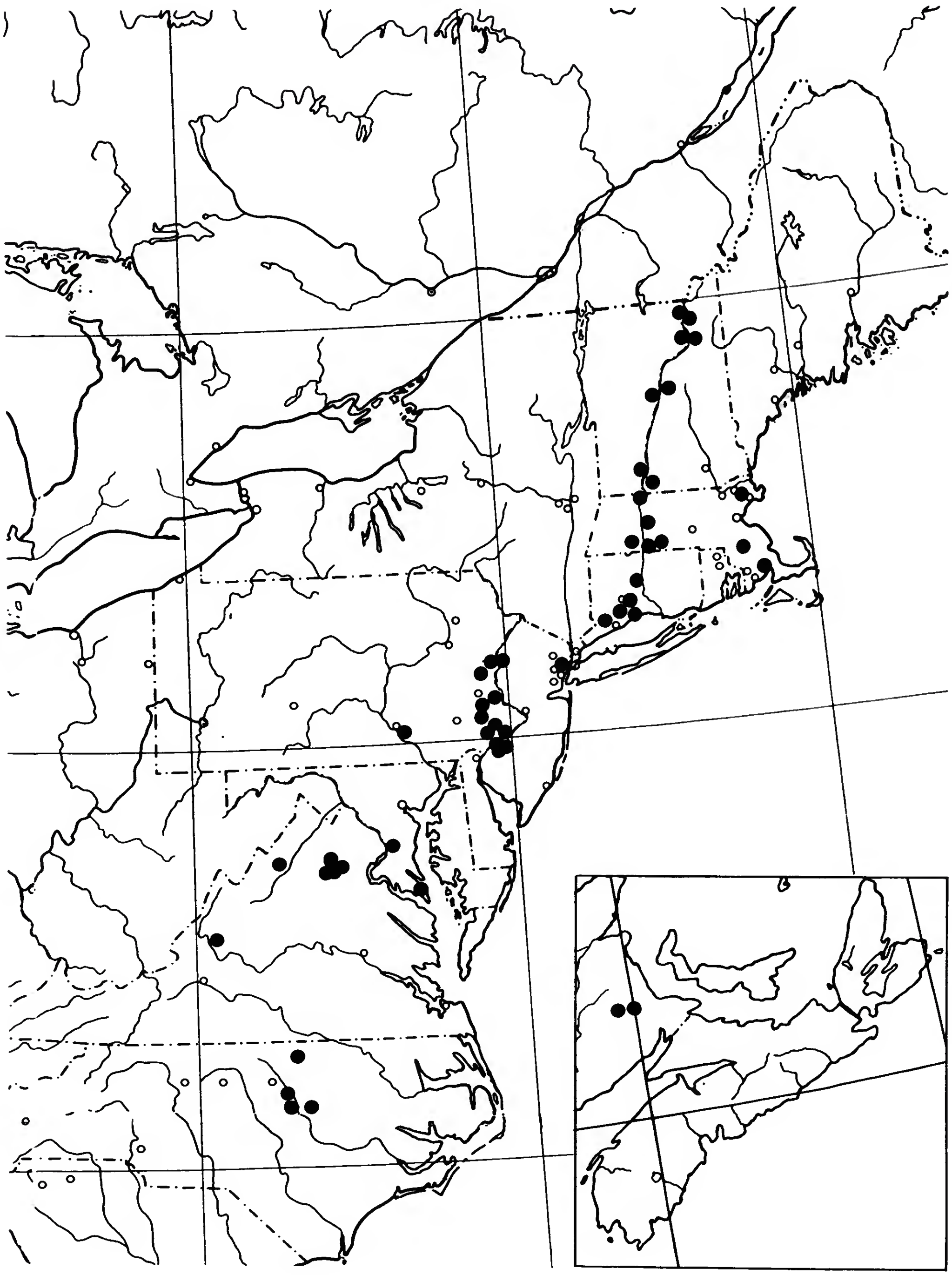

FIGURE 10.—Geographical distribution of *Alasmidonta heterodon* (insert = location of specimens found in New Brunswick).

Hartford Co., Conn. (both USNM). Ashuelot River, 2.5 mi (4.0 km) N of Keene, Cheshire Co. and 2 mi (3.2 km) NW of Keene (both 1954, A. H., A. R. and Louise R. Clarke! (NMC)). Philo Brook, Suffield, Hartford Co., Conn. (1959, S.L.H. Fuller! (MCZ)). Scantic River, 0.5 mi (0.8 km) above Hampden, Hampden Co., Mass. (1951, H. D. Athearn! (MCZ)).

QUINNIPIAC RIVER SYSTEM, CONNECTICUT.—Ten Mile River, Mixville, New Haven Co. (ANSP, MCZ). Quinnipiac River, Meriden, New Haven Co. (MCZ). Wilmot Brook, New Haven, New Haven Co. (MCZ).

HACKENSACK RIVER SYSTEM.—Brook flowing W from Closter to Hackensack, Bergen Co., N.J. (ANSP).

DELAWARE RIVER SYSTEM, PENNSYLVANIA.—*Delaware River Drainage*: Delaware River, Shawnee, Monroe Co. (Ortmann, 1919). Princess Creek, Kunkleton, Monroe Co. (Ortmann, 1919). Pohopoco Creek, 6 mi (9.6 km) E of Leighton, Carbon Co. (USNM). Delaware River, Bucks Co. (MCZ).

Schuylkill River Drainage: Big Neshaminy Creek near Ederson, Bucks Co. (ANSP; Ortmann, 1919). Schuylkill River at Hazellea, Chester Co. (ANSP); also at junction with Darby Creek, Delaware Co. (Ortmann, 1919); Canal, Manayunk, Philadelphia Co. (ANSP; Ortmann, 1919); below Fairmont Dam, Philadelphia Co. (Ortmann, 1919).

SUSQUEHANNA RIVER SYSTEM.—Susquehanna River, Columbia, Lancaster Co., Pa. (ANSP).

POTOMAC RIVER SYSTEM.—Potomac River near Washington, D.C. (USNM). McIntosh Run, 4 mi (6.4 km) N Leonardstown, St. Mary's Co., Md. (Johnson, 1970).

RAPPAHANOCK RIVER SYSTEM, VIRGINIA.—*Rappahanock River Drainage*: Mountain Run, Culpeper Co. (Ortmann, 1919). Marsh Run, 3 mi (4.8 km) SE of Remington, Fauquier Co. (Ortmann, 1919).

Rapidan River Drainage: Blue River, Orange Co. (USNM; Johnson, 1970).

JAMES RIVER SYSTEM, VIRGINIA.—North River, Lexington, Rockbridge Co. (ANSP and USNM).

PAMLICO RIVER SYSTEM, NORTH CAROLINA.—Tar River, Hwy 15, 5 mi (8 km) N of Creedmore, Granville Co. (1977, A. H. and J. J. Clarke! (USNM)).

NEUSE RIVER SYSTEM, NORTH CAROLINA.—Neuse River at Poolec Bridge, Wake Co. (MCZ); Raleigh, Wake Co. (MCZ); 6 mi (9.6 km) E of Raleigh (Johnson, 1970); and NE of Wendell, Wake Co. (USNM). Little River at Tarpley's Mill, 2 mi (3.2 km) NE of Wendell, Wake Co., (1950–51, W. Walter! (MCZ); Walter, 1956).

Subgenus *Alasmidens,* new subgenus

TYPE-SPECIES.—*Alasmidonta mccordi* Athearn, here designated.

Alasmidonta (*Alasmidens*) *mccordi* is principally distinguished by its weak beak sculpturing which does not extend more than 6 mm beyond the umbonal apex, by the presence of a lunule, and by the pseudocardinal teeth in the right valve that are curved, placed one above the other, and oriented parallel with the lunule. Other members of *Alasmidonta* (sensu lato) have stronger beak sculpturing, do not possess a lunule, and the pseudocardinal teeth in the right valve, if well-developed, are placed beside each other and are approximately perpendicular with the dorsal margin. *Alasmidonta* (*Alasmidens*) *mccordi* is probably now extinct.

Alasmidonta (*Alasmidens*) *mccordi* Athearn, 1964

FIGURES 11 and 17

Alasmidonta mccordi Athearn, 1964:134, pl. 9: figs. a and b. [Type-locality: "Coosa River, Ten Island Shoals, just below old Lock 2 Dam, 3 2/10 mi [5.1 km] S of Greenport, St. Clair Co., Alabama." Holotype in the National Museum of Natural Sciences, National Museums of Canada, catalog number 20094.]

THE SHELL

FIGURE 11

DESCRIPTIONS.—Shell triangular-ovate, somewhat compressed, 58.0 mm long, 41.5 mm high, and 26.0 mm wide, slightly thickened anteriorly (2.5 mm thick) and thinner (1.2 mm) posteriorly. Anterior margin roundly curved (more sharply curved above than below), ventral margin broadly curved, posterior margin sharply rounded below and broadly and diagonally curved above, continuing smoothly into the curved dorsal margin that is convex posteriorly and concave anteriorly. Maximum inflation at a point about 39% from anterior to posterior and above the midline (27% from dorsal to ventral margin). Beaks rounded, not large, located about 1/3 the distance from anterior to posterior, and projecting slightly above the hinge line. Posterior ridge flatly rounded in the left valve and not prominent, in the right valve it is narrow, slightly elevated, and sharply rounded. Posterior slope of

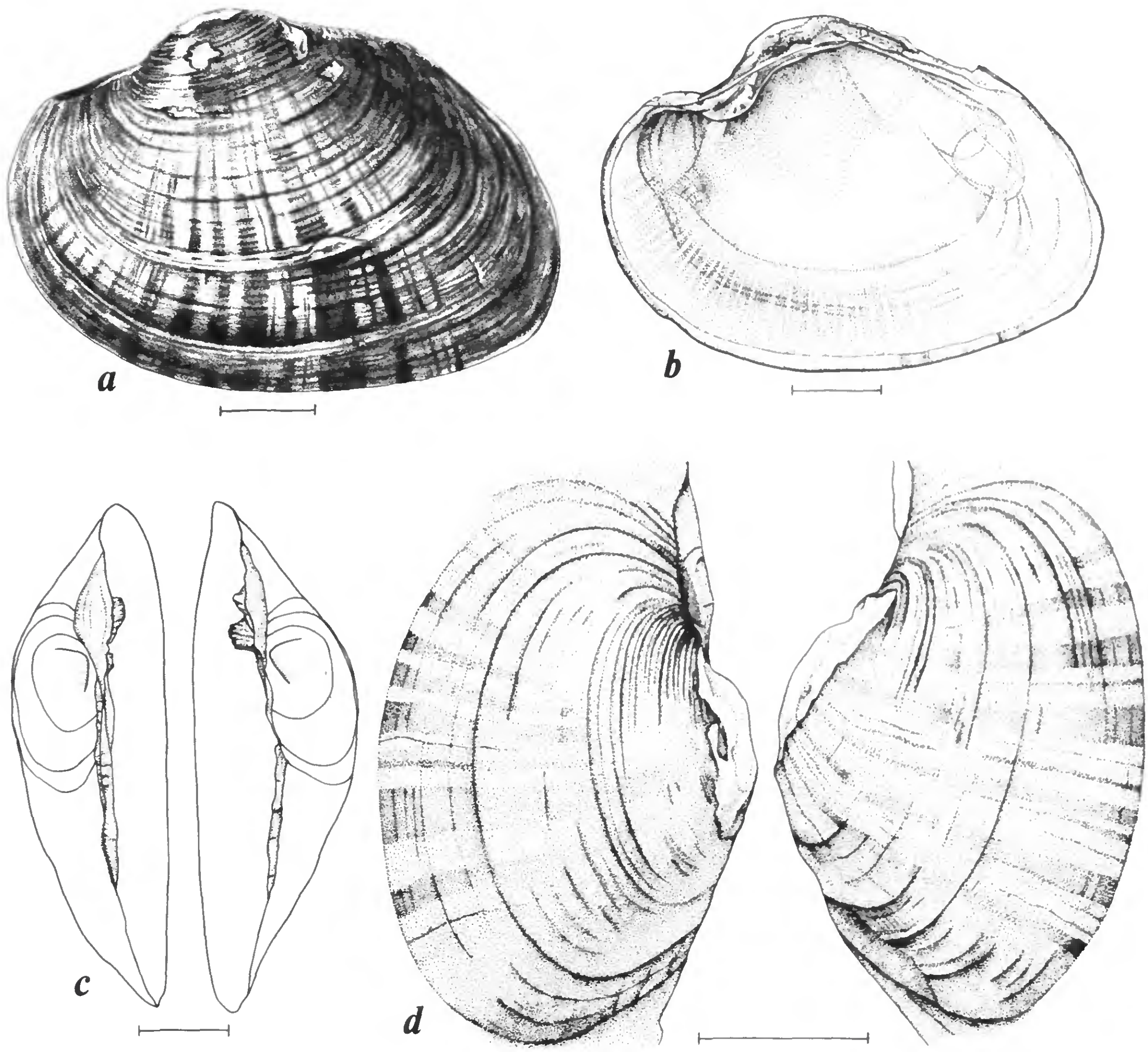

FIGURE 11.—*Alasmidonta mccordi*: *a–d*, holotype, NMC 20094, Coosa River, Ten Island Shoals, Alabama. (Scale = 1 cm.)

medium width, convex throughout, and faintly sculptured. Annual growth increments marked by a few shallow, concentric ridges and grooves that are pale in color and interrupt the periostracal rays. Additional post-juvenile sculpturing consisting of numerous low, concentric, growth wrinkles; a few short, raised, widely and irregularly-spaced threads on the posterior slope of the left valve; fine, obscure corrugations on the posterior ridge of the right valve; and a raised, radial, thread-like ridge on the posterior slope of the right valve. Periostracum with wide and narrow green rays covering the pale yellowish brown ground color except that on the posterior slope the shell is blackened. Ligament of medium length and thickness, pale brown generally but with dark brown areas centrally.

Hinge teeth narrow and incomplete but rather strong. Pseudocardinal tooth single in the left valve and elevated, compressed, subparallel with the dorsal margin, serrated, and confluent with the small, obscure interdental projection. Pseudocardinal teeth in right valve double, narrow, compressed, curved, serrated, one above the other and both parallel with the concave anterior-dorsal margin. Pseudocardinals in each valve buttressed by a flattened ridge below. Lateral teeth obsolete and indicated by low, partly obscure ridges that do not articulate but number one in the left valve and two in the right. The ridge in the left valve is stronger than those in the right. Beak cavity excavated and of medium depth. Anterior muscle scars impressed (in fact slightly excavated beside the cardinal tooth buttresses), pallial line complete and well marked but not impressed, posterior muscle scars very shallow but clearly apparent, and scars within beak cavity consisting of a few rather deep, elongate pits on the back of the hinge plate beneath the umbones and parallel with the hinge plate and also of numerous, faint corrugations near the apex of the beak cavity and distributed in the terminal groove for a short distance anteriorly and posteriorly from that apex. Nacre pearly white, lustrous anteriorly and iridescent posteriorly, and with yellowish stains in and close to the beak cavities.

Beak sculpture obscure in the single specimen examined (only two faint remnants of bars, suggesting a single-looped pattern, are visible) but apparently not extending beyond 6 mm from the umbonal apex.

Life History

Nothing is known about the anatomy, glochidia, breeding period, or natural host of this species.

Athearn (1964:135) has described the habitat of *A. mccordi* as follows: "The specimen was collected alive on a sand and gravelly bottom which was thickly strewn with rock debris from Lock 2 Dam. The water here was swift and shallow."

The Coosa River has been impounded by a series of dams and *A. mccordi* is probably now extinct.

Geographic Records

Figure 17

The only specimen known is from the type locality.

Remarks

Alasmidonta mccordi shows relationship to *Arcidens* (*Arkansia*) *wheeleri* by its possession of a lunule and, in the left valve, of a curved anterior pseudocardinal tooth that is parallel to the lunule. Its central geographical location (Coosa River), between *Alasmidonta* sensu stricto (Atlantic and eastern Gulf drainage) and *Arcidens* (Mississippi River and western Gulf drainages) is probably also significant. *Alasmidonta mccordi* has more shell characters that link it to *Alasmidonta* (sensu lato) than to *Arcidens*, however, e.g. the absence of tubercles on diagonal ridges across the central part of the shell, the lateral teeth that are absent or vestigial, the presence of prominent periostracal color rays, etc. It is therefore retained within *Alasmidonta* (sensu lato) but, as a disparate element, it is placed in a distinct subgenus (*Alasmidens*).

Subgenus *Alasmidonta*, sensu stricto

The glochidia of *A. undulata* and *A. arcula* are both elevated pyriform, higher than long, and have lingulate stylets that bear about 6 longitudinal rows of major microstylets on their distal halves.

Comparative features of the adults are: the shells are medium-sized (about 54–80 mm long), are of medium to tall relative height (H/L about 0.60–0.83), have rather inflated umbones and possess rudimentary to well-developed sculpturing on the posterior slope. There is no sexual dimorphism in the shells. Well developed cardinal teeth and interdental projection are characteristic but lateral teeth are rudimentary. The anal mantle opening is not papillate or crenulate and the inner lamina of the inner demibranch is fully attached to the visceral mass in most specimens and partly attached in some.

Alasmidonta (Alasmidonta) undulata (Say, 1817)

FIGURES 12-14

U[nio] undulata Say, 1817 [no pagination; species 9 under genus *Unio*, pl. 3: fig. 3]. [Type-locality: "Delaware River." Original type material lost.]

"*Unio glabratus*? Lamarck" Sowerby, 1823 [no pagination; species 3, fig. 3]. [No type-locality. Original specimen lost. Not *Unio glabratus* Lamarck, 1819.]

Unio hians Valenciennes, 1827:235, figs. 2a, b. [Type-locality: "les eaux douces des invirons de Philadelphie." Location of original material unknown.]

Alasmodonta sculptilis Say, 1829:339. [Type-locality: "Virginia." Original type material lost.]

Uniopsis radiata Swainson, 1840:289, fig. 62. [Implied type-locality: North America. Location of original material unknown. Not in British Museum (Natural History).]

U[niopsis] mytiloides Swainson, 1840:382, fig. 62. [Implied type-locality: North America. Location of original material unknown. An objective synonym of *Uniopsis radiata*. Not in British Museum (Natural History).]

Margaritana triangulata Lea, 1858:138 [Latin description and specimen localities]; 1859(a):46, pl. 32: fig. 111; 1859(b): 46, pl. 32: fig. 11 [both 1859 references are the same as in 1858, with English description, comments, and illustrations added]. [Specimen localities: upper Chattahoochee, Georgia; Columbus, Georgia; Potato Creek, Georgia; and Sawney's Creek, South Carolina. The specimen figured by Lea (USNM 86249), from Upper Chattahoochee [River], Georgia, is herein selected as lectotype.]

Unio swainsoni Sowerby, 1868, pl. 76: fig. 396, and accompanying text. [Type-locality not specified. Figured holotype in British Museum (Natural History), 1900.3. 19.21. The holotype is so similar to specimens of *Alasmidonta undulata* from the Ottawa-St. Lawrence River System in Ontario and Quebec that its origin there is clearly indicated. Specimens from that area are characteristic and easily recognized (see "Remarks").]

THE SHELL

FIGURES 12*a-e*, *g*

DESCRIPTION.—Shell ovate or triangulate-ovate, up to 75 mm long, 45 mm high, and 35 mm wide, thickened and strong anteriorly (up to 6 mm thick) and thin and fragile posteriorly. Anterior margin rounded, ventral margin broadly and evenly curved or flattened posteriorly, posterior margin roundly pointed below the midline and obliquely flattened above, and dorsal margin short or moderate in length and straight or a little curved. Maximum inflation at middle of shell or slightly anterior of middle. Beaks barely inflated, located about 1/3 the distance from anterior to posterior, and projecting somewhat above the hinge line. Posterior ridge well-marked, rounded or subangular proximally, and flatly rounded distally. Posterior slope concave. Growth increments marked by concentric lines and low, irregular ridges and grooves. Additional post-juvenile sculpturing consisting of one to three coarse radial ridges on the posterior slope and, on some specimens, numerous fine radial ridges between these coarse ridges and/or short, oblique corrugations proximal to the umbones or distributed farther out on the slope. Periostracum smooth and shiny, yellowish with broad green or blackish rays in juveniles, brownish black or black in adults but with rays still visible by transmitted light. Ligament relatively short, thick, and strong.

Hinge teeth prominent but incomplete. Pseudocardinal teeth stumpy, thick, strong, in some specimens deeply grooved, buttressed below by a heavy ridge, and numbering one in the right valve and two in the left, the anterior one being larger. Interdental projection in left valve clearly developed in most specimens. Lateral teeth short and vestigial or absent. Beak cavity triangular, compressed, and rather deep. Anterior muscle scars deep and variously grooved, pallial line complete and well-marked, posterior muscle scars shallow but clearly defined, and scars within beak cavity consisting of irregular grooves on the back of the hinge plate and one or two radial grooves extending from within the cavity and beyond toward the posterior extremity. Nacre glossy throughout, thick and white anteriorly, thin, bluish, and iridescent posteriorly, and variously modified with salmon or pink.

Beak sculpture very heavy and composed of

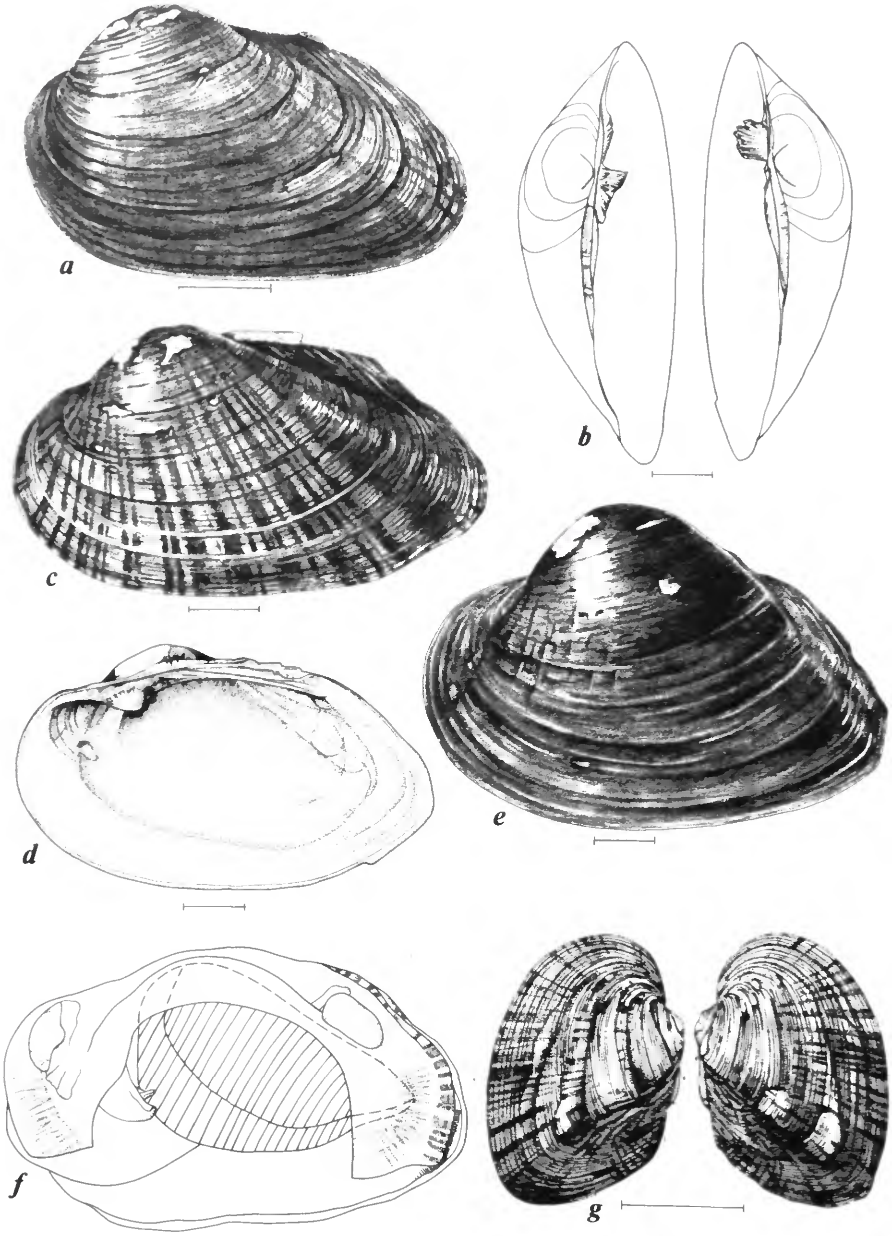

FIGURE 12.—*Alasmidonta undulata*: *a*, morph *swainsoni*, NMC 11330, St. Lawrence River, Quebec, Canada; *b–d*, morph *undulata*, sensu stricto, USNM 86232, Passaic River, Passaic, New Jersey; *e*, morph *triangulata*, USNM 758696, Apalachicola River near Blountstown, Florida; *f*, morph *undulata*, sensu stricto, OSUM 20952, Unadilla River near Norwich, New York; *g*, morph *undulata*, sensu stricto, details of beak sculpturing, USNM 590585, Monocacy River, Maryland. (Scale = 1 cm.)

about 5 prominent, single-looped, curved ridges that extend far out on the shell surface (about 10 mm from the umbonal apex). The loops are asymmetrical, i.e. expanded on the posterior ridge, but the bars are either not thickened there, or only slightly thickened.

VARIATION.—An analysis of variation in relative shell weight is given in Tables 1 and 2 and in the Introduction. Two other characters, hinge plate thickness and anterior-ventral thickening, are shown to be directly correlated with relative shell weight and all of these appear to be related to water quality.

During the study of this material pink nacre was commonly observed in southern populations and only rarely in northern populations. Beak sculpturing and posterior slope sculpturing are also more strongly developed in southern than in northern populations. The significance of these trends is discussed under Remarks.

TOPOGRAPHIC ANATOMY

FIGURE 12*f*

SPECIMEN DESCRIBED.—From Ashuelot River, 4 mi (6.4 km) N of Keene, Westmoreland Co., N.H., collected 8 August 1978 (USNM 795076, A. H. Clarke station 1601); anesthetized with nembutal, fixed in 10% formalin, and preserved in 70% ethyl alcohol; shell length 42.4 mm, sex female (inferred).

DESCRIPTIONS.—Mantle white and translucent but appearing yellowish white because of color of demibranchs within. Small rectangular patches of dark pigment are scattered along the posterior edge of the mantle. (In some specimens they are fused and form a dark band.) Edges of posterior mantle openings flush with pigmented edges of mantle, i.e. not surrounded by a lip. The incurrent opening is 5.5 mm long and surrounded within by 4 rows of pyramidal, interdigitating, pale brown tentacles, the outer tentacles short and located at the mantle edge, the inner tentacles progressively larger in rows 2, 3, and 4 to a maximum of about 1.3 mm. Appressed portion of mantle edges between incurrent and anal openings short (0.5 mm). Anal opening with edges slightly crenulated, without papillae, and 5.0 mm long. Mantle connection between anal and supra-anal openings long (4.4 mm). Supra-anal opening narrow and slit-like, inner edge with reddish brown subapical band and a diffuse, paler band above and below, and 5.6 mm long.

Demibranchs pale yellowish brown. Outer demibranch 25 mm long, 12 mm high, with rounded, free, ventral margin, radial wrinkles, and with about 10 double filaments and 2.0 water tubes per mm. Inner demibranch larger, projecting 2 or 3 mm beyond outer demibranch, and with about 10 double filaments and 0.8 water tubes per mm. The inner lamina of the inner demibranch is connected along only part of its edge with the visceral mass.

Labial palpi pale yellowish brown, bilobate distally, with curved ventral margin, and with distal edges rolled outward; outer surface of each palpus of each pair smooth; inner opposing surfaces radially furrowed (about 5 furrows per mm at margin). Each palpus is joined below its dorsal margin to its corresponding member for about half of its length, or a little less, and the distal ends of the palpi do not touch the inner demibranch but lie 1.0 mm from it.

Fresh specimens from the Tar River were observed to have the mantle edges suffused with orange but details of the colors of other organs were not recorded at the time of collection. Ortmann (1912:296) has described fresh specimens from Pennsylvania as follows: "mantle transparent gray shading into brownish or brownish orange on the margin anteriorly and into white posteriorly; mantle edge brown, mottled with black spots, and posteriorly orange; adductor muscles grayish to brownish; demibranchs grayish brown shading into orange; labial palps whitish to orange-brown; foot pale white or orange brown; abdominal sac whitish." The female outer demibranchs are described as pale yellow when containing eggs and brownish when containing glochidia.

Finally, Table 9 shows that a dichotomy exists in numbers of water tubes per mm in the outer demibranchs of non-gravid individuals. Those specimens with 1.5 to 2.0 water tubes per mm are considered as probable females and those with 1.0 or fewer water tubes per mm are interpreted as probable males. See "Indirect Determination of Sex" (page 000).

VARIATION.—Table 9 contains measurements and observations made on the soft parts of all available preserved specimens of *Alasmidonta undulata*, arranged in geographical order from north to south. The characters reported are those that have been considered significant for species discrimination by other workers or are otherwise of interest in the present investigation.

It can be seen that the extent and the strength of mantle pigmentation varies from extensive and heavy (specimen 12) to complete absence (specimen 1). The distance (A-SA) between the anal (A) and the supra-anal (SA) openings is less than

TABLE 9.—*Alasmidonta undulata:* Variation in topographic anatomy (abbreviations same as Table 4)

		Mantle pigmentation		*Relative length of mantle features (as % of L)*				*Incurrent papillae*		*Labial palps*		*Water tubes*		*Pre-preserv. treatment*	
Spec. No.	*Length (mm)*	*Extent*	*Strength*	*Inc.*	*Anal*	*A-SA*	*SA*	*Ranks*	*Max. Ht. (mm)*	*Posit.*	*Grooves per mm*	*N/ mm**	*Sex*	*Nemb. relax.*	*Form. fixed*
						Long Lake, Masham Twp., Quebec (NMC 3359)									
1	54.8	0	A	15	10	9	14	3	1.2	NT	10	1.5	(F)	-	?
2	50.0	1	W	16	9	6	14	1	0.6	NT	14	0.8	(M)	-	?
						Petitcodiac River, 1.9 mi WSW of Moncton, New Brunswick (NMC 46073)									
3	53.3	3	W	20	16	8	15	4	1.3	NT	8	0.9	(M)	-	-
4	52.0	Inc. Op.	H	17	17	9	13	5	1.4	NT	9	1.5	(F)	-	-
5	51.5	3	M	17	14	8	14	4	1.3	NT	7	0.8	(M)	-	-
6	49.8	Inc. Op.	H	16	13	8	14	4	1.3	NT	7	0.8	(M)	-	-
7	49.4	Inc. Op.	H	16	14	10	12	4	1.3	NT	9	2.0	(F)	-	-
8	48.1	Inc. Op.	H	17	10	9	12	3	1.6	NT	9	2.0	(F)	-	-
9	43.7	Inc. Op.	H	19	14	9	16	4	1.1	NT	8	0.8	(M)	-	-
10	41.5	Inc. Op.	H	21	13	11	16	4	1.2	NT	14	2.0	(F)	-	-
11	38.6	Inc. Op.	W	19	16	7	14	4	1.6	NT	5	2.0	(F)	-	-
						Ashuelot River, 4 mi N of Keene, N.H. (NMC uncat.)									
12	42.4	3	H	13	12	10	13	4	1.3	NT	5	2.0	(F)	+	+
13	37.5	2	W	14	11	12	17	4	1.8	T	9	-	GF	+	+
						Unadilla River, 15 mi NE of Norwich, N.Y. (OSUM 20952)									
14	41.3	1	M	16	14	11	14	2	1.0	T	8	-	GF	-	-
15	38.4	1	M	15	14	6	19	3	1.1	OV	6	1.5	(F)	-	-
						Gunpowder River, Gunpowder Falls, Md. (NMC 59513)									
16	38.0	2	M	19	16	(tissue torn)		3	2.0	T	10	-	GF	-	-
						Christian Creek, 4 mi SE of Staunton, Va. (OSUM 20528)									
17	46.7	2	H	14	11	12	11	3	1.2	OV	8	-	GF	-	-
18	45.4	1	M	16	14	11	13	3	1.0	T	8	-	GF	-	-
						Tar River, Franklin Co., N.C. (USNM 758696, 795077)									
19	58.8	2	W	15	7	12	15	4	1.4	OV	9	1.0	(M)	+	+
20	50.0	Inc. Op.	W	15	9	9	21	3	2.0	OV	6	-	GF	+	+
21	49.4	1	M	16	10	16	10	4	1.4	OV	5	0.8	(M)	+	+
22	41.0	2	M	12	7	8	11	4	1.8	OV	10	-	GF	+	+
23	38.1	2	M	16	14	13	14	2	0.9	OV	10	2.0	(F)	+	+
24	18.5	1	W	22	12	10	14	4	0.8	OV	9	-	-	+	+

* Refers to outer demibranchs of non-gravid specimens.

the length of the anal opening in most specimens (17), the same in one, and larger in five. A-SA is also shorter than the supra-anal opening in most (21) of the 23 undamaged specimens examined. (Ortmann (1912:296) states that A-SA is longer than A and longer than SA in Pennsylvania specimens.) A geographical trend may exist here.

The number of ranks of papillae within the edge of the incurrent opening varies from one to five, and the papillae also vary in maximum height (0.6 to 2.0 mm). As with pigmentation, minimum development of this character occurs in the most northern population.

A pronounced geographical trend appears to exist in regard to the relative position of the labial palpi: the palpi do not touch the inner demibranchs in the most northern populations, some touch and some overlap in intermediate populations, and all overlap in the most southerly population examined. According to Ortmann (1912: 296) the labial palpi of Pennsylvania specimens do not touch the inner demibranchs.

Other characters examined in all specimens, but omitted from Table 9, were the number and extent of anal papillae (absent in all specimens) and the connection between the inner lamina of the inner demibranch and the visceral mass. In the latter character the described specimen (which showed an incomplete connection) was anomalous: in all other specimens, but one, the connection was complete. In the other exception the connection extended along the whole demibranch margin but a few small holes were present.

Glochidium

Figure 13

Description.—Glochidium pyriform, somewhat asymmetrical, 0.370 mm high, 0.310 mm long, 0.103 mm in single valve convexity. The posterior margin is more convex and protuberant than the anterior. The apex is located about 46% of the distance from anterior to posterior (measured parallel to the hinge axis). The surface is finely malleated (depressions shallow, subcircular, and about 5–10 μm wide) and pitted. The pits are about 2 μm wide and number about 1 to 5 in each depression. The apical area is unsculptured, except for fine, concentric lines, and is thickened. The hinge is flatly sinuate, about 0.200 mm long, and the ligament is very narrow.

Each apical stylet is flatly recurved, directed somewhat posteriorly, about 0.125 mm long, 0.052 mm wide at the base, triangular in cross-section, and gradually narrowing to a rounded, blade-like, slightly recurved tip. Each stylet is also supported on each side, for about half its length, by a membrane that is connected to the ventral edge of the valve. Except for small areas at the apex and along the lateral edges, the flatly-rounded, exposed surface of each stylet is covered with approximately 125 microstylets, each about 10 μm long, and arranged in about 8 rows (5 rows near the apex), the rows more-or-less parallel with the midline of the stylet. The microstylets are directed toward the distal end of the stylet and are lanceolate or spatulate, compressed, with 2 to 4 sharp lateral edges and a sharp, curved apex. Other smaller (1–2 μm long), pyramidal microstylets occur on the base of the stylet and continue as tiny (<0.5 μm) micropoints along the ventral edges of the valves.

The above description is of a glochidium taken from an adult specimen (OSUM 20528) collected at Christian Creek, 4 mi (6.4 km) SE of Staunton, Virginia, by D. H. Stansbery and W. J. Clench on 8 September 1968. A glochidium from another specimen (20952, from Unadilla River, 15 mi (24 km) NE of Norwich, N.Y., collected by Carol B. Stein on 28 September 1965) is 0.330 mm wide, and 0.095 mm in single valve convexity. The stylets are roundly curved and the microstylets are multifaceted with up to 6 sharp cutting edges, i.e. with the cross-section a flattened hexagon. Another glochidium from the same parent has symmetrically expanded lateral edges on one stylet and straight edges on the other. Still another glochidium from the same parent is 0.282 mm wide and has a stylet with laterally expanded edges that are markedly asymmetrical.

Another glochidium, from an adult specimen

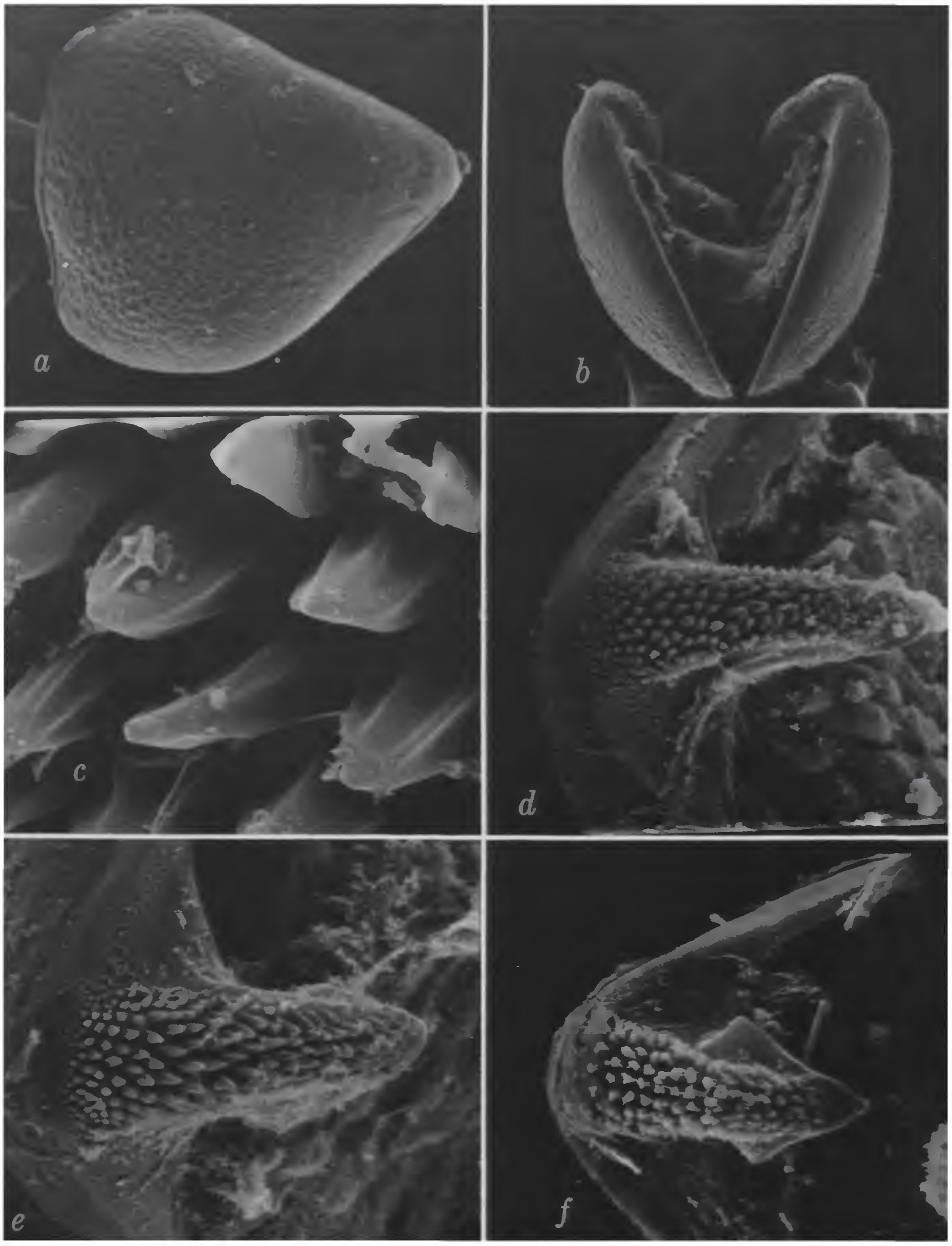

FIGURE 13.—Glochidia of *Alasmidonta undulata*: *a*, OSUM 20528, Christian Creek near Staunton, Virginia; *b-f*, OSUM 20952 (location same as 12*f*), (*a* × 175; *b* × 140; *c* × 4350; *d* × 460; *e* × 520; *f* × 460.)

collected from the Tar River, 2.3 mi (3.7 km) E of Raynor, North Carolina by A. H. Clarke and J. J. Clarke on 28 August 1977, is about 0.378 mm high and 0.330 mm wide. It is apparently identical to other glochidia of *A. undulata* in shape and surface sculpturing but differs from them by having short, blunt stylets and soft, pliable microstylets. This difference is no doubt attributable to immaturity.

Life History

Gravid Period.—Ortmann (1919:178) cites 17 dates, spanning the period from 18 July to the following 14 June, on which he collected gravid specimens. The gravid specimens examined for the present study were collected between 28 August and 24 October.

Natural Host.—Not recorded.

Habitat.—"A common species in the Atlantic drainage in Pennsylvania; but it is quite evident that it avoids the larger rivers, and prefers the smaller streams, where it becomes locally very abundant, going far up towards the headwaters . . . It does not seem to favor riffles and very rough water, but is found chiefly where a steady flow of water prevails. It does not like slackwater, but occasionally it is found in ponds and canals . . . It lives mostly in a mixture of coarser or finer gravel with sand and mud; but I have taken it also in eddies with slow current embedded in the mud deposited between larger stones" (Ortmann, 1919:18).

The above comments conform with my observations in Canada, New England, New York, and North Carolina. It is also abundant and large in outlet streams just below lakes. Its usual associates, in North Carolina and northward, are *Elliptio complanata* and (secondarily) *Strophitus undulatus*.

Geographical Records

Figure 14

St. Lawrence River System.—*Ottawa River Drainage:* Bousquet River, 20 mi (32.0 km) E of Rouyn, Que. (1960, A. H. Clarke, L. R. Clarke, A. R. Clarke! (NMC)). Madawaska River, Algonquin Park, Ont. (ANSP); Hyde Creek, Cedar Lake, near Denbigh, Ont. (ANSP); Mill Pond, Denbigh, Ont. (ANSP, NMC, USNM). Meach Lake, Que. (NMC). Meach Creek, Que.; outlet of Harrington Lake, Que.; Gatineau River, Que.; Chilcott Lake, Que. (all La Rocque, 1962). Ottawa River: Nepean, Ont.; Ottawa, Ont. (both USNM, NMC); Duck Island [near Ottawa] (LaRocque, 1962).

Richelieu River Drainage: Winooski River, 2 mi (3.2 km) SE of Williston, Vt. (1958, W. J. Clench and R. D. Turner! (MCZ)); Chimney Point, Lake Champlain, Vt. (USNM); 2 mi (3.2 km) W of West Milton, Lake Champlain, Vt. (USNM).

Bellechasse River Drainage: Bellechasse River, St. Vallier, Que. (1953, E. L. Bousfield! (NMC)).

St. Lawrence River: Sheek Island, Long Sault Rapids, 8 mi (12.8 km) W of Cornwall, Ont. (1957, A. H. Clarke! (see Clarke, 1959)); near Montreal and Quebec, Que. (LaRocque, 1962 (NMC)).

Coastal Drainages, Nova Scotia.—Cumberland Co.: Halfway River West Lake, 1 mi (1.6 km) S of Newville; River Hebert, Newville. Inverness Co.: McIntyre Lake, 8 mi (12.8 km) ENE of Port Hawkesbury; River Inhabitants, 3 mi (4.8 km) SSW of Glendale. Halifax Co.: Musquodoboit River, 2 mi (3.2 km) N of Musquodoboit Harbour; Fish Lake, 2 mi (3.2 km) S of Waverly; outlet of Fish Lake, 2 mi (3.2 km) S of Waverly; Lake William, at outlet, Waverly; small lake 3 mi (4.8 km) E of Lower Sackville; Gays River, Gays River; outlet of Fletcher Lake, Wellington Station; Shubenacadie River, 1 mi (1.6 km) S of Enfield. Hants Co.: Kennetcook River, 3 mi (4.8 km) E of Clarksville. Colchester Co.: Stewiacke River, 5 mi (8.0 km) E of Stewiacke (all 1946–54, H. D. Athearn! or 1960, A. H. Clarke, L. R. Clarke, and A. R. Clarke! (see Athearn and Clarke, 1962) (NMC)).

St. John River System.—Oak Point, Portage Lake, Aroostook Co., Me. (1955, A. H. Clarke and L. R. Clarke! (NMC)). Square Lake, Aroostook Co., (ANSP); Fish River, Eagle Lake, Aroostook Co. (Ortmann, 1919). Aroostook River, Caribou, Aroostook Co. (USNM, ANSP). St. John River, Connors, Madawaska County, N. B. and Fort Kent, Aroostook Co., Me. (Nylander, 1914).

Penobscot River System, Maine.—Mattawamkeg River, Haynesville, Aroostook Co. (1952, A. H. Clarke! (NMC)).

Sennebec River System, Maine.—South Pond, Warren, Lincoln Co. (USNM).

Kennebec River System, Maine.—Moose River, Rockwood, Somerset Co. (MCZ) and Sidney, Kennebec Co. (ANSP).

Merrimac River System.—Beaver Brook, Pelham, Hillsborough Co., N.H. (this survey) (USNM); Assabet River, Concord, Middlesex Co., Mass. (USNM); Sudbury River, Farmington, Middlesex Co., Mass. (ANSP); Sudbury River,

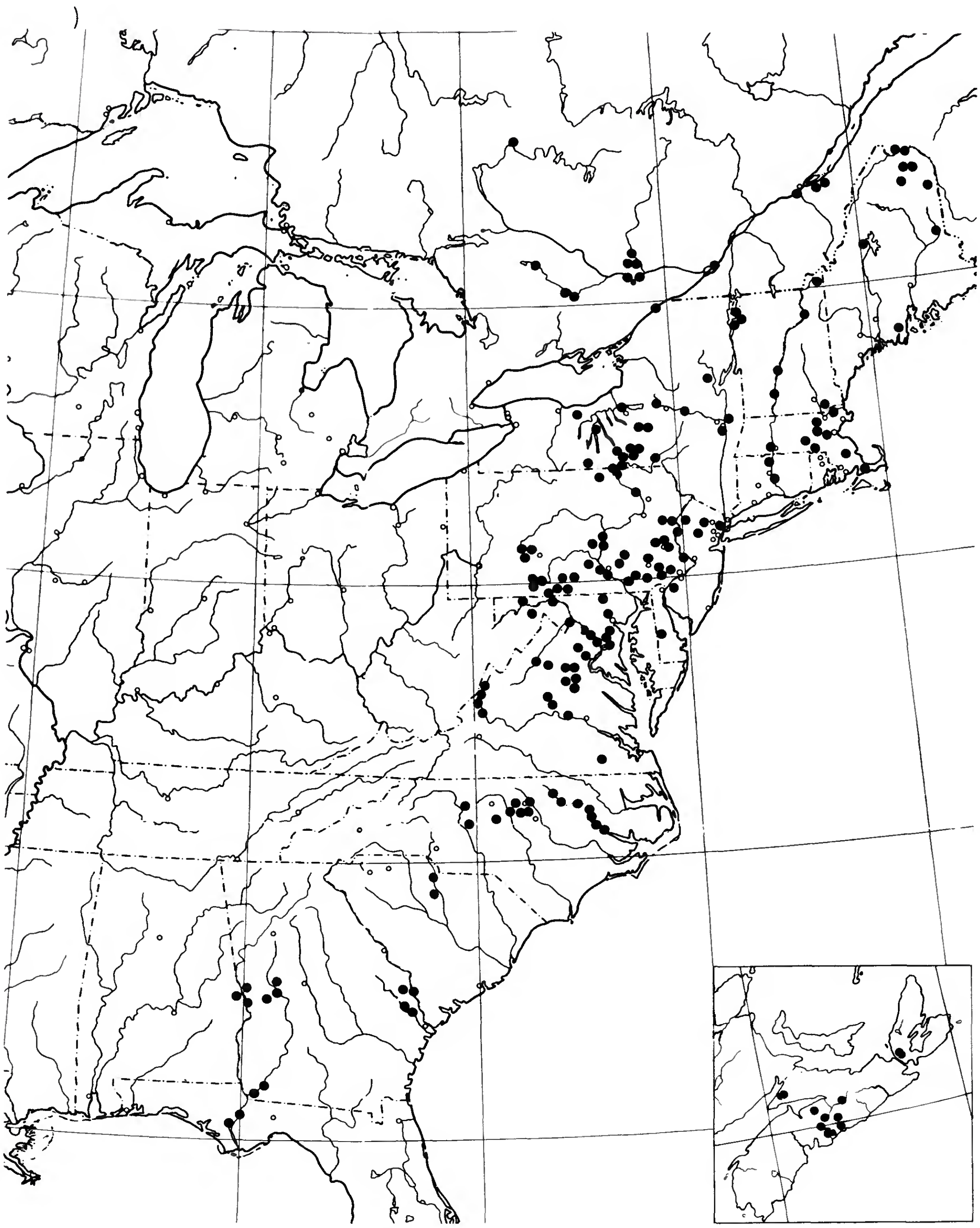

FIGURE 14.—Geographical distribution of *Alasmidonta undulata* (insert = location of specimens found in Nova Scotia).

1 mi (1.6 km) from Concord River, Middlesex Co., Mass.; Merrimac River, Haverhill, Essex Co., Mass. (both USNM).

CHARLES RIVER SYSTEM, MASSACHUSETTS.—Charles River, Newton, Middlesex Co. (MCZ).

SOUTHEASTERN MASSACHUSETTS.—Halfway Pond, near Plymouth, Plymouth Co. (1952, A. H. Clarke, L. R. Clarke! (NMC)); Mashpee Pond, Mashpee, Barnstable Co. (NMC); Blackstone River, Worcester and Uxbridge, both Worcester Co. (both USNM).

CONNECTICUT RIVER SYSTEM.—First Connecticut Lake at outlet, Coos Co., N.H. (headwaters of Connecticut River) (1953, A. H. Clarke and L. R. Clarke! (NMC)); Connecticut River: Northumberland, Coos Co., N.H. (ANSP); Hartland, Windsor Co., Vt.; Bellows Falls, Windham Co., Vt.; Westfield, Hampden Co., Mass. (all USNM); North end Windsor Locks Canal, Suffield, Hartford Co., Conn. (1974, S.L.H. Fuller and J. Bereza! (ANSP)) and South Glastonbury, Hartford Co., Conn. (USNM).

HUDSON RIVER SYSTEM, NEW YORK.—*Erie Barge Canal-Mohawk River Drainage:* Monroe Co.; Seneca Lake; Erie Barge Canal, Onondaga Co. (all 19th-century records cited in Clarke and Berg, 1959); Lake Oneida (Baker, 1916); Erie Canal, Mohawk, Mohawk Co. (USNM); Beaver Creek, 8 mi (12.8 km) S of Mohawk (ANSP).

Hudson River Drainage: Thirteenth Lake, North River, Warren Co.; Troy; Norman's Kill, Albany (all USNM).

PASSAIC RIVER SYSTEM, NEW JERSEY.—Near Morris Plains, Morris Co.; Passaic, Bergen Co. (both USNM).

RARITAN RIVER SYSTEM, NEW JERSEY.—North Branch Raritan River, North Branch, Somerset Co. (ANSP).

DELAWARE RIVER SYSTEM.—*Delaware River Drainage:* Smartwood Lake, Sussex County, N.J. (ANSP). Delaware River, "Foul Rift," Warren Co., N.J. (USNM); Shawnee, Monroe Co., Pa.; Yardley, Bucks Co., Pa. (both Ortmann, 1919) and "Washington Park" [Mercer Co.], N.J. (ANSP). Raccoon Creek, Mullica Hill, Gloucester Co., N.J. (USNM). "Valley Creek" [Sucker Run], southwest of Coatesville, Chester Co., Pa. (ANSP).

Lehigh River Drainage: Princess Creek, Kunkletown, Monroe Co., Pa. (Ortmann, 1919).

Schuylkill River Drainage, Pennsylvania: Manatawny Creek near Earlville, Berks Co. (ANSP); Sancony Creek, Kutztown, Berks Co. (Ortmann, 1919); Maiden Creek, Berks Co.; Pequea Creek, Paradise, Lancaster County; Perkiomen Creek, Chester County (all ANSP); White Clay Creek, Avondale, Chester Co.; Kimberton Dam, near Phoenixville, Chester Co. (both Ortmann, 1919); Pickering Creek, Chester Co. (USNM); Schuylkill River and Canal, Philadelphia (several localities; ANSP, USNM; Ortmann, 1919).

CHOPTANK RIVER SYSTEM.—"Choptank Mills," Kent Co. Del. (ANSP).

SUSQUEHANNA RIVER SYSTEM.—*Upper Susquehanna River Drainage, New York:* Tioga River (Marshall, 1895). Catatonk Creek 2 mi (3.2 km) SE of Candor and at Owego, Tioga Co.; Tioughnioga River, Itaska, Broome Co.; Otselic River near Upper Lisle, Broome Co. (all 1955–58, A. H. Clarke, A. R. Clarke and L. R. Clarke! (see Clarke and Berg, 1959)). Eaton and West Eaton, Madison Co. (both USNM). Chenango River, 3 mi (4.8 km) NE of Greene, Chenango Co. and at Chenango Forks, Broome Co.; Susquehanna River at Afton, Chenango Co. and at Smithboro, Tioga Co. (all 1955-58, A. H. Clarke, L. R. Clarke, and A. R. Clarke! (see Clarke and Berg, 1959)).

Lower Susquehanna River Drainage, Pennsylvania: Mill-race of Crooked Creek, Tioga, Tioga Co.; Chemung River, South Waverly, Bradford Co.; (both Ortmann, 1919). Dennings Creek, Bedford, Bedford Co. (USNM). Conodoguinet Creek, Carlisle, Cumberland Co. (USNM). Beaver Dam Creek, Flinton, Cambria Co.; Swartz Run, Ashville, Cambria Co.; Chest Creek, Patton, Cambria Co.; Frankstown Branch Juniata River, Hollidaysburg, Blair Co.; Raystown Branch Juniata River, Everett, Bedford Co.; Shobers Run, Bedford Springs, Bedford Co.; West Branch Mahantango Creek, Richfield, Juniata Co.; Conewago Creek, Table Rock, Adams Co.; Muddy Creek, Lancaster Co. (all Ortmann, 1919). Conestoga Creek, Lancaster, Lancaster Co. (USNM). Susquehanna River at Athens, Bradford Co. (1956, A. H. Clarke and L. R. Clarke! (see Clarke and Berg, 1959)); Towanda, Bradford Co. (ANSP); Selinsgrove, Northumberland Co. (Ortmann, 1919); "York Furnace," [York Co.] (ANSP); and Columbia, Lancaster Co. (MCZ).

GUNPOWDER FALLS RIVER SYSTEM, MARYLAND.—Gunpowder Falls, 2 mi (3.2 km) SE of Lineboro, Carroll Co. (1964, F. W. Grimm! (NMC)).

PATAPSCO RIVER SYSTEM, MARYLAND.—Gwynn's Falls, Pikesville, Baltimore Co. (1959, F. W. Grimm! (NMC)).

PATUXENT RIVER SYSTEM, MARYLAND.—Patuxent River at Laurel, Prince Georges Co. (3 records, USNM).

POTOMAC RIVER SYSTEM.*—*Upper Potomac River Drainage:* South Branch Potomac River, Romney, Hampshire County, W. Va.; Wills Creek, Ellerslie, Allegany Co., Md.; Great Tonoloway Creek, Thompson Township, Fulton Co., Pa.; Franklin Co., Pa. at West Branch Conococheague Creek, Mercersburg Junction; Conococheague Creek, Greencastle

* Except for the Tar River specimens collected by me, most of the records from the Potomac drainage south to and including the Ogeechee drainage are also cited by Johnson (1970:150–152) under *A. undulata* and *A. triangulata.* Unless otherwise stated, the museum specimens and literature records listed here have also been examined by me and the original sources are therefore cited.

and Scotland; and East Branch Little Antietam Creek, Waynesboro. Potomac River, Hancock, Washington Co., Md. (all Ortmann, 1919).

Shenandoah River Drainage: North Fork Shenandoah River, Broadway, Rockingham Co., Va.; South Fork Shenandoah River, Elkton, Rockingham Co., Va.; Shenandoah River, Harpers Ferry, Jefferson Co., W. Va. (all Ortmann, 1919).

Lower Potomac River Drainage: [Rock Creek], Silver Spring, Montgomery County, Md.; Bull Run, between US 28 and US 29/211 highways, Prince William Co., Va.; Occoquan Creek above the falls, Occoquan, boundary of Fairfax and Prince William counties, Va.; Potomac River, 0.4 mi (0.6 km) S of Seneca Dam, [near Seneca, Montgomery Co., Md.] and 2 mi (3.2 km) above Great Falls to Great Falls, Maryland and Virginia (several localities) (all USNM).

RAPPAHANNOCK RIVER SYSTEM, VIRGINIA.—*Rappahannock River Drainage:* Rappahannock River, Remington, Fauquier Co. and Marsh Run, Remington (both Ortmann, 1919).

Rapidan River Drainage: [Rapidan River], Orange, Orange Co. (USNM). Blue Run and Mountain Run, Orange Co. (both "UMMZ," Johnson, 1970).

YORK RIVER SYSTEM, VIRGINIA.—*North Anna River Drainage:* Mine Run, Orange Co. ("UMMZ"; Johnson, 1970).

JAMES RIVER SYSTEM, VIRGINIA.—Calfpasture River, Rockbridge Co. ("Conrad, 1846" [not seen], cited by Johnson, 1970). North River 1 mi (1.6 km) above bridge at Lexington; North River, Lexington, Rockbridge Co.; North River, 2 mi (3.2 km) WNW of Lexington (UMMZ; Johnson, 1970); North River, 1 mi (1.6 km) above bridge at Lexington; at upper end of Goshen Pass, Rockbridge Co. (all J.P.E. Morrison! (USNM)). Rivanna River, 4 mi (6.4 km) NNW and 3 mi (4.8 km) SE of Palmyra, Fluvanna Co. (both MCZ) and 2 mi (3.2 km) W of Columbia, Fluvanna Co. (Johnson, 1970). James River opposite Maidens, in Powhatten Co. (W. J. Clench and K. J. Boss, 1967) (MCZ).

CHOWAN RIVER SYSTEM.—Nottaway River, 3 mi (4.8 km) E of Rawlings, Brunswick Co., Va. (Johnson, 1970).

PAMLICO RIVER SYSTEM, NORTH CAROLINA.—Tar River at the following sites: 3.8 mi (6.1 km) N of Franklinton, Franklin Co.; 3 mi (4.8 km) N of Bunn, Franklin Co.; 4.5 mi (7.2 km) W of Rocky Mount, Nash Co.; Penny Hill, 8 mi (12.8 km) SE of Tarboro, in Pitt Co.; 1 mi (1.6 km) E of Falkland, Pitt Co. (all 1977–78, A. H. Clarke and J. J. Clarke! (USNM)); Old Sparta, 3.5 mi (5.6 km) W of Pinetops, Edgecombe Co.; and Bruce, 9 mi (14.4 km) NW of Greenville, Pitt Co. (both Johnson, 1970 (MCZ)).

NEUSE RIVER SYSTEM, NORTH CAROLINA.—Neuse River, Raleigh (MCZ); 5.75 mi (9.2 km) E of Raleigh Center (MCZ, USNM); Neuse River Falls (MCZ); Milburnie [7 mi (11.2 km) E of Raleigh] (MCZ) (all Wake Co.). Swift Creek, 3 mi (4.8 km) SSW of Garner, Wake Co. (MCZ, USNM). Middle Creek, 6.25 mi (10.0 km) SE of Apex, Wake Co. (Johnson, 1970). Little River, Tarpley's Mill, 2 mi (3.2 km) NE of Wendell, Wake Co. (Johnson, 1970).

CAPE FEAR RIVER SYSTEM, NORTH CAROLINA.—Morgan Creek, 1 mi (1.6 km) SE of Chapel Hill, Orange Co. ("UMMZ," Johnson, 1970). Rocky River, 11 mi (17.6 km) N of Sanford, Chatham Co. (UMMZ and 1978, A. H. Clarke and J. J. Clarke! (USNM)). Cape Fear River (UMMZ).

YADKIN-PEE DEE RIVER SYSTEM.—Uwharrie River, [Randolph or Montgomery Co.], N.C. ("USNM," Johnson, 1970). Salem [Yadkin River, Winston-Salem], N.C. (USNM).

SANTEE RIVER SYSTEM.—*Wateree River Drainage:* Sawney's Creek, [8 mi (12.8 km) NW of] Camden, [Kershaw Co.], S.C. (USNM).

Catawba River Drainage: Catawba River ("UMMZ," Johnson, 1970).

SAVANNAH RIVER SYSTEM.—Savannah River 10 mi (16.0 km) W of Allendale, Allendale Co. S.C. ("UMMZ," Johnson, 1970). Mill Race, 2 mi (3.2 km) N of Sardis, Burke Co., Ga. (Johnson, 1970).

OGEECHEE RIVER SYSTEM, GEORGIA.—Ogeechee River, Scarboro, Screven Co. and at bridge, 1 mi (1.6 km) S of Dover, Screven Co. (both "UMMZ," Johnson, 1970).

APALACHICOLA RIVER SYSTEM.—*Flint River Drainage, Georgia:* Flint River, 2 mi (3.2 km) W of Nakomis, Crawford Co. (MCZ). Patsaliga Creek, Taylor Co. (MCZ). Potato Creek, [Upson County?] (USNM). Flint River, Bainbridge, Decatur Co. and Hutchinson's Ferry, Recovery, Decatur Co. (both MCZ).

Chattahoochee River Drainage: Mulberry Creek, Mitchell Bridge, 3 mi (4.8 km) SSE of Mountain Hill, Harris Co., Ga. (MCZ). [Chattahoochee River], Columbus, Muscogee Co., Ga. (USNM). Uchee Creek near Nuckols, Russell Co., Ala. (UMMZ).

Apalachicola River Drainage, Florida: Apalachicola River, 6 mi (9.6 km) N of Blountstown, Calhoun Co. (USNM) and Chattahoochee, Gadsden Co. (Clench and Turner, 1956). Dead Lake, Chipola River, Chipola Park, Calhoun Co. (Clench and Turner, 1956 (MCZ)).

REMARKS

A previous discussion (pages 2–5) has indicated that, among the characters used to differentiate the southern populations (*Alasmidonta "triangulata"*) of this group from the northern populations (*A. undulata* sensu stricto), those that relate to relative shell weight (relative overall thickness, anterior thickness, and hinge plate width) are probably ecophenotypic and not genetic. Other shell characters must also be considered.

As stated previously, in our experience, nacre does tend to be pink in southern populations and not in northern populations, and that may be significant, but that character is difficult to assess from museum collections because pink nacre fades to white in a few years. Beak sculpturing, posterior slope sculpturing, and relative height (H/L, see Table 2) are also more strongly developed in southern populations and although those characters may be genetic or a function of more rapid growth, at least in this species group they are too irregularly expressed to be reliable taxonomic discriminants. No correlations were found between the relative position of the umbones (B-A/L) and distribution, or between relative obesity (see Table 2) and distribution.

Among anatomical characters analyzed, a few seem to be at least partially related to geography. Some northern specimens have reduced mantle pigmentation and fewer ranks of papillae within the incurrent opening than southern specimens but no clear geographic trend is apparent. The positions of the distal extremities of the labial palps relative to the inner demibranchs does appear to be correlated with geography. This trend seems to exist in *Alasmidonta varicosa* also. It does not appear to be related to increased demibranch size in southern populations. The trend is a gradual one, at any rate, and does not seem to be useful for taxonomic purposes.

The glochidia of northern and southern populations were also compared and no differences attributable to genetic divergence were evident.

The evidence therefore indicates that *Alasmidonta "triangulata"* is not taxonomically distinct from *Alasmidonta undulata*. For similar reasons the relatively thick-shelled populations corresponding to *Unio swainsoni* Sowerby (see Figure 12*a*) of the Ottawa and lower St. Lawrence River systems are also not accorded separate taxonomic status.

Alasmidonta (Alasmidonta) arcula (Lea, 1838)

FIGURES 15–17

Margarita (Margaritana) arcula Lea, 1838:71, pl. 22: fig. 69. [Type locality: Altamaha [River], Liberty [now Long] Co., Georgia. The lectotype herein selected, Lea's figured specimen, is in the Smithsonian Institution (USNM 86170).]

THE SHELL

FIGURE 15*a,b,d,e*

DESCRIPTION.—Shell triangulate, greatly inflated, up to 80 mm long, 60 mm high, and 53 mm wide, somewhat thickened anteriorly (up to about 3 mm thick) and thinner and rather fragile posteriorly. Anterior margin sharply curved, especially above; ventral margin flatly rounded; posterior margin bluntly pointed basally and obliquely truncated above in adults (squarely truncated in juveniles); and dorsal margin oblique, sigmoid, and rather short. Maximum inflation at or in front of center in adults, at posterior ridge in juveniles. Beaks greatly enlarged, triangular, located about ⅓ the distance from anterior to posterior or a little more, and projecting far above the hinge line. Posterior ridge elevated and sharply angular except becoming rounded near the margin in adults. A second, low ridge above the first is also present. Posterior slope broad and concave near the shell margin. Growth increments marked by irregular ridges, threads, and grooves. Additional post-juvenile sculpturing consisting of a few, poorly defined, oblique threads on the posterior slope. Periostracum yellowish brown with numerous narrow and wide green rays in juveniles; rays partly obscure in adults but visible with transmitted light. Ligament short, thick, and strong.

Hinge teeth peculiar and incomplete. Pseudocardinal teeth greatly compressed and flattened, elongated, deeply serrated, buttressed below by a strong ridge, and numbering 1 in the right valve and 1 or 2 in the left. The pseudocardinal in the right valve and the posterior pseudocardinal in the left are both irregularly produced posteriorly and in some specimens are confluent with the one or two irregular interdental projections that occur in each valve. Lateral teeth vestigial or absent. Beak cavity broad, inflated, and deep. Anterior muscle scars partly impressed and well defined, pallial line clearly defined anteriorly but obsolete posteriorly, posterior muscle scars shallow and almost imperceptible, and scars within beak cavity consisting of one or two radial ridges and

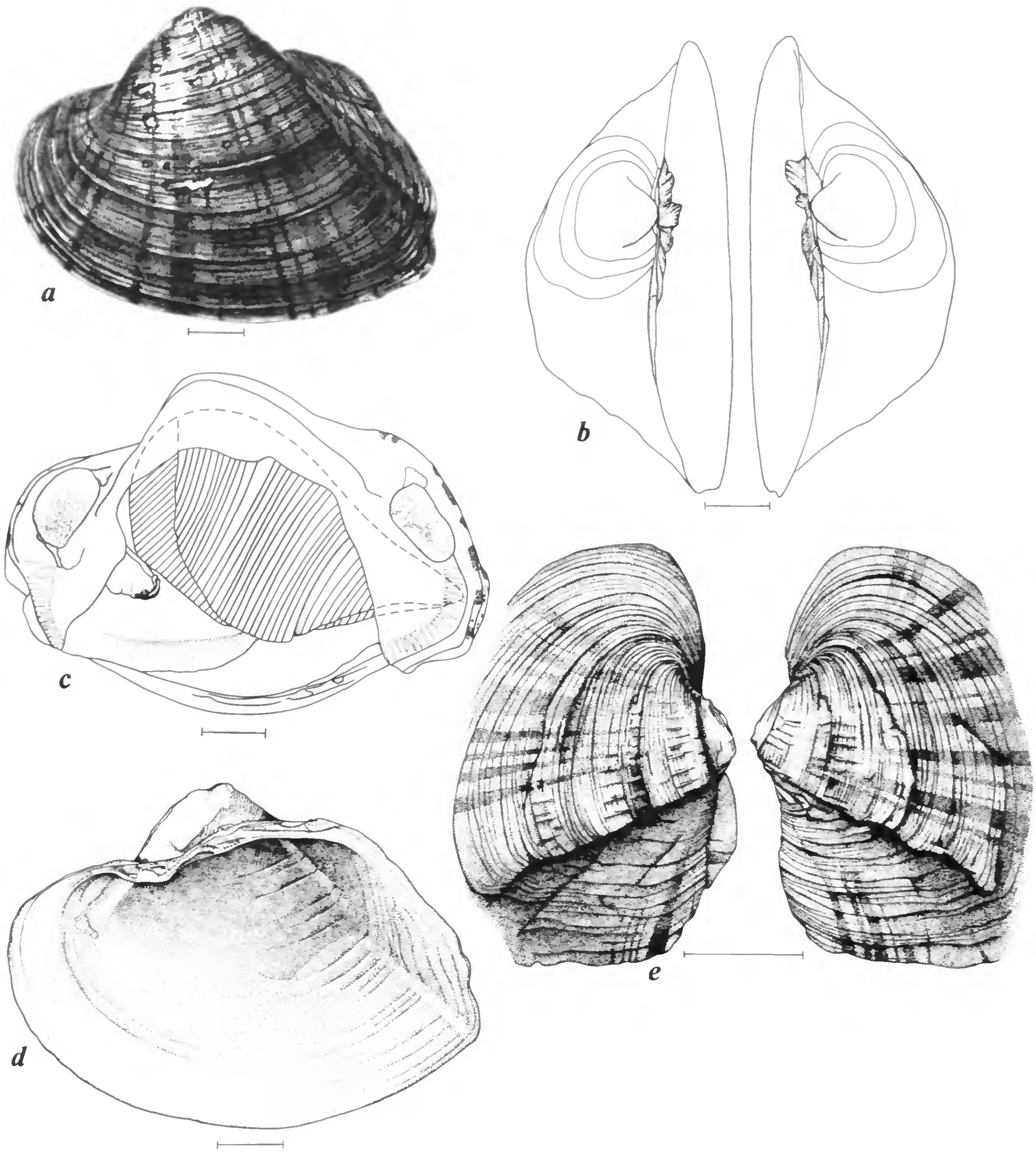

FIGURE 15.—*Alasmidonta arcula*: *a,b,d*, USNM 86170, Altamaha River, Georgia; *c*, OSUM 40165, Ohoopee River near Reidsville, Georgia; *e*, details of beak sculpturing, USNM 123219, Altamaha River, Georgia. (Scale = 1 cm.)

grooves on the back of the hinge plate. External features of sculpturing are also visible within the shell. Nacre bluish white and shiny, iridescent posteriorly and toward the beak cavity.

Beak sculpture very heavy and composed of six or seven short, broad, swollen, irregular, concentric ridges in the center of the shell and extending about 20 mm from the umbonal apices. Ridges very prominent both in young specimens and in mature specimens.

VARIATION.—Table 10 demonstrates that there is considerable variation, especially in the relative thickness of the hinge plate and in relative weight, and that this variation is not attributable to relative maturity. The exceedingly inflated form, sharp posterior ridge, large size, incurved umbones, and exaggerated beak sculpturing are characteristic features and serve to readily distinguish *A. arcula* from its most closely related congener, *A. undulata*. Anatomical and glochidial differences are also diagnostic.

TABLE 10.—*Alasmidonta arcula:* Shell measurements (A = USNM 707224, Altamaha River, Georgia; B = USNM 123219, Altamaha River, Georgia; C = UMMZ 101195, Altamaha River, Georgia; D = USNM 86170, Altamaha River, Long County, Georgia; E = UMMZ 164140, Ohoopee River, near Leman, Georgia)

Lot	L (mm)	H/L	W/L	B-A/L	HP/L	$\frac{Wt \times 10^3}{L \times H \times W}$
A	86.20	0.736	0.698	0.376	0.0359	0.0925
B	81.65	0.750	0.644	0.358	0.0469	0.0616
C	79.25	0.804	0.709	0.368	0.0362	0.0777
D	77.56	0.765	0.638	0.325	0.0512	0.0988
C	77.20	0.749	0.650	0.299	0.0499	0.1250
C	75.25	0.800	0.655	0.375	0.0469	0.0931
C	73.85	0.777	0.667	0.356	0.0540	0.0997
D	71.90	0.745	0.664	0.364	0.0428	0.0917
A	65.00	0.799	0.717	0.349	0.0674	0.0823
C	63.09	0.780	0.693	0.405	0.0462	0.1060
C	63.05	0.764	0.668	0.388	0.0572	0.1280
C	61.15	0.838	0.710	0.360	0.0409	0.0815
C	61.11	0.805	0.709	0.316	0.0420	0.0982
A	61.05	0.804	0.722	0.383	0.0442	0.0638
E	60.43	0.725	0.666	0.344	0.0513	0.1150
D	57.38	0.812	0.736	0.368	0.0453	0.0886
C	55.00	0.782	0.696	0.332	0.0454	–
D	38.91	0.830	0.810	0.345	0.0304	0.0589
B	37.69	0.830	0.733	0.354	0.0544	–
D	21.44	0.765	0.641	0.332	0.0513	–

TOPOGRAPHIC ANATOMY

FIGURE 15*c*

SPECIMEN DESCRIBED.—From Ohoopee River, Ga. Rt. 147 bridge, 5.7 mi (9.1 km) SSW of Reidsville, Tattnall Co., Georgia, collected 22 August 1976 (E. P. Keferl, B. Marzluf, OSUM 40165.4); preserved in 70% ethyl alcohol, body length 75.7 mm, sex male (inferred).

DESCRIPTION.—Mantle of preserved specimen whitish, somewhat translucent, slightly darkened by branchial color showing through. An interrupted brown band of pigment borders the mantle edge throughout and is especially prominent posteriorly where it resembles a thick dashed line. This pigmented band is adjacent to the edges of the posterior mantle openings, i.e. no separating lip is present. The incurrent opening is 10.9 mm long and surrounded just within the edge by a single (partly double) row of small, very short (up to 0.6 mm), blunt papillae. Papillae pale orange-tan and gray in preserved specimen (but reddish brown according to Lea, 1863). Portions of mantle edges, which are appressed in life and separate the incurrent and anal openings, very short (0.5 mm). Anal opening with thickened, smooth edges, without papillae, and 7.2 mm long. Mantle connection between anal and supra-anal opening long (13.0 mm). Supra-anal opening narrow and slit-like, with an internal, narrow gray band, and 10.0 mm long.

Demibranchs of preserved specimen tan-brown, the inner somewhat darker than the outer. Outer demibranch 50 mm long, 30 mm high, with anterior and ventral margins curved and evenly convex, the posterior margin broadly concave below (the demibranch becoming narrow posteriorly), with 2 or 3 prominent radial wrinkles in its central portion, several wrinkles in the posterior portion, and with about 11 double filaments on the surface and about 1.0 underlying water tube per mm. Inner demibranch about 55 mm long and 30 mm high, with free margin rounded, and extending beyond the outer demibranch anteriorly (5 mm beyond) and posterior-ventrally (2.5 mm) but centrally slightly overlapped (1 mm) by the outer demibranch. Inner demibranch with about 11 double filaments per mm and 1.0 underlying water tube per mm. The inner lamina of the inner demibranch of the specimen examined is not completely attached to the visceral mass but exhibits definite breaks in that attachment.

Labial palpi pale yellowish brown, wide and somewhat irregular, bluntly expanded distally, with everted edges, with outer surfaces of each pair smooth, inner surfaces radially furrowed (about 4 furrows per mm at margin). Each palpus is joined below its dorsal margin to its corresponding member for more than half its length.

VARIATION.—Table 11 contains measurements, derived from all of the available preserved specimens, of the same soft-part characteristics listed for other species. The material is not sufficient to reveal very much about intraspecific variability. Some contrasts with *Alasmidonta undulata* are apparent, however, viz. in *A. arcula* A-SA tends to be longer than the anal opening (6 out of 6 specimens) and longer than the supra-anal opening (5 out of 6) but that tendency is reversed in *A. undulata*, the papillae within the incurrent opening are fewer and much smaller in *A. arcula* than in *A. undulata*.

Other characters examined were the number and extent of anal papillae (absent in all specimens) and the extent of the connection between the inner lamina of the inner demibranch and the visceral mass. Specimens 2, 4, 5, and 6 were completely connected but specimens 1 and 3 were not. The outer demibranch is radially wrinkled in this species (in contrast to *A. undulata*) even, as in specimens 3, 4, and 5, when thickened and charged with eggs or glochidia. The latter character, i.e. and incomplete connection between the inner demibranch and the visceral mass (in 2 of 6 specimens examined), and the "crimpled" appearance of the outer demibranch, were also observed by Lea (1863:83).

GLOCHIDIUM

FIGURE 16

DESCRIPTION.—Glochidium pyriform, asymmetrical, about 0.339 mm high, 0.270 mm long, and 0.181 mm in width. The posterior margin is much more convex and protuberant than the anterior, the anterior portion is more inflated than the posterior, and the apex is located about 37% of the distance from anterior to posterior. The surface is malleated (depressions shallow,

TABLE 11.—*Alasmidonta arcula:* Variation in topographic anatomy (abbreviations same as Table 4)

Spec. No.	Length (mm)	Mantle pigmentation: Extent	Mantle pigmentation: Strength	Relative length of mantle features (as % of L): Inc.	Anal	A-SA	SA	Incurrent papillae: Ranks	Max. Ht. (mm)	Labial palps: Posit.	Grooves per mm	Water tubes: N/mm*	Sex	Pre-preserv. treatment: Nemb. relax.	Form. fixed
			Ohoopee River, 5.7 mi SSW of Reidsville, Georgia (OSUM 40165)												
1	75.7	2	H	14	10	17	13	1	0.6	OV	4	1.0	(M)	–	–
2	57.1	2	H	19	10	13	18	2	0.8	OV	4	1.0	(M)	–	–
3	48.4	3	H	18	10	18	12	1	0.6	OV	3	–	GF	–	–
4	39.4	3	H	22	13	17	14	1	0.5	OV	4	–	GF	–	–
			Little Ocmulgee River, nearly Lumberton, Georgia (USNM 801396)												
5	64.4	4	H	19	12	15	9	1	0.6	OV	4	–	GF	+	+
6	57.8	2	M	19	11	17	8	3	1.7	OV	5	2.0	(F)	+	+

* Refers to outer demibranchs of non-gravid specimens.

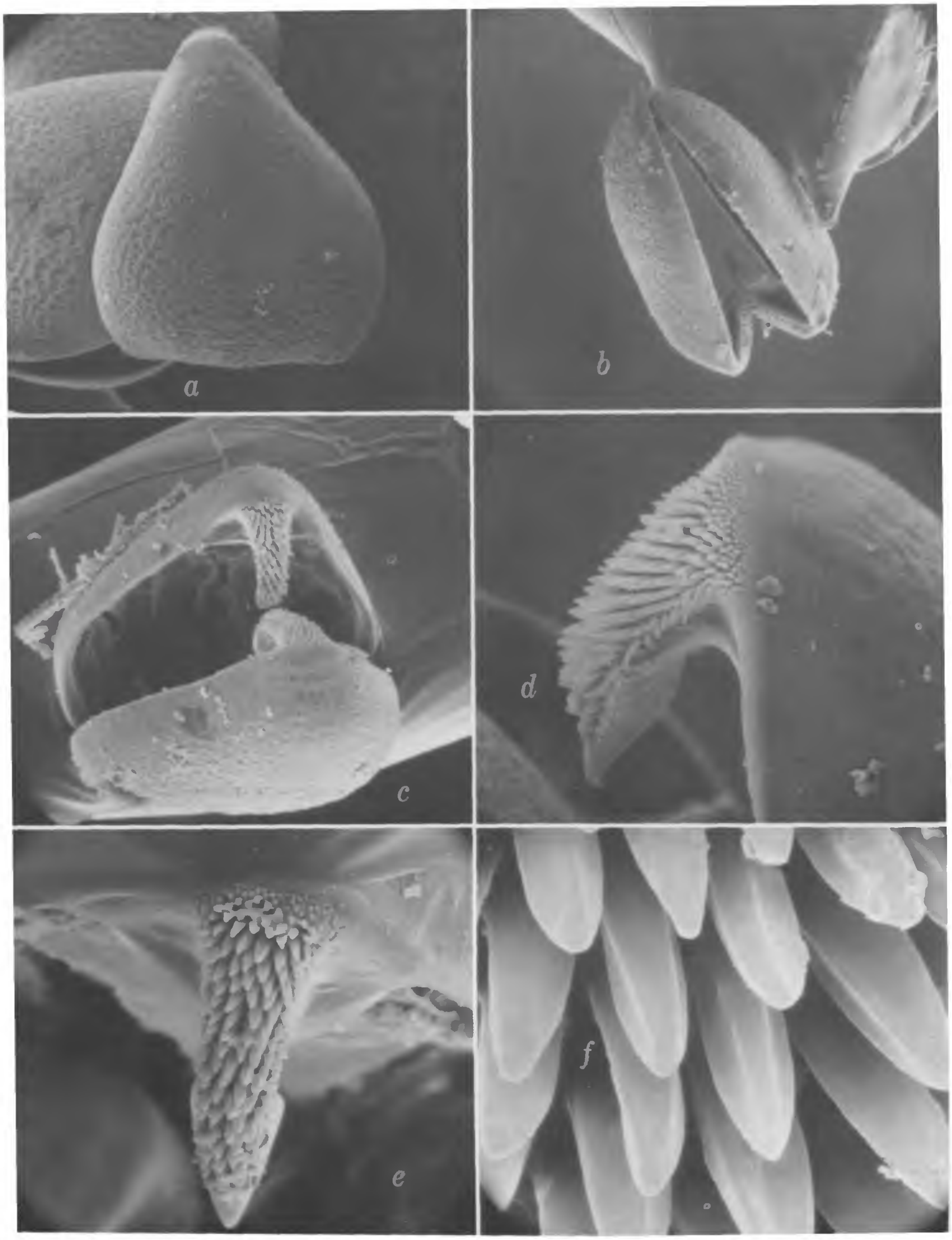

FIGURE 16.—Glochidia of *Alasmidonta arcula*: *a-f*, USNM 801396, Little Ocmulgee River near Lumber City, Georgia. (*a* × 170; *b* × 135; *c* × 185; *d* × 520; *e* × 455; *f* × 3700.)

subcircular or polygonal, and about 6–14 μm wide) and pitted. The pits are about 2 μm wide and number about 1-6 in each depression. The apical and marginal areas are without pits or depressions but there are fine, concentric wrinkles near the apex and low, obscure ridges perpendicular to the margin on the marginal areas. The hinge is flatly sinuate, about 0.200 mm long, and the ligament is narrow.

Each apical stylet is recurved, about 0.112 mm long, 0.043 mm wide at the base, subtriangular in cross-section, and gradually narrowing to a pointed, lancehead-shaped terminal flange. Each stylet is also supported on each side, for about ⅗ of its length, by a membrane that is connected to the ventral edge of the valve. Except for lateral and terminal parts of the flange, the flatly rounded and exposed surface of each stylet is covered with about 110 microstylets, each about 15 μm long, and arranged in about 8 rows (about 4 rows near the apex), the rows approximately parallel with the midline of the stylet. The microstylets are directed toward the distal end of the stylet and are lanceolate or spatulate, compressed, with 2 to 6 sharp, lateral, cutting edges and a roundly-pointed apex. Other smaller (1–2 μm long) pyramidal microstylets occur on the edges and on the base of the stylet and continue as tiny (0.5–1 μm), rounded, micropoints along the ventral edges of the valves.

This description has been drawn from views of three glochidia taken from an adult specimen collected in Little Ocmulgee River near Lumber City, Wheeler/Telfair County, Georgia on 28 May 1979, by A. H. Clarke and J. J. Clarke. There is some variation among the numerous specimens mounted for examination with the SEM, especially in that some of the stylets were without laterally-expanded apices and in that the cross-sectioned shapes of the microstylets were diverse. In general, however, they resemble the glochidia of *Alasmidonta undulata* except that they are much more asymmetrical and are somewhat smaller.

Life History

Gravid Period.—Two of the specimens from the Ohoopee River (see Table 11), collected on 22 August 1976 by E. P. Keferl and R. Marzluf, contained eggs, each about 0.2 mm in diameter. This date is probably close to the beginning of the gravid period for this species. One of the specimens collected in Little Ocmulgee River on 28 May 1979 by me had mature glochidia remaining only in the anterior portion of the outer demibranch. That date, then, is probably very close to the end of the gravid period for *A. arcula*.

Natural Host.—Not determined.

Habitat.—According to Johnson (1970:353) *A. arcula* "lives in sandy mud below sand bars in sluggish water and eddies." This is confirmed by our observations. In Little Ocmulgee River we collected four specimens in mid-river, on a sand bar, and in sand below the bar, in water depths of 0.2 to 0.8 M. The river is about 25 M wide at that point, up to about 1.5 M deep and with sandy bottom throughout. All of the other records for this species are also from riverine habitats in the Altamaha River System.

Geographical Records

Figure 17

Altamaha River System, Georgia,—*Ocmulgee River Drainage:* Limestone Creek, near Hartford, Pulaski Co. (Johnson, 1970). Ocmulgee River at Hawkinsville, Pulaski Co., and below Lumber City, Telfair Co. (Johnson, 1970); and 4 mi (6.4 km) E of Lumber City, Wheeler Co.-Jeff Davis Co. (1962, H. D. Athearn and M. A. Athearn! (NMC, OSUM)).

Little Ocmulgee River Drainage: Gum Swamp Creek at bridge, Scotland, Wheeler Co.-Telfair Co. boundary and below Ga. Highway 134 at Towns, Wheeler Co.-Telfair Co. boundary (both 1965, C. B. Stein and J. Scofield! (OSUM)). Little Ocmulgee River at Ga. Highway No. 134 bridge, Towns, Wheeler Co.-Telfair Co. boundary (1976, K. Wright! (OSUM)). Little Ocmulgee River, ½ mi (0.8 km) W of Ga. Hwy 19, near Lumber City, Wheeler Co.-Telfair Co. boundary (1979, A. H. Clarke and J. J. Clarke! (USNM)).

Ohoopee River Drainage: Ohoopee River, 3 mi (4.8 km) N of Lehman, Emanuel Co. (Johnson, 1970); and at Ga. Hwy. 147 bridge, 5.7 mi (9.1 km) SSW of Reidsville, Tattnall Co. (1976, E. P. Keferl and B. Marzluf! (OSUM)).

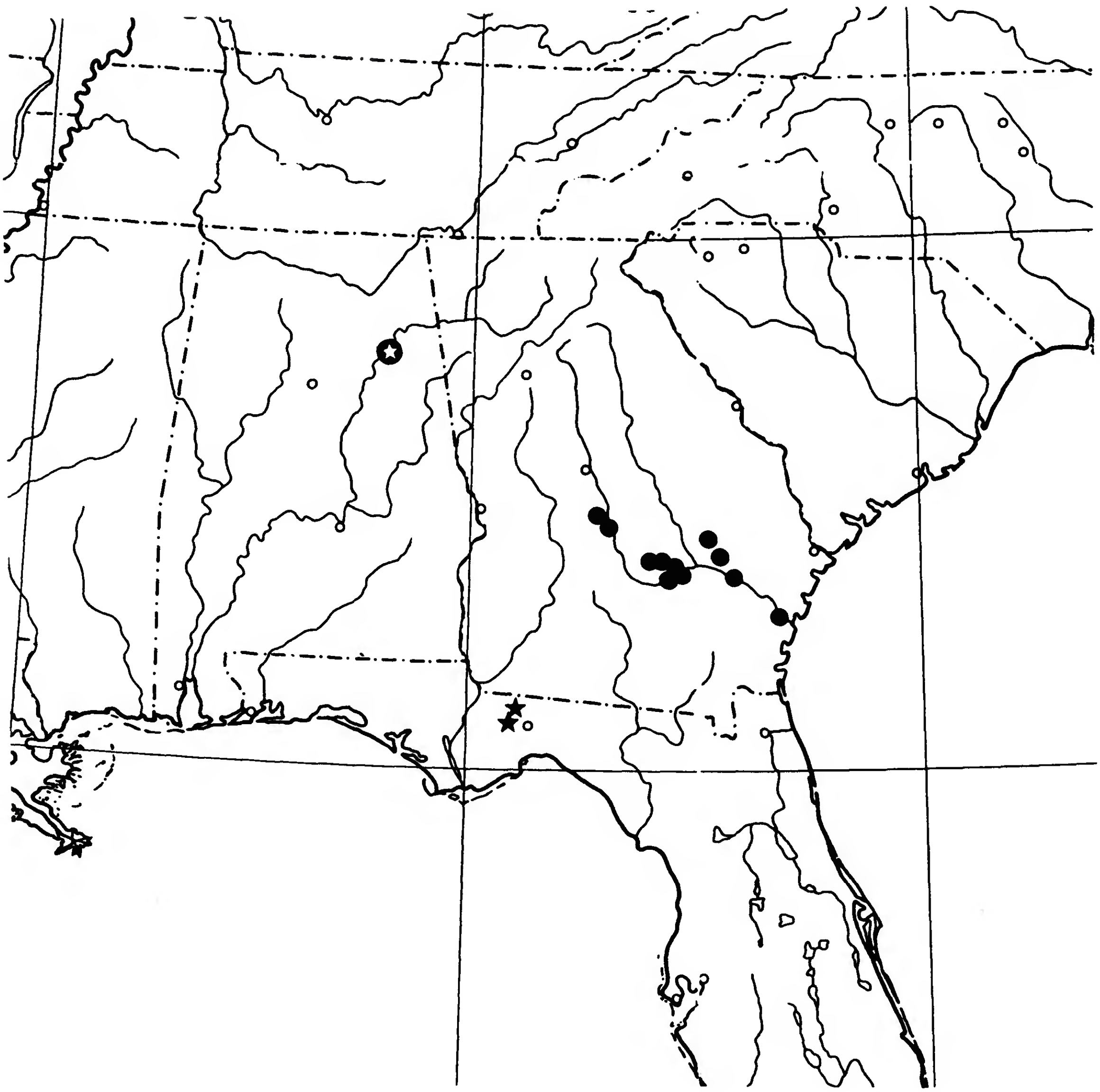

FIGURE 17.—Geographical distribution of *Alasmidonta arcula* (solid circles), *A. wrightiana* (stars), and *A. mccordi* (star within circle).

Altamaha River (main channel): Altamaha River at U.S. Hwy. 301, 5 mi (8.0 km) NNE of Jesup, Long Co.-Wayne Co. boundary (1965, F. J. Moore!; 1965, E. P. Keferl!; and 1970, W. J. Clench and D. H. Stansbery! (all OSUM)); at Liberty Co. (USNM); at Fort Barrington, McIntosh Co. (ANSP) and "near Darien," [McIntosh Co.] (Lea, 1863).

Alasmidonta (Alasmidonta) wrightiana (Walker, 1901)

FIGURES 17 and 18

Strophitus wrightianus Walker, 1901:65–66, pl. 3. [Type-locality: originally Flint River, Baker Co., Georgia but later (*in* Simpson, 1914:357) corrected by Walker to Ochlockonee River, Florida. Holotype in University of Michigan, Museum of Zoology, catalog number 74938.]

The Shell

Figure 18*a-d*

Description.—Shell rhomboid-ovoid, moderately inflated and solid, up to 54 mm long, 38 mm high, and 30.5 mm wide, somewhat thickened anteriorly (up to about 2½ mm thick) and thinner, but not excessively fragile, posteriorly. Anterior margin sharply curved, ventral margin broadly and evenly rounded, posterior margin bluntly biangulate below and obliquely flattened above, and dorsal margin sigmoid and of medium length. Maximum inflation above middle of shell. Beaks inflated, broad, rounded, located about ⅓

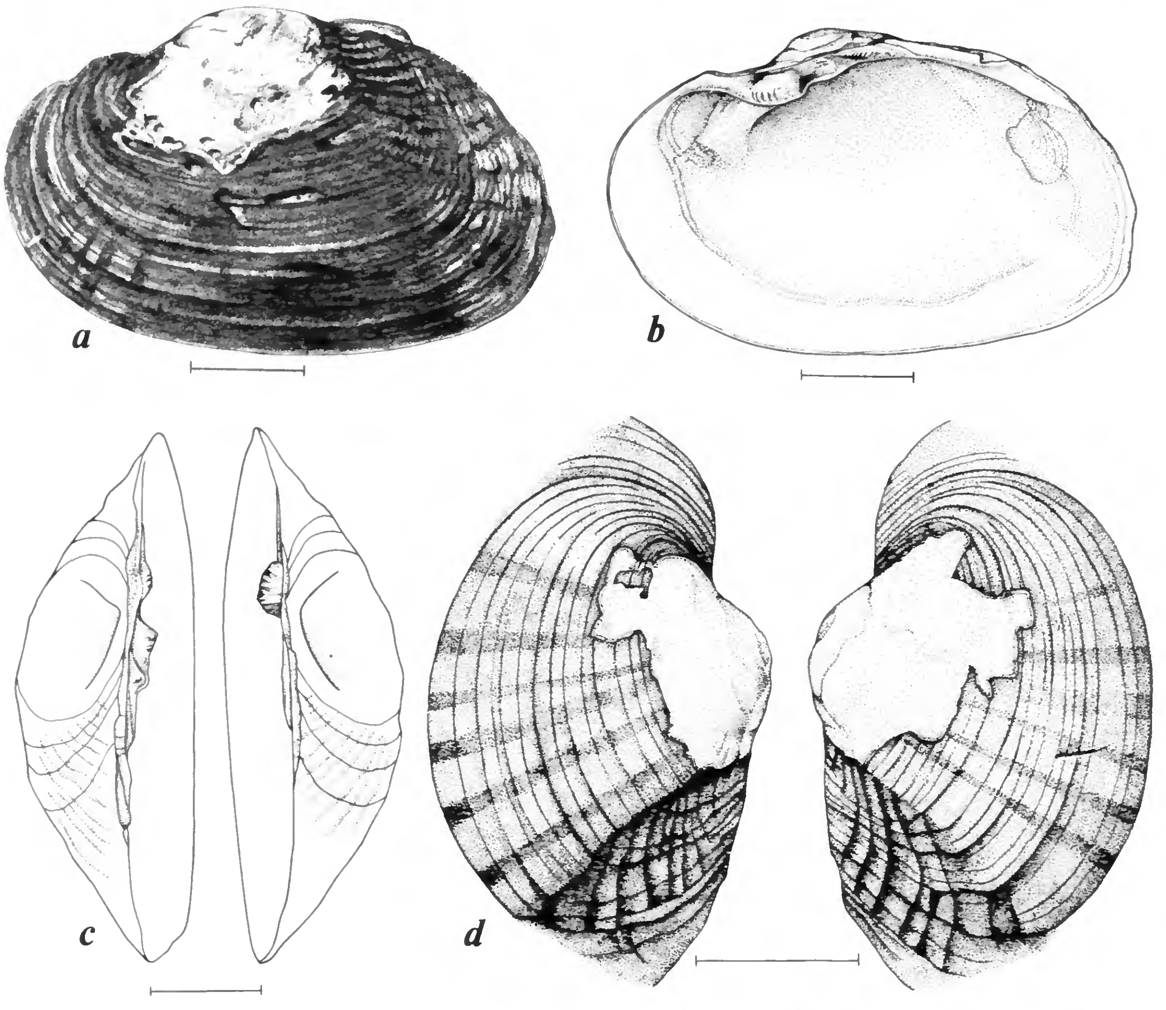

Figure 18.—*Alasmidonta wrightiana*: *a-c*, MCZ 239259, Ocklockonee River near Tallahassee, Florida; *d*, details of umbonal area in best preserved specimen, UMMZ 197239, Ochlockonee River near Tallahassee, Florida. (Scale = 1 cm.)

the distance (or more) from anterior to posterior, and projecting well above the hinge line. Posterior ridge roundly angular. Posterior slope broad, slightly concave above, and heavily sculptured. Growth increments marked by numerous, low, irregular ridges and grooves. Post-juvenile sculpturing consisting of crowded, strong corrugations generally distributed on the posterior slope and oriented perpendicular to the lines of growth. Corrugations finer near the umbones. A few irregular, low, nearly obsolete, radial ridges also occur on the disc in some specimens, especially anteriorly. Periostracum cloth-like and, in adults, covered with dark, broad and narrow blackish green rays spread over a brownish background. Rays most easily visible by transmitted light. Juveniles not seen but presumably more conspicuously rayed. Ligament rather short, broad, strong, and brown.

Hinge teeth of medium size, strong, and incomplete. Pseudocardinal teeth ragged, compressed, pyramidal, and numbering 1 or 2 in the right valve and 2 in the left. Interdental projection present in left valve but irregular and low. Lateral teeth very short; anterior portion nearly obscure. Beak cavity broad and deeply excavated. Anterior muscle scars rather small but deeply impressed, pallial line faintly marked, posterior muscle scars only lightly etched, and scars within beak cavity consisting of one short, well marked, lateral impression bordered by a low ridge on each side, parallel with the hinge plate and located on the back of the hinge plate below the umbone. Nacre silvery white fading into bluish posteriorly, bluish within the anterior muscle scars, and somewhat pinkish near the beak cavity. Nacre iridescent posteriorly.

Beak sculpture coarse and composed of a few heavy, curved ridges that extend about 7½ mm beyond the umbonal apices. The beak sculpture is not well preserved in the specimens available for examination.

VARIATION.—Table 12 demonstrated that apparently normal variation occurs in this species. The posterior slope sculpturing is so extreme that the species is unmistakable but in other shell characters it is quite similar to *Alasmidonta undulata*.

TABLE 12.—*Alasmidonta wrightiana:* Shell measurements

Length (mm)	*H/L*	*W/L*	*B-A/L*	*Hp/L*
Ocklokonee River, 11 mi NW of Tallahassee, Florida (UMMZ 197239)				
44.4	0.691	0.580	0.315	0.0580
39.8	0.708	0.552	0.331	0.0688
Ocklokonee River, bridge 8 mi W of Tallahassee, Florida (MCZ 239259)				
48.5	0.632	0.495	0.370	0.0676
Ocklokonee River, Florida (holotype, data from Walker, 1901)				
54	0.703	0.582	0.392	

LIFE HISTORY

The breeding period and the natural host of this species are unknown.

Aside from the fact that *A. wrightiana* is a riverine species restricted to the Ochlokonee River, and parenthetically that it is very rare, we know nothing about its habitat. Walker (1901: 65) found only a single specimen among two barrels of Unionidae sent to him by Messrs. B. F. King and G. H. King, supposedly from tributaries of the Flint River, Baker County, Georgia. Walker later corrected the locality to Ochlokonee River, Florida, but what proportion of the two barrels of Unionidae came from that river is unknown. Dr. W. H. Heard, an experienced collector, has informed me (pers. comm.) that he has collected many unionid species in the Ochlokonee River, on numerous occasions, and at both of the localities near Tallahassee, Florida (cited herein) and has never found *A. wrightiana*. (See Johnson (1967b) for further comments.)

GEOGRAPHICAL RECORDS

FIGURE 17

OCHLOKONEE RIVER SYSTEM, FLORIDA.—*Ochlokonee River Drainage:* Ochlokonee River, 11 mi (17.6 km) NW of Tallahassee, Leon Co. (UMMZ 197239) and 8 mi (12.8 km) W of Tallahassee, at Fla. Hwy. 1 bridge, Leon Co. (MCZ 239259).

Subgenus *Decurambis* Rafinesque, 1831

Decurambis Rafinesque, 1831:5 [Binney and Tryon's 1864 reprint of Rafinesque's work, page 80]. [Type-species: *Alasmidonta scriptum* Rafinesque, 1831 (=*Alasmidonta marginata* Say, 1818) by subsequent designation (Ortmann and Walker, 1922).]

Rugifera Simpson, 1900:670. [Type-species: *Alasmodonta* [sic] *marginata* Say (1818) by original designation.]

The glochidium of only one species of subgenus *Decurambis* is known, viz. that of *Alasmidonta marginata* (Figure 20), the type-species. It is elevated pyriform, higher than long, and has wide triangular stylets that bear numerous longitudinal rows of major microstylets that decrease on the distal half from about 10 to about 3 rows near the apex.

Comparative features of the adults are: the shells are medium-sized to rather large (about 70 mm to 110 mm long); of low to moderate relative height (H/L about 0.44–0.67); have low, uninflated umbones; and in most species the posterior slope is sculptured with prominent corrugations. The pseudocardinal teeth and interdental projection are well developed and (in most species) small but the lateral teeth are rudimentary or entirely lacking. The anal mantle opening is not papillate or crenulate and the inner lamina of the inner demibranchs is completely attached to the visceral mass.

Alasmidonta (*Decurambis*) *marginata* Say, 1818

FIGURES 19–21

Alasmidonta marginata Say, 1818:459, 460. [Type-locality: Scioto River [Ohio]. Type-material not in the Academy of Natural Science of Philadelphia (Baker and Johnson, 1973) and presumably lost.]

[?] *Mya rugulosa* Wood, 1828:3, pl. 1: fig. 7 [of *Mya*]. [Type-locality: "North America, Fresh Water." Type-material not in British Museum (Johnson, 1971) and presumably lost. Identification uncertain.]

Alasmodon (*Decurambis*) *scriptum* Rafinesque, 1831:4. [Type-locality: Green River [Kentucky]. Original type-material lost.]

Margaritana marginata "var. *truncata*" B. H. Wright, 1898:124. [Type locality: "occurs in eastern as well as western waters and into Virginia and Tennessee." Lectotype in Smithsonian Institution, USNM 150545, from Clinch River, Virginia (Johnson, 1967 (a):9).]

Alasmidonta (*Decurambis*) *marginata susquehannae* Ortmann, 1919:187, pl. 12: fig. 4. [Type-locality: Susquehanna River Selinsgrove, Snyder Co., Pennsylvania. Syntypes in Carnegie Museum, 61.4679.]

Alasmidonta marginata variabilis F. C. Baker, 1928:194, pl. 69: fig. 4–9. [Type-locality: Red Cedar River, near Cheteck, Barron Co., Wisconsin. Lectotype in the Museum of the Wisconsin Geological and Natural History Survey, University of Wisconsin, catalog number 935a (Franzen, 1957: 33).]

THE SHELL

FIGURE 19*a,b,d,e*

DESCRIPTION.—Shell ovate-trapezoidal in shape; up to about 110 mm long, 54 mm high, and 46 mm wide; and thin or of medium thickness (up to 3 mm thick anteriorly) and fairly strong. Anterior margin evenly rounded; ventral margin broadly and flatly curved throughout or centrally straight (or even slightly concave); posterior margin abruptly rounded to biangulate below, diagonally and flatly curved above, and in many species, concave centrally: dorsal margin long and flatly curved. Maximum inflation at posterior ridge behind center of shell. Beaks broad, moderately elevated, located above the hinge line. Posterior ridge prominent, strong, high, and sharply angled. Posterior slope broad, truncated, and flattened or concave.

Annual growth increments marked by grooves with dark periostracum, but other low concentric ridges also cover the surface. Other post-juvenile sculpturing consisting of crowded, rather strong, low corrugations, at right angles to lines of growth, and covering all of the posterior slope or fading out before reaching the posterior margin. Periostracum yellowish brown with wide and narrow green rays. These are particularly prominent in juveniles but as the background color darkens in adults they become less apparent. Ligament strong, broad, and of medium length.

Hinge teeth moderately well-developed but incomplete. Pseudocardinal teeth narrow, dorso-

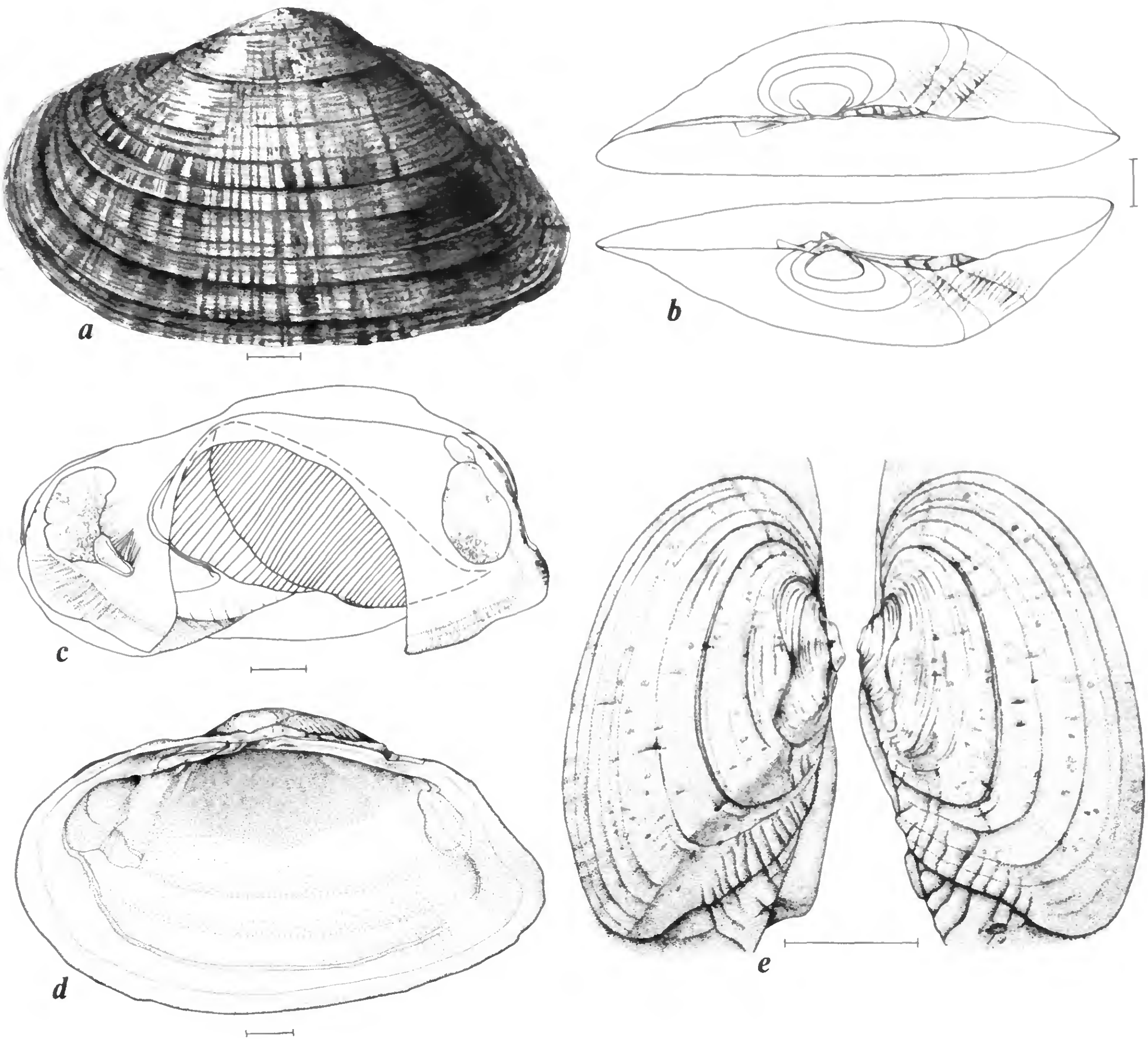

FIGURE 19.—*Alasmidonta marginata*: *a,b,d*, USNM 504885, Iowa City, Iowa; *c*, OSUM 4305, Olentangy River, Ohio; *e*, detail of umbonal area, USNM 504540, West Okoboji Lake, Iowa. (Scale = 1 cm.)

ventrally compressed, erect, pointed, directed anteriorly, and numbering 1 in the right valve and 1 in the left. Interdental projection in left valve prominent, irregular, lamellate, more or less confluent with the pseudocardinal tooth, and articulating with a depression in the right valve. Lateral teeth vestigial and indicated only by a short, poorly defined, proximal, lamellate protuberance in one or both valves. Beak cavity excavated but not deep. Anterior muscle scars impressed, pallial line shallow but clearly discernible in most specimens, posterior muscle scars shallow and not well-defined, and scars within beak cavity consisting of two short parallel grooves with marginal ridges parallel to the hinge plate and located on the back of the hinge plate posterior to the pseudocardinal teeth. Nacre white or bluish white, glossy and (in some individuals) slightly iridescent posteriorly. A high proportion of specimens from the Susquehanna River system, and a few specimens from elsewhere, have pinkish or reddish suffusions. The edge of the shell is bordered by a greenish or grayish band or (in some specimens) the marginal nacre is so thin that external periostracal colors are visible.

Beak sculpture coarse and composed of about 5, broadly double-looped, rounded ridges, all terminating at the posterior ridge, the outermost of which extends about 12 mm beyond the umbonal apex. Ridges best seen in young specimens or specimens from hard water.

VARIATION.—Baker (1928) has shown that at least two well-marked ecophenotypes exist in this species, a form living in creeks and small rivers ("typical" *marginata*) in which the shell is more cylindrical and smaller than the form occurring in large and medium-sized rivers (*truncata*). In form *marginata* "the distance from anterior end to umbones varies from 31 to 36 percent, while in the large river form ["*truncata*"] it varies from 33 to 47 per cent" (Baker, 1928:192). This trend is amply demonstrated by the material available in the Smithsonian Institution and, since Baker clearly indicated that "*truncata*" is an ecophenotype of *marginata* sensu stricto, there is no taxonomic need to evaluate the point statistically.

Baker (1928) also described another race of *marginata* (*A. marginata variabilis*) that was said to differ from typical *marginata* in being smaller, not as sharply truncated, with umbones nearer the anterior end, and with a salmon colored nacre rather than white. The measurements that he gives for *variabilis*, however, fall well within the range of variation quoted on earlier pages for *marginata* sensu stricto. Posterior ridge angulation is a variable character and nacre color, although significant, has already been dealt with in regard to the evaluation of another subspecies (*A. marginata susquehannae* Ortmann (1918), see Clarke and Berg, (1959)) and is not a sufficient basis for subspecific recognition.

TABLE 13.—*Alasmidonta marginata*: Shell measurements

Feature	*N*	*Range*	*Mean* ($\bar{x}$)	*S*
	Cincinnati, Ohio (USNM 86171)			
Length (mm)	10	46.14 -91.12	70.109	16.005
H/L	10	0.532- 0.618	0.576	0.029
W/L	8	0.408- 0.447	0.428	0.016
B-A/L	10	0.319- 0.434	0.377	0.046
Hp/L	9	0.030- 0.046	0.0384	0.0051
	Tippecanoe River, Indiana (USNM 677544, 677420)			
Length (mm)	10	56.20 -71.25	66.403	4.596
H/L	10	0.493- 0.563	0.529	0.023
W/L	8	0.386- 0.459	0.415	0.021
B-A/L	10	0.281- 0.388	0.324	0.040
Hp/L	9	0.039- 0.054	0.048	0.0049
	Fox River, Illinois (USNM 25591)			
Length (mm)	7	44.75 -79.78	61.694	12.712
H/L	7	0.522- 0.556	0.542	0.012
W/L	6	0.402- 0.434	0.417	0.014
B-A/L	7	0.317- 0.339	0.324	0.010
Hp/L	7	0.031- 0.047	0.0398	0.0056

TOPOGRAPHIC ANATOMY

FIGURE 19*c*

SPECIMEN DESCRIBED.—From Clinch River, 2.6 mi (4.2 km) E of Kyles Ford, (0.5 mi (0.8 km) E of Wallens Bend), Hancock Co., Tenn., collected 13 August 1977 (USNM 758835, A. H. Clarke Station 1500); anaesthetized with nembutal, fixed in 10% formalin, preserved in 70% ethyl alcohol; shell length 87.0 mm, sex female (gravid).

DESCRIPTION.—Mantle whitish, transparent centrally, and with branchiae clearly showing through. A broken band of separated and coalesced, brown, rectangular pigment spots, which are pale on the anterior portion of the mantle and become dark posteriorly, occurs around the anterior, ventral, and posterior edges of the mantle. The pigmented band is not separated from the posterior mantle openings. The incurrent opening is 11 mm long and surrounded by a double row of medium-sized, pale brown, flattened papillae that are partially fused along their length to the mantle edge. The mantle edges between the incurrent and anal siphons are separate but are constricted into blunt, opposing points about 1 mm wide that are appressed in life and thereby separate the openings. Anal opening about 6 mm long, with slightly reflected, irregular edges but without a circle of papillae. The mantle edges between the anal and supra-anal openings are fused over a short distance (2 mm) but the junction is easily ruptured during preservation. The supra-anal opening is 16 mm long and has sides extending up and out from the opening. In the specimen examined the opening is sealed by the distended intestine.

Demibranchs of preserved specimen pale brown. Outer demibranch 52 mm long, 18 mm high, roundly truncated anteriorly, broadly rounded ventrally, and becoming narrowed posteriorly. Narrow, pale orange, longitudinal bands (composed of tiny, irregular pigment spots) are oriented parallel to the radial filaments (but less numerous, about 1 band for every 8 double radial filaments), and are distributed across both the outer (gravid) *and* inner demibranchs, although they are irregularly spaced on the latter. There are about 9 double radial filaments per mm in each demibranch. Inner demibranch about 54 mm long and 21 mm high; anterior portion broad and truncated, ventral margin evenly convex, and posterior end narrowing to point at the upper margin; the anterior and ventral margins extend beyond the outer demibranch (6 mm and 5 mm, respectively) but the posterior-ventral margin is slightly overlapped by the outer demibranch. In the gravid female, with developing glochidia, the entire outer demibranch is turgid and thickened (about 5 mm thick). The inner lamina of the inner demibranch is completely attached to the visceral mass.

Labial palps pale brown and rounded-subtriangular with curved ventral and posterior-dorsal margins. The inner membrane is slightly longer than the outer. The outer surface of each is smooth and the inner opposing surfaces are radially furrowed (about 6 furrows per mm at the margin). Each palpus is fused subdorsally to its corresponding member for nearly its entire length.

Variation.—Table 14 demonstrates that substantial variation occurs in the strength and extent of mantle pigmentation, in the number of ranks of papillae at the incurrent openings, in the lengths of those papillae, and in the number of grooves per mm on the inner faces of the labial palps. Ortmann (1912:297), who then confused *A. varicosa* and *A. marginata*, stated that A-SA is much shorter in *A. marginata* than in *A. undulata.* That is borne out by present data, which also indicate that both the incurrent and anal openings in *A. marginata* are also somewhat shorter than in *A. undulata.*

Ortmann (1912:297) also stated that the inner lamina of the inner demibranch is connected to the visceral mass in all specimens that he has examined, although Lea (1863) reported that, in some specimens, it was more or less free at the posterior end. My data agrees with those of Ortmann.

Glochidium

Figure 20

Description.—Glochidium pyriform, 0.341 mm high, 0.346 mm long, single valve convexity 0.092 mm. The valves are only approximately symmetrical: the posterior margin is more broadly curved than the anterior and the apices are located about 42% of the distance from anterior to posterior (measured parallel to the hinge axis). Surface of glochidium finely malleated and pitted except for the distal apical areas (about 80 μm high) and the edges of the valves (about 27 μm wide) that are generally malleated but not pitted. The malleate depressions are subcircular and about 2–10 μm wide and the pits are about 1.5–5 μm wide and are located within and outside of the depressions. The apical third of the valves, and especially the apical tips, are also sculptured with narrow, curved, concentric ridges. Hinge flattened, slightly convex centrally, and about 0.210 mm long. Ligament not observed.

TABLE 14.—*Alasmidonta marginata*: Variation in topographic anatomy (abbreviations same as Table 4)

Spec. No.	Length (mm)	Mantle pigmentation: Extent	Mantle pigmentation: Strength	Relative length of mantle features (as % of L): Inc.	Anal	A-SA	SA	Incurrent papillae: Ranks	Max. ht. (mm)	Labial palps: Posit.	Grooves per mm	Water tubes: N/mm*	Sex	Pre-preserv. treatment: Nemb. relax.	Form. fixed
	Grand River, Brantford Twp., Ontario (NMC 66005)														
1	80.4	1	H	10	7	(tissue torn)		3	1.5	OV	6	-	GF	-	?
2	77.8	3	H	10	8	(tissue torn)		3	1.5	OV	11	-	GF	-	?
3	53.6	Inc. Op.	W	13	8	(tissue torn)		2	1.0	OV	2	-	GF	-	?
	Olentangy River, Sharon Twp. Ohio (OSUM 4305)														
4	95.7	2	H	13	7	3	11	2	1.5	T	6	-	-	-	-
5	85.7	2	H	12	7	2	16	3	1.2	OV	8	-	GF	-	-
	Clinch River, Clinchport, Virginia (OSUM 25759)														
6	64.1	2	H	16	14	3	15	3	2.1	T	9	-	GF	-	-
	Clinch River, Kyles Ford, Tennessee (USNM 758835)														
7	79.6	6	H	12	8	4	20	3	3.1	T	6	-	GF	+	+
	Spring River, Carthage, Missouri (OSUM 13692)														
8	83.2	1	H	12	10	4	torn	1	0.7	T	8	-	GF	-	-
9	80.8	1	M	11	12	4	torn	2	0.5	OV	7	-	GF	-	-
10	67.5	2	H	14	12	4	20	1	0.4	OV	13	-	-	-	-

* Refers to outer demibranchs of non-gravid specimens.

Each apical stylet is recurved, bent inward distally of center, and is about 0.107 mm long, 0.050 mm wide at the base, triangular in cross section, and gradually narrowing to an asymmetrical, blade-like tip that projects from the stylet apically and on the posterior side. Each stylet is also supported on each side, for about half its length, by an (apparently) horny membrane that is broadly connected to the ventral edge of each valve. Except for the knife-like apical projection, the flatly-rounded, exposed side of each stylet is covered with about 180 microstylets, each about 8–12 μm long. The microstylets are arranged approximately in rows parallel to the long axis of the stylet; there are 16 to 20 rows near the base of the stylet and these decrease to about 4 rows near its apex. The microstylets are directed toward the apex of the stylet and are lanceolate to spatulate; many are compressed perpendicularly to the long axis of the stylet and all have sharp, curved apices and 2 to 6 sharp lateral edges. Numerous, smaller (1–2 μm), pyramidal microstylets occur on the base of the stylet where they merge imperceptibly with the larger microstylets and along the adjacent edges of the valves, and as still smaller microstylets (<0.5 μm) or micropoints onto the membrane near the stylet and within the ventral edge of the valves.

The above description is of a glochidium taken from an adult specimen (OSUM 4305A) collected from the Olentangy River in Sharon Township, Franklin Co., Ohio by D. H. Stansbery on 12 December 1962. Another glochidium from the same adult has a membrane connecting the edges of the valve to the edges of the stylet throughout its whole length. In still another glochidium, from an adult specimen (OSUM 25759) collected from the Clinch River at Clinchport, Scott Co., Va. by D. H. Stansbery and W. J. Clench on 7 October 1970, the shell is 0.323 mm high and 0.300 mm long; the microstylets are less numerous (about 100) but they are also grouped in a triangular mass (as in OSUM 4305A), with poorly defined parallel radial rows. Another glochidium, from OSUM 13692 collected from Spring River at the north edge of Carthage, Jasper Co., Missouri, by Carol B. Stein on 20 October 1964, is 0.362 mm high and each valve has a convexity of 0.091 mm.

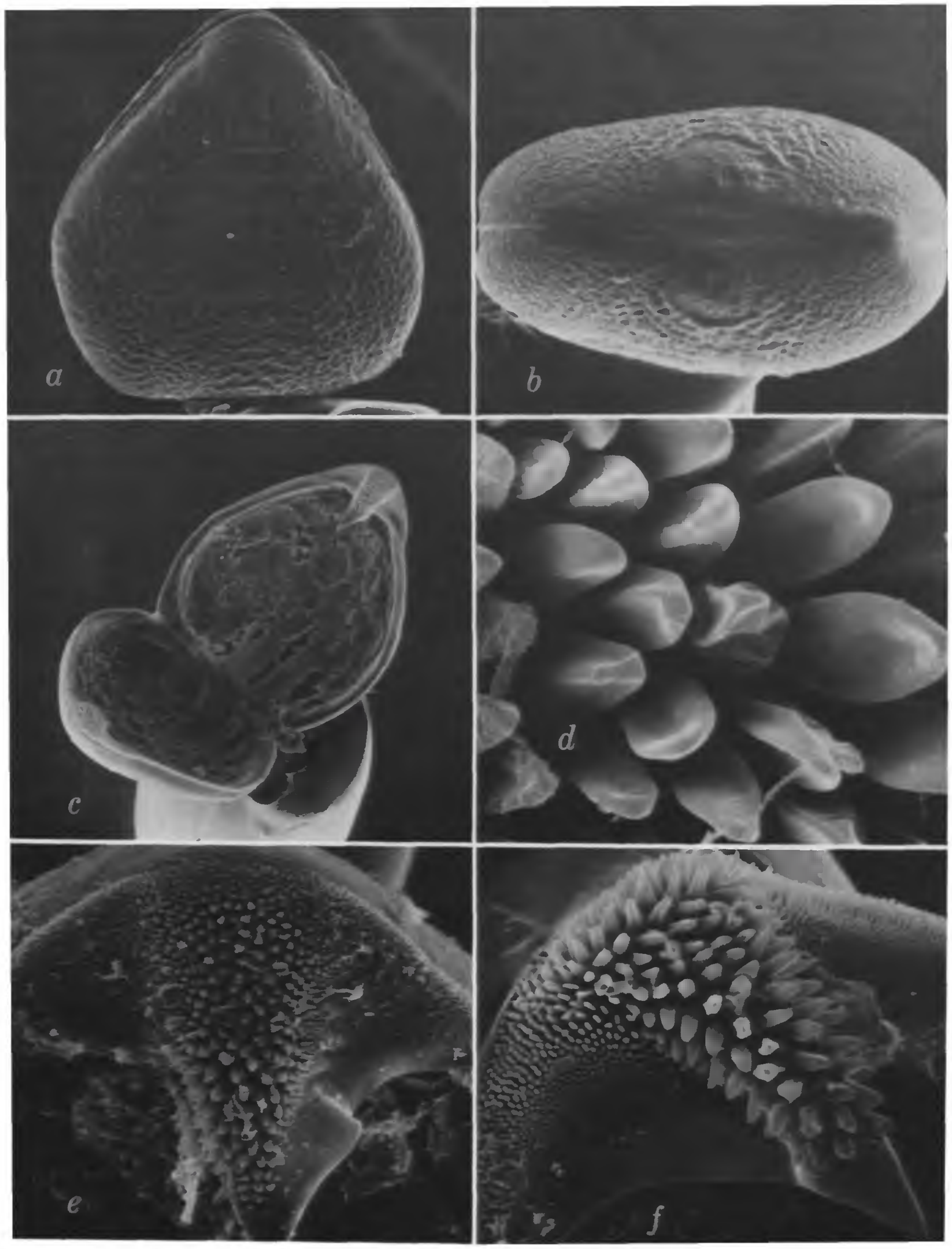

FIGURE 20.—Glochidia of *Alasmidonta marginata*: *a,d,e*, OSUM 4305 (same location as 19*c*); *b,c,f*, OSUM 25759, Clinch River, Virginia. (*a* × 165; *b* × 210; *c* × 130; *d* × 380; *e* × 590; *f* × 910.)

It is clear that the glochidia of *Alasmidonta marginata* are quite variable, even among specimens from the same parent. The broadly triangular mass of numerous (100–180) microstylets, the prominent asymmetry of the stylet, and the general shape of the valves (about equally as high as long, or up to about 8% higher than long) appear to be characteristic features.

Life History

Breeding Period.—Ortmann (1919:103) gives dates spanning the period from 19 July to 23 October (eggs but no glochidia prior to 2 September) for this species. A specimen with glochidia, cited above, was collected by D. H. Stansbery from the Olentangy River, Ohio on 12 December 1962. No spring-collected gravid specimens are on record, but it is nevertheless likely that *A. marginata*, like other alasmidontids, releases its glochidia in the spring.

Natural Host.—According to Howard and Anson (1922) and Fuller (1974) the hosts of *A. marginata* include the following fishes: *Catostomus commersoni* (Lacapede), white sucker; *Hypentelium*

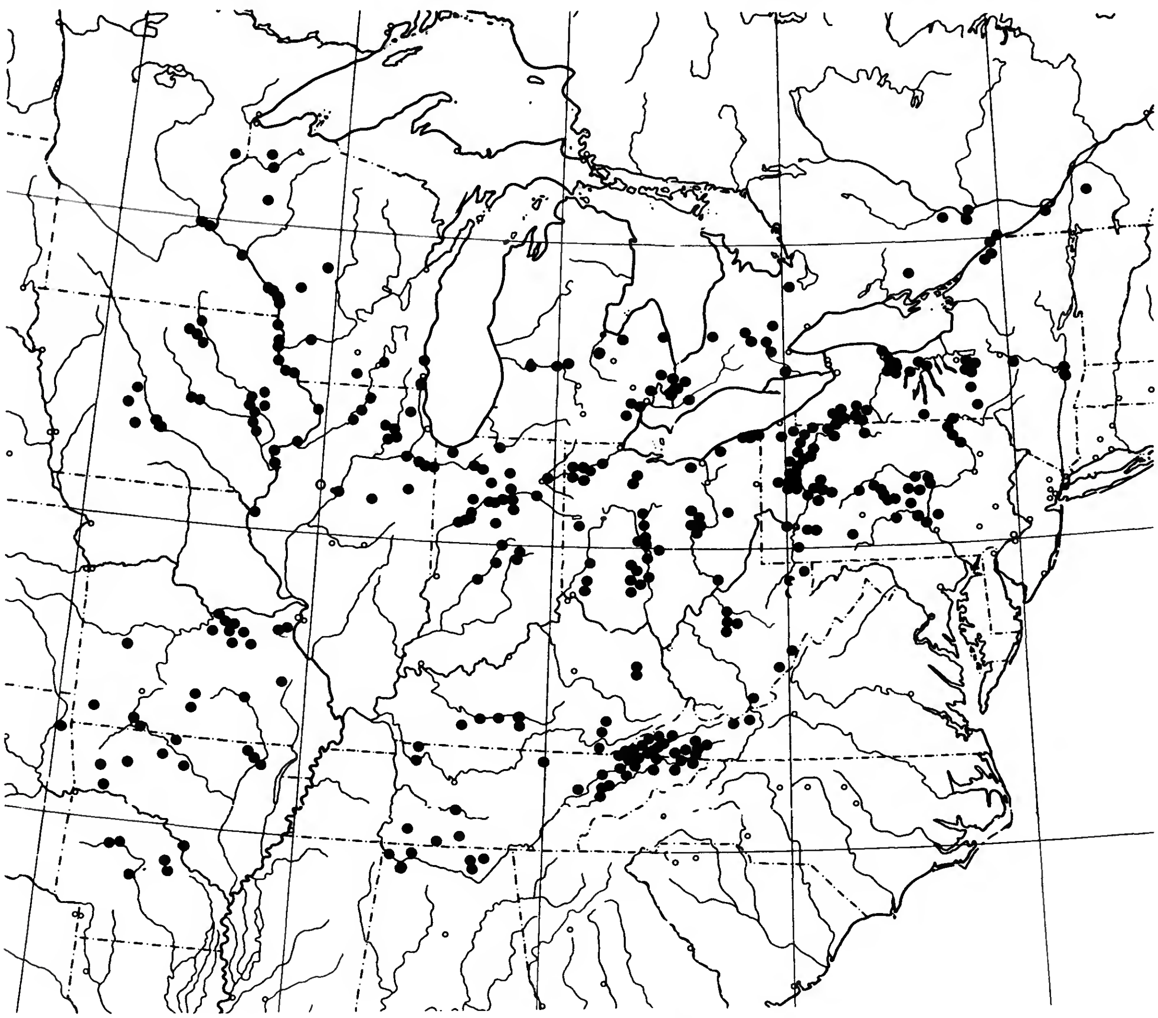

Figure 21.—Geographical distribution of *Alasmidonta marginata*.

nigricans (Lesueur), northern hog sucker; *Moxostoma macrolepidotum* (Lesueur), shorthead redhorse (all Catastomidae); *Ambloplites rupestris* (Rafinesque), rock bass; and *Lepomis gulosus* (Cuvier), warmouth (both Centrarchidae).

HABITAT.—"*A. marginata* is most common in rocky and gravel substrates of large and middle-sized streams, and especially in rapids or riffles. It is one of the very few species that are more abundant in such habitats than elsewhere" (Clarke and Berg, 1959:28). Throughout its range it is found with several other riverine species in diverse mussel communities and ordinarily as a relatively minor element in such communities.

GEOGRAPHICAL RECORDS

FIGURE 21

GREAT LAKES—ST. LAWRENCE RIVER SYSTEM.—*Lake Michigan Drainage*: Sheboygan River, Wisc. (USNM). Lake Michigan, Chicago, Cook Co., Ill. (ANSP). [St. Joseph River], South Bend, St. Joseph Co., Ind.; Kalamazoo River, Kalamazoo, Kalamazoo Co., Mich. (both USNM). Stony Creek, just S of Pewamo, Ionia Co., Mich. (1966, C. B. Stein! (OSUM)). Stony Creek, 1 mi (1.6 km) east of Muir, Ionia Co., Mich. (MCZ). Grand River, 4 mi (6.4 km) above Ionia, Ionia Co., Mich. (ANSP, MCZ).

Lake Huron Drainage: Shiawassee River, Genessee Co., Mich.; Cass River, NE of Caro, Tuscola Co., Mich. (both MCZ). Cass River, 3 mi (4.8 km) NE of Caro, Mich. (1967, D. H. Stansbery! (OSUM)). Black River, near Lexington, Sanilac Co., Mich. (USNM). Maitland River, Auburn, Huron Co., Ont. (ANSP, NMC). Nottawasago River, a few mi NE of Alliston, Simcoe Co., Ont. (NMC).

Lake St. Clair Drainage: Belle River, 4.8 mi (7.9 km) NW of St. Clair, St. Clair Co., Mich.; North Branch, Clinton River, 1 mi (1.6 km) N of Mount Clemens, Macomb Co., Mich. (both 1965, C. B. Stein! (OSUM)). [Clinton River], Utica, Macomb Co., Mich., (MCZ, USNM). Sydenham River, S edge of Florence, Lambton Co., Ont. (1965, C. B. Stein (OSUM)) and NE edge of Alvinston, Lambton Co., Ont. (1967, C. B. Stein and K. A. Heffelfinger! (OSUM)). Sydenham River, 3 mi (4.8 km) NE of Alvinston, and 3.7 mi (5.9 km) S of Alvinston (both 1971, A. H. Clarke and L. R. Clarke! (NMC)); 1.8 mi (2.9 km) NE of Shetland, Lambton Co., (1963, H. D. Athearn! (NMC)) and 0.5 mi (0.8 km) N of Dawn Mills, Kent Co. (1971, A. H. Clarke and L. R. Clarke! (NMC), all Clarke, 1973(a)).

Lake Erie Drainage: Huron River, Ann Arbor, Mich. (several records in MCZ, UMMZ, and USNM; van der Schalie, 1938). Raisin River, 0.5 mi (0.8 km) S of Manchester, Mich. (1958, W. J. Clench and J. Rosewater! (USNM)). St. Joseph River and canal, Fort Wayne, Ind. (USNM). Maumee River, Cecil and near Sherwood, both Defiance Co., Ohio (both OSUM); Defiance, Defiance Co.; Florida, Henry Co.; and Grand Rapids, Wood Co., Ohio (all USNM). Tymochtee Creek, Tymochtee, Wyandot Co., Ohio (1970, R. E. Bowen! (OSUM)). Sandusky River, 1 mi (1.6 km) W of Upper Sandusky, Wyandot Co., Ohio (1974, H. G. and E. Stansbery! (OSUM)). East Branch, Black River, 2 mi (3.2 km) E of Lagrange, Lorain Co., Ohio (1961, C. B. Stein! (OSUM)). [Chagrin River], Chagrin, Ohio (USNM). Grand River, Painesville Township, Lake Co., Ohio (1977, R. Dawson! (OSUM)). Ashtabula River, Gageville, Ashtabula Co., Ohio (1969, R. P. and M. L. Klein! (OSUM)). Conneaut Creek, 3 mi (4.8 km) S of Conneaut, Ashtabula Co., Ohio (1969, J. K. Bissell! (OSUM)). Tonawanda Creek at Willow Bend Inn, Route 5, Genesee Co., N.Y. and Erie Barge Canal, Clover Road, Pittsford, Monroe Co., N.Y. (both Robertson and Blakeslee, 1948). Nith River tributary near New Hamburg, Wilmot Township, Waterloo Co., Ont. (1966, J. Oughton! (NMC)). Conestogo River, Conestogo, Waterloo Co., Ont. (Ortmann, 1919). Grand River, Route 86, West Montrose, Waterloo Co., Ont. (1970, B. T. Kidd! (NMC)) and Galt, Waterloo Co., Ont. (1958, A. H. Clarke and L. R. Clarke! (NMC)).

Lake Ontario Drainage: Genesee River at Avon, N.Y.; South Park, Rochester, N.Y. ("Baker, 1898") and 2 mi (3.2 km) SW of Genesee, N.Y. (all Clarke and Berg, 1959). Honeoye Creek at Route 315, Monroe Co., N.Y. (Robertson and Blakeslee, 1948). Outlet of Canandaigua Lake, N.Y. (MCZ). Seneca River, N.Y. (MCZ). Chittenango Creek, Kirkville and 5 mi (8.0 km) S of Bridgeport, both Madison Co., N.Y. (both 1955–57: A. H. Clarke and L. R. Clarke; Clarke and Berg, 1959). Oneida Creek, 1 mi (1.6 km) SW of Oneida Valley and Little Salmon River, 2 mi (3.2 km) S of Bombay, both Franklin Co., N.Y. (Clarke and Berg, 1959). Erie Barge Canal and Mohawk River, Mohawk, N.Y. (ANSP, MCZ, OSUM, USNM). Skootamatta River, Actinolite, Hastings Co., Ont. (1964, H. B. Herrington! (NMC)).

Ottawa River Drainage: Mississippi River, Pakenham, Ont. (1962, D. E. McAllister, F. R. Cook, J. Cook! (NMC)). Ottawa River, Carleton Co., Ont. (ANSP). Rideau River, 1 mi (1.6 km) N of Hogs Back and at Hogs Back, Ottawa, Carleton Co., Ont. (both 1965, A. H. Clarke, L. R. Clarke and C. B. Stein! (NMC)).

Lower St. Lawrence River Drainage: St. Lawrence River near Sheek Island, 5 mi (8.0 km) W of Cornwall, Stormont Co., Ont. (1957, A. H. Clarke, O. J. Flint, Domenic Pirone! (NMC)) and near Montreal, Que. (La Rocque, 1962). Raquette River, 1 mi (1.6 km) S of Pottsdam, St. Lawrence Co., N.Y. (MCZ). Yamaska River near St. Hyacinthe, St. Hyacinthe Co., Que. (La Rocque, 1962).

SUSQUEHANNA RIVER SYSTEM.—*Upper Susquehanna River Drainage, New York*: Tioga River ("Marshall, 1895," Clarke and Berg, 1959). Susquehanna River at Afton, Afton Co. and Smithboro, Tioga Co.; Catatonk Creek at "Oswego" [sic., Owego] and 2 mi (3.2 km) SE of Candor, both Tioga Co.; Tioughnioga River at Itaska, Broome Co.; Otselic River near Upper Lisle, Broome Co.; Chenango River, 3 mi (4.8 km) NE of Greene, Chenango Co.; and Chenango Forks, Broome Co. (all 1955-57, A. H. Clarke and L. R. Clarke!, Clarke and Berg, 1959). Canisteo River, 17.5 mi (28.0 km) W of Elmira, Steuben Co., at highways 15 and 17 (1966, W. N. Harman! (OSUM)).

Lower Susquehanna River Drainage, Pennsylvania: Susquehanna River at Athens, Bradford Co. (1955, A. H. Clarke and L. R. Clarke! (NMC)); Towanda, Bradford Co. (ANSP); ½-2 mi (0.8-3.2 km) S of Meshoppen, Wyoming Co. (1965, S.L.H. Fuller! (MCZ)); Tunkhannock, Wyoming Co. (Ortmann, 1919). Williamsport, West Branch Susquehanna River, Lycoming Co. (ANSP). Susquehanna River at Selinsgrove, Snyder Co. and Duncannon, Perry Co. (both Ortmann, 1919). Raystown Branch Juniata River at U.S. highway 30 bridge, 1 mi (1.6 km) W of Breezewood, Bedford Co. (1966, J. J. Jenkinson! (OSUM)); Ardenheim, Huntington Co. (ANSP) and Mount Dallas, Bedford Co. (Ortmann, 1919). Frankstown Branch Juniata River at Huntington and Alexandria, Huntington Co. (both Ortmann, 1919). Juniata River at Mount Union, Huntington Co.; near Newton-Hamilton, Mifflin Co.; Tuscarora, Juniata Co. (all ANSP); and Juniata Bridge, Perry Co. (Ortmann, 1919). Conodoguinet Creek, Carlisle, Cumberland Co. (Ortmann, 1919). Swatara Creek, Jonestown, Lebanon Co. (MCZ).

OHIO RIVER SYSTEM.—*Allegheny River Drainage, Pennsylvania*: Allegheny River in McKean Co., ¼ mi (0.4 km) SW of Turtle Point (1976, L. T. McGeehan! (OSUM)) and Larabee (Ortmann, 1919); in Warren Co. 5 mi (8.0 km) above Warren (1965, C. B. Stein! (OSUM)) and at Warren (Ortmann, 1919); in Forest Co. at Hickory (Ortmann, 1919), West Hickory (1972, R. E. Winters! (OSUM)), Tionesta (Ortmann, 1919), and 13 mi (20.8 km) ENE of Oil City (1970, D. P. Tanner! (OSUM)); in Venango Co. 9.5 mi (15.2 km) S of Franklin (1970, R. E. Winters! (OSUM)) and at Walnut Bend (Ortmann, 1919); and in Armstrong Co. at Templeton, Kelly, and Godfrey (all Ortmann, 1919). Connewango Creek, Russell, Warren Co. (Ortmann, 1919). French Creek in Erie Co. 2 mi (3.2 km) W of Mill Village (1965, C. B. Stein! (OSUM)); Crawford Co. at Cambridge Springs, Meadville, and Cochranton (all Ortmann, 1919); and in Venango Co. at Utica, 7 mi (11.2 km) WNW of Franklin (Ortmann, 1919; also 1970, R. E. Winters! (OSUM)). Little Mahoning Creek, Goodville, Indiana Co.; Crooked Creek, Rosston, Armstrong Co.; Quemahonig Creek, Stanton's Mill, Somerset Co.; Loyalhanna River, Ligonier and Idlepark, both Westmoreland Co., Buffalo Creek, Harbison, Butler Co. (all Ortmann, 1919).

Monongahela River Drainage: West Fork River at Weston, Lewis Co., W. Va. and Lynch Mines, Harrison Co., Pa. Cheat River at Mount Chateau and Jaco, both Monongalia Co., W. Va. (all Ortmann, 1919).

Main Channel of Ohio River: Ohio River at Coraopolis, Pa. (ANSP).

Beaver River Drainage, Pennsylvania: Shenango River in Mercer Co. at Jamestown, Shenango, Clarksville, and Sharpsville and in Lawrence Co. at Pulaski and Harbor Bridge (all Ortmann, 1919). Little Shenango River, Greenville, Mercer Co. (MCZ).; Wolf Creek, Grove City, Mercer Co.; Pymatuning Creek, Pymatuning Township, Mercer Co.; Neshammock Creek: in Mercer Co. at Leesburg and in Lawrence Co. at Volant and Estabrook (all Ortmann, 1919). Beaver River, Wampum, Lawrence Co. (ANSP, MCZ, USNM).; Connoquenessing Creek, Ellwood City, Lawrence Co.; Slipperyrock Creek in Lawrence Co. at Rose Point and Wurtemberg. Mahoning River, Mahongstown, Lawrence Co.; Little Beaver Creek, Cannelton, Beaver Co., (all Ortmann, 1919).

Muskingum River Drainage, Ohio: Clear Fork of Mohican River, Hanover Township, Ashland Co. (1959, D. H. Stansbery! (OSUM)). Tuscarawas River, New Philadelphia, Tuscarawas Co. (ANSP, MCZ). Mohican River at mouth, 0.7 mi (1.1 km) W of Walhonding, Coshocton Co. (1977, D. H. Stansbery! (OSUM)). Killbuck Creek, 1 mi (1.6 km) N of highway 77 bridge, Coshocton Co. (1962, D. H. Stansbery! (OSUM)). Walhonding River, 1.2 mi (1.9 km) E of Warsaw, Coshocton Co. (1973, D. H. Stansbery! (OSUM)). Muskingum River, 1.6 mi (2.6 km) S of Conesville, Coshocton Co. (1976, C. B. James! (OSUM)) and at highway 14, below dam at Lowell, Washington Co. (1969, D. H. Stansbery! (OSUM)).

Kanawha River Drainage: Wolfe Creek, Grapefield, Bland Co., Va. (1968, D. H. Stansbery and W. J. Clench! (OSUM)). Walker Creek, State highway 100 bridge, Bane, Giles Co., Va. (1966, D. H. Stansbery! (OSUM)). Read Creek, Wytheville, Wythe Co., Va. (Ortmann, 1919). Indian Creek, ca. 4 mi (6.4 km) SE of Greenville, Monroe Co., W. Va. (1965, G. Dowdy! (OSUM)). Greenbriar River at state highway 7 bridge, Cass, Pocahontas Co., W. Va. and at state highway 219 bridge, 1 mi (1.6 km) E of Renick, Greenbriar Co., W. Va. (both 1969, D. H. Stansbery and W. J. Clench! (OSUM)); and at Ronceverte, Greenbriar Co., W. Va. (Ortmann, 1919). Elk River, Gassaway, Braxton Co., W. Va. and Shelton, Clay Co., W. Va.; North Fork Highes River, Cornwallis, Ritchie Co., W. Va.; and Little Kanawha River, Grantsville, Calhoun Co., W. Va. (all Ortmann, 1919).

Scioto River Drainage, Ohio: Olentangy River at Liberty Township, Delaware Co. (1960, D. H. Stansbery! (OSUM)); at Delaware, Delaware Co. (NMC, USNM); at Mount Air, Franklin Co. (1974, C. B. Stein! (OSUM)); and 7 mi (11.2 km) NNW of center of Columbus, Franklin Co. (1974, J. Frederick, Jr.! (OSUM)). Big Walnut Creek, Madison Township, Franklin Co. (1960, C. B. Stein and D. H.

Stansbery! (OSUM)). Scioto River at Colvin's Quarry, Franklin Township, Franklin Co. (1961, C. B. Stein and D. H. Stansbery! (OSUM)); at Columbus (USNM); and at mouth of Big Darby Creek, Pickaway Co. (OSUM). Big Darby Creek 0.5 mi (0.8 km) S of Fox, Pickaway Co. (1972, R. F. Jezerinac! (OSUM)); 16.2 mi (25.9 km) SW of Columbus, in Pickaway Co. (1976, D. H. Stansbery! (OSUM)); and 4 mi (6.4 km) NW of Circleville, Pickaway Co. (1973, J. M. Condit! (OSUM)). Deer Creek, western edge of Williamsport, Pickaway Co. (1978, K. Borror! (OSUM)) and just north of Pancoastburg, Fayette Co. (1961, S. D. English! (OSUM)). Paint Creek, Rock Mills, Fayette Co. (1967, J. A. Jennings! (OSUM)).

Little Miami River Drainage, Ohio: Little Miami River at Foster, Warren Co. (1977, K. Lammers! (OSUM)) and 6 mi (9.6 km) SSW of Lebanon, Warren Co. (1976, S. C. Lezan! (OSUM)).

Miami River Drainage, Ohio: Laramie Creek, Section 3, Laramie Township, Shelby Co. (MCZ). Miami River, Dayton, Montgomery Co. (1976, R. Bay! (OSUM) (empty shell)).

Kentucky River Drainage, Kentucky: North Fork Red River, 6 mi (9.6 km) N of Campton, Wolfe Co. (1974, E. Secora! (OSUM)). Red River near Campton. (1977, R. Thoma! (OSUM)).

Rolling Fork River Drainage, Kentucky: Rolling Fork River, Lebonon, Marion Co. (MCZ).

Green River Drainage, Kentucky: Russell Creek, Green Co. (USNM). Green River at Greensburg, Green Co. (USNM); Rio, Hart Co. (MCZ); Mumfordville, Hart Co. (USNM); and Mammoth Cave, Edmonson Co. (MCZ, USNM). Barren River, Bowling Green, Warren Co. (USNM).

Wabash River Drainage, Indiana: Flatrock Creek, Shelby Co. (MCZ) and 8 mi (12.8 km) S of Shelbyville, Shelby Co. (1964, C. B. Stein! (OSUM)). Salmonia River, Mount Etna, Huntington Co. and Mississinewa River, 1 mi (1.6 km) below Somerset, Wabash Co. (both USNM). Wabash River at Wabash, Wabash Co. (USNM); Peru, Miami Co. (1969, C. B. Stein! (OSUM), subfossil); 2.5 mi (4.0 km) above Lewisburg, Cass Co. (USNM); Delphi, Carroll Co. (USNM); and Lafayette, Tippecanoe Co. (MCZ). Eel River at Laketon, Wabash Co. (1970, B. F. Snyder! (OSUM) and Logansport, Cass Co. (USNM). Tippecanoe River at highway 30, west of Warsaw, Kosciusko Co. (1963, C. B. Stein! (OSUM)); White Co. (MCZ); and De Long, Fulton Co. (USNM). Wildcat Creek, Burlington, Carroll Co. (USNM). White River, 3 mi (4.8 km) above Noblesville, Hamilton Co.; Noblesville; and Spencer, Owen Co. (all USNM). West Fork White River, Indianapolis (OSUM).

CUMBERLAND RIVER SYSTEM.—*Rockcastle River Drainage, Kentucky*: Rockcastle River at ford, Livingston, Rockcastle Co. (1963, C. B. Stein and D. H. Stansbery! (OSUM)) and at highway 80 bridge between Somerset and London, Rockcastle/Laurel Co. (1963, C. B. Stein and D. H. Stansbery! (OSUM)).

Cumberland River Drainage: Cumberland River, Williamsburg, Whitely Co., Ky. (MCZ). Wolf River, 7 mi (11.2 km) SE of Byrdstown, Pickett Co., Tenn. (USNM).

Red River Drainage, Tennessee: Red River, 4.3 mi (6.9 km) NE of Adams, Robertson Co. and at U.S. highway 41 bridge 1.3 mi (2.1 km) W of Adams, Robertson Co. (both 1966, D. H. Stansbery! (OSUM)).

TENNESSEE RIVER SYSTEM.—*Nolichucky River Drainage*: Nolichucky River, 3.5 mi (5.6 km) SE of Warrensburg at State highway 2486 bridge, Green Co., Tenn. (1968, W. J. Clench and D. H. Stansbery! (MCZ, OSUM)).

Powell River Drainage: Big Mocassin Creek, Mocassin Gap, Scott Co., Va. (Ortmann, 1919). Powell River: 2.5 mi (4.0 km) S of Jonesville, Lee Co., Va. (MCZ); Dryden, Lee Co., Va.; Combs, Claiborne Co., Tenn. (both Ortmann, 1919); and near Hoop, 9 mi (14.4 km) NE of Tazewell, Claiborne Co., Tenn. (1967, D. H. Stansbery! (OSUM)).

Clinch River Drainage: Clinch River at Richland, Tazewell Co., Va.; Fink and Cleveland, Russell Co., Va.; St. Paul, Wise Co., Va.; Clinchport and Speers Ferry, Scott Co., Va. (all Ortmann, 1919); 5.5 mi (8.8 km) below Fort Blackmore, Scott Co., Va. (1953, H. D. Athearn (NMC)); Hill Station, 5.5 mi (8.8 km) below Fort Blackmore, Scott Co., Va. (1953, H. D. Athearn! (OSUM)); 1.5 mi (2.4 km) S of Fairview, Scott Co., Va. (ANSP); Kyles Ford, Hancock Co., Tenn. (1978, A. H. Clarke and J. J. Clarke (USNM)); 0.25 mi (0.4 km) below Kyles Ford (1965, D. H. Stansbery and J. J. Jenkinson! (OSUM)); "The Rounds," [near Kyles Ford] (MCZ); mouth of Possumtrot Run, 4.8 mi (7.7 km) ENE of Sneedville, Hancock Co., Tenn. (1969, D. H. Stansbery! (OSUM)); and 4 mi (6.4 km) NE of Maynardville, Union Co., Tenn. (MCZ). (See Bates and Dennis, 1977 for additional Clinch River records.) Clear Fork Creek, Rugby, Morgan Co. Tenn. (MCZ).

Holston River Drainage: North Fork Holston River at Seven Mile Ford, Smyth Co., Va. (ANSP); Saltville, Smyth Co., Va.; Mendota, Washington Co., Va.; Hilton, Scott Co., Va.; and Rotherwood, Hawkins Co., Tenn. (all Ortmann, 1919). Middle Fork Holston River at Chilhowie, Smyth Co., Va. (Ortmann, 1919); 5 mi (8.0 km) ESE of Abington, Washington Co., Va. (1968, W. J. Clench and D. H. Stansbery! (OSUM)); and 5.3 mi (8.5 km) SW of Glade Springs, Washington Co., Va. (1970, D. H. Stansbery! (OSUM)). Watauga River near Johnson City, Washington Co., Va. (ANSP). South Fork Holston River at Emmett, Bluff City, and Pactolus, all Sullivan Co., Tenn. (all Ortmann, 1919). Holston River at Austin Mill, Hawkins Co., Tenn.; Holston Station and Turley Mill, both Grainer Co., Tenn.; Hodges, Jefferson Co., Tenn. (all Ortmann, 1919); Three Springs, 1 mi (1.6 km) NW of Needmore, Hamblen Co., Tenn. (OSUM); and Mascot, Knox Co., Tenn. (Ortmann, 1919).

Tennessee River, Main Channel: Tennessee River, Knoxville, Knox Co., Tenn. (MCZ) and Tuscumbia, Ala. (USNM)).

Paint Rock River Drainage: Paint Rock River, Trenton and Paint Rock, both Jackson Co., Ala. (both ANSP).

Flint River Drainage: Flint River, Gurley, Madison Co., Ala. (ANSP).

Elk River Drainage: Elk River, Fayettevile, Lincoln Co., Tenn. (ANSP, USNM).

Shoals Creek Drainage: Shoals Creek, Lauderdale Co., Ala. (Ortmann, 1919).

Bear Creek Drainage: Bear Creek, Burleson, Franklin Co., Ala. (Ortmann, 1919).

Buffalo River Drainage: Buffalo River, 10 mi (16.0 km) N of Waynesboro, Wayne Co., Tenn. (1965, B. Isom and P. Yokley! (OSUM)).

Duck River Drainage: Duck River, Hardison's Mill, 12 mi (19.2 km) NW of Lewisburg, Marshall Co., Tenn. (MCZ).

UPPER MISSISSIPPI RIVER SYSTEM.—*Minnesota River Drainage*: Minnesota River, Fort Snelling, Hennepin Co., Minn. (subfossil, USNM).

Mississippi River, Main Channel: Mississippi River, 1 mi (1.6 km) S of St. Paul, Minn.; Homer, Winona Co., Minn.; foot of Lake Pepin, Buffalo Co., Wisc.; 7.5 mi (12.0 km) NW of La Crosse, La Crosse Co., Wisc. (in Minn.); La Crosse, La Crosse Co., Wisc.; Prairie du Chien, Crawford Co., Wisc.; 2.8 mi (4.5 km) SW of Prairie du Chien, (west channel); N of Marquette, Clayton Co., Iowa; Clayton, Clayton Co.; Feuleys Landing, Grant Co., Wisc. (10 mi (16.0 km) NNE of Dubuque, Dubuque Co., Iowa); 9 mi (14.4 km) N of Dubuque; Sabula, Jackson Co., Iowa; Crescent Bridge, Davenport, Scott Co., Iowa (all USNM); Davenport (ANSP); Muscatine, Muscatine Co., Iowa; and Keokuk, Lee Co., Iowa (both USNM).

St. Croix River Drainage: Eau Claire River, 3.5 mi (5.6 km) ESE of Gordon, Douglas Co., Wisc. Namekagon River, 2 mi (3.2 km) SE of Stanbery, Washburn Co., Wisc. (both 1971, M. J. Imlay! (OSUM)). Kettle River. [Pine Co.], Minn. (USNM).

Black River Drainage, Wisconsin: Black River, 0.5 mi (0.8 km) SW of Greenwood, Clark Co. (1967, J. W. Reese! (OSUM)). East Fork Black River, 2 mi (3.2 km) N of Pray, Jackson Co., (1976, H. A. Mathiak! (OSUM)).

Wisconsin River Drainage, Wisconsin: Wisconsin River, Port Andrews, Richland Co. (1976, H. A. Mathiak! (OSUM)).

Wapsipinicon River Drainage, Iowa: Wapsipinicon River at Independence, Buchanan Co. and below Troy, Linn Co. (both USNM).

Rock River Drainage: Sugar River, 3 mi (4.8 km) SW of Brodhead, Green Co., Wisc. (1976, H. A. Mathiak! (OSUM)). Rock River at Jefferson Co., Wisc. (USNM); Rockton, Winnebago Co., Ill. (1969, T. Miller! (OSUM)); Rockford, Winnebago Co., Ill. (MCZ, USNM); and 5 mi (8.0 km) NW of Byron, Ogle Co., Ill. (1969, T. Miller! (OSUM)). Kishwaukee River, DeKalb Co., Ill. (MCZ).

Cedar River Drainage, Iowa: Cedar River south of Osage, Mitchell Co. and at Cedar Rapids, Linn Co. (MCZ, USNM). Shell Rock River at Nora Springs, Floyd Co.; Rockford, Floyd Co.; and Greene, Butler Co. (all USNM).

Iowa River Drainage, Iowa: Iowa River at Iowa Falls, Hardin Co.; Eldora, Hardin Co. (both USNM) and Iowa City, Johnson Co. (MCZ, USNM).

Des Moines River Drainage, Iowa: Lizard Creek, Fort Dodge, Webster Co. (MCZ). "Coon" [=Raccoon] River, Lanesboro, Carroll Co. (USNM) and Van Meter, Dallas Co. (MCZ). Des Moines River, Des Moines, Polk Co. (MCZ, USNM).

Illinois River Drainage: Yellow River, North Hibbard, Marshall Co., Ind. (USNM). Forked Creek, Wilmington, Will Co., Ill. (OSUM). Kankakee River at Momence, Kankakee Co., Ill. (OSUM) and 0.25 mi (0.4 km) below mouth of Horse Creek, Will Co., Ill. (1976, E. Perry! (OSUM)). Sammonauk Creek, Waterman, Dekalb Co., Ill. (ANSP). Illinois River at Morris, Grundy Co., Ill. and Peoria, Peoria Co., Ill. (both USNM). Fox River, 1.5 mi (2.4 km) S of Rochester, Racine Co., Wisc. (1976, H. A. Mathiak! (OSUM)); Yorkville, Kendall Co., Ill. and Millington, Kendall Co., Ill. (both MCZ). Salt Fork Vermilion River, Homer Park, Ogden Township, Champaign Co., Ill. (OSUM). Mackinaw River near Bloomington, McLean Co., Ill. (USNM).

MISSOURI RIVER SYSTEM.—*Missouri River Drainage*: Big Sioux River, west of Granite, Lyon Co., Iowa (USNM). Pomme de Terre River, 11 mi (17.6 km) S of Warsaw, Benton Co., Mo. (fairly fresh valves) (1966, R. McMillan! (OSUM)). Big Piney River, 10 mi (16.0 km) N of Licking, Texas Co., Mo. (MCZ).

Gasconade River Drainage, Missouri: Gasconade River at Gascondy, Osage Co. (MCZ); Gasconade, Gasconade Co. (Ortmann, 1919); and 3 mi (4.8 km) N of Mount Sterling, Gasconade Co. (1964, D. H. Stansbery and J. J. Jenkinson! (MCZ)). Bourbeuse River, 5 mi (8.0 km) S of Owensville, Gasconade Co. (1964, D. H. Stansbery and J. J. Jenkinson! (OSUM)) and Union, Franklin Co. (1977, D. H. Stansbery! (OSUM)).

Meramec River Drainage, Missouri: Meramec River, 1.3 mi (2.1 km) NW of Steelville, Crawford Co. (1977, D. H. Stansbery! (OSUM)); state highway 155 bridge, Franklin Co. (1977, W. L. Pfinger! (OSUM)); near Eureka, St. Louis Co. (1977, D. Oesch! (OSUM)); and Times Beach, 0.5 mi (0.8 km) E of Eureka (MCZ). Mine-a-Breton Creek, Postosi, Washington Co. (USNM).

LOWER MISSISSIPPI RIVER SYSTEM.—*St. Francis River Drainage*: Silvermines Creek near Silver Mines, Madison Co., Mo. (1957, V. B. Haid! (MCZ)).

White River Drainage: White River at 0.3 mi (0.5 km) E of Elkins, Washington Co., Ark. (1976, K. Wright! (OSUM)) and Cotter, Baxter Co., Ark. (Ortmann, 1919). James River, Stone Co., Mo. (USNM); SE edge of Galena, Stone Co. (1973, D. H. Stansbery! (OSUM)); and Galena (Ortmann, 1919). War Eagle Creek, about 1.8 mi (2.9 km) E of Huntsville, Madison Co., Ark. (1977, K. Wright! (OSUM)). Buffalo River, 12.3 mi (19.7 km) SE of Yellville, Marion Co., Ark. (1973, D. H. Stansbery! (OSUM)). Current River, Shannon Co., Mo. (MCZ). Spring River, 1 mi (1.6 km) from Ravenden, Randolph Co., Ark. (USNM) and 0.2 mi (0.3 km) E of Ravenden (1966, G. and E. Pond! (OSUM)). Black River, Kincaid Bar, 2 mi (3.2 km) N of Black Rock, Randolph Co., Ark. (USNM).

Arkansas River Drainage: Illinois River just above mouth of Flint Creek, 1.3 mi (2.1 km) SSW of Flint, Delaware Co., Okla. (1969, M. R. Collum! (OSUM)). Spring River at Carthage, Jasper Co., Mo. (MCZ) and near mouth of Cow Creek at State Hwy. 96, R 25N, T 33S, Cherokee Co., Kan. (Branson, 1966). Mulberry River, 12.5 mi (20.0 km) WNW of Ozard, Franklin/Crawford Co. boundary, Ark. (1976, K. and R. Wright! (OSUM)). Arkansas River, Little Rock, Pulaski Co., Ark. (USNM).

Ouachita River Drainage, Arkansas: Ouachita River at Baker's Landing, 3 mi (4.8 km) above Sims, Montgomery Co. and U.S. highway 270, 3 mi (4.8 km) SE of Pencil Bluff, Montgomery Co.; Caddo River, 4 mi (6.4 km) above mouth, Caddo Valley, Clark Co.; and Saline River, 11 mi (17.6 km) SSE of Benton, Grant Co./Saline Co. (all 1964, C. B. Stein! (OSUM)) and 3 mi (4.8 km) E of Poyen, Grant Co. (1971, D. H. Stansbery! (OSUM)).

Alasmidonta (Decurambis) atropurpurea (Rafinesque, 1831)

FIGURE 22

Alasmodon atropurpureum Rafinesque, 1831:9. [Type-locality: "river Cumberland, very rare." Type-material not in Academy of Natural Sciences (Johnson and Baker, 1973) and apparently lost. A neotype, herein selected, is in the Smithsonian Institution (150522). See "Remarks."]

THE SHELL

FIGURE 22*a-c*

DESCRIPTION.—Shell subovate; up to about 90 mm long, 40 mm high, and 25 mm wide; rather thin-shelled throughout but not fragile; and up to about 2 mm thick anteriorly. Anterior margin sharply rounded; ventral margin flatly curved, nearly straight, or concave centrally; posterior margin bluntly pointed and biangulate below, rounded above, and continuing into the dorsal margin that is broadly convex posteriorly and slightly concave anteriorly. Maximum inflation at the posterior ridge a little behind the center of the shell. Beaks of medium width, rounded, located about 1/4 the distance from anterior to posterior, and projecting somewhat above the hinge line. Posterior ridge well marked, broad, rounded or flattened centrally, and becoming double near the margin in some adult specimens. Posterior slope of moderate width, slightly concave proximally, and flattened distally. Growth increments marked by concentric ridges and grooves. Additional post-juvenile sculpturing consisting of faint, moderate, or well-developed, diagonal corrugations (about 6 to 10 in 10 mm) on the posterior slope, approximately perpendicular to the shell margin, and either restricted to the proximal area or more generally distributed over the posterior slope. Periostracum smooth and glossy between growth rests except roughened posteriorly, with clearly visible, extensive, greenish rays spread over a yellowish brown background in juveniles. The periostracum is thicker and dark blackish brown in adults but rays are still apparent in most specimens, particularly by transmitted light. Ligament strong, broad, thick, and of medium length.

Hinge teeth incomplete and variable. Pseudocardinal teeth rather small but conspicuous, pyramidal, and compressed; one in the right valve, anterior-ventrally directed, and two partially confluent teeth in the left valve. Interdental projection variable but in most specimens clearly developed in the left valve, and articulating with a depression in the right valve. In some specimens a small interdental projection also occurs in the right valve behind this depression. Lateral teeth absent or rudimentary. Beak cavity quite shallow. Anterior muscle scars variably shaped and variably impressed, pallial line continuous and well-marked, and posterior muscle scars shallow but clearly apparent. Scars within beak cavity consisting of one or two short, deep grooves on the back of the hinge plate in the left valve and, in many specimens, of a prominent, deep groove on the lower side of the hinge plate in the right valve placed diagonally and clearly indenting the plate margin when viewed perpendicular to the plane of the valve margin. Nacre shiny; bluish or bluish white; salmon, pinkish, or brownish centrally and in the beak cavity; and in some specimens with irregular brownish blotches.

Beak sculpture obliterated in available material.

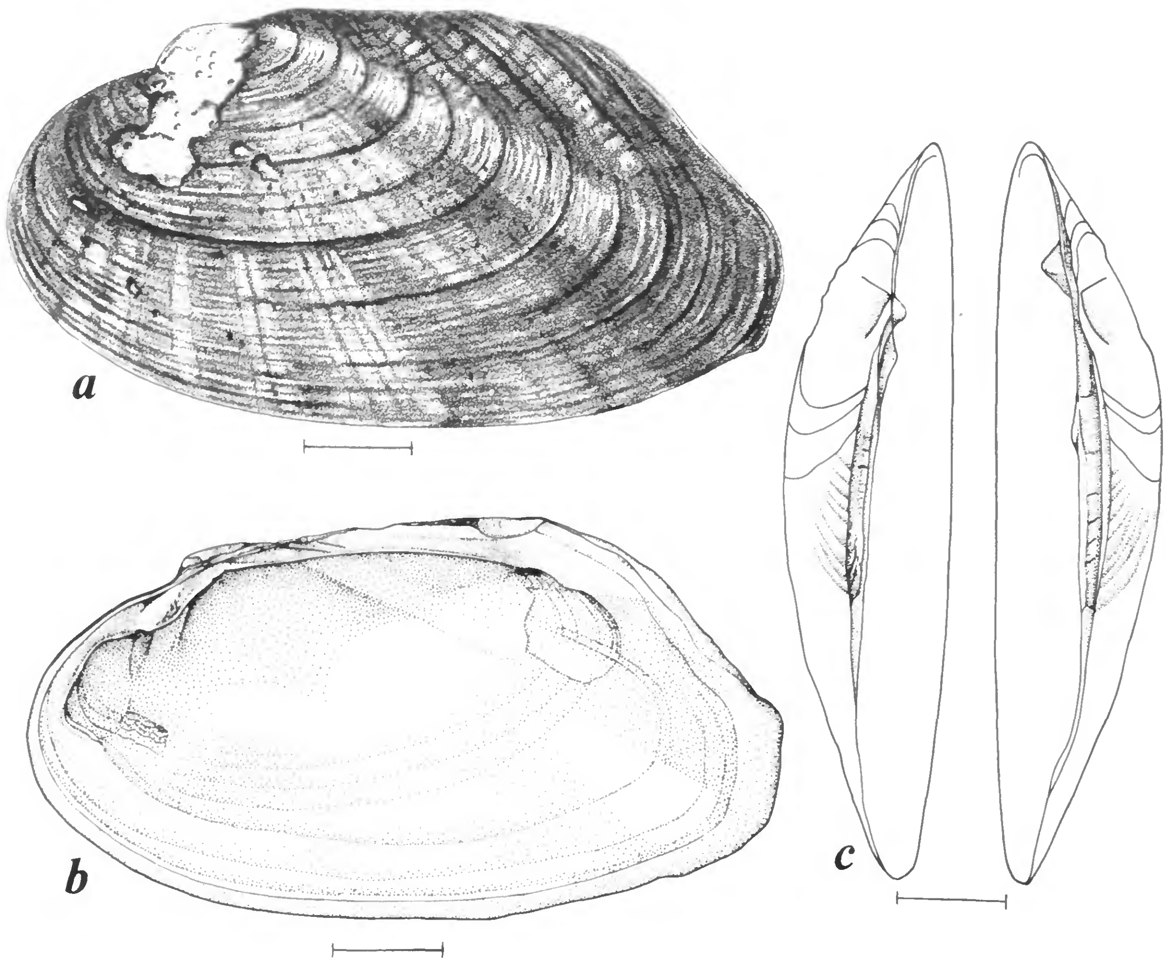

FIGURE 22.—*Alasmidonta atropurpurea*, USNM 150522, Cumberland River, Tennessee. (Scale = 1 cm.)

TOPOGRAPHIC ANATOMY

(not figured)

SPECIMEN DESCRIBED.—USNM 801870, from Marsh Creek, near Brushy Creek, McCreary County, Kentucky, collected 12 July 1980 by S. M. Call and R. D. Stefano; pegged, fixed in 10% formaldehyde and preserved in 70% ethyl alcohol; shell length 77.8 mm, sex male (inferred).

DESCRIPTION.—Mantle whitish, opaque, and slightly thickened between edge and pallial line; grayish, semi-transparent, and very thin within pallial line with the yellow color of the foot and the brownish gray of the demibranchs clearly showing through. The slightly (0.5 mm) thickened edge is about 5.5 mm wide anteriorly and ventrally and 9.5 mm posteriorly; it is suffused with pigment on its inner side, the color being

TABLE 15.—*Alasmidonta atropurpurea*: Shell measurements; specimens from South Fork, Cumberland River, Fentress County, Tennessee (UMMZ 11190)

Feature	*N*	*Range*	*Mean* ($\bar{x}$)	*S*
Length (mm)	11	58.67 -88.27	73.30	9.07
H/L	11	0.509 - 0.555	0.532	0.018
W/L	9	0.307 - 0.375	0.346	0.024
B-A/L	11	0.261 - 0.310	0.292	0.018
Hp/L	11	0.0304- 0.0557	0.0425	0.0085

purple-brown and dense near the posterior openings and orange and less dense elsewhere. A broken band of blackish brown pigment extends around the posterior edge of the mantle externally from the mid-ventral area to the hinge; it is about 1.8 mm wide near the incurrent opening (where it appears as a series of squarish spots that are dark toward the mantle edge and paler away from it) and becomes narrower dorsally and even narrower ventrally.

Incurrent opening 11.3 mm long, purplish brown internally, and surrounded within by a (predominantly) single row of short subcylindrical papillae that are about 0.7 mm long and 0.3 mm wide at their bases. Separation between incurrent and anal openings achieved entirely by the diaphragm; there is no mantle connection. Anal opening 10.5 mm long, with crenulated edges, and darkly pigmented within. Connected portions of mantle edges 5.5 mm long between anal and supra-anal openings. Supra-anal opening 9.4 mm long, with a narrow orange-brown band of pigment between the internal flange and the mantle edge; narrow, and without papillae or crenulations.

Demibranchs brownish gray in the preserved specimen. Outer demibranch 50.2 mm long, 18.7 mm high centrally, with low, dorso-ventral wrinkles overall and a convex, curved central margin. The demibranchs narrow more-or-less evenly from near the center to the anterior and posterior extremities, which are acute. There are about 1.2–1.5 water tubes per mm (with approximately every third septum thicker than those between); about 16 double dorso-ventral surface filaments per mm, and about 5 cross-filaments per mm. Inner demibranch with an obtusely angled anterior extremity, a roundly convex anterior-ventral margin that extends about 8.5 mm beyond the outer demibranch, and a posterior ventral margin that tapers from the point of maximum convexity (located 1/3 of the distance from anterior to posterior) to the acute posterior extremity. The anterior-ventral margin extends about 8.5 mm beyond the outer demibranch but the posterior-ventral margin is flush with that of the outer demibranch. There are also about 1.2–1.5 water tubes per mm, 16 double surface filaments, and 5 cross-filaments per mm in the inner demibranch. The inner lamina of the inner demibranch is fully attached by a membrane to the visceral mass.

The labial palps have undulating dorsal margins, rather sharply rounded posterior margins, and flatly rounded ventral margins. They broadly overlap the inner demibranchs. The outer surfaces are smooth and the inner opposing surfaces of each member are radially furrowed (about 8 furrows per mm at the ventral margin). The outer palpus of each pair is fused to the mantle anteriorly and, for about 3/4 of its length, to the inner palpus.

VARIATION.—Table 16 shows the extent of variation in several characters. The specimen described above in detail (#1 in table) was somewhat unusual in ralative length of A-SA and SA. A sexually related dichotomy clearly exists with respect to number of water tubes per mm in the outer demibranchs. In specimen 6, the septa were not parallel but markedly diagonal to the surficial filaments, and in specimen 4 this condition also obtained (particularly in the posterior part of the demibranch) but to a reduced extent.

In addition to the data presented in the table, it is significant that the anal opening was strongly crenulated in specimen 3 (with tiny papillae 0.2 mm long); moderately crenulated in 1, 2, 5, and 6; and weakly crenulated in 4. The inner demibranch in specimen 3 extended beyond the outer demibranch (by 2.5 mm) in the posterior region as well as in the anterior region. In all specimens the inner demibranch was fully attached, by a membrane, to the visceral mass.

LIFE HISTORY

Alasmidonta atropurpurea is a rare species and, until 1980, almost nothing was known about its ecology. After its discovery in Marsh Creek, McCreary Co., Kentucky in 1979 (see below), however, an extensive description of the physiography, botany, zoology, and water chemistry of Marsh Creek was published (Harker, et al, 1980). Living specimens of *A. atropurpurea* were found

TABLE 16.—*Alasmidonta atropurpurea*: Variation in topographic anatomy (abbreviations same as Table 4)

Spec. No.	Length (mm)	Mantle Pigmentation: Extent	Mantle Pigmentation: Strength	Relative lengths of mantle features (as % of L): Inc.	Ana 1	A-SA	SA	Incurrent Papillae: Ranks	Max. Ht. (mm)	Labial Pipes: Posit.	Grooves per mm	Water tubes N/mm*	Sex	Pre-preserv. treatment: Nemb. relax.	Form. fixed
	Marsh creek, McCreary Co., Kentucky S. M. Call and R. D. Stefano, 12 July 1980														
1	77.8	2	H	15	13	7	12	1+	0.7	0	8	1.2–1.5	(M)	–	+
2	75.0	2	H	18	16	13	8	1+	0.9	0	6	1.0–1.2	(M)	–	+
3	72.3	2.5	H	15	13	13	6	1–2	0.8	0	7	1.5	(M)	–	+
4	71.0	2	H	15	10	16	7	1+	1.0	0	8	2.5–3.0	(F)	–	+
5	68.6	2	H	19	13	12	7	1+	1.0	T	9	1.5	(M)	–	+
6	68.2	2	H	17	13	12	10	1	1.0	0	6	3.0	(F)	–	+

* Refers to outer demibranchs of non-gravid specimens.

there in slow-flowing water among cobbles where they were buried about 1/2 way down in the substrate. Details about the specific ecology of the species will be published by Mr. S. M. Call, Kentucky Nature Preserves Commission, Frankfort, Kentucky.

GEOGRAPHICAL RECORDS

FIGURE 23

CUMBERLAND RIVER SYSTEM.—North Fork Cumberland River (B. H. Wright! (USNM)). South Fork Cumberland River, Armathwaite, Fentress County, Tenn. (J. Lewis! (MCZ)) and Fentress County, Tenn. (B. Walker! (UMMZ)). Lynn Camp Creek, Corbin, Whitley County, Ky. (M. D. Barber! (MCZ)). Marsh Creek (alive) and Rock Creek (an empty shell), both McCreary Co., Ky. (1980, S. M. Call!, not included in Figure 23). Collins River, near Mount Olive, Grundy County, Tenn. (1978, A. E. Bogan!).

REMARKS

Rafinesque's description and his remarks appear to clearly indicate this species. Previous authors have not recognized it, probably because it is rare and because no type material exists. Selection of a neotype is therefore necessary to establish its identity. A neotype from near the original type locality (Cumberland River) and in the same river system, and closely matching Rafinesque's description and measurements, is hereby selected. It is in the Smithsonian Institution (catalog number 150522) and is from South Fork, Cumberland River, Fentress Co., Tennessee collected by B. H. Wright. Its measurements are: length, 74.3 mm; height (including ligament), 43.8 mm; width of both valves appressed, 28.3 mm; distance from umbone to anterior end measured parallel to long axis (B-A), 16.4 mm.

The lot (USNM 783317) from which the neotype was selected contains three other specimens whose measurements are: (a) length 80.0, height (without ligament) 38.6, width 26.5 mm; (b) length 76.7, height (without ligament) 39.8, width 22.5 mm; (c) length 55.3, height (with ligament) 32.3, width 17.8 mm. While specimen (a) is closer to Rafinesque's original measurements (length 3 inches, height 1½ inches, width 1 inch) than the neotype, only the neotype lacks prominent corrugations on the posterior slope. (Rafinesque described *atropurpurea* as smooth.) The neotype is faintly sculptured with corrugations but that is obviously a variable feature in this species.

The neotype and the other specimens in that lot were collected prior to January 1897, the date they were originally catalogued in this museum. No further specimens had been found until 1978, when a pair of disarticulated valves from an apparently freshly-dead specimen were collected from Collins River near Mount Olive, Tennessee by Mr. and Mrs. Arthur Bogan of the University of Tennessee at Knoxville. Soon thereafter (September, 1979), the species was discovered in Rock Creek and Marsh Creek, McCreary Co., Kentucky, by Mr. S. M. Call of the Kentucky Nature Preserves Commission. Later, Mr. Call kindly provided specimens for dissection, but they were

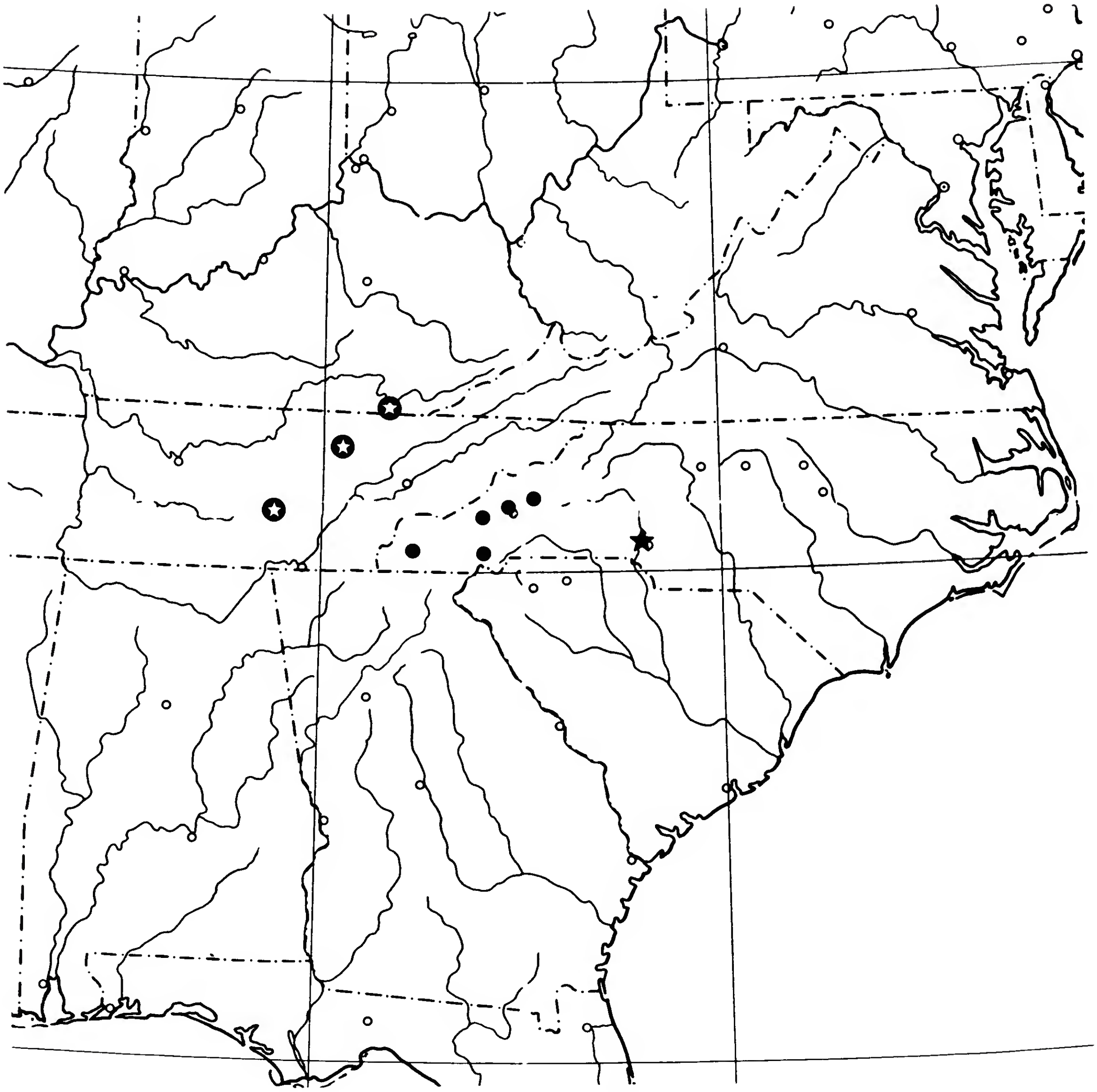

FIGURE 23.—Geographical distribution of *Alasmidonta atropurpurea* (stars in circles); *A. raveneliana* (solid circles); *A. robusta* (star).

received in July 1980, too late to be illustrated here.

Alasmidonta atropurpurea differs from *A. marginata* in that it is much smaller, lacks the high, angular posterior ridge and the truncated and flattened posterior slope, and the corrugations on the posterior slope are much less pronounced. It is similar in some respects to *A. varicosa*, but the posterior ridge in that species is also more elevated than in *A. atropurpurea* and the posterior margin is also more truncated.

Alasmidonta (*Decurambis*) *raveneliana* (Lea, 1834)

FIGURES 23, 24

Margaritana reveneliana Lea, 1834:106, pl. 17: fig. 50. [Type-locality: "French Broad and Swananoe [sic] rivers, North Carolina." The lectotype, herein selected, is apparently

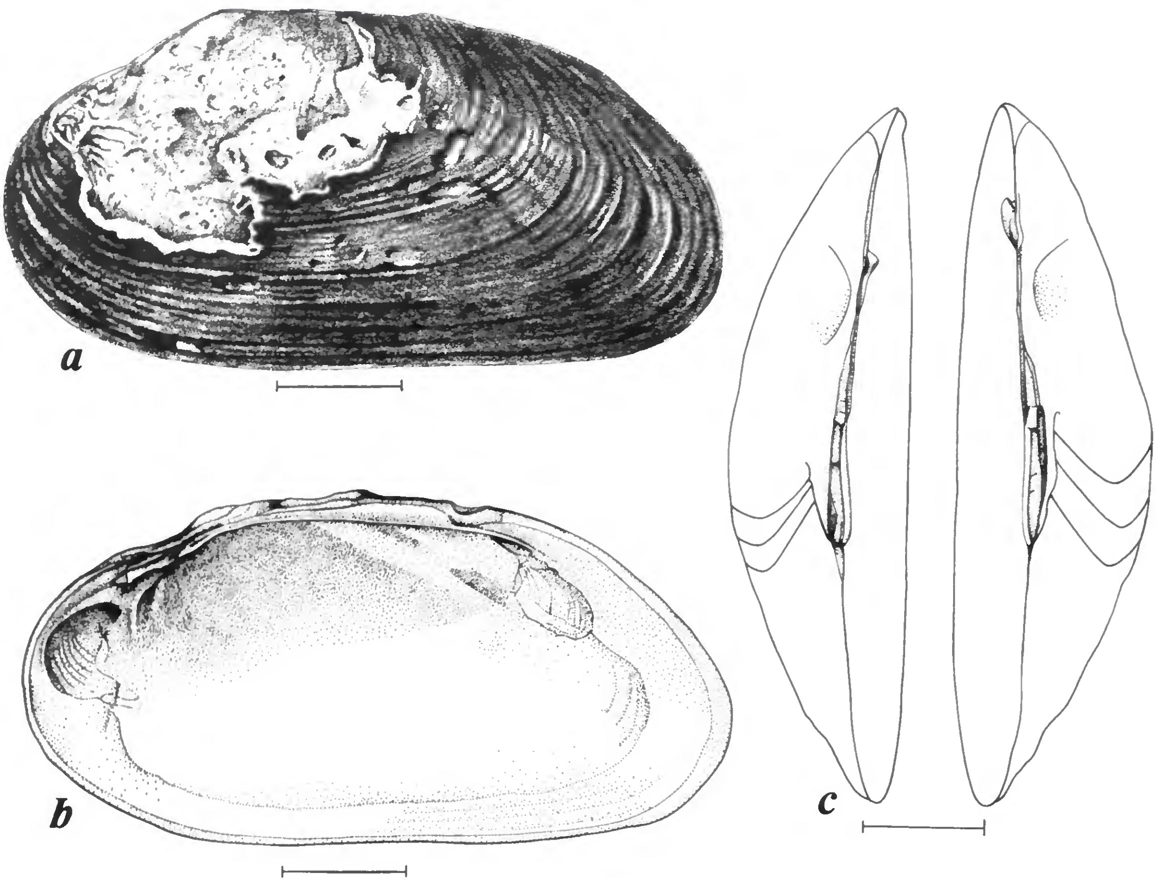

FIGURE 24.—*Alasmidonta raveneliana* (holotype of *Margaritana raveneliana* Lea), USNM 86254, Swannanoa River, North Carolina. (Scale = 1 cm.)

Lea's figured specimen, 86254 in the mollusk collection of the Smithsonian Institution and is from Swannanoa River (Buncombe Co.), North Carolina.]

Unio swananoensis Hanley, 1843:211, pl. 23: fig. 39 [plate published in 1835]. [New name for *Unio ravenelianus* (Lea, 1834) (formerly *Margaritana raveneliana* Lea, 1834), not *Unio ravenelianus* Lea, 1832.]

THE SHELL

FIGURE 24

DESCRIPTION.—Shell subovate or kidney-shaped; up to about 80 mm long, 35 mm high, and 25 mm wide; rather thin-shelled throughout but not fragile; and up to about 1½ mm thick anteriorly. Anterior margin sharply rounded, ventral margin nearly straight or concave centrally, posterior margin roundly pointed below the center and diagonally flattened above, and dorsal margin long and nearly straight posterior to the beaks and sloping or slightly sigmoid anteriorly. Maximum inflation at the posterior ridge near the center of the shell. Beaks of medium width, rounded, located about 28% to 30% the distance from anterior to posterior, and projecting only slightly above the hinge line. Posterior ridge prominent, rounded, and becoming centrally flattened near the margin in some adult specimens. Posterior slope of moderate width and somewhat concave. Growth increments marked by concentric ridges and grooves but disc principally smooth. Additional sculpturing absent except in some juveniles where a trace of plication is visible on the proximal part of the posterior slope. Periostracum smooth in general but roughened posteriorly and with a few, obscure, greenish rays visible in some specimens, especially on the posterior ridge and posterior slope. Juveniles are yellowish brown. The periostracum is thicker and dark brown in adults but some rays are still apparent in many specimens, particularly by transmitted light. Some specimens are prominently rayed. Ligament strong, broad, thick, and of medium height.

Hinge teeth incomplete and variable. Pseudocardinal teeth rather small but conspicuous, pyramidal, and compressed, one in each valve, each anterior-ventrally directed. The one in the right valve is the larger. Interdental projection moderately developed in the left valve. Lateral teeth absent and replaced by a single, nonarticulating thickening of the hinge plate in each valve. Beak cavity quite shallow. Anterior muscle scars variably shaped and impressed, pallial line continuous and well-marked, posterior muscle scars shallow but clearly apparent, and scars within beak cavity consisting of one or two short grooves on the back of the hinge plate of the left valve and a single, deep, oblique groove on the back and on the lower edge of the hinge plate of the right valve. Ridges bounding the posterior slope are also visible on the inside of the shell. Nacre shiny, bluish or bluish white in general but salmon, pinkish, or brownish centrally and in the beak cavity, and in some specimens with irregular brownish blotches.

After completion of the illustrations for this paper two juvenile specimens of *A. raveneliana* with well-preserved beak sculpturing became available. They are from Pigeon River, Canton, North Carolina and were collected by A. E. Ortmann in 1914 (Carnegie Museum, No. 61.7133). The beak sculpture consists of seven moderately heavy bars, the last of which extends 6 mm beyond the umbonal apex. The first 2 or 3 bars are sharply indented adapically and centrally and acutely angled on the posterior ridge. The other bars are slightly curved adapically in one specimen and straight in the other, and in both those bars terminate at the posterior ridge.

TABLE 17.—*Alasmidontta raveneliana*: Shell measurements

Feature	*N*	*Range*	*Mean* ($\bar{x}$)	*S*
	Holston River, Tennessee (ANSP 41281)			
Length (mm)	14	36.16 -68.82	55.20	8.77
H/L	14	0.442- 0.544	0.498	0.0277
W/L	12	0.318- 0.375	0.352	0.0188
B-A/L	14	0.181- 0.267	0.245	0.0300
Hp/L	13	0.023- 0.049	0.0344	0.0067
	Pigeon River, Canton, N.C. (Carnegie Mus. 61.7133)			
Length (mm)	9	48.22 -76.35	66.15	9.23
H/L	9	0.445- 0.571	0.535	0.0216
W/L	9	0.306- 0.348	0.328	0.0144
B-A/L	9	0.234- 0.275	0.248	0.0128
Hp/L	9	0.027- 0.036	0.0335	0.0059

TOPOGRAPHIC ANATOMY

No soft parts were available for study. The following quotation from Ortmann (1921:88) is informative, however.

> The anatomy is the same as that of the genus *Alasmidonta*, as described previously [Ortmann, 1912:297], also with regard to color (inclining to yellowish and orange tints). It should be mentioned that the inner lamina of the inner gills is, in two males and two females, entirely connected with the abdominal sac (as is the case in *A. marginata*); but in one male and two females, it is free in the posterior half or one-third of the abdominal sac. The specimens with the inner lamina partly free are the smaller ones.

GLOCHIDIUM

The only information has been published by Ortmann (1921:88): "Glochidia as usual, triangular, with hooks, about as high as long, L. and H. from 0.29 to 0.32 mm. Thus they are smaller than those of *A. marginata*, where the L. is 0.33, the H. 0.36 mm."

LIFE HISTORY

"I have collected a number of specimens of this species in Pigeon River, at Canton, Haywood Co., N. Car., on May 14, '14. Of three males and four gravid females, all with glochidia, two of them discharging, the soft parts have been preserved. The breeding season thus ends in May"

(Ortmann, 1921:87–88). The host fish of *A. raveneliana* is unknown.

All of the records are from rivers in the mountains of eastern Tennessee or western North Carolina. It is apparently rare but not extinct, judging from the live specimen recently collected from Little River, cited below.

Geographical Records

Figure 23

Tennessee River System.—*Holston River Drainage*: Holston River, Tenn. (S. S. Haldeman! (ANSP)).

Nolichucky River Drainage: Nolichucky River, N.C. (B. Walker! (UMMZ)).

French Broad River Drainage, North Carolina: Little River, Penrose, 5 mi (8.0 km) E of Brevard, Transylvania Co. (1953, M. J. Westfall! (MCZ), one live specimen collected but soft parts not retained). Swannanoa River (Ravenel! (USNM), lectotype and paratype of *Margaritana raveneliana* Lea). French Broad River, Asheville, Buncome Co. (J.F.E. Hardy! (USNM)) and French Broad River (J. S. Phillips! (MCZ, ex. A.A. Gould coll.)). Pigeon River, Canton, Haywood Co. (A. E. Ortmann! (MCZ, UMMZ)).

Little Tennessee River Drainage: [Tulula Creek], Robbinsville, Graham Co., N.C. (S. B. Denton! (USNM)).

Remarks

The most striking feature of this species is the virtually smooth posterior slope of adult specimens. It differs in this respect from all other species in the subgenus *Decurambis*. *A. raveneliana* also tends to exhibit a more concave ventral margin and a more faintly developed interdental projection than is usually seen in *A. marginata* or *A. atropurpurea*. The relative height of *A. raveneliana* (H/L mean 0.498 in Holston River lot) also tends to be lower than in *A. atropurpurea*, *A. marginata*, or *A. varicosa* (H/L means all exceeding 0.516). Finally *A. raveneliana* tends to be more compressed (W/L mean about 0.352) than either *A. marginata* (0.415–0.428) or *A. varicosa* (0.396–0.405) but a little more inflated than *A. atropurpurea* (0.328–0.346).

Alasmidonta (*Decurambis*) *varicosa* (Lamarck, 1819)

Figures 25, 26

Unio varicosa Lamarck, 1819:78–79. [Type-locality: "la riviere de Schuglkill, pres de Philadelphie . . . aussi dans le lac Champlain." Holotype in Geneva Museum, Geneva, Switzerland (Johnson, 1953:95).]

Alasmodon corrugata DeKay, 1843:198, pl. 24: 259. [Type-locality: Passaic River. Type material not in Museum of Comparative Zoology (Johnson, 1956) and probably lost.]

The Shell

Figure 25*a*,*b*,*d*,*e*

Description.—Shell kidney-shaped, up to 70 mm long, 40 mm high, and 30 mm wide, thin-shelled, slightly thickened anteriorly (up to 2 mm thick) but approximately equally strong throughout. Anterior margin abruptly curved, ventral margin long and a little concave centrally, posterior margin roundly biangulate below and obliquely flattened or flatly curved above, and dorsal margin long and gently convex. Maximum inflation at the posterior ridge near the center of the shell. Beaks narrow and bluntly pointed, located about ¼ the distance from anterior to posterior, and barely projecting above the hinge line. Posterior ridge conspicuous, broad, inflated, and rounded. Posterior slope flattened, and somewhat concave. Growth increments marked by concentric ridges and grooves, especially anteriorly. Additional post-juvenile sculpturing consisting of numerous, short, low, poorly-developed corrugations on the posterior slope and at right angle to the lines of growth. The posterior slope corrugations may be virtually absent, principally adapical, generally distributed, or arranged in transverse bands just within lines that apparently mark previous annual growth rests. Periostracum smooth centrally but roughened elsewhere, yellowish and partly or wholly covered by greenish rays in juveniles, brownish and with rays partially obscured in adults. Ligament moderate in length, rather thick, strong, and in longitudinal section clearly exhibiting numerous annual growth rests.

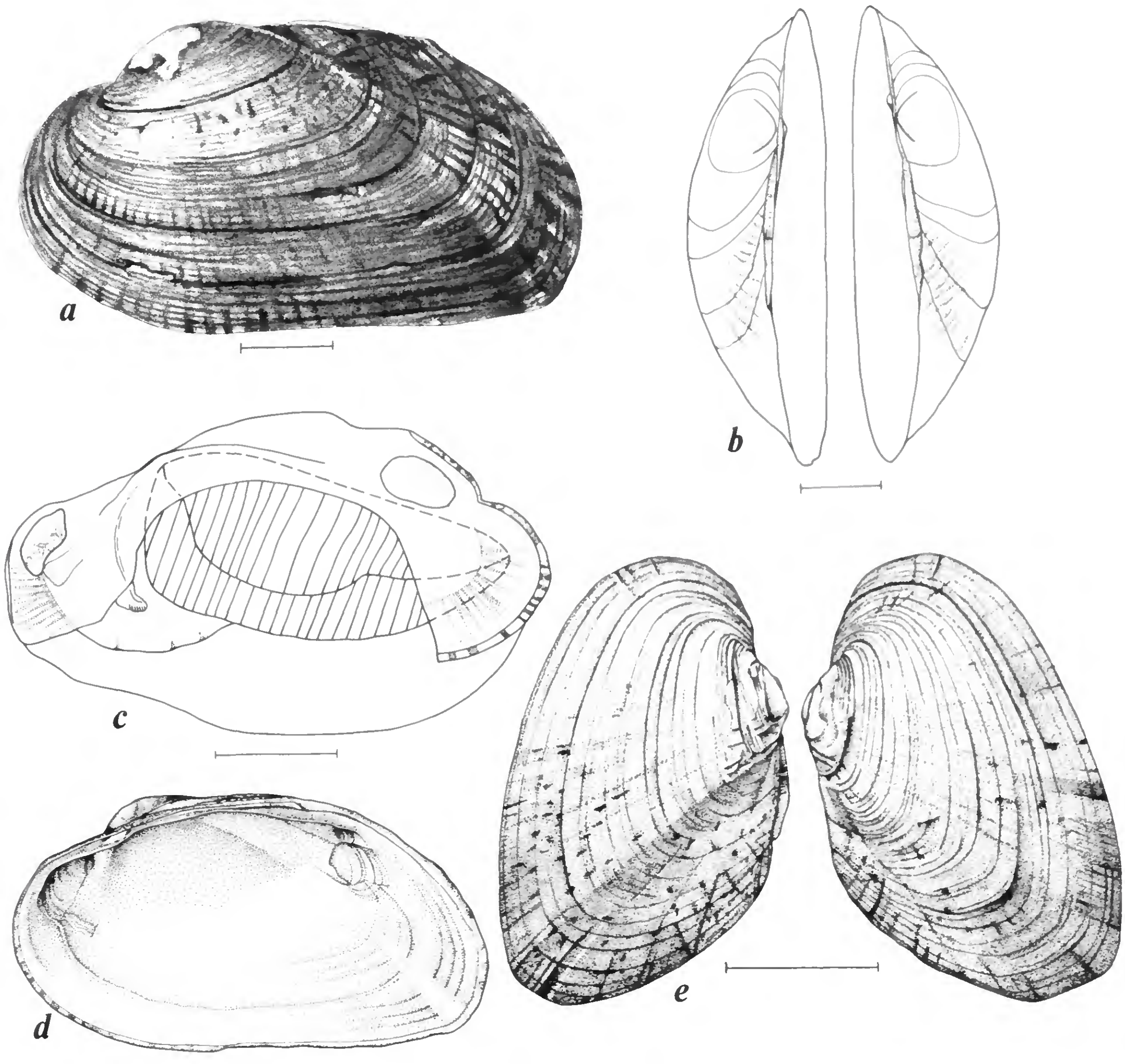

FIGURE 25.—*Alasmidonta varicosa*: *a,b,d*, USNM 452135, Assabet River, Concord, Massachusetts; *c*, NMC 21929, West Branch Tioughnioga River, Homer, New York; *e*, detail of umbonal area, USNM 452141, "Massachusetts." (Scale = 1 cm.)

Hinge teeth poorly developed, variable, and incomplete. Pseudocardinal teeth rather small, rounded, and variously developed or rudimentary, 1 in the right valve and 1 in the left. In some specimens the left valve also bears a vestigial tooth anterior to the major denticle. Interdental projection clearly defined or indicated only by a swelling, which may be barely perceptible, in one or both valves. Lateral teeth vestigial or entirely lacking.

Beak cavity excavated but shallow. Anterior muscle scars impressed, pallial line well marked, especially anteriorly, posterior muscle scars shallow but well-defined, and scars within beak cavity

TABLE 18.—*Alasmidonta varicosa*: Shell measurements

Feature	N	Range	Mean ($\bar{x}$)	S
	Wallace River, 9 mi S of Pugwash, Nova Scotia (NMC 54755)			
Length (mm)	6	53.67 -69.39	59.30	6.08
H/L	6	0.441 - 0.548	0.517	0.040
W/L	6	0.336 - 0.449	0.405	0.038
B-A/L	6	0.198 - 0.229	0.215	0.011
Hp/L	6	0.0295- 0.0407	0.0359	0.0041
	Molunkus Stream, 2.4 mi above Macwahoc, Maine (NMC 20993)			
Length (mm)	7	48.22 -63.86	56.54	5.28
H/L	7	0.508 - 0.554	0.529	0.015
W/L	7	0.372 - 0.424	0.396	0.019
B-A/L	7	0.205 - 0.274	0.246	0.022
Hp/L	7	0.0251- 0.0445	0.0339	0.0066
	Toms's Creek, 6.5 and 7.1 mi SE of Emmitsburg, Md. (NMC 57542, 57557)			
Length (mm)	16	36.86 -64.56	54.05	7.40
H/L	16	0.500 - 0.575	0.539	0.025
W/L	16	0.354 - 0.449	0.405	0.024
B-A/L	16	0.214 - 0.260	0.240	0.013
Hp/L	16	0.0302- 0.0484	0.0408	0.0041
	Conococheaque Creek, Williamsport, Md. (NMC 59581)			
Length (mm)	12	33.27 -53.90	45.73	6.86
H/L	12	0.495 - 0.578	0.536	0.026
W/L	12	0.366 - 0.420	0.392	0.020
B-A/L	12	0.210 - 0.286	0.252	0.026
Hp/L	12	0.0297- 0.0475	0.0407	0.0048

consisting of a few short, low, irregular ridges and grooves behind the hinge plate and subparallel with it, and two shallow, radial grooves directed anterior-ventrally and posterior-ventrally. Nacre glossy, bluish white anteriorly, bluish posteriorly, and yellowish tan olive, or pinkish centrally and in the beak cavity.

Beak sculpture coarse, variable, and composed of a few single-looped or double-looped ridges. The ridges are rarely preserved, however, except in very young individuals.

TOPOGRAPHIC ANATOMY

FIGURE 25*c*

SPECIMEN DESCRIBED.—From Rocky River, 11 mi (17.6 km) N of Sanford, U.S. Hwy. 15 bridge, Chatham Co., N.C., collected 22 June 1978 (USNM 794929, A. H. Clarke Station 1583); anaesthetized with nembutol, fixed in 10% formalin, preserved in 70% ethyl alcohol; shell length 57.0 mm, sex male (inferred).

DESCRIPTION.—Mantle grayish white, translucent, and with color of the branchiae showing through. A broken band of mostly widely-separated, brown, rectangular pigment spots occurs along the mantle edge from the mid-ventral area posteriorly and dorsally to near the posterior end of the ligament. The pigmented band is separated from the posterior mantle openings by a lip. The incurrent opening is 11 mm long and with groups of small papillae, pale gray and orange-brown in color, 2 or 3 rows deep, just within the opening. The central portion (4 mm long) is without papillae. The separation of incurrent and anal openings appear to be achieved by the diaphragm entirely, without appression of mantle edges. The anal opening has smooth but irregular edges, without papillae, and is 8 mm long. The mantle edges between the anal and supra-anal openings are not connected but are simply appressed during life; this area is 5 mm long. The supra-anal opening is slit-like, without papillae, and also 5 mm long.

Demibranchs of preserved specimen pale brown. Outer demibranch 36 mm long, 12 mm high, with anterior portion narrowed and subtruncate, ventral and posterior margins broadly but irregularly rounded, with broad radial wrinkles throughout, and with about 1.0 water tube per mm. Inner demibranch about 40 mm long and 15 mm high, anterior portion broad and truncated, ventral margin more or less evenly convex, and posterior margin sharply rounded; all margins extend beyond the outer demibranch and especially so (5 mm beyond) near the labial palps. Broad radial wrinkles also cover the surface of the inner demibranchs and there is also about 1.0 water tube per mm. Gravid specimens were not seen. The inner lamina of the inner demibranch is completely attached to the visceral mass.

Labial palps pale brown (paler than the demibranchs), wide and hemilunate, broadly curved below and meeting the flattened upper margin in a rounded point, with outer surfaces smooth and lower portion of inner surfaces radially furrowed (about 6 furrows per mm at margin). Each palpus is fused to its corresponding member at its base, but not along its dorsal margin.

VARIATION.—Table 19 indicates that normal anatomical variation occurs in *A. varicosa*. A-SA tends to be longer in this species than in *A. marginata* and the incurrent and anal openings are also longer; in fact in all of these features *A. varicosa* resembles *A. undulata*. As in *A. undulata* a geographic trend is also suggested in regard to the position of the labial palpi; in the northern population the palpi do not touch the inner demibranchs but in the southern populations the palpi tend to touch or overlap these demibranchs.

As in *A. marginata*, the inner lamina of the inner demibranch was fully connected with the visceral mass in all of the specimens examined.

GLOCHIDIA

Glochidia have not been available for study. According to Ortmann (1919:191) they are identical to those of *A. marginata*.

LIFE HISTORY

The period of gravidity for *A. varicosa* spans the interval from August 9 to May 3 in Pennsylvania (Ortmann, 1919:191). A specimen from Rocky River near Sanford, North Carolina, collected on 22 June 1978 had stretched but empty marsupial demibranchs. The host fish is unknown.

"As in *A. marginata*, *A. varicosa* is usually found in rapids or riffles on rock and gravel substrates and also in sandy shoals. It is more abundant in small rivers and creeks, whereas *A. marginata* is

TABLE 19.—*Alasmidonta varicosa*: Variation in topographic anatomy (abbreviations same as Table 4)

Spec. No.	Length (mm)	Mantle pigmentation: Extent	Mantle pigmentation: Strength	Relative length of mantle features (as % of L): Inc.	Anal	A-SA	SA	Incurrent papillae: Ranks	Max. ht. (mm)	Labial palps: Posit.	Grooves per mm	Water tubes N/mm*	Sex	Pre-preserv. treatment: Nemb. relax	Form. fixed
						Petitcodiac River, 19 mi WSW of Moncton, New Brunswick (NMC 46387)									
1	56.3	1	H	15	12	10	11	3	0.8	NT	8	3	(F)	-	-
2	54.2	2	H	26	15	7	13	2	1.0	NT	10	2	(F)	-	-
3	52.1	2	H	15	18	8	22	3	0.8	NT	11	2	(F)	-	-
4	49.2	2	H	18	17	11	14	3	0.9	NT	12	2	(F)	-	-
5	47.8	2	H	18	14	14	18	3	1.0	NT	-	1	(M)	-	-
6	45.0	2	H	18	14	6	16	4	0.6	NT	11	2	(F)	-	-
7	40.3	1	H	17	16	(tissue torn)		2	0.6	NT	13	3	(F)	-	-
8	39.8	2	H	23	18	(tissue torn)		3	0.8	NT	12	1	(M)	-	-
9	36.8	1	H	17	12	9	21	3	0.7	NT	12	2	(F)	-	-
10	27.1	2	M	15	15	(tissue torn)		3	1.0	NT	?	1	(M)	-	-
						West Branch, Tioughnioga River, Homer, New York (OSUM 21929)									
11	48.9	2	M	22	16	6	15	2	1.2	NT	6	3	(F)	-	-
12	43.0	2	H	20	18	6	15	2+	1.0	T	8	1	(M)	-	-
13	40.5	2	H	21	12	4	15	2	1.0	T	11	1	(M)	-	-
						Rocky River, 11 mi N of Sanford, North Carolina (USNM 794929)									
14	56.3	4	H	20	15	7	9	2	0.9	OV	6	-	GF	+	+
15	46.6	2	H	17	12	4	15	3	1.5	OV	6	-	(M)	+	+

* Refers to outer demibranchs of non-gravid specimens.

more abundant in larger streams. The two species often occur together [in the Susquehanna River System], however, and are readily separable" (Clarke and Berg, 1959:29).

This habitat description applies to populations throughout the range of the species. The species most commonly found associated with it are *Elliptio complanata* and, less frequently, *Strophitus undulatus*, *Alasmidonta undulata*, and (in New England and the Canadian Maritime Provinces) *Margaritifera margaritifera*.

Geographical Records

Figure 26

Atlantic Coastal Drainages

Nova Scotia River Systems.—Cumberland Co., Wallace River: 9 mi (14.4 km) S of Pugwash (1960, A. H. Clarke, L. R. Clarke, and A. R. Clarke! (NMC)); Lunenburg Co.: La Have River above Bridgewater (ANSP); Guysborough Co.: St. Mary River, Sherbrooke; Annapolis Co.: Annapolis River, Lawrencetown; Colchester Co.: Stewiacke River, 5 mi (8.0 km) E of Stewiacke (all Athearn and Clarke, 1962).

Petitcodiac River System, New Brunswick.—Petitcodiac River, Petitcodiac, Westmoreland Co. (1967, D. H. Stansbery! (OSUM)); 2 mi (3.2 km) above Salisbury, Westmoreland Co., New Brunswick (1951, H. D. Athearn! (MCZ)).

Renous River System, New Brunswick.—Renous River, Northumberland Co. (MCZ).

Dennys River System, Maine.—Dennys River, Washington Co. (MCZ).

Machias River System, Maine.—Upper Machias River (1961, D. Cameron! (OSUM)).

Penobscot River System, Maine.—Molunkus Stream, 2.4 mi (3.8 km) above Macwahoc, Aroostook Co. (1954, H. D. Athearn! (MCZ)). Mattawamkeag River at Haynesville, Aroostook Co. (1952, A. H. Clarke! (NMC)); and Mattawamkeag, Penobscot Co. (1953, H. D. Athearn! (MCZ)).

Merrimac River System.—Beaver Creek, 2.5 mi (4.0 km) NNE of Pelham, Hillsboro Co., N.H. (1952, H. D. Athearn and A. H. Clarke! (OSUM)). Spicket River, Lawrence, Essex Co., Mass. (MCZ). Shawsheen River, Andover, Essex Co., Mass. (MCZ).

Eastern Massachusetts.—Woburn and Nonesuch Pond, Weston, both Middlesex Co., (both MCZ). Gates Pond, Berlin, Worcester Co. and Abbott Run, North Attleboro, Bristol Co. (both MCZ).

Connecticut River System.—Connecticut River at Turner's Falls, Franklin Co., Mass. (USNM) and Hadley, Hampshire Co., Mass. (MCZ). Westfield River, Westfield, Hampden Co., Mass. (MCZ). Tributary of the South Branch Connecticut River, West Hartford, Hartford Co., Conn. (MCZ).

Passaic River System, New Jersey.—Near Morris Plains, Morris Co. (USNM). Stony Brook, Princeton, Mercer Co. (Ortmann, 1919).

Raritan River System, New Jersey.—North Branch Raritan River, Somerset Co. (ANSP).

Delaware River System.—*Delaware River Drainage*: Delaware River at Columia, Warren Co., N.J. (ANSP); Shawnee, Monroe Co., Pa.; Delaware Water Gap, Monroe Co.; and Northampton Co., Pa. (all Ortmann, 1919); Trenton, Mercer Co., N.J. (ANSP); Bucks Co., Pa. (MCZ; Ortmann, 1919). Paulins Kill, Marksboro, Warren Co., N.J. (ANSP). Lehigh River, Bethlehem, Northampton Co., Pa. (Ortmann, 1919). Big Neshaming Creek near Edderton, Bucks Co., Pa. (ANSP). Pennypack Creek below Valley Falls and near Bethayres, both Montgomery Co., Pa., and Holmesburg, Philadelphia Co., Pa. (all ANSP). Frankford Creek, Philadelphia Co., Pa. (ANSP). White Clay Creek, Avondale, Chester Co., Pa. (Ortmann, 1919). Pickering Creek, Chester Co., Pa. (ANSP, MCZ). Ridley Creek, Delaware Co.; Princess Creek, Kunkletown, Monroe Co.; Lizard Creek, Mantz, Schuylkill Co.; Mahoning Creek, Lehighton, Carbon Co., all Pa. (all Ortmann, 1919). Head of Red Clay Creek, New Castle Co., Del. (ANSP).

Schuylkill River Drainage, Pennsylvania: Manatawny Creek near Earlville, Berks Co.; Maiden Creek, Berks Co.; and Swamps Creek, Zieglerville, Montgomery Co., (all ANSP and Ortmann, 1919).

Susquehanna River System.—*Upper Susquehanna River Drainage, New York*: Unadilla River at Leonardsville, Madison/Otsego Co. (1965, C. B. Stein! (OSUM)); 15 mi (24.0 km) NE of Norwich, Otsego/Chenango Co. (1965, C. B. Stein! (OSUM)). Otselic River, Whitney Point, Broome Co. (1965, E. J. Karlin and C. O. Berg!). Chenango River, Chenango Forks, Broome Co. (Clarke and Berg, 1959). West Branch Tioughnioga River, just N of Homer, Cortland Co., N.Y. (1965, C. B. Stein! (OSUM)); 5.5 mi (8.8 km) N of Cortland, Cortland Co., (Clarke and Berg, 1959). Catatonk Creek below Spencer Lake, Spencer, Tioga Co., (MCZ; Clarke and Berg, 1959); 7 mi (11.2 km) SE of Candor, Tioga Co. (1955, C. O. Berg! (MCZ)); Owego, and 4.5 mi (7.2 km) W of Candor, both Tioga Co. (both Clarke and Berg, 1959).

Lower Susquehanna River Drainage, Pennsylvania: Wyalusing Creek, Stevensville, Bradford Co. (MCZ). Conodoquinet Creek, Carlisle, Cumberland Co. (USNM). Conewago Creek, 10 mi (16.0 km), 8 mi (12.8 km) and 7.5 mi (12.0 km) above Gettysburg, Adams Co. (MCZ; 1957: D. R. Franz! (ANSP)); 1.5 mi (2.4 km) S of, and "near," Boulder, Adams Co. (Ortmann, 1919 and 1952, H. D. Athearn! (MCZ, OSUM)). Muddy Creek, Lancaster Co., Pa. (MCZ). Sinnemahoning Creek, Driftwood, Cameron Co. (Ortmann,

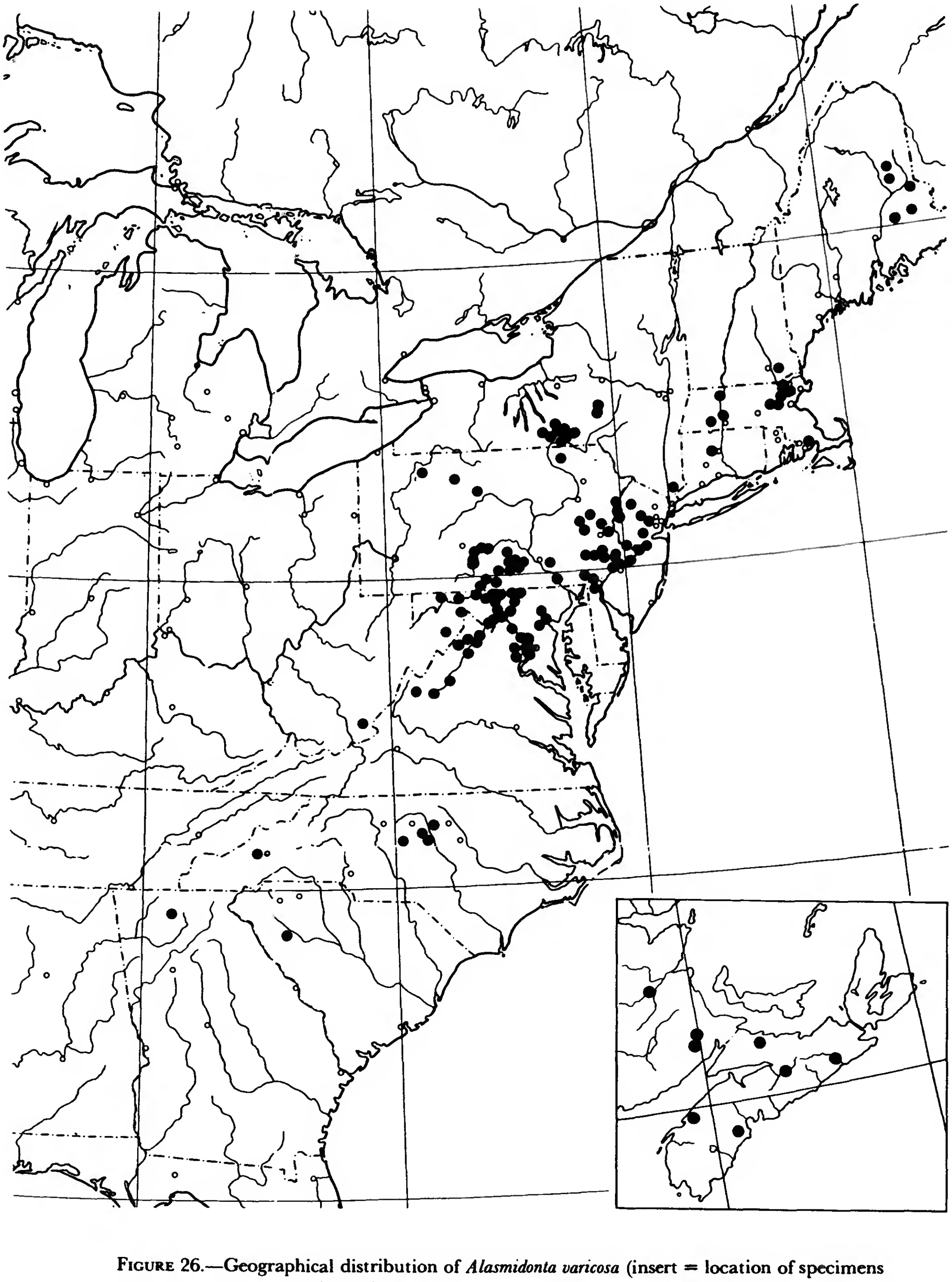

FIGURE 26.—Geographical distribution of *Alasmidonta varicosa* (insert = location of specimens found in New Brunswick and Nova Scotia).

1919); Round Island, Clinton Co. (ANSP). Lancaster, Lancaster Co.; Cush Cushion Creek, Indiana Co. (both Ortmann, 1919). Susquehanna River at Selinsgrove, Snyder Co.; York Haven and "York Furnace," [York], both York Co. (all Ortmann, 1919). Juniata River at Everett, Mount Dallas and Bedford, all Bedford Co., Pa. (all Ortmann, 1919); 1 mi (1.6 km) E of Hollidaysburg, Blair Co. (MCZ). Raystown Branch Juniata River, Huntingdon Co., Pa. (ANSP).

POTOMAC RIVER SYSTEM.—*Upper Potomac River Drainage*: Raystown Creek, 1 mi (1.6 km) W of Breezewood, Bedford Co., Pa. (OSUM). Sideling Creek, Alleghany Co., Md. (ANSP). Wills Creek, Ellerslie, Alleghany Co., Md. (Ortmann, 1919). Lost River, Wardensville, Hardy Co., W. Va. (USNM). Birch Run, Adams Co., Pa. (ANSP). Conococheaque Creek at Greencastle, Scotland, and Mercersburg Junction, Franklin Co., Pa. (all Ortmann, 1919); and Williamsport, Washington Co., Md. (1959, F. W. and G. F. Grimm! (NMC) and 1973, C. B. Stein! (OSUM)). Great Tonoloway Creek, Fulton Co., Pa. (Ortmann, 1919). Tom's Creek, 6.5 mi (10.4 km) and 7.1 mi (11.4 km) SE of Emmitsburg, Frederick Co., Md. (1960, F. W. Grimm! (NMC)). Monocacy River, 12 mi (19.2 km) NNE Frederick, Frederick Co., Md. (1968, H. G. Lee! (OSUM)); 0.5 mi (0.8 km) W of Bridgeport, Frederick/Carroll Co., Md. (1973, C. B. Stein! (OSUM)). South Branch Potomac River, Southbranch, Hampshire Co., W. Va. (Ortmann, 1919). Potomac River at Hancock, Washington Co., Md. (ANSP; 1973, C. B. Stein! (OSUM)); Cherry Run, Morgan Co., W. Va. (ANSP); Harpers Ferry, W. Va. (ANSP) and between Harpers Ferry and Fishers Island, Jefferson Co., W. Va. (1962–65, C. B. Stein! (OSUM)).

Shenandoah River Drainage: North Fork of Shenandoah River, E of Woodstock, Shenandoah Co., Va. (MCZ); 2 mi (3.2 km) SE of Strasburg, Shenandoah Co. (1968, W. J. Clench and D. H. Stansbery! (MCZ)). South River, Waynesboro, Augusta Co., Va. (Ortmann, 1919). South Fork Shenandoah River, Elkton, Rockingham Co., Va. (Ortmann, 1919) and Riverton, Warren Co., Va. (MCZ). Shenandoah River, Clarke Co., Va. (USNM); Milleville, Power Dam, Jefferson Co., W. Va. (USNM); Harpers Ferry, Jefferson Co., W. Va. (ANSP).

Lower Potomac River Drainage: Potomac River at Seneca Falls, Montgomery Co., Md. (USNM); several localities near Great Falls, Maryland and Virginia (MCZ, USNM); High Island, D.C. (USNM). Broad Run, Fairfax Co., Va. (Johnson, 1970). Bull Run, Sudley Church, Prince William Co., Va. (USNM). Occoquan Creek, Prince William Co., Va. (USNM) and 3 mi (4.8 km) W of Manassas, Prince William Co., Va. (Johnson, 1970).

JAMES RIVER SYSTEM, VIRGINIA.—Calf Pasture River (Ortmann, 1919).

CAPE FEAR RIVER SYSTEM, NORTH CAROLINA.—Haw River, 4 mi (6.4 km) ENE of Pittsboro, Chetham Co., Bear Creek, 7 mi (11.2 km) SSW of Pittsboro, (both OSUM). Rocky River, 11 mi (17.6 km) N of Sanford, Chetham (MCZ; Johnson, 1970; 1978, A. H. Clarke and J. J. Clarke (USNM)).

YADKIN RIVER SYSTEM.—Uwharrie River, N.C. (ANSP).

COOPER-SANTEE RIVER SYSTEM.—Catawba River, Bridgewater, Burke Co., N.C. (Ortmann, 1919).

SAVANNAH RIVER SYSTEM.—Turkey Creek, 8 mi (12.8 km) NW of Edgefield, Edgefield Co., S.C. (UMMZ; Johnson, 1970).

Gulf of Mexico Coastal Drainage

COOSA RIVER SYSTEM.—Etowah River, Georgia (ANSP, ex C. M. Wheatley Collection). Locality probably incorrect.

Ohio-Mississippi River Drainage

KANAWAH RIVER SYSTEM.—Greenbrier River, 1 mi (1.6 km) below Fort Spring, Greenbriar Co., W. Va. (1974, K. G. Borror! (OSUM).

***Alasmidonta* (*Decurambis*) *robusta*, new species**

FIGURES 23, 27

THE SHELL

FIGURE 27*a–c*

DESCRIPTION.—Shell subovate, up to about 66 mm long, 43 mm high, and 33 mm wide, rather thin-shelled throughout but not fragile, up to about 2 mm thick anteriorly. Anterior margin well rounded; ventral margin broadly curved (more convex anteriorly than posteriorly); posterior margin terminating in a rounded point below the center and flatly convex and irregular above; and dorsal margin of medium length and curved. Maximum inflation in front of the posterior ridge near the center of the shell. Beaks of medium width, rounded, located about 32% to 39% of the distance from anterior to posterior, and projecting to a variable extent above the hinge line. Posterior ridge well-marked, sharply rounded, becoming more gently rounded near the margin and terminating posterior-ventrally. Posterior slope of moderate width, sharply defined by the posterior ridge, concave proximally and flattened distally.

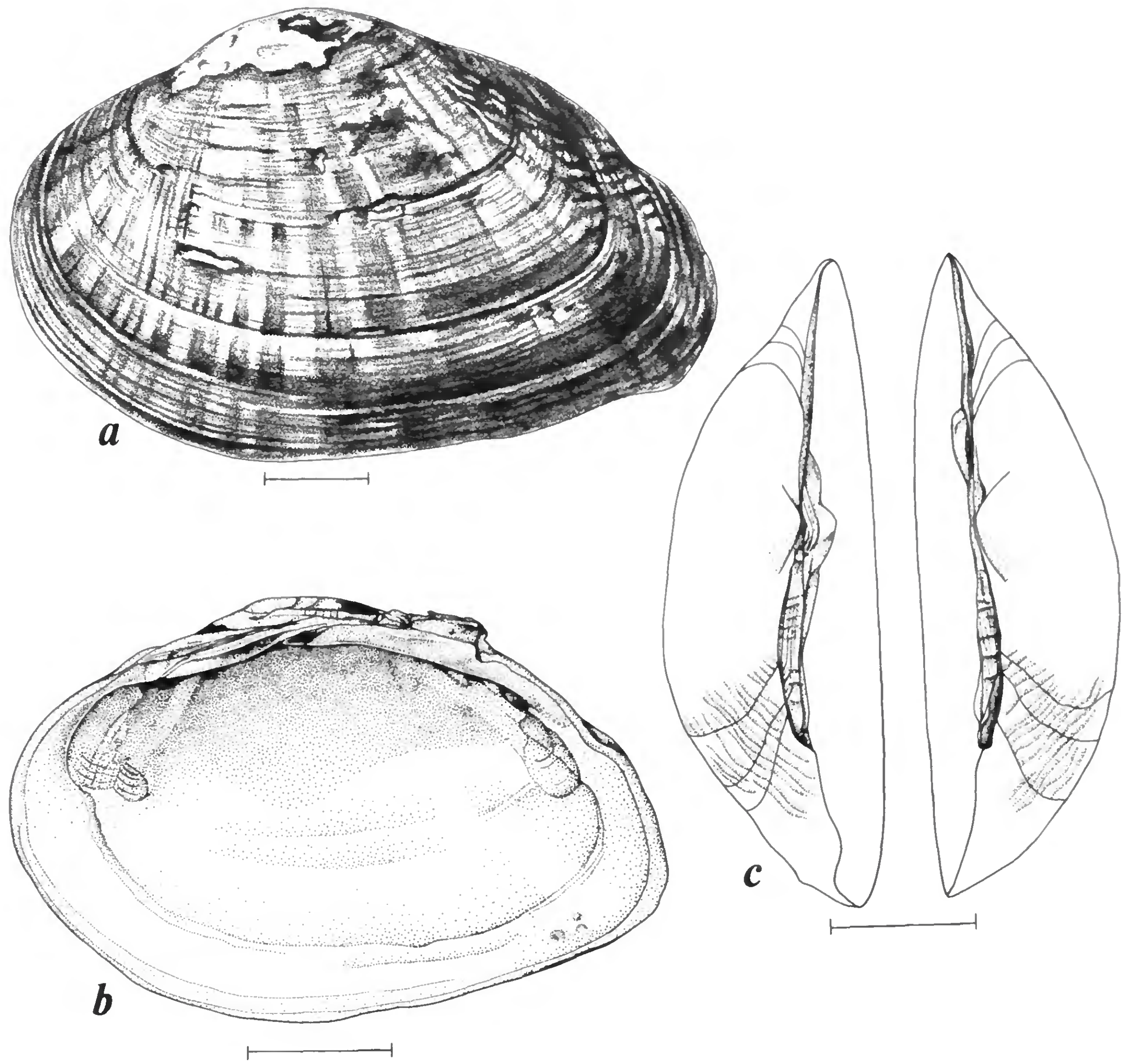

FIGURE 27.—*Alasmidonta robusta*: holotype, ANSP 126755, Long Creek, North Carolina. (Scale = 1 cm.)

Growth increments strongly marked by concentric ridges and grooves but disc otherwise unsculptured. Additional post-juvenile sculpturing consisting of well-developed, diagonal, moderately coarse (about 8 to 15 in 10 mm) corrugations on the posterior slope, approximately perpendicular to the shell margin, and generally distributed over the whole posterior slope. Periostracum smooth and glossy except roughened posteriorly, with clearly visible, extensive, wavy, greenish rays spread over a yellowish brown background. The periostracum is darker in adults but rays are still clearly apparent. Ligament strong, broad, thick, and of medium length.

Hinge teeth incomplete and variable. Pseudocardinal teeth of moderate size, conspicuous, pyramidal, and compressed; one in the right valve, anterior-ventrally directed, and one in the left valve that is confluent with the interdental projection. Interdental projection prominent, long, centrally acute, located in the left valve, more elevated (in most specimens) than the adjacent pseudocardinal tooth, and articulating with a depression in the right valve. Lateral teeth absent and replaced by a single nonarticulating thickening of the hinge plate in each valve. Beak cavities moderately wide and deep. Anterior muscle scars variably shaped, impressed, and bounded by a low, rounded ridge which is decurrent below the pseudocardinal tooth in each valve; pallial line continuous and well-marked; posterior muscle scars shallow but clearly apparent and iridescent, and scars within beak cavity consisting of one or two short, deep grooves on the back of the hinge plate in each valve. Nacre dull or somewhat shiny; bluish or bluish white; and salmon, pinkish, or brownish centrally and in the beak cavity.

Beak sculpture mostly obscure in available material but apparently consisting of a few moderately heavy, concentric, single-looped bars that are angular on the posterior ridge.

TYPES.—The holotype of *A. robusta* is from Long Creek (near Charlotte), Mecklenberg County, North Carolina, originally from the large nineteenth century collection of Charles M. Wheatley. It was later deposited at the University of Pennsylvania and finally in the Philadelphia Academy of Natural Sciences (catalog number 126755). The specimen is 66.0 mm long, 43.0 mm high, 33.2 mm wide (both valves appressed), and the umbones are 25.7 mm from the anterior extremity (measured parallel to the long axis of the shell). There are also four paratypes in the lot (see below). A comparison of *A. robusta* and other species is included under Remarks.

VARIATION.—Measurements of the type lot are given in Table 20.

GEOGRAPHICAL RECORDS

FIGURE 23

The type lot contains the only known specimens of this species. It is probably now extinct. Long Creek is a tributary of the Catawba River, which is part of the Wateree-Santee River System of North and South Carolina.

TABLE 20.—*Alasmidonta robusta*: Shell measurements; specimens from Long Creek, Mecklenburg County, North Carolina (type lot)

Length (mm)	*H/L*	*W/L*	*B-A/L*	*Hp/L*
65.65	0.629	0.498	0.359	0.0565
57.16	0.610	0.446	0.342	0.0621
53.03	0.665	0.466	0.347	0.0578
50.83	0.607	0.432	0.331	0.0521
42.00	0.610	0.436	0.317	0.0607

REMARKS

No information is available about the anatomy, glochidia, or life history of *A. robusta*. About its ecology we know only that it is a localized creek species and that it is now either very rare or extinct. Long Creek traverses an area very close to, and north of, Charlotte, North Carolina. So many of its tributaries have been impounded by dams that it now carries little water. On 29 May 1979, after several days of rain in the area, the main creek channel in a mile-long stretch about 5 miles west northwest of Charlotte carried only 4 to 6 inches of water throughout most of its area. *Corbicula* was common in some depressions and deep channels, and a few empty shells of *Elliptio* and *Lampsilis* show that some unionids may be present. It seems probable that unionid populations would not persist in Long Creek during times of unusual drought and that present populations there, if they exist, are not descended from the same populations that existed there 100 years ago.

The holotype of *A. robusta* bears a striking resemblance to *A. mccordi*. They are similar in shape and size, and are both covered with wide and narrow, wavy, green rays on a yellowish-brown background. They differ markedly in tooth structure, however. *A. mccordi* has strong and unique pseudocardinal teeth, clear remnants of lateral teeth, and no interdental projection. *A.*

robusta has very different pseudocardinal teeth, no remnants of lateral teeth, and a conspicuous interdental projection in the left valve.

Alasmidonta robusta is also similar to some specimens of *A. varicosa*, particularly to those in a lot of unusually large and high specimens collected by C. H. Conner many years ago in Ridley Creek near Philadelphia, Pennsylvania. They differ, however, in that *A. robusta* has a large interdental projection in the left valve; a single, rounded posterior ridge; and mostly wide, wavy, prominent greenish rays even in adult specimens. In *A. varicosa* from Ridley Creek the interdental projection is either absent or vestigial, the posterior ridge has a tendency to be double and rather angular, and the periostracal rays, where visible in adult specimens, are narrow and not wavy.

A. varicosa also occurs in the same drainage system as *A. robusta* and the two species are easily separable. Twelve specimens of *A. varicosa* were collected from the Catawba River at Bridgeport, Burke Co., N.C. by A. E. Ortmann in 1914 (Carnegie Museum, catalog No. 61.7132). They are similar to *A. robusta* except that they lack the prominent interdental projection seen in that species and their shells are thinner, much more quadrate, and their ventral margins are much less convex than in *A. robusta*.

Although *A. robusta* is obviously related to *A. varicosa* and to *A. marginata*, the interdental projection is so striking that one is reminded of the genus *Lasmigona*, in which that feature is characteristic. In 1863 Issac Lea described several unionid species from the Catawba River drainage near Charlotte, North Carolina. One of these was *Unio charlottensis* (now *Lasmigona subviridis* (Conrad, 1834)). Specimens of *Lasmigona* "*charlottensis*," from the vicinity of Charlotte, are up to 116 mm long ((Johnson (1970), also Smithsonian Institution specimens (e.g. USNM 85402)), however, and this is nearly twice as long as the usual maximum length of *L. subviridis* from all other localities. At any rate, *Alasmidonta robusta* differs from *L. subviridis*, (including specimens of *L.* "*charlottensis*") in that *L. subviridis* has well-developed lateral teeth while *A. robusta* has none, in *L. subviridis* the interdental projection is poorly developed while in *A. robusta* it is conspicuous, and the shell in *L. subviridis* is compressed whereas in *A. robusta* it is moderately inflated.

It has been a problem to decide if *Alasmidonta robusta* is specifically distinct from *A. varicosa*. Analysis of a sample of Long Creek water, taken on 29 May 1979 following several days of rain, revealed a total hardness of 40 ppm. Experience has shown that stream water analyzed immediately following substantial rain may be expected to have a much lower $CaCO_3$ concentration than one encounters at the same locality at other times. Therefore, before headwater impoundments were carried out, the average total hardness of Long Creek water may have been much higher than 40 ppm. The fact that *Lasmigona subviridis* from the same area is so large also implies that unusually favorable water quality may occur in the region. (Empty shells of *Elliptio complanata* and *Lampsilis radiata* collected in Long Creek on 29 May 1979, however, were entirely normal.)

Nevertheless, *A. robusta* differs substantially from *A. varicosa*, even when presumably excellent conditions for growth of that species occur, as demonstrated by lots from Ridley Creek and elsewhere. There appears to be no feature of ecology alone that could cause, for example, the interdental projection in *A. varicosa* to become as disproportionately enlarged as we see in *A. robusta*. Significant genetic differences between the taxa are therefore presumed to exist and *A. robusta* is considered a distinct species.

Genus *Arcidens* Simpson, 1900

Arcidens Simpson, 1900:661. [Type-species: *Alasmidonta confragosa* Say, by original designation.]

The glochidium of *Arcidens confragosus* (Figure 31) is pyriform, strongly asymmetrical, with malleated and pitted surfaces and with lingulate stylets that bear about 6 longitudinal rows of major microstylets on both the proximal and the distal halves. The glochidium of *A. wheeleri* is unknown.

Comparative features of the adults are: shells medium-sized to large (about 70–140 mm long), relatively high (H/L >0.70) without sexual dimorphism, with heavy diagonal ridges on the posterior slope and anterior to the posterior ridge, with non-dehiscent periostracum, and with hinge teeth that are well-developed and complete. The anterior-ventral edge of the mantle is not lobate and the mantle edges between the anal and supra-anal openings are fused together.

Subgenus *Arkansia* Ortmann and Walker, 1912, new status

Arkansia Ortmann and Walker, 1912:98. [Type-species: *Arkansia wheeleri* Ortmann and Walker, by original designation.]

The subgenus *Arkansia* is differentiated from *Arcidens* (sensu stricto) by the presence in the former of a lunule; of an anterior pseudocardinal tooth in the left valve, and a pseudocardinal tooth in the right valve, which are both curved and parallel to the lunule; heavy sculpturing only on the posterior half of the shell; and barely perceptible beak sculpturing. In *Arkansia* the external membrane of the outer demibranch is unique: it is openly porous, like a loosely-woven net. The glochidia are unknown.

Arcidens (*Arkansia*) *wheeleri* (Ortmann and Walker, 1912)

FIGURES 28, 29

Arkansia wheeleri Ortmann and Walker, 1912:98, pl. 8. [Type-locality: "Old River [an oxbow of Ouachita River], Arkadelphia, Arkansas." Holotype in the mollusk collection, Museum of Zoology, University of Michigan, Ann Arbor, Michigan, catalog number 105514, labelled "Ouachita Road, 3 miles [4.8 km] above Arkadelphia, Clark Co., Arkansas."]

THE SHELL

FIGURE 28*a,b,e,f*

DESCRIPTION.—Shell quadrate-ovate or subcircular, subinflated, up to about 110 mm long, 73 mm high, and 48 mm wide, moderately heavy, somewhat thickened anteriorly (up to about 6 mm thick) and half as thick posteriorly. Anterior margin broadly rounded and continuing smoothly into the ventral margin, which is also evenly rounded throughout or rounded anteriorly and centrally but flattened posteriorly; posterior margin wide, truncated, oblique, and angular above and below; and dorsal margin long, straight behind the umbones and sharply concave for a short distance below the beaks. When viewed with both valves appressed, this anterior-dorsal depression (the lunule) is round, hemispherical, and unusually well-defined. Maximum inflation near the midline, slightly above the center. Beaks inflated, rounded, inclined forward, and located about 26% to 31% the distance from anterior to posterior, and projecting somewhat above the hinge line. Posterior ridge single or double but low and inconspicuous. Posterior slope rather broad and expanded centrally; the shell has a tendency toward being slightly alate. Growth increments marked by concentric, flattened, annual rings that tend to interrupt the surface sculpturing and numerous fine ridges and grooves. Additional post-juvenile sculpturing consisting of about 3 to 5 broad, rounded, diagonal ridges (similar to those in *Amblema plicata* (Say), but lower) that cross the center and the posterior of the shell; irregular, crowded, flattened tubercles or flattened tubercular ridges that cover the posterior half; and broad, rounded corrugations on the posterior ridge and the posterior slope that cross the lines of growth at a 90° angle, and are interrupted by a flattened, radial groove in the center of the posterior slope. In some specimens the corrugations are reduced and appear as non-aligned swellings. Periostracum chestnut brown, with darker concentric bands, and somewhat lustrous. Ligament dark brown, rather long, and fragile when dry.

Hinge teeth heavy but not entirely complete. The left valve has two strong pseudocardinal teeth. The anterior pseudocardinal is compressed, serrated, and parallel with the sharply defined lunule; the posterior pseudocardinal is pyramidal,

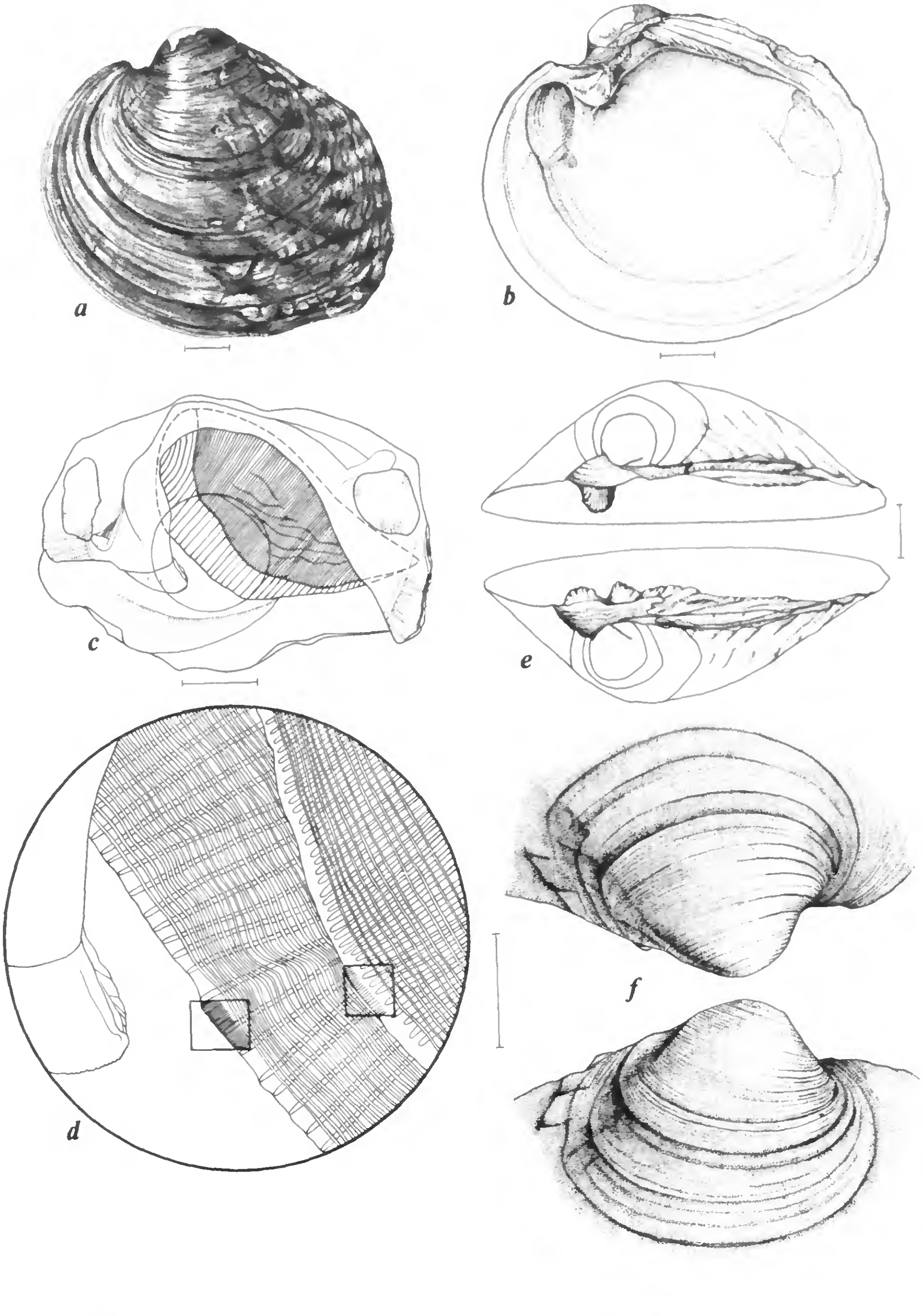

FIGURE 28.—*Arcidens wheeleri*: *a,b,e,f*, USNM 23319, Old River, Arkadelphia, Arkansas (*f* shows umbonal area of best preserved specimen); *c,d*, OSUM 32816, Kiamichi River near Clayton, Oklahoma (*d* is enlargement of circular area indicated in *c*. Scale = 1 cm.)

rounded, thick, irregular, serrated, and not parallel with the lunule. The pseudocardinal teeth are separated by a deep cavity and the posterior member is more or less confluent with a broad, high, arched, serrated, interdental projection. The lateral teeth are double in the left valve and of medium length; the lower lateral is, in fact, confluent with, or an extension of, the interdental projection. The right valve has one heavy, erect, pseudocardinal tooth, convex below and supported by a buttress and concave above and roughly parallel with the lunule, and one strong, straight, lateral tooth of moderate length. Beak cavity excavated, deep, and of moderate width. Anterior adductor muscle scar impressed and rather small, pallial line clearly defined and lightly impressed, posterior adductor muscle scar rather large and well-marked but not impressed, and scars within the beak cavity consisting of 1 to 3 ovate pits on the underside or on the back of the hinge plate. Nacre white or salmon-colored and porcellaneous throughout but iridescent posteriorly. A broad greenish band occurs around the edge where the nacre is thin.

Beak sculpture reduced and fine, consisting of 2 or 3 oblique, double-looped bars that are restricted to the extremity of the beaks and extend only about 4 mm from the umbonal apex. It is visible only on young specimens.

VARIATION.—Table 21 shows that among the material available there is some variation in relative shell dimensions. The largest specimen is relatively the most depressed and the smallest specimen the most elevated (i.e. the most circular) but no clear general trend among other specimens occurs. Relative inflation appears to be inversely related to increased length, however. In most specimens the heavy, diagonal ridges across the middle of the shell are obvious and in other specimens, particularly in young ones, they are obscure.

TABLE 21.—*Arcidens wheeleri*: Shell measurements; specimens from Old River, Arkadelphia, Arkansas (type locality)

Specimen	*Length (mm)*	*H/L*	*W/L*	*B-A/L*	*Hp/L*
Wheeler 1918:112)	109.25	0.796	0.530	–	–
Paratype*	87	0.84	0.55	–	–
MCZ 23319	76.8	0.820	0.548	0.303	0.0956
MCZ 46759	74.9	0.850	0.538	0.274	0.0895
Holotype*	73.5	0.84	0.56	–	–
MCZ 135712	71.1	0.845	0.585	0.292	0.0810
USNM 218946	51.2	0.842	0.578	0.286	0.111
USNM 218946	48.2	0.870	0.560	0.258	0.0854
MCZ 135712	48.0	0.839	0.585	0.297	0.116
Paratype*	35	0.94	0.66	–	–

* Data from Ortmann & Walker, 1912:99.

Wheeler (1918), in describing the nacre of this species, says: "In young shells the entire margin is widely bordered with a rich salmon, in most adults it is a warm cream color, while in some specimens it is an opalescent blue." Normal variation in periostracal color also occurs, the older specimens being the darker.

TOPOGRAPHIC ANATOMY

FIGURE 28*c,d*

SPECIMEN DESCRIBED.—From Kiamichi River, 1.2 mi (1.9 km) SE of Clayton at US Rt. 271 bridge, Pushmataha Co., Oklahoma, collected 22 August 1971 (OSUM 32816.2, D. H. Stansbery!); preserved in 70% ethyl alcohol; length of soft body 66 mm, sex female.

DESCRIPTION.—Mantle pale orange, somewhat translucent in the center, and with color of branchiae and foot showing through. Mantle edge without additional pigment except for a narrow band of pale and dark shades of brown adjacent to the incurrent and anal openings and continuing as an even narrower band around the supra-anal opening. Incurrent opening 11.1 mm long and surrounded by about 3 rows of flattened, small, papillae, the inner papillae the longest (1.1 mm). Separation of the incurrent and anal openings is achieved, at the mantle edge, by appression in life of opposing mantle edges over a very narrow (0.5 mm) distance. The anal opening is 12.1 mm long and is surrounded by a single row of tiny, flattened papillae that are appressed to the sides of the opening and project slightly beyond its edge. The mantle connection between the anal and supra-anal openings is 3.5 mm in length and the supra-anal opening is long (10.3 mm opening, with dorsally expanded edges) and slit-like.

Demibranchs of preserved specimens pale brown. Outer demibranch 43 mm long, 19 mm high, with narrow anterior and posterior extremities and openly curved free margin and with irregular, horizontal wrinkles. The external membrane of the outer demibranch is fragile and porous, appearing more like a closely-woven net (see figure 28*d*) than in any other species seen, with about 11 double sets of radial filaments and about 3½ horizontal cross filaments per mm. The underlying water tubes are thick-walled and number about 3.0 per mm. Inner demibranch 45 mm long, 23 mm high, of the same shape as the outer demibranch but extending beyond it anteriorly (but not reaching the labial palps) and ventrally, and with a few radial wrinkles in the anterior-ventral region. The external membrane of the inner demibranch is also fragile but not so openly porous, and has about 15 double rows of radial filaments per mm, about 2½ horizontal cross filaments, and about 1.0 underlying water tube per mm. The inner laminar of the inner demibranch is not attached to the visceral mass. The diaphragm is split for a short distance at the posterior extremity and perforated there by the open ends of the water tubes.

Labial palps pale brown, wide, flatly curved above, distally rounded below, and pointed above the midline, and with the outer surfaces smooth and the inner surfaces of opposing members radially furrowed (about 5 furrows per mm at margin). The outer palpus is attached to the mantle for ⅔ of its length and the subdorsal interpalpal connection extends for ⅚ of the length of each member.

Variation.—The specimens from the Kiamichi River are the only ones available for anatomical study and they show little variation. They agree in general with Ortmann and Walker's (1912:97–98) description except for some details. In the material examined, the mantle connection between the anal and supra-anal opening is no more than half as long as the anal opening (Table 22); Ortmann and Walker state that A-SA is a little shorter than, or somewhat longer than, the anal opening. The labial palps in one of our three specimens touches the inner demibranchs; according to Ortmann and Walker they do not touch. There is also some variation in strength of mantle pigmentation among Kiamichi River specimens; mantle pigmentation is not mentioned by Ortmann and Walker.

No glochidia from *A. wheeleri* have been available for study and nothing has been published regarding them.

Life History

Nothing is known about the timing or duration of the gravid period of *A. wheeleri*, or about its natural hosts.

Wheeler (1918:112–3) has described Old River, the type locality of *A. wheeleri*, as follows: "Old River . . . is really an ox-bow lake, a former channel of the Ouachita, and is still connected to it by a small creek which does not appear to dry up in summer. Its mouth is about two miles north of Arkadelphia on the left bank, almost lost in a rather dense and difficultly passable swamp. Here, and for a mile or more upstream, Old River is deep and rather wide, with a very sluggish current. In this habitat are found very large specimens of *Anodonta suborbiculata* Say, which are of great beauty, and the largest specimens of *Arkansia wheeleri* Walker and Ortmann [*sic*]. One of the latter measured 109.25 by 87 by 58 mm. In the summer "Half-Moon Lake," the upper channel of Old River, is set off by the subsidence of water on the sand bars, and through the narrow creek which connects it with its lower course it is quite impossible to navigate even a small canoe. Young *Arkansia* are found in the shallow waters both on the sand bars and muddy bottoms, but like other anodontine species they prefer the oozy mud of the river margins where there is little or no current."

Mr. Mark Gordon, a graduate student at the

TABLE 22.—*Arcidens wheeleri*: Variations in topographic anatomy; specimens from Kiamichi River, 1.2 mi SE of Clayton, Oklahoma (OSUM 32816) (abbreviations same as Table 4)

Spec. No.	Length (mm)	Mantle pigmentation: Extent	Mantle pigmentation: Strength	Relative lengths of mantle features (as % of L): Inc.	Anal	A-SA	SA	Incurrent papillae: Ranks	Max. ht. (mm)	Labial palps: Posit.	Grooves per mm	Water tubes N/mm*	Sex	Pre-preserv. treatment: Nemb. relax.	Form. fixed
1	72.6	Inc. Op.	M	19	12	6	17	2	1.1	T	7	2.5	(F)	–	–
2	66.0	Inc. Op.	M	17	12	5	16	3	1.1	N	5	3	(F)	–	–
3	43.0	Inc. Op.	W	18	16	6	14	2	1.0	N	7	3	(F)	–	–

* Refers to outer demibranchs of non-gravid specimens.

University of Arkansas, visited Old River in May 1979 and found the locality now much the same as it was when described by Wheeler. No *Arkansia* were found and high water prevented a more thorough search.

Geographical Records

FIGURE 29

OUACHITA RIVER SYSTEM.—Old River, an oxbow of Ouachita River, near Arkadelphia, Clark Co., Ark. (type-locality) (ANSP, MCZ, USNM). Ouachita River below Arkadelphia (Wheeler, 1918).

RED RIVER SYSTEM.—Kiamichi River, 1.2 mi (1.9 km) SE of Clayton, Pushmataha Co., Okla. (1971, D. H. Stansbery! (OSUM)) and 8.5 mi (13.6 km) NE of Hugo at Spencerville Crossing, Choctaw Co., Okla. (1968, B. Valentine! (OSUM)). Little River, Whitecliffs, Stevier Co.-Little River Co. boundary, Ark. (ANSP).

Subgenus *Arcidens* Simpson, sensu stricto

Arcidens (sensu stricto) may be distinguished from the subgenus *Arkansia* by (in the former) the absence of a lunule, the presence of pyramidal, dorso-ventrally compressed pseudocardinal teeth that are not curved, by heavy sculpturing over nearly the entire surface, and very heavy, pustulous, beak sculpturing. The outer demibranch is not openly porous. The glochidia are pyriform, markedly asymmetrical, and otherwise unusual (see text).

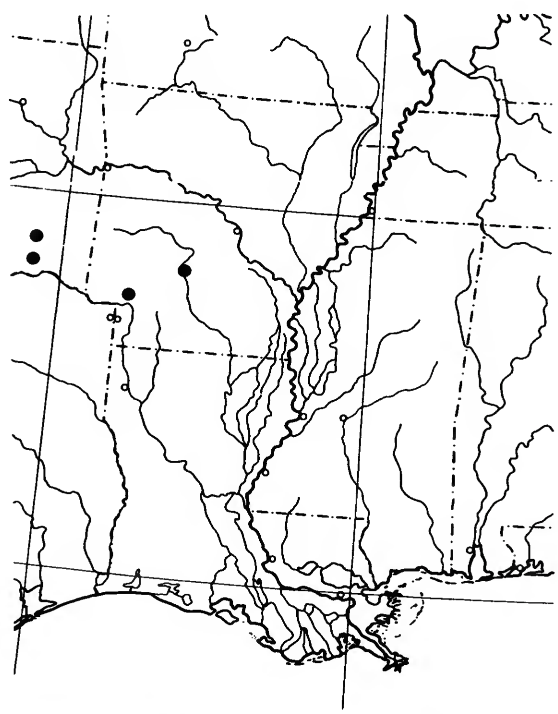

FIGURE 29.—Geographical distribution of *Arcidens wheeleri*.

Arcidens (*Arcidens*) *confragosus* (Say, 1829)

FIGURES 30–32

Alasmidonta confragosus Say, 1829:339; 1831, pl. 21. [Type-locality: "A side stream of the Wabash, called Fox River [Indiana] . . . [and near] New Orleans [Louisiana]." The latter locality was emended by Say in 1832 to "Bayou Teche in the Parish of St. Mary, Louisiana" [see Binney, 1858:195]. Type-material not in Academy of Natural

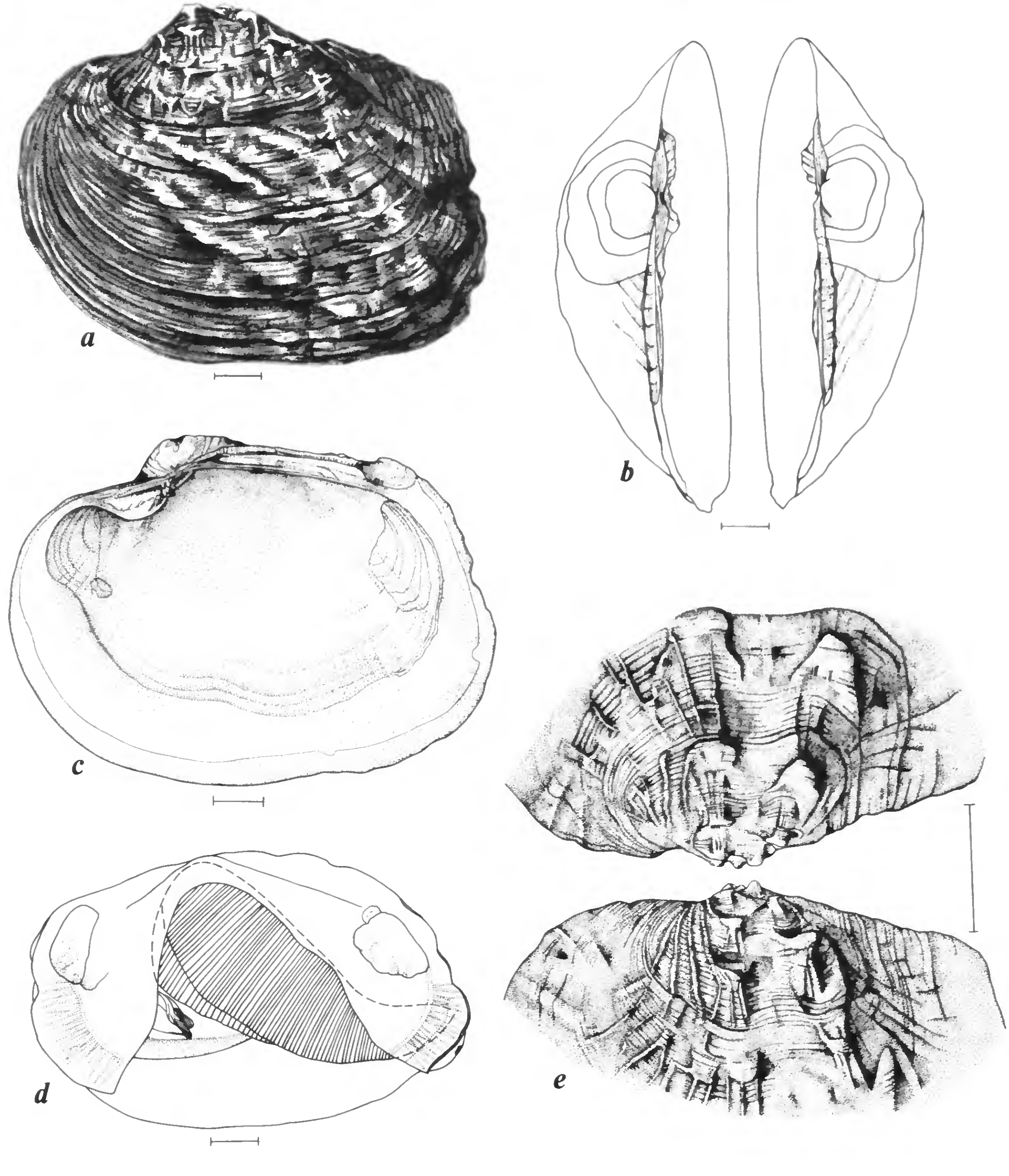

FIGURE 30.—*Arcidens confragosus*: *a-c*, USNM 746008, Mississippi River, York Landing, Iowa; *d*, OSUM 13128, Mississippi River near Burlington, Iowa; *e*, details of beak sculpturing, USNM 540167, Mississippi River, Muscatine, Iowa. (Scale = 1 cm.)

Sciences of Philadelphia (Johnson and Baker, 1973) and presumably lost.]

Arcidens confragosa jacintoensis Strecker, 1931. [Type-locality: San Jacinto River, Texas. Type material in Baylor University Museum, Waco, Texas.]

The Shell

FIGURE 30*a,b,c,e*

DESCRIPTION.—Shell moderately heavy, inflated, and ovate-rhomboid, up to about 144 mm long, 95 mm high, and 66 mm wide, slightly thickened anteriorly (up to 10 mm thick) and about half as thick posteriorly. Anterior margin round, ventral margin flattened or slightly concave posteriorly, posterior margin broadly and roundly pointed below and obliquely flattened above, and dorsal margin long and flatly curved. Maximum width near the center of the shell. Beaks inflated, full, located about 30% to 32% the distance from anterior to posterior, and projecting well above the hinge line. Posterior ridge variable, angular or rounded, and well defined above but becoming obscure below. Posterior slope covered with narrow and wide, low radial ridges perpendicular to the lines of growth. Growth increments marked by wide, concentric, dark bands and by crowded, fine, ridges and grooves. Additional post-juvenile sculpturing very heavy and variable consisting of two radial rows of nodules extending to the middle of the shell (continuations of the beak sculpturing, see below), 4 to 6 broad, diagonal folds extending across the central third of the shell, and numerous, short, rounded radial ridges over nearly the whole surface. Only the lower part of the anterior disc is principally unsculptured. Periostracum greenish and obscurely rayed in juveniles and becoming dark brown (chestnut colored) in adults. Ligament long, thick, and dark brown.

Hinge teeth thick, strong, and dorsoventrally compressed. Pseudocardinal tooth in right valve protuberant, rounded on the lower surface, flattened on the upper, and buttressed below. Anterior pseudocardinal tooth in left valve compressed and sharp, flatly rounded or rounded on the lower surface, flat on the upper, serrated, and also buttressed below. Posterior pseudocardinal tooth coalesced with interdental projection and forming a single, irregular, heavy, and sharp projection under the beak. Lateral teeth of moderate thickness but variable, short, indistinct and incomplete, numbering 1 to 3 in each valve. Beak cavity broad, excavated, and deep. Anterior muscle scars impressed but shallow, pallial line also shallowly impressed, wavy, and intersected from above or crossed by crowded, fine radial grooves; posterior muscle scars shallow and poorly defined; and scars within beak cavity consisting of 2 or 3 small, variable, deep pits located principally, or entirely, deep within the cavity and on the back of the hinge plate. Nacre silvery white and lustrous throughout but not iridescent. A broad yellowish or greenish band occurs along the margin where the nacre becomes thin.

Beak sculpture very heavy and composed of two radial rows of heavy, raised loops (in the form of V-shaped tubercles) that extend far out on the shell and numerous, narrow, radial grooves and ridges posterior to the tubercles and extending onto the posterior slope. Early ridges obliterated in old specimens but distal elements of beak sculpture that continue onto the disc are perennial features.

VARIATION.—*A. confragosus* is quite constant in its morphology. There is some variation in hinge plate thickness (see Table 23) and in the strength and extent of sculpturing. Specimens from Pigeon Creek, Chandler, Indiana (USNM 677485) are heavily sculptured with plicae and irregular, mostly radial, ridges over the whole outer surface whereas some specimens from the Mississippi River (e.g. from Lynxville, Wisconsin, USNM 745921) are nearly smooth. Young specimens tend to be decidedly greenish and more mature specimens are brownish or nearly black. Baker (1928:198) has pointed out that, as in other species, specimens from small streams tend to be more compressed than those from large rivers. The largest specimen, a single left valve from near Burlington, Iowa, is 144.20 mm long, 94.75

TABLE 23.—*Arcidens confragosus*: Shell measurements.

Length (mm)	*H/L*	*W/L*	*B-A/L*	*Hp/L*
Mississippi River near Marquette, Iowa (USNM 54003)				
112.55	0.682	0.498	0.316	0.0548
109.20	0.724	0.487	0.306	0.0582
102.50	0.721	0.479	0.327	0.0653
96.93	0.758	0.505	0.336	0.0892
93.05	0.757	0.463	0.332	0.0715
87.45	0.798	0.490	0.320	0.0619
Illinois River, Dividing Ridge Twp., Calhoun Co., Ill. (USNM 756505)				
87.65	0.698	0.456	0.260	0.0513
84.85	0.698	0.477	0.312	0.0802
83.60	0.713	0.505	0.301	0.1065
80.30	0.682	0.455	0.281	0.0810

mm high, 33.10 mm in single valve convexity, and 38.00 mm in B-A measurement.

TOPOGRAPHIC ANATOMY

FIGURE 30*d*

SPECIMENS DESCRIBED.—From Mississippi River, 1 mi (1.6 km) S of Burlington, Iowa in Henderson Co., Ill. (OSUM 13128, D. H. Stansbery, et al!); preserved in 70% ethyl alcohol; shell removed, body length 93.0 mm, sex female, gravid.

DESCRIPTION.—Mantle of preserved specimen pale brown and somewhat translucent. A narrow, brown pigmented band occurs along the posterior edge and, in the vicinity of the posterior mantle openings, it is adjacent to their edges. The incurrent opening is 17 mm long and surrounded just within by a dark, pigmented band and about 3 ranks of narrow, pale brown, pyriform or filiform papillae, the inner papillae the longest, i.e., up to 1.5 mm long. The separation of the incurrent and anal openings is achieved in life both by the diaphragm and by appression of the mantle edges over a short (0.5 mm) distance. The anal opening is 6 mm long, with darkly pigmented areas within, and surrounded below the edge by a single row of very short (0.2–0.3 mm) rounded papillae. The mantle connection between the anal and supra-anal openings is short (3.0 mm) and the supra-anal opening is long (15 mm), without papillae, and bordered by lamellate mantle edges that extend 7 mm anterior-dorsally beyond the opening.

Demibranchs of preserved specimen pale brown. Gravid outer demibranch 68 mm long, 26 mm high, and 7 mm thick, fragile, padlike, with free margins rounded anteriorly and posteriorly and more flatly curved centrally and with low radial wrinkles. Outer membrane with about 10 double radial filaments and three horizontal cross-filaments per mm; glochidia-filled radial water tubes about 1 per mm. Inner demibranch 64 mm long, 26 mm high, subtruncated and somewhat oblique anteriorly, flatly curved ventrally, and obliquely narrowing posteriorly to a point. Inner demibranch extending 4 mm beyond the outer demibranch anteriorly but posteriorly it is overlapped by the outer demibranch. Outer membrane also with about 10 double radial filaments and 3 horizontal cross-filaments per mm. Inner lamina of inner demibranch attached to visceral mass only along its anterior third. Diaphragm strongly ridged and perforated by the open ends of the water tubes.

Labial palps pale brown, distally overlapping both the inner and outer demibranchs, broadly curved ventrally, more or less straight dorsally, and with a posterior-dorsal point; outer distal edges rolled outward. Outer surfaces smooth and inner surfaces of opposing members radially furrowed (about 5 furrows per mm). Outer member diagonally attached to the mantle for about half its length and subdorsally attached to the inner member for half of its free length.

VARIATION.—Since only two specimens with soft parts are available little can be said about variation. In the figured specimen the labial palpi do not touch the inner demibranchs. Otherwise, the specimens examined agree with the descriptions by Ortmann (1912:284–5) and Baker (1928: 197).

GLOCHIDIUM

FIGURE 31

DESCRIPTION.—Glochidium pyriform, asymmetrical, 0.360 mm high, 0.359 mm long, 0.115

TABLE 24.—*Arcidens confragosus*: Variation in topographic anatomy; specimens from Mississippi River, 1 mi S of Burlington, Iowa (abbreviations same as Table 4)

Spec. No.	Length (mm)	Mangle pigmentation: Extent	Mangle pigmentation: Strength	Relative lengths of mantle features (as % of L): Inc.	Anal	A-SA	SA	Incurrent papillae: Ranks	Max. ht. (mm)	Labial palps: Posit.	Grooves per mm	Water tubes N/mm*	Sex	Pre-preserv. treatment: Nemb. relax.	Form. fixed
1	93.0	1	W	18	6	3	16	3	1.5	OV	5	-	GF	-	-
2	52.0	1	M	15	9	7	22	3	0.9	OV	6	-	GF	-	-

* Refers to outer demibranchs of non-gravid specimens.

mm single valve convexity. The posterior margin is much more protuberant and rounded than the anterior, but the posterior portion of the glochidial shell, seen in basal view, is markedly less inflated than the anterior. The apex is located about 44% of the distance from anterior to posterior (measured parallel to the hinge axis). The surface is finely malleated (depressions irregular or subcircular and about 4–12 μm wide) and even more finely pitted (pits 1–4 μm wide and located within the depressions) except for the distal apical areas (about 40 μm high) and the edges of the valves that are slightly irregular but not pitted. The apex is also sculptured with concentric curved lines subparallel with the apical margin. Hinge 0.234 mm long, convex centrally but flattened near each end. Ligament narrow (about 5 μm wide) and about 0.220 mm long and apparently in two sections, the posterior portion about 0.100 mm long and separated from the 0.060 mm long anterior section by an interligamental space about 0.060 mm long. It is actually continuous, however, but the central part is hidden by the convex edge of the shell.

Each apical stylet is flatly reflexed and is about 0.100 mm long, 0.024 mm wide at the base and spatulate in form, with a blade-like rounded apex. It is supported on each side, for about ¾ of its length, by a lamellate cartilagenous structure, an expansion of the narrower membrane that projects inward from the whole free edge of each valve. Except for the distal extremity the exposed surface of the stylet is covered with about 75 major microstylets oriented in oblique rows and overlapping somewhat in the manner of shingles on a roof, directed toward the distal end of the stylet, and each about 12 μm in length. The microstylets are principally pyramidal in shape but a few located near the point of the stylet exhibit one or two longitudinal ridges. Other, smaller, pyramidal microstylets (about 2 μm high) occur near the base of the stylet and continue as micropoints (<0.5 μm) onto the ventral edge of the valves and on the supporting membrane.

The glochidium described is from an adult collected in the Mississippi River, 1 mi (1.6 km) S of Burlington, Iowa, on 15 September 1964 by D. H. Stansbery, J. J. Jenkinson, and T. A. Balding (OSUM 13128). In another glochidium from the same adult the microstylets are somewhat less numerous and appear soft, as if in a stage of incomplete development.

LIFE HISTORY

BREEDING SEASON.—"Bradytictic, probably [gravid] from September to June. 'Gravid with active glochidia the latter part of January and with late embryos in the middle of March. Sterile in July and August' (Utterback)" (Baker, 1928: 197).

The gravid specimens reported in this paper were collected on 15 September 1964.

NATURAL HOSTS.—Fuller (1974) gives the following fishes as hosts for *Arcidens confragosus*: American eel, *Anguilla rostrata* (Lesueur); gizzard shad, *Dorosoma cepedianum* (Lesueur); rock bass,

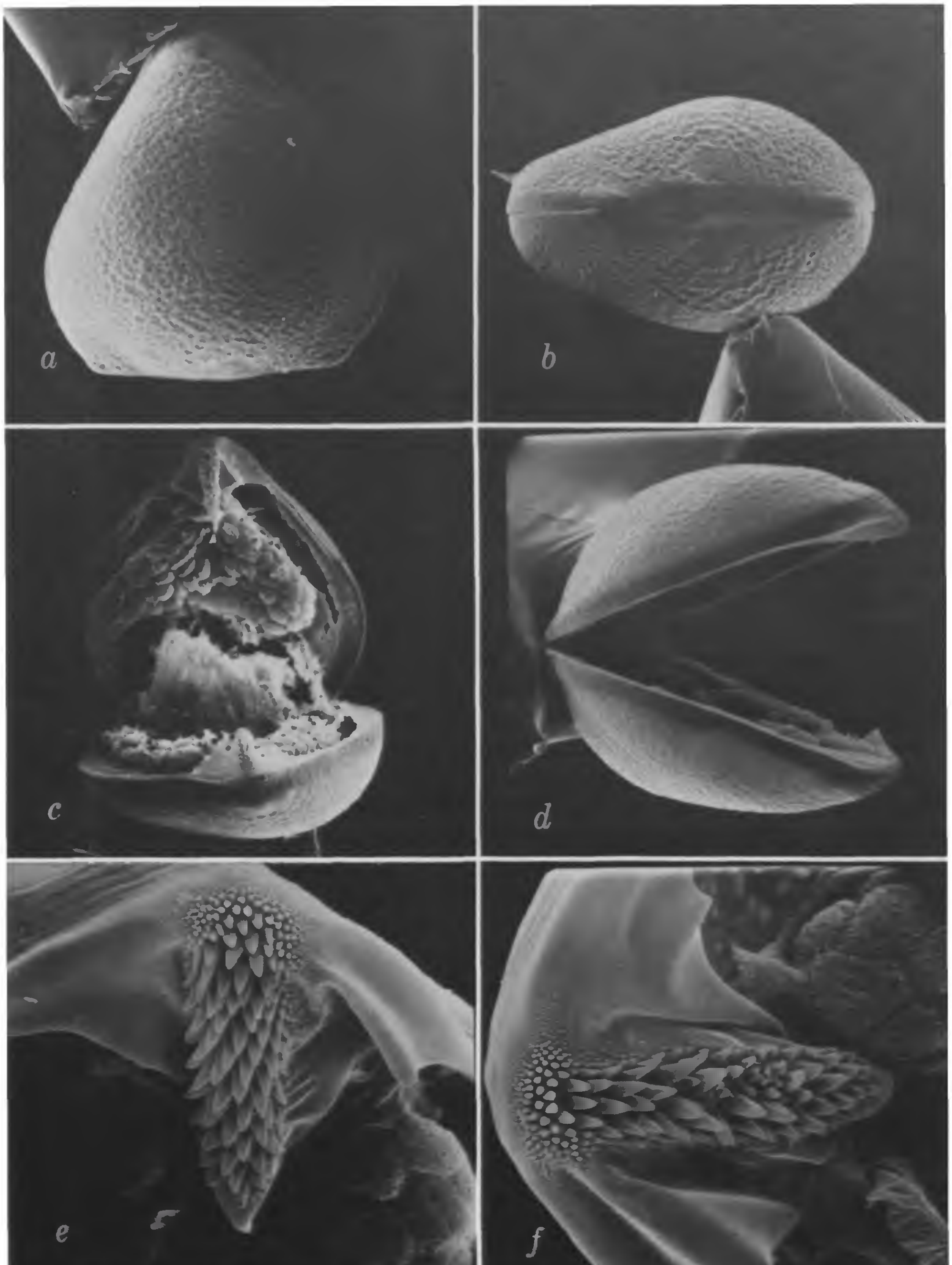

FIGURE 31.—Glochidia of *Arcidens confragosus*: *a-f*, OSUM 13128, (location same as 30*d*). (*a,b,d* × 155; *c* × 130; *e* × 615; *f* × 635.)

Ambloplites rupestris (Rafinesque); white crappie, *Pomoxis annularis* (Rafinesque); and freshwater drum, *Aplodinotus grunniens* (Rafinesque).

HABITAT.—According to Baker (1928:197) this species occurs on sand or mud bottoms, in water a few feet deep, in rapid currents. The species is characteristic of, but not restricted to, large rivers.

GEOGRAPHICAL RECORDS

FIGURE 32

Interior Basin River Systems

OHIO RIVER SYSTEM.—*Green River Drainage, Kentucky:* Green River at Glenmore, 12 mi (19.2 km) N of Bowling Green, Warren Co. (1972, D. H. Stansbery, et al! (OSUM)); 16 mi (25.6 km) ESE of Morgantown, Butler/Warren Co. (1969, D. H. Stansbery and C. B. Stein! (OSUM)).

Rough River Drainage: Rough River at Dundee, Ohio Co., Ky. (MCZ).

Mud River Drainage, Kentucky: Mud River, 3 mi (4.8 km) W of Diamond Spring, Logan Co. (OSUM); Rectors Bridge, 3 mi (4.8 km) E of Dunmar, Muhlenberg Co. (MCZ).

Pigeon Creek Drainage, Indiana: Pigeon Creek, Chandler, Warrick Co. (USNM); Evansville, Vanderburgh Co. (USNM).

Wabash River Drainage: White River at Martin Co., Ind. (1964, C. B. Stein! (OSUM)); West Fork White River, Marysville, Davies Co., Ind. (1967, C. B. Stein! (OSUM)); East Fork White River, 0.5 mi (0.8 km) below Shoals, Martin Co., Ind. (OSUM). Fox River, Richland Co., Ill.; Little Wabash River, Carmi, White Co., Ill. (both MCZ). Wabash River, 7 mi (11.2 km) N of Mt. Carmel, Ill. in White River Township, Knox Co., Ind. (OSUM); New Harmony, Posey Co., Ind. (USNM, MCZ).

Sangamon River Drainage: Sangamon River at Springfield, Sangamon Co., Ill. (MCZ).

TENNESSEE RIVER SYSTEM.—Kentucky Lake of Tennessee River, 6 mi (9.6 km) above New Johnsville, Benton Co., Tenn. (1964, D. H. Stansbery! (OSUM and MCZ)).

UPPER MISSISSIPPI RIVER SYSTEM.—*Main Mississippi River Drainage:* Mississippi River at Red Wing, Goodhue Co., Minn. (USNM); Vermilion Slough, 7 mi (11.2 km) NW of Red Wing (USNM); Dreshback, Winona Co., Minn. (USNM); 2 mi (3.2 km) SSW of La Crosse, La Crosse Co., Wisc. (1977, M. Havlik! (OSUM)); Prairie du Chien, Crawford Co., Wisc. (1976, M. Havlick! (OSUM; USNM); Baker, 1928); Mouth of Harper's Slough, Crawford Co., Wisc. (USNM); Lynxville, Crawford Co., Wisc. (USNM); Prescott, Pierce Co., Wisc. (USNM); Genoa, Vernon Co., Wisc. (USNM); Feuley's Landing; Grant Co., Wisc. (USNM); 8 mi (12.8 km) below Lansing, Allamakee Co., Iowa (USNM); McGregor Island, Clayton Island, York Landing, N of Marquette, and opposite Sny Magill (all Clayton Co.), Iowa (all USNM); 7 mi (11.2 km) SE of Guttenberg, Clayton Co., Iowa; Pine City and Wilkins Island, both Dubuque Co., Iowa (all USNM): 1.2 mi (1.9 km) N of Bellevue, Jackson Co., Iowa (1977, E. Perry! (OSUM)); Eroys Landing, Jackson Co., Iowa; Savanna, Carroll Co., Ill.; Mouth of Elk River, Clinton Co., Iowa (all USNM); Clinton Co., Iowa (MCZ); Lyons, Clinton Co., Iowa and Albany, Whiteside Co., Ill. (both USNM); Davenport, Scott Co., Iowa (ANSP); Princeton, Scott Co., Iowa (USNM and 1968, I. Baumgarth! (OSUM)); Muscatine, Muscatine Co., Iowa (OSUM; USNM); Rock Island, Rock Island Co., Ill. (1976, E. Perry, et al! (OSUM)); Moline, Rock Island Co., Ill. (MCZ, USNM); near Cordova, Rock Island Co., Ill. (OSUM); New Boston, Mercer Co., Ill. (USNM); Parker's Landing, Louesa Co., Iowa (USNM); Burlington Island, Des Moines Co., Iowa (USNM); rapids, 1.5 mi (2.4 km) S. of Montrose, Lee Co., Iowa (USNM); Dallas, Hancock Co., Ill. (USNM); 2 mi (3.2 km) N of Nauvoo Island, Hancock Co., Ill. (USNM); below Burlington, Des Moines Co., Iowa (1964, D. H. Stansbery, et al! (MCZ)); Benton Slough, Henderson Co., Ill. (MCZ); Warsaw, Hancock Co., Ill. (MCZ); Quincy, Adams Co., Ill. (MCZ); 3 mi (4.8 km) S of Hannibal, Ralls Co., Mo (USNM); ¼ mi (0.4 km) below Peark, Pulaski Co., Ill. (USNM); Baton Rouge, E. Baton Rouge Parish, La. (MCZ).

Minnesota River Drainage: Minnesota River, 2.8 mi (4.5 km) SSW of Bloomington, Hennepin Co., Minn. (1977, D. H. Stansbery, et al! (OSUM)).

Rock River Drainage: Pecotonica River, Ill. (MCZ).

Illinois River Drainage: Illinois River at Peru, La Salle Co. (MCZ); many sites between Peoria, Peoria Co. and junction with Mississippi River (1966, W. Starrett, et al!; Starrett, 1971); Peoria, Peoria Co. (OSUM); Liverpool, Fulton Co. (USNM; Starrett, 1971); Quiver Lake and Havana, both Mason Co. (both Starrett, 1971); Frederick, Schuyler Co. (Starrett, 1971); Meredosia, Morgan Co. (MCZ); Naples and Pearl, both Pike Co. (both Starrett, 1971); below Hardin, Calhoun Co. (USNM).

Kaskaskia River Drainage, Illinois: Flat Branch of Kaskaskia River, Humbolt, Coles Co. (OSUM). Kaskaskia River, Washington Co. (MCZ).

Grand River Drainage: Grand River, Clinton, Henry Co., Mo. (ANSP).

Marais des Cygnes River Drainage: Marais des Cygnes River, 3 mi (4.8 km) E of Ottawa, Franklin Co., Kan.

Osage River Drainage: Osage River 5 mi (8.0 km) N of Schell City, Bates/Vernon Co., Mo. (1964, C. B. Stein! (OSUM).

Meramec River Drainage: Meramec River, 2.7 mi (4.3 km) SSE of Fenton, St. Louis/Jefferson Co., Mo. (OSUM).

LOWER MISSISSIPPI RIVER SYSTEM.—*St. Francis River Drainage:* St. Francis River, Poinsett Co., Ark. (OSUM).

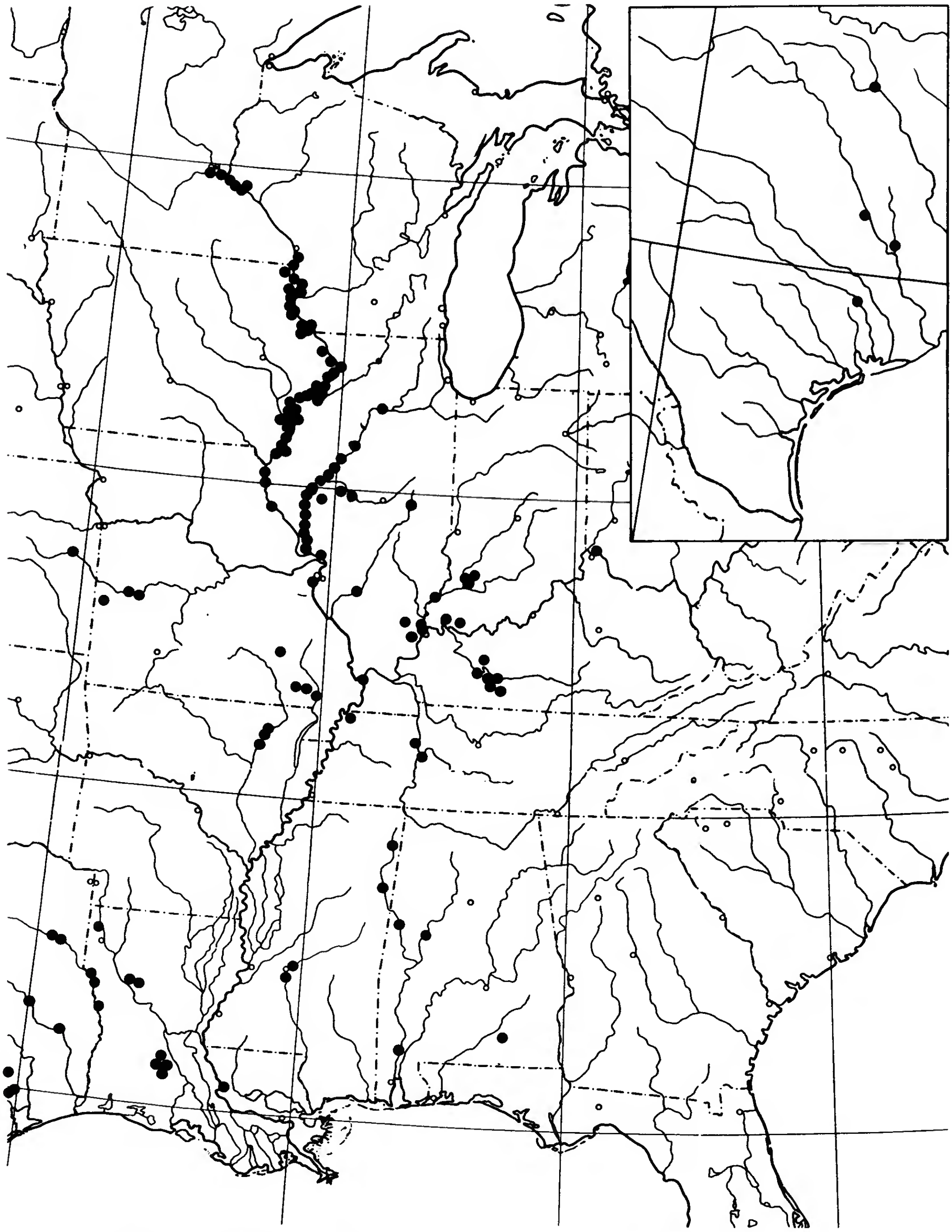

FIGURE 32.—Geographical distribution of *Arcidens confragosus* (insert = locations of specimens found in central Texas.)

Reelfoot Lake Drainage: Reelfoot Lake, Obion Co., Tenn. (ANSP).

Black River Drainage: Black River, W of Hendrickson, Butler Co., Mo. (1964, C. B. Stein! (OSUM)); Pocahontas, Randolph Co., Ark. (1964, C. B. Stein!); Kincaid Bar, Randolph Co., Ark.; Black Rock, Lawrence Co., Ark. (both USNM).

Red River Drainage, Louisiana: Frierson Mill, De Soto Parish (USNM). Saline Bayou, 7 mi (11.6 km) E of Natchitoches, Natchitoches Parish (1964, J. E. Allen! (OSUM)).

Atchafalaya River Drainage, Louisiana: Bayou des Glaises, NE of Opelousac, St. Landry Parish (1964, C. B. Stein, et al! (OSUM)). Bayou Waukasha, 3 mi (4.8 km) SW of Lebeau, St. Landry Parish (1953, H. D. Athearn! (MCZ, NMC)). Arm of Atchafalaya River, 10 mi (16.0 km) SE of Lebeau (1964, R. I. Johnson and C. B. Stein! (MCZ)).

Gulf of Mexico River Systems

Choctawatchee River System.—Double Bridge Creek, Enterprise, Coffee Co., Ala. (USNM).

Mobile River System.—*Tombigbee River Drainage:* East Fork, Tombigbee River, 11.3 mi (18.1 km) S of Fulton, Itawamba Co., Miss. (1974, J. D. Williams, et al! (OSUM)). Tombigbee River, 9.6 mi (15.4 km) NW of Columbus, Lowndes Co., Miss. and 4 mi (6.4 km) S of Pickensville, Pickens Co., Ala. (both 1974–1975, J. D. Williams, et al! (OSUM)). Black Warrior River, 5.8 mi (9.3 km) SE of Eutaw, Greene Co., Ala. (1975, J. D. Williams, et al! (OSUM)).

Main Mobile River Drainage: Bayou Mache, Mobile River, 30 mi (48.0 km) N of Mobile, Mobile Co., Ala. (MCZ).

Pearl River System, Mississippi.—Pearl River, Jackson, Hinds Co. (ANSP, MCZ, USNM).

Sabine River System.—Sabine River, 13.5 mi (21.6 km) W and 10.0 mi (16.0 km) SW of Marshall, Harrison Co., Tex. (1964, C. B. Stein! (OSUM)); Logansport, DeSoto Parish, La. (MCZ and 1964, C. B. Stein! (OSUM)); 10.5 mi (16.8 km) W of Zwolle, Sabine Parish, La. (1964, C. B. Stein, et al! (OSUM)).

Neches River System, Texas.—*Angelina River Drainage:* Angelina River, Angelina Co. (1972, H. Kemper, et al! (OSUM)).

Main Neches River Drainage: Neches River, 18 mi (28.8 km) E of Woodville, Tyler Co. (1964, R. Long! (OSUM)).

Trinity River System, Texas.—Trinity River, Dallas, Dallas Co. (MCZ).

San Jacinto River System, Texas.—*Main San Jacinto River Drainage:* West Fork San Jacinto River, 4.5 mi (7.2 km) S of Conroe, Montgomery Co. (1960, D. H. Stansbery! (OSUM)).

Buffalo Bayou Drainage: Buffalo Bayou, Houston, Harris Co. (USNM); near Eureka, Harris Co. (MCZ).

Brazos River System, Texas.—*Brazos River Drainage:* Brazos River, Cameron, Milam Co. (USNM).

Navesota River Drainage: Navesota River, 2.3 mi (3.7 km) NW of Navesota, Grimes Co. (1968, C. Boone! (OSUM)).

Colorado River System, Texas.—Colorado River (USNM). Skull Creek, Colorado Co. (USNM).

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Front matter (preceding the text) should include: **title page** with only title and author and no other information, **abstract page** with author/title/series/etc., following the established format, **table of contents** with indents reflecting the heads and structure of the paper.

First page of text should carry the title and author at the top of the page and an unnumbered footnote at the bottom consisting of author's name and professional mailing address.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but with no other preparation (such as all caps or underline). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or formal, numbered table heads.

Formal tables (numbered, with table heads, boxheads, stubs, rules) should be submitted as camera copy, but the author must contact the series section of the Press for editorial attention and preparation assistance before final typing of this matter.

Taxonomic keys in natural history papers should use the alined-couplet form in the zoology and paleobiology series and the multi-level indent form in the botany series. If cross-referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa with their corresponding heads in the text.

Synonymy in the zoology and paleobiology series must use the short form (taxon, author, year:page), with a full reference at the end of the paper under "Literature Cited." For the botany series, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in the "Literature Cited") is optional.

Footnotes, when few in number, whether annotative or bibliographic, should be typed at the bottom of the text page on which the reference occurs. Extensive notes must appear at the end of the text in a notes section. If bibliographic footnotes are required, use the short form (author/brief title/page) with the full reference in the bibliography.

Text-reference system (author/year/page within the text, with the full reference in a "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all scientific series and is strongly recommended in the history and technology series: "(Jones, 1910:122)" or ". . . Jones (1910:122)."

Bibliography, depending upon use, is termed "References," "Selected References," or "Literature Cited." Spell out book, journal, and article titles, using initial caps in all major words. For capitalization of titles in foreign languages, follow the national practice of each language. Underline (for italics) book and journal titles. Use the colon-parentheses system for volume/number/page citations: "10(2):5–9." For alinement and arrangement of elements, follow the format of the series for which the manuscript is intended.

Legends for illustrations must not be attached to the art nor included within the text but must be submitted at the end of the manuscript—with as many legends typed, double-spaced, to a page as convenient.

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A few points of style: (1) Do not use periods after such abbreviations as "mm, ft, yds, USNM, NNE, AM, BC." (2) Use hyphens in spelled-out fractions: "two-thirds." (3) Spell out numbers "one" through "nine" in expository text, but use numerals in all other cases if possible. (4) Use the metric system of measurement, where possible, instead of the English system. (5) Use the decimal system, where possible, in place of fractions. (6) Use day/month/year sequence for dates: "9 April 1976." (7) For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc.

Arrange and paginate sequentially EVERY sheet of manuscript—including ALL front matter and ALL legends, etc., at the back of the text—in the following order: (1) title page, (2) abstract, (3) table of contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes, (8) glossary, (9) bibliography, (10) index, (11) legends.