The Tribe Alasmidontini (Unionidae: Anodontinae), Part II: *Lasmigona* and *Simpsonaias*

ARTHUR H. CLARKE

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ABSTRACT

Clarke, Arthur H. The Tribe Alasmidontini (Unionidae; Anodontinae), Part II: *Lasmigona* and *Simpsonaias*. *Smithsonian Contributions to Zoology*, number 399, 75 pages, 22 figures, 14 tables, 1985.—The taxonomy, morphology, life history, and distribution of eight species and subspecies, comprising two genera, are described. As in Part 1, discussions of morphology include descriptions of the shell, anatomy, and glochidium (where possible) of each species and subspecies, and of character variation, together with statistical tables, illustrations, and scanning electron micrographs. Distributional data include organized lists of all specimens in the major museum collections, with distribution maps, and with special reference to recently collected material that is likely to represent living populations. Species and subspecies recognized are: *Lasmigona* (*Alasminota*) *holstonia* (Lea), *L.* (*Lasmigona*) *costata* (Rafinesque), *L.* (*L.*) *complanata complanata* (Barnes), *L.* (*L.*) *complanata alabamensis*, new subspecies, *L.* (*Platynaias*) *compressa* (Lea), *L.* (*P.*) *subviridis* (Conrad), *L.* (*P.*) *decorata* (Lea), and *Simpsonaias ambigua* (Say). Addenda provide additional information about some of the species included in Part 1 of this monograph, including a description and SEM micrographs of the glochidia of *Alasmidonta* (*Decurambis*) *varicosa* (Lamarck).

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Contents

The Tribe Alasmidontini (Unionidae: Anodontinae), Part II: *Lasmigona* and *Simpsonaias*

Arthur H. Clarke

Introduction

This is the second and final part of a taxonomic monograph on the Tribe Alasmidontini (Family Unionidae, Subfamily Anodontinae), an endemic group of North American freshwater mussels. Part I of this study, treating the genera *Pegias*, *Alasmidonta*, and *Arcidens*, was published in 1981 as *Smithsonian Contributions to Zoology*, number 326.

As in the first part, the sequence in which species and species groups are discussed is based on my estimate of phylogenetic relationships. Although extensive information is now available about the morphology of adult shells and glochidia, topographic anatomy, ecology, and distribution of the 22 species and subspecies that are discussed, I do not wish to attempt constructing a phylogenetic tree at this time. Comparative information is still lacking about topographic anatomy in 6 species and subspecies, and about glochidial morphology in 9. The identity of the natural host(s) of 16 species and subspecies is also unknown. Further, there is almost a complete lack of information about biochemical and internal anatomical characters. That is unfortunate because, as demonstrated by several recent studies (e.g., Davis and Fuller, 1981; Kat, 1983), such information offers new and useful insights into phylogenetic relationships.

It is significant that 9 of the species discussed in Parts I and II appear to be either threatened, endangered, or recently extinct. These are: *Pegias fabula*, *Alasmidonta heterodon*, *A. maccordi*, *A. wrightiana*, *A. raveneliana*, *A. robusta*, *Arcidens wheeleri*, *Lasmigona decorata*, and *Simpsonaias ambigua*. The need for further studies on the survival status of these species, and for formulation of programs for the protection of those that are endangered, is clearly evident.

The specimen records listed are principally those from the collections of the Academy of Natural Sciences of Philadelphia (ANSP); the Carnegie Museum (CM); 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); the University of Michigan Museum of Zoology (UMMZ); and the Museum of the Wisconsin Geological and Natural History Survey, University of Wisconsin (MWGNH).

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shell exterior of *Simpsonaias ambigua*, Ms. Julia Kelly for technical assistance, Ms. Mary Jacque Mann and Ms. Susann Braden for making the scanning electron microscope photographs of most of the species, and Ms. Juel Rembert for typing part of the manuscript. The SEM micrographs of *Alasmidonta varicosa* were made by Mr. Edward Sellick of Harvard University. My wife Judith also deserves thanks for her frequent field assistance and for her forbearance. Valuable specimens for this study were also provided by J.B. Bates, R.G. Biggins, S.M. Call, Sally E. Dennis, G.J. Fallo, David Lenat, H.A. Mathiak, D.G. Smith, and D.H. Stansbery. Several museum curators have also assisted by providing access to collections under their care, viz, K.J. Boss, J.B. Burch, G.M. Davis, C.G. Cruchy, R.I. Johnson, J.J. Parodiz, Muriel F.I. Smith, D.H. Stansbery, and Ruth D. Turner. R.I. Johnson also read a draft of the manuscript and provided useful criticism. I also wish to thank Mr. S. Dillon Ripley and the Trustees of the Smithsonian Institution for the generous financial support that made most of this work possible. Final preparation of the manuscript and illustrations, and acquisition of information given in the Addenda, were funded by ECOSEARCH, Inc.

Genus *Lasmigona* Rafinesque, 1831

Symphynota Lea, sensu Simpson (1900:662; 1914:480), Ortmann (1914:42) and other authors. [*Symphynota* Lea, 1829, is a junior synonym of *Proptera* Rafinesque, 1818, because both have the same type-species (*Unio alatus* Say). See Frierson, 1914b:40.]

Lasmigona Rafinesque, 1831:4. [Type-species *Alasmodon rugosum* Barnes, 1823 by subsequent designation of Simpson, 1900; = *Lasmigona* (*L.*) costata.]

Amblasmodon Rafinesque, 1831:4. [Type-species, by monotypy, "*Alasmodon* [sic] *hians* (*Amblasmodon hians*)."]

[?]*Sulcularia* Rafinesque, 1831:4. [Type-species: "*Alasm. badium* (*Sulcularia badia* disc. 1821.)" by subsequent designation of Frierson (1914a).]

Pterosyna Rafinesque, 1831:5. [Type-species, by original designation: "*A*[*lasmodon*] *complanata* Say"; = *Alasmodonta complanata* Barnes, 1823.]

Amblasmadon.—Rafinesque, 1831:5. [Lapsus calami for *Amblasmodon* Rafinesque.]

[?]*Megadomus* Swainson, 1840:265, 378. [Type-species, by original designation: "*M*[*egadomus*] *gigas*" Swainson, 1840 (= *Unio gigas* Swainson, 1824), both nomen dubia.]

Complanaria Swainson, 1840:228, 290, 382. [Type-species by original designation: *C*[*omplanaria*] *gigas* Swainson, 1840 (= *Alasmidonta complanata* Barnes).]

Elasmogona Agassiz, 1846:583. [Unjustified emendation of *Lasmigona* Rafinesque, 1831.]

Elasmigena.—Herrmannsen, 1852:49. [Lapsus calami for *Elasmogona* Agassiz, 1848.]

Pterosygna Simpson, 1900:665. [Lapsus calami for *Pterosyna* Rafinesque, 1831.]

Alasminota Ortmann, 1914:42. [Type-species: *Symphynota* (*Alasminota*) *holstonia* (Lea), by original designation.]

Platynaias Walker, 1918:2. [Type-species, by original designation, "*Symphynota compressa* Lea."]

REMARKS.—The glochidia of five species of *Lasmigona* are known (*L. costata*, *L. complanata*, *L. compressa*, *L. subviridis*, and *L. holstonia*). All are pyriform or triangular-ovate, asymmetrical, with malleated and pitted surfaces and with stylets that are linguate and bear numerous (~ 75+) microstylets or narrowly acuminate and with fewer (~ 25–60) microstylets.

Comparative features of the adult are (1) shell moderately small to large (about 60 to 200 mm long), (2) of moderate to large relative height (H/L about 0.51–0.75), (3) compressed or of only moderate inflation, with dorsal alation in most species, and (4) monoecious (hermaphroditic) or dioecious with or without mild sexual dimorphism. Post-juvenile sculpturing absent in four species but present in two, in which it is comprised principally of corrugations on the posterior slope. Beak sculpturing in *Lasmigona* is principally double-looped whereas in *Alasmidonta* it is principally single-looped. Periostracum is closely adherent. Both psuedocardinal and lateral teeth may be present or the lateral teeth may be reduced or absent but in all species a prominent or moderately prominent interdental projection exists. The mantle edges between the anal and supra-anal openings are normally fused together and, in contrast to *Alasmidonta*, the inner demibranchs are entirely, or principally, free from the visceral mass.

Subgenus *Alasminota* Ortmann, 1914

[?]*Sulcularia* Rafinesque, 1831:4. [Type-species: "*Alasm. badium* (*Sulcularia badia* disc. 1821.)" by original designation.

As shown below under *Lasmigona holstonia*, the identity of "*Alasm. badium*" is uncertain. *Sulcularia* is therefore a nomen dubium.]

Alasminota Ortmann, 1914:42. [Type-species: "*Symphynota (Alasminota) holstonia* (Lea)" [=*Margaritana holstonia* Lea, 1836], by original designation.]

REMARKS.—The glochidia of *Lasmigona holstonia* are ovate-pyriform, with convex adapical sides, height about 0.300 mm or somewhat less, with length approximately equal to height, with acuminate stylets each bearing few (~ 25–30) microstylets, with exterior epiapical micropoints, and with a conspicuous, long larval thread.

Comparative features of the adults are: the shells are rather small (up to about 60 mm long), without a dorsal alation, of medium relative height (H/L about 0.51–0.64), without radial sculpturing on the posterior slope, with poorly developed lateral hinge teeth or without lateral hinge teeth, and with double-looped beak sculpturing. The single included species is dioecious. The supra-anal mantle opening is shorter than the anal opening.

No other species within the Alasmidontini is known to have a larval thread, but such a structure does occur in the closely related genus *Anodonta* and in the genera *Margaritifera*, *Unio*, and *Elliptio* (Lillie, 1895; Lefevre and Curtis, 1912: 151). Since no features appear to contradict, I conclude that *Lasmigona holstonia* is the most primitive living species of *Lasmigona*, and probably the most primitive living species in the Alasmidontini.

Lasmigona (Alasminota) holstonia (Lea, 1838)

Figures 1–3

[?]*Alasm*[*odon*] (*Sulcularia*) *badium* Rafinesque, 1831:5. [Type-locality: "Small streams of the Knobs, rare." Type specimens apparently lost. Identification uncertain; see "Remarks."]

Margaritana holstonia Lea, 1838:42, pl. 13: fig. 37. [Type-locality: "Holston River" (USNM 86320).]

Margaritana etowaensis Conrad, 1849:154. [Type-locality: "Etowah River." Type specimen lost (Johnson and Baker, 1973:155).]

Margaritana etowahensis Lea, 1858:138 [without figure]. [Type-locality: "Tennessee" and "Etowah River, Georgia." Figured later by Lea (1859:227, pl. 31: fig. 110). Type specimen USNM 86259.]

Margaritana georgiana Lea, 1859, errata. [New name for *Margaritana etowahensis* Lea, 1858, considered preoccupied by *M. etowaensis* Conrad, 1849.]

Alasmodon impressa Anthony, 1865:157, pl. 12: fig. 4. [Type-locality: "Tennessee." Holotype is MCZ 150666 (Turner, 1946:102).]

Unio holstonianus Sowerby, 1868, pl. 76, species 398. [An unjustified emendation or lapsus calami for *Margaritana holstonia* Lea.]

THE SHELL

FIGURE 1*a*, *c–e*

DESCRIPTION (Holston River drainage specimens).—Shell long ovate or ovate-lenticular, moderately inflated, and unsculptured, up to about 61 mm long, 34 mm high, and 22 mm wide. Slightly thicker anteriorly (up to 1.5 mm thick) and thinner posteriorly (0.8 mm). Anterior margin sharply rounded, ventral margin broadly rounded near its extremities but flattened centrally, posterior margin sharply rounded below and obliquely subtruncated above, and dorsal margin broadly curved throughout or slightly indented in front of the beaks. Maximum inflation at a point a little above the middle of the shell. Beaks slightly inflated, located about 26% to 34% the distance from anterior to posterior, and projecting slightly above the hinge line. Posterior ridge rounded, not clearly defined below but contrasting above from the narrow posterior slope that is traversed by two radial ridges with a shallow groove between them.

Growth increments marked by shallow, concentric grooves over which the periostracum is darker than elsewhere. Additional post-juvenile sculpturing consisting only of low, concentric lines and ridges of growth. Periostracum yellow, yellowish brown, or brownish and with mostly obscure, narrow, radial greenish or brown rays over part or all of the shell surface (or absent entirely) and with one or two darker rays on the ridges of the posterior slope. Unlike most species, juveniles are not more conspicuously rayed than adults. Ligament pale brown to dark brown, of moderate length and thickness, and brittle when dry.

Hinge teeth only partially developed. Pseudo-

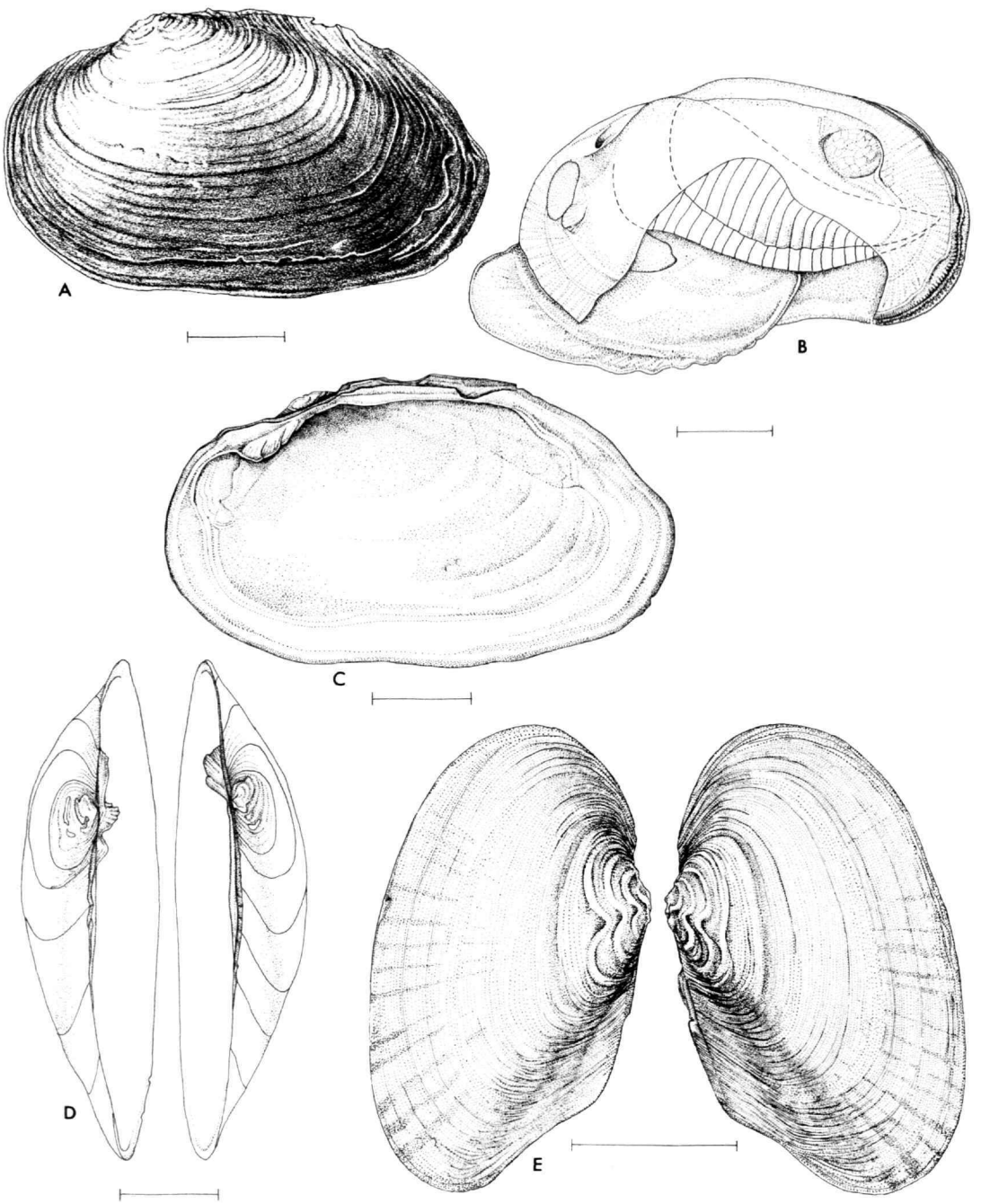

FIGURE 1.—*Lasmigona holstonia: a,c,d*, USNM 86323, Lea's Spring, Blount County, Tennessee; *b*, USNM 801973, headwaters of Holston River, Virginia; *e*, details of umbonal area, USNM 341418, South Fork Pistol Creek, Maryville, Blount County, Tennessee. (Scale = 1 cm.)

cardinal teeth fairly thick and strong: the right valve has 1 moderately large, flattened, elevated tooth, serrated and (in some specimens) distally bilobed or jagged, and directed anterio-ventrally; the left valve has 2 rather small, compressed, sublamellate, elevated and irregular teeth which are also directed anterior-ventrally. A small, flange-like interdental projection also occurs in the left valve where it is partly confluent with the posterior pseudocardinal. Lateral teeth absent or indicated by 1 or 2 poorly defined ridges close to the umbones in each valve. Beak cavity excavated but shallow, with small, variable, irregular muscle scars within, and with a shallow radial groove (corresponding to the lower ridge on the posterior slope) running from it toward the mid-posterior margin. Major anterior muscle scars rather small and impressed, especially on their proximal sides; pallial band distinct, impressed anteriorly and more lightly etched posteriorly or only lightly etched throughout, and crossed by numerous fine radial lines; posterior muscle scars of moderate size and lightly etched but clearly visible in most specimens. Nacre whitish anteriorly and bluish white posteriorly, only moderately shiny in most specimens but posteriorly iridescent in some. Around the margin the nacre is thin and the color of the periostracum shows through.

Beak sculpture double-looped, of moderate strength, variable, and consisting of about 6 concentric ridges. The first is very small, single-looped, and oblique, the second has a shallow re-entering sinus and is also oblique (i.e., expanded more anteriorly than posteriorly), and the third and subsequent ridges are strongly double-looped, each with a broadly rounded anterior loop and a more narrowly rounded posterior loop, and (except for the sinus) the central, elevated parts are more or less parallel with the lines of growth. The narrow extremities of these ridges curve back sharply toward the umbone. In some specimens the sinuses are so deep that they intersect the preceeding bars while in other specimens the sinuses are shallow and cause the bars to undulate only centrally and to be almost single-looped.

VARIATION—Table 1 provides an indication of the variability in relative dimensions of *L. holstonia*. Coefficients of variability for relative height (H/L) ranged from 3.1 to 4.3 in the samples measured, for relative obesity (W/L) they ranged from 5.4 to 7.6, and for relative position of the umbones $\left(\frac{B\text{-}A}{L}\right)$ they ranged from 8.9 to 9.8.

Although no other trends were evident, a positive correlation between L and W/L appeared to exist. The presumed correlation was therefore evaluated by use of the Spearman Rank Coefficient (Siegel, 1956). The sequence of longest to shortest specimens was compared with the sequence of greatest to least relative inflation in each sample. The values compared are: (Station Creek sample) 1½, 1; 1½, 9; 3, 3; 4, 2; 5, 19; 6, 10½; 7, 8; 8, 5; 9, 4; 10, 13; 11, 10½; 12, 14½; 13, 5; 14, 16; 15½, 12; 15½, 14½; 17, 7; 18, 18; 19, 17; (Gatlin Brook sample) 1, 5; 2, 3½; 3, 14; 4, 1; 5, 10; 6, 13; 7, 11; 8, 8½; 9, 2; 10, 8½; 11, 3½; 12, 12; 13, 16; 14, 15; 15, 18½; 16, 22; 17, 6; 18, 18½; 19, 17; 20, 7; 21, 21; 22, 20; 23, 24; 24, 23; (Armuchee Creek sample) 1, 10; 2, 17,

TABLE 1.—*Lasmigona holstonia:* shell measurements.

Feature	N	Range	Mean ($\bar{x}$)	S
	Station Creek, Lee Co., Va.; date? B. Walker!, MCZ 30233			
Length (mm)	19	17.9–48.8	35.9	7.33
H/L	19	0.574–0.645	0.619	0.0190
W/L	19	0.298–0.422	0.369	0.0280
B-A/L	19	0.235–0.334	0.285	0.0263
	Gatlin Brook, Bradley Co., Tenn.; 29 May 1956, H.D. Athearn!, MCZ 222463			
Length (mm)	24	20.0–57.7	41.2	9.37
H/L	24	0.510–0.615	0.580	0.0250
W/L	24	0.289–0.408	0.358	0.0273
B-A/L	24	0.222–0.295	0.259	0.0231
	Armuchee Creek, Floyd Co., Ga. 11 Aug 1956, H.D. Athearn!, MCZ 222459			
Length (mm)	23	16.6–55.1	43.7	8.28
H/L	23	0.522–0.616	0.570	0.0223
W/L	23	0.319–0.396	0.365	0.0196
B-A/L	23	0.219–0.307	0.265	0.0261

3, 13; 4, 21; 5, 15; 6, 5; 7, 22; 8, 2; 9, 4; 11, 9; 11, 14; 11, 19½; 13, 3; 14, 18; 15, 1; 16, 16; 17, 19½; 18, 8; 19, 12; 20, 6½; 21, 11; 22, 6½; 23, 23;

The results showed that L and W/L for Station Creek sample were correlated at the 90% level of confidence ($r_s = 0.564$, $t = 2.816$), for the Gatlin Brook sample the correlation was at the 99% level ($r_s = 0.700$, $t = 4.598$), and for the Armuchee Creek sample there was no correlation ($r_s = 0.06$; $t = -0.2755$). The meaning of this diversity of correlation is not clear but it may be related to differences in the amount of constancy of food supply among the localities. At any rate it provides another caveat against proposal of morphological correlations in unionids based on less than comprehensive evidence.

Other variable features include periostracum (pale yellowish brown to blackish brown) and nacre color (white to bluish and with suffusions of salmon or yellow near the beak cavity). The shape and relative strength of the pseudocardinal teeth and the interdental projection are also somewhat variable and appear to be related to shell thickness that, in turn, may be related to water temperature and hardness as in *Alasmidonta undulata* (see Clarke, 1981). Insufficient data are available to test for such a relationship in this species, however.

Topographic Anatomy

Figure 1*b*

Specimen Described.—USNM 801973, from the headwaters of the Holston River, Virginia, collected by Ms. Sally Dennis, October, 1979; relaxed with propylene phenoxetol, fixed in 10% formalin and preserved in 70% ethyl alcohol; shell length 46.1 mm, sex female (gravid, with glochidia).

Description.—Mantle whitish and translucent, especially within the muscular border, and revealing the purplish demibranches within. Foot white; adductor muscles yellowish white. Muscular border of mantle about 7 mm wide and 0.8 mm thick all around and with numerous whitish radial muscle strands visible in the posterior portion. A narrow, continuous, pale, purplish brown, pigmented band begins mid-ventrally and continues posteriorly along the outer edge of the inner lip of the mantle and becomes broader (0.5 mm) along the posterior mantle openings. Another narrow (0.2 mm), irregular broken, regionally double brownish band occurs along the outer edge of the outer mantle lip near the posterior mantle openings.

Incurrent opening 14.6 mm long, with an irregular band (about 1.0 mm wide) of purplish brown pigment along the inner margin, and with a single to double row of pale papillae on the margin and just within it. Papillae digitate, about 0.8 mm long and 0.2 mm wide at the base, and single, bifid, or trifid in shape. Similar papillae have not been seen in other species. Portions of mantle edges between incurrent and anal opening 2.2 mm long. Anal and supra-anal openings continuous, not separated by a mantle connection. The lower (anal) portion (9.7 mm long) is broader, has crenulated margins, and is broadly pigmented with purplish brown within.

Outer demibranch 30.2 mm long, 7.5 mm high, engorged with glochidia throughout except in its posterior (7.5 mm long) portion, with its free ventral margin broadly and irregularly curved, of nearly the same height throughout but a little narrower posteriorly, and with abrupt, subtruncated extremities. There are about 1.8–2.0 water tubes per mm, and 10 surficial radial filaments and 4 cross-filaments per mm. Inner demibranch about 32.0 mm long, 12.8 mm high, broadly truncated anteriorly and regularly narrowing posteriorly, and extending about 2 mm beyond the outer demibranch anteriorly and 5 mm anterior-ventrally. It has about 0.6–0.8 water tubes per mm and about 10 surficial, radial filaments and 3 cross-filaments per mm. The inner lamina of the inner demibranch is attached to the anterior third of its interface with the visceral mass but not attached along the posterior two-thirds of that interface.

Labial palpi rounded below, somewhat

rounded above, and with up-turned tips (Figure 1*b*). They barely touch the inner demibranch. The outer surface of each palpus of each pair is smooth but the inner surface of each opposing member is radially furrowed (about 5 furrows per mm). The outer palpus of each pair is fused anteriorly to the mantle and subdorsally, for about ¾ its length, to the inner palpus.

VARIATION.—*Lasmigona holstonia* is variable in several features, as shown in Table 2. The specimen described in detail above is apparently anomalous in the absence of a mantle connection between the anal and supra-anal openings, since all other specimens seen have a connection, and the presence of a connection is also reported by Ortmann (1914:43). The anal openings of Ortmann's specimens were crenulated, as in the specimen described above, but in the specimens enumerated in Table 2 crenulations were absent.

Bifid and trifid incurrent papillae were observed in the described specimen but among the specimens reported in Table 2, except for specimen 3, which had a few bifid papillae, no split papillae were seen. In all specimens tabulated the inner demibranchs were entirely free from the visceral mass.

GLOCHIDIUM

FIGURE 2*a–f*

DESCRIPTION.—Glochidium ovate pyriform, 0.280 mm in height and in length, 0.183 mm in convexity (both valves together). The valves are slightly asymmetrical: The posterior margin is a little more convex than the anterior, the apices are placed about 46% of the distance from anterior to posterior, and the area of maximum inflation is somewhat posterior of center. Surface of glochidium finely malleated and pitted except for a band, about 12 μm wide (20 μm wide near the apices), around the margin of each valve. The malleate depressions, which are from about 6 to 10 μm in diameter, are joined to form a series of about 20 irregular and shallow undulations, arranged concentrically around a point

TABLE 2.—*Lasmigona holstonia:* variation in topographic anatomy

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 in OD (N/mm)	Sex	Pre-preserv. treatment: Nemb. relax.	Form. fixed
	Mud Creek, 1 mi SE of Olinger, Lee Co., Va. D.H. Stansbery! 19 Sep 1967 (OSUM 22481)														
1	42.0	2	M	25	17	6.2	12	1–2	1.1	OV	7	2.3	(F)	–	–
2	40.5	1	W	28	15	6.9	13	2–3	1.3	OV	6	grav.	GF	–	–
3	40.4	1	M	30	16	5.2	13	1–2	1.2	OV	8	1.0	(M)	–	–
4	38.2	1.5	M–H	26	13	7.3	12	1–2	1.0	OV	7–8	3.3	(F)	–	–
5	36.5	1.5	M	30	16	5.5	15	2	1.1	OV	6	1.8	(F)	–	–

Terminology:

Mantle Pigmentation: Extent = anterior extent of posterior pigmentation (1 = beginning at posterior ventral margin; 2 = beginning at mid-ventral margin; 3 = beginning at anterior ventral margin); Strength (H = heavy; M = moderate; W = weak).

Relative length of mantle features: Inc. = incurrent opening; Anal = anal opening; A-AS = distance between anal and supra-anal openings; SA = supra-anal opening.

Labial palps: Posit. = position of distal end relative to inner demibranchs (OV = overlapping; T = touching; NT = not touching).

Water tubes in OD: OD = outer demibranch.

Sex: F = female; (F) = female (inferred); GF = gravid female; (M) = male (inferred). (Sexes inferred from number of water tubes per mm in outer demibranch (previous column.))

Pre-preserv. treatment: Nemb. relax. = relaxed with nembutal; Form. fixed = fixed with formalin.

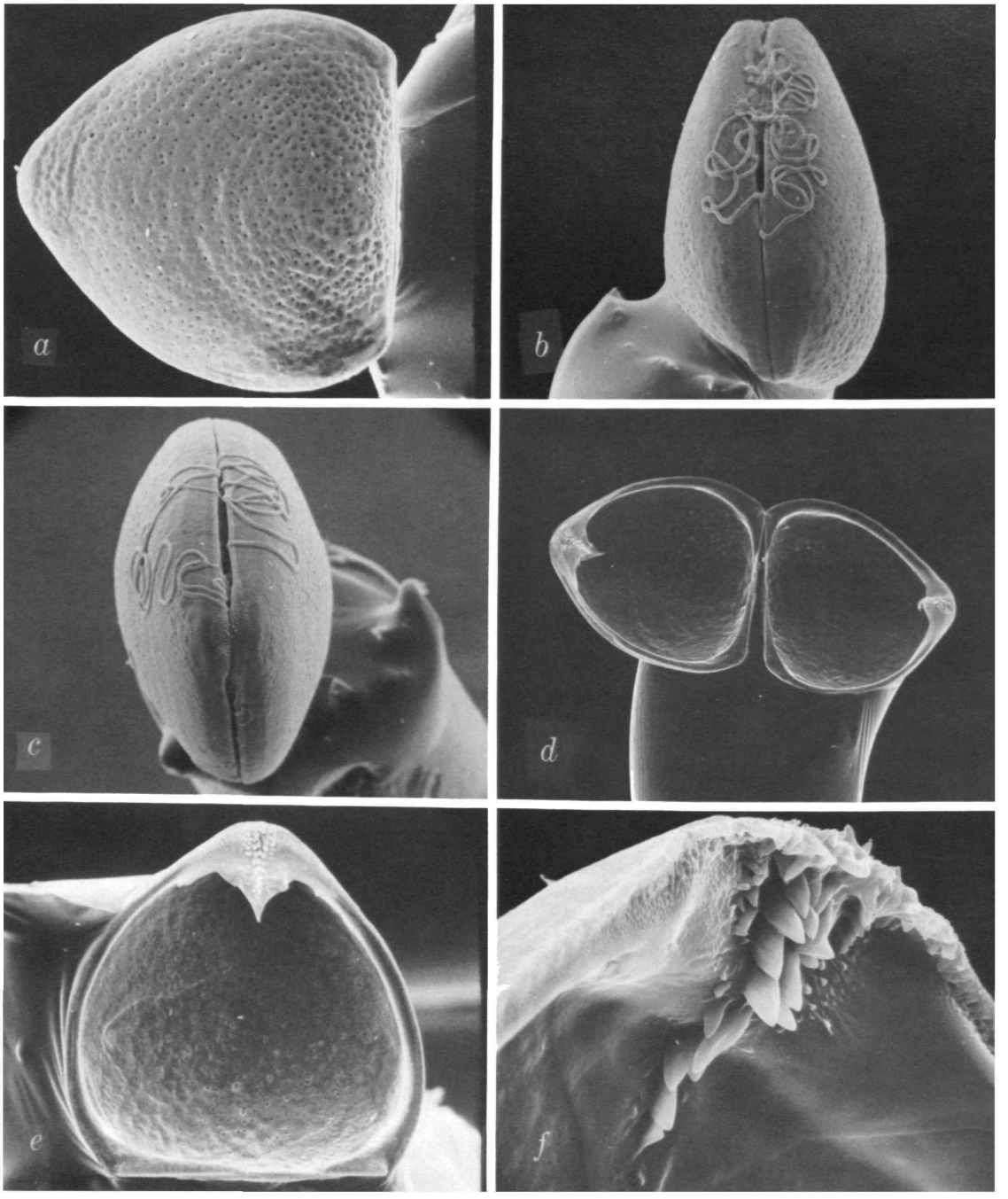

FIGURE 2.—Glochidia of *Lasmigona holstonia: a,d,e,* USNM 801973, headwaters of Holston River, Virginia; *b,c,f,* OSUM 15759, North Fork Clinch River, Tazewell, Virginia (*a,e,* × 228; *b,c* × 192; *d* × 140; *f* × 1120).

above the center of the hinge, and extending to the valve margins. The pits, which are from about 2 to 3 μm in diameter, are located in the depressions, are more numerous on the lower part of the shell (i.e., near the hinge) than on the upper, and are absent near the apices. The hinge is about 0.220 mm long and nearly straight, being only slightly convex centrally. The ligament is narrow and long, slightly exposed externally along its whole length and exposed internally in a shallow sinus that is 65 μm long and centered about 35% of the distance from anterior to posterior.

The stylets are not mature in our material, i.e., the microstylets are still irregularly developed and the stylets themselves appear soft and not fully formed, so the following description will not be entirely applicable to mature specimens. Some features are clear, however, viz, the stylets are approximately 67 μm long, 38 μm wide at their bases, and are apically rostrate. They are attached on each side for most of their length by a flexible membrane. The microstylets appear to be few in number (about 20) and to measure about 7 μm in length and 4 μm in width at their bases. Smaller microstylets (~ 2 μm wide) and micropoints (0.5–1 μm wide) extended laterally from the bases of the stylets along the edges of the valves., and on the outside of the valves at their apices.

This description is of a glochidium from an adult specimen (USNM 801973) collected from a small tributary of the upper Holston River, Virginia, by Ms. Sally Dennis in October 1979. In 2 other glochidia, taken from a specimen (OSUM 15759) collected in the North Fork of the Clinch River at U.S. Route 19, Tazewell, Tazewell County, Virginia, by D.H. Stansbery and J.J. Jenkinson on 5 October 1965, the height and length measurements are 0.287 × 0.313 mm and 0.303 × 0.301 mm. The stylets also appear to be not fully developed but each has about 20 multi-faceted dagger-like microstylets (up to 9 μm long and 6 μm wide at their bases) arranged in a narrow, V-shaped area with only one microstylet in each horizontal distal row and 3 or 4 in proximal rows. In two specimens that were dried and mounted without removing the soft parts, a well-developed larval thread about 1.0 mm long was seen (Figure 2*b*,*c*). A larval thread has not been observed in any other species of the Tribe Alasmidontini. Such a structure does occur in *Anodonta*, however (*A. cygnea*, see Wood, 1974), and in *Margaritifera*, *Unio*, and *Elliptio*.

Life History

GRAVID PERIOD.—Four lots containing gravid specimens have been seen in the Mollusk Collection of the Ohio State University Museum, all from the Clinch River (both North and South Forks) near Tazewell, Tazewell Co., Va. They were collected on 19 August 1969 (glochidia just beginning to form), 29 August 1970, and 5 October 1965 (2 lots), by D.H. Stansbery et al. Thus the gravid period begins about the middle of August and probably continues to the spring of the following year.

NATURAL HOST.—The fish host of *L. holstonia* is unknown.

HABITAT.—Characteristic of small streams where, in many localities, it is the only unionid present. Ortmann (1918:557) has reported finding it in larger streams (Holston River at Church Hill, Hawkins Co., Tenn. and Hiawassee River at Austral, Polk Co., Tenn.) but "in both cases the specimens came from a small slough." It avoids the main channel of large rivers.

Geographical Records

FIGURE 3

TENNESSEE RIVER SYSTEM.—*Powell River Drainage:* Cane Creek, 2 mi (3.2 km) W of Pennington Gap, Lee Co., Va. (UMMZ). Station Creek, Lee Co., Va. (MCZ). Mud Creek, 1 mi (1.6 km) SE of Olinger, 6 mi (9.6 km) SW of Big Stone Gap, Lee Co., Va. (1961, D.H. Stansbery! (OSUM)). Wallen Creek, Sheep Shank, Lee Co., Va. (MCZ, UMMZ). Indian Creek, Cumberland Gap, Claibourne Co., Tenn. (UMMZ). South Fork Powell River, Big Stone Gap, Wise Co., Va. (UMMZ). Powell River at Norton, Wise Co., Va. (UMMZ). Big Stone Gap, Wise Co., Va. (MCZ). Dickson Ford, 2 mi (3.2 km) SE of Jonesville, Lee Co., Va. (UMMZ), and 2½ mi (4 km) S of Jonesville, Lee Co., Va. (MCZ).

Clinch River Drainage: Maiden Spring Creek, Va. Rt. 16, Thompson Valley, below Benbow, Tazewell Co., Va. (1954,

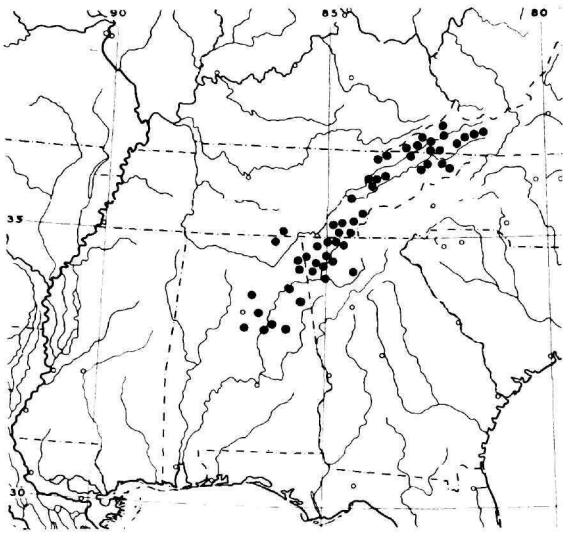

FIGURE 3.—Geographical distribution of *Lasmigona holstonia* (small open circles = cities).

H.D. Athearn! (MCZ)). Jesse Creek, Scott Co., Va. (MCZ). West Blackwater Creek, Blackwater, Lee Co., Va. (UMMZ). Copper Creek, 6 mi (9.6 km) N of Bolton, Russell Co., Va. (UMMZ). Cove Creek, Caryville, Campbell Co., Tenn; Bullrun Creek, Heiskell, Knox Co., Tenn; and Knob Fork Creek, 6 mi (9.6 km) N of Dante, Knox Co., Tenn. (all MCZ). North Fork Clinch River at Whitten's Mill (RR crossing below Willow Chapel), 4.0 mi (6.4 km) NE of Tazewell, Tazewell Co., Va. (1973, D.H. Stansbery! (OSUM)); U.S. Rt.19 bridge, 4 mi (6.4 km) NE of Tazewell (1965, D.H. Stansbery and J.J. Jenkinson! (OSUM)); bridge, 0.3 mi (0.5 km) ENE of Five Oaks, 3.0 mi (4.8 km) NE of center of Tazewell; 1.1 mi (1.8 km) S of Five Oaks, 1.8 mi (2.9 km) NE of center of Tazewell (both 1965, D.H. Stansbery! (OSUM)); and U.S. Rt. 19 bridge, N city limits of Tazewell (1965, D.H. Stansbery and J.J. Jenkinson! (OSUM)). South Fork Clinch River at Va. Rt. 61 bridge, 1.5 mi (2.4 km) ENE of Tazewell, Tazewell Co., Va. (1967, 1969, W.J. Clench et al.! (MCZ, OSUM)); above and at U.S. Rt. 19 bridge, Tazewell (1963, 1965, D.H. Stansbery et al.! (MCZ, OSUM)); E edge of Tazewell (1970, D.H. Stansbery! (OSUM)). Clinch River at N. Tazewell, above Va. Rt. 16A bridge, Tazewell Co., Va. (1965, D.H. Stansbery and J.J. Jenkinson! (MCZ, OSUM)); Va. Rt. 460 bridge, Richlands, Tazewell Co., Va. (1965, D.H. Stansbery et al.! (OSUM)); Lowland, Wise Co., Va. (MCZ); and 1½ mi (2.4 km) S of Dona, Lee Co., Va. (in Hancock Co., Tenn.) (MCZ).

Holston River Drainage: Wolf Creek along Va. Rt. 80, 0.6 mi (1 km) S of Hayter's Gap, 2 mi (3.2 km) NW of Lindell, Washington Co., Va. (1963, W.J. Clench and D.H. Stansbery! (MCZ, OSUM)). Horse Creek, 2 mi (3.2 km) N of Falls Branch, Sullivan Co., Tenn. (MCZ, UMMZ). Whitehorn Creek, Bulls Gap, Hawkins Co., Tenn. (UMMZ). Tributary of Holston River near tributary mouth, 4 mi (6.4 km) S of Rogersville, Hawkins Co., Tenn. (1954, W.J. Clench et al.! (MCZ, UMMZ)). Big Flat Creek, Corryton, Knox Co., Tenn. (MCZ). Middle Fork Holston River at Va. Rt. 682 bridge, 9.5 mi (15.2 km) ENE of Marion, Smyth Co., Va.; U.S. Rt. 11 bridge, 8.5 mi (13.6 km) ENE of Marion; and at Va. Rt. 684 bridge, 8.0 mi (12.8 km) ENE of Marion (all 1970, D.H. Stansbery! (OSUM)). Holston River, "E. Tennessee" (ANSP).

French Broad River Drainage: Jockey Creek, U.S. Rt. 11 bridge, 1 mi (1.6 km) NW of Limestone, 11.8 mi (18.9 km) ENE of Greenville, Greene/Washington Co., Tenn. (1968, W.J. Clench and D.H. Stansbery! (OSUM)).

First Creek Drainage, Knox Co., Tenn.: Whites Creek, near Greenway; Adam's Creek, near Fountain City; First Creek, Knoxville (all MCZ).

Third Creek Drainage, Knox Co., Tenn.: Third Creek (UMMZ).

Hiawassee River Drainage: Valley River, Cherokee Co., N.C. (ANSP). Williams Branch, Monroe Co., Tenn. [not located] (ANSP). Conasauga Creek, Monroe Co., Tenn. (ANSP, MCZ, UMMZ). Pell Branch, 4.6 mi (7.4 km) NE of Benton, Polk Co., Tenn. (1965, H.D. Athearn! (MCZ)). Gatlin Branch, 4.4 mi (7 km) WSW of Benton, in Bradley Co., Tenn. and just above mouth of Clark Branch, 2.2 mi (3.5 km) NW of Ocoee, in Bradley Co., Tenn. (both 1956, H.D. Athearn! (MCZ, OSUM)).

Jones Creek Drainage: Jones Creek, Bridgeport, Jackson Co., Ala. (UMMZ).

Crownover Branch Drainage: Crownover Branch, opposite Russell Cove National Monument, Jackson Co., Ala. (1964, H.D. Athearn! (MCZ, NMC)).

Crow Creek Drainage: Crow Creek, Sherwood, Franklin Co., Tenn. (1966, D.H. Stansbery! (OSUM)).

Paint Rock River Drainage: Larkin Fork of Paint Rock River, 3 mi (4.8 km) S of Francisco, Jackson Co., Ala. (1966, D.H. Stansbery! (OSUM)).

ALABAMA RIVER SYSTEM.—*Coosa River Drainage:* Oostanaula Watershed: Climer Branch at Climer Road, 9 mi (14.4 km) ENE of Cleveland, Bradley Co., Tenn. (1969, H.D. Athearn! (MCZ)). Sugar Creek, 12 mi (19.2 km) SSE of Cleveland, Tenn. (1964, H.D. Athearn! (OSUM)) and near upper King's Bridge, Murray Co., Ga. (UMMZ). Mill Creek at Ga. Rt. 225, Chatsworth, Murray Co., Ga. (1961, H.D. Athearn! (NMC)). Swamp Creek, Murray Co., Ga. (MCZ, UMMZ). Mills Creek, 1.6 mi (2.6 km) NNE of Cohutta, Whitfield Co., Ga. (1958, H.D. Athearn! (MCZ)). Spring Creek, branch of Cuahulla Creek, Varnell, Whitfield Co., Ga. (UMMZ). Little's Creek [not located]; Job's Creek, 2½

mi (4 km) NW of Tilton (all Whitfield Co., Ga. (MCZ)). Swamp Creek, 2 mi (3.2 km) NE of Tilton (1962, H.D. Athearn! (MCZ)). Conasauga River, 10 mi (16 km) N of Eton, Murray Co., Ga. (1958, W.J. Clench and J. Rosewater! (MCZ)). Buckhout Spring Branch, 3 mi (4.8 km) N of Calhoun (MCZ) and 3 mi (4.8 km) NE of Calhoun (UMMZ), Gordon Co., Ga. Armuchee Creek, 0.8 mi (1.3 km) W of Armuchee, Floyd Co., Ga. (1956, H.D. Athearn! (MCZ)) and ½ mi (0.8 km) S of Armuchee (1960, H.D. Athearn! (UMMZ)).

Etowah Watershed: "Shinbone Creek" [not located], Cherokee Co., Ga. (UMMZ). Little Pine Log Creek, Bartow Co., Ga. (MCZ). Etowah River, Ga. (UMMZ).

Chattooga Watershed: Dixon's Branch and Duck Creek [neither located]. Walker Co., Ga. (MCZ, UMMZ). Allen's Branch (MCZ). Harlow's Branch (MCZ, NMC, UMMZ); Lowe's Branch, Summerville (MCZ, UMMZ); Raccoon Creek (MCZ); Spring Creek (MCZ); and Telloga Creek (MCZ), all Chattooga Co., Ga. Daniels Branch (small stream flowing into Little River); Shinbone Creek; and Waterloo Branch, all Cherokee Co., Ala. (all MCZ). Chattooga River at Martindale, Walker Co., Ga. (UMMZ); Trion, Chattooga Co., Ga. (1951, H.D. Athearn! (NMC)); and near Summerville, Chattooga Co., Ga. (MCZ, UMMZ).

Coosa Watershed: Dry Creek No. 3 (MCZ); Dykes Creek (MCZ, UMMZ), Horse Lake Creek (MCZ), and Silver Creek, all Rome, Floyd Co., Ga. Ohatchee Creek, Reeds, Calhoun Co., Ala. (1951, H.D. Athearn! (MCZ, OSUM)). Spring tributary of Carp Creek, Calhoun Co., Ala. (UMMZ). Mill Creek, tributary to Waxahatchee Creek, Shelby Co., Ala. (ANSP, UMMZ). Clear Creek, Montevallo, Shelby Co., Ala. (UMMZ). Spring Creek, 3 mi (4.8 km) NW of Calera, Shelby Co., Ala. (ANSP, UMMZ). Periwinkle Creek, Fayetteville, Talladega Co., Ala. (ANSP, UMMZ). Talladega Springs, Talladega Co., Ala. (MCZ, UMMZ). Cool River, Talladega Springs, Talladega Co., Ala. (MCZ).

Cahaba River Drainage: Little Cahaba River, 2 mi (3.2 km) NE of Leeds, Jefferson Co., Ala. (MCZ) and 6 mi (9.6 km) below Leeds (UMMZ).

Tombigbee River Drainage: Village Creek, Jefferson Co., Ala. (MCZ).

Remarks

Morrison (1969:23) has stated that *Alasmodon badium* Rafinesque, 1831 is the earliest name for the species herein recognized as *Lasmigona holstonia* (Lea, 1836) (= *Margaritana holstonia* Lea, 1836). After carefully reviewing Rafinesque's description of *badium*, however, I have come to the same conclusion as Ortmann and Walker (1922:36), i.e., that one "cannot be sure that *M. holstonia* Lea was intended." I also believe that the description of *badium* more closely agrees with the small-stream morph of *Alasmidonta viridis* (Rafinesque, 1820) (= *Unio viridis* Rafinesque, 1820) later described by Lea (1845) as *Margaritana minor*. As discussed earlier (Clarke, 1981), in 1831 Rafinesque must have forgotten what he had described in 1820 as *Unio viridis*, because he then transferred the name to another species. This error may have led him to believe that the species he had originally described as *Unio viridis* was still nameless and his new name *badium* may have been proposed to supply a name for it.

On the basis of preliminary studies, Hurd (1974:83) has stated that *L. holstonia* (Lea, 1838) and *L. georgiana* (Lea, 1859) are distinct and that both occur in the Coosa River Systems. He writes that *L. georgiana* may be distinguished from *L. holstonia* by differences in size, coloration, and dentition. Although I have examined many specimens, I have been unable to confirm the existence of any significant morphological differences other than those attributable to more rapid growth in some more southern populations. I therefore concur with Ortmann (1923:129, 30) in the opinion that *L. georgiana* and *L. holstonia* are synonymous names for one variable species.

Subgenus *Lasmigona* (sensu stricto)

The glochidia are pyriform, more than 0.320 mm in height, with height greater than length, with concave adapical sides, with acuminate or lingulate stylets each bearing numerous (75+) major microstylets, without exterior micropoints on the apices, and without a byssus.

Comparative features of the adults are: the shells are more than 150 mm long, with or without a dorsal alation, are of medium to great relative height (H/L about 0.46–0.82), have prominent radial sculpturing in most specimens on the posterior slope, have short or rudimentary lateral hinge teeth, and have undulate or double-looped beak sculpturing. The included species

are dioecious. The supra-anal mantle opening is longer than the anal opening.

Lasmigona (Lasmigona) costata (Rafinesque, 1820)

FIGURES 4–6

Alasmidonta costata Rafinesque, 1820:318, pl. 83:15, 16. [Type-locality: "la riviere Kentucky, ou elle parait etre rare." Holotype not in Academy of Natural Sciences of Philadelphia (Johnson and Baker, 1973) and presumably lost.]

Alasmidonta rugosa Barnes, 1823:278, fig. 21. [Type-locality: "Wisconsan [sic] [and] Fox River [Wisconsin]." Location of type specimens unknown; they are probably lost.]

Alasmodon hians Rafinesque, 1831:5. [Type-locality: "River Tennessee." Types found neither in Academy of Natural Sciences of Philadelphia nor in the Paris Museum (Johnson and Baker, 1973:157). Rafinesque's description and subsequent remarks by Ferussac (1835:31), in my opinion, clearly identify this species.]

Lasmigona costata var. *eriganensis* Grier, 1918:10. [Type-locality: Big Bend, Presque Isle Bay, Lake Erie. Type lot is CM 61.422.3.]

Lasmigona costata pepinensis Baker, 1928:144. [Type-locality: "Lake Pepin" [Wisconsin]. Holotype and paratype are WGNHM 357 and 358, respectively. They are labelled "Lake Pepin, Lake City, Wis." (Franzen, 1957:33).]

Lasmigona costata nuda Baker, 1928:145. [Type-locality: "Red Cedar River, west of Chetek, Barron, Co." [Wisconsin]. Holotype is WGNHM 900; paratypes are 901–904 (Franzen, 1957:33).]

THE SHELL

FIGURE 4*a*, *c–e*

DESCRIPTION.—Shell long-ovate, subrhomboid or subtrapezoid, heavily sculptured, up to about 162 mm long, 81 mm high, and 46 mm wide. Somewhat thickened anteriorly (up to 7 mm thick) and thinner, but not fragile, posteriorly. Anterior margin sharply curved and, in some specimens, more abruptly curved above than below; ventral margin broadly convex throughout or broadly convex distally and flattened centrally; posterior margin roundly pointed below and broadly curved or flattened above, and dorsal margin nearly straight except somewhat depressed anterior to the umbones. The point of maximum inflation is about 40% of the distance from anterior to posterior or, in inflated specimens, anterior to the posterior ridge. Beaks low, rather narrow, located about ⅓ the distance from anterior to posterior, and projecting only slightly above the hinge line. Posterior ridge slightly elevated or low and rounded, more prominent adapically than abapically. Posterior slope well defined and somewhat convex to slightly concave.

Growth increments marked by shallow grooves that are darkly pigmented in most specimens. Post-juvenile sculpturing typically consisting of (a) about 12 to 20 strong, rounded ridges on the posterior slope, extending from the posterior ridge to the posterior margin and oriented perpendicularly to the lines of growth; (b) a few, shallow, irregular depressions anterior to the posterior ridge; and (c) low, irregular, concentric undulations traversing the entire surface. Periostracum yellowish brown and covered with numerous broad and narrow, dark greenish rays in juveniles but becoming dark brown and with mostly obscure rays in adults. Ligament long, thick, horny externally, and brittle when dry.

Hinge teeth heavy and thick. Pseudocardinal teeth elevated, pyramidal, serrated, and numbering 1 or 2 in the right valve and 2 in the left. Interdental projection prominent in the left valve, irregular, serrated, and more or less flange-like. Lateral teeth short and rudimentary or absent. Beak cavity shallow and with irregular muscle scars beneath the pseudocardinal teeth. Anterior muscle scars impressed, especially so close to the low buttress located below the pseudocardinal teeth, pallial band impressed and crossed by numerous fine ridges and grooves, and posterior muscle scar conspicuous but shallow. Scars within beak cavity consisting, in many specimens, of two subcircular pits behind the anterior portion of the interdental projection of the left valve (this is variable—up to 8 pits of various shapes and sizes occur in some specimens) and 2 or more irregular pits behind and below the hinge plate anterior to the pseudocardinal teeth in the right valve. Nacre white or bluish white and, in many specimens, tinged centrally

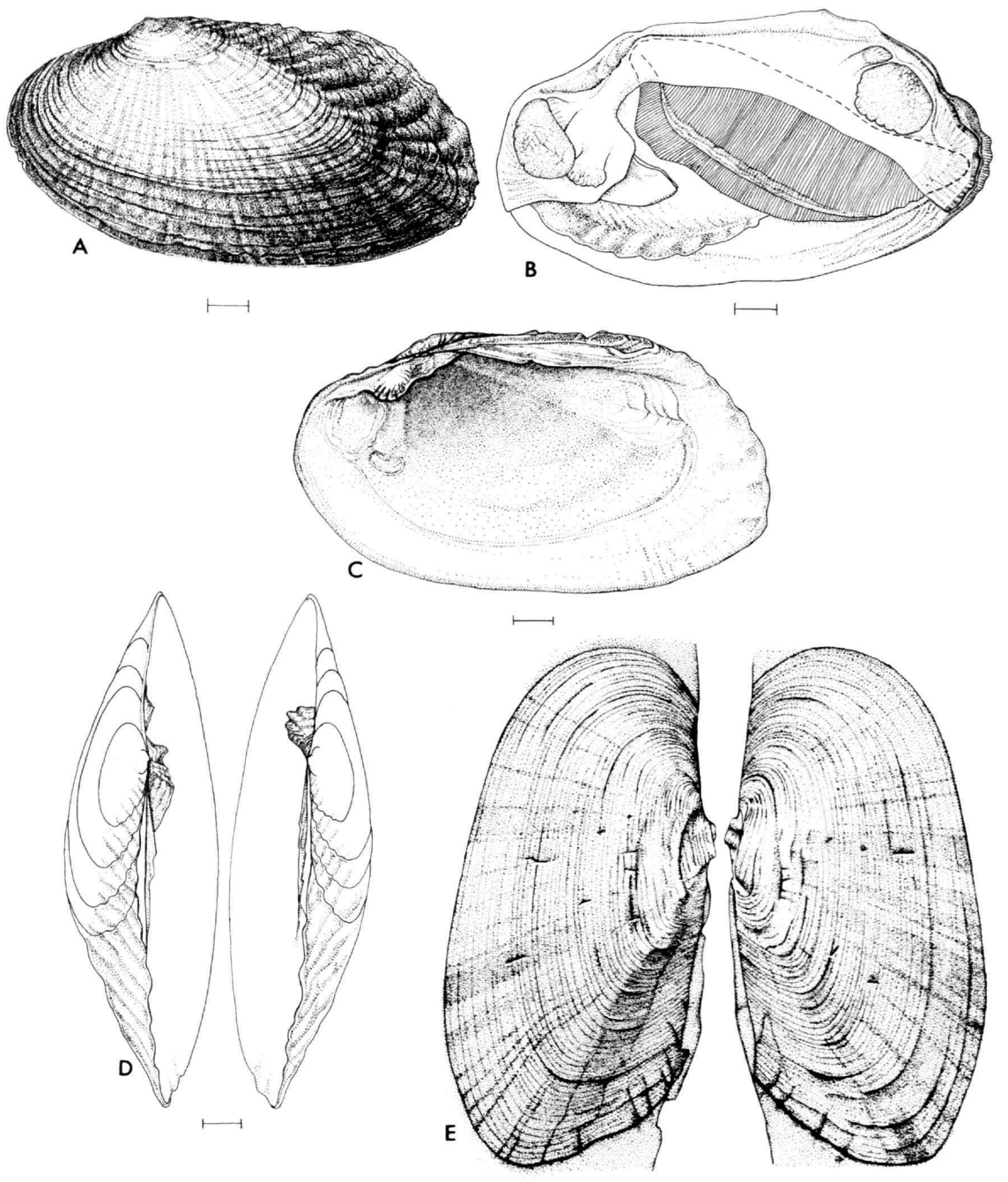

FIGURE 4.—*Lasmigona costata: a,c,d*, USNM 738227, Miami River, Logan County, Ohio; *b*, USNM 801317, Milwaukee River, Thiensville, Ozaukee County, Wisconsin; *e*, details of umbonal area, USNM 540130, [Cedar River], Cedar Rapids, Linn County, Iowa. (Scale = 1 cm.)

with yellow or salmon pink. At the margin the nacre in grayish.

Beak sculpture heavy and composed of 5 or 6 approximately concentric ridges. The first ridge is a tiny, rounded elevation, the second is roundly U-shaped and somewhat asymmetrical, the third is similar but narrower on the anterior and posterior portion, elevated on the central portion, and elevated and angular on the posterior ridge, on the fourth the anterior and posterior portions become nearly obsolete and the elevated portion is more extreme, and in the fifth the anterior and posterior portions are missing. The third, fourth, and fifth ridges are nearly straight centrally or are more or less indented, inclining toward the double-looped condition. The beak sculpturing in most post-juvenile specimens (except those from some hard-water rivers) is partly or wholly obliterated from corrosion.

VARIATION.—Ortmann (1919:126) found that most large specimens of *L. costata* that are swollen just in front of the posterior ridge are females, but that exceptions are so frequently seen that shells cannot be relied upon for sexual interpretation. A summary of his measurements for relative inflation, taken from 9 sexed specimens from a total of 6 Pennsylvania localities, is given in Table 3. Measurements are also presented there of 9 specimens collected from a single locality in Wisconsin (Milwaukee River, Sec. 25, T12N, R20E, Washington Co.) by Walter Ma-

Table 3.—Relationship of shell inflation to sex in *Lasmigona costata*.

Pennsylvanian specimens (Ortmann, 1919)			Wisconsin specimens		
Length (mm)	W/L	Sex	Length (mm)	W/L	Sex
149	0.336	♀	138	0.270	♀
137	0.270	♀	136	0.327	♀
134	0.336	♀	131	0.310	♀
126	0.278	♂	122	0.304	♀
126	0.286	♀	121	0.269	♂
122	0.287	♂	120	0.308	♂
122	0.262	♀	118	0.312	♀
75	0.253	♂	114	0.256	♂
73	0.247	♀	111	0.309	♂

TABLE 4.—*Lasmigona costata:* shell measurements.

Feature	N	Range	Mean ($\bar{x}$)	S
	French Creek, Sagerstown, Crawford Co., Pa. (OSUM 25678)			
Length (mm)	11	88.6–128.6	109.8	14.66
H/L	11	0.529–0.614	0.560	0.0241
W/L	11	0.221–0.306	0.271	0.0259
B-A/L	11	0.278–0.336	0.311	0.0157
$(Wt \times 10^3) \div (L \cdot H \cdot W)$	11	0.270–0.358	0.330	0.0368
	Clinch River, Kyles Ford, Hancock Co., Tenn. (ANSP 335047)			
Length (mm)	26	97.7–141.2	120.5	8.22
H/L	26	0.460–0.557	0.513	0.0221
W/L	26	0.218–0.339	0.272	0.0243
B-A/L	26	0.213–0.316	0.251	0.0260
$(Wt \times 10^3) \div (L \cdot H \cdot W)$	26	0.204–0.455	0.325	0.0648
	Olentangy River, Columbus, Franklin Co., Ohio (OSUM 4386)			
Length (mm)	13	66.6–148.5	120.0	20.56
H/L	13	0.511–0.627	0.565	0.0351
W/L	13	0.239–0.328	0.290	0.0286
B-A/L	13	0.259–0.363	0.317	0.0289
$(Wt \times 10^3) \div (L \cdot H \cdot W)$	13	0.242–0.480	0.355	0.0562
	Mississippi River between St. Paul, Minn. and Davenport, Iowa (USNM, 12 lots)[1]			
Length (mm)	17	61.9–124.3	103.1	18.92
H/L	17	0.466–0.579	0.526	0.0310
W/L	17	0.242–0.396	0.328	0.0384
B-A/L	17	0.264–0.338	0.301	0.0174
$(Wt \times 10^3) \div (L \cdot H \cdot W)$	17	0.388–0.658	0.500	0.0748

[1] USNM 745495, 745535, 745553, 745625, 745642, 745670, 745941, 745956, 746012, 746033, 746051, and 746113.

thiak on 24 May 1980. (All of the females were gravid and the males were sexed by microscopic examination of the demibranchs). Both sets of data support Ortmann's conclusion. All shell measurements (mm) from each population sample of *L. costata* are therefore combined in Table 4 without attempting to subdivide the samples by sex from characteristics of the shells.

The most variable shell characters in this species are size, shape, relative thickness, and sculp-

turing. The largest specimen I have seen was collected in Stone's River, at Tenn. Hwy. 10 bridge, Walterhill, Rutherford Co., Tennessee by Louise R. Clarke and me in 1953. Its measurements are: L, 184.4 mm; H, 93.4 mm; W, 61.3 mm; and B-A 60.0 mm. Several other specimens from that locality were nearly as large. Ortmann (1919:127) has pointed out that in some small streams only small specimens occur, whereas in others many specimens are unusually large.

The extent to which shape varies within some populations of *L. costata* is shown in Table 4. Coefficients of variation ($CV = (S \div \bar{X}) \times 100$) vary from 4.30 to 6.21 for relative height (H/L), from 8.93 to 11.71 for relative obesity (W/L), and from 5.05 to 10.36 for relative placement of the umbones $\left(\frac{B\text{-}A}{L}\right)$.

Specimens from Lake Erie at Presque Isle Bay, Erie Co., Pennsylvania, named "var. *eriganensis*" by Grier (1918:10), are reported to be smaller, more elongate, and more inflated than in *costata* (sensu stricto). According to Grier the relative height of *eriganensis* is 0.53 and the relative inflation is 0.32, whereas in typical *costata* H/L is 0.56 and W/L is 0.27. Ortmann's (1919:131) measurements of 5 "*eriganensis*" specimens give H/L ratios of 0.489–0.541 ($\bar{x} = 0.517$) and W/L ratios of 0.295–0.368 ($\bar{x} = 0.338$). These values are within the ranges of variation seen in other populations of *L. costata* (Table 4). Specimens from Lake Erie do exhibit a characteristic facies but this is undoubtedly an ecophenotypic response and not an expression of genetic distinction. (See Clarke, 1973b, for similar cases involving other species in Lake Erie.)

Specimens from the Mississippi River are subcylindrical and remarkably heavy (Table 4). In this respect they resemble ecophenotypes of *Alasmidonta undulata* from cold, hard-water localities in Canada (Clarke, 1981) and they may be parallel ecophenotypes. Published information on water quality (see Briggs and Ficke, 1977) does not appear to be useful in revealing possible relationships between morphology and ecology, however, perhaps because of non-concordance between the depths where water temperatures were taken in this large river and the depths where the mussels were collected. The problem needs further study but, in general, *L. costata* appears to be unable to tolerate soft water to the extent exhibited by *A. undulata*, and possible effects of temperature and hardness on shell thickness are less likely to be apparent.

Previous authors (e.g., Ortmann, 1919:127; Baker, 1928:145) have cited populations of *L. costata* in which rib-sculpturing of the posterior slope is absent. The occurrence of such populations is irregular and this morph does not constitute a discernable geographical subspecies. Some populations also exhibit more intense or more widespread sculpturing than one usually sees. Such populations are irregularly distributed in the central and southern portions of the species range and are also not taxonomically separable.

Topographic Anatomy

FIGURE 4*b*

SPECIMEN DESCRIBED.—USNM 801317, from Milwaukee River, at Rte. 67 crossing in Thiensville, Ozaukee County, Wisconsin collected 6 November 1979 by H.A. Mathiak; fixed directly in 10% formaldehyde and preserved in alcohol; shell length 148.0 mm, sex female (gravid, with eggs).

DESCRIPTION.—Mantle whitish and translucent, with the colors of the demibranchs and other organs showing through, with a thickened muscular edge (about 7 mm wide anteriorly and 3.5 mm wide posterioventrally) and with a continuous narrow band of pale orange pigment, close to the mantle edge anteriorly and ventrally, which is joined in the central area by a broken brownish pigment band. Both continue posteriorly and dorsally to the hinge-line, the broken brownish band widening somewhat posteriorly.

Incurrent opening 20 mm long, with purplish brown pigment along the edge and to a depth of about 4.0 mm within, and surrounded within by 2 rows of pyramidal papillae, the exposed pa-

pillae each about 1.6 mm long, 0.6 mm wide at the base, and tapering to a narrow (0.1 mm), rounded point. Portions of mantle edges between incurrent and anal openings about 1.0 mm long. Anal opening with edges strongly crenulate but not papillate, pigmented within (like the incurrent opening), and 12.0 mm long. Mantle connection between anal and supra-anal openings 5.0 mm long. Supra-anal opening with a very narrow (0.1 mm), internal, brown-pigmented band, without papillae or crenulations, narrow and slit-like, and 17.5 mm long.

Demibranchs brownish in preserved specimens. Outer demibranch 78.5 mm long, 20.5 mm high in the center, with a broadly curved free ventral margin that narrows to a more-or-less rounded point anteriorly and posteriorly, and with about 1.0 to 1.5 water tubes per mm (when swollen with developing eggs) and about 9–10 dorsoventral surface filaments per mm and 5 cross-filaments per mm. Inner demibranch similarly shaped except with a short anterior lobe and with about 1.2 water tubes per mm and with surface filaments as in the outer demibranch. Edge of inner demibranch extending 7 mm beyond edge of outer demibranch anteriorly (the lobe extends 3 mm further) and flush with it posteriorly. The inner laminae of the inner demibranchs are attached to each other posteriorly but are not attached to the visceral mass.

Labial palpi with broadly sigmoid margins dorsally, rounded margins ventrally, roundly pointed anteriorly, and not touching the inner demibranchs. The outer surfaces are smooth and the inner opposing surfaces of each member are radially furrowed (about 4 furrows per mm at the margin). The outer palpus of each pair is fused to the mantle anteriorly and subdorsally, for about ¾ of its length, to the inner palpus.

In live, non-gravid specimens collected in the Clinch River, 2.4 mi (3.8 km) E of Kyles Ford, Tennessee, on 1 October 1979 the foot was orange and the demibranchs were brown. Ortmann (1912:284) says: "Color of soft parts rather remarkable. Orange tints are often found, similar to those seen in certain forms of *Alasmidonta*. The ground color is yellowish brown; foot, margins of mantle, and adductors often deep orange. The gills are brown, the edge of the mantle, as usual, blackish. The marsupium, when charged, varies from yellowish to brown."

VARIATION.—Table 5 shows that some variation occurs in all observed anatomical features. According to Ortmann (1912:283) the anal opening is long, and exceeds the length of the mantle connection between the anal and supra-anal openings. The present material agrees with this. The incurrent opening is about the same length as the supra-anal opening, or longer, and the anal opening in most specimens (at least in those seen from Wisconsin) is about half to two-thirds as long as the incurrent opening. The lengths of the incurrent papillae and the number of ranks of papillae are both quite variable. In the specimens available, the septa of the outer demibranchs are nearly, or approximately, twice as far apart in males as in sterile females.

Some observed aspects of variation, not apparent from the table, are that (a) in specimens 1 (described in detail above), 7, and 9, the pigmented mantle band was broken but in the other specimens it was continuous and (b) in specimen 3, both of the inner demibranchs were bilobate, i.e., they were radially split near the posterior edge of the foot. In no specimens were the inner demibranchs attached to the visceral mass.

GLOCHIDIUM

FIGURE 5*a–f*

DESCRIPTION.—Glochidium pyriform, 0.364 mm high, 0.333 mm long, 0.210 mm in maximum convexity (both valves appressed). The valves are asymmetrical: the posterior margin is more convex than the anterior, the valves are more inflated anteriorly than posteriorly and the apices are located about 42% of the distance from anterior to posterior (measured parallel to the hinge line). Both the anterior and posterior margins are distinctly concave near the apex. Surface of glochidium finely and irregularly malleated and ridged and also irregularly pitted ex-

TABLE 5.—*Lasmigona costata:* variation in topographic anatomy (terminology same as Table 2).

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 in OD (N/mm)	Sex	Pre-preserv. treatment: Nemb. relax.	Form. fixed
								Milwaukee River, Thiensville, Ozaukee Co. Wisc.; H.A. Mathiak! 6 Nov 1979 (USNM 801317)							
1	148	1	M	14	8	3	12	2	1.6	T	4	–	GF	–	+
2	138	1	M	15	7	3	15	1–2	1.0	OV	9	–	GF	–	+
								Milwaukee River, Sec. 25, T12N, R20E, Washington Co., Wisc.; H.A. Mathiak! 24 May 1980 (USNM 801473)							
3	113	2	M–H	13	8	2	12	1+	1.3	T	5	1.2–1.3	(F)	–	+
4	120	1	M	14	7	1	17	1	1.6	T	5	1.0–1.3	(F)	–	+
5	130	2	M	15	10	1	16	1	1.0	T	5	–	(F)	–	+
								Cedar Creek, Sec. 23, T10N, R21E, Ozaukee Co., Wisc.; H.A. Mathiak! 3 Nov 1979 (USNM 801312)							
6	121	1	M	15	9	2	15	1–2	1.4	T	6	–	GF	–	+
7	118	1	M	13	9	2	13	2	1.6	OV	4	–	GF	–	+
								Clinch River, 2½ mi E of Kyles Ford, Hancock Co., Tenn.; A.H. Clarke! 28 June 1978 (USNM 782518)							
8	126	1	M	19	6	?(torn)	?	1	0.6	OV	5	0.6–0.8	(M)	+	+
9	98	1	M	15	15	2	14	1+	0.9	OV	6	0.6–0.8	(M)	+	+
								Castor River below Zalma, Bollinger Co., Mo.; M. Lipford, P. Manning! 12 Aug. 1979							
10	117	1	M	22	21	3	14	1	0.5	OV	6	1.3–1.5	(F)	–	+

cept for the distal apical areas (about 50 μm high) and the area near the edges of the valves (about 20 μm wide). The malleated depressions are irregular, about 3–7 μm wide, and the pits are about 1–3 μm wide and located within the depressions. Low, regular, concentric ridges occur near the apices and near the valve margins and low, very irregular, subconcentric ridges and grooves, formed by confluence of the malleations, occur over the valve surface. Hinge flattened except noticeably convex centrally and about 0.230 mm long. Ligament exposed externally along its whole length and exposed internally, for a length of about 75 μm in an excavated area centered about 45% of the distance from anterior to posterior.

Each apical stylet is slightly curved throughout, about 0.110 mm long, about 0.050 mm wide at the base, subtriangular in cross-section, and narrowing distally to an acute rostrate point. Each stylet is supported along each side, for about 80% of its length, by horny membrane that is broadly connected to the ventral edge of each valve and continues as a flexible flange within the edges of each valve as far as the hinge. Except for the talon-like apical projection, the flatly rounded, exposed side of each stylet is covered with about 75 major microstylets, each about 7–8 μm long. The microstylets are arranged approximately in V-shaped rows; there are about 8 major microstylets across the base of the stylet and 1–4 near its apex. The microstylets are directed perpendicularly to the upper surface of the stylet, not toward its apex, and most are quadrate to hexagonal in cross-section (i.e., with about 4–6 cutting edges running the length of the microstylet) and bluntly pointed. Numerous, smaller (1–3 μm), pyramidal microstylets occur on the base of the stylet and along its edges, where they merge imperceptibly with the major microstylets, and still smaller microstylets extend onto the membranes near the stylet and along the inner edges of the valves.

The above description is of a glochidium taken

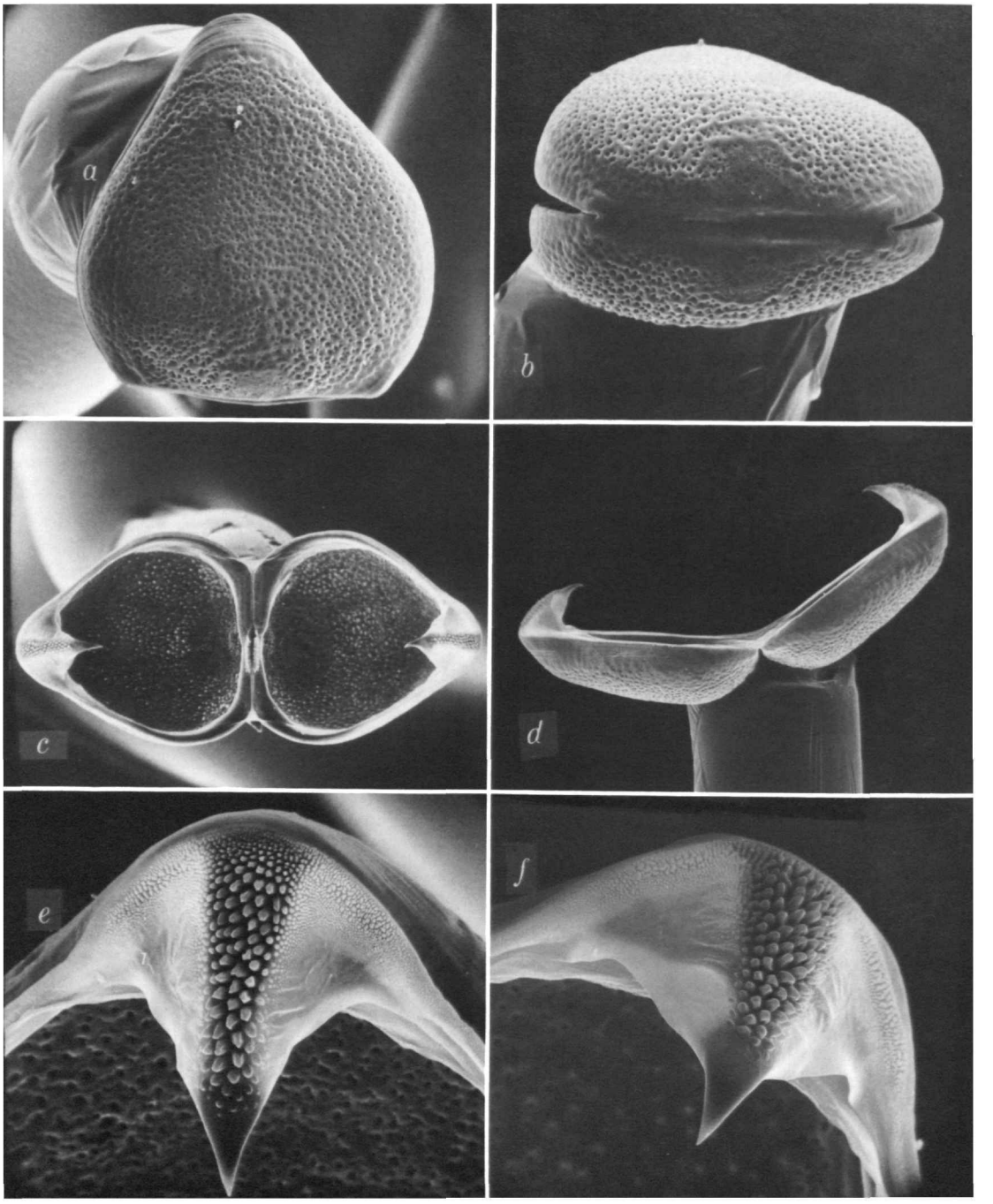

FIGURE 5.—Glochidia of *Lasmigona costata: a–f,* USNM 801473, Milwaukee River, Washington County, Wisconsin (*a* × 175; *b* × 195; *c* × 110; *d* × 100; *e* × 450; *f* × 485).

from an adult specimen (in lot USNM 801473) collected from the Milwaukee River, Sec. 25, T12N, R20E, Washington County, Wisconsin by H.A. Mathiak on 24 May 1980. Other glochidia from the same specimen were very similar. Glochidia from specimens collected at the same locality by Mr. Mathiak on 25 October 1979, had only partially developed microstylets, the membranes that support the stylets were less extensive, and the stylet apices were free for a greater part of their lengths and were asymmetrical. Another glochidium, from a Milwaukee River specimen (Thiensville, Ozaukee Co., Wisconsin, H.A. Mathiak, 5 November 1979) and apparently mature, is 0.357 mm high and 0.336 mm long, and the margins near the apices are only barely concave, i.e., nearly straight. A glochidium taken from a specimen collected in Birch River near McMunn in extreme western Ontario, Canada (Nelson River drainage) by Louise R. Clarke and me on 11 August 1961, is 0.380 mm high, 0.340 mm long, and quite asymmetrical (apex 38% of distance from anterior to posterior). The glochidium is immature, however, with only partly developed stylets.

The glochidia of *Lasmigona costata* are somewhat variable but they are characterized by their pyriform, somewhat asymmetrical form, their dimensions (height about 0.357–0.390 and length ÷ height ~ 0.89–0.94) and their rather small microstylets, which number only approximately 75. These observations are in general agreement with Baker (1928:143) who, quoting earlier authors, gives height 0.390, length 0.385 mm, and height 0.37, length 0.34 mm. They are similar to glochidia of *Alasmidonta marginata* (Clarke, 1981) but the valves are more swollen anteriorly in *L. costata* and the number of microstylets on each stylet are only about half as numerous as in *A. marginata*.

Life History

GRAVID PERIOD.—"Bradytictic. Breeding season beginning in August, glochidia being present in September. They are carried through the winter and discharged about the middle of May. No gravid females seen in June or July, which forms a resting period." (Baker, 1928:143). As noted above, specimens with immature glochidia was taken on 11 August (in Manitoba) and 25 October (in Wisconsin) and mature glochidia were seen in Wisconsin specimens taken on 5 November and on 24 May.

NATURAL HOSTS.—The carp, *Cyprinus carpio* L., has been successfully utilized, under laboratory conditions, as a host for *L. costata* (Lefevre and Curtis, 1910:104). Other fishes must also serve, however, because the carp is not native to North America but was introduced from Europe only 150 years ago (McCrimmon, 1968:17).

HABITAT.—Baker (1928:143) gives: "Abundant in situations of various kinds, in large as well as in small rivers. Prefers gravel in riffles, but also found in sand and fine gravel in quiet waters. Rare in mud." My observations agree with this except that in the Clinch River near Kyles Ford, Tennessee I have found *L. costata* most frequently near river banks under overhanging trees. It also occurs rarely in Lake Erie.

Geographical Records

FIGURE 6

Canadian Interior Basin Drainage Systems

NELSON RIVER SYSTEM.—*Winnipeg River Drainage:* Birch River at Trans-Canada Highway, near McMunn, Man. (1961, A.H. and L.R. Clarke!).

Red River Drainage: Little Pine Lake outlet, Otter Tail Lake outlet, and Otter Tail River, Perham, all Otter Tail Co., Minn. (Wilson and Danglade, 1914:12). Red Lake River, Minn. (Dawley, 1947:679 ; Cvancara, 1967:189). Roseau River, Man. (Dall, 1905:131).

Atlantic Drainage Systems

GREAT LAKES–ST. LAWRENCE SYSTEM.—*Lake Michigan Drainage:* Millecoquins River, Mackinac Co., Mich. (NMC). Sturgeon River, 6 mi (9.6 km) above Loretto and 3 mi (4.8 km) E of Vulcan, both Dickinson Co., Mich. (UMMZ). Big Cedar River, 3 mi (4.8 km) N of Cedar River, Memominee Co., Mich. (1969, D.H. Stansbery and C.B. Stein!). Menominee, Peshtigo, Oconto, Wolf, Embarass, Fox, West Twin,

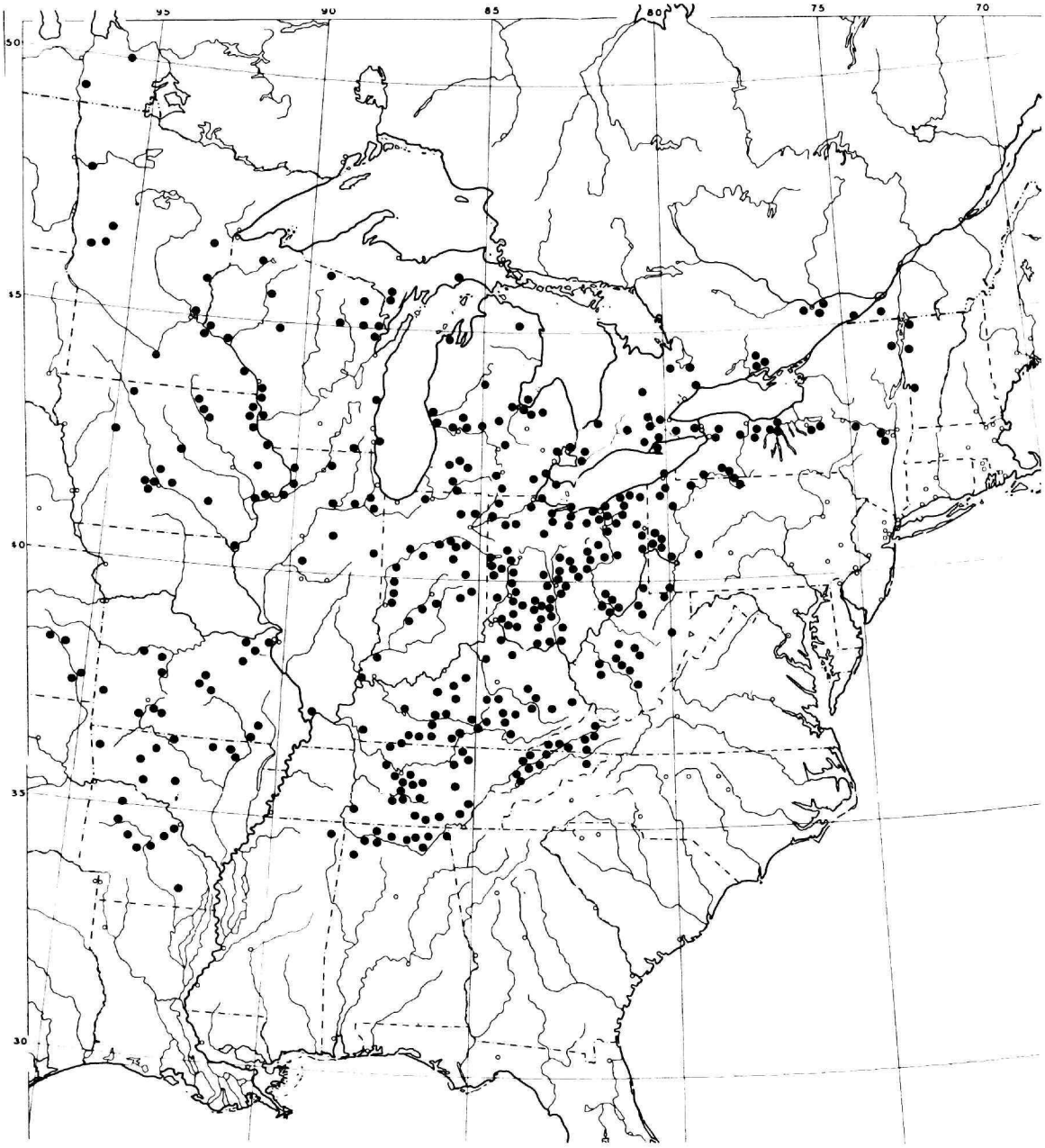

FIGURE 6.—Geographical distribution of *Lasmigona costata* (small open circles = cities).

Manitowoc, and Milwaukee Rivers, all Wisconsin (numerous recent records, Mathiak, 1979:30). White Pigeon River, 2 mi (3.2 km) S of Mottsville, St. Joseph Co., Mich. (1962, C.B. Stein!). St. Joseph River, Three Rivers, St. Joseph Co., Mich. (MCZ) and South Bend, St. Joseph Co., Ind. (USNM). Kalamazoo River, Mich. (several records, MCZ and NMC). Grand River and tributaries (Wabasis Creek, Stony Creek, and Maple River), Mich. (MCZ, USNM). Muskegon River at mouth of Hersey Creek, Osceola Co., Mich. (MCZ). Crystal River, Glen Arbor and Platt River, 10 mi (16 km) S of Glen Arbor, both Leelanau Co., Mich. (MCZ).

Lake Huron Drainage: West Branch of Thunder Bay River, 1 mi (1.6 km) S of Atlanta, Montmorency Co., Mich. (UMMZ). Saginaw River, Saginaw, Saginaw Co., Mich. (1965, G. Ahrens!). Saginaw Bay, Mich. (ANSP). Cass River, 3 mi (4.8 km) NE of Caro and 5 mi (8 km) NE of Vassar, both Tuscola Co., Mich. (NMC, MCZ). Black River, Pefferlaw, York Co., Ont. (1963, H.D. Athearn!). Nottawasaga River near Cookstown, Simcoe Co., Ont. (ANSP). Au Sable River, Hungry Hollow, Arkona, Lambton Co., Ont. (1950, I. Reimann!).

Lake St. Clair Drainage: Belle River, 4 mi (6.4 km) above Marine City, St. Clair Co., Mich. (1951, H.D. Athearn!). North Branch Clinton River, 2 mi (3.2 km) N of Mt. Clemens, Macomb Co., Mich. (MCZ). Clinton River, Utica, Macomb Co., Mich. (USNM). East Branch Sydenham River, 6 localities between 10 mi (16 km) SW of Strathroy, Middlesex Co. and 0.5 mi (0.8 km) N of Dawn Mills, Kent Co., Ont. (Clarke, 1973b:63, 64). Thames River below Woodstock, Oxford Co., Ont. (MCZ) and Chatham, Kent Co., Ont. (NMC). Lake St. Clair, shore 1 mi (1.6 km) N of mouth of Thames River, Kent Co., Ont. (1965, C.B. Stein!).

Lake Erie Drainage: Detroit River 3 mi (4.8 km) below Windsor, Essex Co., Ont. (NMC). Saline River, 1 mi (1.6 km) below Saline, Washtenaw Co., Mich. (USNM). East Fork of West Branch St. Joseph River, Sec. 28, Woodbridge Twp., Hilldale Co., Mich. (USNM). St. Joseph River at St. Joseph/Milford Twps., Williams/Defiance Co., Ind. (1963, C.B. Stein!) and near St. Joe, DeKalb Co., Ind. (1962, D.H. Stansbery!). Beaver Creek, U.S. Hwy. 127, 2 mi (3.2 km) NE of Bryan, Williams Co., Ohio (1966, P. Stromberg!). Blanchard River, 5.6 mi (9 km) E of Dupont, Putnam Co., Ohio (1968, C.B. Stein!). Auglaize River, Moulton Twp., Auglaize Co. (MCZ) and Kalida, Putnam Co., Ohio (ANSP). Maumee river at Crane Twp., Paulding Co. (MCZ), below dam at Grand Rapids, Wood Co. (1959, G. Asker and E. Dickerman!), and Waterville Twp., Lucas Co., Ohio (MCZ). Numerous records, including many recent ones, from Sandusky River, Wolf Creek, Huron River, Vermilion River, Rocky River, Cuyahoga River, Cry River, Mill Creek, and Grand River, Ohio (ANSP, MCZ, NMC, OSUM, UMMZ, USNM). Grand River and its tributaries, Ont. (numerous records, chiefly NMC but also OSUM, USNM). Lake Erie at Toledo Beach, Lucas Co., Ohio (ANSP); Sandusky Bay, Sandusky, Erie Co., Ohio (ANSP); Presque Isle Bay, Pa. (ANSP); Port Rowan, Norfolk Co., Ont. (UMMZ); and Port Dover, Norfolk Co., Ont. (NMC).

Lake Ontario Drainage: Cayuga Creek, Buffalo, Erie Co., N.Y. (ANSP). Baker's Creek, Niagara River, 4 mi (6.4 km) N of Lake Erie, Ont. (1957, H.D. Athearn!). Tonawanda Creek near Pembroke, Genesee Co., N.Y. (NMC). Numerous recent and historical records from Genesee River, Erie Barge Canal, and confluent rivers and lakes (Clarke and Berg, 1959:34). Rouge River, Markham, York Co., Ont. (NMC). Skootamatta River, Actinolite, Hastings Co., Ont. (1964, H.B. Herrington!). Moira River east of Thomasburg, Hastings Co., Ont. (UMMZ). Salmon River, Roblin, Lennox and Addington Co., Ont. (NMC).

St. Lawrence River and Tributaries: Rideau River at Billings Bridge (NMC), west of Billings Bridge (NMC), and Hogs Back (1965, A.H. and L.R. Clarke and C.B. Stein!). Chateauguay River, Howick, Chateauguay Co., Que. (1960, A.H. and L.R. Clarke!). St. Lawrence River near Sheek Island, Mille Roche (now flooded by St. Lawrence Seaway), 8 mi (12.8 km) W of Cornwall, Stormont Co., Ont. (1957, A.H. Clarke!, Clarke, 1959:99). Poultney River, 2 mi (3.2 km) W of Fair Haven, Rutland Co., Vt. (1952, H.D. Athearn!). Little Otter Creek at U.S. Hwy. 7, near Vergennes, Addison Co., Vt. (1955, A.H. and L.R. Clarke!). Lake Champlain, Crown Point, Essex Co., N.Y. (MCZ). Missiquoi River, Swanton, Franklin Co., Vt. (USNM).

HUDSON RIVER SYSTEM.—*Hudson River Drainage, New York:* [Mohawk River], Mohawk, Herkimer Co. (18??, J. Lewis!, USNM). Schoharie Creek, Sloansville, Schoharie Co. (1948, H. D. Athearn!, MCZ). Norman's Kill, Albany, Albany Co. (18??, MCZ).

U.S. Interior Basin Drainage Systems

OHIO RIVER SYSTEM.—*Allegheny River Drainage:* Allegheny River 5 mi (8 km) N of Olean, Cattaraugus Co., N. Y. (MCZ); Olean (ANSP): Turtlepoint, McKean Co., Pa. (1950, H.D. and D.R. Athearn!); Larabee, McKean Co., Pa. (ANSP); and Warren, Warren Co., Pa. (ANSP). French Creek at Hwy. 6, 2 mi (3.2 km) W of Mill Village, Erie Co., Pa. (1965, C.B. Stein!); ½ mi (0.8 km) N of U.S. Hwy 19 at Venango, Crawford Co., Pa. (1975, D. Snyder!); Saegertown, Crawford Co., Pa. (1978, R.F. Winters!); and Utica, Venango Co., Pa. (1979, R. Winters!)

Monongahela River Drainage: Loyalhanna River, Ligonier, Westmoreland Co., Pa. (ANSP). Tygart Valley River, 3.4 mi (5.4 km) SSW of Beverly, Randolph Co., W.Va. (1969, W.J. Clench and D.H. Stansbery!). Dunkard Creek at Worley, Monongalia Co., W.Va. (1969, D.P. Tanner!) and Mount Morris, Green Co., Pa. (1969, W.J. Clench and D. H. Stansbery!).

Beaver River Drainage: Mahoning River near Garrettsville, Portage Co., Ohio (USNM). [Mill Creek], Poland, Mahoning Co., Ohio (USNM). Slippery Rock Creek, Wurtemburg, Lawrence Co., Pa. (1951 H.D. and D.R. Athearn!). Connoquenessing Creek, Ellwood City, Lawrence Co., Pa. (MCZ). Beaver River below Wampum, Lawrence Co., Pa. (ANSP).

Little Beaver Creek Drainage: Little Beaver Creek, 1.9 mi (3 km) SW of Clarkson, Columbiana Co., Ohio (1969, M. West!). For historical Pennsylvania records see Ortmann, 1919.

Fish Creek Drainage: Fish Creek, 1 mi (1.6 km) ENE of Adeline, Marshall Co., W.Va. (1969, D. Tanner!).

Middle Island Creek Drainage: Middle Island Creek, 4.3 mi (6.9 km) W of Shirley, 5.8 mi (9.3 km) ENE of Middlebourne, and 0.5 mi (0.8 km) W of Middlebourne, all Tyler Co., W.Va. (all 1969, D. Tanner!).

Little Muskingum River Drainage: Little Muskingum River, Lawrence Twp., Washington Co., Ohio (1962, D.H. Stansbery and C.B. Stein!).

Muskingum River Drainage, Ohio: Numerous recent and historical records from Killbuck Creek, Lake Fork of Mohican River, Kokosing River, Walhonding River, Licking River, Meigs Creek, Olive Green Creek, Wolf Creek, and Muskingum River (chiefly OSUM; also MCZ, NMC, USNM).

Little Kanawha River Drainage: Laurel Run, Hwy. 33 bridge, Spencer Twp., Roane Co. W.Va. (1962, C.B. Stein and M. Lightner!).

Kanawha River Drainage, West Virginia: Elk River, 1 mi (1.6 km) above Gassaway, Braxton Co. (1959 H.D. Athearn!) and 2.6 mi (4.2 km) SSW of Elkview, Kanawha Co. (1963, C.B. Stein!). Little Sandy Creek, Elk Twp., Kanawha Co. (1962, C.B. Stein and M. Lightner!). Coal River, ½ mi (0.8 km) W of Peytona, Boone Co. (UMMZ) and Lower Falls, 2 mi (3.2 km) W of St. Albans, Kanawha Co. (1969, C.B. Stein and K.G. Borror!). Kanawha River, just below Kanawha Falls (1976, K.G. Borror!), 0.6 mi (1 km) below falls, (1969, W.J. Clench and D.H. Stansbery!), and above Deepwater (1969, C.B. Stein and K.G. Borror!), all Fayette Co.

Twelvepole Creek Drainage: Twelvepole Creek at mouth of Sugar Run, Cabwaylingo State Forest, Wayne Co., W.Va. (1959, R. Preston!).

Big Sandy River Drainage: Levisa Fork of Big Sandy River, 6 mi (9.6 km) N of Allen, Floyd Co., Ky. (1963, C.B. Stein!).

Scioto River Drainage, Ohio: Numerous historical and recent records from Whetstone Creek, Olentangy River, Alum Creek, Big Walnut Creek, Big Darby Creek, Little Darby Creek, Deer Creek, Sugar Creek, Paint Creek, Rocky Fork, North Fork, Little Salt Creek, and Scioto River (chiefly OSUM; also MCZ, NMC, USNM).

Ohio Brush Creek Drainage: Ohio Brush Creek opposite Buzzardsroost Rock, Tiffin/Ohio Brush Twp., Adams Co., Ohio. (1963, E.R. Trautman!).

Little Miami River Drainage Ohio: Caesar's Creek, 2 mi (3.2 km) N of Harveysburg, Warren Co. (MCZ). Little Miami River, several recent and historical records (chiefly OSUM, also ANSP, MCZ, USNM).

Licking River Drainage, Kentucky: Licking River at Blue Licks, Bourbon Co. (1964, D.H. Stansbery!); at Hwy. 27 bridge, Butler, Pendleton Co. (1958, W.J. Clench and J. Rosewater!); and at several other localities (OSUM).

Miami River Drainage, Ohio: Miami River, Stokes Twp., Logan Co. (MCZ), Salem Twp., Shelby Co. (MCZ), and ¼ mi (0.4 km) above Taylorsville Dam, 1 mi (1.6 km) E of Vandelia, Montgomery Co. (1966, P. Stromberg!). Loramie Creek, Newport, Shelby Co. (MCZ). Stillwater River 3 mi (4.8 km) SW of Versailles, Darke Co. (1965, J.J. Jenkinson!); Webster, Darke Co. (MCZ); and above Siebenthaler Ave. bridge, Dayton, Montgomery Co. (1965, E. and J. Keferl!). Twin Creek, Twin Twp., Sec. 10, Preble Co. (MCZ).

Kentucky River Drainage, Kentucky: North Fork Kentucky River, Frozen Creek P.O., Breathitt Co. (1959, H.D. Athearn!). Middle Fork Kentucky River, 1 mi W of Tallega, Lee Co. (1958, W.J. Clench and J. Rosewater!). South Fork Kentucky River, Booneville, Ousley Co. (1958, W.J. Clench and J. Rosewater!). Red River, 6.3 mi (10.1 km) NNW to 5.6 mi (9 km) NNE of Campton, Wolf Co. (1977, R. Thoma!). Dix River, 5 mi (8 km) E of Stanford, Lincoln Co. (MCZ). Elkhorn Creek, 3 mi (4.8 km) S of Swallowfield, Franklin Co. (ca. 1958, H.D. and D.R. Athearn). North Fork Salt River, 5 mi (8 km) W of Taylorsville, Spencer Co.; Rolling Fork Salt River, 1 mi (1.6 km) S of New Haven, Nelson Co.; and Beech Fork Salt River, 3 mi (4.8 km) S of Bardstown, Nelson Co. (all 1958, W.J. Clench and J. Rosewater!).

Green River Drainage, Kentucky: Green River at 1 mi (1.6 km) N of Yosemite, Casey Co. (1964, D. and E. Bickel!); 2 mi (3.2 km) NE of Dunnville, Casey Co. (MCZ); 8 mi (12.8 km) S of Campbellsville, Taylor Co. (MCZ); near Wilsons Park, Hart Co. (1964, D.H. Stansbery and D. Bickel!); Munfordville, Hart Co. (1964, D.H. Stansbery!); Mammoth Cave, Edmondson Co. (MCZ); and ½–2 mi (0.8–3.2 km) below dam at Rochester, in Muhlenberg Co. (1965, S.L.H. Fuller!). Nolan River, 1½ mi (2.4 km) S of Glendale, Hardin Co. (MCZ). Barren River, Hick's Ford, 2 mi (3.2 km) SE of Austin, Barren Co. and Ewings Ford, 4 mi (6.4 km) E of Bowling Green, Warren Co. (MCZ). Bays Fork, ¼ mi (0.4 km) E of Claypool, Warren Co. (MCZ). West Fork Drake Creek, Massey Mill, Warren Co. (MCZ). Gasper River, 9 mi (14.4 km) WNW of Bowling Green, Warren Co. (1969, D.H. and M.L. Stansbery!).

Wabash River Drainage: Salamonia River, Mt. Etna, Huntington Co., Ind. (OSUM). Mississinewa River, 3.5 mi (5.6 km) SW of Albany, Delaware Co., Ind. (1969, D. Tanner!) and 1 mi (1.6 km) below Somerset, Wabash Co., Ind. (USNM). Blue River [Thorn Creek?], Columbia City, [Whitley Co.], Ind. (USNM). Tippecanoe River, DeLong,

Fulton Co., Ind. (USNM). Wild Cat Creek near Burlington, Carroll Co., Ind. (USNM). Coal Creek, Veedersburg, Fountain Co., Ind. (1968, C.B. Stein!). Sugar Creek at U.S. Hwy 41 bridge, 9 mi (14.4 km) N of Rockville, Parke Co., Ind. (1968, C.B. Stein!). Salt Fork of Vermilion River, Homer Park, Ill. (1974, H. van der Schalie and A. LaRocque!). Wabash River at Sec. 36, Greenville Twp., Mercer Co., Ohio (MCZ); Andrews, Huntington Co., Ind. (USNM); Peru, Miami Co., Ind. (USNM); and New Harmony, Posey Co., Ind. (USNM). White River, 6 mi (9.6 km) above Noblesville, Hamilton Co.; Martinsville, Morgan Co.; and Worthington, Greene Co., Ind. (all USNM). (See Clark, 1976 for additional records from Wabash and White rivers.) Big Walnut Creek [Eel River], 1.7 mi (2.7 km) E of Bainbridge, Putnam Co., Ind. (1968, C.B. Stein!). Walnut Creek, 7.5 mi (12 km) ESE of Brazil, Putnam Co. [Clay Co.], Ind. (1967, D.H. Stansbery and C.B. Stein!). Big Blue River at Hwy. 40, E end of Knightstown, Hewig Co., Ind. (1964, C.B. Stein!). Sixmile Creek, about 4 mi (6.4 km) NE of Morristown, Hancock Co., Ind. (1975, E. Secora!). Flatrock Creek, 8 mi (12.8 km) S of Shelbyville, Shelby Co., Ind. (1964, C.B. Stein!).

Ohio River: Ohio River above Coraopolis, Allegheny Co., Pa. (ANSP).

CUMBERLAND RIVER SYSTEM.—*Rockcastle River Drainage, Kentucky:* Middle Fork Rockcastle River, Flat Top Church Ford, Jackson Co., (1964, D.H. Stansbery!). Rockcastle River, Livingston, Rockcastle Co. (MCZ) and first bridge S of Livingston (USNM).

Obey River Drainage, Tennessee: East Fork Obey River, Riverton, Fentress Co. (USNM). Obey River at mouth of Hurricane Creek, 3 mi (4.8 km) S of Byrdstown, Pickett Co., Tenn. and Celina, Clay Co. (both MCZ).

Caney Fork River Drainage, Tennessee: Caney Fork River, Mine Run Shoals, DeKalb Co. (ANSP) and 5 mi (8 km) SE of Carthage, Smith Co. (MCZ).

Stones River Drainage, Tennessee: East Fork Stones River, ¼ mi (0.4 km) below Brown's Mill, 2 mi (3.2 km) S of Lascassus, Rutherford Co. (1980, A.H. Clarke!) 1 mi (1.6 km) NW of Readyville, in Rutherford Co. (1965, D.H. Stansbery!) and Hwy. 10, Walterhill, Rutherford Co. (1953, A.H. and L.R. Clarke!). Stones River, 1.2 mi (1.9 km) W of Couchville, Davidson Co. (MCZ) and above Couchville Pike bridge, SE of Nashville, Davidson Co. (1964, B.G. Isom and R.M. Sinclair!).

Harpeth River Drainage, Tennessee: Harpeth River, about 2 mi (3.2 km) NW of Franklin, Williamson Co. (1966, D.H. Stansbery!); also Davidson Co. (MCZ).

Red River Drainage: Whippoorwill Creek at state Hwy. 96 bridge, 1 mi (1.6 km) W of Dot, Logan Co., Ky. (1968, D.H. Stansbery and C.B. Stein!). Red River, 4.5 mi (7.2 km) W of Adams, Robertson Co., Tenn. (1969, D.H. Stansbery!) and Port Royal, mouth of Sulfur Fork, Montgomery Co., Tenn. (1966, D.H. Stansbery!).

Little River Drainage: Little River, 5 mi (8 km) above Cadiz, Trigg Co., Ky. (MCZ).

Cumberland River, Kentucky: South Fork Cumberland River, Barnside, Pulaski Co. (USNM). Cumberland River, 4 mi (6.4 km) S of Jamestown and Creelsboro, (both Russell Co.) and Burksville, Cumberland Co. (all MCZ).

TENNESSEE RIVER SYSTEM.—*Holston River Drainage:* Watauga River near Johnson City, Washington Co., Tenn. (ANSP). South Fork Holston River, 1.0 m (1.6 km) SSW of Friendship, Buck Bridge, Wright Bridge, and Rambeaux Bridge, all Washington Co., Va. (Stansbery and Clench, 1978). Middle Fork Holston River, Chilhowie, Smyth Co., Va. to Shallow Ford Bridge, Washington Co., Va. (Stansbery and Clench, 1974). North Fork Holston River at North Fork Church near Holston, Washington Co., Va.; above Hwy. 33 bridge, Scott Co., Va.; Click Island, Scott Co. (all Ahlstedt, 1980); and Hwy. 23 bridge, Scott Co. (1965, D.H. Stansbery and J.J. Jenkinson!).

Clinch River Drainage: Numerous records from near Tazewell, Tazewell Co., Va. to Norris Reservoir, Claiborne/Granger Co., Tenn. (1953–1979, H.D. Athearn!, A.H. Clarke!, W.J. Clench!, J.J. Jenkinson!, D.H. Stansbery! and others; see Bates and Dennis, 1978). Powell River at Flannery Ford, 7 mi (11.2 km) SW of Jonesville, Lee Co., Va.; 8–10 mi (12.8–16 km) S of Tazewell, Claiborne Co., Tenn. (both 1954, W.J. Clench, R.D. Turner, and D.J. McMichael!) and several records between Va. Hwy. 833 bridge, Lee Co., Va. and Tenn. Hwy. 25 E bridge, Claiborne Co., Tenn. (Ahlstedt and Brown, 1980). Wallen Creek, Lee Co., Va. (USNM).

Sequatchie River Drainage, Tennessee: Sequatchie River, Lee Station, 5 mi (8 km) S of Pikeville, Bledsoe Co. (USNM); 2½ mi (4 km) SSE of Dunlap, Sequatchie Co. (MCZ); and 1 mi (1.6 km) SSE of Whitwell, Marion Co. (1955, J.R. Hood!).

Crow Creek Drainage: Crow Creek, Sherwood, Franklin Co., Tenn. (1966, D.H. Stansbery!).

Paint Rock River Drainage, Alabama: Hurricane Creek near Gurley [?] in Jackson Co. (MCZ). Paint Rock River, Rocky Hollow Ford, 2 mi (3.2 km) below Holly Tree, Jackson Co. (1966, D.H. Stansbery!); 0.2 mi (0.3 km) above Trenton, Jackson Co. (1967, D.H. Stansbery and W.J. Clench!); and 1 mi (1.6 km) S of New Hope, Madison Co. (UMMZ)

Flint River Drainage: Flint River, Madison Co., Ala. (UMMZ).

Limestone Creek Drainage: Limestone Creek, Mooresville, Limestone Co., Ala. (UMMZ).

Elk River Drainage: Elk River at Estill Springs, Franklin Co., Tenn. (USNM); 3 mi (4.8 km) W of Pelham, Franklin/Marion Co., Tenn.; ¾ mi (1.2 km) SE of Fayetteville, Lincoln Co., Tenn. (both 1953, A.H. and L.R. Clarke!); and West of Athens, Limestone Co., Ala. (UMMZ).

Big Nance Creek Drainage: Big Nance Creek at Red Bank Baptist Church, also 4–5 mi (6.4–8 km) above its mouth, both Lawrence Co., Ala. (1966, D.H. Stansbery!).

Shoal Creek Drainage: Shoal Creek, Lauderdale Co., Ala. (UMMZ).

Spring Creek Drainage: Spring Creek, Colbert Co., Tuscumbia, Ala. (USNM).

Bear Creek Drainage: Bear Creek, "Burleson"[?], Franklin Co., Ala. (UMMZ).

Duck River Drainage, Tennessee: Duck River at Shelbyville, Bedford Co. (MCZ); below Lillard Mill, Milltown, Marshall Co. (1956, H.D. Athearn!); 3 mi (4.8 km) S of Chapel Hill, Marshall Co. (1964, D.H. Stansbery!); and Columbia, Mawry Co. (USNM).

Tennessee River: Tennessee River at Knoxville, Knox Co., Tenn.; and Jackson Co., Ala. (both 19th Century records, ANSP).

UPPER MISSISSIPPI RIVER SYSTEM.—*Minnesota River Drainage, Minnesota:* Watonwan River, Blue Earth Co. Minnesota River, 1 mi (1.6 km) N of St. Paul, Washington Co. (both MCZ).

St. Croix River Drainage: Moose River, Sturgeon Lake, Pine Co., Minn. (1970, M.J. Imlay!). Moose River, Namekagon River, St. Croix River and tributaries in Wisc. (several recent records, Mathiak, 1979:30).

Chippewa and Black River Drainages, Wisconsin: Several recent records (Mathiak, 1979:30). Black River, 0.5 mi (0.8 km) SW of Greenwood, Clark Co. (1967, S.W. Reese and J.S. Buker!).

Wisconsin River Drainage: Wisconsin River, 1 mi (1.6 km) S of Land O'Lakes, Vilas Co. (1962, A.H. and L.R. Clarke, and I. Lubinsky!). Several other recent records from headwaters to Portage Co. in Wisconsin River and tributaries (Mathiak, 1979:30).

Skunk River Drainage: Skunk River, Jasper Co., Iowa (USNM).

Pecatonica River Drainage: Pecatonica River near Calamine, Lafayette Co., Wisc. (Mathiak, 1979:30).

Des Moines River Drainage, Iowa: Lower West Fork Des Moines River, Estherville, Emmet Co. (USNM). Des Moines River at Boone, Boone Co. (MCZ) and Des Moines, Polk Co. (USNM). Raccoon River at Sac City, Sac Co. (ANSP); Adel, Dallas Co. (MCZ); and Van Meter, Dallas Co. (MCZ).

Illinois River Drainage, Illinois: Fox River and tributaries, southeastern Wisc. (4 records, Mathiak, 1979:30). Des Plaines River, Joliet, Will Co. (OSUM). Kankakee River, Wilmington, Will Co. (OSUM). Mackinaw River [near] Bloomington, McLean Co. (USNM). Sangamon River, Athens, Menard Co. (ANSP). Illinois River, Morris, Grundy Co. (USNM; see also Starrett, 1971:313).

Upper Mississippi River: Mississippi River at Prescott, Pierce Co., Wisc.; Vermilion Slough, 7 mi (11.2 km) NW of Red Wing, Goodhue Co., Minn.; 1.6 mi (2.6 km) E of Red Wing, Winona, Winona Co., Minn.; Dreshback, Winona Co.; south of Stoddard, Vernon Co., Wisc.; Victory, Vernon Co.; Genoa, Vernon Co.; 14.5 mi (23.2 km) N of Prairie du Chien, Crawford Co., Wisc.; Prairie du Chien; Agnes Landing, 2 mi (3.2 km) N of McGregor, Clayton Co., Iowa; York Landing, north of McGregor; Lynxville, Crawford Co., Wisc; Clayton, Clayton Co., Iowa; Pine City, 9 mi (14.4 km) N of Dubuque, Dubuque Co., Iowa; Wilkins, 11 mi (17.6 km) SE of Dubuque; Savanna, Carroll Co., Ill; Albany, Whiteside Co., Ill.; East Moline, Rock Island Co., Ill.; and 12.5 mi (20 km) and 25 mi (40 km) SW of Davenport, Muscatine Co., Iowa (all 1907, P. Bartsch!, (USNM)).

MISSOURI RIVER SYSTEM.—*Osage River Drainage, Missouri:* Pomme de Terre River, 11 mi (17.6 km) S of Warsaw, Benton Co., (1966, R.B. McMillan!). Niangua River, 4 mi (6.4 km) W of Windyville, Dallas Co. (MCZ). Little Niangua River, Camden Co. (ANSP).

Gasconade River Drainage; Gasconade River, Gascondy, Osage Co., Mo. (MCZ).

Meramec River Drainage, Missouri: Bourbeuse River, 5 mi (8 km) S of Ohensville, Gasconade Co. (1964, D.H. Stansbery and J.J. Jenkinson!). Meramec River at Hwy. 19 bridge just above Steelville, Crawford Co. (1964, D.H. Stansbery and J.J. Jenkinson!); at Hwy. 155 bridge, 11.0 mi (17.6 km) W of St. Clair, Franklin Co. (1977, W. Pflinger!); and at Times Beach, 1.9 mi (3 km) ENE of Eureka, Louis Co. (1977, D.H. Stansbery and A. Buchanan!). Numerous other records from Bourbeuse, Big, and Meramec rivers and tributaries (Buchanan, 1980:24).

LOWER MISSISSIPPI RIVER SYSTEM.—*Hatchie River Drainage:* Big Hatchie River, Crum's Mill, Tippah Co., Miss. (USNM).

White River Drainage: Spring River, Imbiden, Lawrence/Randolph Co., Ark. (1978, C.B. Stein and W.N. Kasson!). Current River, 1 mi (1.6 km) SW of Doniphan, Ripley Co. Mo. (1959, H.D. Athearn!). Black River at Williamsville, Wynn Co., Mo.; Black Rock, Lawrence Co., Ark.; and Kincaid Bar, 2 mi (3.2 km) N of Black Rock (all USNM). Finley Creek, 4 mi (6.4 km) S of Nixa, Christian Co., Mo. and James River, 7 mi (11.2 km) NW of Ozark, Christian Co. (1965, W.H. Dieffenbach!). James River, Galena, Stone Co., Mo. (USNM). Rocky Creek, Cotter, Baxter Co., Ark. (USNM). Buffalo River, 1.7 mi (2.7 km) W of Gilbert, Searcy Co., Ark. (1977, R. and K. Wright!). Middle Fork Little Red River near Clinton, Van Buren Co., Ark. (USNM) and Shirley, Van Buren Co., Ark. (1967, E.R. and R.M. Kinsen!).

Arkansas River Drainage: Neosho River, Americus, Lyon Co., Kan. (USNM); Emporia, Lyon Co., Kan. (USNM); and Ioda, Allen Co., Kan. (MCZ). Spring River, Carthage, Jasper Co., Mo. (1971, C.B. Stein!). Center Creek, Webb City, Jasper Co., Mo. (USNM). Fouch LaFave River, 1 mi (1.6 km) ENE of Bluffton, Yell Co., Ark. (1967, E. Kinser!).

Ouachita River Drainage, Arkansas: Ouachita River, Pencil Bluff, Montgomery Co. (1964, C.B. Stein!) and shoal off Carter Road, Arkadelphia, Clark Co. (1975, D.M. Martin and S.L.H. Fuller!). Caddo River, Caddo Gap, Montgomery Co. and 4 mi (6.4 km) above mouth at Caddo Valley, Clark Co. (both MCZ). Saline River, Benton, Saline Co. (MCZ) and 3½ mi (5.6 km) SE of Traskwood, Grant/Saline Co. (1964, C.B. Stein!).

Lasmigona (Lasmigona) complanata complanata (Barnes, 1823)

FIGURES 7–9

Alasmidonta complanata Barnes, 1823:278, fig. 22. [Type-locality: "Fox River" and "Wisconsin." Type specimen not located; it is probably lost.]

[?] *Unio gigas* Swainson, 1824:15–17. [Type-locality doubtfully specified as "Oronokoo River." Location of type material unknown.]

Unio Katherinae Lea, 1838:143. [Type-locality: "Lake Superior." Type specimen retained by Lady Katherine Douglas, St. Mary's Isles, Scotland, according to Lea.]

Complanaria gigas Swainson, 1840:258, 290, 382. [Type-locality not specified. Location of type specimen unknown. Refers to fig. 141 in Sowerby (1839), which is of *Alasmidonta complanata* Barnes (= *Lasmigona (L.) complanata complanata* (Barnes)).]

THE SHELL

FIGURE 7*a*, *c–e*

DESCRIPTION.—Shell ovate, alate, obliquely subtruncate posteriorly, and compressed; up to about 200 mm long, 150 mm high, and 62 mm wide. Shell thickened anteriorly (up to 11 mm thick) and thin posteriorly (2.5 mm in a large specimen). Anterior margin rounded, ventral margin long and broadly curved, posterior margin biangulate below (at the termination of the posterior ridge) and obliquely subtruncate above, and dorsal margin alate, compressed, and gently curved or nearly straight. Maximum inflation at about the middle of the shell. Beaks low, not inflated, projecting only slightly above the hinge line, and located about 25% the distance from anterior to posterior. Dorsal wing-like expansion prominent (especially in young specimens), much compressed and fragile. In young specimens this causes the shell to be proportionately high (H/L ~ 0.90) but in mature specimens the "wing" is shorter and the shell is therefore proportionately lower (H/L ~ 0.75). Posterior ridge low but distinctly double, i.e., it is a flattened surface defined by two well-marked, narrow, radial ridges. Another radial ridge also occurs above the posterior ridges. Growth rests well-marked by concentric, darkly-pigmented grooves. Post-juvenile sculpturing consisting of lines of growth, other surficial irregularities, and in many specimens, of 12 or more distinct, wide, radial corrugations on the dorsal expansion. Periostracum in juveniles covered with wide and narrow dark green radial rays on a pale green background; the rays are also intersected by concentric dark and light green bands. In adults the periostracum is brown and more uniform except paler near the umbones and, if not eroded away, still faintly exhibiting dark green radial rays in that area. Ligament of moderate length, compressed, strong, and thickened above the lateral teeth but also narrowly extending between the dorsal extensions of both valves and uniting them to each other at their dorsal edges and along their opposing faces.

Hinge teeth heavy but incomplete. Pseudocardinal teeth large, approximately pyramidal, serrated, and directed ventrally, 1 in the right valve and 2 in the left. Interdental projection flange-like, elevated, short, located in the left valve and more or less confluent with the second pseudocardinal. The interdental cavity in the right valve is deep and in some specimens it completely severs the hinge plate. The lateral teeth are thick but mainly proximal and become obsolete distally. There is 1 in the right valve and 1 or 2 in the left. Beak cavity in left valve shallow, not excavated or only slightly so, with an irregular ridge below and with several irregular and deep muscle scars within. Major anterior muscle scars large, well impressed, and deep on the proximal side; pallial band narrow and incised, especially anteriorly, and posterior muscle scars large and shallow but clearly visible (at least in adults). Nacre pearly white and shining; bluish and iridescent centrally and posteriorly; thin and revealing the external periostracal colors around the entire edge of the shell in juveniles but only around the posterior edge in adults.

Beak sculpture strong and composed of about 7 concentric ridges. The earliest 1 or 2 ridges are single-looped but all following ridges are strongly double-looped. In some specimens these loops are regular and nodulous on both their lower extremities, in others the anterior loops

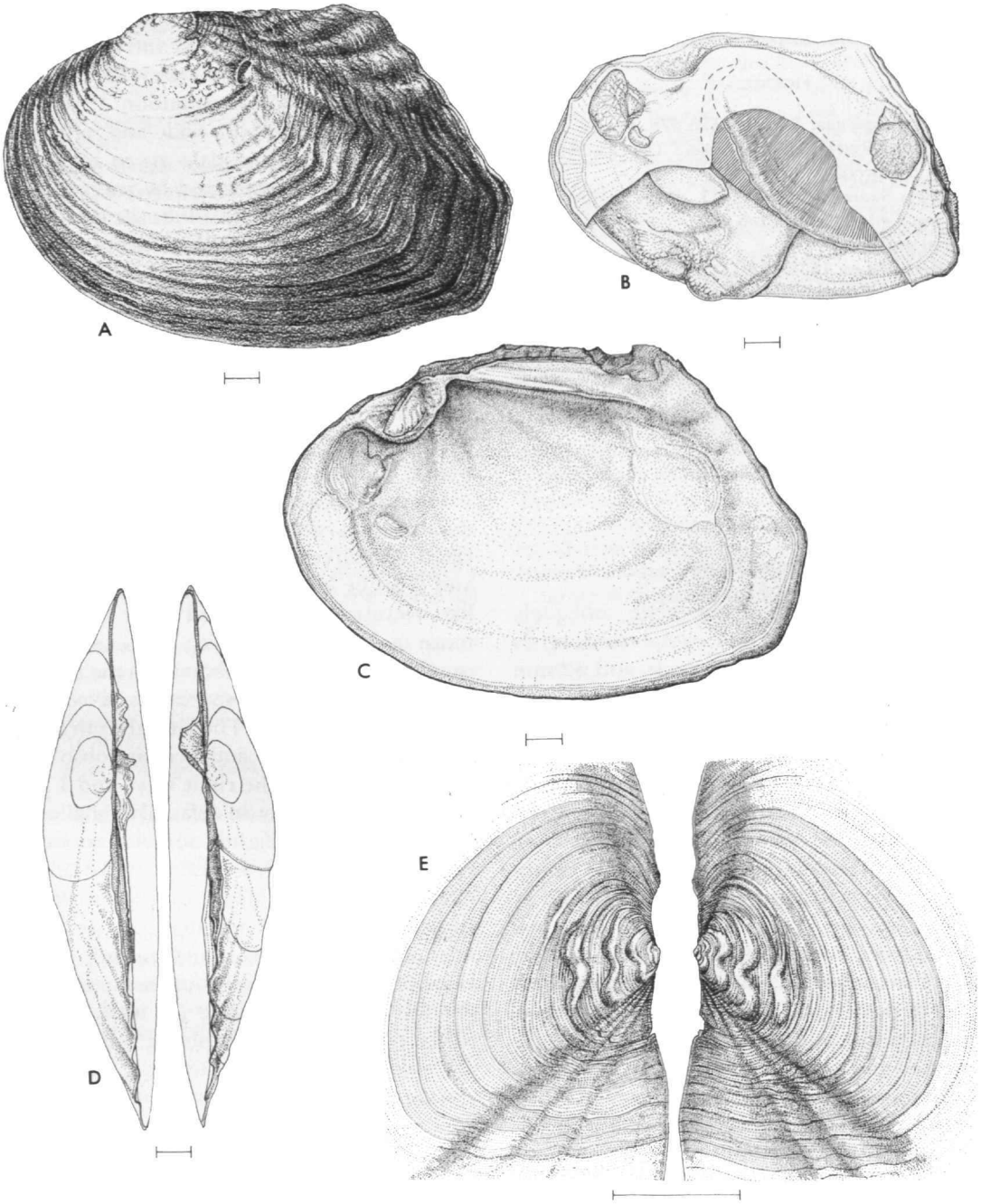

FIGURE 7.—*Lasmigona complanata complanata: a,c,d*, USNM 37303, Des Moines River, Des Moines, Polk County, Iowa; *b*, OSUM 9290, Licking River, Falls Township, Muskingum County, Ohio; *e*, details of umbonal area, USNM 86161, Cincinnati, Cuyahoga County, Ohio. (Scale = 1cm.)

TABLE 6.—*Lasmigona complanata:* shell measurements.

Feature	N	Range	Mean ($\bar{x}$)	S
	Big Walnut Creek, Franklin Co., Ohio (OSUM 6088)			
Length (mm)	6	162.0–177.0	168.5	5.05
H/L	6	0.704–0.749	0.734	0.0185
W/L	6	0.254–0.323	0.282	0.0311
B-A/L	6	0.205–0.296	0.236	0.0296
	Des Moines River, Des Moines, Iowa (USNM 37303)			
Length (mm)	11	123.8–141.2	132.6	5.66
H/L	11	0.698–0.820	0.731	0.0350
W/L	11	0.290–0.329	0.312	0.0131
B-A/L	11	0.201–0.314	0.260	0.0322
	Mukwonago River, Mukwonago, Wisc. (USNM 801484)			
Length (mm)	7	97.5–114.4	107.2	6.14
H/L	7	0.687–0.809	0.747	0.0377
W/L	7	0.265–0.371	0.299	0.0346
B-A/L	7	0.213–0.289	0.253	0.0248
	Milwaukee River, Thiensville, Wisc. (USNM 801322)			
Length (mm)	17	130.8–182.0	161.8	13.54
H/L	17	0.627–0.739	0.660	0.0268
W/L	17	0.285–0.352	0.312	0.0604
B-A/L	17	0.190–0.291	0.243	0.0347

are broken and only the posterior loops are nodulous. The lateral arms of the loops form a series of subparallel radial ridges both anteriorly and posteriorly of the major loops. Supplimentary subparallel radial ridges, on some specimens, extend anteriorly and posteriorly father onto the shell surface.

VARIATION.—Ortmann (1919:133), in contrast to previous authors, states that there are no sexually related differences in the shapes of the shells. I agree in principle with this conclusion.

The Milwaukee River lot (Table 6) contains 7 males and 10 females. Their mean and standard deviation measurements are: (for W/L) ♂ 0.316 ± 0.0195, ♀ 0.310 ± 0.0173; $\left(\text{for } \frac{\text{B-A}}{\text{L}}\right)$ ♂ 0.236 ± 0.0269, ♀ 0.248 ± 0.0325. These pairs of measurements are not statistically different. In the lot from Mukwonago River, however, (7 specimens) 3 of the 4 females had higher W/L values (0.295–0.371) than any of the 3 males (0.265–0.289), although 1 female did not (0.278). In relative position of the beaks there were no indications of difference (♂ 0.257–0.270, ♀ 0.213–0.289). These data indicate that no reliable sexual differences exist in regard to shell shape but, as in *L. costata*, in some populations the most inflated specimens may tend to be females.

Table 6 gives measurements of 4 lots of *L. complanata* from the Ohio-Mississippi River System in the United States. In a previous paper (Clarke, 1973a:47–48) detailed measurements for L (36.9–183.5), H/L (0.643–0.817) and W/L (0.242–0.401) are given for 4 lots from the Nelson River System (James Bay Drainage) in North Dakota and Canada. These latter populations correspond to morph *katherinae* (Lea, 1836). The principle diagnostic features of that morph are smaller maximum size and slower rate of growth (in most populations) and lack of radial costation on the dorsal wing. As discussed previously (Clarke, 1973a:49), those characters related to growth are not taxonomically useful and morph *katherinae* does not merit distinct taxonomic status. The significance of dorsal costation is more complex, however, and is discussed below under *L. complanata alabamensis*.

TOPOGRAPHIC ANATOMY

FIGURE 7*b*

SPECIMEN DESCRIBED.—USNM 801484, from Mukwonago River, Mukwonago, Sec. 25,36; T5N, R18E, Waukesha Co., Wisconsin, collected 8 November 1979 by H.A. Mathiak; fixed directly in 10% formaldehyde and preserved in 70% ethyl alcohol; shell length 111.0 mm, sex female (gravid, with glochidia).

DESCRIPTION.—Mantle pale grayish brown, translucent with the colors of the demibranchs and foot showing through, with a thickened muscular edge (about 14 mm wide, 1.0 mm thick anteriorly and 5 mm wide, 1.5 mm thick posterioventrally). A continous narrow band of pale orange pigment close to the mantle edge posterioventrally and posteriorly is joined, a little anterior to the incurrent opening, by a very narrow

band of dark, purple-brown pigment on the very edge, which continues posteriorly and dorsally to the dorsal margin and becomes broad along the inner edges of the mantle openings.

Incurrent opening 19.0 mm long and surrounded within by 3–4 rows of flattened filiform papillae, those of the inner row the longest (about 1.2 mm long) and 0.2 mm wide at the base. Portions of mantle edges between incurrent and anal openings about 1 mm long. Anal opening, 11.2 mm long and surrounded internally and near its edge by a narrow crenulated ridge. Mantle connection between anal and supra-anal opening 3.7 mm long. Supra-anal narrow, slit-like, and 23.0 mm long.

Outer demibranch about 63 mm long and 32 mm high (torn), thick (7.7 mm), pad-like, engorged with glochidia, and fragile. The free ventral margin is broadly curved and there are about 1.0–1.5 water tubes per mm and 10 surficial filaments and 5 cross filaments per mm. Inner demibranch about 62.5 mm long, 30.0 mm high, rounded anteriorly and ventrally and narrow posteriorly. There are about 1.2–1.6 water tubes per mm, and 12 surficial filaments and 3 cross filaments per mm. The inner lamina of the inner demibranch is attached to the visceral mass anteriorly but not attached centrally or posteriorly.

The labial palpi are nearly straight or somewhat concave above, more or less evenly convex below, and with pointed apices. The palpi do not touch the inner demibranchs. The outer surface of the outer palpus is smooth and the inner opposing surfaces of each member are radially furrowed (about 5 furrows per mm at the margin). The outer palpus of each pair is fused to the mantle for about ¾ of its length and subdorsally, for about ⅞ of its length, to the inner palpus.

Ortmann (1912:283) writes: "Color whitish when young, but foot and gills browner when old. Abdominal sac brown-orange, marsupium pale yellow to brown." Baker (1928:149) states: "Color whitish in young specimens; in mature individuals the foot, gills, and abdominal sac are brownish or yellowish; when gravid the gills are brownish." The colors of the specimens reported above and in Table 7 are in agreement with those statements.

VARIATION.—Table 7 demonstrates that all of the characters tabulated are variable. The number of rows of papillae at the edge of the incurrent opening is particularly inconstant, ranging from 1 to about 3½, and their maximum heights also vary extensively (0.7–2.2 mm). The relative position of the labial palps with respect to contact with the inner demibranchs is also quite variable but the number of grooves per mm on opposing surfaces of the palps is rather constant.

According to Ortmann (1912:282) and Baker (1928:149) the mantle connection between the anal and supra-anal openings is as long as the anal opening, and the supra-anal opening is somewhat longer than either. In more than two-thirds of the specimens reported above, however, the mantle connection is distinctly shorter than the anal opening and in all of the specimens reported the supra-anal opening is longer (in most it is much longer) than the mantle connection or the anal opening. Since the supra-anal opening extends from that mantle connection nearly to the dorsal margin, in young specimens (see specimen 14) with a high dorsal wing the supra-anal opening is very long.

As in *Lasmigona costata*, sterile females are distinguishable from males by the presence of about twice as many septa per mm in the outer demibranch of the females than in the males, but in *L. complanata* the corresponding numbers of septa are greater.

Other variable features were also observed. The margin of the anal opening is crenulated in most specimens but with a more-or-less distinct row of short (0.2–0.3 mm) papillae in some (specimens 2, 6, and 14). In two specimens (2 and 11) the inner demibranchs were not at all connected to the visceral mass but in the other specimens examined a short connection was present along the anterior end of the demibranch.

GLOCHIDIUM

FIGURE 8

DESCRIPTION.—Glochidium ovate pyriform, 0.337 mm in height and in length, and 0.116

TABLE 7.—*Lasmigona complanata:* variation in topographic anatomy (terminology same as Table 2).

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 in OD (N/mm)	Sex	Pre-preserv. treatment: Nemb. relax.	Form. fixed
								Mukwonago River, Mukwonago, Waukesha Co., Wisc., H.A. Mathiak, 8 Nov 1979							
1	114	2	M	18	12	3	21	1–2	1.5	OV	4	grav.	GF	–	+
2	112	2	W	19	11	3	22	2	1.6	torn	5	grav.	GF	–	+
3	111	1	M	17	10	3	21	3–4	1.2	NT	5	grav.	GF	–	+
4	109	1	W	18	10	4	21	2–3	1.8	NT	5	0.7–0.8	(M)	–	+
5	103	1	W	18	12	3	21	2	1.5	OV	5	0.5–0.8	(M)	–	+
6	102	2	W	13	12	3	21	2	1.6	NT	5	0.7–0.9	(M)	–	+
7	98	1	W	17	14	4	24	2–3	1.3	T	6	grav.	GF	–	+
								Milwaukee River, Washington Co., Wisc., H.A. Mathiak, 24 May 1980							
8	144	2	M	16	7	4	21	1	1.3	NT	5	1.6–2.0	(F)	–	+
9	122	2	M	19	8	12	14	1–2	1.2	T	5	grav.	GF	–	+
10	115	2	M	18	8	9	17	1	1.5	NT	4	0.7–1.1	(M)	–	+
								St. Francis River, S of Marked Tree, Poinsett Co., Ark., M. Lipford and T. Manning, 12 Nov 1979							
11	144	1	M	23	12	8	24	3–4	2.2	OV	4	grav	GF	–	+
								St. Francis River, 1½ mi N of Fisk, Butler/Stoddard Co., Mo., T. Manning and M. Lipford, 26 Jun 1979							
12	114	2	W	21	9	15	18	1+	0.7	OV	5	0.9–1.0	(M)	–	+
								St. Francis River, N of Rombouer, Butler/Stoddard Co., Mo., T. Manning and M. Lipford, 26 Jun 1979							
13	112	1	M	21	9	9	16	2	1.5	NT	5	1.7–2.0	(F)	–	+
								Black River, mile 1, N of Point Ferry, Independence/Jackson Co., Ark., T. Manning and M. Lipford, 15 Oct 1979							
14	86	1	W	15	7	14	33	2	1.2	NT	5	1.8–2.0	(F)	–	+

mm in single valve convexity. The valves are somewhat asymmetrical: the anterior margin is more evenly convex and the point of maximum convexity is lower than on the posterior margin, the apices are located about 46% of the distance from anterior to posterior, and the point of maximum inflation is posterior of center. Surface of glochidium finely malleated and pitted, except for a band at the edges of the valves, which is ridged and somewhat malleated but not pitted. The band is about 35 μm wide at the apex and 20–25 μm wide elsewhere. The malleated depressions are subcircular or polygonal and about 5–6 μm wide and the pits are about 1.5–4 μm wide and are located, in groups of 1 to 5, within the depressions. The hinge is flattened, somewhat convex centrally, and about 0.225 mm long. The ligament is external and partly internal, being exposed internally within a 60 μm-long excavated portion of the hinge, which is centered about 43% of the distance from anterior to posterior.

Each apical stylet is rostrate, subtriangular in cross-section, about 0.070 mm long and 0.035 mm wide at the base, with a convex (and microstylet-bearing) outer surface and a narrow, sharp, somewhat recurved distal point. Each stylet is also supported on each side, for about ⅓ of its length, by a membrane that continues around, and is joined to, the edges of the shell. The membrane is continuous across the hinge and along the corresponding margin on the opposite valve and appears to serve to elevate the stylet when stretched by the opening of the valves. The microstylets, which (except for the tips) cover the exposed surface of each stylet, are up to 9 μm

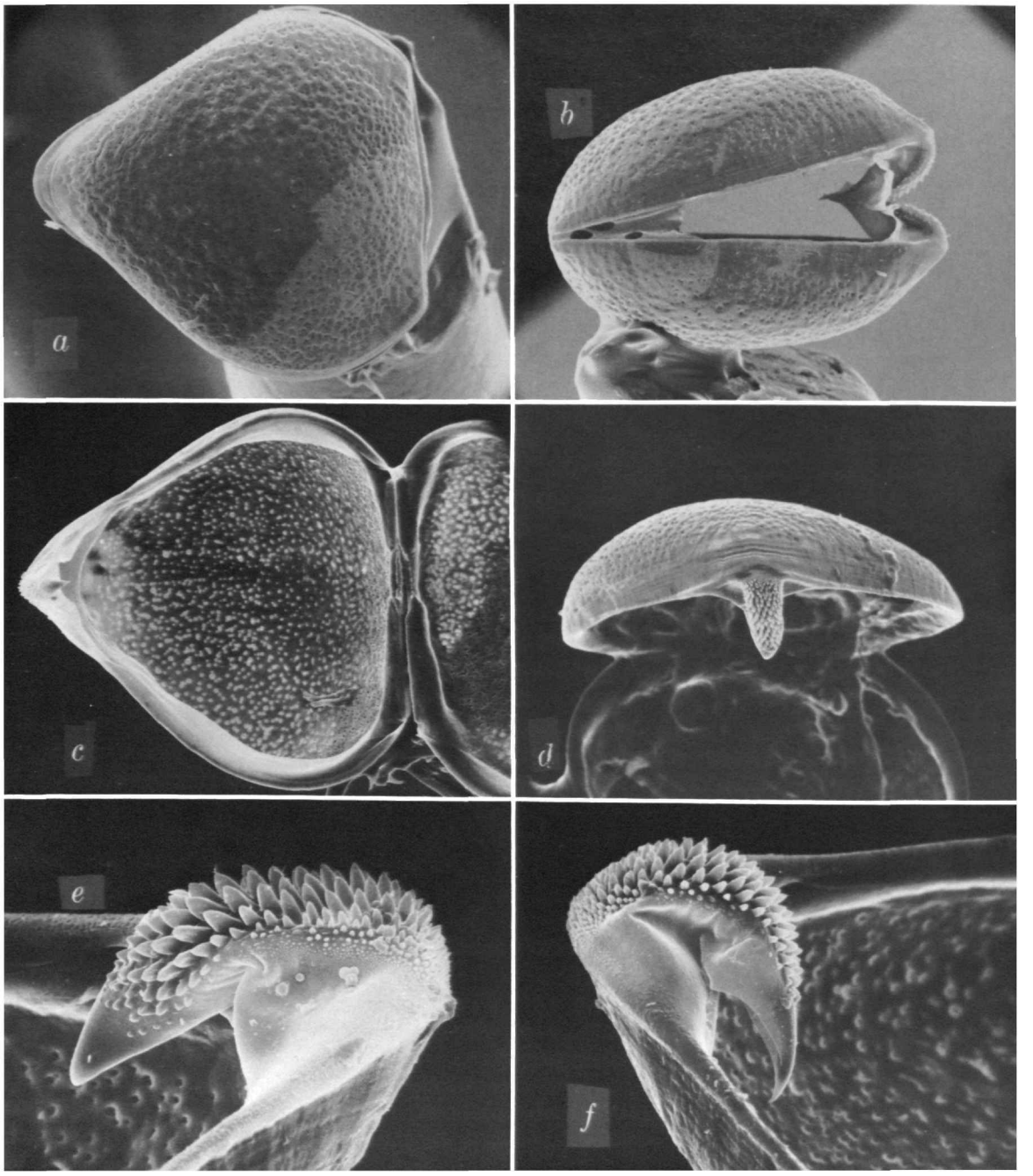

FIGURE 8.—Glochidia of *Lasmigona complanata complanata: a,b,d–f*, USNM 801484, Mukwonago River, Mukwonago, Waukesha County, Wisconsin; *c*, USNM 801474, Milwaukee River, Washington County, Wisconsin (*a,d* × 195; *b* × 205; *c* × 185; *e* × 700; *f* × 510).

long, 4.5 μm wide at their bases, subquadrate in cross-section with about 4 cutting edges, inclined forward toward the apex of the stylet, are arranged approximately in intersecting diagonal rows, and number about 80–90 on each stylet. Numerous, smaller (1–2 μm long) pyramidal microstylets are on the bases of the stylets and these give way to tiny (<0.5 μm) micropoints that extend laterally onto the rims of the valves.

The description is of a glochidium from an adult specimen (USNM 801474) collected from the Milwaukee River, Washington County (Sec. 25, T12N, R20E), Wisconsin by Mr. Harold A. Mathiak on 24 May 1980. (Many of the glochidia had already been discharged.) Another glochidium from the same adult, is 0.345 mm high and 0.340 mm long, the points of maximum convexity of the anterior and posterior margins are of equal height above the hinge, and the apex is located 42% of the distance from anterior to posterior. In another glochidium taken from a somewhat deformed specimen (USNM 801484) collected in the Mukwonago River at Mukwonago, Waukesha County, Wisconsin by Mr. Mathiak on 8 November 1979, the height is only 0.303 mm, the width is 0.287 mm, single valve convexity is 0.086 mm, and the stylets have 1 or 2 subapical lateral flanges. In still another glochidium, taken from an apparently normal specimen from the same lot, the height is 0.327 mm, the length is 0.317, the width is 0.181 mm, and the stylet is about 0.115 mm long.

Other authors, quoted by Baker (1928:149), give height and length measurements of 0.320 × 0.310 mm, 0.30 × 0.29 mm, 0.34 × 0.34 mm, and 0.32 × 0.31 mm.

Life History

Gravid Period.—Mature glochidia were taken from Wisconsin specimens collected on 8 November and 24 May. A specimen in an early stage of gravidity (with developing eggs) was collected in Manitoba on 9 August (Clarke, 1973a:49). According to Baker (1928:150), in Wisconsin *L. complanata* is gravid from September to April or May and not gravid in July and August.

Natural Hosts.—Fish hosts of *L. complanata* include carp (*Cyprinus carpio* L.), green sunfish (*Lepomis cyanellus* Rafinesque), largemouth bass (*Micropterus salmoides* (Lacepede)), and white crappie (*Pomoxis annularis* Rafinesque) (Fuller, 1974:234).

Habitat.—In Western Canada, L. *complanata* was found in rivers from 25 to 200 feet wide, with rapid to slow current, among sparse to moderately abundant aquatic macrophytes, and on sand or mud bottoms (Clarke, 1973a:48, 49). Baker (1928:150) gives large and small rivers and creeks on a mud (usually), sand, or fine gravel bottom in depths of a few cm to a meter.

Geographical Records

Figure 9

Canadian Interior Basin Drainage Systems

Nelson River System.—*Winnipeg River Drainage:* Whitemouth River near Whitemouth, Man. (1951, W.E. Godfrey!; 1961, A.H. and L.R. Clarke!). Birch River near McMunn, Man. (1961, A.H. and L.R. Clarke!). Historical records cited in Clarke (1973a:48).

Red River Drainage: Numerous recent and historical records from Red River, Assiniboine River, Qu'Appelle River, and tributaries in Man., Sask., and N. Dak., cited in Clarke (1973a:48) and Cvancara (1967:189).

Saskatchewan River and Lake Winnipegosis Drainage: Recent and historical records from White Earth Creek, Sturgeon River, Battle River, Turtlelake River, Shell River, Carrot River, Shoal River, Valley River, Woody River, Swan River, and Red Deer River in Man., Sask. and Alta. cited in Clarke (1973a:48).

Nelson River Drainage: Recent and historical records from Lake Winnipeg, Pigeon River, Gunisao River, Nelson River, and Burntwood River in Man. cited in Clarke (1973a:48).

Atlantic Drainage Systems

St. Lawrence River System.—*Lake Superior Drainage:* Lake Superior (Lea, 1838; type-locality of *Unio katherinae* Lea). Red Cliff Creek, Bayfield Co., Wisc. (Baker, 1928:151). Not recorded in Lake Superior Drainage by Mathiak (1979:31).

Lake Michigan Drainage: Numerous recent records from Oconto River, Oconto Co.; Kewaunee River, Kewaunee Co.;

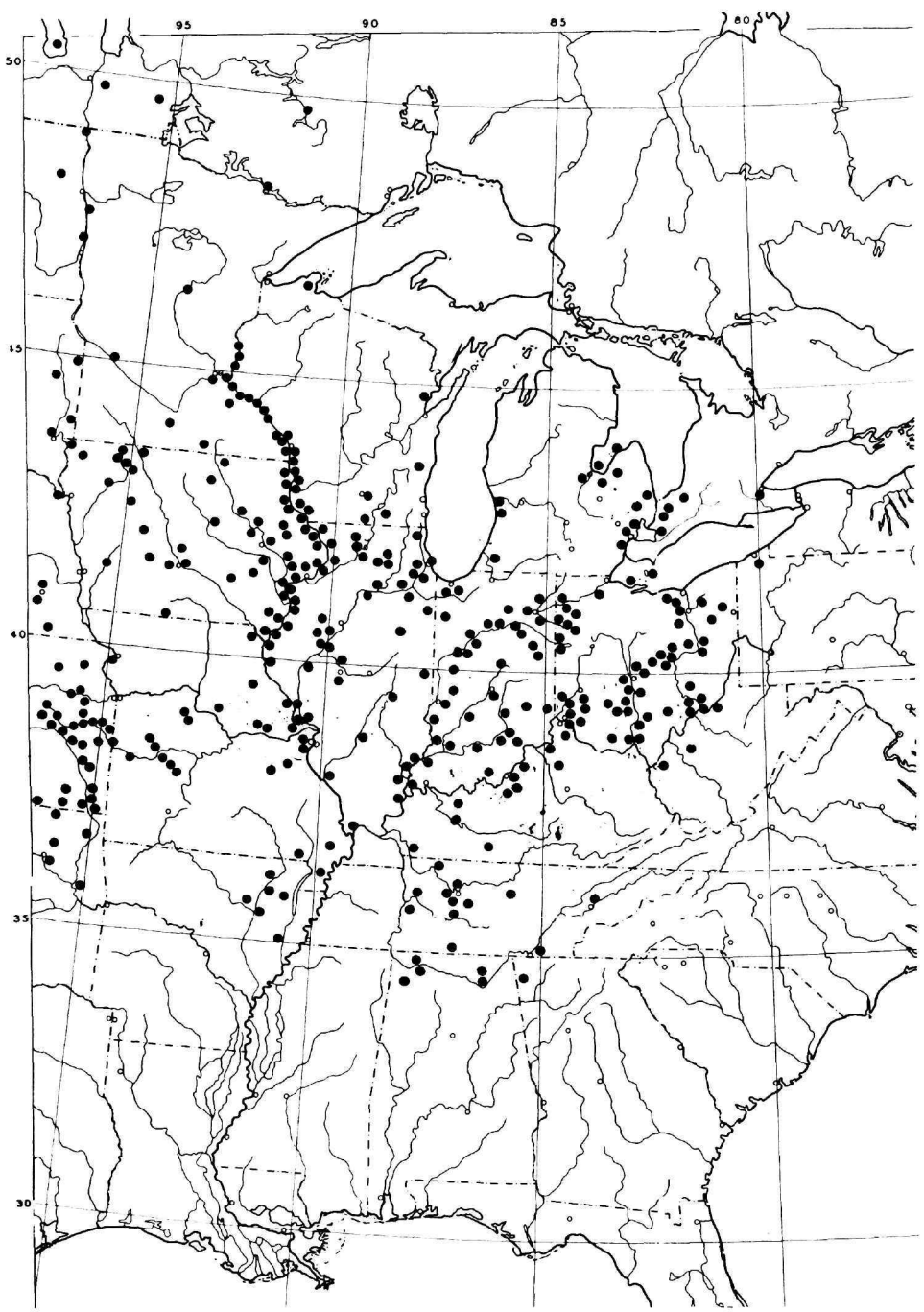

FIGURE 9.—Geographical distribution of *Lasmigona complanata complanata*. (See "Geographical Records" for localities in North Dakota, South Dakota, Nebraska, Kansas, and Oklahoma that are not plotted; for western Canadian localities, see Clarke, 1973a:48, 49; small open circles = cities.)

East and West Twin River, Manitowoc Co.; Manitowoc River, Calumet Co.; Milwaukee River, Washington, Ozaukee, and Milwaukee counties; and small streams in Racine and Kenosha counties, all Wisconsin (Mathiak, 1979:31). Salt Creek, Porter Co., Ind. (MCZ). St. Joseph River, Berrien Springs, Berrien Co., Mich (ANSP). Black River, 2 mi (3.2 km) S of Holland, Ottawa Co., Mich. (UMMZ). Grand River, Mich. (MCZ).

Lake Huron Drainage, Michigan: Saginaw River, 5 mi (8 km) below Saginaw, Saginaw Co. (1964, G. and F. Ahrens!); Cass River, 3 mi (4.8 km) NE of Caro, Tuscola Co. (1967, G. and F. Ahrens!); and Frankenmuth, Saginaw Co. (UMMZ). Saginaw Bay near mouth of Kawkawlin River, Bay County, and State Park, Bay City, Bay County (both UMMZ).

Lake St. Clair Drainage: Mill Creek, 3 mi (4.8 km) W of Yale; St. Clair Co., Mich. (MCZ). Belle River, 4 mi (6.4 km) S of Capac, St. Clair Co. (MCZ) and 4 mi (6.4 km) above Marine City, St. Clair Co. (1951, H.D. Athearn!). Bear Creek, 3½ mi (5.6 km) SSW of Brigden, Moore Twp., Lambton Co., Ont. (1972, C.G. Gruchy!, 1974, A.H. Clarke!) and 0.3 mi (0.5 km) from mouth, near Wilkesport, Lambton Co. (1973, W. Scott!). East Branch Sydenham River, 10 mi (16 km) SW of Strathroy, Middlesex Co., Ont. (1971, A.H. and L.R. Clarke!). McGregor Creek, in cemetary, Chatham, Kent Co., Ont. (1963, H.D. Athearn!). North Branch Clinton River, 2.3 mi (3.7 km) N of Mt. Clemens, Macomb Co., Mich. (1978, C.B. Stein!). Rouge River, Thirteen Mile Road, 2 mi (3.2 km) S of Birmingham, Oakland Co., Mich. (MCZ). Detroit River, Mich. (USNM).

Lake Erie Drainage: St. Joseph River, 3 mi (4.8 km) SW of Cedarville, Allen Co., Ind. (1978 M. Henschen!) and Fort Wayne, Allen Co., (USNM). Canal, Fort Wayne, Allen Co., Ind. (USNM). St. Mary's River, 4 mi (6.4 km) above Rockford, Mercer Co., Ohio (1951, H.D. Athearn!). Willshire, Van Wert Co., Ohio (OSUM); and south of Fort Wayne, Allen Co., Ind. (1962, D.H. Stansbery!). Maumee River, Sec. 12, Crane Twp., Paulding Co., Ohio (MCZ). Auglaize River, Sec. 28, Duchouquet Twp., Auglaize Co., Ohio (MCZ); 4.8 mi (7.7 km) ENE of Kossuth, Auglaize Co. (OSUM); mouth of Blue Creek, Brown Twp., Paulding Co. (1965, H.F. Price!); and 1 mi (1.6 km) S of Powell River, Defiance Co. (OSUM). Ottawa River, Kalida, Putnam Co., Ohio (ANSP). Flatrock Creek, Sec. 35, Emerald Twp., Paulding Co., Ohio (MCZ). Gordon Creek, 2 mi (3.2 km) SSW of Mark Center, Defiance Co., Ohio (1975, C.E. Cichra!). Beaver Creek, 1.3 mi (2.1 km) SE of Grand Rapids, Wood Co., Ohio (1977, T.E. Linkous!). East Branch Black River, 3 mi (4.8 km) E of Bolden, Lorain Co., Ohio (OSUM) and Lagrange Twp., Lorain Co. (1964, B.J. Zahwranec!). Cuyahoga River, Hwy. 303 bridge, Shalersville Twp., Portage Co., Ohio (1964, D.H. Stansbery!). Ohio Canal, Akron, Summit Co., Ohio (MCZ). Grand River, Caledonia, Haldimand Co., Ont. (MCZ). Lake Erie at Crane Beach State Park, near Lucas/Ottawa County boundary, 17–19 mi (27.2–30.4 km) E of Toledo, Lucus Co., Ohio (1966, D.G. De Weese!); beach at Locust Point, 9 mi (14.4 km) NW of Port Clinton, Ottawa Co., Ohio; and Fish Point, south end of Pelee Island, Essex Co., Ont. (both 1977, B.D. Valentine!).

U.S. Interior Basin Drainage Systems

OHIO RIVER SYSTEM.—*Allegheny River Drainage:* Leboeuf Creek, Waterford, Erie Co., Pa. (UMMZ). Mahoning River, Alliance, Stark Co., Ohio (MCZ). West Branch Mahoning River, below dam at Newton Falls, Trumbull Co., Ohio (1966, D.H. and M.L. Stansbery!). Eagle Creek, Garrettsville, Portage Co., Ohio (MCZ).

Middle Island Creek Drainage: Middle Island Creek, 2.0 mi (3.2 km) ENE of Arvilla, Pleasants Co., W.Va. (1969, D. Tanner!).

Muskingum River Drainage, Ohio: Chippewa Lake, Medina Co. (ANSP). Sugar Creek, 2 mi (3.2 km) S of Orrville, Wayne Co. (1974, E.P. Keferl!). Conotton Creek, 1.1 mi (1.8 km) ESE of Leesville, Carroll Co. (1979, R. Sanders!). Ohio Canal New Philadelphia, Tuscarawas Co. (MCZ). Killbuck Creek, 1 mi (1.6 km) N of Hwy. 77 bridge, Bethleham/Clark Twp., Coshocton Co. (1962, D.H. Stansbery!). Mohican River at mouth, Coshocton Co. (1977, D.H. Stansbery and K.G. Borror!). Little Stillwater Creek, 2.2 mi (3.5 km) ENE of Dennison, Tuscarawas Co. (OSUM). Numerous other recent records from Tuscarawas River, Walhonding River, Little Wakatomika Creek, Raccoon Creek, Wolf Creek, and Little Muskingum River (OSUM). Historical records from Meigs Creek near Relief, Morgan Co. and East Branch of Little Hocking River, 1.2 mi (1.9 km) W of Constitution, Washington Co. (OSUM). Numerous (40 +) recent records from Muskingum River (OSUM).

Hocking River Drainage: Hocking River, 1.7 mi (2.7 km) SSE of Haydenville, Hocking Co., Ohio (OSUM).

Kanawha River Drainage: Pocatalico River, Hicumbottom, Kanawha Co., W.Va. (1969, C.B. Stein and K.B. Borror!).

Guyandotte River Drainage: Guyandotte River, Huntington, Cabell Co., W.Va. (UMMZ).

Scioto River Drainage, Ohio: Numerous recent records from Alum Creek, Blacklick Creek, Big Walnut Creek, Big Darby Creek, Deer Creek, Paint Creek, Salt Creek, and Scioto River (OSUM).

Little Miami River Drainage, Ohio: Caesar Creek, 0.2 mi (0.3 km) above its mouth, 7.0 mi (11.2 km) NE of Lebanon, Warren Co., (1972, D.H. Stansbery and C.B. Stein!). Todd Fork, 0.8 mi (1.3 km) NW of Middleboro, Warren Co. (1972, S.A. Dole!). East Fork Little Miami River, Batavia Twp., Clermont Co. (MCZ). Little Miami River, Sec. 10, Wayne Twp., Warren Co. and Cincinnati, Hamilton Co. (both MCZ).

Miami River Drainage: Miami River, Hamilton, Butler Co., Ohio (MCZ). Whitewater River, Brookville, Franklin Co., Ind. (MCZ).

Licking River Drainage: Licking River at Hwy. 27 bridge, Butler, Pendleton Co., Ky. (1958, W.J. Clench and J. Rosewater!).

Kentucky River Drainage: Elkhorn Creek near Ky. Hwy. 1, Franklin Co., Ky. (1963. U. Soelinger!). Kentucky River, Hewig Co., Ky. (USNM).

Salt River Drainage, Kentucky: Floyds Fork Salt River, 4 mi (6.4 km) E of Anchorage, Jefferson Co. (OSUM). North Fork Salt River at Barnes, 5 mi (8 km) west of Taylorville, Spencer Co. and 1 mi (1.6 km) SE of Mt. Washington, Bullitt Co. (both 1958, W.J. Clench and J. Rosewater!). Rolling Fork Salt River, New Haven and ½ mi (0.8 km) S of New Haven, Nelson Co. Ky. (both MCZ). Beech Fork Salt River, 1 mi (1.6 km) SW of Bardstown, Nelson Co. (MCZ).

Blue River Drainage: Blue River, 3 mi (4.8 km) below Milltown, Crawford Co., Ind. (1950, H.D. and D. R. Athearn!).

Green River Drainage, Kentucky: Rough River, Dundee, Ohio Co. (MCZ). Green River below Lock 5 Dam at Glenmore, Warren Co. (1978, D.H. Stansbery and K.G. Borror!) and ½–2 mi (0.8–3.2 km) below dam at Rochester, Muhlenberg Co. (1965, S.L.H. Fuller!).

Wabash River Drainage: Wabash River, just east of Wabash, Mercer Co., Ohio (1962, D.H. Stansbery and C.B. Stein!). Sec. 21, Recovery Twp., Mercer Co., Ohio and near Geneva, Adams Co., Ind. (both MCZ); Makon, Jackson Twp., Huntington Co., Ind. (1950, H.D. Athearn!); Peru, Miami Co., Ind. (1969, C.B. Stein!); Logansport, Cass Co., Ind. (USNM); Lafayette, Tippecanoe Co., Ind. (MCZ) and below Lafayette (1964, D.H. Stansbery and R.I. Johnson!); Terre Haute, Vigo Co., Ind. (MCZ): Graysville, Sullivan Co., Ind. (1975, C.F. Clark!); Vincennes, Knox Co., Ind. (UMMZ): east of Maumee, White Co., Ill. (1975, C.F. Clark!); and Juno Island, New Harmony, Posey Co., Ind. (MCZ). Brooks Creek, Jay Co., Ind. (MCZ). Salamonia River, Montpelier, Blackford Co., Ind.; near Monument City, Huntington Co., Ind. (both UMMZ); and Grant Co., Ind. (MCZ). Eel River, North Manchester, Wabash Co., Ind. (MCZ). Tippecanoe River, White Co., Ind. (MCZ) and Freeman Lake, Ind. (1965, J. Bates and R. Wakefield!). Wildcat Creek, 10 mi (16.1 km) above mouth, 10 mi (16.1 km) ENE of Lafayette, Tippecanoe Co., Ind. (1963, C.B. King!). Salt Fork Vermilion River, Homer, Champaign Co., Ill. (NMC). Sugar Creek, 9 mi (14.4 km) N of Rockville, Parke Co., Ind. (1968, C.B. Stein!). Little Wabash River, White Co., Ill. (UMMZ). West Fork White River, Strawtown, Hamilton Co., Ind.; Worthington, Greene Co., Ind. (both UMMZ); and Maysville, Davies Co., Ind. (1961, C.B. Stein!). White River, Indianapolis, Marion Co., Ind. Big Walnut Creek, North Road, Floyd Twp., Putnam Co., Ind. (both MCZ). Flatrock Creek, Waldron, Shelby Co., Ind. (MCZ). Clifty Creek, 2.7 mi (4.3 km) E of center of Columbus, Bartholomew Co., Ind. (1979, G.R. Finni!). Muscatatuck River, 12 mi (19.2 km) N of Salem, Washington Co., Ind. (UMMZ). East Fork White River, east of Medora, Jackson Co., Ind.; Brownsville, Jackson Co. (both UMMZ); and Shoals, Martin Co., Ind. (1961, C.B. Stein!).

Ohio River: Cincinnati, Hamilton Co., Ohio (MCZ) and just below mouth of Wabash River, Gallatin Co., Ill. (UMMZ).

CUMBERLAND RIVER SYSTEM.—*Cumberland River Drainage:* Mine Run Shoals, Caney Fork River, DeKalb Co., Tenn. (ANSP). East Fork Stone's River, Walterhill, Rutherford Co., Tenn. (1967, W.J. Clench and D.H. Stansbery!). Harpeth River, Davidson Co., Tenn. (1955, S.T. Dillon!) and west of Shacklett, Cheatham Co., Tenn. (UMMZ). Little River, Cadiz, Trigg Co., Ky. (MCZ). Cumberland River, Edenwold, Davidson Co., Tenn. (MCZ) and Red Rock Bar, Clarksville, Montgomery Co., Tenn. (UMMZ).

TENNESSEE RIVER SYSTEM.—*Tennessee River Drainage:* Holston River between Big Flat Creek and Morday Island, Knox Co., Tenn. (1970, B. Gilson!). Paint Rock River, 0.2 mi (0.3 km) above Trenton, Jackson Co., Ala. (1967, W.J. Clench and D.H. Stansbery!) and New Hope, Marshall Co., Ala. (ANSP). Elk River, Elkton, Giles Co., Tenn. (UMMZ). Cedar Creek, 1 mi (1.6 km) E of Pogo, Franklin Co., Ala. (1966, D.H. Stansbery and P. Yokley!). Duck River at Williamsport, Maury Co., Tenn. (UMMZ); 4 mi (6.4 km) east of Columbia, Maury Co. (MCZ); and south of Waverly, Humphreys Co., Tenn. (UMMZ). Buffalo River, 5 mi (8 km) N of Lobelville, Perry Co., Tenn. (UMMZ). Tennessee River at Harrison, Hamilton Co., Tenn. (1963, C.B. Stein!) and Muscle Shoals (canal), Lauderdale Co., Ala. (ANSP).

UPPER MISSISSIPPI RIVER SYSTEM.—*Minnesota River Drainage, Minnesota:* Minnesota River at Montevideo, Chippewa Co. (1964, A.H. and L.R. Clarke!) and 2.8 mi (4.5 km) SSW of Bloomington, Hennepen/Scott Co. (1977, D.H. Stansbery and M. Havlik!). Watonwan River, Blue Earth Co. (MCZ).

St. Croix River Drainage: Clam River near Clam Falls, Polk Co., Wisc. (Mathiak, 1979:31). St. Croix River at Stillwater, Washington Co., Minn. (USNM); Hudson, St. Croix Co., Wisc. (1977, S.L.H. Fuller!; Mathiak, 1979:31); and Prescott, Pierce Co., Wisc. (USNM).

Cannon River Drainage: Cannon River, Faribault, Rice Co., Minn. (USMM).

Chippewa River Drainage, Wisconsin: Eau Claire River, Eau Claire and Clark counties (Mathiak, 1979:31). Chippewa River, in accessory channel, Maxville Twp., Buffalo Co. (Mathiak, 1979:31).

Black River Drainage, Wisconsin: Beaver Creek, Galesville, Trempealeau Co. Black River, Irving, Jackson Co. (both Mathiak, 1979:31).

Wisconsin River Drainage, Wisconsin: Wisconsin River at Rhinelander, Oneida Co.; near Plover, Portage Co.; and near Lone Rock, Sauk Co. (all Mathiak, 1979:31). Tributary of Wisconsin River near Wausau, Marathon Co. (Mathiak, 1979:31). Yellow River near Marshfield, Wood Co. and Necedah, Juneau Co. (both Mathiak, 1979:31). Lemonweir River at Mauston, Juneau Co. (Mathiak, 1979:31).

Rock River Drainage: [Rock River], Madison, Dane Co., Wisc. Turtle Creek, 3 mi (4.8 km) N of Darien, Walworth Co., Wisc. (1976, H. Mathiak!). Sugar River, Wisc. (MCZ). Yellow Creek, Freeport, Stephenson Co., Ill. (UMMZ). Kishwaukee River, Winnebago Co., Ill. (UMMZ). Kishwaukee Creek, Sycamore and DeKalb, DeKalb Co., Ill. (both MCZ). Rock River, 1 mi (1.6 km) S of Rockford, Winnebago Co., Ill. (UMMZ).

Wapsipinicon River Drainage, Iowa: Wapsipinicon River at Waubeek, Linn Co., and Anamosa, Jones Co. (both USNM).

Iowa River Drainage: Lake Albert Lea, Freeborn Co., Minn. (ANSP). [Shellrock River], Rockford, Floyd Co., Iowa (USNM). [Little] Cedar River, Stacyville, Mitchell Co., Iowa (USNM). Cedar River at Cedar Falls, Blackhawk Co., Iowa; Vinton, Benton Co., Iowa (both OSUM); Cedar Rapids, Linn Co., Iowa (UMMZ); and near Rochester, Cedar Co., Iowa (USNM). Pratt Creek, Monroe Twp., Johnson Co., Iowa (USNM). English River, Wessonville Mill, Washington Co., Iowa (OSUM). Iowa River, Iowa Falls, Hardin Co., Iowa (USNM) and Iowa City, Johnson Co., Iowa (MCZ). Mud Creek, Wilton, Muscatine Co., Iowa (USNM).

Skunk River Drainage, Iowa: Skunk River, Orchard Mills, 6 mi (9.6 km) S of Mt. Pleasant, Hewig Co. (MCZ). South Skunk River above waterworks N of Oskaloosa, (USNM).

Des Moines River Drainage: Beaver Creek, Dove Woods, N of Des Moines, Polk Co., Iowa (1953, E. and J. Karlin!). Raccoon River at Sac City, Sac Co.; Iowa (USNM); Lanesboro, Carroll Co., Iowa (USNM); and Dallas Co., Iowa (MCZ). Des Moines River at Estherville, Emmet Co., Iowa (MCZ); 5 mi (8 km) W of Boone on U.S. Hwy 30, Boone Co., Iowa (UMMZ); Des Moines, Polk Co., Iowa (MCZ); and Clark Co., Mo. (USNM).

Illinois River Drainage: Des Plaines River near Libertyville, Lake Co., Ill. Du Page River at 1 mi (1.6 km) NW of Naperville, Du Page Co., Ill. and at boundary of Du Page and Will counties, Ill. (both UMMZ). Iroquois River, Ind. and 3 mi (4.8 km) above L'Erable, Iroquois Co., Ill. (both USNM). Kankakee River, Shelby, Lake Co., Ind. (UMMZ). Mazon Creek, Mazon, Grundy Co., Ill. (MCZ). Spoon River, just above Elmore, Knox Co., Ill. (UMMZ) and Ellisville, Fulton Co., Ill. (MCZ). Sangamon River at Mahomet, Champaign Co., Ill. (MCZ); Lake Springfield, Sangamon Co. (USNM); and Athens, Menard Co., Ill. (ANSP). Illinois River, Ill. at Summit, Cook Co. (UMMZ); Joliet, Will Co. (MCZ): Morris, Grundy Co. (USNM): Peru, La Salle Co. (MCZ): Havana, Mason Co. (UMMZ); Meredosia, Morgan Co. (MCZ) all pre-1950 records) and river mile 10.5–15.1 to river mile 140.5–149.7 (1966, W.C. Starrett!; Starrett, 1971:374).

Mississippi River Drainage (*signifies specimen(s) collected by Paul Bartsch, 1907): Mississippi River at 1 mi (1.6 km) S of St. Paul, Washington Co., Minn.; Prescott, Pierce Co., Wisc. (both USNM); head of Lake Pepin, about 4 mi (6.4 km) E of Red Wing, Goodhue Co., Minn.; Vermilion Slough, Goodhue Co., Minn.; foot of Lake Pepin, Pepin Co., Wisc.; 1 mi (1.6 km) above Wabasha, Wabasha Co., Minn. (all USNM*); just below Alma Light, Buffalo Co., Wisc. (MCZ); Winona, Winona Co., Minn.; Dreshback, Winona Co., Minn. (USNM*); 5 mi (8 km) above La Crosse, La Crosse Co., Wisc. (MCZ): Brownsville, Houston Co., Minn.; south of Stoddard, Vernon Co., Wisc., Victory, Vernon Co., Wisc.; Lafayette Twp., Allamakee Co., Iowa; mouth of Harpers Slough, Seneca Twp., Crawford Co., Wisc.; (all USNM*); Marquette, Iowa (USNM); Lynnville, Crawford Co., Wisc. (UMMZ); Prairie du Chien, east channel of river, Crawford Co., Wisc. (1979, M. Havlik!); Clayton, Clayton Co., Iowa; Guttenberg, Clayton Co.; Cassville, Grant Co., Wisc.; 10 mi (16.1 km) NNE of Dubuque, Dubuque Co., Iowa in Potosi Twp., Grant Co., Wisc. (all USNM*); Hurricane Chute, 1 mi (1.6 km) E of Waupeton, Dubuque Co., Iowa (1977, S.L.H. Fuller!); Mosalem Twp., about 11 mi (17.6 km) SE of Dubuque, Dubuque Co., Iowa; Sand Prairie, J. Daviess Co., Ill.; 2 mi (3.2 km) below Belleview, Jackson Co., Iowa; mouth of Elk River, Clinton Co., Iowa (all USNM*); Savanna, Carroll Co., Ill. (1977, S.L.H. Fuller!); Le Clair, Scott Co., Iowa; Albany, Whiteside Co., Ill. (both USNM*); 6 mi (9.6 km) NNE of Cardova, Rock Island Co., Ill. (1977, Dome Pipeline Co.); Davenport, Scott Co., Iowa; Montepelier, Muscatine Co., Iowa (both USNM*); Muscatine, Muscatine Co., Iowa (MCZ); Parkers Landing, Louise Co., (USNM); Keithsburg, Mercer Co., Ill. (UMMZ); canal, O'Connell Island, 3 mi (4.8 km) NNE of Burlington, Des Moines Co., Iowa; Dallas, Hancock Co., Ill; 2 mi (3.2 km) N of Nauvoo, Hancock Co., Ill. (all USNM*) mouth of Price's Creek near Sandusky, Lee Co., Iowa (UMMZ); bar, Keokuk, Lee Co., Iowa (UMMZ); Warsaw, Hancock Co.; Ill., Quincy, Adams Co., Ill.; Clarksville, Pike Co., Mo. (all MCZ); Hamburg, Calhoun Co., Ill.; above Golden Eagle, Calhoun Co., Ill.; and Peruque, St. Charles Co., Mo. (all UMMZ).

Missouri River System.—*Missouri River Drainage:* Knife River, Bulah, Mercer Co., N. Dak. (UMMZ). Green River, 7 mi (11.2 km) N of Dickinson, Stark Co., N. Dak. (1965, J. Williams!). Heart River, 10 mi (16.1 km) SW of Richardton, Stark Co., N. Dak. (UMMZ). Cannonball River (north branch), Mott, Hettinger Co., N. Dak. (UMMZ). Apple Creek about 5 mi (8 km) ESE of Bismark, Burleigh Co., N. Dak. (1978, E.R. Roach!). Crow Creek, 11 mi (17.6 km) NE of Chamberlain, Brule Co. (in Buffalo Co.), S. Dak. (UMMZ). Pipestem River, Buchanan, Stuttsman Co., N. Dak. (UMMZ). Aowa Creek, Ponca, Dixon Co., Nebr. (USNM). Big Mud Lake, between Kenmoor and Halls, Buchanan Co., Mo. (MCZ).

Big Sioux River Drainage: Clear Lake, Deuel Co., S. Dak. Lake Kampeska, Codington Co., S. Dak. Split Rock River, Palisades, Minnehaha Co., S. Dak. (all UMMZ). Big Sioux River at western edge of Sioux Falls, Minnehaha Co., S. Dak. (1971, K. Perkins!) and at Klondike, Lyon Co., Iowa (USNM). Rock River, Rock Valley, Sioux Co., Iowa (USNM).

Little Sioux River Drainage, Iowa: Little Sioux River at

"loop" near Lake Okoboji, Dickinson Co. (MCZ); east of Milford, Dickinson Co. (UMMZ); and southeast of Sutherland, O'Brien Co. (USNM). Ocheyedan River, Spencer, Clay Co. (MCZ). Spillway at Trumbull Lake, Clay Co. (E.L. Waffle!, UMMZ).

Platte River Drainage, Nebraska: Wood River, Gibbon, Buffalo Co. (MCZ). Oak Creek, Lincoln, Lancaster Co. (USNM).

Nishnabotna River Drainage: Nishnabotna River, Shelby Co., Iowa (MCZ).

Kansas River Drainage: Republican River, Cambridge, Furnas Co., Nebr. (UMMZ). Smoky Hill River, Salina, Saline Co., Kans. (USNM) and Abilene, Dickinson Co., Kans. (UMMZ). Mud Creek, Abilene, Dickinson Co., Kans. (UMMZ). Big Blue River at Milford, Seward Co., Nebr. (UMMZ); Wymore, Gage Co., Nebr. (1957, W.H. Coil!); and Garrison, Pottawatomie Co., Kans. (UMMZ). Vermilion Creek, Onaga, Pottawatomie Co., Kans. Elk Creek, Holton, Jackson Co., Kans. (USNM). Soldier Creek, Shawnee Co., Kans. (MCZ). "Silver Lake," Shawnee Co., Kans. (ANSP). Wakarusa River, 5 mi (8 km) SW of Lawrence, Douglas Co., Kans. (MCZ).

Grand River Drainage: Grand River, Iowa (USNM).

Blackwater River Drainage, Missouri: Muddy Creek, 4 mi (6.4 km) SE of La Monte, Pettis Co. (UMMZ). Flat Creek, Pettis Co. (UMMZ).

Roche Perche Creek Drainage: Roche Perche Creek, Columbia, Boone Co., Mo. (UMMZ).

Osage River Drainage: Dragoon Creek, 4.1 (6.6 km) N, 1.0 mi (1.6 km) W of Quenemo, Osage Co., Kans. (USNM). Marais des Cygnes River at Lyon Co., Kans. (MCZ); 6 mi (9.6 km) SSW of Lyndon, Osage Co., Kans. (UMMZ); near Peoria, Franklin Co., Kans. (MCZ); near Ottawa, Franklin Co., Kans. (MCZ); and La Cygne, Linn Co., Kans. (USNM). Pottawatomie Creek, 5 mi (8 km) SW of Lane, Franklin Co., Kans. (1950, R.W. Reese!). South Fork Pottawatomie Creek, 4½ mi (7.2 km) S of Garnet, Anderson Co., Kans. (MCZ). Bull Creek and Wea Creek, Miami Co., Kans. (UMMZ). Grand River, Clinton, Henry Co., Mo. (ANSP). Pomme de Terre River, Hwy. 58 between Wheatland and Hermitage, Hickory Co., Mo. (1964, C.B. Stein!). Osage River, 5 mi (8 km) N of Schell City, Bates/Vernon Co., Mo. and Osceola, St. Clair Co., Mo. (both 1964, C.B. Stein!). See also Murray and Leonard (1962:87–90).

Auxvasse Creek Drainage: Auxvasse Creek at Hwy. I-70 bridge, between Williamsburg and Kingdom City, Callaway Co., Mo. (1964, C.B. Stein!).

Loutre River Drainage: Loutre River between Williamsburg and Danville, Montgomery Co., Mo. (1964, C.B. Stein!).

LOWER MISSISSIPPI RIVER SYSTEM.—*Meramec River Drainage, Missouri:* Dry Fork Creek, 3.1 mi (5 km) SE of St. James, Phelps Co. (1963, W.H. Dieffenbach!). Meramec River, Corisande Beach, St. Louis Co. (1965, E. Haid!). Numerous records from Bourbeuse, Big, and Meramec rivers (Buchanan, 1980:23).

Kaskaskia River Drainage, Illinois: Flat Branch of Kaskaskia River, Humboldt, 9 mi (14.4 km) NE of Matoon, Coles Co. (OSUM). Kaskaskia River, Vandalia, Fayette Co. (USNM).

Portage Bayou Drainage: Castor River, between Sikeston and Dexter, in Stoddard Co., Mo. (1964, C.B. Stein!).

St. Francis River Drainage: Drainage ditch, 5½ mi (8.8 km) SE of Gideon, New Madrid Co., Mo. (1964, C.B. Stein!). St. Francis River, 1 mi (1.6 km) SW of Parkin, Crosse Co., Ark. (1964, C.B. Stein!) and 3 mi (4.8 km) N of Widener, St. Francis Co., Ark. (1978, C.B. Stein and W.N. Masson!).

White River Drainage: [Bayou de Vue], Jonesboro, Craighead Co., Ark. (UMMZ). Black River at Hendrickson, Butler Co., Mo.; Pocahontas, Randolph Co., Ark. (both 1964, C.B. Stein!); and Black Rock, Lawrence Co., Ark. (UMMZ). White River, 4.8 mi (7.7 km) SSW of Newark, Independence Co., Ark. (1977, K. and R. Wright!) and Newport, Jackson Co., Ark. (UMMZ).

Arkansas River Drainage: Grouse Creek, 1.0 mi (1.6 km) NNW of Dexter, Cowley Co., Kans. (1971, A.L. Metcalf!). Little Arkansas River, Wichita, Sedgwick Co., Kans. (UMMZ). Caney Creek, 5 mi (8 km) SE of Cedarvale, Chautauqua Co., Kans. (USNM). Middle Caney Creek, 1.7 mi (2.7 km) NE of Niotaze, Chautauqua Co., Kans. (1978, A.C. Metcalf!). Little Caney River, 2.1 mi (3.4 km) NW of Copan, Washington Co., Okla. (1978, A.L. Metcalf!). Caney River, below Hulah Dam, 2.5 mi (4 km) W of Hulah, Osage Co., Okla. (1978, A.L. Metcalf!). Verdegris River, rocky shoal 10 mi (16.1 km) N of Fredonia, Wilson Co., Kans. and at Oalagah, Rogers Co., Okla. (both UMMZ). Bird Creek, 2.0 mi (3.2 km) ENE of Sperry, Tulsa Co., Okla. (OSUM). Neosho River at NW ⅛, SE ¼, S 4, T 17 S, R 9 E, Morris Co., Kans. (1956, B. Leonard and H.D. Murray!); 1 mi (1.6 km) N of Emporia, Lyon Co., Kans. (UMMZ); S 4, T 23 S, R 16 E, Coffey Co., Kans. (1957, H.D. Murray!); Iola, Allen Co., Kans. (MCZ); SE ¼, S 16, T 29, R 20 E, Neosho Co., Kans.; N ½, S 16, T 32 S, R 21 E, Labelle Co., Kans. (both 1957, H.D. Murray!); Erie, Neosho Co., Kans.; 30 mi (48 km) SW of Pittsburgh, in Cherokee Co., Kans. (both UMMZ). Cottonwood River, Lyon Co., Kans. (USNM). Big Creek, Allen Co., Kans. (UMMZ). Cabin Creek, Vinita, Craig Co., Okla. (UMMZ). Greenleaf Creek, at mouth, Braggs, Muskogee Co., Okla. (1950, G.H. Brick!).

Red River Drainage, Oklahoma: Blue River, Johnston Co., (1970, W. Gale!). Tributaries of Red River near Lake Texoma (1966, collector? (OSUM)).

Lasmigona (Lasmigona) complanata alabamensis, new subspecies

THE SHELL

FIGURE 10

DESCRIPTION.—Shell triangular-ovate, strongly alate, prominently sculptured, and com-

pressed; up to about 150 mm long, 125 mm high, and 38 mm wide. Shell slightly thickened anteriorly (up to 6 mm thick), thin posteriorly (1.5 mm in a large specimen) and fragile. Anterior margin generally rounded but sharply concave in front of the umbones, ventral margin broadly curved at the ends and flat or slightly concave in the center, posterior margin rather sharply rounded or roundly pointed centrally, and dorsal margin with a high, broad alation that is acutely rounded apically. Maximum inflation at about the middle of the shell. Beaks low, compressed, barely protruding, and located about 15% to 17% of the distance from anterior to posterior. Dorsal, wing-like expansion very prominent, much compressed, strongly ribbed, and partly broken in most specimens, especially in adults. Posterior ridge double, located high on the shell, of low relief but clearly marked, and both defining a narrow, slightly concave area. Growth rests well-marked by concentric, darkly-pigmented grooves. Post-juvenile sculpturing

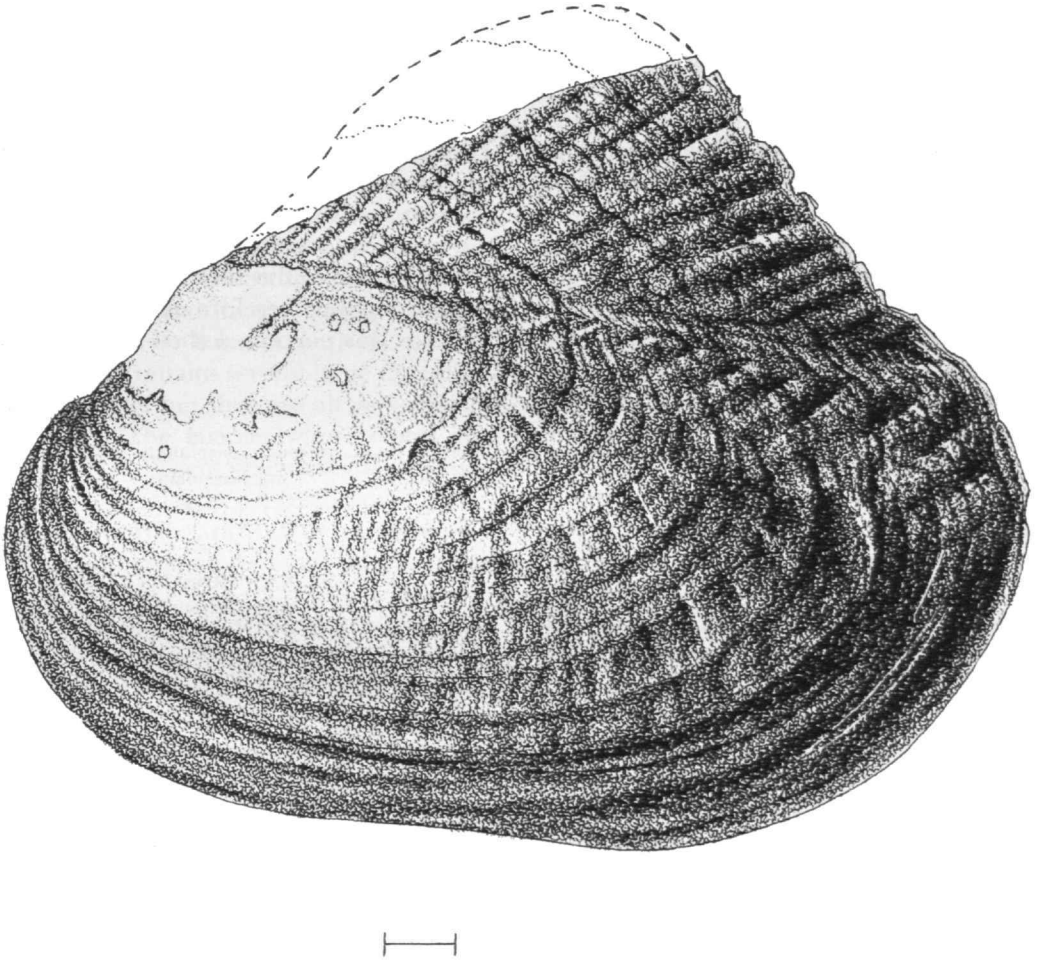

FIGURE 10.—*Lasmigona complanata alabamensis:* USNM 809996, holotype, H. Neely Henry Lake, Coosa River, Calhoun County, Alabama. (Scale = 1 cm.)

consisting of numerous wrinkled, radial corrugations on the dorsal wing and on the posterior and central areas of the shell, being chiefly absent only on the anterior ventral area. Radial corrugations widest and most prominent on the dorsal wing and on the posterior ridges and in the area between them and becoming variable, but in many specimens narrow and more crowded, in the central portion of the shell. Periostracum in juveniles yellowish brown to chestnut brown, with or without numerous narrow, darker rays. Adults are darker and some are greenish yellow or grass green, especially anterior-ventrally, and with crowded, very narrow, green rays. Ligament quite long, compressed, strong, thickened above the lateral teeth, extended between the dorsal wings, and uniting them to each other along their dorsal edges and over their opposing faces.

Hinge teeth somewhat thickened but incomplete. Pseudocardinal teeth moderately large, pyramidal, strongly grooved, and directed ventrally, 1 in the right valve and 2 in the left. Interdental projection flange-like, elevated more than the pseudocardinals, of medium length, located in the left valve and confluent with the second pseudocardinal and with a lateral. The interdental cavity in the right valve is wide and deep and severs the hinge plate at the umbone. The lateral teeth are fairly short, somewhat thickened (especially anteriorly), and straight or slightly curved, 1 in the right valve and 1 or 2 in the left. Beak cavity in left valve more or less excavated but narrow and not deep and with irregular muscle scars within; beak cavity in right valve is the triangular interdental cavity. Anterior adductor muscle scar medium-sized, quadrate-ovate and impressed dorsally; pallial band shallow, complete, and approximately parallel with the margin; posterior adductor scar quite large, irregular, and lightly etched. Nacre white, iridescent centrally and posteriorly, and much thinner in a band around the edge, especially in juveniles.

Beak sculpture not clearly visible in available material but it appears to be composed of a series of quite strong, double-looped ridges with their central, inverted, V-shaped portions more elevated than the other portions.

TYPES.—The holotype, illustrated in Figure 10, was collected by Dr. John C. Hurd (now at the Department of Biology, LaGrange College, LaGrange, Georgia), during his 1971–1973 survey of the mussels of the Coosa River. It is from H. Neely Henry Lake, Coosa River, Calhoun County, Georgia and it is now deposited in the Smithsonian Institution's Collection of Mollusks (USNM 809996). It's measurements are: length 147.7 mm, height 114.5 mm, width 36.3 mm, and B-A 24.7 mm. Comparative measurements of the holotype and of 7 specimens (including the 3 paratypes) in Dr. Hurd's personal collection, are given in Table 8.

VARIATION.—Normal variation in color is apparent (Table 8). Adults are blackish brown or chestnut brown and juveniles are chestnut brown or yellowish brown. Some adults and juveniles are also partly greenish,

Prominent sculpturing is the principle diagnostic feature of this subspecies and variation in sculpturing was therefore examined in some detail. For this purpose 4 shell areas were differ-

TABLE 8.—*Lasmigona complanata alabamensis:* shell measurements.

Length	H/L	W/L	B-A/L
	H. Neely Henry Lake, Coosa River, Calhoun Co., Ala.		
149.6	0.843	0.239	0.150
147.7*	0.775	0.246	0.167
124.1	0.811	0.199	0.218
81.7	0.747**	0.247	0.217
	Lake Jordan, Coosa River, Elmore Co., Ala.		
124.2	0.848	0.228	0.200
96.3	0.871	0.218	0.153
91.4	0.844	0.229	0.191
84.6	0.863	0.227	0.165

* Holotype and figured specimen; upper part of wing broken away.

** Wing deformed.

entiated, viz, dorsal wing (DW), posterior slope (PS), mid-ventral region (MV), and anterior area of disc (AA). Sculpturing was scored as: 4 (very strong), 3 (strong), 2 (moderate), 1 (weak), or 0 (absent). The holotype illustrated in Figure 10, has a score of : DW, 4; PS, 3; MV, 2; AA, 1 (the weak sculpturing on the anterior area is not visible in the illustration).

All specimens in the collection of *L. complanata* from the Mobile River System in the collection of the University of Michigan (UMMZ) and in the personal collection of Dr. J.C. Hurd were scored for strength of sculpturing. The UMMZ contained 7 specimens from the Cahaba River (DW, 3–4; PS, 2–4; MV, 1–4; AA, 0–1), 1 from the Chattooga River (DW, 4; PS, 4; MV, 3; AA, 0) and 1 from Yellowleaf Creek, Shelby Co., Alabama (DW, 4; PS, 3; MV, 2; AA, 0.5). The Hurd collection contained 8 specimens from 2 lakes in the Coosa River (DW, 3–4; PS, 2–4; MV, 1.5–3; AA, 0–2). These values have been combined and are given in Table 9. For comparative purposes, sculpturing scores are also given for those lots in the MCZ Collection that contain 6 or more specimens and for the largest lot from the Canadian Interior Basin in the NMC Collection. (The latter contains several large Canadian population samples but they are all very similar in sculpturing.) The samples whose scores are listed are from divergent geographical localities and appear to be clearly representative of the trends in sculpturing variability seen in the numerous small lots examined from throughout the range of the species.

Inspection of Table 9 demonstrates that the population from the Mobile River System is much different from all other populations cited with regard to sculpturing. There differences are especially pronounced in regard to sculpturing on the posterior slope and on the mid-ventral area but they are also significant in regard to the dorsal wing. These values illustrate numerically a fact that is also apparent visually, i.e., that the Mobile River System population is strikingly different from all other populations and that it merits separate taxonomic status.

TABLE 9.—Sculpturing scores for *Lasmigona complanata* sensu lato (abbreviations: DW = dorsal wing; PS = posterior slope; MW = midventral; AA = anterior area).

Area of shell	N	Range	Mean ($\bar{x}$)	S
	Mobile River system (all UMMZ and J.C. Hurd specimens)			
DW	17	3–4	3.78	0.44
PS	17	2–4	3.18	0.64
MV	17	1–4	2.26	0.83
AA	17	0–2	0.62	0.65
	Salt River (North Fork and Rolling Fork), Ky. (MCZ 220214, 220216, 220368)			
DW	13	0–3	1.69	1.19
PS	13	0–1	0.19	0.26
MV	13	0–0.5	0.08	0.19
AA	13	0	0	0
	Wood River, Gibbon, Buffalo Co., Neb. (MCZ 61005)			
DW	10	0.5–2	1.40	0.52
PS	10	0–0.5	0.05	0.16
MV	10	0–0.5	0.10	0.22
AA	10	0	0	0
	Wabash River, Juno Lake, New Harmony, Ind. (MCZ 58094)			
DW	6	1.5–3	1.83	0.68
PS	6	0	0	0
MV	6	0	0	0
AA	6	0	0	0
	Swan River, 8 mi N of Norquay, Saskatchewan (NMC)			
DW	17	0–1	0.20	0.29
PS	17	0–0.5	0.06	0.28
MV	17	0	0	0
AA	17	0	0	0

ANATOMY, GLOCHIDIA, AND LIFE HISTORY

Unfortunately nothing is known about the anatomy, glochidia, or reproduction of this subspecies but it is probably very much like the nominate subspecies in those respects. Its habitat includes lakes and rivers. A note by H.H. Smith, the collector, on the label accompanying a specimen from Yellowleaf Creek, Shelby Co., Alabama (MCZ 28912) states: ". . . in mud in deep water. . . one in 15 ft. . . rarely in muskrat piles." According to van der Schalie (1938:10): "In the

Cahaba *complanata* is confined to medium-sized and large-river conditions. It is by no means a common species. . . ."

Geographical Records

Figure 11

Gulf of Mexico River Systems

Mobile River System.—*Tombigbee River Drainage:* East Fork Tombigee River, 0.5 mi (0.8 km) NE of mouth of Bull Mountain Creek, 11.3 mi (18.1 km) S of Fulton, Itawamba Co., Miss. (1974, J.D. Williams!, OSUM). Tombigee River at Columbus, Lowndes Co., Miss. (MCZ); 2 mi (3.2 km) SW of Pickensville, Pickens Co., Ala. and 10 mi (16.1 km) NW of Aliceville, Pickens Co. (both 1974, J.D. Williams!, OSUM). Locust Fork Black Warrior River, Island Ford, 1 mi (1.6 km) E of Sayre, Jefferson Co., Ala. (1978, H.D. Athearn!, NMC). Black Warrior River, Squaw Shoals, Jefferson Co., Ala. (UMMZ).

Alabama River Drainage: Cahaba River at Nunley Ford, W of Helena, Shelby Co., Ala.; Gurney, Shelby Co.; Lily Shoals, about 6 mi (9.6 km) S of Blockton, Bibb Co., Ala.; 7 mi (11.2 km) below Centerville, Bibb Co.; and 8 mi (12.8 km) N of Spratt, Perry Co., Ala. (all UMMZ). Chattooga River near Lyerly, Chattooga Co., Ga. (UMMZ). Yellowleaf Creek, Shelby Co., Ala. (UMMZ). Coosa River at H. Neely Henry Lake, Calhoun Co., Ala. and Lake Jordan, Elmore Co., Ala. (both ca. 1972, J.C. Hurd!).

Three other specimens from the Gulf of Mexico coastal region have also been seen but they are either deformed or are otherwise unusual and cannot be placed in either *L. complanata* (sensu stricto) or *L. complanata alabamensis*. They are all from Mississippi, viz, the Pearl River at Jackson, Hinds Co., (1910, B. Walker!, MCZ) and Monticello, Lawrence Co. (1964, D.H. Stansbery!, OSUM) and the Pascagoula River, west of Lucedale, George Co., (1964, F. Yrabedre and son!, MCZ).

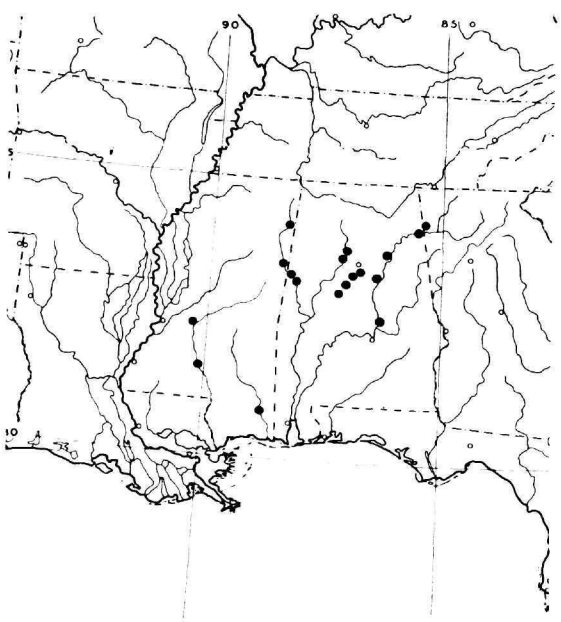

Figure 11.—Geographical distribution of *Lasmigona complanata alabamensis* (small open circles = cities).

Subgenus *Platynaias* Walker, 1918

Platynaias Walker, 1918:2. [Type-species, by original designation: "*Symphynota compressa* Lea"]

The glochidia of both *L. compressa* and *L. subviridis* are triangular-ovate, with convex adapical sides, less than 0.300 mm in height, with height less than length, with acuminate stylets each bearing relatively few (30–60) major microstylets, with exterior epiapical micropoints, and without a larval thread. The glochidia of *L. decorata* are unknown.

Comparative features of the adults are: the shells are rather small to medium-sized (about 50 to 115 mm long), with a dorsal alation (at least in juveniles), are of medium relative height (H/L about 0.52–0.68), lack radial sculpturing on the posterior slope, have well-developed lateral hinge teeth, and have double-looped beak sculpturing. Two of the included species are monoecious (hermaphroditic) and the other (*L. decorata*) is unknown in this regard but it is probably also monoecious. The supra-anal mantle opening is longer than, or approximately as long as, the anal opening.

Lasmigona (Platynaias) compressa (Lea, 1829)

Figures 12–14

Symphynota compressa Lea, 1829:450, pl. 12: 22. [Type-locality: "Ohio and Norman's Kill, near Albany" [New York]. A lectotype, which is apparently Lea's figured specimen, is herein selected (USNM 83961) and is labeled "Yellow Cr., Cincinnati, Ohio, T.G. Lea."]

Unio alasmodontina (ex Barnes), Lea 1829:451. [Published as a synonym of *Symphynota compressa* Lea.]

Unio pressus Lea, 1842:237. [Proposed as a substitute name for *Unio compressus* (Lea, 1829) not Sowerby (1828). The species had been previously transferred from *Symphynoto* to *Unio* by Lea (1836:11). Later Simpson (1900:663) replaced the species in *Symphynota* and returned to the use of *compressa*. I herein retain *compressa*, both for Simpson's reasons and also because it has now been in continuous use for more than 80 years.]

Unio compressus var. *plebeius* Adams, 1842:16. [Type-locality: "a small brook in Middlebury [Vermont]." The lectotype, selected by Johnson (1956:130), is MCZ 154961. It was later illustrated by Johnson and Boss (1972, pl. 39: fig. 5).]

The Shell

FIGURE 12*a*, *c–e*

DESCRIPTION.—Shell ovate-trapezoid, compressed, and principally unsculptured; up to about 114 mm long, 65 mm high, and 35 mm wide. Somewhat thicker anteriorly (up to 2.8 mm thick) than posteriorly (up to 1.4 mm). Anterior margin roundly curved, ventral margin broadly curved anteriorly and flatly curved, straight, or even slightly arcuate centrally, posterior margin rounded below and obliquely truncated above, and dorsal margin broadly curved, flattened, or slightly sinuate. Young specimens are markedly compressed and alate posterior-dorsally. Maximum inflation in adults slightly above the midpoint of the shell. Beaks not inflated, located about ⅓ the distance from anterior to posterior, and projecting slightly above the hinge line. Posterior ridge low and either more-or-less distinctly double, one ridge terminating postbasally and the other mid-posteriorly, or obscure and rounded. Posterior slope narrow and centrally concave.

Growth increments marked by shallow concentric grooves or incised lines that are darkly pigmented. Post-juvenile sculpturing principally absent but consisting, in some specimens, of a few, obscure, serial indentations on the posterior slope and, in some other specimens, of a shallow radial groove in front of the lower posterior ridge and/or a few irregular indentations elsewhere on the shell. Periostracum shining to dull and covered with broad and narrow green or greenish rays on a brownish or yellowish background. In some specimens the rays are obscure and the periostracum is brownish throughout. Ligament long, brown in color, and fragile when dry.

Hinge teeth well-developed in most specimens. Pseudocardinal teeth narrow and laminar but strong, more or less parallel with the anterior-dorsal margin, and numbering 1 in the right valve and 2 in the left. Interdental projection present in the left valve, prominent, compressed, and bilobed, the posterior lobe (located beneath the umbone) the larger. The interdental cavity in the right valve completely, or nearly, severs the hinge plate. Lateral teeth in most specimens strong but narrow and of medium length, 1 in the left valve and 2 in the right. In some specimens the laterals are incomplete. Beak cavity shallow and compressed and with irregular and variable muscle scars beneath the unbones. Many specimens clearly exhibit 1 of these small scars in the right valve and 2 in the left but in others the scars are obscure. Anterior major muscle scars large, prominent, and impressed; posterior scars also large and clearly apparent but only lightly impressed; pallial line (band) also clearly visible, lightly impressed, and crossed or not crossed by ridges and grooves; its inner margin is irregularly crenulated, especially anteriorly, and its outer margin is more or less regular. Nacre silvery white and, especially posteriorly and in the posterior muscle scar, iridescent. At the margin the nacre is thin and appears greenish gray.

Beak sculpture heavy and composed of about 6 or 7 principally double-looped concentric ridges. The earliest ridges are rounded anteriorly, with a deep sinus posterior of center, and expanded and V-shaped posteriorly. Later ridges are similar but tend to be jagged anteriorly and discontinuous. The beak sculpturing of most post-juvenile specimens, except those from hard water environments, is obliterated by corrosion.

VARIATION.—Table 10 shows that *L. compressa* is not unusually variable in relative dimensions. Coefficients of variability vary from 2.80 to 7.59 for relative height (H/L), 4.95 to 8.78 for relative obesity (W/L), and 5.54 to 7.04 for relative

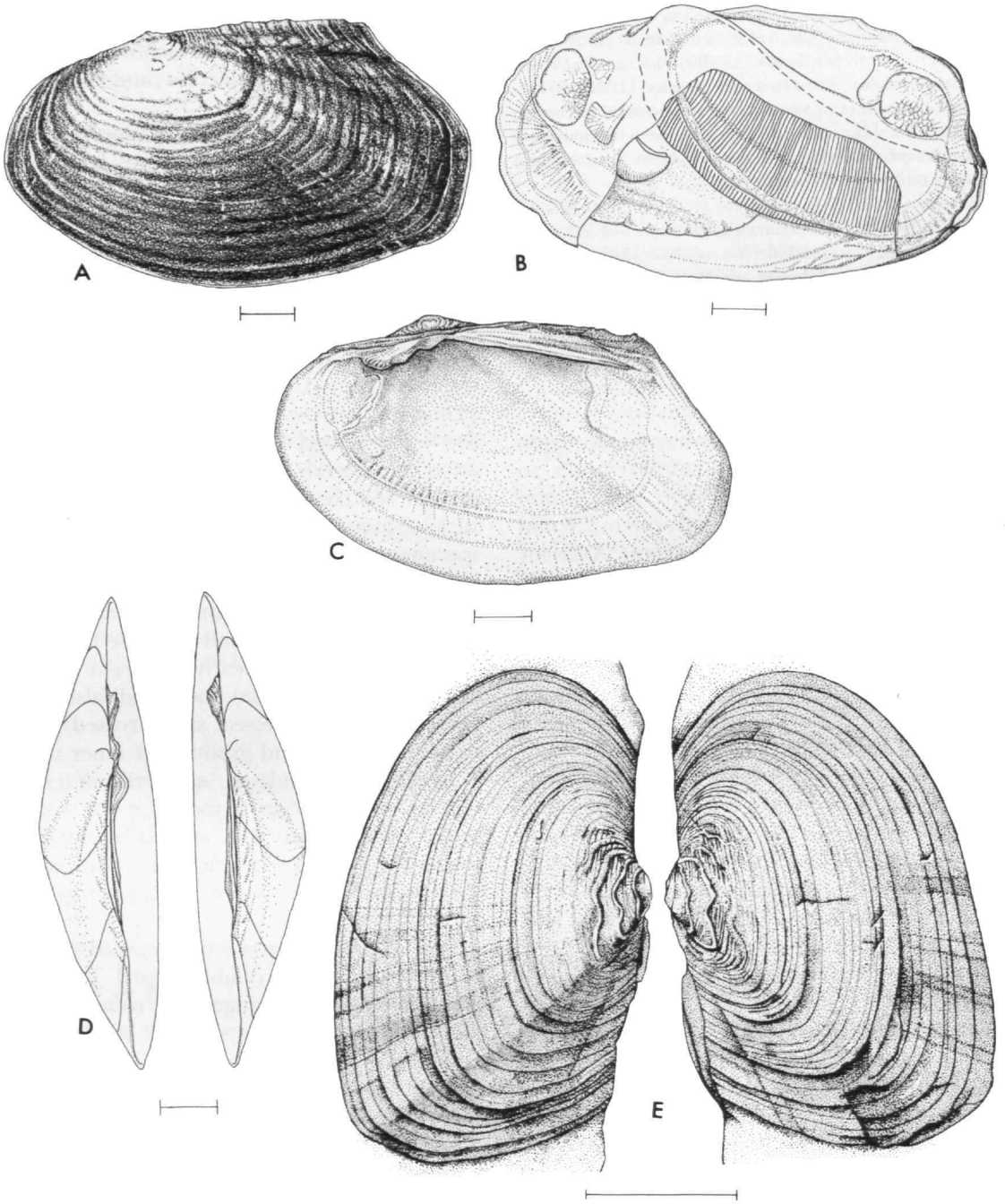

FIGURE 12.—*Lasmigona compressa: a,c,d,* USNM 26106, White River, Indiana; *b,* USNM 801452, Cedar Creek, Ozaukee County, Wisconsin; *e,* USNM 505941, details of umbonal area, [Shellrock River], Rockford, Floyd County, Iowa. (Scale = 1 cm.)

TABLE 10.—*Lasmigona compressa:* shell measurements.

Feature	N	Range	Mean ($\bar{x}$)	S
		Black River, Pefferlaw, Ont. (NMC 62927)		
Length (mm)	30	46.8–113.6	77.4	16.99
H/L	30	0.562–0.634	0.585	0.0164
W/L	30	0.227–0.317	0.270	0.0237
B-A/L	30	0.312–0.399	0.347	0.0195
		Sand Creek, Ottawa Co., Mich. (MCZ 150173)		
Length (mm)	9	43.8–94.3	78.1	16.12
H/L	9	0.516–0.638	0.551	0.0418
W/L	9	0.279–0.330	0.309	0.0153
B-A/L	9	0.283–0.347	0.316	0.0175
		Kent's Creek, Rockford, Ill. (MCZ 145617)		
Length (mm)	13	52.5–82.7	73.3	9.25
H/L	13	0.573–0.615	0.586	0.0158
W/L	13	0.256–0.326	0.280	0.0191
B-A/L	13	0.242–0.306	0.277	0.0195

placement of the beaks (B-A/L). In contrast to *L. costata*, *L. compressa* is normally hermaphroditic, so sexual dimorphism in the shells does not contribute to enhanced variability.

It is of interest that the population sample from Black River, Pefferlaw, Ontario showed a distinct trend for the longest specimens to be relatively more inflated than the shortest specimens. This apparent correlation was tested by comparing the sequence of longest to shortest specimens with the sequence of greatest to least relative inflation (W/L) by use of the Spearman Rank Coefficient (Siegel, 1956). The values compared are: 1, 6; 2, 9; 3, 1; 4, 8; 5, 7; 6, 5; 7, 10; 8, 2; 9, 5; 10, 3; 11, 12; 12, 16.5; 13, 13; 14, 11; 15, 20; 16, 28; 17, 16.5; 18, 26; 19, 19; 20, 23.5; 21, 22; 22, 27; 23, 15; 24, 21; 25, 30; 26, 14; 27, 25; 28, 29; 29, 18; and 30, 23.5. The results obtained ($r_s = 0.794$, $t = 6.91$) indicate that, at the 99% confidence level, a positive correlation exists between increasing length and increasing relative obesity. For reasons that are not apparent, however, no such correlation exists between L and W/L for the Sand Creek or Kent's Creek population samples.

It is also of interest that although young specimens of *L. compressa* tend to have relatively higher dorsal wings than older specimens, there is so much variation in relative height of post-juvenile specimens that no significant statistical relationship can be demonstrated between L and H/L in the available material. Perhaps this is because juvenile specimens were uncommon in the samples that were large enough for statistical analysis. In addition, no correlation of L with $\frac{\text{B-A}}{\text{L}}$ are apparent.

Other variable features are the color of periostracum (brownish black, brown, or yellowish), the extent to which rays are present, and the color of the nacre (white or bluish). Specimens from northern Ontario, at the northern edge of the range, attain only modest length, i.e., up to about 70 mm at 10 years of age. (See measurements in Clarke, 1973a:45.)

TOPOGRAPHIC ANATOMY

FIGURE 12*b*

SPECIMEN DESCRIBED.—USNM 801452, from Cedar Creek, Route 60, Sec. 23, T 10N, R 21E, Ozaukee County, Wisconsin collected 3 November 1979 by H.A. Mathiak; fixed directly in 10% formaldehyde and preserved in alcohol; shell length 104.8 mm, sex female (gravid, with glochidia).

DESCRIPTION.—Mantle very pale brown, almost whitish, with tiny pale pigment patches separated by lace-like darker lines; translucent with colors of other organs showing through but with a thickened muscular edge (about 6–8 mm wide, 0.8 mm thick anteriorly and 1.5 mm thick posterioventrally). There is a narrow, continuous, very pale orange band of pigment close to the mantle edge anteriorly and ventrally that is joined posterioventrally by a narrow, continuous, dark brown band of pigment. Both continue posteriorly and dorsally to the hinge line, the brownish band widening somewhat (to about 1.1 mm) posteriorly. The mantle margin in front of the incurrent opening is crenulated.

Incurrent opening 21.2 mm long (with posterior tips of outer demibranchs protruding slightly

beyond the opening) and surrounded within by 2 rows of curved, narrow papillae, the exposed members each about 1.2 mm long, 0.25 mm wide at the base, and tapering to a narrow (0.05 mm), rounded point. Portions of mantle edges between incurrent and anal openings about 1.0 mm long. Anal opening with edges nearly smooth (not papillate or crenulate), wide, and about 10.0 mm long. Mantle connection between anal and supra-anal opening 5.2 mm long. Supra-anal opening with smooth edges, narrow and slit-like, and 13.7 mm long. The incurrent and anal openings are both bordered within along their edges and to a depth of about 1.5 mm with purplish brown pigment but the supra-anal opening is bordered within by a paler, narrower (0.5 mm), brownish pigment band.

Outer (gravid) demibranchs are pale reddish brown, 61.0 mm long, 23.2 mm high, thick (4–5 mm) and pad-like, and with their posterior ends protruding about 1.5 mm beyond the edge of the incurrent opening. The free ventral margin is broadly curved throughout its whole length except at its narrow extremities where it is subangular anteriorly and sharply rounded posteriorly. There are about 1.6 water tubes per mm and about 10 radial surficial filaments and about 5 cross-filaments per mm. The inner demibranchs are pale brown, project about 7 mm beyond the outer demibranch anteriorly and about 1 mm anterioventrally, and are overlapped (3 mm) by the outer demibranchs posterioventrally. There are about 0.8–1.0 water tubes per mm and about 10 radial surficial filaments and 5 cross filaments per mm. The inner lamina of the inner demibranch is not attached to the visceral mass.

Labial palpi pale yellowish white, with nearly straight dorsal margins, sharply rounded posteriodorsal apices, and crescent-shaped ventral margins, and touching the inner demibranch. The outer surfaces are smooth and the inner opposing surfaces of each member are radially furrowed (about 5 furrows per mm) at the margin. The outer palpus of each pair is fused anteriorly to the mantle and fused subdorsally, for about ¾ of its length, to the inner palpus.

Ortmann (1912:282) states: "Color of soft parts whitish, edge of mantle black, chiefly so posteriorly. The foot is pale brownish yellow, the gills grayish. The abdominal sac is often pinkish. The charged marsupium varies greatly in color, this variation depending at least in part on the stage of development of the embryos. It may be white, cream-color, pinkish, pale orange, or various shades of brown." According to Baker (1928:140): "Color of animal whitish; mantle edged with black, especially near the siphonal openings; gills grayish-white; foot yellowish-brown; marsupium whitish in sterile, brownish or orange in gravid specimens."

VARIATION.—Table 11 indicates that the characters observed are not particularly variable, at least among the specimens examined. The reported numbers of ranks of papillae are approximations, but in some specimens the incurrent papillae are more densely packed than in others. In all specimens examined the posterior mantle pigmentation was in the form of a continuous black band, the anal opening was crenulated (the degree of crenulation was variable), and the inner demibranch was attached to the visceral mass only along its anterior extremity.

In specimen 7 the inner demibranch had about 0.8 water tubes per mm whereas the outer demibranch had about 2.5. This indicates that the outer demibranch is potentially marsupial. Even the juvenile specimen (2) showed similar demibranch structures. All other specimens were obviously gravid. This is in agreement with Ortmann's (1911:281) observation that, with very rare exceptions, all specimens of *L. compressa* are female. Van der Schalie (1970:106) has further clarified this fact by demonstrating that this species is normally hermaphroditic.

GLOCHIDIUM

FIGURE 13

DESCRIPTION.—Glochidium triangular-ovate, 0.275 mm in height, 0.344 mm in length, and 0.105 mm in single valve convexity. The valves are noticeably asymmetrical: the posterior margin is longer, the apices are placed about 45% of

TABLE 11.—*Lasmigona compressa:* variation in topographic anatomy (terminology same as Table 2).

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 in OD (N/mm)	Sex	Pre-preserv. treatment: Nemb. relax.	Form. fixed
Raisin River, Sharon Hollow, Washtenaw Co., Mich., Collector?, 15 Apr 1961 (UMMZ uncataloged)															
1	78.8	bleached by alcohol		22	13	4	15	2	1.5	NT	5	–	GF	–	–
2	41.5	bleached by alcohol		19	12	6	14	1½	0.6	OV	8	2.5	(F)	–	–
Mukwonago River, Mukwonago, Waukesha Co., Wisc., H.A., Mathiak! 21 Oct 1979 (USNM 801979)															
3	83.5	2	M	23	12	4	14	3	1.2	OV	6	–	GF	–	–
4	78.4	2	M	21	10	5	15	3	1.5	OV	6	–	GF	–	–
5	78.1	1	M	19	13	5	11	2–4	1.2	OV	6	–	GF	–	–
6	77.8	1½	M	21	12	4	14	3	1.7	OV	6	–	GF	–	–
7	77.4	1½	M	20	11	6	12	2–3	1.6	OV	6	2.5	(F)	–	–
8	76.7	1	M	17	13	7	9	3	1.2	T	5	–	GF	–	–
9	76.2	2	M	23	11	6	13	2	1.4	OV	6	–	GF	–	–
10	73.1	2	M	17	10	3	15	3	1.0	OV	5	–	GF	–	–
11	71.8	1½	M	21	14	4	14	3	1.2	OV	5	–	GF	–	–

the distance from anterior to posterior, and the area of maximum inflation is also slightly anterior of center. Surface of glochidium malleate and punctate except for a narrow marginal band, about 20 μm wide, which is sculptured with low collabral ridges. The malleations are about 6–10 μm in diameter, polygonal, and distributed in irregular, subconcentric groups. The pits are about 2 to 3 μm in diameter, located in the depressions, and generally distributed. The hinge is virtually straight and is about 0.243 mm long. The ligament is long and narrow, exposed externally along its whole length and internally within a narrow sinus, about 88 μm long, which is nearly centrally located on the hinge.

The stylets are about 105 μm long, 24 μm wide at their bases, narrowly attenuate, with a narrow, rostate apex, and supported along both sides for nearly their whole lengths by the mantle membrane. The microstylets are about 10 μm long, 5 μm wide at their bases, pyramidal, multifaceted, and arranged in single file on the distal ends of the stylet and 3 or 4 abreast on the proximal end. Slightly smaller (8 μm × 4 μm) microstylets project around the base of the stylets and continue as a dense band of micropoints (1–2 μm long) along the outer edges of the shell. This area is brown in fresh specimens and contrasts with the yellowish color of the valves.

The above description is of a glochidium from an adult specimen (USNM 801452) collected in Cedar Creek, Ozaukee County (Sec. 23, T10N, R21E) Wisconsin by Harold A. Mathiak on 3 November 1979. Three other glochidia, from a specimen collected in the Raisin River at Sharon Hollow, Washtenaw County, Michigan by University of Michigan personnel on 15 April 1961 measure 0.293 mm in height, 0.358 mm in length, and 0.110 mm in single valve convexity; 0.282 mm in height, 0.331 mm in length, and 0.214 mm in total convexity; and 0.277 mm in height and 0.326 mm in length.

Baker (1928:141), quoting 2 other authors, gives 0.313 × 0.353 mm and 0.28 × 0.34 mm for height and length measurements of glochidia from *L. compressa.*

LIFE HISTORY

GRAVID PERIODS.—Mature glochidia were found in specimens collected in Wisconsin on 3 November and in Michigan on 15 April. This is

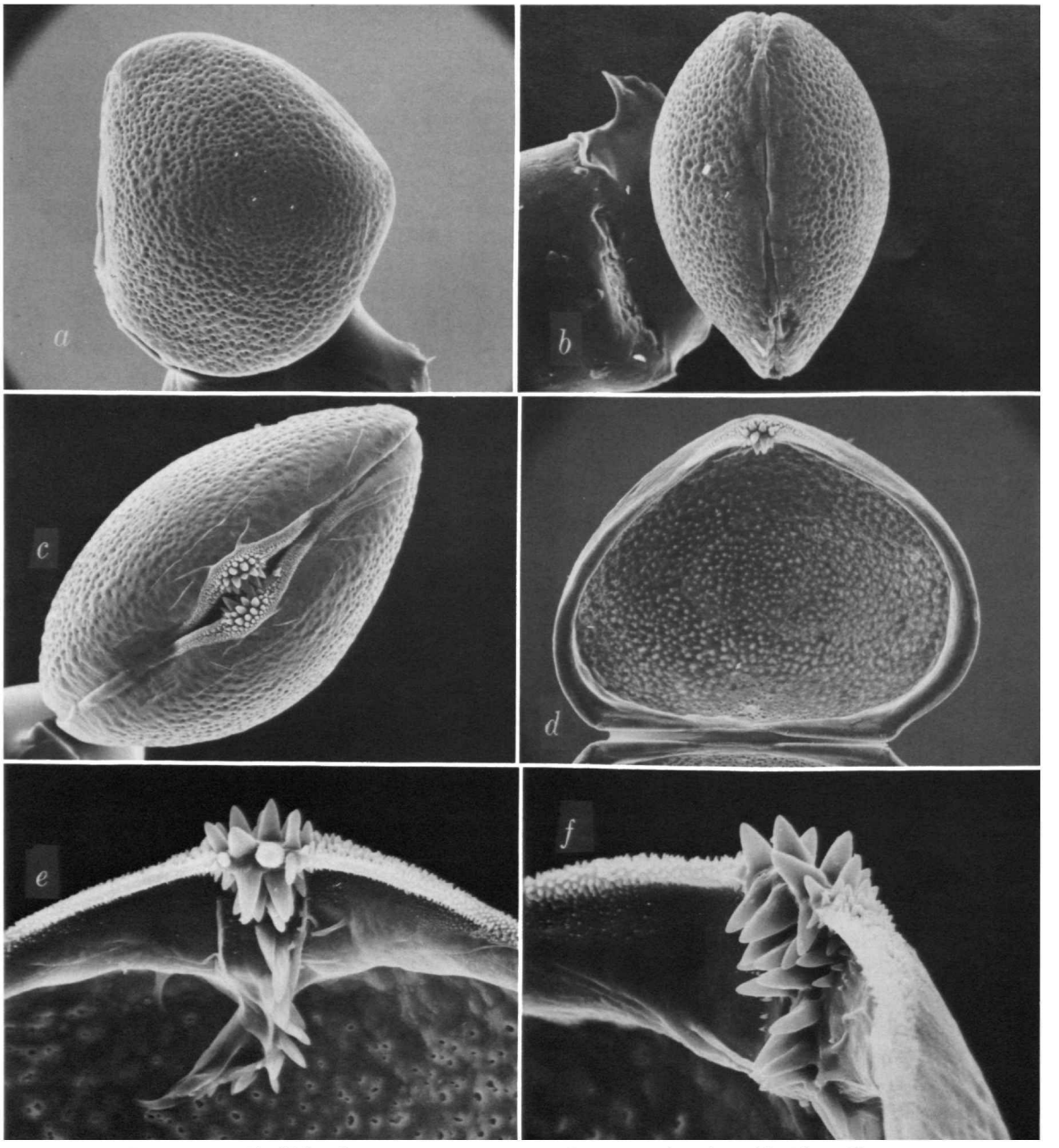

FIGURE 13.—Glochidia of *Lasmigona compressa: a–c,* UM (uncataloged), Raisin River, Sharon Hollow, Michigan; *d–f,* USNM 801452, Cedar Creek, Ozaukee County, Wisconsin (*a* × 170; *b* × 180; *c* × 205; *d* × 200; *e* × 590; *f* × 790).

in agreement with Baker (1928:141) who gives August to May or June as the gravid period.

NATURAL HOSTS.—The identity of the host(s) of *L. compressa* has not been determined.

HABITAT.—Found in large to small rivers and in creeks down to about 2 m in width and in gravel, sand, and mud. The hermaphroditic and (presumably) self-fertilizing capability of this species is apparently adaptive for ascending very narrow streams and for passive dispersal by birds. The few records from lakes probably all represent empty valves washed in from rivers or creeks. Baker (1928:141) notes that it is "not usually found in riffles, but below them in small pools, 0.3–1 m deep, on fine sand or mud bottom. More rarely [it is found] on gravel bottom, swift current, water 0.3–6 m deep."

GEOGRAPHICAL RECORDS

FIGURE 14

Canadian Interior Basin Drainage Systems

MOOSE RIVER SYSTEM.—*Moose River Drainage:* Missinaibi River, 20 mi (32 km) E of Hearst, Ontario (NMC).

ALBANY RIVER SYSTEM.—*Albany River Drainage:* Shekak

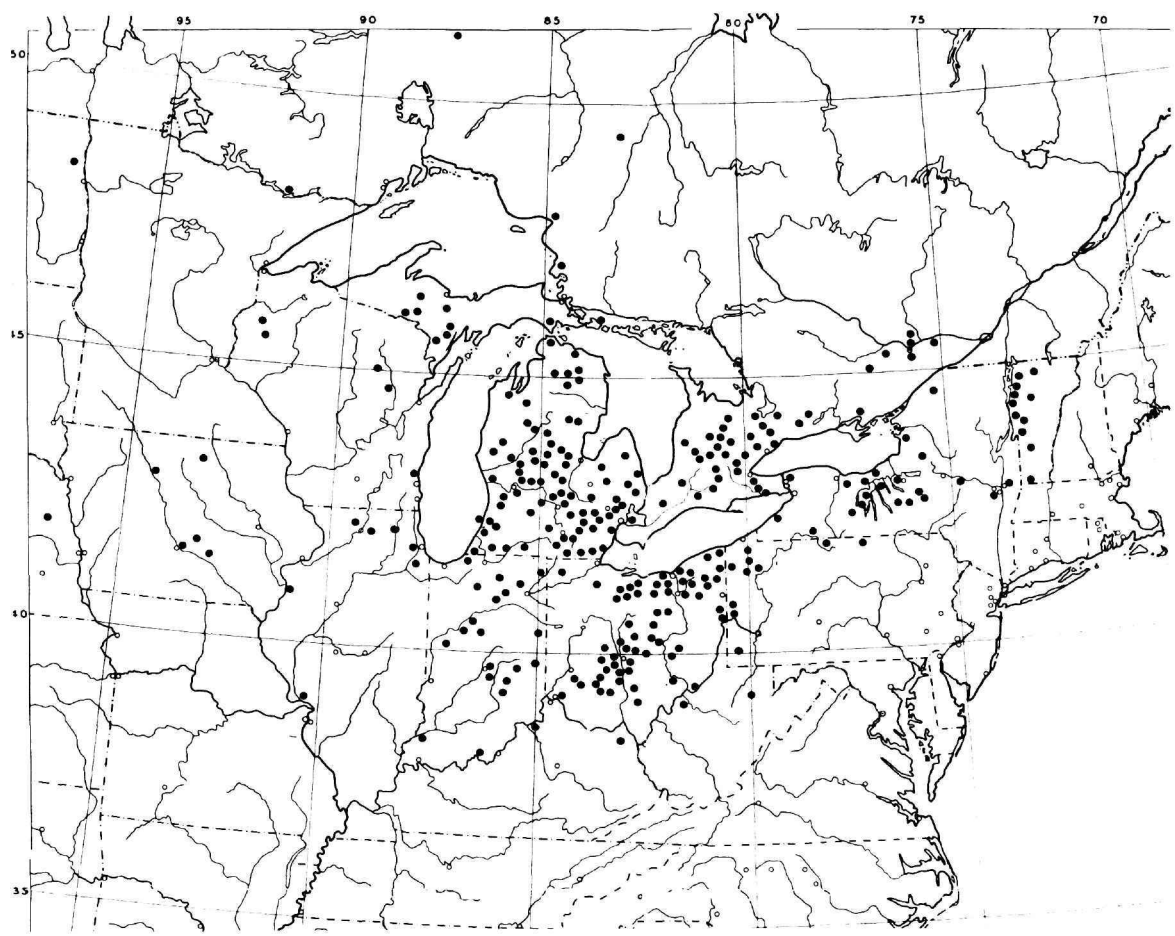

FIGURE 14.—Geographical distribution of *Lasmigona compressa*. (For Canadian localities that are not shown, see Clarke, 1973a:43, 45; small open circles = cities.)

River, 34 mi (54.4 km) W of Hearst, Ontario (1960, A.H., L.R., and A.R. Clarke!, (NMC)). Nagagami River, 40 mi (64 km) W of Hearst (1965, H.D. Athearn! (NMC)).

ATTAWAPISKAT RIVER SYSTEM.—*Attawapiskat River Drainage:* "Boulder River" [Pebble River], about 170 mi (272 km) N of Geraldton, Ont. (NMC). Drinking River, Lake Attawapiskat Region, Ontario (UMMZ).

NELSON RIVER SYSTEM.—Many records from the Winnipeg, Red, and Saskatchewan river drainage, and the Lake Manitoba-Lake Winnipegosis drainage area, from western Ontario to Saskatchewan and south in North Dakota and Minnesota, are given in Clarke (1973a:45).

Atlantic Drainage Systems

ST. LAWRENCE RIVER SYSTEM.—*Lake Superior Drainage:* West side Michipicoten River at mouth (1961, J.V. Wright! (NMC)). Montreal River, NE shore of Lake Superior (USNM).

Lake Michigan Drainage, Michigan: Galien River, [Berrien Co.]. Outlet of Half-Moon Lake, 3 mi (4.8 km) E of Jonesville, Hillsdale Co. (both USNM). Creek outlet of Sherwood Lake, Sherwood Twp., Branch Co. (MCZ). St. Joseph River, below dam at Mottville, St. Joseph Co. (1963, C.B. Stein! (OSUM)). South Dowagiac Creek, La Grange, Cass Co. (MCZ). Pawpaw River at 8 mi (12.8 km) NW of Pawpaw, Van Buren Co. and also at 2½ mi (4 km) NE of Watervliet, Berrien Co. Black River, 1½ mi (2.4 km) W of Bangor, Van Buren Co. 5 mi (8 km) NW of Bangor; and 3 mi (4.8 km) NE of South Haven, Van Buren Co.; Battle Creek River, 7½ mi (12 km) NE of Battle Creek, Calhoun Co. (all UMMZ). Kalamazoo River, 1 mi (1.6 km) W of Concord, Jackson Co. (MCZ). Rabbit River, Hamilton, Allegan Co. (UMMZ). Grand River and tributaries, many records (UMMZ, MCZ, OSUM, USNM). Hayworth Creek, 5 mi (8 km) NE of Fowler, Clinton Co. (1966, C.B. Stein!, OSUM). Muskegon River tributaries, several records (UMMZ, ANSP). Tributaries of Lake Michigan in Oceana, Newago, Traverse, Emmet, Shewano, Iron, Menominee, Dickinson, and Marquette counties, numerous records (UMMZ); Pigeon River near Vanderbilt, Otsego Co. (1967, S. Taub! (OSUM)).

Lake Huron Drainage: Creek mouth, Aux Chene Creek, Mackinac Co., Mich. Potaganissing River, 2 mi (3.2 km) from mouth, Drummond Island, Chippewa Co., Mich. Ocqueoc River, N of Millersburg, Presque Isle Co., Mich. (all UMMZ). Thunder Bay River system at Sage Lake, 0.8 mi (1.3 km) NE of Road 612, Montmorency Co., Mich. (MCZ); Thunder Bay River, 1 mi (1.6 km) S of Atlarata, Montmorency Co., Mich.; Wolf Creek, Oscoda Co., Mich. and East Branch Au Sable River, 6 mi (9.6 km) W of Lovell, Crawford Co., Mich. (all UMMZ). Rifle River, Ogemaw Co., Mich. (UMMZ). Saginaw River system at numerous localities (UMMZ) including S. Branch Tobacco River at bridge just S of Farwell, Clare Co., Mich.; N. Branch Chippewa River, 4 mi (6.4 km) W of Mount Pleasant, Isabella Co., Mich.; and 5 mi (8.0 km) WSW of Rosebush, Isabella Co., (all 1966, C.B. Stein! (OSUM)). Unnamed creek about 2 mi (3.2 km) W of Stroud, Simcoe Co., Ont. (OSUM). River at Pefferlaw, York Co., Ont. (1963, H.D. Athearn! (NMC)). Portageville Creek, Portageville, King Twp., York Co., Ont. (UMMZ). Maitland River, Auburn, Huron Co., Ont. (UMMZ). Whitefish Creek, Lake Simcoe, Simcoe Co., Ont. (UMMZ).

Lake St. Clair Drainage: Sydenham River, 15.5 mi (24.8 km) SW of Strathroy, Lambton Co., Ont. (1967, C.B. Stein and K. Heffelfinger! (OSUM)). Thames River at headwaters, Mitchell, Perth Co., Ont. (UMMZ). Medway Canal, 5 mi (8 km) N of Arva, Middlesex Co., Ont. (UMMZ). Avon River, 1¼ mi (2 km) above Stratford, Perth Co., Ont. (UMMZ). South Branch Thames River at Dorchester, Middlesex Co., Ont. and below Woodstock, Oxford Co., Ont. (both UMMZ). Black River, 1½ mi (2.4 km) W of Amadore, Sanilac Co., Mich. (UMMZ). Mill Creek, 9 mi (14.4 km) N of Capac, St. Clair Co., Mich. (UMMZ). Belle River at Indian Trail Road bridge, 4.8 mi (7.7 km) NW of St. Clair, St. Clair Co., Mich. (1965, C.B. Stein! (OSUM)). Clinton River, Pontiac, Oakland Co., Mich. (UMMZ). North Branch Clinton River, 1 mi (1.6 km) N of Mount Clemons, Macomb Co., Mich. (1965, C.B. Stein and J. Stillwell! (OSUM)). Paint River near Rochester, Oakland Co., Mich. (UMMZ).

Lake Erie Drainage: Rouge River, Birmingham, Oakland Co., Mich. and Detroit, Oakland Co., Mich. (both UMMZ). Detroit River, Fighting Isle, Wayne Co., Mich. (UMMZ). Huron River at Dexter, Ann Arbor (Washtenaw Co.) and many other localities (all UMMZ). Portage River, 2 mi (3.2 km) SW of Pinckney, Livingston Co., Mich. (UMMZ). North Branch Saline River, Washtenaw Co., Mich. (MCZ). Goose Creek just N of Brooklyn, Jackson Co., Mich. (UMMZ). River Raisin at 3 mi (4.8 km) NW of Norwell, Jackson Co., Mich. (UMMZ); millrace below dam 2 mi (3.2 km) S of Tecumseh, Lenawee Co., Mich. and 1 mi (1.6 km) SE of Manchester, Washtenaw Co., Mich. (both MCZ). Otter River, LaSalle, Monroe Co., Mich. (UMMZ). St. Joseph River (of the Maumee), 3 mi (4.8 km) W of Waldron, Hillsdale Co., Mich. (UMMZ). and at bridge, Newville, DeKalb Co., Ind. (1962, D.H. Stansbery! (OSUM)). Beaver Creek, Williams Co., Ohio (MCZ). The Outlet at Ohio Rt. 568 bridge, 5.5 mi (8.8 km) E of Findlay, Hancock Co., Ohio (1968, C.B. Stein and J.J. Jenkinson! (OSUM)). Tymochtee Creek, 0.5 mi (0.8 km) N of Tymochtee and 3.2 mi (5.1 km) E of Kirby, both Wyandot Co., Ohio (both 1970, R. Bowers! (OSUM)). Sandusky River, 2.1 mi (3.4 km) NE of Little Sandusky and 5.3 mi (8.5 km) E of Crawford, both Wyandot Co., Ohio (both 1970, R. Bowers! (OSUM)). Huron River about 2 mi (3.2 km) SW of Milan, Erie Co., Ohio (1969, M. Trautman! (OSUM)). West Branch Huron River, 7.4 mi (11.8 km) SW of Norwalk, Huron Co., Ohio (1969, R. Bowers! (OSUM)). Vermilion River, 3.6 (5.8 km) and 3.8 mi (6.1 km) NE of Clarksfield, 5.9 mi (9.4 km) NW of New London (all Huron Co., Ohio), and 6.4 mi (10.2 km) S of Vermilion, Erie Co., Ohio (all 1968, R. Bowers! (OSUM)).

East Branch Black River at Ohio Rt. 303, Lorian Co., Ohio (1959, D.H. Stansbery! (OSUM)) and at River Corners, Medina Co., Ohio (1964, M. Trautman! (OSUM)). West Branch Black River, 1.8 mi (2.9 km) WNW of Wellington, Lorain Co., Ohio (1978, R. Bowers!, (OSUM)). West Branch Cuyahoga River, 1.9 mi (3 km) W of Burton, Geauga Co., Ohio (1971, C.B. Stein! (OSUM)). Cuyahoga River, Mantua, Portage Co., Ohio (MCZ). Mill Creek at Forman Road bridge, Eaglesville, Ashtabula Co., Ohio (1969, J. Bissell and R. Klein! (OSUM)). Grand River at covered bridge, about 1 mi (1.6 km) NW of Rock Creek, Morgan Twp., Ashtabula Co., Ohio (1966, D.H. Stansbery! (OSUM)). Ashtabula River, 6.8 mi (10.9 km) N of Giddings, Ashtabula Co., Ohio (1969, M. Klein and J. Bissell! (OSUM)). Conneaut Creek, 3 mi (4.8 km) S of Conneaut, Ashtabula Co., Ohio (1969, J. Bissell! (OSUM)). Crooked Creek, Dunkink, Chautauqua Co., N.Y. (MCZ). Grand River (Ontario) at Leggett, 1.8 mi (2.9 km) S of Keldon (both East Luther Twp. Dufferin Co.), (1971, B.T. Kidd! (NMC)); Fergus, Wellington Co., (NMC); Byng, Haldimand Co., (MCZ); and Caledonia, Haldimand Co., (UMMZ). Willow Brook, 2.2 mi (3.5 km) ENE of Grand Valley, Dufferin Co., Ont. (1971, B.T. Kidd! (NMC)). Irvine Creek, 2 mi (3.2 km NNW) of Dracon, Wellington Co., Ont. (1969, J. Oughton! (NMC)). Galt Creek, 1¼ mi (2 km) SSW of Aberfoyle, Wellington Co., Ont. (1969, J. Oughton! (NMC)). Eramosa Creek, Wellington Co., Ont. (1968, J. Oughton! (NMC)). Speed River near N city limits of Guelph, Wellington Co., Ont. (1965, U. Soehngen! (OSUM)). Canagigique River, Floradale, Waterloo Co., Ont. (UMMZ). Small Creek near Hespler, Waterloo Co., Ont. (1968, J. Oughton! (NMC)). Nith River, Plattsville, Oxford Co., Ont. (1969, J. Oughton! (NMC)); and 2.9 mi (4.6 km) W of Paris, Brant Co., Ont. (1963, H.D. Athearn! (NMC)).

Lake Ontario Drainage: Niagara River, N.Y. (USNM). Mono Mills, Peel Co., Ont. (MCZ). Credit River, 4 mi (6.4 km) SW of Victoria, Peel Co., Ont. (1968, H.D. Athearn! (NMC)) and tributary above Georgetown, Halton Co., Ont. (UMMZ). East Branch Don River, Toronto, York Co., Ont. (UMMZ). Indian River, Peterborough Co., Ont. (1953, H.B. Herrington! (UMMZ)). Creek branch at Bethany, Hwy. 7A, Manvers Twp., Durham Co., Ont. (1958, H.B. Herrington! (UMMZ)). Moira River, Hastings Co., Ont. (MCZ). Erie Canal, Pittsford, Monroe Co., N.Y. and Palmyra, Wayne Co., N.Y. (both MCZ). West River, (specimen very large), Penn Yan, and Flint Creek (all Yates Co., N.Y. (MCZ)). Seneca Lake, Rod and Gun Club, S of Geneva, Ontario Co., N.Y. (1962, A. Weir! (NMC)). Owasco Lake outlet, Cayuga, Cayuga Co., N.Y. (USNM). Seneca River, Baldwinsville, Onondaga Co., N.Y. (UMMZ). Sphaerium Brook, McLean, Tompkins Co., N.Y. (1955, A.H. Clarke! (MCZ)). Wood Creek near Kenwood, Oneida Co., N.Y. (MCZ). Wolcott Creek, 2 mi (3.2 km) below Wolcott, Wayne Co., N.Y. (ANSP). Stony Creek, Jefferson Co., N.Y. (MCZ).

St. Lawrence River Drainage (main river): Racquette River, 1 mi (1.6 km) S of Potsdam, St. Lawrence Co., N.Y. (MCZ). Mill Pond, Madawaska River, Denbigh, Lennox and Addington Co., Ont. (UMMZ). Old mill stream, Pakenham, Lanark Co., Ont. (UMMZ). Rideau River, Ottawa, Carleton Co., Ont. (UMMZ). Richardson Lake, Clarendon Twp., Pontiac Co., Que. (1966, G. Gibson! (UMMZ)). Masham, [Gatineau Co.], Que. (UMMZ). Brook, Hull, Gatineau Co., Que. (MCZ). Greens Creek, Hwy. 17, 10.3 mi (16.5 km) W of Cumberland, [Carleton Co.], Ont. (1960, D.E. McAllister! (NMC)).

Lake Champlain Drainage, Vermont: Otter Creek, East Danby, Rutland Co. (1952, H.D. Athearn! (MCZ)) and near Vergennes, Addison Co. (MCZ). Fairhaven, Rutland Co. and Cornwall, Addison Co. (both USNM). Chimney Point, Lake Champlain (USNM). Small brook, Middlebury, Addison Co. (holotype of *Unio compressus* var. *plebeius* Adams (MCZ)). Winooski River, Jonesville and Winooski (both Chittendon Co.) (MCZ). Creek near Mallett's Bay, Lake Champlain, Chittendon Co. (MCZ). Lamoille River, Cambridge, Lamoille Co. and 2 mi (3.2 km) N of Milton, Chittendon Co. (both MCZ).

HUDSON RIVER SYSTEM.—*Hudson River Drainage:* Hoosic River, Eagle Bridge, Bennington Co., Vt. (USNM). Hydraulic Canal, Herkimer, Herkimer Co., N.Y. (MCZ). Champlain Canal, near Troy, Rensselaer Co., N.Y. (MCZ). Norman's Kill, near Albany, Albany Co., N.Y. (MCZ).

U.S. Interior Basin Drainage Systems

OHIO RIVER SYSTEM.—*Alleghany River Drainage:* Ischua Creek, Cattaraugus Co., N.Y. (MCZ). French Creek, 9 mi (14.4 km) N of Meadville, Crawford Co., Pa. (1975, D. Snyder! (OSUM)); Saegertown, Crawford Co., Pa. (1978, R.E. Winters! (MCZ)); and below mouth of Patchel Run, 1.8 mi (2.9 km) N of Franklin, Venango Co., Pa. (1975, C.B. Stein! (OSUM)). Sandy Creek, 5 mi (8 km) SW of Franklin, Venango Co., Pa. (1967, S.L.H. Fuller! (MCZ)). Allegheny River, Larabee, McKean Co., Pa. (ANSP).

Monongahela River Drainage: Tygarts River, W.Va. (USNM). North Fork Ten Mile Creek, 1.0 mi (1.6 km) SE of Prosperity, Washington Co., Pa. (1969, D. Tanner! (OSUM)).

Beaver River Drainage: Shenango River, Jamestown, Mercer Co., Pa. (ANSP). Deer Creek, 2 mi (3.2 km) W of Limaville, Stark Co., Ohio (OSUM). Hiram, Portage Co., Ohio (MCZ). Garretsville, Portage Co., Ohio (USNM). Lesser branch of Mahoning River, Newton Falls, Trumbull Co., Ohio (MCZ). Mahoning River, Leavittsburgh, Trumball Co., Ohio (USNM). Beaver River below Wampum, Lawrence Co., Pa. (ANSP).

Little Beaver Creek Drainage: Little Beaver Creek, Cannelton, Beaver Co., Pa. (MCZ); ½ mi (0.8 km) S of Gaston's Mill, Columbiana Co., Ohio (1963, R. Sagar! (OSUM)); and Beaver Creek State Forest, 1.9 mi (3 km) SW of Clarkson. Columbiana Co., Ohio (1969, M. West! (OSUM)).

Muskingum River Drainage, Ohio: Little Muskingum River,

Washington Co., (1962, D.H. Stansbery and C.B. Stein! (OSUM)). Shreve Run of Killbuck Creek, Shreve, Wayne Co. (ca. 1960, M. Trautman! (OSUM)). Muddy Fork of Mohican River, N of Blackleyville, Wayne Co. (1964, M. Trautman! (OSUM)). Owl Creek Branch of Kokosing River, ½ mi (0.8 km) NE of Fredericktown, Knox Co. (1967, G. Yost! (OSUM)). Walhonding River just below confluence of Mohican and Kokosing rivers, Coshocton Co. (1967, C.B. Stein! (OSUM)). Little Wakatomica Creek, 8.6 mi (13.8 km) S of Nellie, Coshocton Co. (1972, D.H. Stansbery et al.! (OSUM)). South Fork Licking River, just NE of Hebron, Licking Co. (1975, D. Ross and M. Brenner! (OSUM)). White Eyes Creek, 2.7 mi (4.3 km) S of Otsego, Muskingum Co; West and South branches, Wolf Creek at Ohio Rt. 76 bridge, 1 mi (1.6 km) S of Waterford, Washington Co. (all 1969, D. Tanner! (OSUM)).

Little Kanawha River Drainage: Reedy Creek at W.Va. Rt. 14 bridge, Wirt Co., W.Va. (1961, D.H. Stansbery! (OSUM)).

Little Sandy River Drainage: Little Sandy River, just E of Grayson, Carter Co., Ky. (1975, J. MaGregor! (OSUM)).

Scioto River Drainage, Ohio. (all OSUM records): Olentangy River above Mud River, below county road 196 bridge, Marion Co. (1961, C.B. Stein!); E bank below Ohio Rt. 750 bridge, Delaware Co. (1960, D.H. Stansbery!); and Dodridge Street bridge, Columbus, Franklin Co. (1958, D.H. Stansbery!). Alum Creek, 2.9 mi (4.6 km) S of Kilbourne and 4.8 mi (7.7 km) W of Galena, both Delaware Co. (both 1969, D.H. Stansbery!). Big Walnut Creek, Groveport Road bridge, Obetz, Franklin Co. (1959, D.H. Stansbery!). Raccoon Creek, 3.1 mi (5 km) NNW of Union Station, 0.5 mi (0.8 km) SW of Granville, at Granville, and 2.6 mi (4.2 km) ESE of Granville, Licking Co. (all 1975, G. Miller!). Little Walnut Creek, U.S. Rt. 23 bridge, Jackson Twp., Pickaway Co. (1958, D.H. Stansbery!). Big Darby Creek, Allen Zane Twp., Union/Logan county line (1959, D. Mount!); 5.7 mi (9.1 km) NNW of Georgesville, Franklin Co. (1972, C.B. Stein and D.H. Stansbery!); Orient, 12.5 mi (20 km) SW of Columbus, in Pickering Co. (1971, D.H. Stansbery!); and Rt. 104 bridge S of Fox, Pickaway Co. (1963, C.B. Stein and D.H. Stansbery!). Little Darby Creek, U.S. Rt. 40 bridge, West Jefferson, Madison Co. (1975, D.H. Stansbery!) and 1.5 mi (2.4 km) E of Plumwood, Madison Co. (1963, D.H. Stansbery and C.B. Stein!). Scioto River, Columbus, Franklin Co. Opossum Run, 2.5 mi (4 km) NE of Mount Sterling, Pickaway Co. (1969, J. Stillwell!). Deer Creek, Ohio Rt. 104 bridge, 5 mi (8 km) S of Yellowbud, Union Twp., Ross Co. (1969, J. Stillwell and J. Bissell!). Sugar Creek, 4 mi (6.4 km) S of Washington Court House, Fayette Co. (1967, K. Jennings and J. Reese!). North Fork, 8.2 mi (13.1 km) E of Washington Court House, Fayette Co. (1967, K. Jennings and R. Hughes!). Paint Creek, 1 mi (1.6 km) N of Rock Mills, Fayette Co.; at Rock Mills; and 5 mi (8 km) S of Greenfield, Highland Co. (all 1967, K. Jennings and J. Reese!). Salt Creek along Dixon Mill Road, 1.4 mi (2.2 km) ESE of Londonderry, Ross Co. (1975, A. Spreitzer and M. Vrabec!). Little Salt Creek below Hickman Road bridge, 1.6 mi (2.6 km) SSE of Brooks Corner, Jackson Co. (1974, J.J. Jenkinson!).

Little Miami River Drainage, Ohio: Caesar Creek, 0.2 mi (0.3 km) above its mouth, 2.8 (4.5 km) SSE of Waynesville, Warren Co. (1972, D.H. Stansbery! (OSUM)). Little Miami River, Telegraph Mill bridge, Corwin, Warren Co. (1956, D.H. Stansbery et al! (OSUM)).

Whitewater River Drainage: Green's Fork, 1 mi (1.6 km) E of Pennville, Wayne Co., Ind. (1964, C.B. Stein! (OSUM)).

Wabash River Drainage, Indiana: Mississinewa River, 1.2 mi (1.9 km) W of Deerfield, Randolph Co. (1969, D. Tanner! (OSUM)). Blue River, Columbia City, Whitley Co. (USNM). Eel River, N Manchester, (MCZ) and 11.5 mi (18.4 km) N of Wabash (1970, B. Snyder! (OSUM)), both Wabash Co.. Tippecanoe River, bridge S of Atwood, Koskiusko Co. (1963, C.B. Stein! (OSUM)) and DeLong, Fulton Co. (USNM). Wabash River, Lafayette, Tippecanoe Co. (MCZ) and Delphi, Carroll Co. (USNM). Honey Creek, Russiaville, Howard Co. (USNM). Coal Creek, Waynestown, Montgomery Co. (UMMZ). Canal at Indianapolis, Marion Co. (MCZ). Big Blue River, near Newcastle, Henry Co. (1975, B. Crawford! (OSUM)). Brandywine Creek, 0.8 mi (1.3 km) SE of Fountaintown, Shelby Co. (1964, C.B. Stein! (OSUM)). Flatrock Creek, 8 mi (12.8 km) S of Shelbyville, Shelby Co. (1964, C.B. Stein! (OSUM)). Clifty Creek, 2.7 mi (4.3 km) E of center of Columbus, Bartholomew Co. (1979, G. Finni and W. McClain! (OSUM)). White River, Ind. (USNM).

Ohio River (main stem): Ohio River, Cincinnati, Hamilton Co., Ohio (MCZ).

UPPER MISSISSIPPI RIVER SYSTEM.—*St. Croix River Drainage, Wisconsin:* Yellow River, 5–6 mi (8–9.6 km) W of Spooner, Washburn Co. (1976, H. Mathiak! (OSUM)). East Branch Eau Claire River, 4.5 mi (7.2 km) W of Antigo, Langdale Co. (1969, D.H. Stansbery! (OSUM)). (For many other recent Wisconsin records see Mathiak, 1979.)

Rock River Drainage: Kent's Creek, NW of Rockford, Kent Co., Ill. (MCZ).

Iowa River Drainage: [Shell River], Rockford, Floyd Co., Iowa (USNM).

Skunk River Drainage: Skunk River, Jasper Co., Iowa (USNM).

Des Moines River Drainage, Iowa: Lizard Creek, First Dodge, Webster Co. (MCZ). Des Moines River, Des Moines, Polk Co. (MCZ).

Illinois River Drainage: Dupage River, Plainfield, Will Co., Ill. (ANSP). Little Kankakee River, LaPorte, LaPorte Co., Ind. (MCZ). Fox River, Algonquin, McHenry Co., Ill. (MCZ). Illinois River, Joliet, Will Co., Ill. (USNM).

Missouri River Drainage: [Elkhorn River], West Point, Cuming Co., Neb (USNM).

Lasmigona (Platynaias) subviridis (Conrad, 1835)

FIGURES 15–17

Unio subviridis Conrad, 1835:4 (appendix), pl. 9: fig. 1. [In text under "*Unio viridis*" as "this may be a different species [from *U. viridis* Rafinesque] and in that case I propose to call the present shell *subviridis*." Type-locality: "Schuylkill River, Juniata River, creeks in Lancaster Co., Penn." The holotype, originally catalogued under number 2105 in the Academy of Natural Sciences of Philadelphia, and now lost, was labelled "creeks in Lancaster Co." (Johnson and Baker, 1973:172; see also Frierson, 1915).]

Unio tappanianus Lea, 1838:62, pl. 17: 55. [An unnecessary replacement name for "*U[nio] viridis* Rafinesque sensu Conrad and therefore it takes the same type specimen and type-locality as above. A specimen (USNM 86133) is almost certainly the specimen on which Lea's figure was based.]

Unio hyalinus Lea, 1845:164, pl. 2: 4. [Type-locality: [James River] Richmond, Virginia. Holotype is USNM 96131.]

Margaritana quadrata Lea, 1861:41. [Type-locality: "East Tennessee" [undoubtedly incorrect]. The holotype, figured by Lea (1862:210, pl. 32: fig. 279), is USNM 86264. It appears to be a deformed specimen of *Unio subviridis* Conrad.]

Unio pertenius Lea, 1863:193. [Type-locality: "Neuse River, near Raleigh, N. Carolina." The holotype, figured by Lea (1866:8, pl. 2: fig. 4), is USNM 86139.]

THE SHELL

FIGURE 15*a,c–d*

DESCRIPTION (of Susquehanna River system specimens).—Shell ovate trapezoid, unsculptured, up to 62 mm long, 33 mm high, and 20 mm wide, rather fragile, somewhat thicker anteriorly (up to 1.5 mm thick) and thinner (0.5 mm) posteriorly. Anterior margin rounded above and more openly curved below, ventral margin slightly convex throughout or centrally flattened, posterior margin sharply rounded, subacute, or somewhat biangulate below and obliquely flattened above, and dorsal margin broadly sinuate to gently convex throughout. Maximum inflation at a point a little above the center of the shell. Beaks depressed, projecting only little above the hinge line, and located about 27% to 34% the distance from anterior to posterior. Posterior ridge rounded in most specimens or, in some, obscurely double and subangular. Posterior slope compressed and concave, in some juveniles it is dorsally expanded and subalate. Growth increments marked by concentric grooves that are darkly pigmented in most specimens. Post-juveniles sculpturing consisting only of growth rests and, in some specimens, of a few irregularities of growth. Periostracum pale yellowish or brownish overlaid with numerous narrow and wide green or blackish rays. Rays are particularly conspicous in juveniles. Ligament narrow, thin, rather short, and fragile when dry.

Hinge teeth well developed but rather small and delicate. Pseudocardinal teeth somewhat elevated, serrated, moderately sharp, directed anterior-ventrally, and numbering 2 in the left valve and (ordinarily) 1 in the right. Interdental projection present in the left valve but not well developed; it is low, flange-like, variable, and confluent with the pseudocardinals. The interdental depression in the right valve severs the hinge plate in many specimens. Lateral teeth narrow and sharp, of only moderate length, and ordinarily numbering 1 in the right valve and 2 in the left. In many specimens, however, the lateral teeth are incomplete or partly indistinct. Beak cavity shallow, quite narrow, and exhibiting irregular, small, muscle scars. Anterior adductor muscle scars conspicuous but small and shallow. Posterior muscle scars clearly discernable but only lightly etched. Pallial band narrow, well marked but not deep, and with inner margin subcrenulate but outer margin mainly smooth. Nacre shiny, whitish anterio-ventrally, bluish and iridescent posteriorly, and, in many specimens, with yellowish or pale salmon suffusions centrally and near the beak cavity. At the margin the nacre is thin and the periostracal colors and patterns shows through.

Beak sculpture variable but fundamentally double looped and consisting of about 6 concentric ridges and smaller accessory anterior and posterior radial ridges. In one specimen the first ridge is single-looped, expanded anteriorly, and not at all parallel with lines of growth; the second ridge is similar but nodulous posteriorly; the

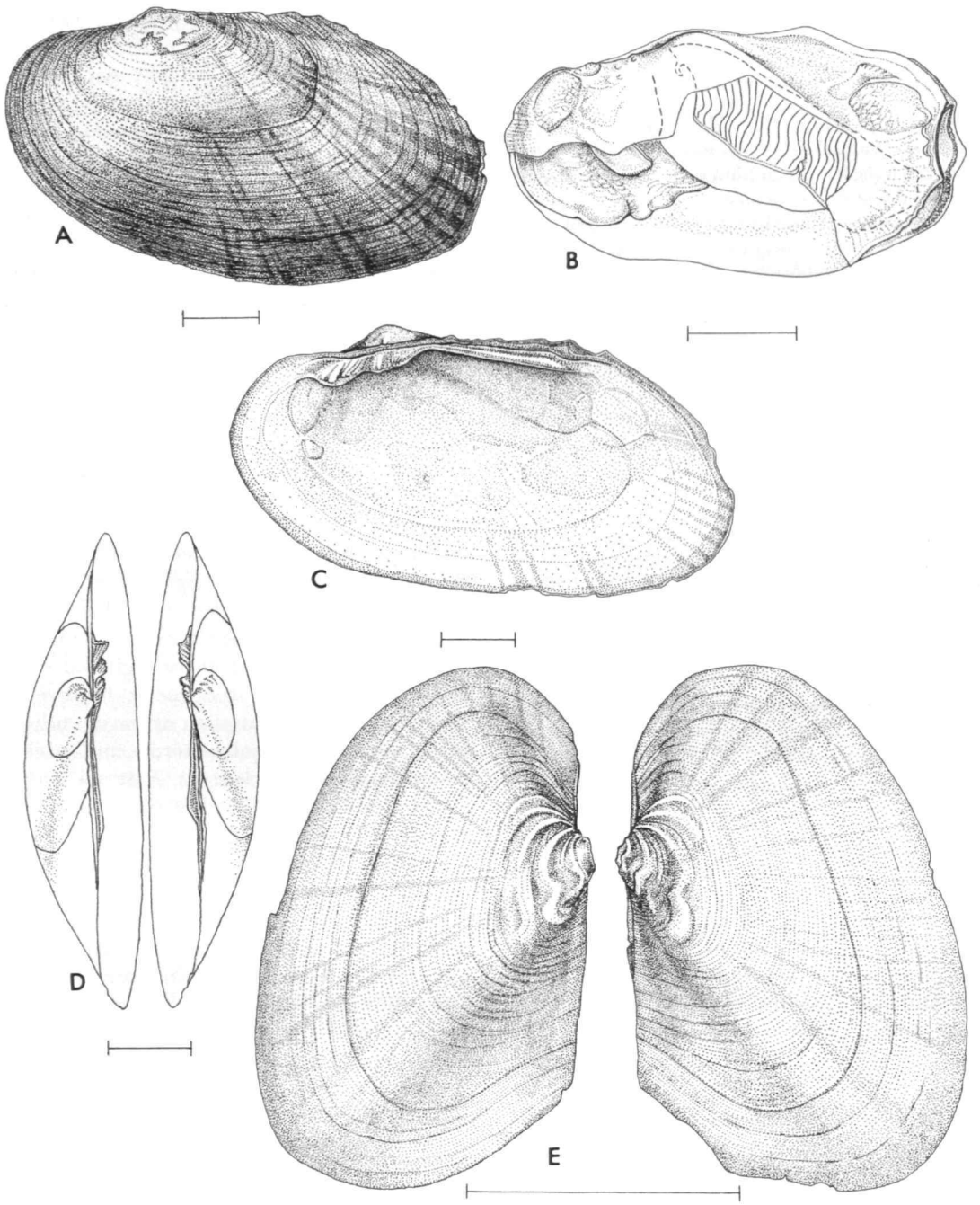

FIGURE 15.—*Lasmigona subviridis: a,c,d*, USNM 152972, Cortland, Cortland County, New York; *b*, USNM 758868, Little River, 5 mi (8 km) NW of Zebulon, Wake County, North Carolina; *e*, USNM 618640, 4–6 mi (6.4–9.6 km) N on Rt. 64 of Raleigh, Wake County, North Carolina. (Scale = 1 cm.)

third is transitional; the fourth and fifth are strongly double-looped with the anterior loop rounded and the posterior loop narrower but equally expanded; and the sixth loop is nearly obliterated. In another specimen there are about 8 bars and the re-entering sinus ridges intersect previous ridges and produce an anastomosing network. In another specimen with 8 bars the bars are broken but widely spaced and do not intersect. Most of the beak sculpture ridges are still visible on many adult specimens.

VARIATION.—The population samples of *L. subviridis* examined (Table 12) are not unusually variable. Their coefficients of variability for H/L reach a maximum of 5.4, for W/L a maximum of 7.5, and for $\frac{B\text{-}A}{L}$ a maximum of 6.7. Ortmann (1919:122) has already pointed out that the most variable feature of the shell is the color of the periostracum. Among specimens in the Smithsonian Institution this varies from green to yellowish brown and to brown, with rays being visible in most specimens but particularly so in green or yellowish individuals.

Inter-population variation in size of *L. subviridis* is discussed below under *L. decorata* (Lea, 1852).

TABLE 12.—*Lasmigona subviridis:* shell measurements.

Feature	N	Range	Mean ($\bar{x}$)	S
		Mohawk River, Mohawk, N.Y. J. Lewis! date? USNM 519836		
Length (mm)	7	32.1–42.0	37.8	3.53
H/L	7	0.595–0.678	0.630	0.0341
W/L	7	0.340–0.406	0.370	0.0279
B-A/L	7	0.303–0.355	0.329	0.0190
		Potomac River, 1 mi SE of Seneca, Md. F.W. Grimm! 22 Aug 1959 (NMC)		
Length (mm)	16	33.2–50.3	44.2	3.83
H/L	16	0.583–0.676	0.640	0.0249
W/L	16	0.325–0.381	0.358	0.0178
B-A/L	16	0.292–0.552	0.326	0.0190
		Pamunky Creek, Orange Co., Va. (USNM 424444, 424445)		
Length (mm)	5	40.2–54.7	46.3	7.13
H/L	5	0.612–0.634	0.621	0.0110
W/L	5	0.358–0.405	0.389	0.0190
B-A/L	5	0.239–0.281	0.268	0.0179
		James River, Lynchburg, Va. (USNM 451973)		
Length (mm)	4	34.2–36.5	35.1	0.99
H/L	4	0.641–0.649	0.644	0.0037
W/L	4	0.307–0.318	0.317	0.0082
B-A/L	4	0.256–0.296	0.278	0.0202

TOPOGRAPHIC ANATOMY

FIGURE 15*b*

SPECIMEN DESCRIBED.—USNM 758865, from Little River (Neuse River system), 5 mi (8 km) NW of Zebulon, Wake County, North Carolina collected by A.H. Clarke (station 1486) on 20 May 1977; specimen killed accidentally with X-rays, fixed in 10% formaldehyde and preserved in 70% ethyl alcohol; shell length 45.6 mm, sex female (gravid, with eggs).

DESCRIPTION.—Mantle yellowish white at the marginal muscle band, near the adductor muscles and over the diaphragm; translucent centrally and above the diaphragm. Foot orange, visceral mass yellowish white, and adductor muscles pale yellowish brown. Marginal muscle band 6.0 mm wide and 0.4 mm thick anterior-ventrally, 4.5 mm wide and 0.6 mm thick posterior ventrally, and bent inwardly near the posterior mantle openings. Mantle with a narrow (0.5 mm) band of dark brown pigment along the margin only near the incurrent and anal openings.

Incurrent opening 8.4 mm long, surrounded just within the edge by a partially double row of flattened pyriform papillae that are pigmented principally only along their adjoining sides. Inner papillae about 0.5 mm long and 0.2 mm wide at their bases. Mantle edge between incurrent and anal openings about 0.5 mm long. Anal opening 5.4 mm long, 5.4 mm wide, surrounded by a single row of tiny (0.1 mm long), pyramidal papillae, and more darkly pigmented than the incurrent opening. Mantle connection between anal and supra-anal openings 2.0 mm long. Supra-anal opening 7.9 mm long, slit-like, with smooth, flanged edges, and without pigmentation.

Outer demibranch pale orange, 23.5 mm long, 7.2 mm wide at its broadest part (posteriorly),

with an irregular free margin (narrowly lobate anteriorly and cleft centrally), and with narrow extremities. There are about 3 water tubes per mm, about 14 radial surficial filaments per mm in the anterior portion, and about 25 radial surficial filaments per mm in the posterior portion, and 5 cross filaments per mm. Inner demibranch also pale orange, 25.5 mm long, 11.4 mm high, projecting 5.3 mm beyond the outer demibranch anterior-ventrally, roundly subtruncate anteriorly and narrowing posteriorly, with about 1.0–1.5 water tubes per mm and 14 surficial radial filaments and 5–6 cross filaments per mm. The inner lamina of the inner demibranch is connected to the visceral mass only in its anterior portion.

Labial palpi more or less straight dorsally, rounded ventrally, with upturned tips and not touching the inner demibranchs. The outer surface of the outer palpus of each pair bears low, irregular ridges and the inner opposing surface of each member is furrowed (about 5 furrows per mm). The outer palpus of each pair is fused basally to the mantle and subdorsally, for about ⅚ of its length, to the inner palpus.

According to Ortman (1912:282) the marsupia are "cream color, pale orange, or brown." The anatomy is there reported to be the same as in *Lasmigona compressa* (Lea), and *L. subviridis* is also described as hermaphroditic, with female gill structure occurring in the outer demibranchs of all specimens.

Glochidium

Figure 16

Description.—Glochidium subovate, 0.285 mm high, 0.372 mm long, and 0.184 mm in total convexity (both valves appressed). The valves are markedly asymmetrical; the apices tip forward and are located about 41% of the distance from anterior to posterior, the posterior margin is more distended than the anterior and its point of maximum expansion is higher, and the area of maximum valve inflation is anterior of center. Surface of glochidium finely malleate and punctate except for a narrow marginal band, about 36 μm wide near the apex and about 26 μm wide elsewhere, which is sculptured with low collabral ridges. The malleations are subcircular, about 4–8 μm in diameter, and generally distributed. The pits are about 1–3 μm wide, circular, and with about 1 located in each depression. The hinge is about 0.258 mm long and nearly straight but very slightly convex. The ligament is long, narrow, and visible externally.

The stylets are approximately 100 μm long (the stylets were not fully visible in our material), about 30 μm wide at their bases, narrowly attenuate, and supported along most of their length by the mantle membrane. The microstylets are about 9 μm long, 6 μm wide at their bases, pyramidal, multifaceted, and arranged in single file on the distal end of the stylet and about 6 abreast on the proximal end. At the bases of the stylets and occupying a V-shaped confluent area are numerous slightly smaller microstylets (6–7 μm high) that extend onto the rims of the valves. Numerous micropoints (0.5–2 μm) also continue along the rim for a long distance on each side and along the edges of the stylet. The expansion of microstylets and micropoints does not continue onto the outer sides of the valves as it does in *L. compressa*.

The above description is of a glochidium from an adult specimen collected in the Unadilla River at South Edmeston, Otsego/Chenango County, New York, by Dr. Carol B. Stein on 28 September 1965. Two other glochidia, from the same specimen, are 0.290 mm in height, 0.350 mm in length, and 0.287 mm in height, 0.358 mm in length. There is also some variation in shape (see Figure 16). According to Ortmann (1919:122) the glochidia are 0.30 mm high and 0.36 mm long. According to the figures in Lea (1874b, pl. 21 (two figures, both numbered 14)) of 2 glochidia from a specimen from Columbia, Pennsylvania (Susquehanna River?), the shape is variable and the height and length may be approximately equal.

Life History

Gravid Period.—The glochidia described above are from a specimen collected on 28 Sep-

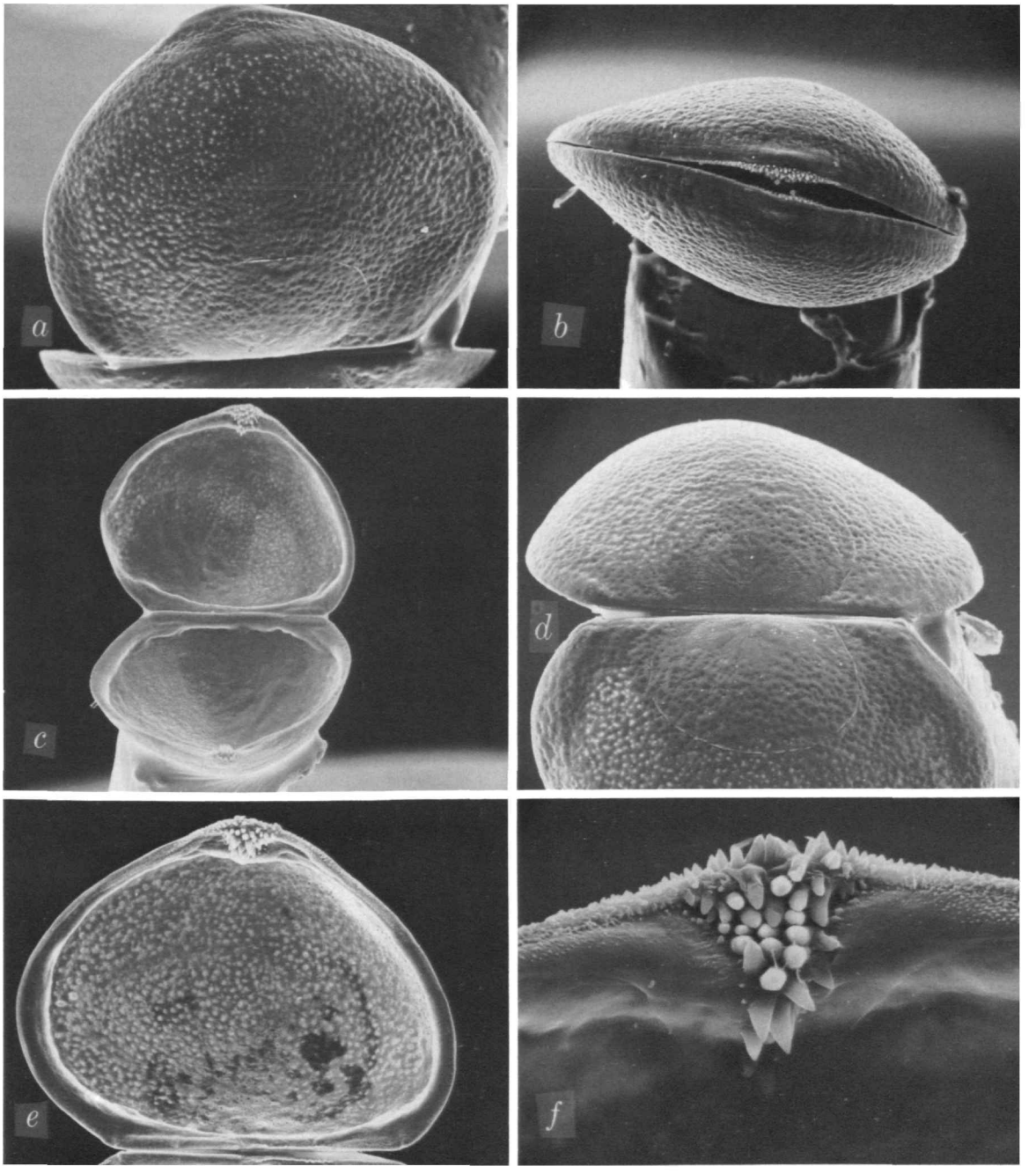

FIGURE 16.—Glochidia of *Lasmigona subviridis: a–f*, OSUM 20954, Unadilla River, South Edmeston, Chenango/Otsego Counties, New York (*a,b* × 205; *c* × 120; *d* × 195; *e* × 675; *f* × 820).

tember. Ortmann (1919:122) reported gravid specimens had been collected in Pennsylvania from 13 August to the following 8 June.

NATURAL HOSTS.—The fish host(s) of this species are unknown.

HABITAT.—I agree fully with Ortmann (1919:124) who says: "[*L. subviridis*] is very erratic in its distribution . . . [;] it avoids the larger rivers and prefers smaller streams. . . . The specimens found by myself in larger rivers generally are few, and often in small branches of the river. But even in small streams, it is not everywhere present. But generally, when found, it turned up abundantly. Like [*L. compressa*] . . ., it is averse to very strong current, and prefers the quiet parts, pools or eddies with gravelly and sandy bottoms, and it also goes into canals, where it seems to flourish." Perhaps significantly, it has not been found in association with *L. compressa* in the region of geographical overlap (Clarke and Berg, 1959:33).

GEOGRAPHICAL RECORDS

FIGURE 17

Atlantic Coastal Drainage

ST. LAWRENCE–HUDSON RIVER SYSTEMS, NEW YORK (canals and associated streams intersecting both systems).—Erie Barge Canal, 9 mi (14.4 km) E of Syracuse, Onondaga Co. (MCZ); Baldwinsville, Onondaga Co. (ANSP); and Mohawk, Herkimer Co. (MCZ). Chittenango Creek, Kirkville, Onondaga Co. (Clarke and Berg, 1959:33). Champlain Canal near Troy, Rensselaer Co. (MCZ).

HUDSON RIVER SYSTEM, NEW YORK.—Hudson River, Albany, Albany Co. (MCZ).

PASSAIC RIVER SYSTEM, NEW JERSEY.—Passaic River, Newark, Essex Co. (MCZ).

RARITAN RIVER SYSTEM, NEW JERSEY.—Raritan River, New Brunswick, Middlesex Co. (ANSP). Delaware-Raritan Canal, Princeton, Mercer Co. (Ortmann, 1919:123).

DELAWARE RIVER SYSTEM.—Pequest River, Great Meadows, Warren Co., N.J. (UMMZ). "Valley Creek" [probably Sucker Creek], SW of Coatsville, Chester Co., Pa. (ANSP). Schuylkill Canal, Manayunk, Philadelphia Co. (Ortmann, 1919:123). Schuylkill River at Phoenixville, Chester Co., Pa. (ANSP). Delaware River at Shawnee, Monroe Co. and Yardley, Bucks Co., Pa. (both Ortmann, 1919:123).

SUSQUEHANNA RIVER SYSTEM.—Susquehanna River 2 mi (3.2 km) W of Otego, Otego Co., N.Y. (1955, A.H. and L.R. Clarke! (NMC)); Afton, Chenango Co., N.Y., Nineveh, Broone Co., N.Y. (all Clarke and Berg, 1959:33); and Dauphin Co., Pa. (ANSP). Unadilla River, S. Edmeston, Otsego/Chenango Co., N.Y., above State Rt. 80 bridge (1965, C.B. Stein! (OSUM)). Catatonk Creek, 7 mi (11.2 km) SE of Candor, Tioga Co., N.Y. (1955, C.O. Berg! (MCZ)) and Owego, Tioga Co., (Clarke and Berg, 1959:33). Willseyville Creek, Willseyville, Tioga Co., N.Y. and Cayuta Creek, Alpine, Schuyler Co., N.Y. (both Clarke and Berg, 1959:33). Chemung River, Chemung, Chemung Co., N.Y.; Corning, Steuben Co., N.Y. (both MCZ); and South Waverly, Bradford Co., Pa. (Ortmann, 1919:123). Cush Cushion Creek, 1 mi (1.6 km) W of Cherry Tree, Indiana Co., Pa. (MCZ) and Green Township, Indiana Co. (Ortmann, 1919:123). Sinnemahoning Creek, opposite Round Island, Clinton Co., Pa. (ANSP). Dunning Creek and Raystown Branch Juniata River, Bedford, Bedford Co., Pa. (Ortmann, 1919:123). Juniata River, 1 mi (1.6 km) E of Hollidaysburg, Blair Co., Pa. (MCZ). Conedoguinet Creek, Carlisle, Cumberland Co., Pa. (Ortmann, 1919:123). Little Swatara Creek, 2½ mi (4 km) S of Fredericksburg, Lebanon Co., Pa. (1964, H.D. Athearn! (MCZ)).

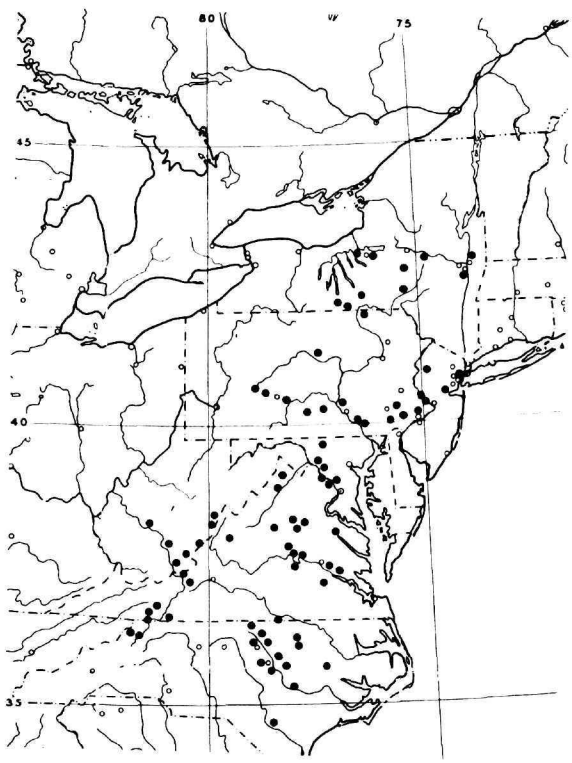

FIGURE 17.—Geographical distribution of *Lasmigona subviridis* (small open circles = cities).

POTOMAC RIVER SYSTEM.—Great Tonoloway Creek, Thompson Twp., Fulton Co., Pa. (Ortmann, 1919:123). Conococheague Creek, Greencastle, Franklin Co., Pa. (Ortmann, 1919:123) and Williamsport, Washington Co., Md. near bridge at Md. Rt. 68 (1959, F.W. Grimm! (NMC)). Tom's Creek, 7.1 mi (11.4 km) SE of Emmitsburg, Sixes Road, Frederick Co., Md. (1960, F.W. Grimm! (NMC)). North Fork Shenandoah River, 2 mi (3.2 km) SE of Strasburg, at Va. Rt. 55 bridge, Shenandoah/Warren Co., Va. (1968, W.J. Clench and D.H. Stansbery! (OSUM)). Opequa Creek, Winchester, Frederick Co., Va. (UMMZ). South Branch Potomac River, South Branch and Romney, Hampshire Co., W.Va. (both Ortmann, 1919:123). Potomac River at Point of Rocks, near bridge at U.S. Rt. 15 and also off NW shore of river, Frederick Co., Md. (1919, F.W. Grimm! (NMC)); 5 mi (8 km) N of Lucketts, Louden Co., Va. (1950, H.D. Athearn! (MCZ)); pool in rocky side channel about 1 mi (1.6 km) SE of Seneca, Montgomery Co., Md.; in Fairfax Co., Va. (1959, J.P.E. Morrison, W. Bell, F.W. Grimm! (NMC)); and Great Falls, [near] Washington, D.C. (MCZ).

RAPPAHANNOCK RIVER SYSTEM, VIRGINIA.—Rapidan River, 3 mi (4.8 km) N of Orange, Orange Co., (MCZ) and near Orange, Orange Co. (UMMZ). Rappahannock River (UMMZ).

YORK RIVER SYSTEM: Pamunkey Creek [North Anna River], Orange, Orange Co., Va. (ANSP).

JAMES RIVER SYSTEM, VIRGINIA.—South Rivanna River at U.S. Rt. 29 bridge, 6 mi (9.6 km) N of Charlottesville, Albermarle Co. (1968, W.J. Clench and D.H. Stansbery! (MCZ)). Rivanna River at Va. Rt. 15 bridge, Palmyra, Fluvanna Co. (1968, W.J. Clench and D.H. Stansbery! MCZ)) and 2 mi (3.2 km) W of Columbia, Fluvanna Co. (Clench and Boss, 1967 (MCZ)). James River opposite Maidens, Goochland Co; Cartersville, Cumberland Co. (both Clench and Boss, 1967 (MCZ)); and Richmond, Henrico Co. (UMMZ). [Appomattox River], Petersburg, Dinwiddie Co. (UMMZ).

ROANOKE RIVER SYSTEM.—Stone River, Occanweechi Island, near Clarksville, Mecklenburg Co., Va. (UMMZ).

PAMLICO RIVER SYSTEM, NORTH CAROLINA.—Tar River, 2 mi (3.2 km) ENE of Bunn, Franklin Co. (1966, A.H. Clarke! (NMC)); Rt. 64 bridge, 2 mi (3.2 km) W of Spring Hope, Franklin Co. (1967(?) W.J. Clench! (MCZ)) and Old Sparta, Edgecombe Co. (1964, R.I. Johnson! (MCZ)).

NEUSE RIVER SYSTEM, NORTH CAROLINA.—Flat River, 2.5 mi (4 km) S of Mt. Tirzah, Person Co. and 2.3 mi (3.7 km) ENE of Rougemont, Durham Co. Eno River, 1.75 mi (2.8 km) ESE of Hillsboro Center, Orange Co. Little River, Tarpley's Mill, 2 mi (3.2 km) SE of Wendell, Wake Co. Stirrup Iron Creek, 2 mi (3.2 km) NE of Morrisville, Wake Co. Swift Creek, 3 mi (4.8 km) SSW of Garner, Wake Co. Neuse River at 9.5 mi (15.2 km) ENE of Durham, Durham Co.; 3 mi (4.8 km) S of Milburnie, Wake Co.; and Selma Prison Camp, 3.5 mi (5.6 km) NNE of Smithfield, Johnson Co. (all 1950–1951, W. Walter! (MCZ)). (Additional locality records have been published by Walter (1956) in the form of spots on a map, but the specific sites are not otherwise described.)

CAPE FEAR RIVER SYSTEM: Cape Fear River, Kinnon, Cumberland Co., (UMMZ).

Ohio-Mississippi River Drainage

KANAWHA RIVER SYSTEM.—Watauga River, along old N.C. Rt. 603, 8.5 mi (13.6 km) WNW of Boone, Watauga Co., N.C. (1974, D.H. Stansbery and W.J. Clench! (OSUM)). Reed Creek, Wytheville, Wythe Co., Va. (UMMZ). Little River at U.S. Rt. 221 bridge, Wood's Store, 5.3 mi (8.5 km) NE of Floyd, Floyd Co., Va. (1968, D.H. Stansbery and W.J. Clench! (MCZ)). Branch, Greenbrier River, 1 mi (1.6 km) W of Kessler's Store, Arbovale, Pocahontas Co., W.Va. (1955, H.D. Athearn! (MCZ)). West Fork Greenbrier River, May, Mill Run, 7.5 mi (12 km) NNE of Durbin, Pocahontas Co., W.Va. (1969, D.H. Stansbery and W.J. Clench! (MCZ)). Greenbier River at Beard, 4.2 mi (6.7 km) S of Hillsboro, Pocahontas Co., W.Va. (OSUM) and at Ronceverte, U.S. Rt. 219 bridge, Greenbrier Co., W.Va. (MCZ). New River at 1½ mi (2.4 km) from U.S. Rt. 421, Watauga Co., N.C. (UMMZ); Edgewater, Grayson Co., Va. (UMMZ); U.S. Rt. 21 bridge, 3½ mi (5.6 km) S of Independence, Grayson Co., Va. (1968, W.J. Clench and D.H. Stansbery! (MCZ) (fragments)); Pearsburg, Giles Co., Va. (UMMZ); 2 mi (3.2 km) S of Hinton, Summers Co., W.Va. (1969, W.J. Clench and D. H. Stansbery! (MCZ)); and 1½ mi (2.4 km) below Prince, Fayette Co., W.Va. (1955, H.D. Athearn! (MCZ)). Kanawha River in middle of Kanawha Falls at Glen Ferris, Fayette Co., W.Va. (1969, C.B. Stein! (OSUM)).

***Lasmigona (Platynaias) decorata* (Lea, 1852)**

FIGURES 18, 19

Unio decoratus Lea, 1852:257, pl. 13: fig. 6. [Type-locality: (probably Saluda-Wateree River System) "Abbeville District, S[outh] C[arolina]." The lectotype, herein selected (Lea's figured specimen), is USNM 83972 and is labelled "Abbeville, S. Carolina."]

Unio charlottensis Lea, 1863:191. [Type-locality; "Near Charlotte, Mecklenberg [sic] County, N. Carolina." The holotype, Lea's figured specimen (1866, pl. 2: fig. 5) is USNM 85402.]

Unio insolidus Lea, 1872:159. [Type-locality: "Abbeville Dist., N.C. and Irwin's Creek, N.C." The lectotype, herein selected, is Lea's figured specimen (1874a, pl. 13: fig. 37). It is USNM 83972 and is labelled "Irwin's Creek, Mecklenburg District, Charlotte, N.C."]

THE SHELL

FIGURE 18

DESCRIPTION.—Except for its much larger size and increased shell thickness, the shells of *L.*

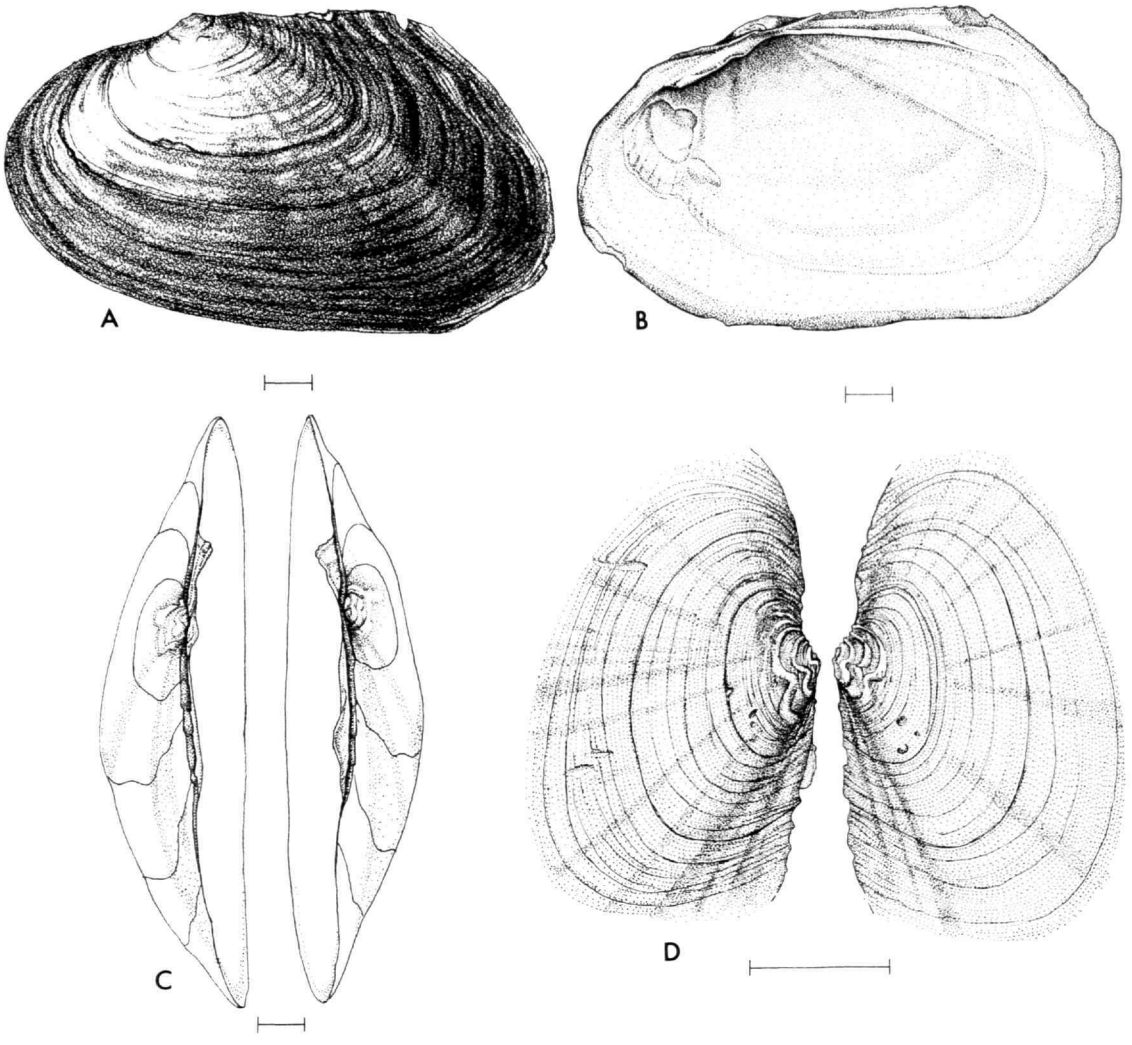

FIGURE 18.—*Lasmigona decorata: a–c*, USNM 85402, holotype of *Unio charlottensis* Lea, "near Charlotte, Mecklenberg County, North Carolina"; *d*, ANSP, Pfeiffer's Pond, [near Charlotte], North Carolina. (Scale = 1 cm.)

decorata do not differ significantly from those of *L. subviridis*. The largest specimen of *L. decorata* is 114.8 mm in length, 68.0 mm in height, and 38.6 mm in width. That is nearly twice as long, and about 8 times as voluminous, as the largest specimens of *L. subviridis*. Annual growth rests are not entirely distinct in this specimen but there appear to be about 5 annuli. The other specimens also exhibit large annual increases in length (up to 15–25 mm) between annuli. The shell wall of the largest specimen is 3.5 mm thick, double the normal thickness for *L. subviridis*. The hinge teeth are also correspondingly heavier but in shells of large specimens the inflation of the valves, while not great, appears to have separated the lateral teeth of each valve so that they artic-

ulate only at their edges. The periostracum is also darker and thicker in this species than in *L. subviridis*.

The presumed significance of these differences is discussed below.

VARIATION.—The lectotype of *Unio decoratus* Lea, which is a juvenile specimen, measures: length 60.5 mm, height 36.8 mm, width 18.8 mm, and B-A 19.3 mm. Other measurements are given in Table 13. The data there do not demonstrate that *L. decorata* is particularly variable but, like *L. subviridis*, juveniles possess a low but distinct posterior alation but adults do not, and the periostracum may be yellowish, greenish, or brown, and with greenish or blackish rays.

ANATOMY, GLOCHIDIUM, LIFE HISTORY

No soft parts of this species are available and nothing is known about its topographic anatomy or glochidia, but both are probably similar to *L. subviridis*. Although it has not been collected for many years, in view of its past occurrence in widely separated localities in the large Wateree-Santee River System, it probably still survives there.

GEOGRAPHICAL RECORDS

FIGURE 19

Atlantic Drainage Systems

Pee Dee River Drainage: "Croziers Branch," Cabarrus Co., N.C. ("Wheatley" (ANSP)).

Wateree-Santee River Drainage, North Carolina: Bissel's Pond, Elias Pond, Flanigan's Pond, and Pfeifer's Pond, all near Charlotte, Mecklenburg Co.; Beaver Creek [not located], Catawba River, Irwins Creek [Mecklenburg Co.]; Sugar Creek, near Charlotte, Mecklenburg Co. (all mid-19th century, C.M. Wheatley! (ANSP)).

REMARKS

The correct systematic placement of the populations of this taxon, nearly all of which are from the vicinity of Charlotte, North Carolina, in the Pee Dee and the Wateree-Santee drainage

TABLE 13.—*Lasmigona decorata:* shell measurements.

Feature	N	Range	Mean ($\bar{x}$)	S
	Sugar Creek, near Charlotte, N.C. (holotype and paratypes of *Unio charlottensis* Lea)			
Length (mm)	6	45.9–114.8	75.7	28.58
H/L	6	0.570–0.665	0.622	0.0349
W/L	6	0.320–0.396	0.350	0.0274
B-A/L	6	0.287–0.337	0.317	0.0174
	Pfeiffer's Pond, Charlotte, N.C.; date? C.M. Wheatley! ANSP 126707			
Length (mm)	13	36.3–104.2	59.5	21.52
H/L	13	0.536–0.652	0.596	0.0315
W/L	13	0.289–0.393	0.337	0.0350
B-A/L	13	0.296–0.367	0.326	0.0196
	Irwin's Creek, Mecklenberg Co., N.C. (holotype and paratypes of *Unio insolidus* Lea)			
Length (mm)	8	33.7–73.6	52.7	11.97
H/L	8	0.552–0.602	0.584	0.0207
W/L	8	0.288–0.355	0.316	0.0256
B-A/L	8	0.252–0.297	0.273	0.0174
	Catawba River, N.C.; date? C.M. Wheatley! ANSP 126711			
Length (mm)	3	72.8–80.7	76.2	–
H/L	3	0.555–0.624	0.590	–
W/L	3	0.306–0.337	0.324	–
B-A/L	3	0.288–0.317	0.298	–

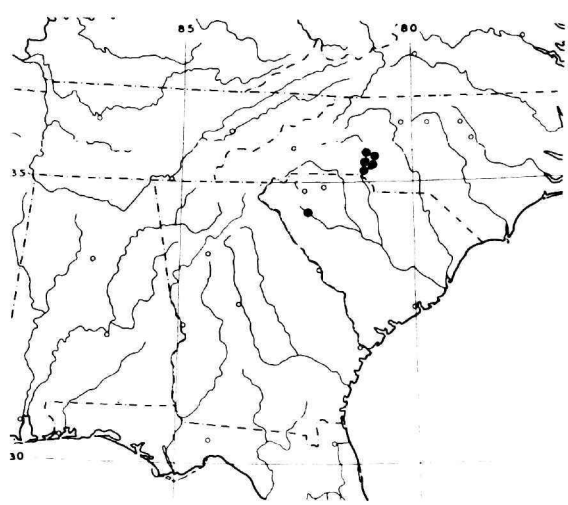

FIGURE 19.—Geographical distribution of *Lasmigona decorata* (small open circles = cities).

systems, has presented a problem. I have been tempted to follow Johnson (1970:343–346, and pers. comm.) who considers them simply robust specimens of *L. subviridis* from particularly favorable habitats, but for the reasons given below I believe that would have been wrong.

The populations samples from the vicinity of Charlotte came from ponds (a most unusual habitat for *L. subviridis*) and creeks in and near the Catawba River drainage and from the Catawba River itself. A diversity of habitats is therefore represented. The Wateree-Santee System is probably the southernmost river system in which the *L. subviridis-L. decorata* complex occurs, and the large size of the specimens might be thought the result of a longer annual growing season. If such were the case, however, a clinal increase in maximum size should exist when population samples are compared along the north to south sequence of river systems running from the Hudson River System to the Wateree-Santee System (see Briggs and Ficke, 1977, for extensive water temperature and water quality data). No such cline occurs, however. Instead, the maximum sizes of specimens in the north to south sequence does not show any significant change until the Wateree-Santee System is reached, and then the maximum length of specimens increase by a factor of approximately 2. Water hardness cannot be invoked either to explain the shift because the Catawba River and its tributaries near Charlotte all have soft water, i.e., $CaCo_3$ concentrations of about 20 ppm.

I am not aware of any species within the Unionidae where such a step shift in size occurs. It is true that unusally favorable habitats are sometimes populated by larger-than-normal specimens. For example, some ponds in New England have unusually large specimens of *Anodonta cataracta* Say. The maximum lengths of these specimens are not more than about 20% above the maximum sizes of specimens from other nearby drainage systems, however. There appears to be no reason, therefore, to expect that the very large size of *L. decorata* is not a result of genetic distinctness, and the populations from the Santee-Wateree System are therefore considered to be taxonomically distinct from those of *L. subviridis*.

It seems reasonable to speculate that the step increase in size of *L. decorata* may indicate that it is polypoid. Like *L. compressa* and *L. subviridis*, *L. decorata* is also probably hermaphroditic and capable of self-fertilization. This condition would certainly be advantageous, and perhaps crucial, to the evolution of a polyploid daughter species from a diploid progenitor (see also Burch and Huber, 1966). At any rate, if *L. decorata* is polypoid, the most appropriate taxonomic option available is to distinguish it from *L. subviridis* at the species level.

The earliest available name for the taxon is *Unio decoratus* Lea, 1852 and although Lea's figured specimen (herein designated as lectotype) is a juvenile, it is clearly this species. The type-locality, "Abbeville District S. Carolina" includes portions of both the Savannah River System and the Saluda River System. The latter is the more likely original source since it is part of the Wateree-Santee System and no *Lasmigona* species are known from the Savannah River System.

Genus *Simpsonaias* Frierson, 1914

Simpsonaias Frierson, 1914a:7. [Type-species, by original designation, *Alasmodonta ambigua* Say.]

Simpsoniconcha Frierson, 1914b:40. [Proposed as a replacement name for *Simpsonaias* Frierson, thought to be preoccupied. This is an error, however, because *Simpsonaias* Frierson is not preoccupied (e.g., see Neave, 1940:199).]

The glochidia of *Simpsonaias* are triangular-ovate, about 0.27 mm in height and 0.25 mm in length, slightly asymmetrical, with malleated [and pitted?] surfaces and with acuminate stylets that are broad at their bases. Other details are not known. No larval thread has been reported.

Unlike other North American unionids, almost all of which require a fish host for their glochidia (a few species undergo direct development without a host), the glochidial host for *S. ambigua* is an amphibian, the mud puppy *Necturus maculosus* Rafinesque.

Comparative features of the adults are: shell small (up to 48 mm long), lenticular-ovate, of low relative height (H/L about 0.464–0.530), rather compressed, dioecious, with sexual dimorphism, and without radial post-juvenile sculpturing. Beak sculpturing composed of parallel, inverted V-shaped ridges or, less commonly, simply of undulating bars. Periostracum nondehiscent. Pseudocardinal teeth are small and one in each valve; lateral teeth are absent. The anal mantle opening is about the same length as the supra-anal opening and the inner demibranchs are entirely free from the visceral mass. The outer demibranchs only are marsupial and are reported to be enormously thickened when charged with glochidia and of contrasting texture above and below.

The phylogenetic position of *S. ambigua* is obscure. It is not closely related to any other living species.

Simpsonaias ambigua (Say, 1825)

FIGURES 20, 21

Alasmodonta ambigua Say, 1825:131. [Type-locality: "Northwest Territory." Type specimens not in the Academy of Natural Sciences of Philadelphia (Johnson and Baker, 1973) and apparently lost.]

Unio hildrethianus Lea, 1834:36, pl. 3: fig. 8. [Type-locality: "Ohio, near Marietta." Syntypes are ANSP 41826 (Johnson and Baker, 1973:157).]

Alasmodonta dubia Ferussac, 1835:26. [Cited as "*Alasmodonta dubia* Say," with *U. hildrethianus* Lea as synonym. In the same paper (page 31), Ferussac also uses the combination *Anodonta dubia* Say as a senior synonym of *U. hildrethianus* Lea, and he cites (page 29) the name *dubia* Say as a valid species in the genus *Cyclas*. Say described only one species with the trivial name *dubia* and that is *Cyclas dubia* Say, 1817 (Family Sphaeriidae).]

THE SHELL

FIGURE 20*a–c*

DESCRIPTION.—Shell lenticular-ovate, moderately inflated, unsculptured, and with only rudimentary hinge teeth; up to about 48 mm long, 22 mm high, and 16 mm wide. Much thicker (2.9 mm) anteriorly than posteriorly (0.5 mm). Anterior margin more or less evenly rounded; ventral margin flatly rounded, flat, or slightly concave just posterior of center; posterior margin also more or less evenly rounded and similar to anterior margin or a little broader; and dorsal margin also flattened or flatly rounded and subparallel with ventral margin except indented in front of the umbones. Maximum inflation (and maximum height) both behind the middle of the shell. Beaks somewhat pointed, directed inwardly and toward the anterior, not inflated, located about 24% to 26% the distance from anterior to posterior, and projecting only a little above the hinge line. Area of posterior ridge convex and inflated but no distinct posterior ridge is discernable in most specimens. Area of posterior slope slightly concave near margin.

Growth increments indicated by dark concentric periostracal bands covering barely discernable concentric grooves. Additional post-juvenile sculpturing consisting only of concentric threads (especially anteriorly), a few obscure radial lines posteriorly, and low lines and grooves of growth. Periostracum predominantly brown or yellowish brown but blackish posteriorly in some specimens. Rarely one sees faint traces of narrow rays over the center of the shell, but most specimens, including juveniles, are entirely unrayed. Ligament rather long or of medium length, of moderate thickness, brown, and fragile when dry.

Hinge teeth unusual, small, and incomplete. The right valve has a single, small, low, rounded, slightly elongated pseudocardinal tooth that arises from the shell wall (not from a thickened hinge plate as in other species) just in front of the umbone. The left valve of some specimens has an ever smaller tooth that arises below and posterior to the umbone, i.e., in the same position as the interdental projection in *Lasmigona* species. This tooth, where present, is low, short, somewhat flange-like, rounded, and irregular. There are no articulating lateral hinge teeth, although the edge of the shell is a little thickened below the ligament and, in some specimens, a poorly defined lateral ridge may be present. Beak

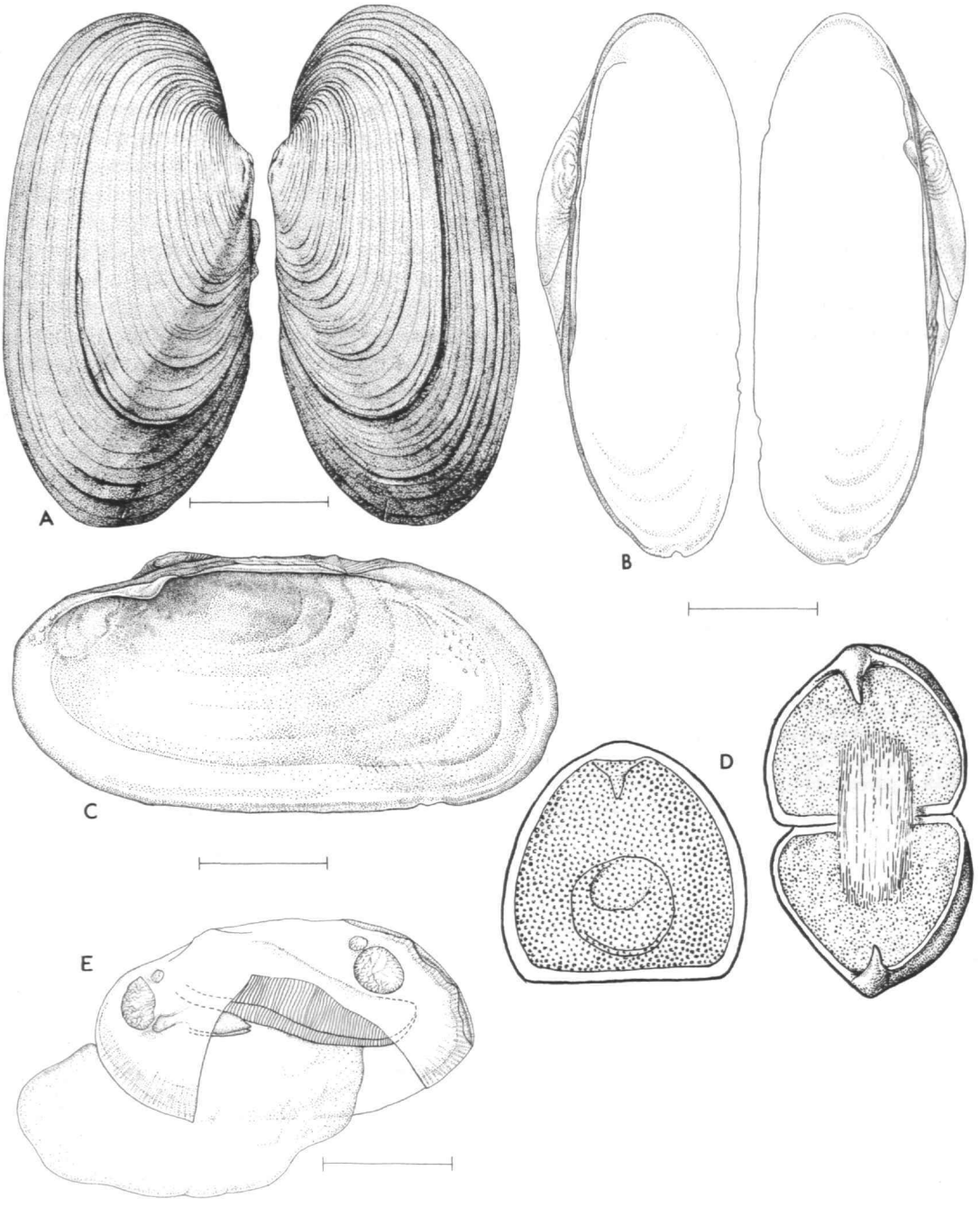

FIGURE 20.—*Simpsonaias ambigua: a–c*, USNM 86266, [Mississippi River], Alton, Madison County, Illinois; *d*, glochidium larva (from Howard, 1951); *e*, A.H. Clarke, Station 1916, Eagle Creek, 4.5 mi (7.2 km) NE of Sparta, Gallatin County, Kentucky. (Scale = 1 cm.)

cavities somewhat excavated but not deep, and with a variable number of small, irregular muscle scars within. Major anterior muscle scars small and shallow but well-marked; pallial band well marked, located quite far from the margin (and more clearly defined) anteriorly but closer to the margin posteriorly, and in some specimens with several tiny, parallel, collabral ridges within the anterior portion; and posterior muscle scars very lightly etched and located distinctly forward of the most posterior portion of the pallial band loop. Nacre bluish white, iridescent posteriorly, with yellowish, salmon, or purplish suffusions in the center and near the beak cavities, and thin in a narrow band around the edge of the shell with the periostracal color showing through.

Beak sculpture composed of about 6 parallel, predominantly inverted, V-shaped ridges, apparently corresponding to the middle portions of the double-looped ridges in *Lasmigona*. The earliest 2 ridges are obscure in available material: they appear to be single-looped and especially expanded anteriorly. Later ridges are inverted V-shaped, with anterior arms short and directed ventrally in their proximal portions but curving anteriorly distally, and with posterior arms also short and more or less straight and parallel with the ligament or slightly curved upward. In some specimens the bars are in the shape of shallow V's and the later bars are simple undulating ridges but in most specimens the bars are deeply indented centrally.

VARIATION.—The data presented in Table 14 show that *S. ambigua* is quite variable in relative dimensions. Simpson (1914:324) has stated that in males "their shells are less inflated, more nearly straight below and not so broad posteriorly; those of the females being decidedly swollen behind, the posterior ridge being very full and widely rounded, the base line sometimes a little incurved in the middle and the hinder end of the shell broad." He also writes that males are much less common than females, but the data in Howard (1915:8; 1951:4) do not support this statement. Because the shells whose measurements are given in Table 14 lacked soft parts and therefore could not be sexed, it is impossible to know whether some of the variation may have been caused by sexual dimorphism.

TABLE 14.—*Simpsonaias ambigua:* shell measurements.

Feature	N	Range	Mean ($\bar{x}$)	S
	Iowa River, Iowa City, Iowa; date?, R.E. Call!, B. Shimek! MCZ 6349, USNM 519653			
Length (mm)	21	20.0–48.0	38.7	8.00
H/L	21	0.464–0.530	0.497	0.0182
W/L	21	0.253–0.360	0.311	0.0317
B-A/L	21	0.213–0.295	0.260	0.0214
	Little Red River near Clinton, Ark.; date? E. Pleas!, USNM 124626, 125631			
Length (mm)	5	27.9–41.5	37.1	5.36
H/L	5	0.511–0.522	0.517	0.0050
W/L	5	0.315–0.376	0.351	0.0229
B-A/L	5	0.258–0.337	0.284	0.0319
	Mississippi River, Davenport, Iowa; date?, D.S. Sheldon!, ANSP 41060, 41285			
Length (mm)	8	26.3–47.2	40.0	7.07
H/L	8	0.445–0.530	0.485	0.0279
W/L	8	0.329–0.387	0.347	0.0179
B-A/L	8	0.219–0.312	0.267	0.0271

S. ambigua also varies somewhat in the shape and size of the small pseudocardinal teeth and in the presence or absence of traces of lateral teeth. The shell is quite distinctive, however, and cannot be confused with any other.

TOPOGRAPHIC ANATOMY

FIGURE 20*e*

SPECIMEN DESCRIBED.—From Eagle Creek, 0.8 mi (1.3 km) W of Glencoe, 4.5 mi (7.2 km) NE of Sparta, Gallatin/Owen County, Kentucky (38°42′33″N, 84°50′06″W), collected 13 July 1982 by A.H. Clarke, S.M. Call, and G.J. Fallo (A.H. Clarke, Station 1916); anaesthetized with nembutal, fixed in 10% formalin, preserved in 70% ethyl alchol; shell length 28.2 mm., sex female (sterile).

DESCRIPTION.—Foot white, broad, and spatulate, 24.5 mm long and 13.8 mm high in the relaxed specimen. Mantle whitish, subopaque,

thickened near the edge, and with a narrow, pale grayish marginal band that is especially apparent posteriorly. Incurrent opening 4.6 mm long and surrounded within by a predominantly double (partly triple) row of narrow, flattened, crowded, simple, pinkish papillae, each about 0.5 mm long. Separation of incurrent and anal openings achieved by the diaphragm and by a narrow (1.1 mm) lobe on each mantle edge that is presumably held in contact with its opposite member during life. Anal opening 3.0 mm long, surrounded within by a narrow, lamellate, and partially crenulated ridge that lies within an irregular, purplish pigmented band. Mantle edges each with a pointed lobe at the incurrent and anal openings. Between the anal and supra-anal openings the mantle edges are fused over a distance of 1.7 mm. Supra-anal opening narrow, unpigmented, and 3.2 mm long.

Demibranchs of preserved specimen whitish and diagonally placed. Outer demibranch 14.3 mm long, 3.8 mm high, flattened ventrally, and curved up anteriorly and posteriorly, with about 16 double filaments per mm and with about 4.0 water tubes per mm. Inner demibranch 16.0 mm long, 4.6 mm high, of similar form to the outer except projecting beyond it 1.7 mm anteriorly and 0.8 mm ventrally. There are about 16 double filaments per mm and 3.0 water tubes per mm. The water tubes do not extend all the way to the lower edge in the inner demibranch but terminate about 1.2 mm from the edge. Inner lamina of inner demibranch not attached to the visceral mase.

Labial palps pale yellowish white, narrow, roundly pointed posteriad, about 7.8 mm long, 1.8 mm high at their highest points (near the free end), and joined together and to the mantle and the visceral mass for about 80% of their lengths. They slightly overlap the inner demibranchs. The outer surfaces are smooth and the inner surfaces are radially furrowed (about 5 furrows per mm).

Simpson's (1914:324) observations on gravid specimens provide important additional information. They are as follows:

> Marsupium filling the entire outer gills and forming enormously thickened pads, the upper part finely vertically striate, the lower part of different texture, lighter colored, wrinkled and granular on the surface: embryos very large; outer and inner gills nearly alike in size, the latter free from the abdominal sac, all united to the mantle to their posterior ends; palpi longated, granular; mantle straight below, thickened on the border; branchial opening large, with numerous light-colored papillae with dark lines; anal opening black, without papillae, separated from the small superanal opening by a long bridge; hinder part of the mantle, branchial and anal openings widely separated by the very thick marsupia. . . . The marsupium is decidedly vertically striate throughout its upper half, the lower half is lighter, granular, and wrinkled externally and in places shows traces of vertical sulci as in the higher Uniones, *Lampsilis*, etc.

Since only one specimen with soft parts is available, nothing can be said about their variation in this species. Simpson's statement about a "long bridge" between the anal and supra-anal openings probably refers to specimens distended with full marsupia.

Glochidia

Description.—"The glochidia are clear white in color, of the triangular type, with well-developed hooks. . . . The dimensions are as follows: height 0.265 to 0.274 mm, length 0.247 to 0.255 mm" (Howard, 1951:4). Howard's figures are repoduced in Figure 20*d*.

Life History

Breeding Period and Natural Host.—Howard (1915:6–8) showed that the natural host of *S. ambigua* is the mud puppy *Necturus maculosus* Rafinesque. The infected hosts were collected on 17 October and kept alive over the winter in the laboratory at Fairport, Iowa, and the glochidia were shed from their hosts in the last week of May. The glochidia were deeply imbedded in the external gills of the hosts. Experimental and accidental attachments of other glochidia to amphibians have been reported (see Howard, 1951:6) but the *N. maculosus–S. ambigua* association is the only obligate host-parasite relationship known that involves an amphibian

and a freshwater mussel. Howard's data further indicate that, unless the mud puppies were infected in the spring and normal release of their glochidial parasites was inhibited by laboratory confinement, then unlike other anodontines, *S. ambigua* may release mature glochidia from the marsupia in the fall rather than the spring. Both alternatives would be rather extraordinary and additional study of this interesting, rare, and elusive species is much to be desired.

HABITAL.—Call (1900:527) states: "It is sometimes found in mud and on gravel bars, but in greatest numbers and perfection hidden in the mud under flat stones; more than 200 have been taken from under a single flat rock about one square foot area." Howard (1915:8) writes: "All of the adult individuals were found under flat stones of the flag-stone type characteristic of the limestone in the region. Beneath a single rock I found four. While exploring the under surface of these I felt and seized a wriggling animal which proved to be a mud-puppy, demonstrating the manner in which *Necturus* becomes innoculated. Glochidia shed by the mussels in such a location would not have a rapid dispersal by currents so that the *Necturus* commonly seeking such a shelter would run the chance of a heavy infection."

Finding live *S. ambigua* is a most unusual occurrence. Baker (1928:184) reported finding dead shells on a gravel bar at the edge of a river in Wisconsin but no living specimens could be found even though search was carried out there for several days. Several of my colleagues, all of whom are experienced field collectors, have occasionally found a few empty shells of *S. ambigua* but never a living specimen. This is in partial agreement with Frierson (1927:24) who says: "The larval stage of the species appears to be developed upon newts, and this accounts for the very local habit of the species, being rarely found, but in abundance when ever found; a hundred have been taken from a square foot."

Two localities from which a rather large number of empty shells have recently been found are the East Fork Stone's River about 100 yards (91 m) below the dam at Brown's Mill, near Lascassus, Rutherford Co., Tennessee (D.H. Stansbery, pers. comm.) and Eagle Creek, 0.8 mi (1.3 km) WSW of Glencoe, Gallatin/Owen Co., Kentucky (G.J. Fallo, pers. comm.). I visited the Stone's River locality and searched it for 4½ hours on 12 and 13 October 1980, and failed to find any empty or living specimens of *S. ambigua*. The river there is about 20–30 m wide, with slow current and a substrate of mud, sand, and gravel, and limestone rocks (many of which are flat), with algae and emergent macrophytes and overhung by deciduous trees.

On 13 July 1982, in company with G.J. Fallo and S.M. Call, I also visited the Eagle Creek locality. A careful search by all of us for 3 hours revealed several empty shells of *S. ambigua* on the shore and one live specimen. The living specimen was found about 8 m below a riffle, buried in gravel, under a flat limestone rock (rock about 20 cm long and wide and 10 cm thick) in about 20 cm of water depth. The creek flows around an island here and has areas of riffles and of slow-moving water. The *S. ambigua* occurred about 20 m below the island where the creek width is about 20 m. Other species taken alive nearby were *Fusconaia flava* (2), *Elliptio dilatata* (6), *Alasmidonta viridis* (5), *Lasmigona complanata* (1), *Strophitus undulatus* (1), *Tritogonia verrucosa* (1), *Lampsilis radiata siliquoidea* (4) and numerous specimens of *Corbicula fluminea* and *Goniobasis* species.

GEOGRAPHICAL RECORDS

FIGURE 21

GREAT LAKES–ST. LAWRENCE RIVER SYSTEM.—*Lake Michigan Drainage:* Wolf River, Shawano Co., Wisc. (H.A. Mathiak, 1979).

Lake Huron Drainage: Saginaw River, Michigan (UMMZ).

Lake St. Clair Drainage: Sydenham River at county Rt. 1 bridge, S of edge of Florence, Lambton Co., Ont. (1965, C.B. Stein and J.E. Stillwell; (OSUM)).

Lake Erie Drainage: Detroit River at Bois Blanc Island, Ont. and Belle Isle, Wayne Co., Mich. (both UMMZ). River Rouge, Wayne Co.; Tiffin River Morenci, Lenawee Co.; Macon Creek at Stowell Road, Monroe Co.; and Lake Erie, La Plaisance Bay, Monroe Co., all Mich. (all UMMZ). St.

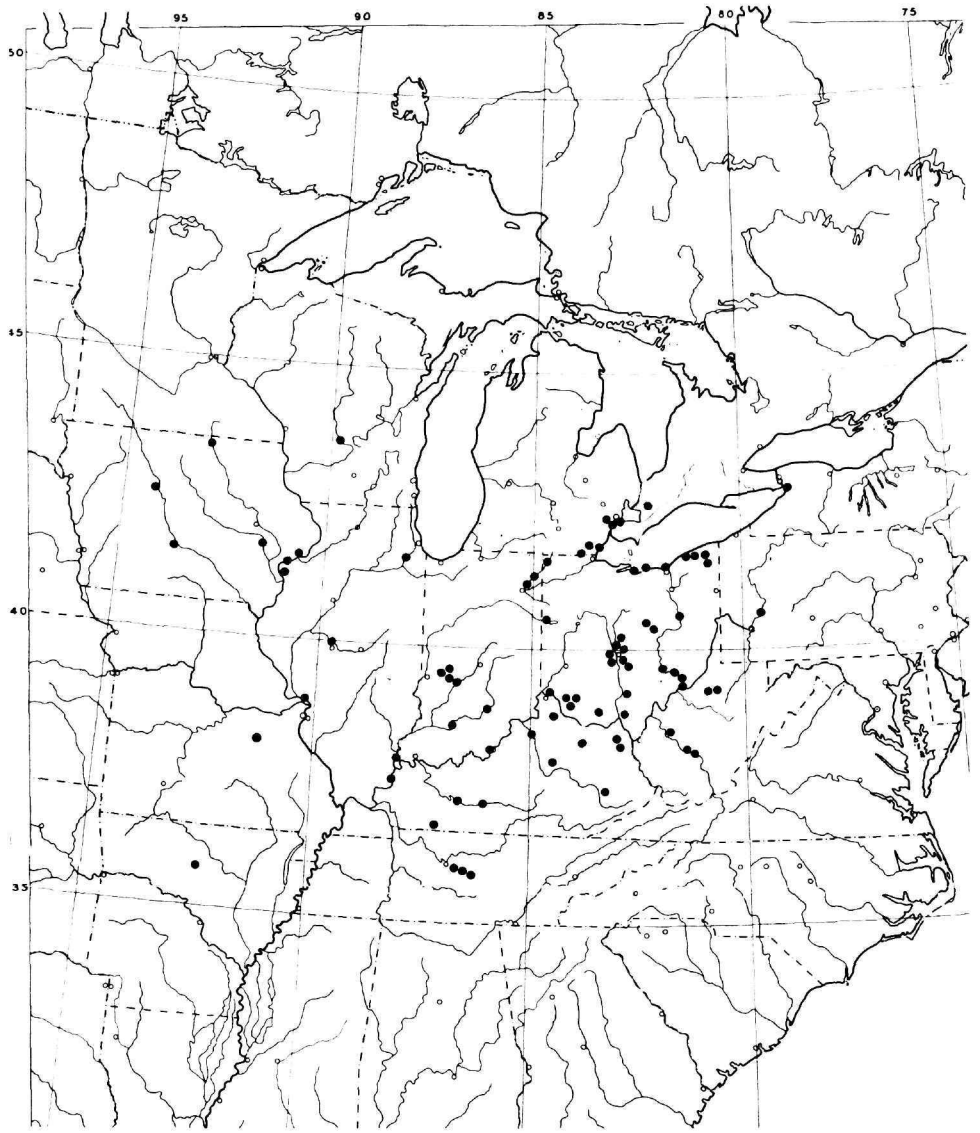

FIGURE 21.–Geographical distribution of *Simpsonaias ambigua* (small open circles = cities).

Joseph River at Ohio Rt. 34 bridge, 8 mi (12.8 km) NW of Bryan, Williams Co., Ohio (1962, D.H. Stansbery! (OSUM)), and at Newville and St. Joe, both DeKalb Co., Ind. (both OSUM). Maumee River, Ohio (UMMZ). Lake Erie at Sandusky Bay, Sandusky, Erie Co. (CM); Vermilion, Erie Co. (CM); and Cleveland, Cuyahuga Co. (MCZ, UMMZ), all Ohio. Grand River, covered bridge about 1 mi (1.6 km) NW of Rock Creek, Ashtabula Co., Ohio (1961, D.H. Stansbery!); at and below covered bridge at Mechanicsville, Austinberg Twp., Ashtabula Co. (1961, D.H. Stansbery!, 1969, K. Borror, et al.!); below covered bridge below dam, Ohio Rt. 534, Harpersfield Twp., Ashtabula Co. (1961, D.H. Stansbery!) and at SE edge of Painesville, about 1 mi (1.6 km) above railroad bridge, Lake Co., all Ohio (all OSUM). Buffalo Creek, Buffalo, Erie Co., N.Y. (MCZ). Lake Erie, Buffalo, Erie Co., N.Y. (ANSP, MCZ).

OHIO RIVER SYSTEM.—*Allegheny River Drainage:* Allegheny River, 9.4 mi (15 km) SW of Kittaning (1970, P.

Doyle! (OSUM)) and 4 mi (6.4 km) ENE of Freeport, at Godfrey, (1969, D. Tanner!), both Gilpin Twp., Armstrong Co., Pa. (both OSUM).

Monongahela River Drainage: West Fork River, Lightburn, Lewis Co., W.Va. (CM).

Muskingum River Drainage, Ohio: Mohican River, 2.2 mi (3.5 km) W of Tiverton Center, Coshocton Co. (1967, D.H. Stansbery, et al.! (OSUM)). Walhonding River, 1¼ mi (2 km) E of Walhonding, Coshocton Co. (1967, D.H. Stansbery! (OSUM)). Ohio Canal, New Philadelphia, Tuscarawas Co. (CM). Tuscarawas River (UMMZ). Muskingum River below McConnelsville Dam, Malta Twp., Morgan Co. (1969, C.B. Stein and K.G. Borror!); below dam at Lowell, Adams Twp., Washington Co. (1967, C.B. Stein and J. Condit!); below dam at Devola, 4.5 mi (7.2 km) NW of Marietta, Washington Co. and West Side Beach, just above river mouth, Marietta (all OSUM).

Little Kanawha River Drainage: West Fork Hughes River, 1.4 mi (2.2 km) NE of Harrisville, Ritchie Co., W.Va. (1968, J.J. Jenkinson! (OSUM)).

Kanawha River Drainage, West Virginia: Pocatelico River, Raymond City, Putnam Co. (CM). Kanawha River just below Kanawha Falls, Glen Ferris, Fayette Co. and at riffle about 1 mi (1.6 km) below Kanawha Falls (both 1969, C.B. Stein and K.G. Borror! (OSUM)).

Little Sandy River Drainage: Little Sandy River just below Grayson, Carter Co., Ky. (1975, J. MacGregor! (OSUM)).

Tygart's Creek Drainage, Tygart's Creek and Cave Branch below Ky. Rt. 12 bridge, 9.2 mi (14.7 km) WNW of Grayson, Carter Co., Ky. (1978, J.J. Jenkinson! (OSUM)).

Scioto River Drainage, Ohio: Alum Creek near Africa, (1955, R. Maly!); at "meanders," about 4 mi (6.4 km) S of Cheshire (1967, D.H. Stansbery, et al.!); S of Lewis Center Road (1961, D.H. Stansbery and C.B. Stein!) and along Rt. 107, above Rt. 109 bridge, all Orange Twp., Delaware Co. (OSUM). Big Walnut Creek at Williams Road bridge, Madison Twp., Franklin Co. (1961, D.H. Stansbery and C.B. Stein! (OSUM)). Olentangy River between Sneuffer and Wilson Bridge Road, Sharon Twp., Franklin Co. (1962, D.H. Stansbery and C.B. Stein! (OSUM)). Big Darby Creek between Commercial Point Road and Borror Riffles, Scioto/Darby Twp.; Orient, Darby Twp.; and Ohio Rt. 104 bridge, Fox, Jackson Twp., all Pickaway Co. (all 1958–1963, D.H. Stansbery et al.! (OSUM)). Salt Creek below U.S. Rt. 35 bridge, 13.3 mi (21.2 km) SSE of Chillicothe, Ross Co. (1980, A.E. Spreitzer! (OSUM)). Little Scioto River, 3 mi (4.8 km) NE of its mouth, Dixon Mill Bridge, Scioto Co. (1965, J.E. Stillwell! (OSUM)). Scioto River, Columbus, Franklin Co. (CU).

Ohio Brush Creek Drainage: Ohio Brush Creek at ford, 2.6 mi (4.2 km) WNW of Peebles, Adams Co., Ohio (1971, J.J. Jenkinson! (OSUM)).

Whiteoak Creek Drainage: Whiteoak Creek, 6 mi (9.6 km) W of Sardinia, Pike Twp., Brown Co., Ohio (OSUM).

Little Miami River Drainage, Ohio: North Fork Little Miami River, 8.8 mi (14.1 km) NE of Batavia, Clermont Co. (1973, J.M. Sears! (OSUM)). East Fork Little Miami River, 8.8 mi (14.1 km) NE of Batavia and 3.4 mi (5.4 km) NW of Batavia (both 1973, J.M. Sears! (OSUM)) and above Rt. 74 bridge, below dam, Batavia, (1972, C.B. Stein! (OSUM)).

Licking River Drainage, Kentucky: Slate Creek at swinging bridge, 5.9 mi (9.4 km) NE of Owingsville, Bath Co. (1978, D.H. Stansbery et al.! (OSUM)). South Fork Licking River, Falmouth, Pendleton Co. (1969, D.H. Stansbery! (OSUM)).

Kentucky River Drainage, Kentucky. Troublesome River, 2.3 mi (3.7 km) above Lost Creek, Breathitt Co. (1959, H.D. Athearn! (MCZ, NMC, UMMZ)). Eagle Creek, 4.5 (7.2 km) and 1.5 mi (2.4 km) NE of Sparta, Gallatin/Owen Co. (1982, S.M. Call, A.H. Clarke, G.J. Fallo!). Kentucky River, Gratz, Owen Co. (1958, W.J. Clench and J. Rosewater! (MCZ)).

Green River Drainage, Kentucky: Green River above bridge, Munfordville, Hart Co. and Glenmore, below Lock and Dam No. 5, 16 mi (25.6 km) ESE of Morgantown, Butler/Warren Co. (both 1969, D.H. Stansbery et al.! (OSUM)).

Wabash River Drainage: Tippecanoe River, Ind. (USNM). Deer Creek, Putnam Co., Ind. (UMMZ). Walnut Creek (Eel River) at Greencastle, Putnam Co., Ind. (MCZ) and at U.S. Rt. 40 bridge, 7.5 mi (12 km) ENE of Brazil, in Washington Twp., Putnam Co., Ind. (1967, D.H. Stansbery et al.! (OSUM)). East Fork White River, Rockford, Jackson Co., Ind. (UMMZ) and about ½ mi (0.8 km) below bridge at Shoals, Martin Co., Ind. (1964, C.B. Stein! (OSUM)). West Fork White River, 5.5 mi (8.8 km) NE of Spencer, Owen/Monroe Co., Ind. (OSUM). Wabash River, 2.1 mi (3.4 km) S of Scudder, Mercer Co., Ohio (1977, W.N. Kasson and D.G. Thompson! (OSUM)) and New Harmony, Posey Co., Ind. (MCZ, UMMZ, USNM).

Ohio River (main channel): Ohio River at Cincinnati, Ohio (MCZ, UMMZ); Louisville Ky. (USNM); and Golconda, Pope Co., Ill. (MCZ).

CUMBERLAND RIVER SYSTEM.—*Red River Drainage:* Red River about ½ mi (0.8 km) above iron bridge at junctions of Ky. Rt. 77 and county Rt. 1067, Logan Co., (1974, C.F. Clark! (UMMZ)).

Stone's River Drainage, Tennessee: E Fork Stone's River, at Brown's Mill, 2.0 mi (3.2 km) SSE of Lascassus, Rutherford Co. and below Walterhill Dam, Rutherford Co. (both 1965, D.H. Stansbery! (OSUM)). Stone's River, above and at Couchville Pike bridge, 1.2 mi (1.9 km) W of Couchville, Davidson Co. (1965, D.H. Stansbery et al.! (MCZ, OSUM)).

MISSISSIPPI RIVER SYSTEM.—*Wisconsin River Drainage:* Wisconsin River, Wisconsin Dells, Kilbourn, Columbia Co., Wisc. (UMMZ).

Iowa River Drainage, Iowa: Cedar River, Osage, Mitchell Co. (USNM). Iowa River, Iowa City, Johnson Co. (ANSP, MCZ, UMMZ).

Des Moines River Drainage, Iowa: Lizard Creek, Fort Dodge, Webster Co. (MCZ). Des Moines River, Des Moines, Polk Co. (ANSP).

Illinois River Drainage, Illinois: Sangamon River, Athens,

Menard Co. (ANSP). Illinois River, Joliet, Will Co. (MCZ).

Meramec River Drainage: Bourbeuse River, about 5 mi (8.0 km) S of Rosebud, Gasconade Co., Mo. (Buchanan, 1980).

Arkansas River Drainage: Little Red River, Clinton, Van Buren Co., Ark. (ANSP, MCZ, UMMZ, USNM). White River, Ark. (UMMZ).

Mississippi River (main channel): Prairie du Chien, Crawford Co., Wisc. (van der Schalie and van der Schalie, 1950). Davenport, Scott Co., Iowa (ANSP, USNM); Muscatine, Muscatine Co., Iowa (USNM); Mercer Co., Ill. (MCZ); Alton, Madison Co., Ill. (USNM). (None of these records includes the name of the water body concerned, but all of the localities mentioned are partially on the Mississippi River.)

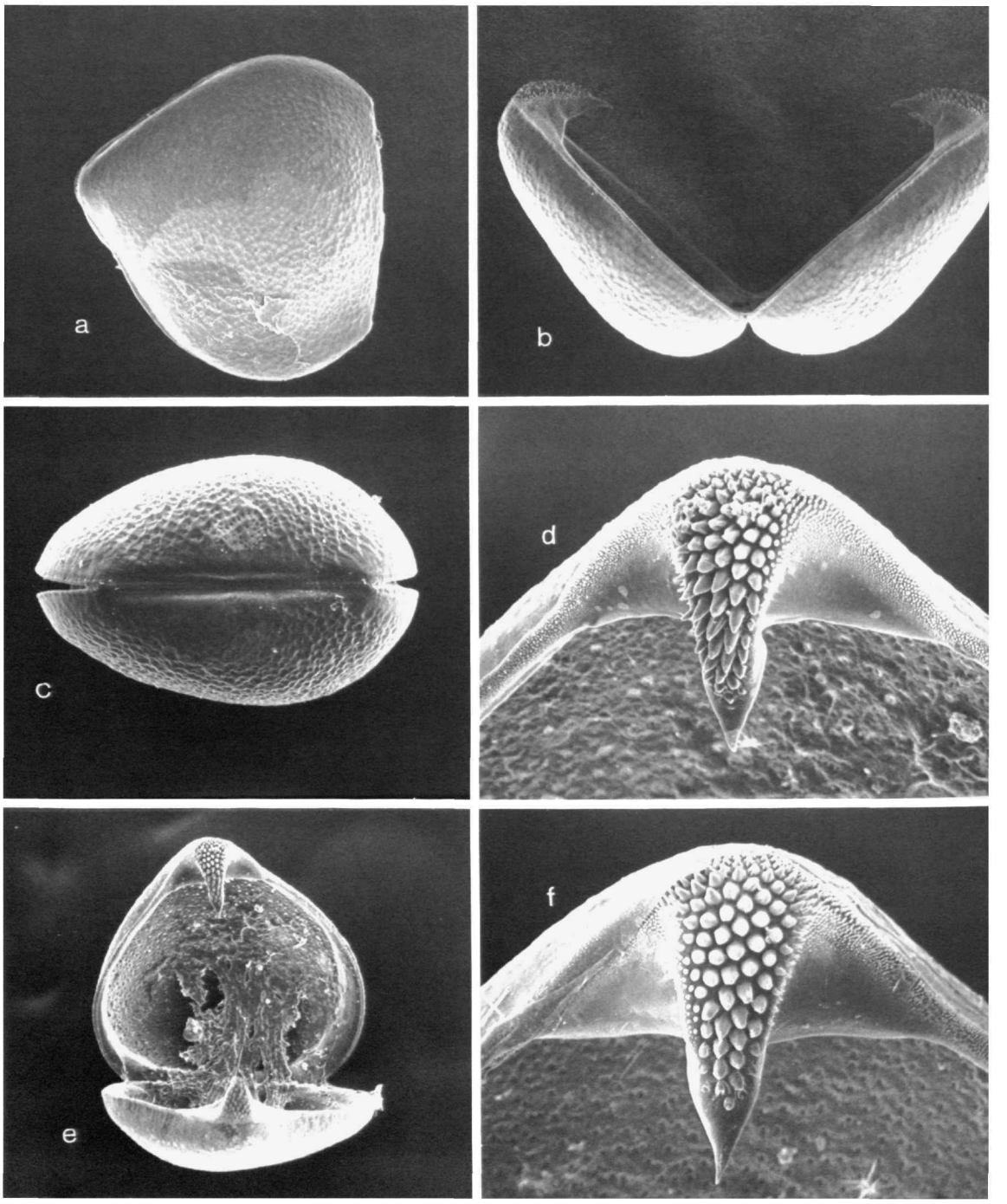

FIGURE 22.—Glochidia of *Alasmidonta varicosa: a–f*, MCZ (uncataloged), West River, Newfane, Windham County, Vermont (*a,c*, × 165; *b* × 155; *d* × 510; *e* × 130; *f* × 500).

axis), and 0.097 mm in single valve convexity. The valves are assymmetrical: the posterior margin is more expanded than the anterior, the apices are located about 44% of the distance from anterior to posterior, and the area of maximum inflation is anterior of center and about 25% of the distance from hinge to apex. Surface of glochidium finely malleated and pitted except for the distal apical areas (about 30 μm high), and the edges of the valves (about 30 μm wide), which are generally malleated but not pitted. The malleated depressions are subcircular and about 6–12 μm wide. The pits are about 2–4 μm wide and most are located within the depressions. The apical unpitted areas of the valves are sculptured with narrow, curved, concentric ridges. Hinge straight, about 0.240 mm long, and recessed centrally within the slightly convex basal margin.

Each apical stylet is recurved, bent inward distally, and is about 100–110 μm long and 45–50 μm wide at the base, triangular in cross section, and gradually narrowing to an assymmetrical tip that has a narrow flange on both sides, the posterior flange being the more extensive. Each stylet is supported on each side, for about half its length, by an (apparently) horny membrace that is broadly connected to the ventral edge of each valve. Except for the blade-like apical extension, the flatly-rounded, exposed side of each stylet is covered with about 80–100 microstylets, each about 7–14 μm long. The microstylets are arranged in rows more-or-less parallel to the long axis of the stylet; there are about 10 rows near the base of the stylet and these decrease to about 3 rows near its apex. The microstylets are not entirely erect but are inclined toward the apex of the stylet and, in the available material, are elongate-pyramidal with rounded sides or are multifaceted with 5–7 sharp edges. Numerous smaller (0.7–2.0 μm high), pyramidal microstylets occur on the bases of the stylets, merge imperceptibly with the larger microstylets, and also extend along the adjacent edges of the valves and on the membrane near the stylets as micropoints (< 0.5 μm).

SEM micrographs reveal that the glochidia of *A. varicosa* and *A. marginata*, thought by Ortmann to be identical (see Clarke, 1981:60–63, 78), exhibit significant differences. In *A. varicosa* the height is less than the length, whereas in *A. marginata* the height is more than, or approximately equal to, the length. (In Part I (1981:60) the length and height measurements for *A. marginata* glochidia were inadvertently reversed.) Furthermore, the microstylets on each stylet in *A. varicosa* are only about half as numerous as those in *A. marginata*.

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