

THE TAXONOMIC STATUS OF *ANODONTA LACUSTRIS*
LEA (BIVALVIA: UNIONIDAE)

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ABSTRACT: Conchological and allozymic evidence is consistent with the taxonomic distinction of *Anodonta lacustris* Lea 1857 (= "*A. marginata*" sensu F. C. Baker 1928, non Say 1817) from *A. grandis* Say 1829. In addition, allozymic evidence supports the distinction of *A. lacustris* from *A. cataracta* Say 1817 and *A. fragilis* Lamarck 1819. Furthermore, justification is provided for the use of the name *A. lacustris* Lea 1857 in lieu of *A. marginata* Say 1817.

Key words: *Anodonta lacustris*, taxonomy, nomenclature, distribution.

INTRODUCTION

The freshwater mussel genus *Anodonta* (Bivalvia: Unionidae) is Holarctic in distribution and comprises approximately 16 species in North America, north of Mexico (Burch, 1975). Due to the phenotypic plasticity of shell characters and the relatively low levels of variation displayed in soft part anatomy (but see Kat, 1983a, 1986), species limits as well as interspecific relationships within this genus are poorly understood. Used in conjunction with morphological analyses, molecular data sets, such as those produced by starch gel electrophoresis of proteins (allozymes), may give fresh insight on long standing taxonomic debates as to the veracity of certain species determinations in this genus (Kat, 1983a, 1986). When a parapatric or sympatric distribution occurs, the absence of morphologically and/or molecularly intermediate individuals in the zone of contact dictates the rejection of the hypothesis of a single gene pool and, therefore, the acceptance of multiple species (Wiley, 1981). In the case of

†Contribution from The University of Michigan Biological Station.

allopatric distributions, the determination of gene pool discreteness is virtually impossible. However, since certain measures of molecular differentiation (e.g., genetic distance and number of fixed allelic differences) are correlated with levels of taxonomic separation (Thorpe, 1983), these measures may provide provisional support for species level distinctness in the case of allopatric taxa (e.g., Davis, 1983; Richardson *et al.*, 1986). Based on empirical observations, Davis (1983) suggested that, for two allopatric unionid taxa, the probability of having distinct species is high if an allozymic analysis with 14 or more loci indicates a Nei's Distance (Nei, 1972) ≥ 0.222 . The purpose of this paper is to reestablish *Anodonta lacustris* Lea 1857 among the recognized species of North American freshwater mussels, to discuss the reasons for this resurrection, to reaffirm the conchological basis for this decision, and to present allozyme data that corroborate these conclusions.

MATERIALS

The specimens on which this study is based include those from our collecting in Indiana, Michigan and Pennsylvania, R. G. Noseworthy's collecting in Newfoundland, specimens from the University of Michigan Museum of Zoology, the National Museum of Canada, and the National Museum of Natural History, Smithsonian Institution. Included in the latter collection is the "Holotype" (see Johnson, 1970, p. 356) of Lea's (1857) *Anodonta lacustris* (USNM cat. no. 86597, Fig. 1) and Lea's (1861) *Anodonta simpsoniana* (USNM cat. no. 86434, Fig. 8). The allozyme data were obtained by standard starch gel techniques (Selander *et al.*, 1971; Ayala *et al.*, 1973). Locality data for the Michigan specimens in Figs. 3, 4, 6, 7 are as follows: *Anodonta lacustris* Lea, beach pool, Lake Michigan shore, Section 19, Bliss Township, R. 6 W., T. 39 N., Emmet County, July, 1988, UMMZ 250670; *Anodonta grandis* Say, North Fishtail Bay, Douglas Lake, Section 22, Munro Township, R. 3 W., T. 37 N., Cheboygan County, July, 1988, UMMZ 250671.

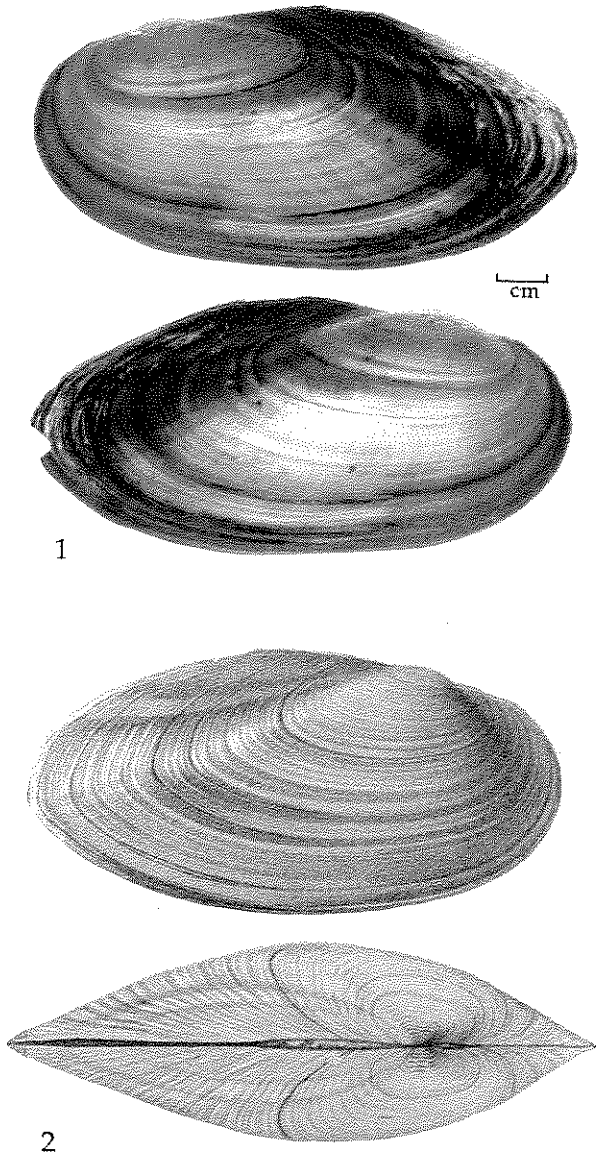
NOMENCLATURE

Anodonta lacustris Lea was recognized by the early North American naturalists (e.g., Latchford, 1882; Latchford & Poirier, 1885; Marshall, 1892, 1895; Taylor, 1892; Letson, 1905). Later it was placed in the synonymy of *A. marginata* Say 1817 (e.g., Simpson, 1900; Wright & Walker, 1902; Dall, 1905; Baker, 1916, 1928; Frierson, 1927). This concept of "*A. marginata*," which we do not believe to represent the actual species Say named, was best presented by Baker (1928). More

recently, van der Schalie (1938) doubted the validity of "*A. marginata*" *sensu* Baker and others, believing it to be only a variation of *A. grandis* Say 1829. Johnson (1970) placed both *A. lacustris* and *A. marginata* in the synonymy of *A. cataracta* Say 1817. *Anodonta lacustris* ("'*Anodonta marginata* Say' of authors but not of Say, 1817" [Clarke, 1973]) has been placed in the synonymy of *A. grandis simpsoniana* Lea 1861 by Clarke (1973). Justification for recognizing *Anodonta lacustris* over *A. marginata* is based on the following: all type material of *A. marginata* is lost, its type locality is unknown, the original description (both figure and text) is uninformative as to the most essential diagnostic character, *i.e.*, beak sculpture, and remarks accompanying the original description (Say, 1817) indicate that *A. marginata* was "very common in our rivers." A "type" of *A. lacustris* from the Isaac Lea collection, on the other hand, is available (USNM cat. no. 86597, Figs. 1, 5), the type locality is known, the shell is well described and illustrated (Fig. 2), and the species is common only in lakes and ponds, and is rarely found in flowing water (Baker, 1928; Hoeh and Burch, unpublished data). The latter, *i.e.*, the habitat difference, indicates to us that the two nominal species, *A. marginata* Say and *A. lacustris* Lea, are not synonymous, so there seems to be no point in subordinating Lea's *A. lacustris* to Say's species, as has been done sometimes in the past. The identity of Say's *A. marginata* should be determined, if possible, because of the name's priority, but whatever the species turns out to be, we are confident that it will not be the same as *A. lacustris*.

DESCRIPTIONS OF ANODONTA LACUSTRIS

In 1857, Isaac Lea named and described *Anodonta lacustris*, one of approximately 90 species of *Anodonta* that he described during his life. As was his usual procedure, he published the first description as several lines of Latin (the language required at the time for new descriptions of undescribed species) and a locality. This established the name as his and fixed the publication date, the latter of prime importance in regard to nomenclatural priority. Then, as was also his custom, Lea later published an English translation of the original Latin description, a more detailed description of the shell, sometimes described (as was the case for *A. lacustris*) the external features



FIGS. 1, 2. *Anodonta lacustris* Lea. Fig. 1. "Holotype," USNM 86597, left and right valves. FIG. 2. Lea's (1860, pl. 62, fig. 188) illustrations, right valve and dorsal view of both valves with beak sculpture. Measurement line = 1 cm.

of the soft anatomy, made additional comments regarding the species, and gave an excellent figure of the shell (Fig. 2). Lea's (1860) translation of his original Latin description of the shell of *Anodonta lacustris* is as follows: "Shell smooth, transverse, somewhat inflated, very inequilateral, subangular behind; valves thin; beaks slightly prominent, closely undulate at the tips; epidermis yellowish olive, eradiate or obsolete radiate, transversely banded; nacre white or reddish brown and iridescent." He (*loc cit.*) expanded on this brief diagnosis as follows: "Shell smooth, transverse, somewhat inflated, very inequilateral, subangular behind; substance of the shell thin; beaks slightly prominent, with numerous closely set, irregular undulations at the tips; ligament long, thin and dark brown; epidermis yellowish olive, without rays or obscurely rayed, transversely banded; umbonial slope raised and rounded; posterior slope carinate, rather wide, with two slightly impressed and three dark lines from the beaks to the margin on each valve; anterior cicatrices confluent, large and slightly impressed; posterior cicatrices confluent, large and very slightly impressed; dorsal cicatrices placed in the center of the cavity of the beaks; cavity of the shell rather deep and wide; cavity of the beaks very shallow, scarcely perceptible; nacre bluish white or reddish brown and iridescent." F. C. Baker (1928), referring to "*Anodonta marginata*," improved on Lea's description, and described so completely our concept of *A. lacustris* that we believe it needs little or no modification: "Long-ovate or elongate elliptical, moderately inflated, usually with thin valves; anterior end rounded; posterior end elongated, pointed, biangulate; ventral margin slightly rounded; dorsal margin straight, slightly sloping at the extremities; beaks slightly raised above the dorsal margin, rather full in some specimens, slightly compressed in others; beak sculpture consisting of 4-5 (rarely 6), somewhat irregularly looped bars, of which the posterior loop is short and v-shaped, and the anterior loop is long and broadly rounded; posterior ridge rounded, faintly double, ending in a rather bluntly biangulate point, which is midway of the posterior margin, the dorsal and ventral margins declining and inclining to meet it; surface with raised growth lines which are more conspicuous on the posterior end, and which are larger and edged with black at rest periods; epi-

dermis olive greenish, brownish, sometimes blotched with reddish-brown on the anterior slope, or the shell may have a brownish cast over a yellowish-green background; region of umbones sometimes of a rich golden color; green rays are more or less distinct on the surface; nacre usually a peculiar dull, silvery tint, iridescent at the posterior end, frequently stained with salmon near the beak cavities, which are shallow. Hinge edentulous."

TYPE LOCALITY OF *ANODONTA LACUSTRIS*

The localities given by Lea with the original description of *Anodonta lacustris* were "Crooked Lake and Little Lakes, New York." The specimens were sent to him by James Lewis, M.D., of Mohawk, N.Y. Whittemore two years later (1859) gave a description of this area of New York, including the Little Lakes. "Little Lakes", shown on an 1829 map ("Entered according to Act of Congress June 5th, 1829, by David H. Burr of the State of New York."; Accession 75350, Maps and Charts, General Library, University of Michigan), are located in the southern end of Warren Township in Herkimer County (Susquehanna River drainage). The two lakes are joined by a stream, and Warren Post Office is located about halfway between the two lakes. An east-west highway, leading eastward to Albany, runs between the two lakes and next to Warren Post Office. Schuyler's Lake is 3.5 miles west southwest of Warren Post Office. The upper of the two "Little Lakes" is now called Weaver Lake and the lower one Young Lake (U. S. Geological Survey topographic map, Richfield Springs, New York, SW/4 Richfield Springs 15' Quadrangle, printed 1960 [data 1943]). On the current quadrangle map, Weaver Lake is shown as surrounded by swamp, and Young Lake is bordered on its west side by swamp. Warren Post Office is now the town of Warren, and the highway bisecting it is U. S. 20. Schuyler's Lake is now called Canadarago Lake, although the town just south of it is named Schuyler Lake. We have not been able to locate "Crooked Lake." It may be Schuyler's Lake (= Canadarago Lake).

DISTRIBUTION OF ANODONTA LACUSTRIS

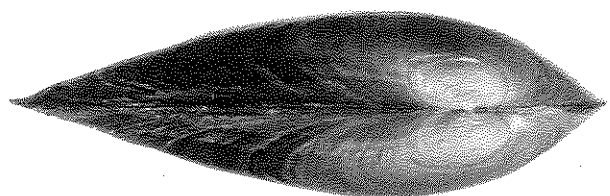
A geographic distribution for *Anodonta lacustris* was given by Marshall (1895): "Occurs in the Eastern [Susquehanna and Hudson River drainages] and St. Lawrence drainage systems. Found in both systems in New York. Confined to a limited area in the Eastern system. Generally distributed in the St. Lawrence system." Baker (1928) gave the general distribution of "*A. marginata*" as: "'St. Lawrence drainage' (Simpson). Specimens from Lake Chetek and lakes in the Wisconsin and Rock drainage indicate that this species also inhabits the Mississippi drainage." Two lots labeled *A. grandis simpsoniana* (National Museums of Canada cat. nos. 31630 [Klotz Lake, 30 miles east of Longlac, Ontario] and 31635 [unnamed lake north of Savant Lake, Ontario]) were found to contain both *A. grandis* and *A. lacustris*. These specimens were collected from the Hudson Bay drainage of the Canadian Interior Basin. From the above, the known distribution of *A. lacustris* comprises the St. Lawrence, upper Susquehanna and Hudson, upper Mississippi, and southern Hudson Bay drainages of North America.

HABITAT OF ANODONTA LACUSTRIS

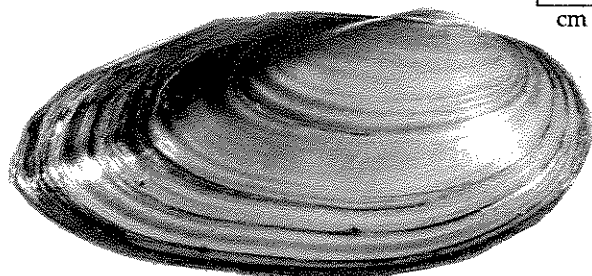
The localities for *Anodonta lacustris* in the original description were lakes. Baker (1916) found it in Oneida Lake, New York, described its habitat, including associated organisms, and compared its habitats in Oneida Lake to those in Tomahawk Lake (Wisconsin) and Saginaw Bay (Michigan). Baker (1928) gave the habitat of "*A. marginata*" in Wisconsin as "Shallow, quiet lakes in mud bottom. Lake Chetek, sand and mud bottom, water .6-1 m. deep, near shore; Sturgeon Bay, near canal, in fine sand, in 1.1 m. of water. This species is for the most part a mussel of lakes and is seldom found in rivers."

OBSERVATIONS AND DISCUSSION

A comparison of shell shape and beak sculpture for *Anodonta lacustris* and *A. grandis* is presented in Figs. 3, 4, 6, 7. According to Baker (1928), "...*Anodonta marginata* [= *A. lacustris*] may be distinguished from *grandis* by its thinner shell, more pointed



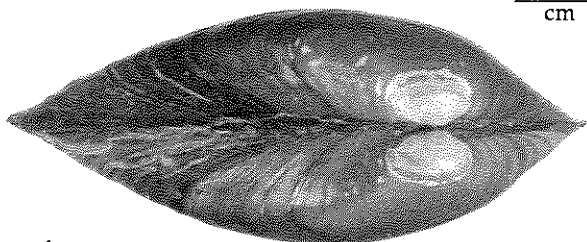
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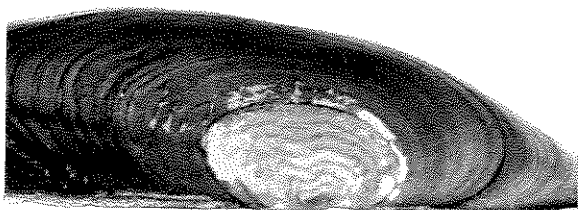


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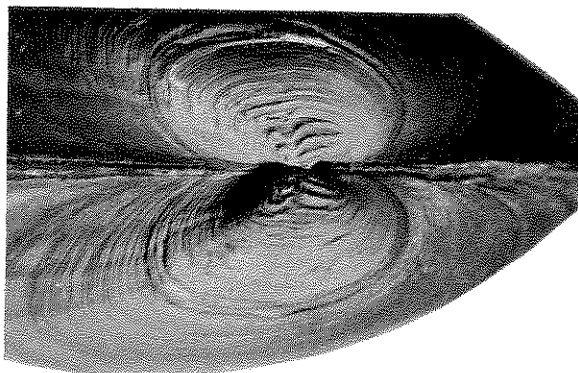


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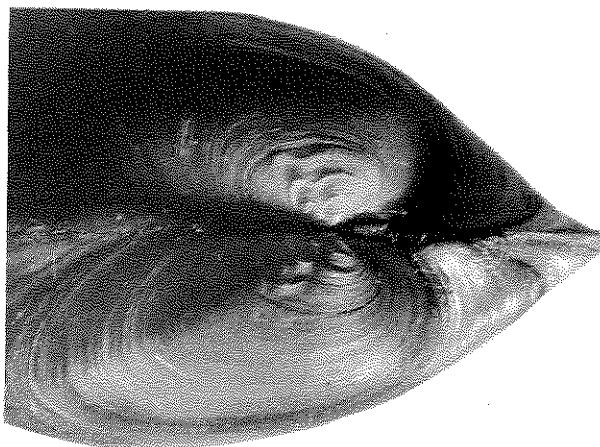
FIG. 3. Dorsal view and right valve of *Anodonta lacustris* (UMMZ 250670). FIG. 4. Right valve and dorsal view of *A. grandis* (UMMZ 250671). Measurement line = 1 cm.



5



6



7

FIG. 5. Beak sculpture of the "Holotype" of *Anodonta lacustris* (USNM 86597). FIG. 6. Beak sculpture of *A. lacustris* (UMMZ 250670). FIG. 7. Beak sculpture of *A. grandis* (UMMZ 250671).

TABLE 1. Nei's genetic distance and number of fixed allelic differences between *Anodonta lacustris*¹ (4)² and conchologically similar species of *Anodonta* (based on 24 presumptive loci).

Species		Nei's genetic distance	No. of fixed allelic diff.
<i>A. cataracta</i> ³	(5) ²	0.325	6
<i>A. fragilis</i> ⁴	(5)	0.372	7
<i>A. grandis</i> ⁵	(5)	0.301	5

¹Lancaster Lake, Cheboygan County, Michigan.

²() = Number of individuals scored in allozymic survey.

³Pickering Creek, Pennsylvania State Highway 23, Phoenixville, Pennsylvania.

⁴Birds Pond, Whitbourne, eastern Newfoundland, Canada.

⁵Mill Creek, below Starve Hollow Lake, Jackson County, Indiana

and elongated posterior end, less elevated and more compressed umbones, peculiar silvery nacre, and the umbonal markings which are finer than *grandis*, differently looped (anterior much longer than posterior), and not nodulous. ... In the *grandis* group the dorso-anterior margin forms a sharp angle with the rounded anterior end, while in the *marginata* from Wisconsin this feature is wholly lacking or only slightly developed." Therefore, at least in the upper St. Lawrence River drainage, *A. lacustris* and *A. grandis* are conchologically quite distinct. Based on an allozymic comparison of allopatric populations, there is a relatively large degree (*sensu* Davis, 1983) of genetic differentiation between *Anodonta lacustris* and *A. grandis* (Table 1). In addition, an allozymic analysis of syntopic individuals of *A. lacustris* and *A. grandis* from Four Mile Lake, Washtenaw Co., Michigan, revealed fixed allelic differences (no intermediates) at three of seven presumptive loci (Hoeh, unpublished data). The conchological and allozymic evidence strongly suggests that *A. lacustris* and *A. grandis* have distinct gene pools and, therefore, are specifically distinct. As mention-

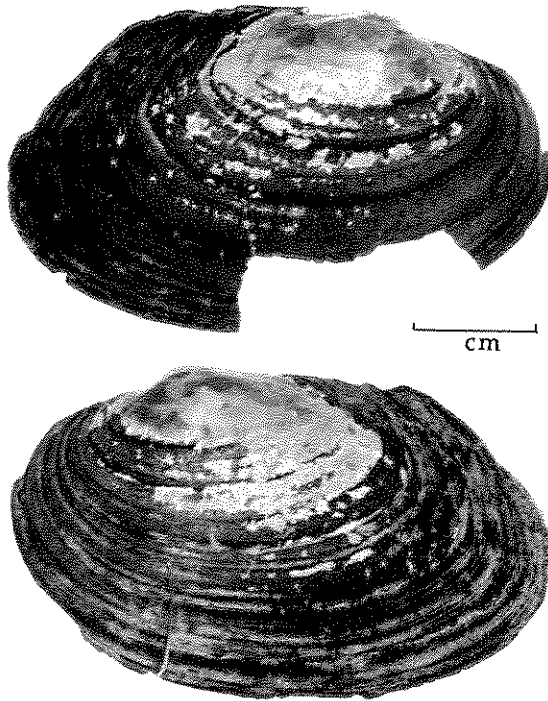


FIG. 8. *Anodonta simpsoniana*, Holotype, USNM 86434. Measurement line = 1 cm.

ed above, *A. grandis* and *A. lacustris* occur sympatrically in the southern Hudson Bay drainage. The maintenance of morphological distinctness in sympatry along with the obvious conchological differences between *A. lacustris* (Figs. 1, 2, 3) and the type of *A. simpsoniana* (Fig. 8) strongly suggest that *A. lacustris* is not a synonym of *A. simpsoniana*. Morphological distinction of *Anodonta lacustris* from congeners located in the lower St. Lawrence River drainage area is more difficult. Simpson (1914) believed that *A. fragilis* was conspecific with *A. lacustris*. However, beak sculpture differences distinguish these two taxa (compare Fig. 6 with fig. 4 in Clarke, 1973). Morrison (personal communication) stated that "... *marginata* [= *A. lacustris*] from the lower St. Lawrence drainage is hard to tell from *A. cataracta*. It is more fragile, has a brilliant nacre,

more loops in the beak sculpture, also more slender than is usual in *cataracta*." From the above, it is apparent that Morrison thought *A. lacustris* (as *A. marginata*) and *A. cataracta* could be distinguished conchologically. In addition, the relatively high levels of allozymic differentiation (*sensu* Davis 1983) observed between *A. lacustris* and both *A. cataracta* and *A. fragilis* corroborate the species level status of *A. lacustris* (Table 1). The geographic distributions of *Anodonta lacustris*, *A. cataracta* and *A. fragilis* (cf. Marshall, 1895; Johnson, 1970; Kat, 1986) suggest that these species may occur parapatrically or sympatrically. Efforts should be made to locate areas of contact and test the common gene pool hypothesis. Further corroboration of species level status for *A. lacustris* should also be sought from a phylogenetic hypothesis of relationships within the genus *Anodonta*. This hypothesis would provide information on character state distributions and, therefore, on additional characteristics potentially diagnostic for *A. lacustris*. Lastly, it is hoped that this work, in conjunction with that of others (Kat, 1983a, 1983b, 1986; Kat & Davis, 1984), will put to rest the presumed subspecific relationships implied by the continued use of trinomials in the case of distinct species such as *Anodonta cataracta*, *A. fragilis* and *A. lacustris* (e.g., see Turgeon *et al.*, 1988).

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