

Malacological Review, 1975, 8: 81-89THE SYSTEMATIC POSITION OF *CYRTONAIAS* (BIVALVIA: UNIONIDAE)

Samuel L. H. Fuller

ABSTRACT

The Central American and Texan freshwater mussel genus *Cyrtonaias* Crosse & Fischer 1894, long of uncertain systematic position, is here determined to be a member of the unionid subfamily Lampsilinae. *Cyrtonaias* is considered to be the most primitive known representative of the Longenae, the most primitive lampsiline tribe. These judgments are based primarily upon the anatomy of Texan specimens of *Unio tampicoensis* Lea 1838, which appears to be identical to *U. berlandierii* Lea 1857, the type species of *Cyrtonaias*. *C. tampicoensis* is homogeneously and delicately papillose along the free mantle margins anteriad from the incurrent mantle aperture and exhibits a marsupium, unique among known Lampsilinae, that occupies the entire outer female demibranch. This species is additionally remarkable for its low degree of sexual dimorphism.

INTRODUCTION

Cyrtonaias was introduced as a section of *Unio* Philipsson by Crosse and Fischer (In: Fischer & Crosse, 1894). The type species of *Cyrtonaias* is *U. berlandierii* Lea 1857, by original designation. In the light of the relevant figures of Lea (1838, 1857) and opinions of Strecker (1931), I agree with the conchologically based judgments of Frierson (1927) and Haas (1969a) that *U. berlandierii* is conspecific with *U. tampicoensis* Lea 1838, which is, also, chronologically first of the many nominal species referred to *Cyrtonaias* by Fischer & Crosse (1894), von Martens (1900), Simpson (1900, 1914), Frierson (1927) and Haas (1969a). Accordingly, I use the combination *C. tampicoensis* (Lea) to typify *Cyrtonaias* in this paper.

Unio tampicoensis and *U. berlandierii* were placed in *Lampsilis* Rafinesque as a subgenus of *Unio* by von Martens (1900). Simpson (1900, 1914) included these species in *Proptera* Rafinesque as a subgenus of *Lampsilis*. Frierson (1927) and Haas (1969a) referred them to *Cyrtonaias* as a subgenus of *Lampsilis*. They were placed in *Lampsilis* without subgeneric designation by Strecker (1931) and Murray & Roy (1968). Haas (1969b) again considered *Cyrtonaias* a subgenus of *Lampsilis*. Finally, other authorities (Modell, 1942, 1964; Morrison, 1967; Heard & Guckert, 1971; Valentine & Stansbery, 1971) have granted *Cyrtonaias* full generic rank. Except for those of Simpson and Frierson, these opinions appear to be uncritical and/or based only upon conchological evidence.

Simpson's (1900, 1914) statement that the marsupium characteristic of his "Group of *Lampsilis umbrosa* [(Lea)]" (in which he included *Unio tampicoensis* and *U. berlandierii*) occupies "the whole outer gills [demibranchs] posteriorly, not projecting much below" is not consistent with Lea's (1860) earlier, accurate observation that the "branchial uterus [marsupium]" of *U. berlandierii* is "filled through the whole length of the outer branchiae [demibranchs]."

Frierson (1927) believed that, were Lea correct, "the group [*Cyrtonaias*] must be placed among the *Elliptio*" (a simplistic response), and he apparently did not consider that Lea (1860) had added, "Branchial opening [incurrent aperture] with papillae on the inner side [inner lobe of the mantle margin], a row of which latter,

diminished in size and wider apart, extends round the basal margin." The latter feature is peculiar to the Unionidae: Lampsilinae (*sensu* Ortmann, 1910) among Nearctic naiades, and, indeed, both of Lea's observations quoted above are consistent with my notes (below) on the anatomy of *C. tampicoensis*.

Often maligned, though sometimes wrongly, Isaac Lea did, in fact and long ago, provide precisely the information needed in order to demonstrate that *Cyrtonaias* belongs, more specifically, to the tribe Lampsilinae: Longenae, recently created by Heard & Guckert (1971). The object of this paper is to support and to amplify this point of view.

MATERIAL

The notes below are based primarily upon 1 male and 1 ovigerous female of *Cyrtonaias tampicoensis* collected 1 August 1972 by Louis E. Sage and myself in the Guadalupe River, about 2 miles southwest of Seguin, Guadalupe County, Texas. (This station is the type locality of *Quadrula (Quincuncina) guadalupensis* Wurtz 1950 (see Wurtz, 1950).) The material is deposited at the Academy of Natural Sciences of Philadelphia (ANSP). The male specimen is catalogued as ANSP 333535 (the shell) and A4484 (the soft tissues in alcohol); the female as 333535 and A4485.

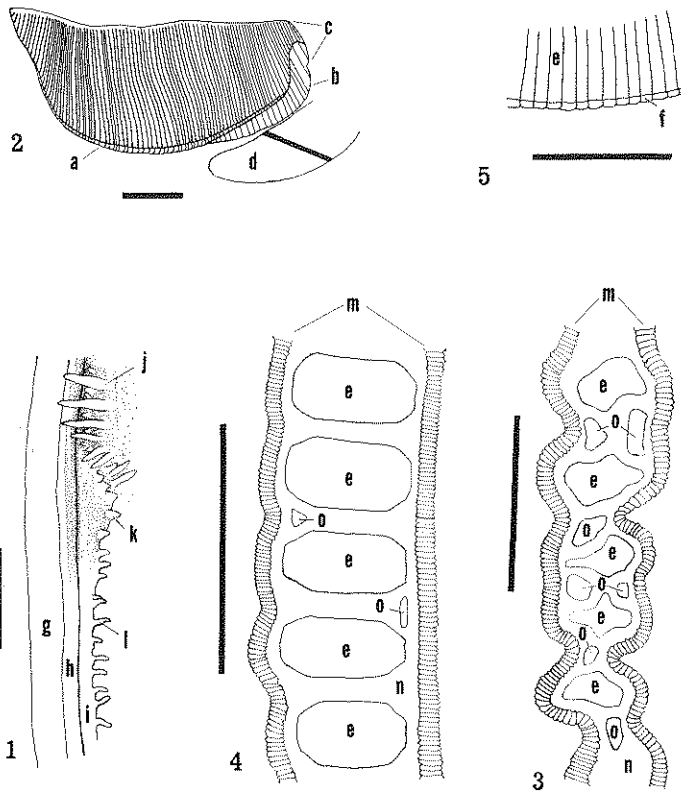
Certain additional observations are included on a series consisting of 10 males, 5 barren females and 1 ovigerous female collected 28 May 1973 by Robert R. Grant, Jr. and myself in the Nueces River at Texas Hwy. 16, about 10.5 miles south of Tilden, McMullen County, Texas. These specimens (ANSP A5266) agree in all essentials with the Guadalupe River material.

All specimens were relaxed with ca. 0.05% sodium nembital, fixed in ca. 5% formalin and stored in ca. 70% ethanol (tap water was the solvent in these volumetric preparations).

In an attempt to evaluate possible sexual dimorphism in *Frierosonia* Ortmann 1912 (the only other genus known in the Lampsilinae: Longenae), large series of shells of *Lampsilis iridella* Pilsbry & Frierson 1908, type species of *Frierosonia* by Ortmann's (1912) original designation, and of *L. semirasa* Pilsbry 1909, considered a synonym of *L. iridella* by Haas (1969a), were examined. The series of *L. iridella* are ANSP 93810, the original lot studied by Pilsbry & Frierson (1908); 93810a, the figured holotype, subsequently identified as such by Johnson & Baker (1973); 98555; and 99531 through 99538. ANSP 98555 includes disintegrated material stored in alcohol; this loss is especially unfortunate because, were a male involved, observations on anatomical sexual dimorphism might have been possible as a complement to Ortmann's (1912) diagnosis of *Frierosonia*, which is based exclusively on shells and female soft tissues. The series of *L. semirasa* are ANSP 99542, the original lot studied by Pilsbry (1909); 99542a, the lectotype, subsequently selected by Johnson & Baker (1973); and 99539 through 99541. All these materials are from numerous, sometimes poorly localized places in the Gulf drainage of eastern Mexico, chiefly from the Panuco River system (see Pilsbry, 1909).

ANATOMY OF *CYRTONAIAS TAMPICOENSIS*

Differentiation of the free mantle margins is limited to papillation of the inner mantle lobe at and anterior from the mantle apertures (Fig. 1). There is a single row of short, erect, closely spaced, and rather delicate papillae on the apical surface of this lobe at the anal aperture. There are 2, somewhat intermingled rows at the incurrent aperture (Fig. 1). Those of the outer row closely resemble the anal papillae; the papillae of the inner row are longer, slightly stouter, subtentaculate, and fused basolaterally to the inner surface of the lobe (Fig. 1). The outer row extends anterior from the incurrent aperture along the apical surface of the inner lobe (Fig. 1) for about 1/2 of the animal's length (cf. Lea, 1860); these



FIGS. 1-5. Aspects of the anatomy of an ovigerous female *Cyrtonaias tampicoensis* (Lea) from the Guadalupe River, about 2 miles southwest of Seguin, Guadalupe County, Texas (ANSP A4485). Scale: the bar equals 5 mm in each figure. Fig. 1. Ventral view of the left post-basal mantle margin at and anterior from the incurrent mantle aperture. Fig. 2. Lateral view of the right gill and outer oral palpus. Mantle removed along heavy line on palpus. Fig. 3. Transverse section of water tubes in a non-marsupial demibranch (i.e., both demibranchs in the male, as well as the inner ones of the female). Fig. 4. Transverse section of ovigerous water tubes (eggs removed) near the posterior end of an outer, marsupial demibranch. Fig. 5. Lateral view of a portion of the ventral margin of an outer, marsupial demibranch.

Abbreviations used: a = outer, marsupial demibranch; b = inner, non-marsupial demibranch; c = region of fusion of demibranchs to visceral mass; d = outer oral palpus; e = watertube; f = portion of water tube extending distad beyond ventral margins of lamellae of outer, marsupial demibranch; g = outer mantle lobe; h = middle mantle lobe; i = inner mantle lobe; j = papilla of inner row at incurrent mantle aperture; k = papilla of outer row at incurrent (and anal) mantle aperture(s); l = papilla of row along apical surface of inner mantle lobe anterior from incurrent mantle aperture; m = gill filaments; n = interlamellar tissue; o = vessel paralleling the gill filaments through the interlamellar tissue.

papillae are somewhat longer and more nearly tentaculate anterior from the aperture (Fig. 1). Immediately anterior from the incurrent aperture the inner mantle lobe is little wider than it is elsewhere along the margin of the animal (Fig. 1).

The mantle apertures are separated functionally in life by a tangency of the apposing free mantle margins, but there is no mantle suture between them. Anal and supra-anal portions of the excurrent aperture are separated by a suture of the

apposing inner mantle lobes, which is usually about equal to the anal aperture in height. Nine of the 16 Nueces River individuals (or 56.3% of this admittedly small lot) have 1 (4 males) or 2 (4 males, 1 female) secondary suture(s) above the primary suture. This additional occlusion varyingly approaches closure of the supra-anal aperture in a few specimens. The supra-anal aperture lacks papillae and is occluded dorsally for a few mm by postbasal extension of the mantle isthmus. The height of the incurrent aperture is about twice that of the anal, than which the supra-anal is usually a little higher.

The inner demibranch hangs somewhat lower than the outer in the male, and (Fig. 2) posteriorly the outer female demibranch hangs about as low as the inner. The anterior margin of the outer demibranch and about the dorsal 1/2 of the anterior margin of the inner demibranch are fused to the visceral mass (Fig. 2). The dorsal margins of the inner lamellae of the inner demibranchs are either fused to the visceral mass all along the foot or free of the mass for a few mm anteriorly. The dorsal margins of the outer lamellae of the outer demibranchs are free of the mantle for a few mm posteriorly (i.e., the diaphragm is very briefly incomplete), and the gills extend posteriad almost to the mantle margin. Thus the horizontal bar is very short.

Interlamellar septa parallel the gill filaments and are complete, uninterrupted, and imperforate, but the surfaces of the marsupial septa are weakly ribbed transversely, perhaps reflecting phylogenetically recent fusion of adjacent interlamellar connectives (see Fuller, 1971, on the Nearctic unionine genus *Uniomerus* Conrad). Septa of both demibranchs in both sexes occur about every 20 gill filaments (Figs. 3, 4), but in marsupial, outer female demibranchs, septa may be more closely spaced, and in non-marsupial demibranchs of both sexes, the exact spacing may be difficult to determine because of the irregular shapes and sizes of the water tubes. All septa are usually about 10 filaments thick at their bases (Figs. 3, 4), but those of the gravid marsupium are stretched until they become much thinner (Fig. 4). The marsupium occupies the entire outer female demibranch except a few water tubes at each end (Fig. 2). Vessels (Figs. 3, 4) parallel the gill filaments through the interlamellar tissue, which is about equally well developed in each sex; they ordinarily occur at the bases of septa. Vessels are rare and usually minute in the marsupium (Fig. 4), but they are abundant and large in non-marsupial demibranchs (Fig. 3), where, it seems, the septa are formed by fusion of the walls of apposing vessels. Thus the apparent origins of marsupial and non-marsupial septa are quite different. The ventral margins of inner demibranchs are furrowed in both sexes, and those of the outer male demibranchs are sharp, but the marsupial water tubes distend slightly beyond their lamellae (Figs. 2, 5), creating the beaded appearance of the ventral margin of the outer female demibranch.

The egg is subspherical, translucent, apparently minute (see below), and with a subcentral, opaque embryo. The egg mass is compressed from front to rear, narrower below, composed of several layers of eggs, and (see Utterback, 1915: 245, and Fuller, 1971, on the egg mass of *Uniomerus*) reflects the uneven surfaces of apposing marsupial septa. The larval stage, if any, is unknown. I have ovigerous females collected 28 May and 1 August. The nature of the breeding season cannot with certainty be inferred from these data. However, the diameter of the eggs collected 28 May is about 0.16 mm; of those collected 1 August, about 0.17 mm. These data suggest that gravidity commences by at least the late spring in Texas and that development proceeds, slowly, into the fall, perhaps leading to an overwintering larva. This notion contrasts with Morrison's (1967) suggestion that "*Cyrtornaias* ... may ... have a short breeding season in the cool winter months" of Mexico.

The outer oral palpi are very slightly larger than the inner. Palpi are large, subfalciform, elongate, and either do not or do barely overlap the inner demibranchs (Fig. 2). The posterior margins of apposing inner and outer palpi are fused together for about the proximal 1/2 of their lengths.

The rectum terminates in a hood, which is slit vertically to form 2 lobes, broader above, whose free margins are crenulate.

Pigment (Fig. 1) consisting of fine dark specks occurs only on the free mantle margins at and for a few mm anterior from the mantle apertures. The outer mantle lobe and the outer and apical surfaces of the middle lobe are unpigmented. The apposing surfaces of the middle and inner lobes are pigmented. The apical surface of the inner lobe, including its papillae, is unpigmented, and pigment occurs on the inner surface of this lobe among the bases of the papillae of the inner incurrent row. These patterns are poorly developed at the supra-anal aperture and faint to obsolete anterior from the incurrent one.

SYSTEMATICS OF *CYRTONAIAS*

Classification

Superfamily: The apparent alliance of *Cyrtonaias* to the Lampsilinae: Longenae (see "Subfamily" and "Tribe" below) suggests that its larva, though unknown, will prove to be the glochidium of the Unionacea (see Parodiz & Bonetto, 1963). Moreover, the only alternative is the Mutelacea, whose members' marsupia are restricted to the inner demibranchs (Ibid.), whereas in *Cyrtonaias* the marsupium occurs only in the outer demibranchs.

Family: Assuming that *Cyrtonaias* is unionacean, I place it in the Unionidae (*sensu* Ortmann, 1911, but not as restricted *sensu* Heard & Guckert, 1971) because of the parallel orientation of its interlamellar septa to its gill filaments and because of the location of its marsupium, in the outer, female demibranchs. (The unionacean families Amblemidae and Hyriidae (*sensu* Heard & Guckert), also, satisfy the former criterion, but their marsupia occur, respectively, in all 4 demibranchs and in only the inner ones.) This has been the choice of all authorities save 2: Modell (1942, 1949 [by implication], 1964), who placed *Cyrtonaias* (with all other Lampsilinae) in his Elliptionidae, ostensibly on the basis of beak sculpture (though the only mention of *Cyrtonaias* is in Modell's lists of lampsiline genera); and, apparently, Morrison (1955), who did not mention *Cyrtonaias*, but included the Lampsilinae in his concept of the Amblemidae.

Subfamily: *Cyrtonaias* appears to fall within the Lampsilinae (*sensu* Ortmann, 1910) because it conforms to the one unifying morphological feature of that subfamily (see Ortmann, 1912): distension of the marsupial water tubes ventrad beyond the limits of the lamellae of the outer female demibranchs. This is the consensus of earlier workers, with few exceptions. Morrison (1967) implied that *Cyrtonaias* is a member of his (1955) Amblemidae: Ambleminae. Valentine & Stansbery (1971) uncritically placed *Cyrtonaias* in the Unionidae: Ambleminae. Heard & Guckert (1971) included *Cyrtonaias* in the Unionidae: Popenaiadinae. It appears that Heard & Guckert shared Frierson's (1927) partial appreciation of Lea's (1860) observations on *Unio berlandierii* (see "Introduction" above), which would have led them to the correct assumption that the marsupium of *Cyrtonaias* is restricted to the outer demibranchs, as is characteristic of their concept of the Unionidae. Also, they were influenced by Morrison's (1967) suggestion that "*Cyrtonaias* . . . may . . . have a short breeding season in the cool winter [misquoted by Heard & Guckert as "summer"] months." Now, a bradytictic (i.e., long) breeding season is the one unique

feature of these authors' Popenaiadinae in the context of their concept of the Unioniidae, but imputation of bradytixis to *Cyrtonaias* contradicts Morrison's point, even though the winter months are characteristically involved in a long breeding season among Nearctic naiades.

Tribe: On the basis of conchological and anatomical features, Parodiz & Bonetto (1963) usefully employed the tribal concept in their classification of South American naiades; this device may be used to advantage elsewhere in naiad classification. Based on marsupial characters alone, Simpson's (1900) lampsiline subdivisions (Ptychogenae, Eschatigenae, Mesogenae and Heterogenae) are biologically (as well as etymologically) inconsistent with the tribes established by Parodiz & Bonetto, but they are, in effect, of tribal rank. To Simpson's concepts Heard & Guckert (1971) added the Longenae, also based on a marsupial character. The type genus of the Longenae, by monotypy (Ibid.), is the Mexican *Frierersonia* Ortmann 1912, whose type species, as noted above (see "Material"), is *Lampsilis iridella* Pilsbry & Frierson 1908, by Ortmann's (1912) original designation. *Frierersonia* is remarkable for its marsupium, unique among Lampsilinae and extending all of the height and not quite the length of the outer female demibranch. The marsupium of *Cyrtonaias* is yet more extensive (Fig. 2), and this genus is unquestionably longenous.

Affinities

As discussed above (see "Introduction"), *Cyrtonaias* has been associated, chiefly on a conchological basis, with only *Lampsilis* and *Proptera* among lampsiline genera recognized by Valentine & Stansbery (1971) and by Heard & Guckert (1971). Shells of *C. tampicoensis* do approximate the shape of those of certain species of *Lampsilis* and *Proptera* (see Burch, 1973), but the latter 2 genera have heterogeneous marsupia (see Ortmann, 1912). Because *Frierersonia* is the only other genus known in the Longenae, only it need be distinguished from *Cyrtonaias* in detail. The differences between these 2 genera are several, including some of great importance, which are evident in the contrast between Ortmann's (1912) notes on *F. iridella* and the anatomy of *C. tampicoensis* given above (plus Lea's (1860) observations on the anatomy of *Unio berlandierii*).

The subcylindrical water tubes of the marsupium of *Frierersonia iridella* extend greatly beyond the distal margins of the lamellae of its demibranch and curve posteriad, producing the postbasal margin of the marsupium into a point. The distal margin of the marsupium is rather sharp. The marsupium exhibits dark pigment and is clearly demarked from a short non-marsupial portion of the outer female demibranch at its anterior end. The glochidia are 0.20 mm long and 0.22 mm wide ("of medium size"). The inner lobe of the mantle margin anterior from the incurrent aperture is crenulate, somewhat broadened, and conspicuously pigmented.

In *Cyrtonaias* the marsupial water tubes extend only slightly beyond the lamellae of the outer female demibranch, thus giving the ventral margin of the marsupium a beaded aspect (Figs. 2, 5). Marsupial water tubes (Fig. 4) are laterally elastic, providing space for a rather broad egg mass. The marsupium (Fig. 2) occupies almost the entire outer female demibranch and is not structurally distinct from the minute non-marsupial region at each end of this demibranch, it is rounded postbasally, and it lacks dark pigment. The eggs are about 0.16 mm in diameter during late May; about 0.17 mm in early August. These data suggest a glochidium smaller than is known for *Frierersonia*. Postbasally, the inner lobe of the mantle margin is narrow, conspicuously papillose, and very faintly pigmented (Fig. 1).

In the context of Ortmann's (1912) lampsiline system, the *Frierersonia* marsupium is the more advanced in that it occupies less of its demibranch and its water tubes are extended conspicuously posteriad, whereas the *Cyrtonaias* marsupium is the

more advanced by virtue of its laterally elastic water tubes (see Fuller, 1974: 109-110). Similarly, the postbasal mantle margin of *Frieria* is well developed in terms of pigmentation and breadth (advanced characters), but weakly papillose (primitive character), while *Cyrtonaias* is opposite in these respects. (Finally, the tendency toward closure of the supra-anal mantle aperture in *Cyrtonaias*, though genetically unstable, is an advanced unionid character.) Thus each genus exhibits a different combination of advanced and primitive characters; perhaps each represents a distinct lineage within the Longenae.

The specimens of *Lampsilis iridella* and *L. semirasa* that I have examined (see "Material" above) consist only of unsexed shells, but the lack of 2 distinct, presumably sexual, morphological types in this large quantity of material supports Ortmann's (1912) statement that "Male and female shells [of *Frieria* are] hardly different." This appears to be true of *Cyrtonaias*, as well. The width/height relationship (an index of obesity, which characteristically differs sexually in the Lampsilinae) of my 10 male Nueces River shells ranges from 55.2% through 68.0%, with an average of 60.3%, while the corresponding figures for the 6 female shells are 58.6% through 67.3%, with an average of 63.8%. Sexual dimorphism of the shell cannot be inferred from these overlapping ranges, and there is no consistent difference in shape between the sexes in these shells. It appears that neither *Frieria* nor *Cyrtonaias* is in advance of the other in terms of sexual dimorphism of the shell.

There is no other information on sexual dimorphism in *Frieria*, but it can be emphasized that in *Cyrtonaias tampicoensis* the morphology of the postbasal mantle margin (Fig. 1) in each sex is identical; that in all demibranchs of each sex there is an almost equal development of interlamellar tissue, including equally thick septa (Figs. 3, 4); and that septa, though often set somewhat more closely together in marsupial than in non-marsupial demibranchs, are usually about equally spaced in both types (Figs. 3, 4). Again in the context of Ortmann's (1912) system of the Lampsilinae, the low degree of sexual dimorphism of both hard and soft tissues in *Cyrtonaias* is an extremely primitive feature.

Once distension of the water tubes distad beyond the ventral margins of the marsupial lamellae was achieved, there were evidently 2 major trends in the evolution of lampsiline anatomy (see Ortmann, 1912): restriction of the marsupium posteriad and ventrad in the outer female demibranch and morphological differentiation of the postbasal mantle margin, especially the inner mantle lobe, anteriad from the incurved aperture. In the former respect, *Cyrtonaias* is undeveloped, and, in the latter, it is weakly developed. Most primitively represented by this genus, the Longenae are probably closer to the original lampsiline stock than is any other extant tribe. Indeed, one or more of the other tribes may bear a derivative relationship to the Longenae (cf. Heard & Guckert, 1971: 344).

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SAMUEL L. H. FULLER

Academy of Natural Sciences of Philadelphia
Philadelphia, Pennsylvania 19103, U.S.A.

