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A RE-EVALUATION OF THE RECENT UNIONACEA (PELECYPODA) OF NORTH AMERICA

William H. Heard and Richard H. Guckert

Florida State University, Tallahassee, Florida 32306, U.S.A.

ABSTRACT

Recent higher classifications of freshwater mussels, based principally on shell characters, do not reflect the phylogenetic relationships of these animals which may be interpreted from reproductive features. Although these 2 types of characters are not consistently mutually exclusive, there is comparatively little overlap. Shell characters have received emphasis in the classification of naiades on a world-wide basis because of convenience of study and because they can be employed in investigations of fossil material. Unfortunately, too little information on reproductive morphology and habits is presently available to permit a wide-scale classification based on these features, and it may prove difficult to relate fossil forms to such a scheme should one eventually be proposed. The choice of one system (*i.e.*, either shell or soft-parts) demonstrates parallel evolution of characters in the other system. It is considered here that a system based on aspects of reproduction, with parallelism in the shell features, more accurately reflects natural, evolutionary affinities than does a system which reverses the emphasis.

In order to stimulate further investigation (particularly of non-Nearctic groups), a revised system of affinities of North American naiades at the familial and subfamilial levels, derived from anatomical and related aspects of reproduction, is presented here. This system concerns such features as (*a*) the number of marsupial demibranchs (4 or 2), (*b*) the location of the marsupial demibranchs (only the inner 2, or only the outer 2), (*c*) specific regions of the marsupial demibranchs which incubate the developing larvae (the entire demibranchs, only the posterior portion, only the central portion, *etc.*), (*d*) the morphology of the marsupial demibranchs (simple or subdivided septa and water-tubes; continuous or interrupted septa and water-tubes), (*e*) the duration of incubation of the larvae (short- or long-term), (*f*) the nature of the glochidial shell (hooked or hookless), and (*g*) other anatomical aspects more subtly related to reproduction in terms of water currents (completeness and composition of the diaphragm; presence/absence of a supra-anal opening).

These characters indicate that Recent representatives of the Margaritiferidae, Amblemidae and Unionidae occur in North America. A fourth family, the Hyriidae, is known from the Nearctic Region only in fossil form; living species are presently confined to South America and Australasia. Nearctic subfamilies and their characters are delineated for these 3 Recent families, and the North American genera of each group are listed. Three new subfamilies are proposed: **Cumberlandinae** (Margaritiferidae), **Megalonaiadinae** (Amblemidae) and **Popenaiadinae** (Unionidae). Notes on related unionacean groups in the Neotropical, Palearctic, Ethiopian, Oriental and Australasian regions are provided.

A suggested relationship of the Mutelacea to the Unionacea is included, and phylogenetic affinities of the families and subfamilies of Nearctic unionaceans are interpreted from reproductive data. The presently-Holarctic Margaritiferidae, the most primitive group of unionaceans, is considered to have independently given rise to the hyriid-mutelacean stock and to the Amblemidae. The Amblemidae, present in all areas but South America and the Australasian Region, in turn is described as ancestral to the Unionidae. The unionids have reached greatest diversification in North America and comprise the vast majority of Nearctic mussels. The more primitive Pleurobeminae (presently confined to North and Central America) is suggested to have given rise independently to (*a*) the Popenaiadinae of the southern United States, Mexico and Central America, (*b*) the Anodontinae of the Northern Hemisphere, and (*c*) the Lampsilinae of North and Central America. The Unioninae s.s. of Eurasia is thought to have been derived from anodontine stock. The Pleurobeminae is considered to be ancestral to the primitive lampsiline stock which subsequently diverged along several lines through specializations of the marsupial demibranchs.

The evolutionary trends in advancement and/or specialization of the Nearctic unionaceans include (*a*) reduction from 4 to 2 (principally the outer pair) marsupial demibranchs, with greatest diversification occurring in present groups in the Northern Hemisphere, (*b*) development of continuous interlamellar septa and water-tubes, (*c*) morphological adaptations of the marsupial demibranchs which reach greatest specialization by restricted regionalization of ovisacs in the unionid Lampsilinae, (*d*) a tendency toward a complete diaphragm formed entirely by the ctenidia, and (*e*) a general change from short-term to long-term incubation of the larvae. Most unionaceans possess hookless glochidia, and the hooked larvae are considered to have evolved independently in the hyriids and in the unionine-anodontine stock.

INTRODUCTION

Modell (1942, 1949, 1964), Morrison (1955, 1966, 1967), McMichael & Hiscock (1958), and Haas (1969a, 1969b) have altered the taxonomic treatment and presented new impressions of the phylogenetic affinities (?) of freshwater mussels of the families Margaritiferidae, Mutelidae and Unionidae as formerly interpreted by Simpson (1896, 1900a, 1914), Ortmann (1910a, 1911a, 1912a, 1921a) and Frierson (1927). However, the work of Parodiz & Bonetto (1963) has demonstrated the necessity of a re-evaluation of these other recent reports and has consequently prompted this extension of their findings.

Modell originally (1942) emphasized beak sculpture as the principal character which he considered to reflect phylogenetic relationships; other shell characters (e.g., form and hinge aspects), anatomical features, and larval type were relegated to secondary importance. Later (1949), Modell fruitlessly attempted to support his concepts with morphological information. His most recent report (1964) shows few digressions from his previous considerations.

While Ortmann's (1910a) system of the "Unionidae," widely followed by North American workers, consists of but 3 subfamilies (viz., Unioninae, Anodontinae and Lampsilinae), Modell's latest (1964) scheme includes the following higher taxa which include Nearctic representatives:

- Family Elliptionidae Modell, 1942
  - Subfamily Pleurobeminae[1] Modell, 1942
  - Subfamily Elliptioninae Modell, 1942
  - Subfamily Ambleminae[2] Modell, 1942
  - Subfamily Alasmidontinae[2] Frierson, 1927
  - Subfamily Lampsilinae von Ihering, 1901
- Family Unionidae[2] Fleming, 1828
  - Subfamily Quadrulinae von Ihering, 1901
  - Subfamily Rectidentinae Modell, 1942
  - Subfamily Anodontinae[2] Swainson, 1840

Morrison (1955) restored Modell's Ambleminae to familial rank (as Refinesque, 1820, employed it) and included in it the subfamilies Ambleminae

[1] This taxon was first employed by Hannibal in 1912.

[2] These taxa were originally proposed by Rafinesque in 1820.

s.s. and Lampsilinae. As Morrison (1967) also pointed out, the family Quadrulidae Hannibal, 1912, and its subfamily Quadrulinae von Ihering, 1901, are synonyms of the Amblemidae and Ambleminae, respectively.

McMichael & Hiscock (1958) recognized the importance of soft-part and reproductive features, but they persisted in subscribing to Modell's scheme based principally on shell characters.

Haas (1969a, 1969b) presents more conservative systems which include the Recent North American unionaceans in the Margaritiferidae and Unionidae (and its subfamilies Unioninae s.s., Quadrulinae, Anodontinae, Alasmidontinae, Lampsilinae and Hyriinae).

In our opinion most classifications of freshwater mussels have (1) overemphasized shell sculpture, paleontological data and seemingly zoogeographic relationships, and (2) only superficially interpreted anatomical features. While Frierson (1909, p 107) stated that "beak sculpture and manner of carrying ova in the gills are not correlated," he preferred to use shell features as the basis of classification. However, as Hannibal (1912, p 117) and Ortmann (1912a, p 230) have pointed out, respectively, shell characters are of "secondary importance in the recognition of groups more comprehensive than genera," and are "unfit to be used for the distinction of the larger groups." Modell's (1942, p 164) suggestion that most anatomical characters "gehen Hand in Hand mit Umbildungen der Schale" would be considered by Hannibal and Ortmann (and by us) to be fallacious.

A number of different schemes of classification of freshwater mussels have been proposed (see McMichael & Hiscock, 1958), each seeming to stress a different combination of characters and/or rearranging the member groups. Van der Schalie (1952) has provided a most informative paper which reviews (1) some of the systems that earlier workers devised, and (2) the personalities of several of these taxonomists/systematists.

Sterki (1898, 1903) indicated that the classification of these mollusks should include their reproductive features, e.g., the number and location of the marsupial demibranchs, the regions of these demibranchs which incubate the developing larvae, the morphology of the marsupial demibranchs, the duration of gravid periods (= "breeding season" of authors), and the nature of the glochidial larvae. Simpson (1900a) created a number of divisions (based upon distinctive marsupial demibranch features) within the subfamilies of the "Unionidae." Ortmann subsequently subscribed to the initial findings of Sterki and Simpson and extended their work in more detail.

In viewing Modell's most recent phylogenetic scheme (1964, figure on p 122), one can immediately detect the composite nature of the families Elliptionidae and Unionidae. In the Elliptionidae (comprising elements of Ortmann's 1910a Unioninae, Anodontinae and Lampsilinae!) are the Lampsilinae and Alasmidontinae which are for the most part bradytictic (i.e., "long-term breeders," retaining developing glochidial larvae except in the Nearctic summer), while others are tachytictic (i.e., "short-term breeders," carrying glochidia only in the Nearctic summer: Pleurobeminae, Elliptioninae and Ambleminae). The Alasmidontinae contains species with hooked glochidia, while the other members of this family Elliptionidae possess hookless larvae. Animals of the Elliptionidae have seven different marsupial gill conditions which Simpson (1900a) termed tetragenae, homogenae, diagenae, heterogenae, mesogenae, eschatigenae and ptychogenae. Modell also included in the "family Unionidae" groups with (1) the tetragenous condition, short-term breeding and hookless glochidia, and (2) the homogenous condition, long-term breeding and hooked glochidia. Furthermore, groups with hooked glochidia, the homogenous condition and long-term breeding were placed in 2 different unionid subfamilies (Rectidentinae and Anodontinae), and genera with these same features were included in the Alasmidontinae of the Elliptionidae. Finally, Modell's Rectidentinae contains (1) *Rectidens* Simpson which is tetragenous and has hookless glochidia, and (2) *Arnoldina* Hannibal, *Utterbackia* Baker and *Pyganodon* Crosse & Fischer[3] which have the homogenous condition and hooked glochidia. These few examples should suffice to demonstrate the shortcomings of Modell's classification.

Hass (1969a, 1969b) has provided the most recent conchological systems, and he lists 6 subfamilies (compared to Modell's 12), in the Unionidae: Unioninae, Quadrulinae, Anodontinae, Alasmidontinae, Lampsilinae and Hyriinae. However, his scheme (1) does not consistently separate tetragenous and homogenous groups, (2) maintains a distinction between the Anodontinae and the Alasmidontinae, and (3), like Modell, retains the Hyriinae[4] in the Unionidae.

In these previous examples we have attempted to show the limited value of using principally (or entirely) shell characters in the classification of freshwater mussels. Ortmann's work remains today as a model of the anatomical/reproductive approach. He recognized, however, that his provisional interpretations could be subject to change in the light of additional information. In addition, he was interested in the natural relationships of these mussels, not just in their nomenclature. We will attempt to follow Ortmann's lead and hopefully extend our knowledge of the evolution of this large and diverse group of animals. To do so, however, requires a re-evaluation of his concept of the unionid subfamilies, particularly the Unioninae (see Ortmann, 1910a, 1912a). His consideration of this group includes several genera with 4 marsupial demibranchs as well as others with only the outer 2 demibranchs marsupial (although all except *Megalonaias* Utterback (tetragenae) and *Popenaias* Frierson (homogenae) are short-term breeders, and all North American groups possess hookless glochidia). His (1910a) Anodontinae (s.l.) encompasses the Alasmidontinae (s.s.) as defined by Rafinesque (1820), Swainson (1840), Frierson (1927), Modell (1942, 1949, 1964) and Haas (1969a, 1969b). Since all species of these 2 groups possess marsupial demibranchs (homogenae in all genera but *Strophitus*, which has the diagenous condition) with secondary interlamellar septa and secondary water-tubes, they are more correctly considered as a single group unlike any other subfamily. Ortmann's (1910a) Lampsilinae (an extension of von Ihering's 1901 taxon) is retained by Modell (1942, 1949, 1964) and Morrison (1955), but is removed to the Elliptionidae and Amblemidae, respectively.

It appears to us that the aforementioned reproductive characters are more significant than Modell, Morrison, McMichael & Hiscock, and Haas have considered, and we find their systems artificial and untenable. Consequently, we recommend a consideration of what we feel are more distinctive features, and we offer here a revised higher classification of the North

[3] These 3 taxa are actually subgenera of *Anodonta* Lamarck which Modell correctly places in the Anodontinae.

[4] McMichael & Hiscock (1958) included the Hyriinae in the Mutelidae (Mutelacea), but Parodiz & Bonetto (1963) correctly restored it to familial rank and placed it in the Unionacea.

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American naiades. Unlike numerical taxonomists who use all characters and give them equal weight, we have subjectively elected to ignore one entire array of characters (i.e., conchological features) and to suggest soft-part anatomy and reproductive habits as pre-eminent in describing phylogenies. There is regretably little specific evidence to support our contention that shell features are the less conservative characteristics. However, ecophenotypic variation in the shell is well documented, and it is difficult (if not impossible) to interpret the possible genetic adaptation(s) of different forms of beak and disc sculpture. Besides, although the shell features of these mussels are indeed convenient, they have not adequately been demonstrated to be more conservative than any other set of characters. Consequently, we have preferred to emphasize reproductive aspects in the manner that systematic botanists favor flowers (i.e., reproductive organs) to such vegetative characters as leaves. Nevertheless, it is hoped that when more information on naiades from other regions becomes available the shell and reproductive features can be correlated into a more meaningful system which more accurately defines the parallel evolution in either or both set(s) of characters on a worldwide basis.

The anatomy and reproductive habits of mussels of the Ethiopian, Oriental and Australasian Regions are still poorly known. While we have provided notes on some species/genera from these areas, we cannot at this time adequately interpret their characters in terms of our proposed system. Future investigations of naiades in these areas will provide information which may well modify the views and concepts presented here. Our objective is to present a format to which future studies (hopefully to be stimulated by this paper) may be compared.

We have listed in this paper the commonly-used generic designations of the different families and subfamilies of the Nearctic unionaceans. However, we wish to stress that a critical re-evaluation of these alleged genera is needed. This is indicated in particular by the presence of some 18 monotypic genera among the 48 genera listed for North America. Superscript numbers in the following section refer to corresponding comments under Notes, which appear at the end of this paper (p 345).

CLASSIFICATION

SUPERFAMILY UNIONACEA
(Fleming, 1828) Thiele, 1935

Freshwater pelecypods with schizodont hinge dentition; ovoviviparous animals, the larvae (= glochidia[1]) being incubated in all 4 or in only some (either the inner or the outer pair) of the demibranchs; glochidia of most species temporarily parasitic on the gills or fins of fishes[2]; for additional features see Thiele (1935, p 815).

Family 1. MARGARITIFERIDAE
Haas, 1940[3]

Type genus: *Margaritifera* Schumacher, 1816[4] (type species: *Mya margaritifera* Linnaeus, 1758). All 4 demibranchs marsupial; glochidia hookless but with irregular small teeth at ventral margin of the valves (Ortmann, 1912a, p 232); interlamellar connections of demibranchs irregularly scattered or forming irregular oblique rows, or incomplete septa which run obliquely to the direction of the gill filaments; ctenidia lacking water-tubes; posterior margins of mantle not united, lacking even a tendency to form anal and branchial siphons; supra-anal opening lacking; diaphragm separating branchial and suprabranchial cavities incomplete, formed only by the ctenidia; tach ~~brad~~ytictic. Present distribution: North America and Eurasia.

Subfamily Margaritiferinae s.s. (Modell, 1942[5])

Type: same as for the family. Interlamellar connections discontinuous, irregularly scattered or falling into oblique rows. Represented in the United States by *Margaritifera margaritifera* (Linnaeus), *M. falcata* (Gould) and *M. hembeli* (Conrad).

Subfamily **Cumberlandinae,** new subfamily

Type genus: *Cumberlandia* Ortmann, 1912b (for *Unio monodonta* Say, 1829). Interlamellar connections of the demibranchs scattered and in interrupted rows, but developed as continuous septa which run obliquely forward. The monotype, *Cumberlandia monodonta* (Say), is confined to the Tennessee, Cumberland and Ohio River systems in the United States.

Family 2. AMBLEMIDAE Rafinesque, 1820

Type genus: *Amblema* Refinesque, 1820 [type species: *Amblema costata* Rafinesque, 1820 = *A. plicata* (Say, 1817)]. All 4 demibranchs marsupial (= tetragenae); glochidia hookless[6]; interlamellar connections usually developed as continuous septa (interrupted in *Gonidea*), parallel to the gill filaments; undivided water-tubes present, either continuous or interrupted (*Gonidea*), but always parallel to the gill filaments; posterior margins of mantle not united but drawn together by the diaphragm, thus separating the branchial and anal siphons; anal siphon closed above, leaving a separate supra-anal opening; diaphragm complete, formed entirely by the ctenidia; principally tachytictic (except in the Megalonaiadinae). Present distribution in the Nearctic Region[7]: principally in the United States, a few species ranging into southern Canada.

Subfamily Gonideinae Ortmann, 1916

Type genus: *Gonidea* Conrad, 1853, for *Anodonta angulata* Lea, 1838. Septa incomplete, interrupted and perforated by subcircular holes so that the water-tubes communicate with each other[8]; tachytictic. The monotype, *Gonidea angulata* (Lea), is presently found in western North America from southern British Columbia into southern California.

Subfamily Ambleminae s.s.

[=Quadrulinae (von Ihering, 1901) Hannibal, 1912]

Type: same as for the family. Septa and water-tubes well-developed and continuous, not perforated; tachytictic. Recent genera in the Nearctic Region are:

Amblema Rafinesque, 1820
Elliptoideus Frierson, 1927
Fusconaia Simpson, 1900a
Plectomerus Conrad, 1853
Quadrula Rafinesque, 1820[9]
Quincuncina Ortmann, 1922
Tritogonia Agassiz, 1852

Subfamily **Megalonaiadinae,** new subfamily

Type genus: *Megalonaias* Utterback, 1915, for *Unio crassus* var. *giganteus* Barnes, 1823. Septa and water-tubes well-developed and continuous; bradytictic. *Megalonaias* Utterback currently ranges from north-central United States into Central America.

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Family 3. HYRIIDAE (Swainson, 1840) Parodiz & Bonetto, 1963

Type genus: *Prisodon* Schumacher, 1817, for *Prisodon obliquus* Schumacher, 1817. Only the 2 inner demibranchs marsupial; glochidia with hooks; marsupial demibranchs with septa-like, interrupted interlamellar connections forming incomplete (discontinuous) water-tubes which run parallel to the gill filaments; distinct branchial and anal openings present, but lacking a separate supra-anal opening; diaphragm complete: anterior part formed by the ctenidia (perforated), posterior part formed by union of the posterior mantle margins; duration of larval incubation little known[10]. Recent species are confined to South America and Australasia, although *Diplodon* is known from the Triassic of Texas and Pennsylvania in the United States (Parodiz & Bonetto, 1963).

Family 4. UNIONIDAE Rafinesque, 1820 [11]

Type genus: *Unio* Philipsson, 1788 [12] (type species: *Mya pictorum* Linnaeus, 1758). Only the 2 outer demibranchs marsupial; glochidia hooked or hookless[13]; interlamellar connections developed as continuous septa; water-tubes usually uninterrupted [14] (but divided in the Anodontinae s.l.); septa and water-tubes parallel to gill filaments except in *Strophitus* (Anodontinae); posterior margins of mantle not united but drawn together by the diaphragm, thus separating the branchial and anal siphons; anal siphon closed above, leaving a separate supra-anal opening[15]; diaphragm complete, formed entirely by the ctenidia: tachytictic or bradytictic. Recent species occur in the Nearctic, Neotropical, Palearctic, Ethiopian, Oriental and Australasian Regions.

Subfamily Unioninae s.s.[16]

Type: same as for the family. Marsupial demibranchs: homogenae (entire outer demibranchs forming smooth pads externally); glochidia usually with hooks[17]; septa and water-tubes (parallel to the gill filaments) undivided, lacking secondary septa and secondary water-tubes; tachytictic. Ortmann (1912a, p 273) suggests that *Unio* of Europe is not equivalent to the similar forms (i.e., Pleurobeminae) of North America, principally because of the presence of hooked glochidia and differences in beak sculpture. Present distribution: Palearctic, Ethiopian, Oriental, and Australasian Regions; absent from the Nearctic and Neotropical Regions.

Subfamily Pleurobeminae (Hannibal, 1912) Modell, 1942

Type genus: *Pleurobema* Rafinesque, 1820 (type species: *Pleurobema mytiloides* Rafinesque, 1820 = *Unio clava* Lamarck, 1819). Marsupial demibranchs: homogenae; glochidia lacking hooks; septa and water-tubes (parallel to gill filaments) undivided, lacking secondary septa and secondary water-tubes; tachytictic. Recent genera are known from southern Canada and the United States (listed below), and the northern Neotropical Region (Central America[18]).

Cyclonaias Pilsbry, 1922
Elliptio Rafinesque, 1820
Hemistena Rafinesque, 1820
Lexingtonia Ortmann, 1914
Plethobasus Simpson, 1900a
Pleurobema Rafinesque, 1820
Uniomerus Conrad, 1853

Subfamily **Popenaiadinae**, new subfamily [19]

Type genus: *Popenaias* Frierson, 1927 (type species: *Unio popei* Lea, 1843).

Marsupial demibranchs: homogenae; glochidia lacking hooks; septa and water-tubes (parallel to gill filaments) undivided, lacking secondary septa and secondary water-tubes; bradytictic. Presently known only from peninsular Florida (*P. buckleyi* (Lea)) and Texas (*P. popei* (Lea)) in the United States; Mexico and Central America.

Popenaias Frierson, 1927
Cyrtonaias Crosse & Fischer, 1893, in Central America

Subfamily Anodontinae (Rafinesque, 1820) Ortmann, 1910a

Type genus : *Anodonta* Lamarck, 1799, for *Mytilus cygneus* Linnaeus, 1758. Marsupial demibranchs: homogenae, or diagenae (in *Strophitus* only: marsupia filling the entire outer 2 demibranchs, with ovisacs subdivided into compartments which are transverse to the demibranchs); glochidia hooked; septa divided from front to rear by secondary septa, producing secondary water-tubes which are parallel to the demibranchs (except in *Strophitus*); bradytictic.[20] Principally North American forms, but also occurring in Central America, Eurasia and the Oriental Region.

Alasmidonta Say, 1818
Anodonta Lamarck, 1799 [21]
Anodontoides Simpson, 1898
Arcidens Simpson, 1900a
Arkansia Ortmann & Walker, 1912
Lasmigona Rafinesque, 1831
Simpsoniconcha Frierson, 1914
Strophitus Rafinesque, 1820

Subfamily Lampsilinae [22] (von Ihering, 1901) Ortmann, 1910a

Type genus: *Lampsilis* Rafinesque, 1820 (type species: *Unio ovatus* Say, 1817). Marsupia represented by ovisacs confined to varying restricted regions of the outer 2 demibranchs: (*a*) longenae=ventral part of entire demibranchs, (*b*) heterogenae=posterior part, (*c*) mesogenae=central part, (*d*) eschatigenae=lower part of posterior region, demibranchs not folded, and (*e*) ptychogenae=lower part of demibranchs which are composed of vertical folds; ovisacs marked externally by sulci, marsupia not forming smooth pads as in tetragenae, homogenae and diagenae; glochidia hookless, or axe-head shaped (*Proptera*); septa and water-tubes undivided, both running parallel to the gill filaments; bradytictic, except *Obliquaria* which is tachytictic; widespread sexual dimorphism in the shell [23] and in the development (in females) of flaps, papillae or caruncles in the mantle below the branchial opening. Recent genera, confined to North and Central America, are:

heterogenae:

Actinonaias Crosse & Fischer, 1893
Carunculina Simpson, 1898
Dysnomia Agassiz, 1852
Ellipsaria Rafinesque, 1820 [24]
Glebula Conrad, 1853
Lampsilis Rafinesque, 1820
Lemiox Rafinesque, 1831 [25]
Leptodea Rafinesque, 1820
Ligumia Swainson, 1840
Medionidus Simpson, 1900b
Obovaria Rafinesque, 1819
Pachynaias Crosse & Fischer, 1893
Proptera Rafinesque, 1819
Truncilla Rafinesque, 1819
Villosa Frierson, 1927

mesogenae:

Cyprogenia Agassiz, 1852
Obliquaria Rafinesque, 1820

eschatigenae:

Dromus Simpson, 1900a [26]

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DISCUSSION

Hannibal (1912), Ortmann (1912a) and Walker (1917) have concluded that the primitive condition of the freshwater mussels is the tetragenous marsupial condition in which all 4 demibranchs incubate the developing glochidial larvae for a short (i.e., tachytictic) duration. Of the 2 groups which exhibit this feature, the Amblemidae is more advanced than the Margaritiferidae because of the typical presence in the former of (*a*) continuous interlamellar septa and water-tubes, (*b*) distinct branchial, anal and supra-anal openings (=" siphons "), and (*c*) a complete diaphragm. While Hannibal and Ortmann derive the Mutelidae and Unionidae (both *sensu lato*) from the Margaritiferidae, Modell (1964) has proposed that the Mutelidae (i.e., his opinion of the superfamily Mutelacea) gave rise independently to the composite Unionidae and to the Margaritiferidae, from which the composite Elliptionidae evolved.

It seems more probable that the tetragenous condition of the Margaritiferidae gave rise to the tetragenous condition of the Amblemidae, and through the loss of the marsupial function of the outer demibranchs also gave rise to the unionacean Hyriidae and to the Mutelacea (Fig. 1). The nature of such a divergence is obscure, particularly concerning the larvae (glochidia in the Unionacea, lasidial forms in Mutelacea). Indeed, our conjecture is in contrast to the view of Parodiz & Bonetto (1963, p 185) that " The two different types of larvae, i.e., glochidium and lasidium, cannot be considered to be derived from any hypothetical direct ancestry."

Through loss of the marsupial function of the inner demibranchs, the tachytictic Amblemidae could account for the origin of the tachytictic Unionidae which could have independently given rise to the subfamilies Unioninae s.s., Anodontinae and Pleurobeminae by adaptations in the larvae (some developing hooks), a tendency toward a bradytictic habit, and morphological changes in the marsupial demibranchs (Anodontinae). The Lampsilinae is considered here to have evolved from the Pleurobeminae through a change in the duration of incubation and in the morphological specialization of the marsupial demibranchs (Fig. 2). Our suggested relationships within the Lampsilinae are outlined in Fig. 3.

Gonidea angulata (Lea) has usually been associated with the family Unionidae *sensu lato*: in the Unioninae s.l., by Ortmann (1916), Frierson (1927), Thiele (1935) and Haas (1969a, 1969b); in the Anodontinae s.l. by Hannibal (1912). Modell (1964), however, saw fit to place it in the margaritiferid subfamily Pseudodontinae Frierson, 1927, which in turn Thiele (1935) considered part of the Unionidae (Unioninae *sensu lato*). Ortmann (1916) investigated the anatomy of this monotypic genus and found some features suggesting the Margaritiferidae (interlamellar septa and water-tubes present, but not continuous) and some recalling the Amblemidae (complete diaphragm; supra-anal opening present), while other aspects were common to both groups (tetragenous gill condition; data suggesting a tachytictic habit). We consider Ortmann's subfamily Gonideinae a valid taxon and place it in the Amblemidae below the more advanced Ambleminae (see Fig. 1).

A number of other peculiarities and exceptions have been previously mentioned (e.g., the bradytictic *Megalonaias* and *Popenaias*, the allegedly ultra-tachytictic *Anodonta imbecilis*, and the tachy-

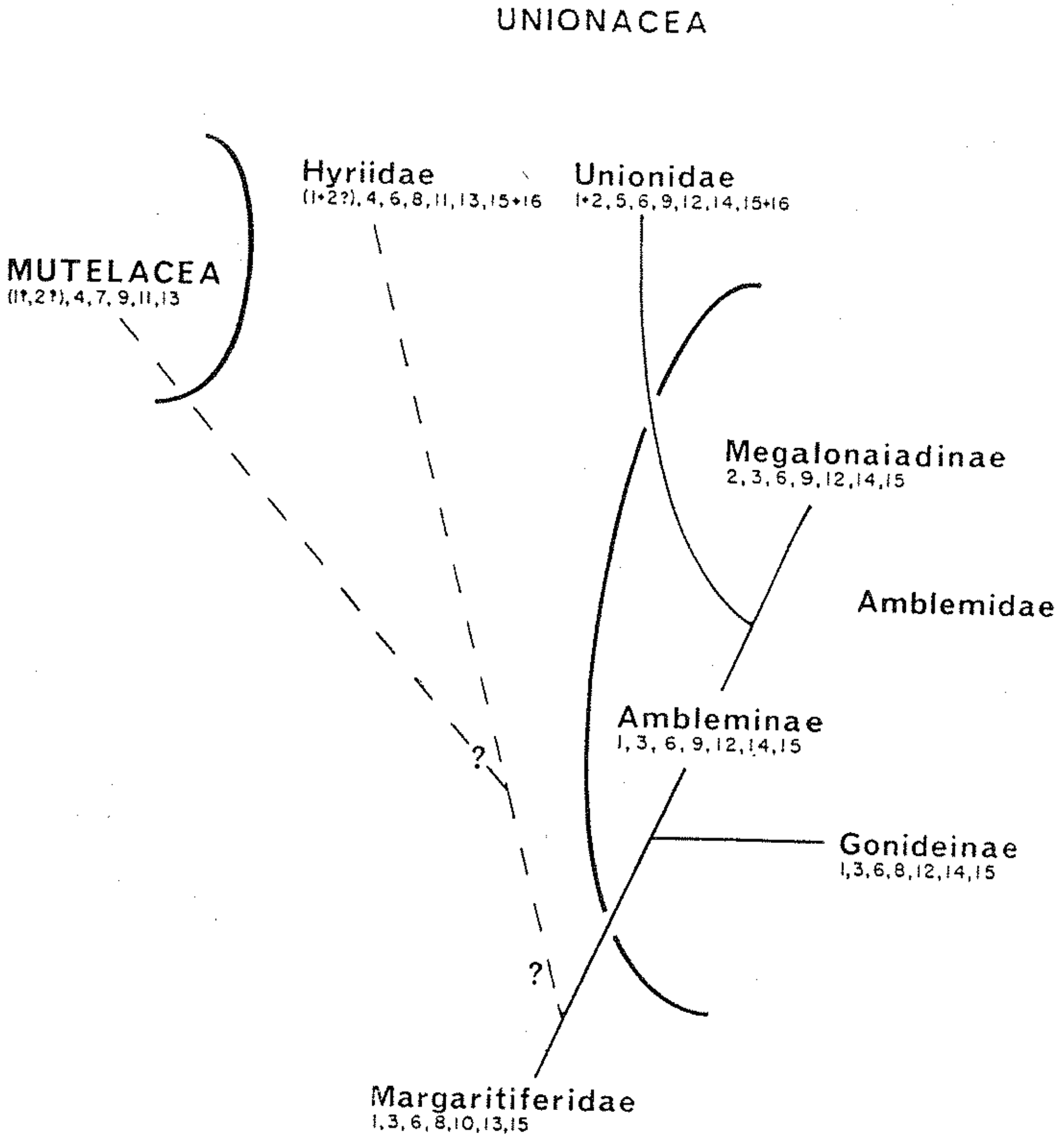

FIG. 1. Proposed affinities of the families of the Unionacea, and the suggested relationship of the Mutelacea to the Unionacea. 1, tachytictic (short-term incubation); 2, bradytictic (long-term incubation); 3, tetragenae (all 4 demibranchs marsupial); 4, only the inner 2 demibranchs marsupial; 5, only the outer 2 demibranchs marsupial; 6, possessing glochidial larvae; 7, possessing lasidial or lasidial-like larvae; 8, interlamellar septa and water-tubes interrupted; 9, interlamellar septa and water-tubes continuous; 10, diaphragm incomplete; 11, diaphragm complete, composed of gill and mantle tissues; 12, diaphragm complete, formed by gills only; 13, supra-anal opening absent; 14, supra-anal opening present; 15, glochidia hookless; 16, glochidia with hooks.

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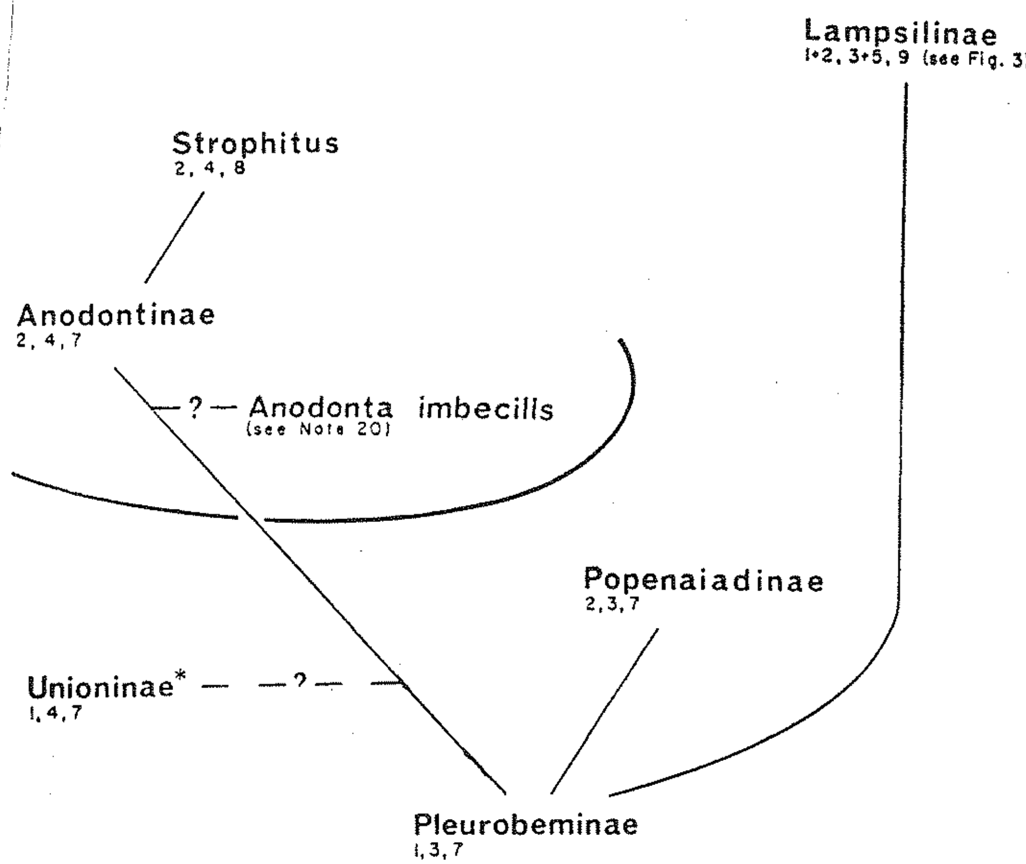

FIG. 2. Proposed affinities of the subfamilies of the Unionidae. *For the Unioninae Ortmann (1912a, p 273), however, suggests that (*a*) *Unio* and the Pleurobeminae arose independently from a tetragenous marsupial condition, and (*b*) the subtriangular hooked glochidium "somewhere near *Unio* was the starting point for the development of the subfamily Anodontinae." 1, tachytictic; 2, bradytictic; 3, glochidia hookless, semielliptical; 4, glochidia hooked, subtriangular; 5, glochidia hookless, axe-head shaped; 6, tetragenae; 7, homogenae; 8, diagenae; 9, marsupial demibranchs other than tetragenae, homogenae or diagenae.

tictic *Obliquaria*). Our interpretation of their phylogenetic affinities is shown in Figs. 2 and 3.

The taxonomy and relationships of most freshwater mussels is still poorly known. Of the 54 genera of the Unio-

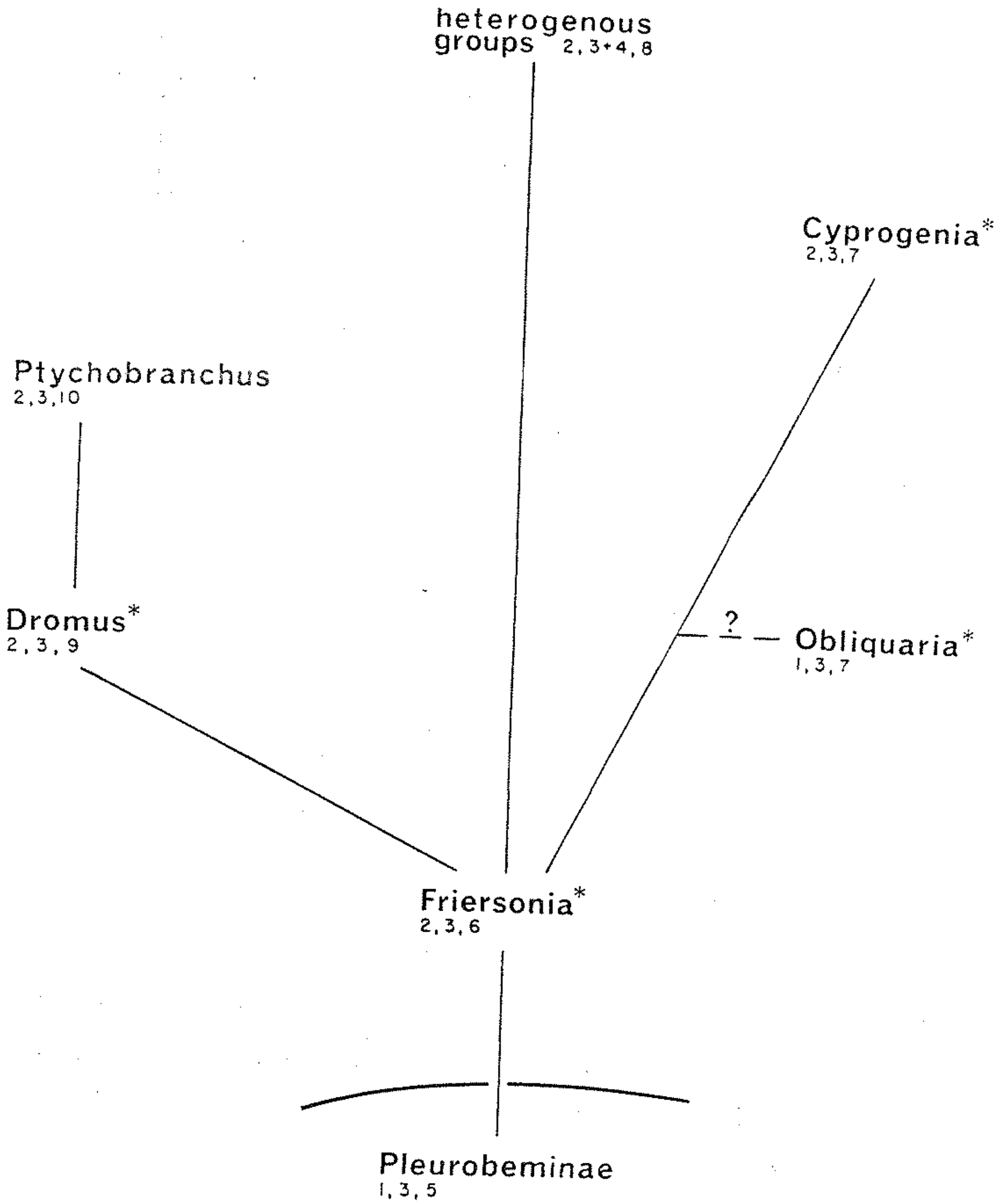

FIG. 3. Possible relationships in the unionid subfamily Lampsilinae. **Cyprogenia*, *Dromus*, *Friersonia* and *Obliquaria* are monotypic genera. 1, tachytictic; 2, bradytictic; 3, glochidia semielliptical; 4, glochidia axe-head shaped (in *Proptera*); 5, homogenae; 6, longenae; 7, mesogenae; 8, heterogenae; 9, eschatigenae; 10, ptychogenae.

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ninae *sensu lato* discussed by Thiele (1935), 24 are listed as "Tier unbekannt;" and of the morphological accounts available, many are superficial. Thiele was able to provide only inconsistent information from the previous literature in his review of the Unioninae. Such information, because it is incomplete, is confusing and at present it is impossible to relate it adequately to our classification.

In our system of the Nearctic freshwater mussels we have attempted to employ with consistency what we feel are the most pertinent features which characterize the various groups. The superfamilies are distinguished principally according to the larval type produced. The families of the Unionacea are separated primarily on the basis of (*a*) the number and location of the marsupial demibranchs, and (*b*) the morphology of these demibranchs. The subfamilies have been characterized largely by the (*a*) morphology of the marsupial demibranchs (i.e., the anatomical conditions of the ovisacs), (*b*) hooked/hookless nature of the glochidia,[5] and (*c*) duration of larval incubation.

Although further studies of soft-part morphology are desirable, continued investigation of the shell features (e.g., beak and disc sculpturing, hinge dentition) and their critical evaluation in the definition of genera, subgenera and species (and their geographic and temporal distribution) is also needed. Chromosome and electrophoretic studies on the Nearctic unionaceans are currently underway in several laboratories, and it is hoped that these approaches will also provide greater insight into a natural classification of these freshwater mussels and allow a better understanding of their evolutionary relationships.

NOTES

[1] The superfamily Mutelacea Parodiz & Bonetto (1963) is characterized principally by the production of lasidial (Mycetopodidae Gray, 1840) or lasidial-like (Mutelidae Gray, 1847) larvae which (like the unionacean Hyriidae) are incubated in the inner two demibranchs.

[2] In the Unionidae s.s., *Anodonta imbecilis* Say and *Strophitus undulatus* (Say) (both Anodontinae s.l.) have been reported to undergo direct development in the marsupia without a parasitic stage (Howard, 1914, and Lefevre & Curtis, 1911, respectively). However, Tucker (1927, 1928) has shown that the glochidia of *A. imbecilis* are facultatively parasitic, utilizing the fish *Lepomis cyanellus* Rafinesque as the host. *Simpsoniconcha ambigua* (Say), also in the Anodontinae s.l., utilizes a salamander [*Necturus maculosus* (Rafinesque)] as the glochidial host. In the hyriid genus *Diplodon* Spix, the subgenus *Diplodon* s.s. possesses parasitic glochidia while the larvae of the subgenus *Rhipidonta* Mörch undergo direct development (Parodiz & Bonetto, 1963).

[3] Official List Name No. 202 (see Flemming, 1958a); =Margaritanidae Ortmann, 1911a.

[4] Official List Name No. 1236 (see Flemming, 1958b); =*Margaritana* Schumacher, 1817 (Official Index Name No. 1082; see Flemming, 1958c).

[5] Margaritiferinae Modell, 1942 = Margaritaninae Ortmann, 1910a (Official Index Name No. 233; see Flemming, 1958d).

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[5] The number of species of *Unio* Philipsson with glochidia possessing/lacking hooks is presently unknown. If the number of species with hooked glochidia is small in relation to the number lacking hooks, the provisional distinction of the subfamilies Unioninae s.s. and Pleurobeminae would seem artificial. If further investigations demonstrate this possibility, the Pleurobeminae might best be considered synonymous with the Unioninae s.s.

[6] Thiele (1935) cites *Rectidens* Simpson (southeast Oriental Region) as having tuberculated glochidia.

[7] According to Bloomer (1931a, 1931b, 1932, 1933, 1946, 1949), Haas (1924, 1954), von Martens (1900), Morrison (1967), Ortmann (1910b, 1911b, 1917), Prashad (1918, 1919a, 1919b) and Thiele (1935), additional tetragenous species occur in Central America and in the southern Palearctic, Ethiopian and/or Oriental Regions: *Balwantia* Prashad, *Brazzaea* Bourguignat, *Caelatura* Conrad, *Contradens* Haas, *Ensidens* Frierson, *Indonaia* Prashad, ? *Lamellidens* Simpson, *Lamprotula* Simpson, *Nitia* Pallary, *Parreysia* Conrad, *Potomida* Swainson, *Pseudodon* Gould, *Psilunio* Stefanescu, *Rhombunio* Germain, *Rectidens* Simpson and *Trapezoideus* Simpson.

However, several discrepancies and/or unusual features may be noted: (1) Bloomer (1931a) reported that *Brazzaea anceyi* Bourguignat from Africa is tetragenous, has a distinct supra-anal opening, and has continuous but perforated septa (except in the inner demibranchs of males). He consequently suggested removing the genus *Brazzaea* from the Mutelidae (Haas, 1969a, nevertheless retained it there as a subgenus of *Aspatharia* Bourguignat; he later, 1969b, removed it to the Unioninae s.l. as a subgenus of *Caelatura* Conrad) and placing it in Ortmann's Unionidae/Unioninae. This taxon would appear to belong to our concept of the amblemid subfamily Gonideinae. (2) *Contradens cambojensis* (Sowerby) from Siam had previously been grouped in the Unionidae s.l. by Ortmann (1917). (3) *Lamellidens* Simpson was cited by Thiele (1935) as containing embryos either in all 4 or only the outer 2 demibranchs, although Prashad (1918, 1919a) and Bloomer (1931b) found that in *L. marginalis* (Lamarck) from India only the outer demibranchs were marsupial. Bloomer (1931b) also noted discontinuous, perforated septa in this species. *Lamellidens consobrinus* (Lea) from India was previously grouped in the Unionidae s.l. by Ortmann (1911b). (4) Thiele (1935) placed *Potomida* Swainson in the Margaritiferidae as a subgenus of "*Margaritana*," although Haas (1969a, 1969b) considers *Potomida* to be a member of the Quadrulinae of the Unionidae s.l. (5) *Pseudodon salwenianus* (Gould) was reported by Prashad (1919a) to be tetragenous, to lack a separate supra-anal opening, and to possess a complete diaphragm formed by the ctenidia only. These features suggest that this species is an amblemid which has secondarily lost the supra-anal opening. (6) "*Psilunio*" *sinuata* (Lamarck), which Haas (1940) listed in the unionid Quadrulinae, was previously demonstrated by Ortmann (1912b) to be a margaritiferid. Haas (1969a, 1969b) eventually concurred and placed this species (as *Pseudunio sinuata*) in a subgenus of *Margaritifera*.

Although no living species of the Amblemidae (?) possessing radial beak sculpture are currently found in North America, a variety of presumably related fossil forms (*Proparreysia* Pilsbry, 1921) have been reported from Cretaceous deposits in Wyoming, Montana, Colorado and New Mexico in the United States. Henderson (1935) placed this group in the subfamily Parreysiinae of the Unionidae s.l.

[8] Perforated marsupial septa are also known in *Brazzaea anceyi* Bourguignat (Bloomer, 1931a), *Caelatura aegyptiaca* (Cailliaud) (Bloomer, 1932, 1949) and *Parreysia acuminata* (H. Adams), *P. bakeri* (H. Adams), *P. ruellani* (Bourguignat) and *P. stuhlmanni* (von Martens) (see Bloomer, 1932), all in the Amblemidae; in *Contradens cambojensis* (Sowerby) and *Hyriopsis* Conrad (see Ortmann, 1917) and *Lamellidens thwaitesii* (Lea) (Bloomer, 1931b), all in the unionid Pleurobeminae (?); and even in *Grandidieria burtoni*

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(Woodward) in the Mutelidae (Bloomer, 1933).

[9] Frierson (1927) listed a number of seemingly meaningless subgeneric names for *Quadrula* Rafinesque and described additional new ones. Morrison (1966) elevated several of these taxa to generic rank.

[10] The 4 Australasian subfamilies of the alleged Mutelidae listed by McMichael & Hiscock (1958) were relocated on anatomical grounds in the family Hyriidae by Parodiz & Bonetto (1963). These groups should be re-examined, and perhaps re-defined, however, particularly in terms of (*a*) the characteristic portion(s) of the inner demibranchs which are marsupial, and (*b*) the gravid periods. It is of special interest that among members of *Hyridella* Swainson (Hyridellinae Iredale) " Breeding apparently seasonal, from spring through summer " (McMichael & Hiscock, 1958, p 439). This time would correspond to the Nearctic fall and winter. Dr. Juan J. Parodiz (of the Carnegie Museum, Pittsburgh, Pennsylvania, U.S.A.) has kindly provided us with unpublished data from his observations on South American hyriids (pers. comm., 1969): " *Diplodon charruanus* (d'Orb.) begins [*incubation*] in summer (Dec., Jan.): maturation in fall (May) to early spring (Sept.). *D. rhuacoicus* (d'Orb.), the same as in *charruanus*. *D. burroughianus* (Lea), spring and summer (Sept. to Feb.), sometimes continues until next fall (May). *D. hylaeus* (d'Orb.), spring and summer (Oct. to Jan.), lasts all winter; maturation next spring. This species lives in rather warmer areas than the others mentioned. *D. delodontus* (Lam.), begins in summer, maturation in fall to next spring and cont.: probably all year around."

[11] Unionidae Fleming, 1828 = Official List Name No. 201 (see Flemming, 1958a). However, as Bowden and Heppell (1968, Note 48, p 250) pointed out, Rafinesque should receive authorship through previous usage.

[12] Official List Name No. 1235 (see Flemming, 1958b). *Unio* Philipsson, 1788 = " *Unio* Retzius, 1788 " (see Simpson, 1900a, p 679).

[13] Morrison (1955) erroneously listed hooked glochidia, as well as divided water-tubes, as a feature of the entire family Unionidae. *Acuticosta* Simpson from China was cited by Thiele (1935) as having tuberculated glochidia.

[14] In *Lamellidens consobrinus* (Lea) (Pleurobeminae) from India most marsupial septa are continuous, although some are incomplete (temporarily, becoming continuous during gravidity?) (Ortmann, 1911b).

[15] The supra-anal opening is secondarily lost in *Cyclonaias tuberculata* Rafinesque (Pleurobeminae) and in *Carunculina parva* (Barnes) (Lampsilinae). A similar condition occurs in *Mutela kamerunensis* (Walker) (Mutelidae) and in *Pseudodon salwenianus* (Gould) (Amblemidae).

[16] Ortmann's, 1910a, Unioninae s.l. encompasses the subfamilies Unioninae s.s. and Pleurobeminae of the Unionidae as well as the entire family Amblemidae as employed here.

[17] Ortmann (1918) reported the absence of hooks on the glochidia of *Unio caffer* Krauss from Africa. However, Ortmann's material may have been comparatively immature. McMichael & Hiscock (1958) have demonstrated that *Velesunio ambiguus* (Philippi) from Australia does indeed possess hooked glochidia (the hooks appear only late in larval development), although this species was considered earlier by Hiscock (1951) to have hookless larvae. A re-examination of *U. caffer* Krauss (the type of Simpson's, 1900a, Section *Cafferia* which Modell, 1964, considered to be a genus in the unionid subfamily Rectidentinae; Haas, 1969a and 1969b, placed it in the Unio-

ninae s.l.) in terminal stages of larval incubation is therefore desirable.

[18] The Central American "genera" *Cinicula* Swainson, *Psoronaias* Crosse & Fischer and *Sintoxia* Rafinesque, which Morrison (1967) listed in the Amblemidae, may belong to the Pleurobeminae.

[19] Ortmann (1912a) noted that "*Elliptio*" *popei* (Lea) from Mexico is gravid in December and January, and Frierson (1913) observed that "*Unio* (*Nephronaias*)" *ortmanni* Frierson from Guatemala is gravid in February. Ortmann (1921c) further reported that 3 other species from Guatemala (viz., "*Elliptio*"[6] *calamitarum* (Morelet), *E. yzabalensis* (Crosse & Fischer) and *E. ravistellus* (Morelet)) are gravid in January and/or February. Finally, Morrison (1967) has indicated that "*Elliptio*" *opacatus* (Crosse & Fischer) and an unidentified species of *Barynaias* Crosse & Fischer from Mexico are gravid in December, and he further suggested that "*Cyrtonaias* mussels may also have a short breeding season in the cool summer months."

Ortmann (1912a: 272) stated for *E. popei* that "Here we would have a so-called summer breeder which breeds in mid-winter. But we know now, that not the season of the year, but the shortness of the breeding season is important, and according to all analogies, *E. popei* should be a form with a short breeding season" (i.e., tachytictic). However, recent investigations have confirmed 1 species with the homogenae type of marsupial demibranchs to be bradytictic and circumstantial evidence suggests that other such species in Texas, Mexico and Central America undergo winter breeding.

In 1965 six bi-monthly collections of what is commonly known as *Elliptio buckleyi* (Lea) (=*Unio buckleyi* Lea, 1843), endemic to the Florida peninsula, were made by the senior author from the Myakka River at the Myakka River State Park 17 miles southeast of Sarasota, Sarasota Co., Florida. The January, March, May, September and November collections contained gravid females; gravid animals were lacking in the July collection (each collection contained more than 100 animals). Although Ortmann (1912a) implied that *E. popei* is tachytictic, it is probable that this species, as well as *E. ortmanni*, *E. calamitarum*, *E. opacatus*, *E. yzabalensis* and *E. ravistellus* (and conceivably others), does not exhibit latitudinal, seasonal variation from the more northern summer-breeding groups but is also bradytictic.

"*Elliptio*" *buckleyi*, *E. calamitarum*, *E. ortmanni*, *E. popei*, *E. ravistellus* and *E. yzabalensis* display the homogenae structure which is found in the species of the pleurobeme genera previously listed. The extended (=winter) breeding habit is the principal character which distinguishes this group from the related tachytictic species of the Pleurobeminae. The occurrence of bradyticy in this group warrants providing these species with a generic designation distinct from those given to their tachytictic allies. The only available name for any of these species is *Popenaias* Frierson, 1927 (p 38).[7] This taxon was originally proposed as a subgenus of *Elliptio* Rafinesque; the type is *P. popei* (Lea) by original designation (p 10). Future taxonomic re-evaluation may necessitate the inclusion of other

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[6] Ortmann considered all Central American naiades with the anatomy of *Elliptio* to belong to that genus.

[7] Haas (1969a, 1969b) considers *Popenaias* (homogenae, bradytictic) to be a subgenus of *Nephronaias* Crosse & Fischer, but the anatomy and breeding habits of the type of *Nephronaias* (*Unio plicatulus* Charpentier) are entirely unknown. Although Haas originally (1969a) placed *Elliptoideus* (tetragenae, tachytictic) as a subgenus of *Elliptio* (homogenae, tachytictic), he later (1969b) included it as a subgenus of *Nephronaias*. This example again demonstrates the misleading value of shell characters.

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species and/or genera in this bradytictic-homogenae group of unionids.

This group of bradytictic, subtropical and tropical, homogenae-unionids with undivided septa and water-tubes is more advanced than the related species of the Pleurobeminae and is here placed in a new subfamily, the Popenaiadinae, which is characterized by long-term gravidity.

[20] Allen (1924) has postulated a very short (3-week), repetitive reproductive habit in *Anodonta imbecilis* Say.

[21] *Anodonta* Lamarck has been divided into several subgenera, one of which (*Arnoldina* Hannibal, 1912) Modell (1964) placed as a genus in the subfamily Rectidentinae, family Unionidae. The type, *Rectidens* Simpson, 1900a, was placed in the Unioninae s.l. by Thiele (1935), who stated that all 4 demibranchs contain glochidia, and by Haas (1969a, 1969b).

[22] Hannibal (1912) raised the Lampsilinae to familial rank, including in it only some of the typical lampsiline genera.

[23] Sexual dimorphism in the shell is noted among the other subfamilies only in *Tritogonia verrucosa* (Rafinesque) of the Ambleminae (Amblemidae).

[24] *Ellipsaria* Rafinesque, 1820 =*Plagiolopsis* Thiele, 1935 =*Plagiola* Rafinesque, 1819 (see Baker, 1964a).

[25] *Lemiox* Rafinesque, 1831 =*Conradilla* Ortmann, 1921b, *fide* Thiele (1935).

[26] *Conchodromus* Haas, 1930 =*Dromus* Simpson, 1900a, *fide* Baker (1964b).

[27] Longenae is a new term (consistent with Simpson's, 1900a, terminology) to describe the nature of the comparatively primitive marsupial demibranchs of *Friersonia* Ortmann, 1912a.

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RÉSUMÉ

UNE REÉVALUATION DES UNIONACES (PELECYPODA) ACTUELS D'AMÉRIQUE DU NORD

W. H. Heard et R. H. Guckert

Les principales classifications récentes des bivalves d'eau douce, basées essentiellement sur le caractère de la coquille, ne reflètent pas les relations phylogénetiques de ces animaux, alors que ces relations peuvent être interprétées à partir de caractéristiques de reproduction. Bien que ces 2 types de caractères ne soient pas en toute logique mutuellement exclusifs, ils se recoupent relativement peu souvent. Les caractères de la coquille ont été exagérés dans la classification des moules d'eau douce dans l'ensemble du monde, d'une part parce qu'ils peuvent être employés dans les recherches sur matériel possible, d'autre part à cause de la facilité d'étude. Malheureusement il y a trop peu d'informations sur le fonctionnement et la morphologie de l'appareil reproducteur pour permettre d'établir, à l'échelle mondiale, une classification basée sur ces caractéristiques, et il serait difficile de mettre en évidence les relations des formes fossiles avec un tel système si jamais on le proposait. Le choix d'un système unique (c.a.d. soit la coquille, soit les parties molles) montre une évolution parallèle des caractères dans l'autre système. D'où l'on considère qu'un système basé sur les aspects de la reproduction, en parallèle avec les caractèristiques de la coquille, reflète les affinites naturelles et évolutives avec plus de précision que ne le ferait un système qui se limiterait à exagérer un autre caractère.

Dans le but de stimuler de nouvelles investigations (en particulier pour les groupes non-Néoarctiques) on présente ci-aprés un systéme revisé des affinités des moules d'eau douce d'Amérique du Nord, en le situant au niveau des familles et sous-familles et en le basant sur l'anatomie et les aspects de la reproduction. Ce système tient compte de caractéristiques telles que (*a*) le nombre de chambres marsupiales (4 ou 2), (*b*) la localisation des chambres marsupiales (seulement les 2 internes ou seulement les 2 externes), (*c*) les régions spécifiques de la chambre interbranchiale qui sert á l'incubation des larves (la chambre entiére, ou seulement la portion centrale etc. . .) (*d*) la morphologie des chambres marsupiales (septa et canaux simples ou subdivisés, septa et canaux continus ou interrompus), (*e*) la durée de l'incubation des larves, (*f*) la nature de la coquille du glochidium (avec ou sans crochet), et (*g*) les autres aspects anatomiques plus subtilement en relation avec la reproduction en matière de courant d'eau (forme et composition du diaphragme, présence/absence d'une ouverture supra-anale).

Ces caractères indiquent que les représentants actuels des Margaritiferidae, Amblemidae et Unionidae se rencontrent en Amérique du Nord. Une 4ème famille, les Hyriidae,

est connue de la région Néoarctique seulement sous forme fossile, les espèces vivantes actuelles sont actuellement confinées à l'Amérique du Sud et l'Australie. Les sous-familles Neoarctiques ont été caractérisées pour ces 3 familles et la liste des genres de chaque groupe a été établie. Trois nouvelles sous-fammilles sont proposées: **Cumberlandinae** (Margaritiferidae), **Megalonaiadinae** (Amblemidae) et **Popenaiadinae** (Unionidae). Des indications sur less roupes d'Unionacés ont été fournies pour les régions Néotropicales, Paléarctiques, Ethiopiennes, Orientales et Autralasiennes.

Un parenté des Mutelacea aux Unionacea a été suggérée et les affinités phylogénétiques des familles et sons-familles d'Unionacés Néoarctiques sont interprétées d'aprés des données de la reproduction. Les Margaritiferidae Holarctiques actuels, le plus primitif des groupes d'Unionacés, est considéré comme ayant donné naissance independamment d'une part au stock mutelacés-hyriidés, d'autre part aux Amblemidae. Les Amblemidae, présents dans toutes les aires sauf de Sud-Amérique et d'Australasie, sont à leur tour décrits comme ancêtres des Unionidae. Les Unionides ont atteint leur plus grande diversification en Amérique du Nord et comprennent la grande majorité des moules d'eau douce Néoarctiques. Les plus primitifs Pleurobeminae (actuellement confinés à l'Amérique du Nord et du Centre) ont, pense-t-on, donné naissance indépendamment (*a*) aux Popenaiadinae du Sud des U.S.A., du Mexique et de l'Amérique Centrale, (*b*) aux Anodontinae de l'hemisphere Nord et (*c*) aux Lampsilinae d'Amerique du Nord et du Centre. Les Unioninae S. S. d'Eurasie ont, semble-t-il, dérivé du stock des Anodontinae. Les Pleurobeminae sont considérés comme les ancêtres du stock primitif des Lampsilinae qui, en conséquence, se separent en plusieurs lignees selon la specialisation du marsupium.

Les tendances évolutives dons la progression et/ou la spécialisation des Unionacés Néoarctiques comprend (*a*) la réduction de 4 à 2 (surtout la paire externe) chambres marsupiales, avec la plus grande diversification apparaissant dans les groupes actuels de l'hémisphère Nord, (*b*) le développement de septa et canaux interlamellaires continus, (*c*) les adaptations morphologiques des marsupiums qui atteignent la plus grande spécialisation par restriction spaciale des ovisacs chez les Lampsilinae, (*d*) une tendance à avoir un diaphragme complet formé entièrement par les cténidies et (*e*) un passage général d'une incubation des larves du court terme au long terme. La plupart des Unionacés possèdent des larves glochidium sans pointes, et les larves à pointes sont considérées comme ayant évolué indépendamment d'une part chez les Hyriidae et d'autre part chez les Unioninae-Anodontinae.

A. L.

АБСТРАКТ

РЕВИЗИЯ СОВРЕМЕННЫХ UNIONACEA (PELECYPODA) СЕВЕРНОЙ АМЕРИКИ

В. ХЕРД и Р. ГУККЕРТ

Современные классификации пресноводных моллюсков на уровне высоких таксонов, основанные, главным образом, на характере строения раковины, не отражают филогенетических отношений этих моллюсков, которые могут быть освещены при учете характера их размножения. Хотя эти два типа особенностей моллюсков не исключают друг друга, но они перекрываются сравнительно мало. На характер раковины особенно обращается внимание в классификации наядид. Эти признаки широко известны, благодаря удобству их применения как на живых, так и на ископаемых раковинах. К сожалению, имеется слишком мало данных по морфологии размножения и по образу жизни личинок, чтобы можно было создать крупно-масштабную классификацию, основанную точно на этих признаках. Если бы такая схема и была предложена, возникают трудности установления родственных связей между современными и ископаемыми формами. При выборе какой-нибудь одной системы (т.е. по морфологии раковины или по морфологии мягких частей тела) выяснилось бы наличие параллельной эволюции признаков.

Авторы считают, что система, основанная на характере размножения, с параллельным учетом признаков строения раковины, точнее отражает естественную эволюцию и близость форм, чем любая другая система.

Чтобы стимулировать дальнейшие исследования (особенно среди не-неоарктических групп), в настоящей статье авторы представляют пересмотренную систему признаков северо-американских наядид на уровне семейств и подсемейств, учитывая анатомические признаки и родственные черты в характере размножения.

Эта система охватывает такие признаки, как: а) количество полужабр с марзупиями (4 или 2); б) расположение полужабр с марзупиями (только 2 внутренних или только 2 внешних); в) особые места, где инкубируются развивающиеся личинки (вся полужабра, или лишь задняя ее часть, или только центральная и т.д.); г) морфология марзупиальной полужабры (простая или разделенная септа и водяные трубки, непрерывная или прерывистая септа и водяные трубки); д) продолжительность инкубации личинок (кратко- или долговременная); е) природа раковины глохидия (с крючками или без них); ж) другие анатомические аспекты, более тонко связанные с характером размножения, например, токи воды (полнота и строение диафрагмы, наличие или отсутствие супра-анального отверстия).

Эти признаки указывают на то, что современные представители семейств Margaritiferidae, Amblemidae и Unionidae встречаются в Северной Америке. Четвертое семейство-Hyriidae, известно из неоарктического района лишь в ископаемом виде. Современные же приурочены к Южной Америке и к австрало-азиатскому району. Для этих трех современных семейств устанавливаются неоарктические подсемейства и указываются их признаки, а также даются списки северо-американских родов для каждой группы. Предлагаются три новых подсемейства: Cumberlandinae (Margaritiferidae), Megalonaiinae (Amblemidae) и Popenaiinae (Unionidae). Приводятся замечания о родственных группах унионид в неотропическом, палеарктическом, эфиопском, восточном и австрало-азиатском районах. Рассматриваются предполагаемые родственные связи между Mutelacea и Unionacea, а также филогенетическая близость семейств и подсемейств неоарктических унионид, которые интерпретируются исходя из особенностей их размножения. Margaritiferidae (самая примитивная группа из унионид), являющаяся в настоящее время холарктической, рассматривается как представляющая собой независимую ветвь от Hyriidae-Mutelacea к Amblemidae. Последние, распространенные во всех областях, кроме Южной Америки и ав-

страло-азиатского района, рассматриваются в свою очередь как предки унионид, которые достигли наибольшего разнообразия в Северной Америке и составляют большую часть неоарктических моллюсков.

Предполагается, что наиболее примитивные Pleurobeminae (в настоящее время приуроченные к Северной и Центральной Америке) восходят непосредственно к а) Popenaiinae из южных районов США, Мексики и Центральной Америки; б) к Anodontinae северного полушария и в) к Lampsilinae Северной и Центральной Америки.

Считается, что Unioninae s.str. Евразии произошли от Anodontinae. Pleurobeminae рассматриваются как предки примитивных лампсилин, которые постепенно разделились на несколько линий путем специализации марзупиальных полужабр. Эволюционные тенденции в развитии и/или в специализации неоарктических унионид включает: а) редукцию с четырех до двух (главным образом, на внешней паре) марзупиальных полужабр, при этом самое большое разнообразие встречается у современных форм в северном полушарии; б) развитие непрерывной интерламеллярной септы и водяных трубок; в) морфологическую адаптацию марзупиальных полужабр, достигающую наибольшей специализации путем усиления локализации яйцевых мешков у Lampsillinae; г) тенденцию к образованию полной диафрагмы, целиком за счет ктенидиев; д) общее изменение периода инкубации личинок с кратковременной на долговременную. Большинство унионид имеют глохидий без крючков, а крючконосые личинки рассматриваются как возникшие независимо у Hyriidae и у унионид-анодонтид.

Z.A.F.