NOTES ON THE UNIONIDÆ AND THEIR CLASSIFICATION.

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The Unionidæ are not only the most conspicuous invertebrates of our fresh waters, and wonderfully rich in species, but they are also very interesting morphologically and physiologically. The publication of Simpson's synopsis of the Naiades, made a new era in our knowledge of these animals. On the one hand, Simpson has undertaken the important and difficult task of revising the enormous number of described species by the careful examination and comparison of an immense mass of material. A large number of nominal species have been referred to those which were believed to be valid, when reduced to synonyms and varieties. On the other hand, he has shown that not only the shells, but principally the soft parts, must be considered in order to build up a proper classification and he has investigated and sifted the attempts of earlier writers in that direction.

Having studied for years such of our Unionidæ, or, more properly, Unioninæ, as were obtainable, their soft parts, propagation, and embryos, I have formed some ideas of my own regarding their classification, which proves to be somewhat at variance with that given by Simpson. At first it seemed preferable to wait, and study and compare further,[1] until now, almost two years later, I feel more satisfied than ever that these views have a real foundation and some scientific value.

The Glochidia.—It has been found long ago, especially by Isaac Lea, that there are considerable differences of shape in the shells of the embryonic young of Unionidæ, but, so far as known, no attempt has been made to apply this fact to classification. The phases and changes of early and embryonal life are more and more regarded as important in estimating the system-

[1] Many living specimens of different groups and species were kept under observation for shorter or longer periods.

atic position and phylogeny of all groups of animals, and must be taken into account in studying the Unionidæ. Since differences between embryos seem to be correlated with circumscribed groups of the adult animals, they must be regarded as a valuable factor in classification. The writer has examined embryos of many species at different stages of development, not only in regard to the shells but also to the soft parts showing decided and interesting differences between the several groups and species.[1] There are three main types of glochidia, so far as known:

1. Those of Anodonta, Alasmidonta, etc. — Their valves are large, rounded-triangular, with a long dorsal commissure, a strong thickening along the margins, and are pointed in the middle of the ventral side, each bearing a large, rough spine, or "hook" (spur) bent inward so as to prevent the closing of the shell, which remains wide open during the embryonal stage of life. This formation is of decided importance, morphologically and physiologically, for doubtless these strong spines facilitate the attachment of the young mussels, after being discharged from the branchiæ of the parent, to the fins, etc., of fish, and possibly to parts of other aquatic animals. It is to be regretted that so little is known in regard to the early postembryonal life of the young Naiades.

2. Those of Proptera, e. g., alata Say. — The dorsal commissure is short, the dorso-ventral diameter being the largest; the ventral margins are rather short, truncated or slightly curved; there is a smooth spine at the anterior and posterior ends (of the ventral margins) of each valve, bent slightly outward and by passing those of the opposite valves, allows the shell to close along the ventral side. The long anterior and posterior sides are truncate, nearly straight, and the shell is widely gaping at both ends, a feature which is permanent, to a degree, in the adult shell.

3. The glochidia of those species which were generally ranged under the old genus Unio, with the exception of Proptera, have a moderately long dorsal commissure, and are generally rounded

[1] It is intended to publish the results of these investigations when they are more advanced.

along the other margins, but otherwise of various shapes, the dorso-ventral diameter (properly altitude) showing considerable differences. There are no spines, the margins of the valves are simple, or nearly so, and the shell can be entirely closed. There are minor differences in the configuration of the shells and the soft parts.

The Hinge. — The species of the old genus Unio, with few exceptions, have perfect [1] hinges, and this seems to be a feature characteristic for the whole group, and is of systematic importance.

In the species ranged under Anodonta, Alasmidonta, etc., on the other hand, the hinges are generally more or less deficient, or wholly wanting. *Symphynota pressa* Lea (*Unio pressus*) is a real, or apparent, exception, it having rather perfect but feeble hinge teeth. Other features of the shell, the soft parts and the embryos, show relationships with Symphynota, such as *S. costata* Raf. Natura non facit saltus.

In this connection should be mentioned the genus Margaritana, some species and varieties of which have perfect and others imperfect hinges, in adult specimens.

The muscles, especially the large adductors, are generally of a different color and texture in the Alasmidonta-Anodonta group than in the "Uniones."

The Marsupia. — It is now generally known that there are two different types of embryo-bearing branchiæ, or parts of such. In Anodonta, Alasmidonta, etc., and in a part of the Uniones (in the older, wider sense) the ova and embryones are lodged only in the outer, or all four branchiæ, which, when not gravid, are of the ordinary formation and appearance. In another group of the Uniones, the marsupia are not only invariably in the outer branchiæ, but also permanently differentiated, so that they may be recognized even when not gravid. They are located in certain parts of the branchiæ, in most species, with approximately fixed numbers of ovisacs for each species, or extending over the outer branchiæ through their whole length, as in Ptycho-

[1] Only as regards the hinges of the Naiades and not in a general sense; the hinge-type of the Cycladidæ, for example, is more perfect, and more constantly so.

branchus; but in the latter genus also they are permanently differentiated in the female.

This fact has possibly not been given due weight, and Simpson has been severely criticised for giving systematic values to physiological features. This character, however, is distinctly an anatomical one, and must be regarded as a factor in classification.

It is well known that in some of the Quadrula all four branchiæ bear ova, or embryos, but it has not been proven that this is so in all, especially in younger specimens, such as *Q. pustulosa* Lea, etc. Neither is it known whether in some species of Unio and Pleurobema the same condition may not be found occasionally. Moreover, Simpson himself says that in *Anodontoides ferussaciana* all branchiæ have been found bearing ova, and Gysser makes the same statement in regard to *Margaritana margaritifera*. This clearly shows that a distinction between two groups cannot be founded on this feature, the more so, since such closely allied forms as Unio, Pleurobema, and Quadrula are separated.

Differences of Male and Female Shells. — For some groups, these differences have long been known, most of the genera Lampsilis and Truncilla being familiar examples. The distension of the female shell near the posterior-inferior end — as a rule — is obviously the result of the demand for space for the voluminous gravid marsupia near the posterior ends of the outer branchiæ. These differences are of various kinds and of very various degrees, as especially among the Truncillæ, not only between different groups but also between species of the same groups, and even between different local forms of one and the same species, *e. g.*, *Lampsilis luteolus* Lam. There are even species where we can speak not only of a *distension* in the female, but of a *different formation* of the entire shell, as in *Plagiola securis* Lea. In other forms the differences may be very slight, as in *Obov. ellipsis* Lea, although its marsupia are of the same type with those of *Lampsilis ventricosus* Barnes. The members of the genus Ptychobranchus though having voluminous, and highly differentiated marsupia, show no outward differences of the shell, and some females may be even less inflated than males of the same size, as has often been observed by the writer. However, there is a

difference of another kind: a deep, oblique sulcus on the inside of each valve, in the female, the space occupied by the marsupium, so that the sexes can readily be distinguished on the empty shells at least in older specimens.

It may be repeated here that in younger examples of Lampsilis, etc., the female shells cannot be distinguished from the males during the first two or three years of life, and the distension is formed only from that age on, with the development of the marsupia.

The female shell of *Tritogonia tuberculata* Barnes, is less inflated posteriorly than the male, and has a flat, thin extension at the posterior end. Here the difference is of another kind than in Lampsilis, a small portion of the branchia, if any, finding room in the extended part of the shell, the genus evidently ranging under another group: with Unio (s. str.), Quadrula, etc., without differentiated marsupia.[1]

In some species of Unio, Quadrula, etc. there are slight, more or less marked differences between the male and female shells, the latter being, generally, more inflated, and sometimes differing in outline so that the sexes can be recognized with some reliability. Yet these differences are not so typical and so constant as in Lampsilis, Tritogonia, etc.

Species of another group, however, show well-marked differences, *e.g.*, *Alasmidonta truncata* H. B. Wright[2] and *A. calceola* Lea. The fact was well known to the older conchologists, and even the late Hy. Moores, three fourths blind, readily discerned the sexes by a touch. The females are more inflated and more voluminous posteriorly, curved down, and having generally a stronger ridge. It is much the same with *Strophitus edentulus*

[1] So far as known, this species has not yet been seen in the gravid condition. Its branchia, however, show no differentiated parts, and are barren during fall and winter, while the ovaries are charged with ova and the testes with sperm, as in Quadrula, etc., which Tritogonia closely resembles in its soft parts and shell. In dissecting a large female, I found a number of thin, grayish, beaded strands, of various lengths, scattered in the outer branchiæ, in all probability rows of abortive and degenerated ova. The strands were between the branchial fibrillæ and parallel with them.

[2] The name is the one given in Simpson's *Synopsis*. Since then it has been asserted by Fox that the Western form is the true *Al. marginata* of Say. (See *Nautilus*, vol. xv, pp. 16, 47.)

Say, and the sexes can generally be recognized by the shape of the shell; and the same may be said of *Symph. costata* Raf. (*rugosa* Barnes).

We have, then, among the Unioninæ with differentiated marsupia, species in which the female shells are decidedly different from the males, others in which they are slightly so, and still others where differences are not recognizable. Those without differentiated marsupia mostly show slight or no such differences, while in Tritogonia, though of another type, it is well marked; and again there are marked differences between male and female shells among the Alasmidonta, etc. It is evident from these facts that much weight cannot be placed on this feature for purpose of classification. If so, natural groups would have to be divided, and discrepant forms united.

The Inner Branchiæ. — The upper edges of the inner branchiæ are adherent to the abdominal sac either immediately, or by an interposed soft membrane of varying width. In some genera, or species, even in the same individual a part of the branchiæ may be of one, the balance of the other type. Simpson has paid considerable attention to this feature, and it seems that there are no constant differences available for classification.

Seasons of Propagation. — Since the publication of my observations several years ago, I have been able fully to confirm the facts then stated. The forms with differentiated marsupia, as Lampsilis, Ptychobranchus, etc., bear embryos during the fall and winter, and discharge their young in spring and early summer, rarely a part of them in autumn. The same was found to be true with the Alasmidonta, Symphynota, etc. On the other hand, the Unio (s. str.), Quadrula, Tritogonia, etc. were invariably found with the branchiæ barren during fall and winter, their ovaries filled with ova and the testes with sperm. This shows that Lampsilis, etc., bear their young during a long period, about eight or nine months. With Unio, etc., the charging of the branchiæ with ova, the development and discharging of the young is all effected within a few summer months. We may properly designate the latter as summer breeders, the former as winter breeders.

This is a purely physiological feature, and, moreover, is proved

only for the animals living in this latitude. But being coincident to a considerable degree with anatomical characters, it certainly is significant, and seems to have some bearing on the phylogenetic origin of these groups, as stated elsewhere. It appears to point to different climatic conditions under which the several groups developed and differentiated from their ancestors.

Reviewing the points discussed above, we find the principal natural divisions as follows:

1. The forms with perfect hinges, typically and generally Their embryonic shells are not pointed in the middle of the ventral margin, and able to close.

2. The forms more or less deficient in, or lacking, hinges, typically and generally. Their embryonic valves are subtriangular, pointed on the ventral side, and each bearing a large spine.

Each of these main groups seems to contain the forms nearest related. Any other arrangement would separate naturally allied forms and unite incongruous ones.

There may be one exception, however, as pointed out above, and that is the genus Proptera. In the members of the genus there are a number of features at variance with those of group 1, *i. e.*, the thin shells; the dorsal wings, anterior and posterior to the beaks; the gaping in front and behind, probably the umbonal sculpture; the slight, and in some species, even deficient hinges. Adding to these the very different form of the embryos, we have a collection of characteristics which place these molluscs not only in a generic rank of equal standing with that of Lampsilis plus its nearly related genera, but as a group by itself. In my opinion they rather represent a third main division between those of Lampsilis-Unio and Alasmidonta-Anodonta. On the other hand they have one characteristic in common with Lampsilis, etc., *i. e.*, the differentiated marsupium, consisting of distinct ovisacs. Whether this feature should be regarded as paramount in contrast with all the others mentioned, may be questioned. For the present, however, I prefer to range them alongside of those which have been regarded as their relatives.

Judging from certain features, there is some similarity between Proptera and Pseudospatha Simpson, in regard to the shells, and

it will be interesting to compare their soft parts and embryos, when obtainable.

If designations are wanted for the main divisions, they might be called: (1.) Holodontes, (2.) Haplodontes.

The former again contains two main subdivisions, — one in which the marsupia are differentiated, the other in which they are not so. Among the first, Ptychobranchus represents a group by itself, equivalent to the balance, owing to the exceptional formation of its branchiæ and ovisacs, and features of the shell. A group represented by *C. fronata* Lea, *reflexa* Raf. and *dromus* Lea seems a natural one, although there are differences in the number and size of the ovisacs, which might be regarded as sufficient for generic distinction. And so it is with the balance, of which Lampsilis is the typical genus. The differences between male and female shells in the several groups of Truncilla are more considerable than between some of the Truncilla and Lampsilis s. str., and so it is in regard to some other features.

Simpson ranges under the Lampsilis group also Cristaria Schum. and Pilsbryoconcha Simpson, the hinge teeth of which are defective or almost wanting, and the soft parts unknown, as are also the embryos. With a knowledge of the latter, their position will be more fully ascertained. In regard to Pseudospatha we refer to what has been said above.

In the second subdivision of the Uniones, Tritogonia is distinguished by its shell. Unio, Pleurobema and Quadrula, constituting a very large and conspicuous part of our fresh-water bivalves, and comprising various plastic and variable forms, are so closely related and almost inseparably connected, that even the highest authority is in doubt under which of these genera certain species should be ranged. In regard to the branchiæ, we refer to what has been said on p. 108.

It may be in place here to mention that these mussels quite generally are not able to open their shells as wide as the Lampsilis, etc., do. And this seems to be in close connection with the fact that their posterior mantle openings, especially the branchial, are much less fringed than those of Lampsilis, the fringes having the function of rakers, preventing the entrance of coarse materials with the inward current of water, as has been seen by

actual observation, *e. g.*, on *L. ventricosus*. Whenever any larger object touches the margin of the mantle, that is the long and partly branched fringes, they at once move inward and by interlacing form a fine network. Some other species also, *e. g.*, *C. irrorata*, with the valves not opening wide, have the papillæ only moderately developed.

The systematic position of Margaritana is still uncertain. In shape and appearance of the shell, and nacre, they resemble more Unio, than Alasmidonta. The hinge is perfect in some and defective in other species, in what seem to be individuals, typically perfect, and in younger specimens. It has been mentioned that Gysser occasionally found all four branchiæ charged with ova, and in all probability they are summer breeders, like Unio, etc. That, however, must be ascertained by actual observation. The crucial test will be found in the examination of the embryos.[1] — I have also seen in some specimens of *Quadrula kirtlandiana* Lea, very numerous, crowded, small muscle scars scattered over the inner surfaces of the valves inside the pallial line, described as characteristic for Margaritana.

The second main division consists of Alasmidonta, Anodonta and their allies, and these two genera seem to represent the two main groups. Among the former, *Strophitus edentulus* Say, shows a somewhat exceptional feature, which may entitle it to generic rank. As regards the shell, soft parts and formation of embryos, it stands very near to Alasmidonta, but the ova and embryos are imbedded, in various numbers, about from ten to twenty, in cylindrical albuminous masses placed transversally in the outer gills. In my opinion, these masses, which have also been compared with and called placentæ, are not homologous and equivalent with the ovisacs of Lampsilis, etc. The question deserves more study and comparison.

Some other species and genera, *e. g.*, *Lastena lata* Raf. need more examination, in order to ascertain some of their characteristics and their exact systematic positions.

The following table, based upon what is written above, will

[1] I should be glad to receive not only whole specimens, but gravid gills, or parts of such, in alcohol, or even dried, of *Marg. margaritifera* Linn. and *M. mondonta* Say. f.

show more plainly a systematic arrangement which appears natural and logical. It is not carried out to all the genera as established and recognized by Simpson, but only to groups showing characteristic, distinctive features. Again it may be pointed out that Proptera, possibly with an additional genus, might be regarded as representing a third (*i. e.*, the second) main division.

I. Hinge typically perfect; embryonic shell with the ventral margin rounded or truncate, able to close.

A. Marsupia permanently differentiated in the outer branchiæ (winter breeders).

1. Shell without dorsal wings, not gaping at the anterior and posterior ends; embryonic shell without spines, with rounded ventral margin, closing all around.

a. Marsupia occupying part of the branchiæ.

aa. Marsupia near the posterior end of the branchiæ, bean- or kidney-shaped; female shell usually distended near the posterior-inferior end; typical genus: . . . . . Lampsilis

bb. Marsupia occupying almost the whole margin of the branchiæ, or a part near the middle; shell short, heavy; female shell not markedly different from the male; typical genus: . . . . . Cyprogenia

b. Marsupia occupying the whole branchiæ forming folds when gravid; shell elongated, not externally different in males and females; . . . . . Ptychobranchus

2. Shell with anterior and posterior dorsal wings (at least in younger specimens), gaping in front and behind; hinge teeth feeble or defective; marsupium in posterior part of branchiæ; embryonic shells with spines at anterior and posterior ends of truncate ventral margin, widely gaping at the truncate anterior and posterior ends: . . . . . Proptera

B. Marsupia not differentiated, the outer, or both pairs of branchiæ serving as brood pouches (summer breeders).

1. Female shell with a flat extension at the posterior end; shell with crowded warts all over: . . . . . Tritogonia

2. Male and female shells slightly or not different; typical genus: Unio

II. Hinge typically more or less defective or wanting; no differentiated marsupia; embryonic valves rounded-triangular, pointed on the ventral side, each with a large spine.

A. Hinge more or less defective (rarely perfect, but feeble); beak

sculpture usually consisting of simple, concentric ridges; male and female shells more or less different.

1. Ova and embryos imbedded in cylindrical albuminous masses lying transversally in the outer branchiæ: . . Strophitus

2. Ova and embryos free in the branchiæ; typical genus: Alasmidonta

B. Hinge teeth wanting; beak sculpture of undulating or two-looped ridges, (animal, at least in some species, hermaphroditic); typical genus: . . . . . Anodonta