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MEMOIRS
OF THE
CARNEGIE MUSEUM.

VOL. IV. NO. 6.

W. J. HOLLAND, EDITOR.

MONOGRAPH OF THE NAJADES OF
PENNSYLVANIA.

SUPPLEMENT
AMERICAN ETHNOLOGY,
1911
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GENERAL INTRODUCTION.

PART I. ANATOMICAL INVESTIGATIONS.

PART II. THE SYSTEM OF THE NORTH AMERICAN NAJADES.

By A. E. ORTMANN, PH.D.

PITTSBURGH.

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CARNEGIE MUSEUM.

VOL. IV.

NO. 6.

A MONOGRAPH OF THE NAJADES OF PENNSYLVANIA.

BY ARNOLD E. ORTMANN, PH.D.

GENERAL INTRODUCTION.

The writer began to collect *Najades* in Pennsylvania as early as 1904. Additional material was incidentally secured in 1905 and 1906, while he was hunting for crawfishes. In 1907 the collecting of mussels was systematically begun, and the particularly favorable seasons of 1908 and 1910, and in part also of 1909, permitted the taking of large numbers of species and specimens. Not only the shells but also the soft parts were collected, and the writer endeavored to find both males and females, the latter in the sterile as well as in the gravid state. In this he generally was successful, and a great quantity of material representing the soft parts was preserved in alcohol, partly with the shell, partly without, but always with the proper records. In this way a collection of the Pennsylvanian *Najades*, both of shells and soft parts, has been brought together, which certainly is superior to any other local collection; in fact, the writer believes that he has at his command a larger assemblage of the soft parts than is found in all other collections combined.

The chief purpose of this work was to secure the material for a systematic monograph of the *Najades* of our state. A preliminary list of the species found in Pennsylvania has been previously published (Ortmann, 1909), but since then, further information has been obtained with respect to the systematic and zoogeographical side of the subject, and in the present monograph a final account will be given. In addition, the writer has investigated the anatomical structure of the mussels, and very important structural features, chiefly in the gills, have been discovered, which had been in part entirely overlooked by previous authors. The knowledge of the anatomical details thus obtained has enabled the writer to revise



the system of the North American *Najades*, and to put it upon a more secure foundation. A preliminary account of this work has also been published (Ortmann, 1910).

The most prominent advance in our ideas as to the systematic arrangement of the fresh-water mussels is marked by the publication of Simpson's paper on the *Najades* (Simpson, 1900). We cannot but admire this work, for the general principles of classification are correctly recognized by Simpson, and the soundness of his views has been amply confirmed by our own investigations. Yet Simpson suffered under two serious disadvantages: he did not possess enough material representing the soft parts to settle all systematic questions, and did not make any microscopical investigation of the anatomical structures. This latter shortcoming has been in part remedied by Sterki (Sterki, 1903). In the present monograph additional observations will be furnished, and with regard to the Pennsylvanian species, it may be said that the soft parts of all of them, with very few exceptions, have been at hand, and they are now sufficiently well known to enable us to assign each species to its proper place in the system. Of course in the case of the species and genera not found in Pennsylvania, this reference remains to be made; but after the main points of view have been indicated, this will be a comparatively easy task. The fact, however, should be emphasized that there is now no excuse whatever for collectors of the *Najades* preserving only the hard parts, and throwing away the soft parts. The soft parts form an integral portion of the animal, and should be preserved and examined together with the hard parts, and this is most imperative in the case of those genera, of which our present knowledge is more or less defective.

The greater portion of the material at hand, forming part of the collections belonging to the Section of Invertebrate Zoölogy in the Carnegie Museum, was secured by the writer in person. The art of collecting mussels has to be learned, because, while it is easy enough to pick them up, it can only be done after a thorough knowledge of the proper places and seasons has been acquired. The *Najades* inhabiting our rivers, creeks, ponds, and lakes, can only be obtained alive by going after them into the water, but as soon as their whereabouts is discovered, it is easy enough to get them. Their discovery cannot be accomplished under all conditions. Part of the season our creeks and rivers have too much water, or the water is too muddy to locate the mussels. This is the case chiefly in early spring, when the snow melts, and in the first half of summer, the time of the copious summer rains.

In Pennsylvania the best season is generally from August to October, when

the water courses are low and clear; but very often there is also a season of low water from the end of April to the end of May. In smaller creeks, where the water is never very deep, any dry period of about a week's duration will bring about favorable conditions, but in the larger rivers successful collecting is generally possible only late in summer and in autumn. The exceptionally dry summers of 1908, 1910, and partly also of 1909, afforded unusual and unexpected facilities for making collections. Collecting in the lakes (Lake Erie for instance) does not depend so much on the season, but it depends a good deal on the weather. Quiet days, when there are no wind and surf, should be selected.

Hand-picking is the best way of securing specimens. Devices like the so-called "clam-dredge" of the mussel fishermen of the Mississippi and Ohio are useless in our rivers on account of the rough and rocky character of their bottoms. Yet in Lake Erie upon sandy and sandy-muddy bottoms I have used a similar apparatus to great advantage. This is a modification of the common "clam dredge," and I am especially indebted to Dr. W. J. Holland for suggestions in constructing

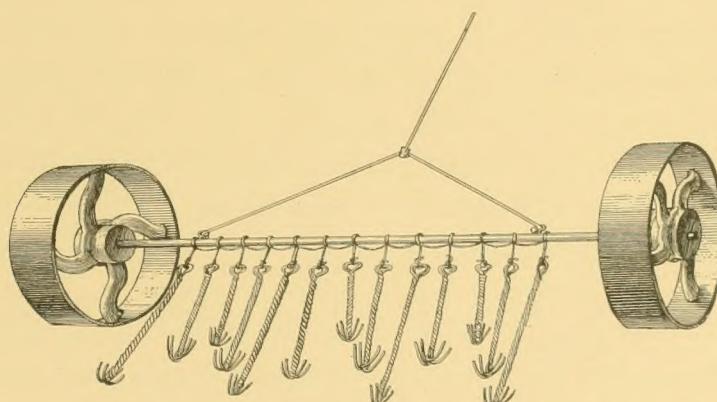


FIG. 1. The Holland Clam-dredge.

this device. It consists (See fig. 1) of a piece of gas-pipe with two wheels at the ends, to which four-pronged hooks are attached. The hooks are made of wire, with their stems rather long (six to ten inches), and they are tied to the gas pipe with *very short* strings: this prevents the tangling up of the whole mass, which is a great nuisance, when, as in the usual clam dredge, *short* hooks with *long* strings are used. With this apparatus, "*the Holland clam-dredge*," I obtained shells in Presque Isle Bay, Lake Erie, at depths of from six to fifteen feet.

In 1910 I had special advantages for collecting *Unionidæ* in Lake Erie, by being offered the opportunity to go out with the "sand-sucker" of the Erie Sand and Gravel Co. I thus obtained specimens at depths of from ten to fifteen feet.

I cannot close these introductory remarks without making public acknowledgement of the encouragement and valuable help furnished to me at all stages of my work by Dr. W. J. Holland, the Director of the Carnegie Museum. First of all, the study of the *Najades* forms part of Dr. Holland's general scheme and his policy of studying our local fauna (See Holland, W. J., in the Proceedings of the American Association of Museums, Vol. III, 1909, p. 12) and thus the general idea of this work, as well as my previous work on the crawfishes (See Memoirs of the Carnegie Museum, II, 1906), is largely due to his suggestion. In addition, he supplied me with the necessary means for carrying on my collecting, and the chief item in such work is the expense. As to this, I can only express my great gratification and sincere thanks for the liberal allotment of funds made to me. Finally, Dr. Holland furnished me with all the paraphernalia for the work of the laboratory, including everything that belongs to its literary and technical side. It goes without saying that he always followed the progress of my studies with the closest attention, helped me along in difficult cases, and was ever ready with suggestions and advice.

The wealth of the subject matter to be treated makes it necessary to divide this memoir into parts. Since it is absolutely essential to lay a proper foundation for the systematic part, and since the anatomical studies furnish this foundation, it is obvious, that the latter should be given first. In the present publication therefore I shall take up questions of anatomy and their bearing upon the system of the North American *Najades*. I reserve for a future publication the description of the various species and their zoögeography.

PART I. ANATOMICAL INVESTIGATIONS.

The anatomy of the European *Unionidae* appears to be rather well known, at least after the fashion in which they are treated in the textbooks. (I have consulted those of Cooke, 1895, and of Taylor, 1894 and 1900.) We have also several accounts of the anatomy of American forms (for instance, Brooks, 1890). But looking more attentively at these, we find that comparatively few genera and species have been studied. This is not astonishing in the case of Europe, where only a few types are found. With reference to the American shells, however, it is very strange that we possess descriptions, more or less satisfactory, only of *Unio* and *Anodonta*, and only of eastern species of these genera. Further, we shall see that even in these some of the most important parts of the anatomy have been neglected.

With regard to the numerous other genera found in the great interior basin, we possess only scanty notes on the gross anatomy. These have been supplied

almost exclusively by Lea and Simpson. The latter in his great "Synopsis" (1900) gives generalized accounts of the soft parts, chiefly in the diagnoses of the higher groups, genera, and their subdivisions; but we often remain in doubt whether a particular species has been examined by Simpson or not. Simpson furnished descriptions of the soft parts of species for another publication (See Baker, 1898), but in this case it is to be observed that he sometimes described the soft parts of a species which he did not examine, or rather that he inferred some of the characters from other species, which he believed to be allied. *Quadrula coccinea* is an instance. The description of the marsupium is here positively incorrect and was introduced apparently in the belief that this species, being supposedly a *Quadrula*, should have the marsupium of this genus.

Nevertheless, Simpson's observations published in the "Synopsis," are of the highest value, for he correctly recognized the most essential part of the anatomy, namely the *marsupium*. In all *Unionidæ* (as in the *Najades* in general), the eggs are carried in the gills, where they develop into larvæ, known as *glochidia*. This is a well known fact; and it was also long ago known (chiefly through Lea) that the marsupium is formed in the different species by different gills, or parts of gills. But this character had never been employed in making a systematic arrangement, and the credit for recognizing the importance of the marsupium, and for using it successfully in the division of the *Unionidæ* into genera and in the grouping of the latter, distinctly belongs to Simpson.

But Simpson studied only the general features of the marsupium, and thus his groups are not in all cases without objection. Further in a number of species he did not succeed in ascertaining the shape of the marsupium, and thus was able to place them only tentatively. As has been said above, several well supported corrections have been introduced by Sterki (1903), who paid attention chiefly to the shape of the glochidium, together with that of the marsupium.

The present writer made it his chief purpose to ascertain the shape of the marsupium in all species which came under his observation, and to this end to obtain gravid females. In this undertaking he was generally successful, and, with very few exceptions, gravid females of all Pennsylvanian species were secured. But when he took up the closer anatomical study, he made a very important discovery, namely that *in all our Unionidæ the anatomical structure of the gills, which serve as marsupia, is permanently differentiated*. It was known and emphasized by Sterki that this is externally the case in a certain group of genera (*Lampsilis*-type), while it was maintained that in the rest no such differentiation was visible in the female, when not gravid. But this latter assumption is incorrect.

There is always in the female an anatomical difference in the marsupial gills, and this difference may be detected even without a microscopical investigation, although the latter is generally advisable in order to render the structure absolutely clear.

In addition the writer has found, chiefly along the edge of the mantle, a number of structural differences which are also important, and will be described below.

A. GENERAL STRUCTURE OF THE GILLS.

The primary elements of the gills are the *gill-filaments* (*gill-tentacles* of Brooks) —cylindrical or somewhat compressed tubes, which arise in two longitudinal rows from a common base (ctenidium) between the foot and the mantle of the mussel, and hang down into the branchial chamber. These filaments are doubled back upon themselves, the outer row outwardly, the inner inwardly. The filaments of each row being connected with each other (See below), there are thus *two gills* on each side of the animal, an *inner* and an *outer* one, each consisting of two *laminæ* (*lamellæ*) composed of filaments, the laminæ including between them a space. The two laminæ are distinguished as the *primary* and the *secondary* limb of the gill, the former being the descending adaxial part, the latter the reflected and ascending part. The latter part is the outer lamina in the outer, and the inner lamina in the inner gill.

On the inside of each lamina, toward the cavity of the gill, there develops a peculiar tissue, called *interlamellar outgrowth* (Taylor, p. 177). This connects the gill-filaments of each lamella, leaving more or less regularly placed open holes (*ostia*), by which the inner cavity of the gill communicates with the outside. This interlamellar tissue forms a rather large part of the gill, in fact the lamella itself appears composed chiefly of this tissue, while the original gill-filaments form only its outer layer, separated from one another by the *intertentacular* (Brooks) or *interfilamentar grooves*. The interlamellar tissue is permeated by lacunar blood-vessels. The filaments develop along their sides *chitinous rods* for the support of the gill. Two such rods belong to each filament, but these rods are not continuous, but interrupted, consisting of longer or shorter, disjointed pieces.

The filaments and their chitinous rods run about vertically, that is to say, from the base toward the edge of the gill; a slightly fan-shaped arrangement is sometimes indicated, corresponding to the curved edge of the gill, upon which they stand vertically.

The interlamellar cavity of each gill is not simple, but is divided. There are "interlamellar partitions" (Brooks) or "interlamellar junctions" (Taylor), which connect the two laminæ of the gill. In most cases, these connections are developed

as *septa*, dividing the inner cavity of the gill. They run about parallel to the gill-filaments, that is to say, vertically toward the edge of the gill, and consist of a tissue similar to that of the interlamellar outgrowth, with differences which will be described below. Most of these septa run continuously all the way from the base to the edge of the gill, while others are shorter, and are intercalated at various distances from the base, but each septum is always continued to the edge. Thus the interlamellar cavity is divided into a number of canals, running from base to edge, which are called *water-tubes*. The size of these water-tubes is variable, and differs considerably according to sex (See below).

There is one exception among the *Najades* known to me from North America, which does not show this arrangement, *Margaritana margaritifera*.¹ Here the gills are also composed of filaments and possess an interlamellar outgrowth, which, however, is rather slightly and irregularly developed. *But there are no septa dividing the cavity of the gills.* Instead of this, the two laminæ are connected by more or less cylindrical or irregular thickenings of the interlamellar outgrowth, which are rather heavy and solid, and are placed quite irregularly. Sometimes these connections are a little elongated in the direction of the filaments, but they never are continuous septa, but rather patches of tissue, and if any regularity is observable, it is a somewhat *diagonal* or *oblique* arrangement. Toward the edge of the gill, and in its hindmost part a vertical arrangement is indicated, but even here there are no complete septa, and consequently no *water-tubes* (See fig. 2).

This peculiar development of the interlamellar junctions in *Margaritana* is in my opinion very important. While the presence of water-tubes is a character common to all our other *Najades*, the absence of this feature in *Margaritana* is very remarkable, and I have no doubt that this character, together with the otherwise slight development of the interlamellar outgrowth, which gives to the primary gill-filaments a greater significance in the whole make-up of the gill, points to a *more primitive stage* in the development of the gill in *Margaritana*, than in any other mussel.

The secondary limb of each gill (outer in the outer, inner in the inner gill)

¹In quoting species, I shall, for the present, use Simpson's nomenclature.

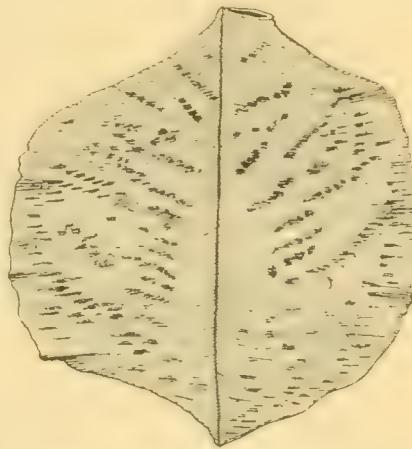


FIG. 2. *Margaritana margaritifera* (L.); right gills spread out and seen from below, showing arrangement of interlamellar connections.

extends upward as far as the base of the primary limb. Its distal margin in the outer gill is fused with the mantle, and thus a small space is cut off from the branchial chamber, which appears as a longitudinal canal along the base of the outer gill—the *suprabranchial* or *cloacal canal* of the outer gill, into which the water-tubes of this gill open. In the case of the inner gill, the secondary (inner) lamella is always connected anteriorly with the wall of the visceral mass (abdominal sac) for a shorter or longer distance; behind this connection it is sometimes free as far as the posterior end of the foot; and behind this point, the two inner laminae of the right and left inner gill are connected with each other up to the posterior end. Thus the inner gill also has a *suprabranchial* or *cloacal canal*, which is double (right and left) anteriorly, lying on either side of the foot and abdominal sac, but becomes united back of the foot into one cavity. In many cases this canal is not entirely closed, but communicates with the branchial chamber through a slit along the sides of the abdominal sac.

There are a number of variations in the development of the characters mentioned in the last paragraph.

The outer lamina of the outer gill is united with the mantle up to the posterior end of the gill in practically all species known to me, the only exception being in the case of *Margaritana margaritifera*. Here (Compare fig. 6) the outer lamella is free posteriorly for a considerable distance, and the posterior end of the gills assumes in consequence a very peculiar shape (See below, under "diaphragm").

As has been stated, the connection of the inner limb of the inner gill with the abdominal sac is variable. In the most primitive condition, such a connection is present only at the anterior end of the gill for a short distance, and in this case the inner lamina is free and leaves a slit-like communication open between the suprabranchial canal and the branchial chamber. In other forms, this slit is more or less, often entirely, closed; and then the whole inner lamina of the inner gill is connected, first to the abdominal sac, and farther behind, back of the hind end of the foot with that of the gill of the other side, and thus the suprabranchial canal of the inner gill is entirely separated from the branchial chamber.

Long ago Louis Agassiz called attention to these differences of structure. Later on their value was doubted by Lea as well as by Simpson, and Sterki also does not consider them as of much systematic significance. I have investigated my material with reference to this question, and find that the connection of the inner lamina of the inner gill with the abdominal sac is indeed variable, and that sometimes it is differently developed in the same individual on the right and left side. *But it is only in certain forms that this variability occurs.* In others this character is quite

constant. Thus in the species placed by Simpson in the genera *Quadrula*, *Pleurobema*, *Unio*, *Margaritana*, *Sympnynota*, *Anodontoides*, and *Anodonta*, I always found the inner lamina of the inner gill entirely free from the abdominal sac, with the exception of its anterior end. This is the more remarkable, since both Lea and Simpson (See Simpson, 1900, p. 766, footnote 2) affirm that in *Quadrula multiplicata*, a species which stands near our *Q. undulata*, the inner gills are sometimes free, sometimes connected. I have not seen that particular species; but of *Q. undulata* I have examined some thirty specimens, and have never seen a connected inner gill. Although the number of specimens investigated in this case seems small, the fact that I never found a connected inner gill in the genera named above, is, I think, rather significant, for I have looked over about four hundred individuals belonging to these genera, and it would be very strange, if variations occur here at all, that I by a curious chance never came across a single one.

Further, I found the inner lamina of the inner gill always almost entirely free in the following species of other genera: *Alasmidonta heterodon* (fifteen specimens investigated) *Lampsilis parva* (three specimens). In *Obliquaria reflexa* (four specimens) the gill is also free, but for a shorter distance, a little more than half of the abdominal sac. The same is the case in *Plagiola securis* (six specimens), where the length of the free edge is somewhat variable (in one case the slit was very short, but only on one side!).

On the other hand there are forms, in which the inner limb of the inner gill is always entirely united to the abdominal sac. This is the case in the genus *Alasmidonta* (excluding *A. heterodon*), in *Obovaria ellipsis*, *circulus*, and *retusa*, in the genus *Truncilla*, and in many species of the genus *Lampsilis* (*gracilis*, *alata*, *recta*, *orbiculata*, *ligamentina*, *radiata*, *luteola*).

In all those not hitherto mentioned, there is variation in this respect. This is most evident in the genera *Strophitus* and *Ptychobranchus*. In fact in the latter genus I have observed all conditions, from an inner lamina almost entirely free to an inner lamina entirely connected. In *Strophitus* it varies from free for about half the length of the abdominal sac to entirely connected. In *Plagiola elegans* (two specimens) the open slit was in one case short, about one fourth of the length of the abdominal sac, and in the other there was only a small hole at the posterior end of the foot. In *Lampsilis iris*, *nasuta*, *multiradiata*, *cariosa*, *ventricosa*, and *ovata*, the inner gill is entirely connected, or has a small hole at the posterior extremity of the foot; and in *Micromya fabalis* (four specimens), the slit is short, from about one fourth to one half of the length of the abdomen.

The closing of the slit proceeds always in an antero-posterior direction, and

if there is only a small opening left, this is never placed anteriorly, but always at the posterior end of the foot.

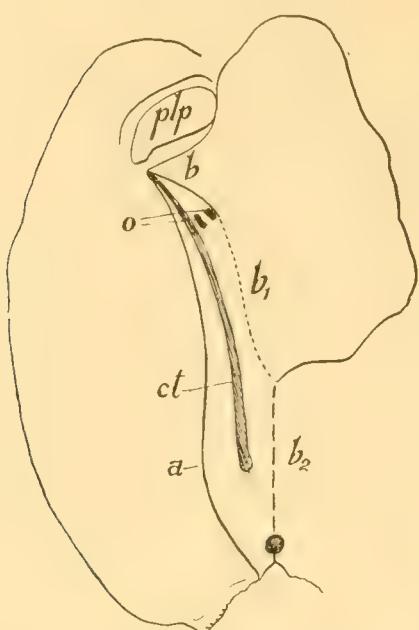
According to these observations, I must attribute to this character a certain limited systematic value. There are a number of forms, in which the primitive condition of an unconnected, free inner lamina of the inner gill is always found.

There are other forms, which belong to the more advanced types, in which this lamina is always entirely, or almost entirely, connected with the abdominal sac. Between these stand others, in which all transitional conditions are found, and in some of these an intermediate condition seems to be characteristic, while in others this character is variable.

As has been mentioned above, posteriorly to the abdominal sac and foot, the inner laminæ of the two inner gills unite in the median line of the body (See fig. 3). By this union, together with the connection of the outer laminæ of the outer gills with the mantle, a complete separation of the branchial chamber from the posterior part of the suprabranchial canals (cloacal chamber) is effected by a septum or *diaphragm*, which forms a horizontal division, from which the gills hang down (See fig. 4). At the posterior end the four suprabranchial canals of the two gills of the right and left side are united into one cavity, the *cloacal chamber*. This is brought about by the fact that

FIG. 3. *Anodonta grandis gigantea* (Lea)
Left half of body, seen from below, with gills removed; showing attachment of gills.—*plp*, palpus; *ct*, ctenidium (base of gills); *a*, line attachment of outer lamina of outer gill to mantle; *b*, attachment of inner lamina of inner gill to abdominal sac; *b*₁, free edge of the latter; *b*₂, line of connection of the two inner laminæ of right and left gill; *o*, sexual and renal orifices.

the gills extend posteriorly beyond their attachment to the body at their base, or rather, that this attachment (ctenidium) does not extend to the posterior end of the body (See fig. 5). This attachment, the common base of the two primary limbs of the gills on each side, runs backward to a point, which generally lies about midway between the posterior end of the foot and the posterior margin of the mantle; beyond this point the inner limbs of the two gills on each side remain connected with each other, but are no longer attached to the body, and the two suprabranchial canals on each side are fused (See figs. 3 and 5). Thus of the four suprabranchial canals present in the anterior part of the body, each of which belongs to one gill, the two median canals are united first immediately behind the



posterior end of the foot; and a little bit farther back, the two outer canals (belonging to the outer gills) open into and unite with this cloacal chamber.²

In a posterior view (See fig. 4) the diaphragm separating the branchial and cloacal openings forms a rather short, simple, horizontal bridge, from which the gills hang down. Sometimes there is a slight median incision, when the two inner laminæ of the inner gills are not fully united to their ends, but according to my investigations this has no systematic value.

We are to note an exception to the normal structure, and this is again *Margaritana margaritifera*. Here (See fig. 6) the diaphragm represents an entirely different aspect, which is due to the fact that, as we have seen above, the outer laminæ of the outer gills are not connected with the mantle up to their ends. Thus on the one hand the outer attachment of the diaphragm is not seen at the outer edge of the mantle, and the outer laminæ of the outer gills are free for a considerable distance, which causes the whole dia-

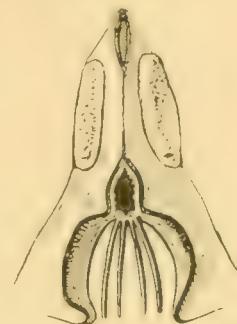


FIG. 4. *Anodonta grandis gigantea* (Lea). Posterior view, showing branchial, anal, and supra-anal openings, diaphragm, and posterior ends of gills.

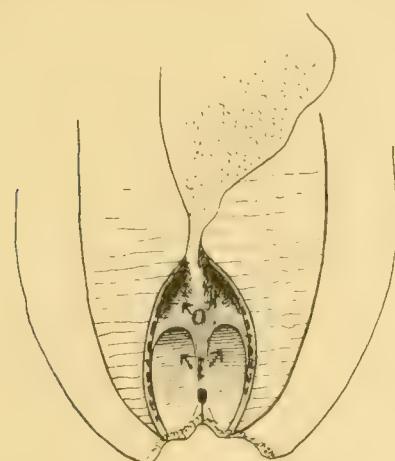


FIG. 5. *Anodonta grandis gigantea* (Lea). Posterior end of body, seen from below, with the diaphragm cut open in the median line, to show cloacal chamber.—*o*, openings of the suprabranchial canals of inner gills; *i*, openings of the suprabranchial canals of outer gills.

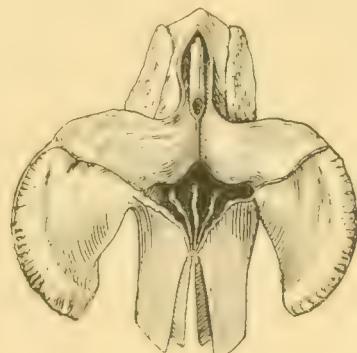


FIG. 6. *Margaritana margaritifera* (L.). Posterior view, showing branchial and anal openings, and the peculiar, incomplete diaphragm. No supra-anal is separated from the anal.

phragm to appear as if it were tapering to a median point; and, on the other hand, the cloacal opening (anal siphon) is much larger than usual.

²This condition is not clearly represented in Brooks' (1890, p. 275, fig. 143) diagrammatic figure. The openings of the suprabranchial canals of the outer gills into the common posterior cloacal cavity are not shown. Their position would be indicated by the two nervous strands starting from the parietosplanchnic ganglia and curving backward toward the posterior end of the gills.

B. STRUCTURAL FEATURES OF THE FINER ANATOMY OF THE GILLS.

1. *The Water-tubes and the Septa dividing them.*

The following description of the water-tubes necessarily leaves out of consideration the peculiar form, *Margaritana margaritifera*, for this has no water-tubes.

We have seen above that the water-tubes are formed by the interlamellar junctions, which run from near the base of the gill to its edge, and are generally developed in the shape of continuous septa, which do not differ in their tissue from that of the interlamellar outgrowth, that is to say, in their normal development their tissue is lacunar, often containing blood-vessels (See Pl. LXXXVI, figs. 1, 5, 6a, 7a, 10a, 12a, 13, 14a, and Pl. LXXXVII, figs. 1, 4, 8).

This simplest structure is always found in both gills of the male, and there is no further differentiation of it in this sex, with the exception that toward the base of the gills the septa become sometimes a little more independent, being wider on account of the greater distance of the two laminae from each other. The water-tubes formed by these septa are rather wide in the longitudinal direction of the gill, since the septa are distant from each other. The distances are variable, and often, chiefly so in the genera *Alasmidonta*, *Strophitus*, *Sympynota*, *Anodontoides*, and *Anodonta*, they are rather large near the base of the gill, where also the septa become irregular, running for a short distance diagonally, and being sometimes somewhat reticulate. In the genera just named there are often as many as forty and even more filaments between two septa. The average is from about fifteen to thirty; in other genera, the average is from about ten to twenty or twenty-five, although there is occasionally a larger or smaller number present. We may say, that normally there are more than fifteen filaments between two septa.

The identical structure is found in those gills of the female, which do not serve as marsupia, that is to say, in the inner gill, when the outer gill alone is used as a marsupium, and in the inner and the anterior part of the outer gill, when only the posterior part of the outer gill is so used (See Pl. LXXXVI, figs. 6a, 7a, 10a, 11a, 12a, 14a; Pl. LXXXVII, fig. 5). In those forms (genus *Quadrula*), where both gills serve as marsupia, this structure is not found at all in the female. (See Pl. LXXXVI, figs. 2, 4.)

In the marsupial gills of the female important structural modifications take place, and these modifications, which we shall describe presently, are quite marked, and invariably characterize the female sex. Consequently it is possible *not only to distinguish a sterile female (with the marsupium not charged) from a male, but also to discover the general character of the marsupium in a sterile female.*

In the *sterile female* the septa separating the water-tubes in the marsupial gill (See Pl. LXXXVI, figs. 2, 4, 7b, 10b, 14b; Pl. LXXXVII, figs. 2, 6, 7, 9) are much more crowded than in the male. There are, on an average, only from about five to ten filaments between two septa, although in some cases this number may increase to twenty. But in every species this number is considerably smaller in the female than in the male. This difference is very striking, and may be detected by the naked eye on holding up the gill toward the light. When I was hunting for sterile females among my material I always used this method in discovering the sex, and the much more crowded septa in the gill examined always indicated the female sex. I never made a mistake, and a specimen selected as a sterile female according to this test always proved to belong to this sex, when a closer microscopical examination was made.

In consequence of the more crowded condition of the septa the water-tubes have a different cross-section and are not elongated in the longitudinal direction of the gills, as those of the male, but are either more rounded or square (See Pl. LXXXVI, figs. 10, 14; Pl. LXXXVII, figs. 2, 9), or even elongated in the transverse direction (See Pl. LXXXVI, fig. 7).

But not only does the more crowded character of the septa indicate a marsupial gill, but *the septa themselves have a different structure*. While in the male and the non-marsupial gill of the female the septa are not much different from the inter-lamellar outgrowth, in the marsupial gill they are considerably altered. They are more strongly developed, appear more as independent structures, and their tissue is more compact, without lacunæ or blood-vessels. Generally, they are thicker, and also longer in the direction from lamina to lamina, and, what is their most striking character, their epithelial layer is quite different. While in the male type, described above, the epithelium, which faces the water-tubes, is a simple layer, in the marsupial gill of the sterile female it is folded and thrown up into wrinkles, which often assume considerable proportions (Compare Pl. LXXXVI, figs. 1 and 2, 7a and 7b; and Pl. LXXXVII, figs. 1 and 2, 8 and 9).

There is no question that this peculiar structure of the septa of the marsupial gills is an adaptation to their function. When the marsupium in the breeding season becomes charged with eggs, these gills naturally must swell, and they actually do so, as is well known. The swelling can be only in one direction, namely transversely to the longitudinal plane of the gill, that is, in the direction from lamina to lamina. This means, that the two laminæ of the gill are forced apart, and since they are connected by the septa, the latter, if they are not to be torn, must be built accordingly. The description and the figures given here of the

structure of these septa show that the latter is highly favorable to stretching, and while they stretch out, they become thinner, and the folds of the epithelium become smoothened and flattened (Compare Pl. LXXXVI, figs. 2 and 3, 8 and 9, 14 and 15; and Pl. LXXXVII, figs. 2 and 3). After the discharge of the mature embryos (glochidia) the gill and its septa assume again their normal shape.

This structural feature of the marsupial gill of the female is met with in all our *Unionidæ*, and in some it is the only one found. To the latter belong the following genera of Simpson: *Quadrula*, *Pleurobema*, *Unio*, and *Tritogonia*. But among these we observe a division into two groups. In some both gills, inner and outer, have the structure of marsupial gills, and become charged with eggs in the breeding season (See Pl. LXXXVI, figs. 2, 3, 4); in others it is only the outer gill which serves this purpose (See Pl. LXXXVI, figs. 6, 7, 10, 11, 12, 14). According to my investigations, in the following species *both gills* are marsupial: *Quadrula subrotunda* (Lea); *Q. kirtlandiana* (Lea); *Q. rubiginosa* (Lea); *Q. trigona* (Lea); *Q. pustulosa* (Lea); *Q. lachrymosa* (Lea) (according to material from Kansas); *Q. metanevra* (Rafinesque); *Q. cylindrica* (Say); *Q. undulata* (Barnes); *Q. hippopæa* (Lea); *Tritogonia tuberculata* (Barnes).

Only the *outer gills* serve as marsupia in: *Quadrula tuberculata* (Rafinesque); *Q. pyramidata* (Lea); *Q. obliqua* (Lamarck); *Q. coccinea* (Conrad); *Q. cooperiana* (Lea); *Pleurobema æsopus* (Green); *P. clava* (Lamarck); *Unio crassidens* Lamarck; *U. gibbosus* Barnes; *U. complanatus* (Dillwyn); *U. productus* Conrad.

The bearing of these facts upon the systematic arrangement will be discussed later.

There are *further structural modifications of the water-tubes* found in an association of forms of *Unionidæ*, which apparently compose a natural group, and have been already recognized as such by Sterki. This group is composed of the genera *Anodontida*, *Anodontoides*, *Sympynota*, *Strophitus*, and *Alasmidonta* of Simpson's "Synopsis." Of these I have investigated the following species: *Anodontida cataracta* Say; *A. grandis* Say; *A. imbecillis* Say; *Anodontoides ferussacianus* (Lea) (and var. *subcylindraceus* (Lea)); *Sympynota compressa* Lea; *S. viridis* (Conrad); *S. costata* (Rafinesque); *S. complanata* (Barnes); *Strophitus edentulus* (Say); *Alasmidonta undulata* (Say); *Alasmidonta marginata* (Say) (and the var. *varicosa* (Lamarck)); *A. heterodon* (Lea).³

³The existence of the structures described in the following paragraphs has been denied by Lefevre and Curtis (1910). As I have pointed out, however, (Ortmann, 1910a), their own figures show them. These lateral water-tubes cannot be blood-vessels, for which they apparently have been taken by these two authors, and this is so easily seen (even macroscopically) that we do not need to discuss it any further.

In all these only the outer gill serves as a marsupium, and during the breeding season, and only during this time, *each water-tube is divided into three tubes running from the base to the edge of the gill*, the division being effected by two secondary septa, which grow out at right angles from the primary septa (or interlamellar junctions). Two of these secondary water-tubes are located toward the faces (*laminæ*) of the gill, while the third one, which is much larger than the lateral ones, occupies the middle, and is separated from the two *laminæ* by the lateral tubes. *Only this central tube contains ova and embryos*, and properly should be called an *ovisac* (See the cross-sections, Pl. LXXXVI, figs. 8, 9, 11b, 16). Thus we see that, while in the forms discussed above the whole water-tube assumes the function of an *ovisac*, in the present cases *only a part of the original water-tube discharges this function*.

In addition, these *ovisacs* of the *Anodonta*-group are also *closed above, at the base of the gill*, by a similar tissue growing out from the septa at their lower ends (See Pl. LXXXVIII, figs. 3a, 11). As far as I can see, this tissue, which forms the *ovisacs* here, is furnished by, and forms part of, the epithelial layer of the septa.

This structure apparently is an adaptation to the lengthened breeding season and the extreme swelling of the marsupium, which is observed in these forms, and serves for the aëration of the mass of embryos. The swelling of the marsupium during the breeding season is very great here, much greater than in any of the forms belonging to the *Quadrula*-group. Thus it might become difficult to furnish the necessary oxygen to the developing eggs in the ordinary way, by the minute ostia perforating the *laminæ*, and the cutting off of a part of each water-tube close to each lamina must have the effect of keeping up a lively current of water within the gill, between the *laminæ* and the central *ovisac*.

As has been said, this threefold division of the tubes is present *only during the breeding season*. I have examined numerous sterile females, in which this structure is not seen (Pl. LXXXVI, fig. 15); in others it is indicated (Pl. LXXXVI, figs. 7b, 12b) by a stronger fold (or group of folds) of the epithelial layer of the septa, near their insertion into the *laminæ*. In specimens where the eggs begin to go into the gills, this structure is sometimes not yet developed, but it appears soon, and the epithelial folds, which form the secondary septa within the water-tubes, begin to grow into the lumen of the water-tubes, and the folds of the opposing faces of the two septa finally unite in the middle. The point of union (cross-section of the line of union) is often distinctly seen in sections. After the discharge of the glochidia these structures disappear rapidly. I have seen them still present in some specimens, from which the embryos had recently been discharged

(Pl. LXXXVI, fig. 12b); in others they were greatly reduced, and the septa had assumed their normal shape; but in specimens of this group, where the marsupium was well filled with eggs or embryos, I have always seen them, although it is sometimes hard to obtain good slides, especially when the embryos have reached the glochidium-stage, since at that time the making of sections is rather difficult.

There is one form among those above enumerated, in which the development of this structure goes a step further. This is *Strophitus*. It was known long ago that this genus is characterized by a peculiar arrangement of the ova in the gills, they forming short, horizontal rows, which run transversely from lamina to lamina. According to my investigations this arrangement is brought about by further outgrowths of the epithelial layers of the septa, which fill the spaces between two septa, or rather only the middle part, the ovisac (See Pl. LXXXVIII, figs. 7, 8, 9), and thus the simple ovisac of *Anodonta* and other genera is here divided into a number of smaller, *secondary ovisacs*, running transversely across the gill, each of which contains a short, more or less cylindrical mass of eggs or embryos. These masses (placentulae) will be discussed later. Also in *Strophitus* these structures are not present in sterile females, and after the discharge of the glochidia they soon disappear. The gradual development is seen in the vertical longitudinal sections of the marsupial gill on Pl. LXXXVIII, figs. 6 to 9.

All other forms of *Unionidae*, which have not thus far been mentioned, have the simple structure of the marsupial gills, as described in the case of *Quadrula*, etc., but there are other differentiating structural features on the edges of the gills, which must be compared with the more primitive forms.

2. *Differentiating Structures on the edge of the gills.*

There is a difference in the structure of the edge of the inner and the outer gill, which is found in all our *Najades*, including *Margaritana*, and of this I shall first speak.

Making vertical cross-sections through the gills of a male (See Pl. LXXXVII, figs. 11, 12, 15; Pl. LXXXVIII, fig. 12), we observe that the edge of the outer gill is simply rounded off, while that of the inner gill possesses a peculiar longitudinal furrow along it, which may also be distinctly seen macroscopically. As to the meaning of this furrow, I can not make any suggestion, and am only able to state the fact of its presence. *By the presence of this furrow an inner may always be distinguished from an outer gill.*

The same difference is found in the inner and outer gill of the female (See Pl. LXXXVII, fig. 13), and the conformation of the edge of the gill is practically

identical with that of the male in all sterile individuals. There is no change in this matter in the gravid females of the genera *Unio*, *Pleurobema*, and *Quadrula*. The result is that the edge of the marsupial gill does not participate in the swelling of the gill. The greatest swelling in these genera occurs near the base or in the middle of the gill, while it decreases toward the edge, which always remains rather sharp, and *this sharp edge of the marsupial gill is a very important macroscopical character* in the species of these genera. A microscopical examination shows that there is no difference of the structure of the edge from that of the sterile female (Compare Pl. LXXXVII, figs. 13, 14, 16; Pl. LXXXVIII, fig. 1).

In our other *Unionidae* it is different, and we distinguish two types of development, though in all cases the differentiation concerns only the edge of the outer, or marsupial gill.

The first type is found in the *Anodonta*-group (in those forms, which have the water-tubes divided into three tubes, as described above). It has already been said that in these forms the marsupium swells to an extreme degree, and this immense swelling also affects the edge. The two laminæ of the gill draw apart at the edge, and this strain would cause a rupture at this point, if it were not for the fact that there is here an extraordinary thickness of tissue, *which is capable of stretching*, and thus keeps the edge of the gill closed (See Pl. LXXXVIII, figs. 2b, 3b, 5, 10). There are no filaments, or chitinous rods, or ostia visible in this elastic tissue.

This transverse stretching of the edge of the gill takes place in various degrees, and is well observed only in marsupia, which are fully distended. Even in fully charged marsupia it is often absent in certain parts, chiefly so toward the anterior and posterior ends of the edge of the gill, which then remains simple, but appears as a kind of ridge or cord upon the swollen marsupium. In the middle of the gill, however, this stretching takes place regularly, and is sometimes accompanied by a slight bulging out of the edge, beyond the original margin of the gill (Pl. LXXXVIII, figs. 3b, 10). In other cases such bulging is hardly noticeable, and the edge of the gill does not appear rounded off, but rather truncated (Pl. LXXXVIII, figs. 2b, 5). The peculiarities of this structure may be easily seen with the naked eye or with an ordinary magnifying glass, and the most striking effect is that the edge of the marsupium in these forms *does not appear sharp*, as in the *Unio*-group, *but blunt, rounded off, or truncated*. The single water-tubes (or ovisacs) are not distinctly marked off externally along the edge of the marsupium.

The other type of the specialization occurring on the edge of the marsupium is found in the *Lampsilis*-group, to which belong the following genera and species of Simpson's "Synopsis," females of which I have investigated:

Truncilla triquetra Rafinesque; *T. perplexa rangiana* (Lea); *Micromya fabalis* (Lea); *Lampsilis ventricosa* (Barnes); *L. ovata* (Say); *L. cariosa* (Say); *L. multiradiata* (Lea); *L. radiata* (Gmelin); *L. luteola* (Lamarek); *L. ligamentina* (Lamarek); *L. orbiculata* (Hildreth); *L. recta* (Lamarek); *L. nasuta* (Say); *L. iris* (Lea); *L. parva* (Barnes); *L. alata* (Say); *L. gracilis* (Barnes); *Obovaria retusa* (Lamarek); *O. circulus* (Lea); *O. ellipsis* (Lea); *Plagiola securis* (Lea); *Obliquaria reflexa* Rafinesque; *Ptychobranchus phaseolus* (Hildreth).

This type resembles the one just described in so far as the two laminæ of the gill yield at the edge to the tendency of the marsupium to swell. The swelling of the gill itself is generally not carried to the same excessive degree as in the *Anodonta*-group, although it is sometimes quite considerable; in its stead, the chief expansion takes place *at the edge itself, and in this case beyond it*. The thickened tissue is not simply stretched out in a transverse direction, but it bulges out, thus protruding beyond the original edge of the gill (See Pl. LXXXVIII, fig. 14). The latter is always clearly indicated by a line at which the filaments and their chitinous rods stop; and this line may be seen with the naked eye or with a low power lens. Beyond this line the gill sometimes projects to a considerable distance, and this projection, into which the septa are continued, acquires a peculiar appearance. It does not project and bulge out uniformly, but the septa on the inside, acting as stays, check the bulging at their lines of insertion, and thus the edge of the marsupium assumes a *beaded appearance*, each bead representing a water-tube, being separated from the adjoining bead by a kind of constriction or sulcus, representing the septum. This protruding, beaded structure of the marsupial edge is very characteristic of these forms, and is distinctly visible to the naked eye. Apparently Simpson's diagnostic character, that here the ovisacs are distinctly "marked out by a sulcus," refers to the edge of the marsupium; for upon the lateral faces of the marsupium there are no such distinct sulci, and there is hardly any difference in the appearance of these faces from what is seen in the other genera, which, according to Simpson, have no such sulci. However, when the water-tubes are very large, as for instance in *Lampsilis alata* and *gracilis*, the sulci are a little more distinct on the lateral faces.

In the genus *Ptychobranchus* (Pl. LXXXVIII, figs. 13, 14), the bulging out of the edge takes place *all along the gill*, which, in addition, is peculiarly folded, as is well known. In the rest of the genera the bulging is localized, and it is always the *posterior section of the outer gill* which shows this structure, sometimes to a greater, sometimes to a lesser extent. The fact that the marsupium is restricted in these genera, is a character emphasized by Simpson. There is some differentia-

tion in this, for instance in *Obliquaria* it is only a small part of the gill immediately behind the middle which forms the marsupium. But this is, in my opinion, rather unimportant, for in the typical forms of *Lampsilis*, *Obovaria*, and *Plagiola* very often the outmost posterior end of the outer gill is not used as marsupium. But it is without exception a rule that the marsupial part always *projects* beyond the original edge of the gill (as marked by the filaments); and this is also noticed, although in a lesser degree, in the sterile female. When the gills are not charged, of course, the protruding, outbulging tissue is much contracted; yet the mass of this tissue is so considerable, that it is even then clearly seen, and it keeps the laminæ of the gill permanently apart at the edge (See Pl. LXXXVIII, figs. 13, 15, 17, 21), so that the beaded appearance is also preserved. By this character a female of these forms may always be recognized even when sterile, and further the marsupial edge may generally be distinguished by its color. Often it appears simply opaque whitish, in distinction from the water-soaked, transparent tissue of the rest of the gill, but in other cases a peculiar dark pigment develops, chiefly on the inner side of this tissue in the epithelial layers (See Pl. LXXXVIII, figs. 15, 17, 18, 19, 20).

The part of the outer gill of the female which is not used as marsupium has the normal structure, that is to say, it corresponds essentially to the structure of the edge of the outer gill of the male. In sterile females it simply forms the anterior continuation of the marsupial part, and is not marked off, except by the lesser elevation of the edge (Pl. LXXXVII, figs. 6, 7, 10). In the gravid female, however, the marsupium swells principally at the edge, and it also increases its longitudinal (antero-posterior) dimension. Thus it is forced to push past the anterior part of the gill, forming a fold with it (See Pl. LXXXVII, fig. 5). This fold probably is analogous to the numerous folds seen in the genus *Ptychobranchus* (Pl. LXXXVII, fig. 3), at any rate it serves the same purpose. Sometimes, when also the hindmost part of the outer gill does not take part in the formation of the marsupium, a similar small fold is also seen posteriorly, but this is rather insignificant and variable. At the anterior fold, the marsupium pushes forward on the *inside* of the anterior, non-marsupial part of the gill.

C. THE OVA AND THE LARVÆ (GLOCHIDIA).⁴

1. Arrangement of the ova and embryos in the marsupium.

As is well known, the sexual orifices are situated on each side of the abdominal sac, and open into the anterior part of the suprabranchial canal of the inner gill.

⁴Wherever I use the words "ova" or "eggs," as distinguished from "glochidia," I mean the eggs and their subsequent stages of development, before the glochidial shell is formed.

From this point the way is open for the eggs all along the base of the inner gill backward to the common cloacal chamber and forward again into the suprabranchial canal of the outer gill. From the suprabranchial canals at the bases of the gills the ova reach the water-tubes in the gills. I have repeatedly found specimens, in which this process was going on, and where both suprabranchial canals were more or less filled with ova. (Instances are *Ptychobranchus phaseolus*, *Strophitus edentulus*, *Alasmidonta undulata*, *Quadrula undulata*.)

After the eggs have reached the water-tubes (*ovisacs*), they are firmly packed together there, until the marsupium is filled to its utmost capacity. In no case have I observed that the ova become connected in any way with the tissue of the gills; on the contrary, they always remain free from them, but generally are connected with each other, so that the contents of each water-tube or ovisac form a more or less solid mass, which in its shape conforms to the shape of the ovisac. The connection of the eggs between themselves is merely a "sticking together," which sometimes is rather slight, but produces in other cases a rather firm mutual adhesion. It is accomplished by the outer egg-membranes, which apparently have the property of freely imbibing water, and thus of becoming gelatinous.⁵ For these gelatinous masses containing the eggs we may use the term *placentæ*, introduced first by Sterki with reference to the genus *Strophitus*. (As will be seen later, I call the *placentæ* of *Strophitus* *placentulæ*.) These *placentæ* may be more or less compact (See Pl. LXXXVI, fig. 3; Pl. LXXXVII, fig. 3; Pl. LXXXVIII, fig. 14); they are well developed in *Quadrula subrotunda*, *kirtlandiana*, and *rubiginosa*, where they are rather cylindrical, since the water-tubes do not expand very much and remain subcylindrical in the charged marsupium. In *Ptychobranchus* the *placentæ* are also very solid, and there is in the outer layer a peculiar brown stain developed, when the glochidia are formed. The *placentæ* are subcylindrical here, but somewhat club-shaped, on account of the swollen distal end. In all these forms, it is easy to take the *placentæ* out of the gill whole, without injury.

In *Quadrula metanevra*, *undulata*, *coccinea*, in the species of *Pleurobema* and *Unio*, in all forms of the *Lampsilis*-type (except *Ptychobranchus*), the water-tubes are more or less stretched out transversely, so that their lumen becomes compressed, and consequently also the *placentæ* have a similar shape, leaf-like, lanceolate, or elliptical. Here the mutual adhesion of the eggs is not so firm, so that they come apart more easily, and it is not feasible to take the *placentæ* out entire. In some of these forms (*Quadrula undulata*, *Unio*, and the *Lampsilis*-species), the adhesion

⁵There may be a secretion furnished by the epithelium of the water-tubes. This question is reserved for further histological investigation.

is noticed only in the eggs, while later on the glochidia are more or less free. In *Quadrula coccinea* and *Pleurobema*, however, the placentaæ are more solid, and remain so until they are discharged (See below).

In *Strophitus*, as we have mentioned, peculiar conditions prevail. The ovisac (inner part of a water-tube) is subdivided into smaller partitions, running cross-wise to the gill; and in each of these compartments, which are almost cylindrical, a small number of ova are located which again stick together rather firmly and can easily be taken out whole. These "placentaæ" of Sterki, consequently, are not entirely homologous to the placentaæ of the other genera, since in the latter each ovisac contains only one placenta, while in *Strophitus* there are many of them in one ovisac. The eggs of *Strophitus* form a single, irregular row in each *placentula*, as I should prefer to call them here, and there are from about two to eight or ten (generally seven) in each *placentula*.⁶

In the genera *Anodonta*, *Anodontoides*, *Sympynota*, and *Alasmidonta*, no placentaæ appear to be present. The eggs as well as the glochidia fill the ovisacs in immense numbers, and seem to be entirely free. At any rate I never succeeded in isolating the egg-mass from an ovisac, but invariably, as soon as an ovisac is injured, the eggs or glochidia flow out freely, without sticking together, although in some instances in some of my sections of the genus *Sympynota*, a placenta-like cohesion is here and there indicated in the younger eggs.

2. *The Glochidia.*

I am not prepared to say where the fertilization of the eggs takes place. It must take place somewhere between their issue from the genital orifice, and their final deposition in the gills. It may take place in the suprabranchial canals, or in the gills. At any rate as soon as the marsupium is well filled cleavage begins, and the eggs develop within the gill into the young larval shell, known as *glochidium*. The development from the egg to the glochidium is rather rapid, while the glochidium may remain unchanged a long time in the marsupium before it is discharged.

We generally find in individual shells a rather uniform stage of development of the embryos, and, as a rule, when there are eggs, there are only eggs, and when there are glochidia, we find only these. Nevertheless, as already observed by Sterki (1898, p. 19) in *Cyprogenia*, there are sometimes cases, where all stages from the egg to the fully developed glochidium are found in one and the same marsupium.

⁶I have evidence in some of my slides that not all eggs in a *placentula* of *Strophitus* develop into glochidia, but that some become abortive. It may possibly be that the latter furnish material for the *placentulae*. In other species also I have seen what looks like abortive eggs (see *Lampsilis alata*, Pl. LXXXIX, fig. 18). This matter should be investigated more closely. Sterki (1898, p. 19) already mentions it.

I have seen the identical condition in *Anodontoides* and *Sympynota*, with young eggs at the base of the gills, glochidia near the edge, and with the intermediate stages in the middle.

The shape of the glochidium has been studied repeatedly by different writers, but the credit of using it successfully for the systematic arrangement of the genera belongs to Sterki. The glochidium of *Anodonta* possibly is best known. It is rather large, subtriangular, with a spine at the tip of each valve (Pl. LXXXIX, fig. 13). Yet this shape cannot be regarded as typical, and it represents a specialization. As Sterki points out, it is found only in that group of genera, which I have repeatedly called the *Anodonta*-group, and it is one of the diagnostic features of this group.

I have seen this glochidium in the following forms: *Strophitus edentulus* (Say); *Anodonta grandis* Say; *A. imbecillis* Say (Pl. LXXXIX, fig. 13); *Anodontoides ferussacianus* (Lea) (Pl. LXXXIX, fig. 12); *Sympynota compressa* Lea (Pl. LXXXIX, fig. 10); *S. viridis* (Conrad); *S. costata* (Rafinesque); *S. complanata* (Barnes) (Pl. LXXXIX, fig. 11); *Alasmidonta undulata* (Say) (Pl. LXXXIX, fig. 9); *A. marginata* (Say); *A. marginata varicosa* (Lamarck); *A. heterodon* (Lea) (Pl. LXXXIX, fig. 8).

In all these the glochidia are rather uniform in size as well as in shape. Generally they are rather high and pointed, but sometimes (*Sympynota compressa* and *viridis*) they are wider and less pointed. We do not need to go into detail here, since most of them have been already figured by Lea (Observ. VI and XIII).⁷ The glochidia of *Alasmidonta undulata* and *Anodontoides ferussacianus* are here figured for the first time (Pl. LXXXIX, figs. 9 and 12).

Lea, who is the only writer, who has furnished drawings of the glochidia, has observed the same type in the following additional species: *Margaritana deltoidea* (= *Alasmidonta calceola*) (See Observ. VI); *Margaritana spillmanni* (= *Strophitus spillmanni*) (See Observ. XIII). They also belong to the same group. On the other hand, Lea says of *Margaritana triangulata* (= *Alasmidonta triangulata*) (See Observ. VI) from Georgia, that he could not observe any hooks, and the same is the case in *Margaritana hildrethiana* (= *Hemilastena ambigua*, see Observ. VI), *Anodonta ferussaciana* (= *Anodontoides ferussaciana* ibid.), and in *Anodonta ovata* (= *grandis*, see Observ. X). All these species should have hooks, if Sterki's theory, that this is a fundamental character of the glochidia of this group, is correct.

⁷A number of Lea's figures are rather unsatisfactory, because they are not drawn to scale. Thus, for instance, the glochidium of *Plagiola securis* (Observ. VI, pl. 5, fig. 6) does not show its real character, being too small in comparison with those of other species (also the gaping margins are not shown). The glochidia on our Plate LXXXIX are all from photographs taken under the same enlargement, and thus show the actual comparative proportions.

And indeed I have seen the hooks in the two last-named species. Lea himself in the case of *Hemilastena* suggests that the glochidia he has seen are too young, and that the hooks might develop later. And this is apparently true, for I have observed in a number of species, that young glochidia have no hooks, while they are present in older ones. In the following cases this was most evident: specimens of *Alasmidonta marginata*, collected Sept. 2, 1907; of *Alasmidonta marginata varicosa*, collected Aug. 13, 1908; of *Sympynota viridis*, collected Sept. 6, 1909; of *Sympynota costata*, collected Aug. 31, 1906, and Sept. 21, 1907; of *Sympynota complanata*, collected Sept. 14, 1909; and of *Strophitus edentulus*, collected Aug. 24, 1909. All had no hooks, and we see that they all were collected in the months of August and September, the beginning of the breeding season. In other specimens of the identical species, collected generally a littler later in the season or in the spring, hooks (spines) were present.

Thus we have every reason to believe that Sterki's opinion that this kind of glochidium is common to, and characteristic of, the genera *Strophitus*, *Alasmidonta*, and *Anodonta*, is essentially correct, and that it should be enlarged so as to embrace all forms belonging to the "Anodonta-group."

A second type of glochidium presents a somewhat rectangular shape, more or less dilated ventrally (celt-shaped), with two spines or hooks, one at each of the ventral corners of the shell; further the lateral (anterior and posterior) margins of this shell are here not in contact all along their edges, as usual, but are gaping. In Pennsylvanian species, I have only observed this type in *Lampsilis alata* (Say) (See Pl. LXXXIX, fig. 18), and in addition in *L. lavigissima* (Lea), from Kansas. Lea describes it (Observ. X and XIII) from the same species and from *L. purpurata* (Lamarck).

These species stand in Simpson's system in the subgenus *Proptera* of *Lampsilis*. This has induced Sterki to believe that this shape of glochidium is common to all forms belonging to *Proptera*, and to elevate it, on that account, to generic rank.

Although I agree with Sterki in making *Proptera* a genus by itself, I would not place all species listed under Simpson's subgenus into it, for we have at least one species, which has a glochidium of a different shape. This is *Lampsilis (Proptera) gracilis* (Barnes) (See Pl. LXXXIX, fig. 19). Here the glochidia are *in shape* similar to those of the third type, to be described presently, but they differ considerably from them *in size*, for they are much smaller. In fact, the glochidia of this species are by far the smallest I know among our *Unionidæ*. The natural consequence is that we are compelled to create a new genus (*Paraptera*) for it.

In the shape of the glochidia *Lampsilis alata* (and the forms allied to it)

stands rather isolated, but the gaping margins are found at least in one other species, *Plagiola securis* (Lea) (See Pl. LXXXIX, fig. 17).⁸ Here the general shape is similar to the third type, but it is rather distinctly spatulate and quite large. I think that the glochidium of *Plagiola securis* is the only one which might be compared with that of *Lampsilis alata*, and it is rather significant that the only glochidium, which permits such a comparison, is found in a group, which, as we shall see later, is rather closely allied to *Proptera*.

The third type of glochidium is found in all the rest of the genera of Simpson investigated by myself. Here the shell is semicircular or semielliptical, the ventral margin evenly rounded, and no spines are present. With the exception of *Plagiola securis* the margins shut completely. There are minor differences in size and shape; as has been mentioned, those of *Paraptera gracilis* are very small (See Pl. LXXXIX, fig. 19). Of those of the genera *Quadrula*, *Pleurobema*, *Unio*, *Ptychobranchus*, and *Obovaria*, we may say, that they are generally rather small, while those of *Lampsilis* and *Truncilla* are somewhat larger.

The following is a list of the Pennsylvanian species, in which I have seen glochidia of this type: *Truncilla triquetra* Rafinesque (Pl. LXXXIX, fig. 24); *Truncilla perplexa rangiana* (Lea); *Lampsilis ventricosa* (Barnes) (Pl. LXXXIX, fig. 23); *L. ovata* (Say); *L. cariosa* (Say); *L. multiradiata* (Lea); *L. luteola* (Lamarck); *L. ligamentina* (Lamarck) (Pl. LXXXIX, fig. 16); *L. orbiculata* (Hildreth) (Pl. LXXXIX, fig. 22); *L. recta* (Lamarck) (Pl. LXXXIX, fig. 21); *L. nasuta* (Say); *L. iris* (Lea) (Pl. LXXXIX, fig. 20); *L. gracilis* (Barnes) (Pl. LXXXIX, fig. 19); *Obovaria circulus* (Lea) (Pl. LXXIX, fig. 15); *Plagiola securis* (Lea) (Pl. LXXXIX, fig. 17); *Ptychobranchus phaseolus* (Hildreth) (Pl. LXXXIX, fig. 14); *Unio crassidens* Lamarck (Pl. LXXXIX, fig. 6); *Unio gibbosus* Barnes (Pl. LXXXIX, fig. 7); *Pleurobema clava* (Lamarck) (Pl. LXXXIX, fig. 5); *Quadrula undulata* (Barnes) (Pl. LXXXIX, fig. 3); *Q. coccinea* (Conrad) (Pl. LXXXIX, fig. 4); *Q. rubiginosa* (Lea) (Pl. LXXXIX, fig. 2); *Q. subrotunda* (Lea); *Q. kirtlandiana* (Lea) (Pl. LXXXIX, fig. 1).

Other Pennsylvanian species, the glochidia of which are known to be of this type (See Lea, Observ. VII and X), but have not been seen by myself, are: *Lampsilis radiata* (Gmelin), *L. parva* (Barnes), and *Obovaria retusa* (Lamarck).

3. The breeding season.

Lea (Observ., II, III, VII, X) had already paid attention to the time of breeding of the *Unionidae*. Sterki (1898 and 1903) has pointed out that there are

⁸See footnote on page 300.

important differences between the different forms with regard to the time, when the marsupium is filled, and the present writer has devoted a special article to this topic as far as it concerns the Pennsylvanian species (*Nautilus*, 1909), which confirms and supplements Sterki's observations. Additional facts have been furnished by Conner (1909, p. 112).

Since the publication of my paper in 1909, I have made a large number of further observations, which generally serve to support my previous conclusions, and the microscopical investigation of the contents of the marsupia of soft parts at hand has added a number of more important facts. These new observations will be reserved for the systematic part, and will be treated under each species. Here I shall give only a condensed statement of the results obtained by Sterki and myself, and a few considerations as to their systematic value.

Among our *Najades*, we have in our latitude two types, *summer-breeders* and *winter-breeders*. Those belonging to the first class, have the marsupium filled only in summer, that is to say, in the period between the end of April and the beginning of August. Of course this indicates the extremes; for in the case of single species and single individuals the breeding season is much shorter; and the month of June, and the beginning of July is generally the time when most of these forms are gravid. The development from the egg to the glochidium takes place within a *very short time* (a few weeks), and, after the glochidia are formed, they are discharged immediately. The consequence is that individuals with glochidia are rather rarely found.

It is a remarkable fact, first pointed out by Sterki, that summer-breeders are found only in a restricted group of genera; and, as we shall see, this physiological character is *always* found in the forms belonging to this group. It is composed of the genera: *Quadrula*, *Pleurobema*, and *Unio* of Simpson, and, as may be seen from the description of their soft parts given above, these, according to their morphological characters, form a group by themselves. Likewise the genus *Margaritana*, which stands by itself in the system, seems to be a summer-breeder; at all events, Conner (1909, p. 112) found gravid females in June and August, but not in November and January, and I failed to find them in the beginning of May, the beginning of June, and on August 4. (At the latter date only one specimen was taken.) In Europe, *Margaritana* is known to breed in July and August (See Harms, 1907, p. 818).

All other genera are winter-breeders. In these the marsupia fill some time in summer, from July to September. The development of the eggs also takes place rapidly, and generally the glochidia are fully developed in September or

October. However, *they are not*, as a rule, *then discharged, but are carried through the winter in the marsupium, and are not set free till warmer weather sets in again, in April, May, or June of the next year.*

Among the winter-breeders we have in some cases the breeding season still more extended, so that in summer (June, July) the end of one season overlaps with the beginning of the next (of course, not in the same individual), and in such forms gravid females may be found all the year round.

In order to understand these conditions, we must inquire what are their essential features. Sterki used the terms *summer-* and *winter-breeders*, and he certainly was right so far as it concerns the species in our latitude.⁹ But in my opinion, the most important difference of the two groups is, that in the one case the breeding season is *short*, and the glochidia are discharged immediately, while in the other case it is *long*, and the glochidia are kept in the marsupium for a long time. This would be well expressed if we call the summer-breeders *tachytic* forms, and the winter-breeders *bradytic* forms.¹⁰ It seems to me, that the former condition is the primitive and original one, while the latter is apparently a special adaptation to the climatic conditions of higher latitudes. From this point of view we gain a rather satisfactory interpretation of the *raison d'être* of the two types, and also ascertain a very significant correlation between these physiological characters and certain morphological features.

If a short breeding season is the more primitive condition, we can understand perfectly well, that those *Najades*, which are *tachytic*, have also a comparatively primitive and simple morphological structure in their marsupium. This is actually the case in *Margaritana* as well as in *Quadrula*, *Pleurobema*, and *Unio*. On the other hand, in the forms with a long breeding season we should expect morphological adaptations conforming to it. And this is actually the case. In the *Anodontata*-group we have seen, that there exists a very complex structure of the marsupium, the purpose of which apparently is, to furnish a proper water circulation for the embryos enclosed in the marsupium (See above, p. 293), and in all members of this group the embryos stay a long time in the marsupium. In the members of the *Lampsilis*-group, which also are *bradytic*, the *Anodontata*-structure is not present. But we have become acquainted above with a peculiar bulging out of the marsupium, which apparently serves the same purpose, namely to bring the glochidia into closer contact with the water, since the membrane which covers this outbulging marsupium is very thin. But in addition, I shall describe below

⁹I know cases of exotic forms, which behave like summer-breeders, but do not breed in "summer."

¹⁰From $\tau\alpha\chi\nu\sigma$ quick, $\beta\rho\alpha\delta\nu\sigma$ slow, and $\tau\iota\kappa\tau\iota\kappa\sigma$ breeding.

certain other structures (flaps and papillæ of the edge of the mantle), which most emphatically serve for the aëration of the marsupium, and thus are to be regarded as adaptations to a long breeding season.

Having thus correlated physiological function with anatomical and morphological structures, we may rest assured, that we have discovered an essential principle in the development of the *Najades*, and we may say with all confidence that a systematic arrangement, which is founded upon such structures, which we are able to understand, must be the correct one. Sterki's discovery of summer- and winter-breeders, although originally not fully understood, thus becomes the most important step in our knowledge of the system of the *Najades*.

4. *The discharge of the Glochidia.*

As may be inferred from the above, the discharging of the glochidia must take place at two different seasons: in the bradytic forms in spring or early summer (April to June),¹¹ in the tachytic forms from the end of June to August. While this fact is beyond doubt, the manner of discharge remains yet to be investigated, and for some time this proved a serious puzzle to me. But now I am satisfied that my observations are complete enough to answer the question.

Lea repeatedly observed the discharge of the glochidia and placentaæ, but he only mentions that they come out of the shell at the posterior end (in *Lampsilis radiata*, *L. parva*, *Strophitus edentulus* (Observ. X), and *Unio complanatus* (Observ. II), and he further quotes (Observ. III) a similar fact as observed by Kirtland in *Quadrula cylindrica*. As we shall see, these observations are probably correct, and represent the normal conditions.

On the other hand, Lea (Observ. II, p. 52) reports that in a gravid female of *Anodonta fluviatilis* (= *cataracta*) he made the young come "from the orifice at the inferior part" (= edge) of the marsupium, by the pressure of his fingers upon the sides of the marsupium. I consider this not normal, but an artificial effect, in fact, there are no such "orifices."

Other authors do not treat of the discharge of the glochidia, except that Simpson (1900, p. 616) incidentally expresses the opinion, that in *Strophitus* the placentaæ are discharged through the walls of the gills, which, as I believe, is entirely wrong.

¹¹Sometimes it is postponed to the beginning of July, chiefly so in Lake Erie. Lea has repeatedly and in various species observed discharges during winter. These always took place, however, in the case of specimens kept in captivity under artificial conditions, which probably induced an abnormally early discharge. Since the glochidia of bradytic forms are fully developed in the beginning of the winter, artificial conditions (temperature for instance) might start the discharge at any time during the winter.

Considering the anatomical structure of the gills, and the fact, that the embryos are contained in the water-tubes, we should expect, *a priori*, that the discharge would take place by the natural channels. This would be by the way of the suprabranchial canals into the cloacal chamber, and thence outward through the anal opening of the mantle. And indeed, I have collected evidence for this natural discharge in a number of cases, which furnish positive proof of it. They are the following: In cutting up specimens of *Quadrula subrotunda*, on June 22 and 24, 1909, I repeatedly observed placentaæ coming out of the anal opening. Of course, this might be due to rough handling, but I have never seen them coming out at any other place, unless I forced them out by so strong a pressure, that the walls of the gills burst open. On June 24, 1909, I collected a good number of specimens of *Quadrula subrotunda* and *coccinea*, which I took home alive, and kept over night in a bucket with water. The next morning I saw quite a number of placentaæ floating in the water and was able to distinguish easily those belonging to the first species, which are subcylindrical and pink, from those belonging to the second, which are flattened (leaf-shaped or lanceolate) and white. On June 23, 1910, I took home a number of gravid *Quadrula coccinea*, and watched the discharge of the placentaæ. They distinctly came out of the anal opening. On June 24, I opened one of these specimens, and saw the placentaæ slowly moving out from the water-tubes through the suprabranchial canal to the anal siphon. While I was holding this specimen in my hand (with the shell opened and the left half of the mantle thrown back), four placentaæ moved out. The coming out was not by a jerk or a squirt, but was slow and gradual, as if carried by a steady current of water. A second specimen, opened shortly after this, exhibited the same phenomenon. On July 25, 1910, two specimens of *Pleurobema asopus* were found in the act of discharging placentaæ. One was seen in the water, with a number of pink placentaæ lying behind the posterior end of the shell, which were greedily devoured by a number of minnows. The other was taken home, and the discharge was observed at leisure in a basin of water. The pink placentaæ came slowly out of the anal opening, often in pairs, and sometimes, when the shell was squirting water out of the anal opening, a number of placentaæ were thrown out. Among my alcoholic material, there are several individuals, which were preserved in the act of discharging glochidia in the natural way. The best specimen is an *Anodontoides ferussacianus*, collected May 14, 1908, which has the posterior half of either marsupium empty (discharged), while the anterior half is yet full. Here I observe, that the suprabranchial canals of the marsupial gills are crowded with loose glochidia back to the cloacal cavity, and a mass of glochidia is located

in the anal opening. The dark brown color of the glochidia contrasts strongly with the whitish, semitransparent tissue at the base of the gills, and thus the suprabranchial canals are easily traced by this color. The same phenomenon was seen in a specimen of *Quadrula undulata*, collected July 8, 1909, where also numerous loose glochidia, but of whitish color, were found in the suprabranchial canals of all four gills. On May 13, 1910, a specimen of *Symplynota costata* was found, also in the act of discharging loose, brown glochidia through the suprabranchial canals. The glochidia were not plentiful in the canals. This specimen was not preserved. An additional case, corresponding closely to the instances just mentioned, was observed on July 12, 1910, in *Anodonta imbecillis*. Finally, I have observed in alcoholic material of five specimens of *Strophitus edentulus* collected April 22 and 24, 1908, a similar condition. But here there were whole placentæ as well as free glochidia in the outer suprabranchial canals, and in no case were they very numerous.

Entirely different from these are the following observations:

In a gravid female of *Ptychobranchus phaseolus* (collected August 31, 1906; probably unusually delayed in the discharge), there were on the margin of the right marsupium about half a dozen placentæ protruding through and beyond the edge, that is to say, in the act of escaping from the marsupium *through openings in the outbulging edge of the gill*. This peculiar fact suggested to me the idea, that the discharge of the glochidia might take place here not by the natural channels and the anal opening, but by breaking through the edge of the marsupium into the branchial cavity, and thence through the branchial opening into the surrounding water. I consequently made a careful search among my material for additional specimens caught in the same act, and I found indeed such evidence for this "unnatural" discharge. What I was able to ascertain is that there are actually, at the time of the discharge, *holes breaking through the edge of the marsupium*, which thus furnish an outlet for the glochidia. These holes may be seen macroscopically, and are also shown quite satisfactorily in some of my slides. The best slides I have are made from *Lampsilis luteola* and *multiradiata* (See Pl. LXXXVIII, figs. 18 and 20). But I also possess such from *Lampsilis nasuta* and *Obovaria circulus*, which show this feature, although less distinctly. I remember further, to have noticed macroscopically these holes in *Lampsilis alata*, but I did not succeed in obtaining a satisfactory slide, and I have a slide of *Lampsilis gracilis* (See Pl. LXXXVIII, fig. 16), which shows, as I believe, the closing up of these holes after the discharge of the contents of the ovisacs.

In 1910 I found similar instances. A specimen of *Ptychobranchus phaseolus*,

collected June 27, had most of the placenta $\ddot{\text{e}}$ discharged, but of the remaining few, some were protruding from the edge of the gill, exactly as described above. Females, discharging glochidia, and with openings in the edge of the marsupium, were seen in the following additional cases: *Lampsilis luteola*, May 6 and July 7 (on the latter date in several individuals); *Lampsilis ventricosa*, May 21 and June 23; *Lampsilis multiradiata*, June 23.

To all appearance, these holes are present only during the actual discharge of the placenta $\ddot{\text{e}}$ or the glochidia, and immediately after it, and close up again very soon, so that it is difficult in sectioning, to strike just the right point of the edge of the gill, where they are best visible, and this may account for my failure to obtain a greater number of good slides. It also should be remembered, that gravid females in the act of discharging, are naturally scarce among material, which was not collected with this question in view, and it is indeed astonishing, that I found so many instances supporting the assumption, that in the *Lampsilis*-group, that is to say, in those forms, in which the edge of the marsupium bulges out beyond the original marginal line of the gill, the glochidia are discharged, not by way of the natural outlets, but by breaking through the marginal wall of the gill. If this is so, a very important correlation is suggested: the anatomical peculiarities of the edge of the marsupium in these forms appear as a direct adaptation to the way of discharging the glochidia: *the edge of the marsupium is built for this purpose*.

Nevertheless this phenomenon should be further studied. I have given here my observations, and I think they are correct and conclusive, for I cannot imagine that conditions as represented in the figures 18 and 20 on Plate LXXXVIII are wholly artificial and abnormal.

From the above instances we see, as well as from some of the older observations of Lea, that in some cases the whole placenta $\ddot{\text{e}}$ are discharged, in others free glochidia. This is connected with the greater or lesser solidity of the placenta $\ddot{\text{e}}$ (See above, p. 298), but its systematic value is not very great; at any rate, each one of the greater groups contains examples of either method of discharge.

D. HERMAPHRODITISM.

Lea and others have demonstrated that most of our *Unionidæ* are *gonochorists*, and the existence of *hermaphrodites* remained doubtful, till Sterki found them. In a number of cases, hermaphroditism is occasional and exceptional, according to Sterki (1898, p. 30), and he names the following instances: *Quadrula rubiginosa*, *Q. pryamidata*, *Lampsilis parva*. But in another case, that of *Anodonta imbecillis* (Nautilus, 12, 1898, p. 87), he found that *hermaphroditism is the normal condition*.

Sterki decided this question by investigating the sexual glands. Since I have found that the sex of any individual may be determined by an examination of the gills, it should be possible, to recognize hermaphroditism by the structure of the latter, for in the case of hermaphroditism *no individual should be found exhibiting the male structure of the gills.*

This is indeed true, and I am not only able to confirm Sterki's observation with reference to *Anodonta imbecillis*, but in addition I think I have discovered among the Pennsylvanian species in *Sympnynota compressa* and *S. viridis*, two other cases in which hermaphroditism is at least the normal condition. The particulars are as follows:

Of *Anodonta imbecillis*, until toward the end of the summer of 1909, I found only 6 specimens (in May and beginning of June), every one gravid. On September 14, 1909, I collected a large number (about thirty) of this species in the outlet of Lake Leboeuf, which again were all gravid with one exception, and the latter proved, upon anatomical examination, to be also an individual with the female structure of the gills. At that time, I was aware of the existence of this question, and was looking out for males, but was unable to find any. In 1910 I collected only a single individual, but again a gravid specimen.

In the case of *Sympnynota compressa* my observations are not so positive, and only during 1909 and 1910 did I pay attention to this species with this point in view. I repeatedly collected specimens, which were not gravid, in May, June, July, and the beginning of August; but these might have been sterile females as well as males. I also collected four specimens, not gravid, on October 10, 1907 (together with gravid specimens). Of these I preserved two, believing them to be males; but upon investigation they proved to possess the female type of gills. During the month of September of 1908 I collected about twenty-five specimens, and among them there was not a single one which was not gravid. On August 18, 1909, I found about twenty specimens at one locality, and on September 27, 1909, about fifteen at another place. On these occasions I was hunting for males, but was unable to find any. On the latter date I found four very young specimens, which were not gravid. Three of these were preserved, but they also had the female gill-structure. In 1910 the result was the same. Of three specimens found every one had the female structure, or was gravid. However, from Professor Charles Brookover in Akron, Ohio, I received a specimen of *S. compressa* coming from Lake Erie, at Cedar Point, Ohio, which had the male anatomy of the gills. This is indeed very remarkable in view of the fact, that among all the specimens collected in Pennsylvania and preserved in alcohol or examined on the spot, there was not a single male, and that I was altogether unable to find a male in our state.

Of the hermaphroditic nature of *Sympynota viridis* I feel more confident. I received thirty-four specimens of this species, collected by Dr. Atkinson on July 11, 1908, and preserved the soft parts of fifteen of them. None was gravid, but they all had the female gills. In August, 1908, April, August, and September, 1909, I found this species repeatedly, altogether from fifty to sixty individuals, but all proved to be gravid, unless they were very young, and even in a number of the latter (in the second and third year of age) the female gill-structure was recognizable. In August, 1910, I collected altogether over one hundred specimens, and examined them in the field one by one, and every one had the female gill-structure. Thus in this case also I hunted in vain for males.

It would be a very strange coincidence, that I should fail to find males only in these two closely allied species, if they exist. In all other species of *Unionidæ* I never had any trouble in discovering males, provided there were more at hand than a few. In fact, it seems that the males generally slightly outnumber the females. Nevertheless I could not find them in the above cases, and even those sterile specimens, which I took home as males, turned out to have the female structure.

I therefore think that the conclusion is justified, that in these two species of *Sympynota* no males exist; and *that they are, as a rule, hermaphrodites*; although occasionally males may turn up, as is shown by the specimen from Cedar Point.

I should also add that the Carnegie Museum possesses from a branch of the Rio Grande at Mercedes, Hidalgo County, Texas, an *Anodonta*, belonging to the *imbecillis*-group, which probably is *A. henryana* Lea. There are seven specimens, and all were collected by Dr. Atkinson on May 15, 1907, and every one of them is gravid. Of course, the number is too small to express a final opinion, yet, according to my experience with other species, even among seven individuals we should expect to find both sexes. Thus in this case also it is suggested, that we have to deal with a hermaphrodite, which is also probable on account of the affinity of this species with *Anodonta imbecillis*.

I may possibly be able to give the results of further investigations of this question in the future.

E. SEX RECOGNITION IN THE YOUNG.

Sterki (1898, p. 29) has pointed out, that in young individuals, from two to four years old, the sexual glands are not developed, and that in those of the *Lampsilis*-type the sexual differences of the shells and the gills are not noticeable; there-

after, the marsupium begins to form, and with increasing age the number of ovisacs increases.

Since I have shown, that there are in the females of all species permanent differentiations of the marsupial gills, the question arises, whether these differences are observable at an early age, and I am able to report the following cases:

The smallest specimen of any species I ever investigated, in which the sex was recognizable, was a specimen of *Strophitus edentulus*, 17 mm. long. Here (See Pl. LXXXVI, fig. 10), in a cross-section, the septa of the outer gills were decidedly more crowded and more solid than those of the inner gills. However, the peculiar folding of the epithelium of the water-tubes (as shown in older specimens, see Pl. LXXXVI, fig. 7b) was not yet developed. This specimen upon the outer surface of the shell exhibited *one* growth-rest; assuming that this was formed in the first winter, this specimen would have been in its *second year*.¹²

Additional evidence, that in some species already in the *second year* the female structure of the gills begins to develop, is furnished by the following cases.

Anodonta grandis gigantea Lea. Here I found a young individual, 46 mm. long, but with only one growth-line, distinctly possessing the female structure (Pl. LXXXVI, fig. 14).

Sympnynota compressa Lea. A specimen, 44 mm. long, with only one growth-rest had the female structure fully developed.

Sympnynota viridis (Conrad). A number of young ones, of various sizes (18 to 31 mm. long), showed distinct traces of the female structure, and one of them (31 mm.) was even gravid (Pl. LXXXVI, fig. 11).

Besides these cases, I did not find the female type of gills in the *second year* in any other species, although I examined specimens of *Quadrula undulata hippopœa*, *Unio complanatus*, *Lampsilis ligamentina*, *L. multiradiata*, *L. ventricosa*, and *L. ovata*.

That specimens in the *third year* have the female structure, is shown in a specimen of *Sympnynota complanata*, 35 mm. long, with two growth-lines. Here the difference of the septa of the outer gill became very striking, when compared with a male, 54 mm. long, with three growth-lines.

¹²I am aware of the fact that the value of growth-rests for the determination of age has been disputed. It is, however, beyond doubt that during each winter a growth-line is formed. It is also established, that growth-lines may form at any other time, whenever unfavorable conditions prevail. But the latter are undoubtedly abnormal and irregular. In young specimens, we may safely assume, that the first few growth-rests, chiefly when they are regular, correspond to the stoppage of growth in winter. In older ones, it is more difficult to recognize the annual growth-lines, and to distinguish them from the accidental lines. Yet in well developed specimens they may be told apart. It may incidentally be mentioned here, that in shells from Lake Erie the growth-lines are often extremely regular, simply because in the lake accidental disturbance of the summer growth is very rare, and thus only annual lines are developed.

In *Quadrula undulata hippopaea*, I found a specimen distinctly of the female type, which was 36 mm. long, and had two growth-lines; here again the female structure became very evident, after a comparison was made with a male specimen, 34 mm. long, also possessing two growth-lines.

I have an individual of *Lampsilis nasuta*, 38 mm. long, with two growth-lines, which is gravid.

That absolute size is no proper criterion in this question, is shown, for instance, in the case of *Lampsilis iris*, of which I have a specimen 33 mm. long (smaller than in the instance just mentioned) which is gravid, but has at least three distinct growth-lines, and consequently would be at least in its *fourth* year.

All other females observed, sterile or gravid, had at least three growth-rests, and should be considered as being in their *fourth year* of age, or older.

Thus it becomes apparent, that the female structure, at least in some species, develops as early as the second year, and that one at least (*Sympynota viridis*) may already become sexually mature at this time. In others, the female structure is distinctly seen in the third year, and some of them (*Lampsilis nasuta*) may bring forth progeny. Later, from the fourth year onward, the time of maturity is reached in most of the species.

F. DIFFERENTIATING STRUCTURES OF THE EDGE OF THE MANTLE.

Simpson in the diagnosis of a number of genera states that the edge of the mantle is "double." According to my observations, it is double along its whole extent in *all* forms. While the outer edge is closely adjacent to the margin of the hard shell, and is always simple, the inner edge, which is generally parallel and close to the outer edge, is more or less expansile, and is able to fill and close the gap between the two halves of the shell, when the adductor muscles relax, that is to say, when the shell "opens." And further, this *inner edge* of the mantle is not uniform in its structure all along its margin, but shows certain differentiating structures, some of which are systematically valuable.

1. *The anal and branchial openings ("siphons")*.

The part of the edge of the mantle at and near the posterior end of the shell is modified so as to form what is known as the *anal* and *branchial openings*, the former lying more dorsally, and immediately above the latter. They are formed by the mutual approach of the edges of the inner mantle at certain points, and sometimes by their coalescence. The two openings are separated from one another by the diaphragm, discussed above (See p. 288), composed of the posterior ends of

the gills, which serve to draw the mantle together, although, in our species, the two sides of the latter never unite at this point (Compare fig. 4, on p. 289). The part above this point is the *anal opening*, which forms the outlet for the supra-branchial canals and the cloacal cavity (with the anus). Its upper (dorsal) boundary will be discussed below (see supra-anal opening).

Below the diaphragm is the *branchial opening*, which leads into the branchial chamber, into which the gills hang down. Its lower or anterior boundary is marked by slightly projecting lobes of the inner edge of the mantle (often indicated only by a curve reaching from posterior to the lower margin), which approach each other, and beyond which the edges of the inner mantle touch each other, but without growing together.

Anal and branchial openings generally possess on the inner edge peculiar crenulations, teeth, or papillæ, which were already studied by Lea, who took special pains to describe them accurately, believing that they might be of systematic value. He lays great stress upon the presence or absence of papillæ on the inner edge of the *anal siphon*. But according to my observations, this is not an important feature. There may be papillæ, which may be larger or smaller (always smaller than those of the branchial opening), and they pass gradually into fine teeth, scallops, or crenulations; or the edge may be practically smooth. Sometimes the teeth, or crenulations, appear different according to the state of preservation.

In most cases crenulations (wrinkles or small folds), fine teeth, or very fine papillæ are present. A smooth or almost smooth edge is found principally in the following forms: *Quadrula metanevra*, *Q. cylindrica*, *Q. tuberculata* (Rafinesque), *Anodonta grandis*, and *A. imbecillis*. In *Anodonta cataracta* I found crenulations of very variable character. On the other hand more distinct papillæ appear in *Pleurobema clava*, *Unio crassidens*, *U. gibbosus*, *U. complanatus*, *U. productus*, and *Anodontoides ferussacianus*.

The *branchial opening* always has papillæ, and they offer, although slightly varying in their development, no remarkable differentiations. They may be simpler or more complex (arborescent), and may be larger or smaller.

2. *The supra-anal opening.*

In most of our species, the upper part of the anal opening is separated from the anal by a complete union of the inner edges of the mantle, and is called the *supra-anal opening* (See fig. 4, on p. 289). This opening communicates under the united edges of the mantle with the anal opening, and its purpose is rather obscure. I am inclined to believe, that the connection of the edges of the two halves of the

mantle is the essential feature of this structure, which serves to close and define the anal siphon dorsally, while the upper opening (supra-anal), which remains unclosed, is only incidental to this, so to speak a by-product.¹³

There are a few forms, in which *no supra-anal opening* is present, that is to say, where the edges of the mantle do not at all coalesce. In our state, we have only two such forms, *Margaritana margaritifera* (See fig. 6, p. 289) and *Quadrula (Rotundaria) tuberculata*, and in each of them, we have a large, single, undivided anal opening. This feature was known previously, and in my opinion is rather significant, as showing the preservation of a primitive condition.

In all other forms, there is a connection of the margins of the mantle separating a supra-anal from the anal opening. Yet in a number of species this connection is very short, and sometimes deciduous; or it may be torn easily, or may be occasionally altogether absent. I have observed specimens with this connection missing in the following species: *Quadrula subrotunda*, *Q. rubiginosa*, *Q. coccinea*, *Q. obliqua*, *Q. undulata*, *Pleurobema œsopus*, *Unio crassidens*, and *U. gibbosus*. But on the whole, such specimens are rare and in all of these species I have found other individuals with this connection present. In some cases it seemed that this connection was naturally lacking, while in others it had been apparently torn apart by rough handling, which may happen easily, since in all these cases the connection is very short.

In other instances the connection is a little longer, but it is generally situated so that the supra-anal is a good deal longer than the connection, and than the anal opening. This condition of a rather short connection is found in all species not mentioned here as possessing a different conformation.

In certain forms the connection of the mantle becomes somewhat longer, so that it is about as long as the anal opening, and also about as long as the supra-anal. I have observed this in *Alasmidonta undulata*, *Sympnynota complanata*, and *Anodontoides ferussacianus*.

In still other forms the connection becomes rather long, restricting the supra-anal a good deal, so that the latter is distinctly shorter than the connection, and hardly longer than the anal opening. These species are *Anodonta grandis* (fig. 4, p. 289), *Anodonta cataracta*, and *Anodonta imbecillis*.

Finally, in one case, that of *Lampsilis parva*, I found the supra-anal opening entirely closed. Of this I have only three specimens, and in one I think I have seen a very small supra-anal opening, while in the other two the inner edges of the

¹³In rare and individual cases, there is a double connection. Lea mentions a few such instances, and I have observed the same thing in *Obovaria retusa*. I consider this an abnormality.

mantle were entirely connected as far as the posterior dorsal end. Of course the outer edges of the mantle remain separated, and if only superficially investigated, the appearance of a slit-like supra-anal, identical to that of other forms, is imitated.

3. *The edge of the mantle in front of the branchial opening.*

Anterior to the branchial opening the margin of the mantle is originally without any special differentiation. The two edges are about parallel and close together to the anterior end of the animal, and do not possess any appendages in the shape of papillæ and the like. At most the inner edge is slightly crenulated, scalloped, or wrinkled, and the latter appearance often depends on the state of preservation (it becomes wrinkled by strong contraction in alcohol). The commonest condition is when the papillæ of the branchial opening suddenly become small, assume the shape of crenulations, which soon disappear, and thenceforward the inner edge appears more or less smooth. The margin of the mantle (the part under both edges), which is thickened at the branchial opening, thins out gradually, and the thickening is hardly any longer noticeable at a short distance in front of the branchial opening.

This condition is seen in all species investigated belonging to the following genera of Simpson: *Quadrula*, *Pleurobema*, *Unio*, *Tritogonia*, *Alasmidonta*, *Strophitus*, *Sympnynota*, *Anodontoides*, *Anodonta*, and *Ptychobranchus*.

In *Margaritana* Lea (Observ. VII, Pl. 29, fig. 104) has figured strong, papillæ-like crenulations on the edge of the mantle for a considerable distance in front of the anal opening. He does not give a detailed description of this structure in the text. In the specimens in my possession I find that the inner edge of the mantle in this region is strongly wrinkled and crenulated, the crenulations passing posteriorly into strong papillæ, such as are usually found at the branchial opening. I do not regard this as a special differentiation of structure, but it rather appears to me to be a forward continuation of the papillæ of the branchial opening; so that we should in this case regard the branchial opening as less distinctly defined anteriorly. In fact I cannot discern any sharp demarcation of the latter, such as is seen in other species. The branchial opening in *Margaritana* is ill defined, and passes gradually into the anterior margin of the mantle, a condition which again emphasizes the primitive character of this genus.

There remain a number of genera, which are characterized by the peculiar structure of the marsupium, and in which it is restricted to the posterior part of the outer gills, and projects beyond the margin of the latter. These are the genera *Obliquaria*, *Plagiola*, *Obovaria*, *Lampsilis*, *Micromya*, and *Truncilla*. Among these we meet with interesting special structures on the edge of the mantle.

As has been said, *Ptychobranchus*, which is also associated with these genera, has the normal structure. The same holds true of *Obliquaria*, *Plagiola*, *Obovaria*, and certain species of Simpson's *Lampsilis*, namely: *L. ligamentina*, *alata*, and *gracilis*. But the beginning of a differentiation is here indicated. In all these the thickening of the margin of the mantle is more distinct, and extends farther forwards, sometimes as far as the middle of the ventral margin, where it disappears rather suddenly. Along this thickening we observe the inner edge of the mantle as a distinct keel, which is more or less crenulated or toothed. These teeth, which are the continuation of the papillæ of the branchial opening, are also sometimes found for a short distance in normal cases, as described above; in the present genera, however, they extend farther forward, generally as far as the thickening of the margin of the mantle, and disappear beyond, or give way to mere crenulations. *But in no case do these teeth assume the shape of papillæ*, or appear as the main feature of this structure. They are rather elements accessory to the edge of the mantle itself, which is a narrow keel or lamella, projecting from the thickened margin of the mantle. This lamellar, projecting character is most evident in *Lampsilis alata* and *gracilis*.

This structure of the edge of the mantle is present in both male and female, but it is generally more distinct in the female, chiefly so far as it refers to the thickening of the margin of the mantle and the size of the crenulations or teeth.

While we may say that in these forms the structure of the margin of the mantle is practically normal, except that its thickening, and the crenulations of the inner edge are more emphasized; we find in the remaining species of *Lampsilis*, and in *Micromya* and *Truncilla*, other and more strongly pronounced differentiations, and there are two types observable within the genus *Lampsilis* (including *Micromya*), while in *Truncilla* peculiar conditions prevail.

The first type is found in the following species: *Lampsilis parva*, *iris*, *nasuta*, *recta*, and *Micromya fabalis*. In these the thickening of the margin of the mantle is rather pronounced, and along it runs the inner lamelliform edge, which, however, is not simply crenulated or toothed, but possesses *distinct, well developed, conical, more or less regular papillæ*, which are rather sharply distinguished from the irregular, crowded, or massed papillæ of the branchial opening. These papillæ run forward in various extent, and disappear rather suddenly; generally with the disappearance of the thickening of the margin, and give way to the normal crenulations or the normal smoothness of the anterior edge. In the different species, the papillæ show the following peculiarities:

Lampsilis parva. In this species, Lea already had described and figured (Observ. VII, Pl. 29, fig. 102), what he called a "caruncle" on the edge of the mantle, just in front of the branchial opening. This is according to him a black, spongy mass, which, being quite expansible and retractile, may assume various shapes. In the three gravid specimens before me, I see a group of black, projecting papillæ standing upon the marginal thickening of the mantle, which extends about as far as the middle of the ventral margin of the mantle. This group of papillæ is rather short, and resembles indeed a "caruncle," yet does not differ in any essential respect from the structures, which will be described in the other species belonging here. It is composed of from four to six larger, and some smaller papillæ, and in front of it the inner edge is smooth.

Micromya fabalis. Lea (Observ. X) calls the edge of the mantle below the branchial opening "fringed," and Simpson (1900, p. 525) says in the generic diagnosis of *Micromya*, that it is "fringed," and in the female is "developed into a flap with a distinct, toothed ridge inside." In the only (sterile) female of *Micromya fabalis* I have seen, the structure of the edge of the mantle is similar to that of *Lampsilis parva*, only the group of papillæ extends farther forward, but not quite as far as the thickening of the margin of the mantle. The number of papillæ is greater. There are from eight to ten larger ones, and a few smaller ones, and they are further apart from each other than in *L. parva*. In the male the same structure is present, but the thickening is very slightly developed, and the papillæ are decidedly smaller, and occupy a shorter space on the edge.

Lampsilis iris. The mantle of this species (as *novi-eboraci*) has also been described by Lea (Observ. X) as "fringed," and he says that there are large, distant papillæ. This is quite correct. I observe in my specimens, that in the female there are from four to ten (according to age) very large, conical papillæ upon the inner edge of the mantle in front of the branchial opening. There are a few smaller papillæ between the larger ones, and the latter are rather remote from each other, and are placed at irregular intervals. This row of papillæ extends forwards for a considerable distance, but not quite as far as the middle of the ventral margin. It stops very suddenly, and beyond this point the inner edge of the mantle is only finely crenulated or smooth. In the male, the papillæ are much smaller.

Lampsilis nasuta. The female agrees with that of *L. iris* in the presence of papillæ, but the latter are very small, fine, and crowded, forming a rather regular row, running forward almost to the middle of the ventral margin, where they disappear rather gradually, and pass into the smooth anterior part of the inner edge of the mantle. In this species the inner edge in front of the branchial opening is

more lamellar, and the papillæ form merely a fringe on this narrow lamella. In the male of this species, the papillæ are extremely small.

Lampsilis recta. The female is like that of *L. nasuta*, but the papillæ are much larger (sometimes with two tips), rather regular, and form a crowded, very distinct row, which stops quite suddenly at about the middle of the ventral margin. The largest papillæ stand just at the point where they stop, but the difference in size is not very great, and the increase in size is slight in the postero-anterior direction. The strong development of the papillæ makes the inner edge of the mantle, on which they stand, appear as distinctly projecting beyond the irregularly crenulated or smooth anterior part. In the male, the margin of the mantle is less thickened, and the papillæ are much smaller, yet they are present.

The second type of development of the inner edge of the mantle, found in the genus *Lampsilis*, is observed in the following species: *L. luteola*, *radiata*, *orbiculata*, *ventricosa*, *ovata*, *multiradiata*, and *cariosa*. Here the specialization is shown not by a development of papillæ, but the inner edge itself is greatly enlarged. It forms a *rather broad, lamellar keel*, which stands upon the thickened margin of the mantle, possesses great powers of expansion and retraction, and occupies a considerable distance from the branchial opening forwards, as far as to about the middle of the ventral margin. Here the lamella suddenly stops, but is prolonged anteriorly into a *free, longer or shorter, ribbon-like flap*, which also may be expanded to a considerable length and again retracted.

This peculiar "flap" has been noticed by Lea in several species (*radiata*, *luteola*, *ventricosa*, *ovata*, *multiradiata*). He also has observed that there is, in some forms on the posterior end of the lamellar expansion, right in front of the branchial opening, a very curious "eye spot" (dark, round spot, upon a light background).

Simpson mentions this character for his section *Lampsilis* of the genus *Lampsilis*, and says also that in the section *Eurynia* it is "sometimes" present. All of the species of the first section known to me possess it, but not all of the second one. Apparently Simpson did not attribute much value to this feature, and he says that it is found only in the female, and during the breeding season. According to my experience, however, it is a regular character of all species, where it is observed; and is found not only in the female, but also in the male, although in the latter only in a rudimentary condition. I have been able to make it out in all males investigated. I consider it a very important systematic character, which is connected with the aeration of the embryos in the marsupium, and consequently developed at its best in the female during the breeding season, but it is permanently present. Probably also in the other species of *Lampsilis* described above the corresponding papillæ have the same physiological function.

Lea has figured this "flap" of *Lampsilis radiata* (Observ. II, Pl. 15, figs. 48 and 49) and of *L. ventricosa* (Observ. VII, Pl. 30, fig. 107), and he calls special attention in *L. radiata* to its different shape in different individuals. Indeed in his two figures (figs. 48 and 49), there is a great difference in so far that in fig. 48 the anterior prolongation of the flap is not seen. But disregarding the possibility that this figure may be inaccurate,¹⁴ the condition shown in fig. 48 may be either abnormal, or the anterior end of the flap may be injured, or it may not be fully expanded. (I think the latter is very likely the case.) Fig. 49 is rather correct, and also the figure of the flap of *L. ventricosa*.

I have repeatedly observed this flap in life, and have seen it in function. I made the best observations in the case of *L. ventricosa* and *multiradiata*. When the animal is undisturbed, and the posterior end of the shell is gaping, we notice, in the gravid female, that the marsupia, which are easily recognized, are pushed outward, so that they project even a little beyond the shell (already observed by Lea). They show below and in front of the branchial opening (See fig. 7). The lamellar expansions of the inner edge of the mantle occupy exactly the place, where the marsupia are visible, and are expanded on both sides of the latter, projecting beyond the margin of the shell and beyond the marsupia, forming a lateral wall on each side of the latter. In addition, the free flaps are fully expanded, appearing as prolongations of the lamellar portions, floating free in the water. This whole apparatus performs rhythmical, wave-like contractions, beginning at the posterior end, and ending at the free tips of the flaps. The contractions follow each other in quick succession (two to three in a second), and must produce a very lively current of water over the exposed edges of the marsupia. The position of the shell being generally much tilted, the animal almost "standing upon its head," and the shell being directed with its anterior end against the current, the flaps float horizontally in and with the current. I once (Sept. 15, 1909) had a chance to depict the flaps in action, standing knee-deep in the water of the Allegheny

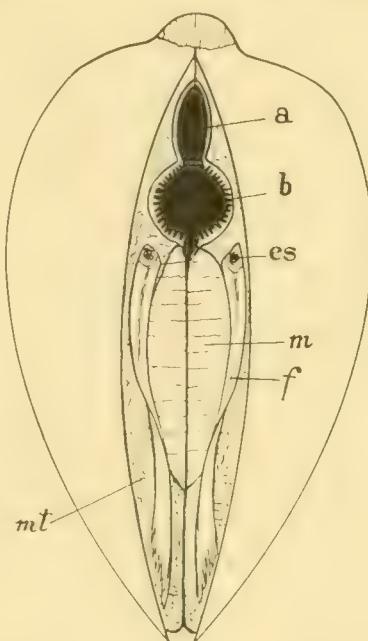


FIG. 7. *Lampsilis ventricosa* (Barnes).
Shell of gravid female, seen from above and
behind, showing: a, anal opening; b, bran-
chial opening; m, marsupia; mt, mantle;
and f, mantle flap in front of branchial
opening.

¹⁴This is suggested by the generally poor character of the figures on this plate, which are extremely superficial and unsatisfactory.

River, at Warren, Pa. The figure here given (fig. 7) is a reproduction of this sketch. It represents a shell as seen from above, with its hind portion turned up. Allowance must be made for the difficult conditions, under which this sketch, which is rather diagrammatic, was made.

The general shape of the lamella and flap in *L. ventricosa*, is ribbon-like, much longer than wide, and the free anterior projection is rather long. It arises rather suddenly at the posterior end near to and immediately in front of the branchial opening, forming there an angle, at which the eye spot is situated. The edge of the ribbon (inner edge of mantle) is, when expanded, rather smooth, but there are, chiefly toward and at the free anterior lobe, a few irregular teeth, which give to this lobe a lacerated appearance. These teeth are quite variable. When contracted, the edge is wrinkled and crenulated, and the free lobe is much shorter, triangularly pointed or rounded off. Immediately in front of the lobe, the inner edge has a few small teeth, or it is scalloped, and becomes smooth anteriorly.



FIG. 8. *Lampsilis ventricosa* (Barnes), female. Right Mantle Flap, seen from inside.

This peculiar lamella or flap is also distinguished by its color. In *L. ventricosa* it is gray on the outside; on the inside it is a beautiful pale orange, with a blackish longitudinal line (See fig. 8). The thickened margin of the mantle between the inner and outer edge is also pale orange, or light brown, with black mottlings.

Together with the eye spot, mentioned above, and with the whitish marsupium with its black markings on the edge, being visible between the flaps, the whole aspect of these parts in the living shell in this condition becomes rather attractive.

In the male the lamella and flap are similar, but smaller in all dimensions, the colors are less sharply defined, and the free lobe is very small, yet distinctly present.

Practically the same apparatus is seen in *L. ovata*, *multiradiata*, and *cariosa*, only in the two latter species the teeth of the edge are more numerous, and the black line is often missing in *L. ovata* and *cariosa*. Altogether there is much variation in the intensity of the color, the light parts shading from deep brown to light orange. The eye spot is always present in the female, but indistinct in the male. In alcoholic material, of course, the colors largely fade.

In *L. orbiculata* the same flap as in *L. ventricosa* is developed quite typically; in alcoholic material a distinct black line is seen, and between this line and the edge the flap is rather dark black. The only difference is that here the teeth along the edge are more numerous and more crowded, increasing in size in the postero-anterior direction. *L. orbiculata* generally is placed with *L. ligamentina* in the

system, but I think, according to the above observation, that it has no closer relationship with this species. The latter has no trace of a flap, in fact, it hardly shows any differentiation on the edge of the mantle. *Lampsilis ligamentina* is no *Lampsilis* at all. It is true, the males of these two species are very similar; but this is not true of the females. The peculiar shape of the female shell of *L. orbiculata* is quite remarkable, and entirely unlike that of the female *L. ligamentina*.

Lampsilis luteola and *radiata* possess a similar flap, and are practically identical with each other in this respect. Here the edge of the ribbon possesses numerous, irregular teeth, increasing in size toward the anterior free lobe; and further, there are distinct teeth on the inner edge of the mantle in front of the free lobe, diminishing in size anteriorly till the edge becomes almost smooth. In the male, the anterior end of the flap is indicated by large teeth, which gradually pass into the scalloped and smooth anterior edge, and again all parts are smaller in the male, and less typically developed. On the inside of the flap and lamella there is a broad band of black color, and there is also an eye spot posteriorly, but this is hard to see in contracted alcoholic material.

There remains the genus *Truncilla* to be discussed. In *T. triquetra* we see conditions, which somewhat approach the first group of *Lampsilis*, where there are papillæ in front of the branchial opening. The swelling of the margin of the mantle is distinct, but does not extend far forward, and the inner edge along the swelling possesses a number (four to six) of conical papillæ, which are not very large, and are followed farther forward by a number of still smaller papillæ diminishing in size. In front of these the edge is smooth. But in this species we see a feature in the female, which, although not very striking, distinctly indicates the beginning of the most prominent peculiarity of *T. perplexa rangiana*, to be discussed below. The inner edge of the mantle, where it carries the papillæ, is not quite close and parallel to the outer edge, but runs at a certain distance from the latter, and the space between the two edges has a peculiar spongy structure. This spongy structure is also developed to a certain degree in the species of *Lampsilis*, but it is not so markedly restricted to the posterior part of the margin, just in front of the branchial opening. In the male of *T. triquetra* the two edges are almost parallel and close together, and the papillæ of the inner edge are rather small. While in the female *T. triquetra* the separation of the inner edge from the outer is barely indicated, this condition furnishes the most striking feature in *T. perplexa rangiana*. Lea already described it (Observ. X), and Simpson (1900, p. 516) mentions it in the generic diagnosis, but without having properly understood this structure. In the female of *T. perplexa rangiana*, the inner edge of the mantle is

posteriorly, in front of the branchial opening, *widely separated from the outer edge*, and approaches the latter again at about the middle of the ventral margin. In the space between the two edges, the margin of the mantle is thick, white, and spongy, and of a peculiar structure. Thus the inner edges cut off in part a *separate chamber within the shell* at the posterior lower end of the latter. Along the inner edge in this region are fine papillæ, the largest behind, diminishing anteriorly, and becoming effaced before the edges come together again. Farther in front, the inner edge is smooth. In the male of this species, this peculiarity is not found. In this sex the two edges are almost parallel, and the papillæ of the inner are extremely small. There is no doubt, that this structure also has something to do with the aëration of the glochidia during the prolonged breeding season. But its particular action should be further studied.

I have tried to find other features of the soft parts, which might offer differentiations available for the general systematic arrangement of the *Najades* of our region, but was not successful. Thus, for instance, as Lea has already pointed out, the palpi show certain differences, but these are rather slight, and of no systematic value, and it is not necessary to give a detailed description of the latter.

We are now ready, to discuss the general system of our *Najades* with reference to the characters described above.

PART II. THE SYSTEM OF THE NORTH AMERICAN NAJADES.

A. DIVISION INTO FAMILIES AND SUBFAMILIES.

In the course of the preceding investigation of the soft parts we took occasion to point out that *Margaritana margaritifera* is unique among our mussels. In fact some of the anatomical characters are so unusual, that this species appears as a stranger in our fauna, differing fundamentally from all other species. The most striking features are: (1) the absence of water-tubes in the gills; (2) the peculiar conformation of the diaphragm at the posterior end of the gills. There is not a single species among those which I have investigated, which shows even an approach to the structure seen in *Margaritana*, and the first one of these is something quite unexpected in so far that it does not conform at all to the type of gill-structure, as laid down in the text-books.

In addition, the lack of a separate supra-anal opening and the incomplete demarcation of the anterior boundary of the branchial opening present additional peculiarities. Further, although I have not seen gravid females, and am unacquainted with the marsupium and the larvæ, these are known in the European

Margaritana through the studies of Harms (1907, pp. 817 and 818). The marsupium is formed by all four gills, and the glochidium is apparently of the *Quadrula*-type.¹⁵ These characters we must regard as expressing a distinctly primitive type of development in the case of *Margaritana*.

All this is sufficient to impress upon *Margaritana* the stamp of oddity and singularity, which justifies us in saying that this form stands by itself in the system, and should not be associated with any other form. This is best expressed by creating a family for it (*Margaritanidae*).

Yet there is possibly another species, which may go with it, *Margaritana monodonta* (Say). The soft parts of this have been described by Lea (Observ. X), and as far as the description goes, we may say that it agrees with *Margaritana margaritifera*. Lea especially emphasizes the peculiar diaphragm and the absence of a defined supra-anal opening.

Leaving the genus *Margaritana* aside and turning our attention to the rest of our *Najades*, we find that the most prominent differentiations are found in the sexual apparatus, and chiefly in the general form and the finer anatomical structure of the marsupium. This part of the anatomy has been used by Simpson for his system. But his classification only serves in part to bring out the natural affinities. Summing up what has been discussed above, we are led to distinguish three groups among our *Unionidae* according to the structure of the gills.

1. In some the water-tubes of all or of some gills serve, in the gravid female, as ovisacs (receptacula for the ova and embryos). Their only differentiation is in the development of the septa separating the ovisacs, which more closely approach each other, are stronger, and possess a folded epithelium, adapted to the swelling of the marsupial gill in the breeding season. There are no other modifications, and the edge of the marsupial gill is not changed, and always remains sharp. It goes without saying, that this is clearly the most primitive type of the three. There are no special adaptations to an extended breeding season, and the latter is short in all these forms,—they are tachytic. This type is found in Simpson's genera *Unio*, *Pleurobema*, *Quadrula*, and *Tritogonia*.

I have given above the essential characters of the soft parts. Of less importance are the following: marsupial gill little or only moderately swollen in the breeding season; marsupium either formed by all four gills, or only by the outer gills in their whole length; supra-anal opening only in rare instances not separated from the anal, generally well defined by the connection of the margins of the

¹⁵Harms (p. 820) describes "rather strong" hooks in the glochidium, but in his figure (p. 818, fig. 4) there are only mere traces of them, and they cannot be compared, by any means, with those of the *Anodonta*-glochidium.

mantle, which is rather short, and leaves a supra-anal of considerable length; branchial opening rather well defined anteriorly; no papillæ or special structures on the edge of the mantle in front of the branchial opening; inner lamina of inner gills free from the abdominal sac;¹⁶ glochidia imbedded in rather well developed placentæ, or placentæ poorly developed; glochidia small or of medium size, semicircular or semielliptical, with rounded ventral margin, and without spines. The discharge of the glochidia is by the natural channels through the anal opening. These forms are tachytictic.

With regard to the characters of the shell little can be said, for the shape of the shell is very variable. Generally the shell in this group is rather heavy, from more or less rounded to more or less elongate. The colors of the epidermis are dull or brighter, rarely with bright markings (rays); sometimes peculiar, odd shapes of the shell are met. The sculpture of the beak is variable, concentric, or with indications of double loops, or pustulous, or even with traces of zig-zag sculpture toward the disc. Very often the sculpture of the beak is obsolete; hinge always complete, with well developed teeth, often quite heavy; male and female shell in most cases absolutely undistinguishable.

Remarks: It is practically impossible to recognize this group by shell characters, although there are certain peculiar types of shell, which are found in this group alone. Simpson failed entirely to recognize the close affinity of the genera belonging to this group, and places them in three different divisions of his system, bringing his *Unio* and *Pleurobema* together with the *Anodonta*-group, with which there is no close relationship whatever, and removing *Tritogonia* entirely from them. The genera of Simpson's system belonging here cannot be maintained as defined by Simpson, and material changes will be necessary as will be shown hereafter.

2. The second group comprises the following genera of Simpson: *Strophitus*, *Anodonta*, *Anodontoides*, *Sympnynota*, and *Alasmidonta*.

Here each ovisac of the gravid female is not formed by a whole water-tube, but only by a part of it, the middle one, which is separated from two lateral canals by a folding up of the epithelium of the septa. In addition, the ovisacs are closed above at the base of the marsupial gill, thus forming a completely closed sac within each water-tube. In one case (*Strophitus*) this sac is again divided into secondary compartments. The edge of the marsupial gill becomes adapted to the swelling of the gill in the breeding season, and gives way, the two laminæ drawing apart;

¹⁶This holds good only for the Pennsylvanian species examined by me. In exotic forms belonging to this group, the inner lamina may be connected with the abdominal sac (See *Nautilus*, 23, April, 1910, p. 139).

and there is heavy tissue at the edge capable of being stretched out. This causes a rounded or truncated edge in the charged marsupium. This peculiar structure of the marsupial gill is developed only in the gravid female, and is absent in the sterile female.

These characters are apparently connected with the prolonged breeding season, and the peculiar secondary water-tubes serve for the aération of the embryos in the marsupium. The stretching of the edge of the gill is easily understood.

Other characters are the following: marsupial gills always extremely swollen and marsupium always formed by the outer gills alone in their whole length; supra-anal opening well separated from the anal; the separating connection of the margins of the mantle well developed, sometimes short, but normally somewhat longer, and even quite long, thus leaving only a short slit for the supra-anal; branchial opening well defined anteriorly; no papillæ or other special structures on the edge of the mantle in front of the branchial opening; inner lamina of inner gills free from the abdominal sac, more rarely more or less connected with it; glochidia very remarkable, and furnishing a very important character of this group. They are generally very large, subtriangular, in rare instances almost semicircular in shape, and are more or less pointed in the middle of the ventral margin, where they possess a peculiar spine or hook (this spine is undeveloped in very young glochidia). The glochidia are sometimes imbedded in well developed placentæ or placentulæ. Sometimes the placentæ are poorly developed, or the glochidia appear completely isolated. The discharge is by the natural channels and the anal opening, and these forms are bradyticic.

The essential characters of this group are found in the shape and structure of the marsupium, which represent adaptations to the extreme swelling of the latter, and to the long breeding season, for all forms belonging here are bradyticic. The formation of lateral water-canals in the marsupium undoubtedly is a device to provide proper aération for the glochidia enclosed so long a time in the marsupium. Whether the special hooks of the glochidia are connected with a differentiation of function from that in the *Quadrula*-group is yet unknown.

The shell of the forms belonging to this group is never very heavy and solid, and never distinctly rounded, but it is more or less elongate, rather thin, often with distinctly colored epidermis (banded and rayed). The sculpture of the beak is of two types: either more or less distinctly double-looped, or concentric; in the latter case often very heavy. The hinge-teeth have a distinct tendency to become obsolete. They are present in some forms, but are then often of peculiar shape, and in others they exhibit all stages of reduction to complete disappearance.

The male and female shells are generally quite undistinguishable, only in rare cases is there a slight differentiation.

Remarks: The genera belonging here stand together in Simpson's system, but associated with others, which do not belong here, and the essential characters of this group have been entirely overlooked. Sterki has correctly recognized their natural affinity, relying chiefly upon the remarkable shape of the glochidium. But, as we have seen, there are additional characters in the gills of the gravid female, which are common to all these forms, which are so peculiar, and so strongly marked, that there cannot be the slightest doubt, that this is a natural group.

3. All the remaining genera form a third group, and are more closely allied to each other than to any one of the groups thus far discussed. This comprises the following of Simpson's genera: *Truncilla*, *Micromya*, *Lampsilis*, *Obovaria*, *Plagiola*, *Obliquaria*, *Cyprogenia*, and *Ptychobranchus*.

They all agree in that here again each ovisac is formed by only one water-tube, and that this remains simple. But we have here a special structure at the edge of the gills, which permits a bulging out of the ovisacs beyond the original edge of the gills, and this causes a projection of the marsupial gills beyond the original edge, indicated by the ends of the gill-filaments. The swelling of the marsupium takes place chiefly at and near the edge of the gill, and since near the base no swelling in a longitudinal direction is possible, the arrangement of the ovisacs often is fan-like, they being narrower and thinner near the base, and thicker (club-like) toward the edge. This necessarily causes a folding of the edge of the gill, which is most pronounced in one genus (*Ptychobranchus*), where the whole outer gill is used as marsupium. In all other genera it is only the posterior section of the outer gill, which serves as marsupium (sometimes only part of this section); and here the marsupium is almost kidney-shaped and forms only a single, irregular fold with the non-marsupial anterior part, and sometimes a smaller fold with a posterior non-marsupial section of the gill. The edge of the marsupial gill is peculiarly beaded, the beads corresponding to the protruding ovisacs, the furrows between them to the septa on the inside of the gill.

The marsupium is generally much swollen, and the ovisacs are rather large, and, toward the edge, rather sharply defined externally; supra-anal opening always well separated from the anal; the connection of the mantle generally short or of medium length, leaving a rather large supra-anal opening; only rarely is the latter small, or entirely closed; branchial opening well defined in front; anterior to it there may be no special structures, or such may be present in the shape of papillæ or flaps on the mantle edge; inner lamina of inner gill generally entirely connected with the abdominal sac, more rarely partly or almost entirely free.

Glochidia generally of medium size and normally of simple shape, semicircular or semielliptical, without spines; yet in certain forms peculiar glochidia are found (See p. 301). Placentæ more or less well developed, but often atrophied, so that the glochidia appear free. The discharge of the glochidia takes place in an unusual manner, through the edge of the marsupium.

The essential characters of this group (marsupium and edge of mantle) undoubtedly are connected with the prolonged breeding season (all these forms are bradytic), and with the unusual manner of discharging the glochidia. The soft parts are built according to a special plan, which is adapted to this peculiar discharge, and facilitates the proper aeration of the glochidia during the long breeding season, but this latter adaptation is different from that seen in the *Anodonta*-group serving the same purpose.

Shape of the shell very variable, round and heavy, or more or less elongated and lighter. Color of epidermis dull or bright. Sculpture of beak generally more or less double-looped, more rarely concentric, often obsolete. Hinge mostly well developed, with strong teeth, rarely somewhat reduced. Male and female shells more or less differentiated, sometimes only very slightly, but in other cases the differences between the shells of the two sexes are very striking.

Remarks: The essential structure of the marsupium of this group has been entirely overlooked by Simpson. He, indeed, brings these forms together in his system, but groups them according to characters, which are rather unimportant. In addition, his generic divisions are not at all satisfactory, and need complete revision, as we shall see below. Sterki also has recognized the mutual affinity of these forms, but on account of the similarity of the glochidia to those of the genera of the first group (*Quadrula*, etc.), he brings them too near to the latter. The structure of the marsupium in this group is again so unique, that it alone suffices to sharply separate the group from all others.

I do not think there should be any doubt or hesitation in recognizing these groups as natural. The differences are such and so uniform, that we must regard them as fundamental. They concern in the first instance the *sexual apparatus*, and the development and specialization of the structures, which serve the physiological process of propagation, we are compelled to take as the surest indication of a phylogenetic progress within the group. One of the most important characters of the fresh-water shells, called *Najades*, is found in the way they take care of their young, not discharging the eggs directly into the water, but keeping them for a time in the gills; and it is only natural that this peculiar feature, after it had once developed, is further improved, complicated, and specialized.

All modifications of the gills are directly or indirectly correlated with the sexual apparatus, and besides a number of other characters of the soft parts as well as the hard parts are connected with it; in fact the sexual apparatus is the most important feature of the *Najades*. This is not at all astonishing; we find the same conditions in so many other groups of animals. Thus it is clear that a system founded upon these characters must be a natural one, and that it shou'd be fitted to furnish us the key for the proper understanding of the systematic relations.

Thus we are to regard the above three groups (excluding *Margaritana*) as so many natural divisions of the family UNIONIDÆ, which then, of course, should rank as subfamilies,¹⁷⁾ namely: the UNIONINÆ, ANODONTINÆ, and LAMPSILINÆ. For *Margaritana* it is unquestionably best to create a new family, the MARGARITANIDÆ.

It is evident, even without the knowledge of certain details of the sexual apparatus, that the *Margaritanidæ* form the most primitive group of the *Najades*. The character of the gills surely indicates this, and also the character of the branchial and anal openings, although possibly the shell may not represent the most ancient type.

Of the *Unionidæ*, the *Unioninæ* are certainly more primitive than the other two subfamilies, as is evidenced by the simple character of the structure of the marsupial gills. The *Anodontinæ* and *Lampsilinæ* are more advanced, but they have advanced in different directions, and each has developed special features of the sexual apparatus. Generally speaking, the *Lampsilinæ* contain the most highly advanced types, as is shown by the restriction of the marsupium to a part of the outer gill, and by the strong expression of the sexual differentiation in the outer shell. Yet there are forms among the *Anodontinæ*, which show extremely complex structures (*Strophitus*), unparalleled in any other genus, and the peculiar glochidia of the *Anodontinæ* surely mark a high stage of development. The arrangement and sequence of the families and subfamilies would possibly be the best as given above; but we must not forget that, while, for instance, the *Lampsilinæ* show relations in the structure of the edge of the gill to the *Anodontinæ*, they more nearly approach the *Unioninæ* in the shape of the glochidia. This is, however, the usual difficulty in all our systematic arrangements.

¹⁷⁾Simpson unites all these forms in one subfamily, *Unioninæ*, from which he distinguishes as a second subfamily the *Hyriinae* (properly *Hyriinae*), with the marsupium formed by the inner gills alone, and with radial beak sculpture. The conception of the latter subfamily on the part of Simpson is entirely wrong. Very little is known about their anatomy, but I recently have been able to investigate some of the genera, and find that some are really *Unioninæ* (in the new sense), while others rather agree with the family *Mutelidae* (See *Nautilus*, 23, April, 1910, p. 139, and January, 1911). With regard to the sculpture of the beak, serious mistakes have been made. The shape of the marsupium certainly is important, but at present in many genera is unknown. The *Mutelidae* are reported to possess a lasidium in place of the glochidium, but again the larvæ of many genera of these are entirely unknown. I hope to be able to contribute to the solution of this question in the near future, on the basis of a splendid collection representing the "*Hyriinae*" from South America.

I think that the families and also the three subfamilies of the *Unionidae* are *geologically rather old*, and we cannot say that one descended from the other. They probably go back to a common ancestral group, which probably stood somewhere between the present *Margaritanidae* and *Unioninae*. It is not my object, at present, to go into detail in this respect, and to discuss the phylogeny of the *Najades*. This will be possible only after a fuller knowledge is at hand of the exotic forms, and by studying also the fossil *Najades*. But I may here incidentally mention that I believe that these main groups probably go back to the Cretaceous, but the *Lampsilinae* may be a little, but not much, younger. This is also expressed in the geographical distribution, the *Lampsilinae* alone being restricted to North America (including Central America), while the others are also found in the Old World. But I shall leave this question for the present.

B. THE GENERA.

1. The *Margaritanidae* consist solely of the genus *Margaritana*.
2. The *Unioninae* contain the following genera of Simpson: *Tritogonia*, *Unio*, *Pleurobema*, *Quadrula*. With regard to *Tritogonia*, Sterki (*Nautilus*, 21, 1907, p. 48) was the first to point out that it possesses the marsupium attributed by Simpson to the genus *Quadrula*, and my own investigations have convinced me that this is quite correct, and that *Tritogonia* is a true *Quadrula*. The other three genera fall according to Simpson into two groups. In *Unio* and *Pleurobema* only the outer gills serve as the marsupium, while in *Quadrula* both outer and inner gills become charged with ova.

My investigations have shown that there are indeed a number of species, in which all four gills are marsupial, while there are others, in which this is true only of the outer gills. This is an absolutely constant character, and I have not seen a single instance in any species, where there was any variation in this respect. Thus it is evident, that this character, emphasized by Simpson, is important, and it is indeed, so far as I can see, the most important one which marks a division within this subfamily. Thus we must retain the genus *Quadrula* in the sense that it comprises those species, in which all four gills serve as marsupium. However, Simpson placed in the genus *Quadrula* a number of species, which according to my observations have the marsupium formed only by the outer gills. This he did, of course, because he did not know the marsupium. As long as we were unable to recognize the shape of the marsupium, unless we had gravid females, it was impossible to assign the proper place to any species, in which the gravid female was unknown. But since I have shown that the sex of any specimen may be

ascertained by the septa of the gills, and that we are able to make out the character of the marsupium also from the sterile female, it is now possible to properly place all species of which females are at hand. Thus I have ascertained, that the following forms of Simpson are true *Quadrulas*: *Q. subrotunda*, *kirtlandiana*, *ruginosa*, *trigona*, *pustulosa*, *metanevra*, *cylindrica*, *undulata*, *plicata hippopæa*, and *Tritogonia tuberculata*. *Q. lachrymosa* also belongs here, judging from specimens obtained in Kansas and from the middle Ohio River.

Of other forms of Simpson's *Quadrula* which I have investigated the following proved to have only the outer gills built to receive eggs: *Q. tuberculata*, *coccinea*, *pyramidata*, *obliqua*, *cooperiana*. With the exception of the first these all fall under *Pleurobema*, in Simpson's sense, but it is somewhat different in the case of *Q. tuberculata*. Here we have additional characters, which have already been pointed out by Simpson, and which induced him to place this species in a separate subgenus, *Rotundaria*. The chief features are the absence of a supra-anal opening and the peculiar sculpture of the beak. The structure of the hinge and the color of the nacre are also rather peculiar, and there are so many distinctive characters in evidence, that I feel fully justified in elevating the subgenus *Rotundaria* to the rank of a genus.

All other forms with only the outer gills serving as marsupium should belong to the two genera *Pleurobema* and *Unio*. There are no differences whatever in their soft parts, and these two genera can be distinguished only by the characters of the shell. Looking over Simpson's elaborate diagnoses (they are rather descriptions), it is hard to find well-marked differential characters. The shape of the shell may be taken as the most important criterion. In *Pleurobema* it is quite solid, triangular, rhomboidal, or subovate, more or less distinctly oblique, that is to say, with the two axes giving the two principal dimensions (height and length) forming a distinct and sharp angle with each other. This causes the umbonal region, which is more or less elevated, to assume an anterior location in the shell. In *Unio* on the contrary the shell varies from oval to elongate, is straight, with the axes very nearly vertical to each other, with the result that the umbonal region is less elevated and less anterior. Further, in *Pleurobema* the color of the epidermis is from dark brown to light brown or olive, with prevalence of the lighter shades, and the color of the nacre is white or silvery, rarely lighter or darker pinkish or salmon-red, but never purple. In *Unio*, the epidermis is brown to black, very rarely lighter, with prevalence of the darker shades, and the nacre may be white, but more often assumes red to purple tints.¹⁸

¹⁸As will be shown elsewhere, the North American genus *Unio* should be separated from the typical European *Unio* (Type: *pictorum* Linnæus). For the former the name *Elliptio* Rafinesque 1819 is available.

The Pennsylvanian species placed under *Unio* are unquestionably more closely allied to each other than to those placed under *Pleurobema*, but there are other extralimital species, which cannot be so easily associated with this genus. Furthermore, we have several types included in the genus *Pleurobema* which are rather distinct, and which may be entitled to generic rank, unless we prefer to leave all these forms united in the old genus *Unio*. The Pennsylvanian material representing the species of this group is scarcely extensive enough to enable us to settle this question. There are a multitude of forms of *Unio* and *Pleurobema* in the central and southern parts of North America, many of which apparently form connecting links. Before these have been more closely studied, and before it has been positively ascertained that they belong in this group, it is futile to attempt a final classification of these forms. Thus I retain the main divisions (*Unio* and *Pleurobema*) introduced by Simpson, adding to the latter genus the species removed from *Quadrula*. With regard to *Q. cooperiana* it is absolutely certain that it stands close to another species placed by Simpson in *Pleurobema*, *P. aesopus*, and is still more closely allied to *P. cicatricosum*. With regard to *Q. coccinea*, *pyramidata*, and *obliqua*, this is not so evident, but I think that there are some southern types of *Pleurobema*, with which these should be associated.

I assume that *Quadrula* having four gills serving as marsupium, represents a more primitive stage than the others, where only the outer gills have this function and the corresponding structure. It appears, as a matter of course, that the differentiation between the gills, the inner serving exclusively the function of breathing, and the outer exclusively that of propagation, represents a higher stage of development than in those cases in which all gills serve both functions; and this is further supported by the fact that in certain species of *Quadrula* (*subrotunda*, *kirtlandiana*, *rubiginosa*) we have types, in which the swelling of the marsupium in the breeding season is so small, that the water-tubes and their contents remain subcylindrical, which undoubtedly is a primitive condition. The fact that the most primitive form, *Margaritana*, has also all four gills marsupial, further speaks for our assumption. Yet I cannot suppress the thought that the opposite opinion has something in its favor, and the evidence for this is furnished by the fundamental differentiation of the edge of the inner and outer gill, as is shown by my description of the peculiar furrow along the edge of the inner gill, which is absent in the outer gill. As stated above, I cannot surmise what the meaning of this feature is. It may be possible that it represents an old, primitive differentiation of the two gills, the edge of the outer gill indicating the original restriction of the function of propagation of this gill. Then, of course, we would have to assume that in *Quadrula*

this function spread secondarily to the inner gill. I must confess that this idea appears to me as unlikely, since it means a going back to a less specialized stage, two organs, each of which originally served a different function, now assuming both. The balance of evidence is, I think, in favor of the assumption made here, but the question is open to further study.

3. The *Anodontinae*. Simpson's genera: *Strophitus*, *Anodonta*, *Anodontoides*, *Sympynota*, and *Alasmidonta* belong here. The definition of these according to shell characters, as given by Simpson, is rather satisfactory, and I merely suggest another arrangement of them. There is no question that *Strophitus*, in spite of the peculiarity of the marsupium, comes nearer to *Alasmidonta*, than to any other genus, which is chiefly shown by the heavy sculpture of the beak, and the tendency of the inner lamina of the inner gill to become united with the abdominal sac. On the other hand *Sympynota* and *Anodonta* are more closely allied, as is shown by the sculpture of the beak. *Anodontoides* is essentially an *Anodonta*, but with different sculpture of the beak. We apparently are dealing here with a number of types, which have developed independently from a common source, and of which each has preserved one or the other primitive character, while it is more advanced in other features. *Strophitus* is extreme in the structure of the marsupium; *Anodonta* is extreme in the reduction of the hinge-teeth. With regard to the hinge-teeth we observe that we have primitive types in *Alasmidonta heterodon*, and *Sympynota compressa* and *viridis*; yet they are again peculiarly transformed. The inner lamina of the inner gills is more primitive (free) in *Anodonta*, *Anodontoides*, and *Sympynota*, while a more advanced stage is observed in *Alasmidonta* and *Strophitus*. *Anodonta* represents an extreme stage in the development of the supra-anal opening. The following sequence possibly would be advisable: *Alasmidonta*, *Strophitus*, *Sympynota*, *Anodontoides*, *Anodonta*.

4. *Lampsilinæ*. The following genera of Simpson's "Synopsis" belong here: *Truncilla*, *Micromya*, *Lampsilis*, *Obovaria*, *Plagiola*, *Obliquaria*, *Cyprogenia*, *Ptychobranchus*. Some of them are very well defined, while others stand in need of a thorough revision.

First of all, *Ptychobranchus* stands by itself, on account of its very unique marsupium, the peculiarity of which is fully appreciated by Simpson. Yet, as we have seen, *Ptychobranchus* is truly *lampsiline*, for it has the characteristic structure of the edge of the marsupium. There is no question that it is the most primitive form in this subfamily, although possibly the present condition of the marsupium is not the original one.

Among the others we see that the structure of the marsupium is practically

alike; there are very few minor differences, but the genera, *Obliquaria* and *Cyprogenia*, stand out more prominently among them.¹⁹ They possess a remarkably small number of ovisae, which stand rather in the middle of the outer gill, and the shell also is peculiar in its shape and ornamentation. *Cyprogenia* is in addition distinguished by the great prolongation of the marsupium, which forces it to coil up within the shell. Thus these two genera are well defined.

As has been seen above, there is among the *Lampsilinæ* a further differentiation connected with the sexual apparatus, which, in my opinion, is of prime value. This is the development of special structures on the edge of the mantle in front of the branchial opening. Although some of these structures have been noticed by previous writers, no importance has been attached to them.

We have observed, that in the genera *Truncilla*, *Micromya*, and in certain species of *Lampsilis* such structures are present, while in other species of *Lampsilis*, as well as in *Obovaria*, *Plagiola*, *Obliquaria*, *Cyprogenia*, and *Ptychobranchus*, they are absent, or barely indicated. We have seen, that *Ptychobranchus*, *Obliquaria*, and *Cyprogenia* may be distinguished on other grounds. This leaves certain species of *Lampsilis* (*ligamentina*, *alata*, *gracilis*), and the genera *Obovaria* and *Plagiola* as a group, possessing a similar conformation of the edge of the mantle. *Plagiola*, *Obovaria*, and *Lampsilis ligamentina* are practically identical in the entire structure of the soft parts, and in the form of the shell they also stand rather close together. With regard to *Lampsilis ligamentina*, I do not see any reason why it should not be placed with *Obovaria*; in fact it fully agrees with Simpson's diagnosis of *Obovaria*, and could be grouped very well with *O. ellipsis*. *Plagiola* can be distinguished from *Obovaria* only by the characters of the shell, chief among which are the presence of a distinct posterior ridge and the peculiar markings of the epidermis. (In addition, *P. securis* has a peculiar glochidium, but the writer does not know whether this glochidium is found in other species of *Plagiola*.)

Lampsilis alata and *gracilis* have been placed by Simpson in a separate subgenus, *Proptera*, on account of the peculiarities of the shell (general shape and character of hinge-teeth). Sterki has proposed to elevate it to the rank of a genus on account of the odd glochidium of *L. alata*, assuming, that this shape is also found in the other species of *Proptera*. Since I have shown, that the glochidium of *L. gracilis* differs fundamentally from that of *L. alata*, and also from all other *Lampsilinæ*, we are forced to restrict the genus *Proptera* to those forms, which have a glochidium like *L. alata* (*purpurata*, *lævissima*), and should create a new

¹⁹Recently, Sept. 24, 1910, I found a gravid female of *Cyprogenia irrorata* in the Ohio River at Portsmouth, Scioto Co., Ohio, and had a chance to study its soft parts.

genus for *L. gracilis*. I propose here the name of *Paraptera* for it. *Paraptera* and *Proptera* are closely allied in the structure of the soft parts, and agree especially in the edge of the mantle.²⁰ They also have many similarities in the shell, and greatly differ in this respect from *Obovaria* and *Plagiola*.

The separation of the species would leave in the genus *Lampsilis* the following species: *parva*, *iris*, *nasuta*, *recta* (forming a group with papillæ on the edge of the mantle); and *ventricosa*, *ovata*, *multiradiata*, *cariosa*, *orbiculata* (with a flap on the edge of the mantle). But I also unite with this genus *Micromya fabalis*, which does not differ in any essential point from *Lampsilis*, and possesses on the edge of the mantle the characteristic papillæ of the first group of *Lampsilis*.

Lastly we have the genus *Truncilla*, which is not only characterized by the soft parts, as we have seen above, but more emphatically by the shape of the shell. Simpson's division of this genus into subgenera is well supported.

It is clear, that *Truncilla* and *Lampsilis* are the most advanced types of this subfamily, and that *Ptychobranchus* in the first line, and then *Obliquaria*, *Obovaria*, and *Plagiola* are rather primitive. *Cyprogenia*, *Paraptera*, and *Proptera* represent special modifications of this primitive type.

We thus obtain the following arrangement of the families, subfamilies, and genera of the *Najades* found in Pennsylvania. (Compare my Preliminary Report, 1910, p. 114.)

1. Family MARGARITANIDÆ Ortmann (*Nautilus*, February, 1911).

Diaphragm incomplete, formed by the gills; posteriorly the outer lamina of the outer gills not connected with the mantle for a considerable distance; anterior end of the inner gills separated from the palpi by a gap;²¹ branchial and anal openings ill-defined, and the latter not closed above; no supra-anal developed; gills without water-tubes, and with scattered interlamellar connections, which in certain places form irregular diagonal rows; marsupium formed by all four gills; larva a small, semicircular glochidium, without distinct hooks; shell elongated; sculpture of the beak concentric; hinge-teeth imperfect; epidermis blackish.

Genus *Margaritana* Schumacher.²²

²⁰I do not understand Simpson's description (1900, p. 567) of the edge of the mantle of *Proptera*, and have not seen anything which could be called a "thickened flap of the outer fold."

²¹This item should be inserted in the diagnosis on account of the different structure found in the *Mutelidae* (See *Nautilus*, January and February, 1911).

²²Certain writers (See Thiele, in Brauer, Suesswasserfauna Deutschlands, Heft 19, 1909, p. 32) consider *Margaritana* the type of the genus *Unio*, and call *Unio* by the name of *Lymnium* Oken 1815. This is not correct, as Simpson has already clearly shown (1900, p. 674, footnote 1).

2. Family UNIONIDÆ (d'Orbigny), Ortmann (*Nautilus*, February, 1911).

Diaphragm complete, formed by the gills; posteriorly the outer lamina of the outer gill connected with the mantle to its posterior end; anterior end of the inner gills separated from the palpi by a gap; branchial and anal openings sharply separated from one another by the diaphragm; anal opening very rarely not closed above and without supra-anal, generally closed and with a supra-anal opening (which very rarely may be obliterated); gills with water-tubes and distinct, continuous interlamellar septa, running parallel to the filaments. Marsupium in all four gills, or only in the outer gills; larva a glochidium. Shell of very variable shape; sculpture of the beak more or less reduced, of various types, but originally of the concentric or zig-zag pattern; hinge-teeth perfect or imperfect; epidermis plain or with color-markings.

1. Subfamily UNIONINÆ (Swainson) Ortmann.

Inner lamina of inner gills generally free from the abdominal sac (sometimes, in extralimital forms connected); supra-anal opening sometimes not separated from the anal, normally present, the closed part rather short; branchial opening well-defined; no papillæ or flaps on edge of mantle in front; marsupium formed by all four gills, or by the outer gills only; edge of marsupium always sharp and not distending; water-tubes not divided in the gravid female; glochidium semi-elliptic or semicircular, without spine; shell generally heavy and solid, rounded to elongated, mostly with dull-colored epidermis; sculpture of the beak generally rather indistinct, concentric, or pustulous, or with indications of double loops or zig-zag bars; hinge always complete, with rather strong teeth; generally no difference of sex shown in the shell.

GENERA

a¹. All four gills serving as marsupium; anal and supra-anal opening separated, but separation often deciduous; shell of various shapes, always rather heavy, outside smooth or with sculpturings.

Genus *Quadrula* Rafinesque.

a². Only the outer gills serving as marsupium.

b¹. Supra-anal not separated from the anal opening; sculpture of the beak consisting of numerous, fine, irregular corrugations; shell rounded; beak-cavities very deep; nacre dark violet or purple.

Genus *Rotundaria* Rafinesque.

b². Supra-anal opening separated from the anal; sculpture of the beak consisting of few, generally concentric ridges; shell rounded or elongated; beak-cavities of medium depth, or shallow.

c¹. Shell oblique, ovate, or rhomboidal, with prominent beaks, which are placed rather anteriorly; color of epidermis brown to light, generally not very dark, often with rays; nacre varying from light red to white.

Genus *Pleurobema* Rafinesque.

- c². Shell ovate or elongate; beaks not very prominent, and not much produced; color of epidermis brown to black, only indistinctly rayed, if at all; nacre varying from white to deep purple, with the dark shades prevailing.

Genus **Elliptio** Rafinesque.²

2. Subfamily ANODONTINÆ Ortmann.

Inner lamina of inner gill free from the abdominal sac or more or less connected with it, rarely entirely connected; supra-anal opening well separated from the anal, sometimes the connection of the mantle separating it from the anal is very long, and the supra-anal is quite short; branchial opening well defined, no papillæ or flaps in front of it on the edge of the mantle; marsupium formed by the outer gills in their whole length, distending, when charged, and the thickened tissue at the edge capable of stretching out in a direction transverse to the gill, but not beyond the edge (or only slightly so); water-tubes in the gravid female divided longitudinally into three tubes, with only the one in the middle used as an ovisac, and closed at the base of the gill; glochidium semicircular or triangular, with a spine (hook) in the middle of the ventral margin of each valve; shell generally not very heavy, often thin, never round, but more or less elongated; color of epidermis generally bright and with color markings; sculpture of the beak double-looped or concentric, in the latter case often extremely heavy; hinge rarely complete, and if so, of peculiar structure; generally there is a distinct tendency toward the reduction of the hinge-teeth, and often they are completely absent; sexual differences in the shell very rarely present.

GENERA

- a¹. Sculpture of the beak concentric, heavy; inner lamina of inner gills having a tendency to become united with the abdominal sac.

- b¹. Shell with cardinal teeth; lateral teeth present or wanting; ovisac of each water-tube in the gravid female not subdivided; placenta poorly developed, and glochidia practically free.

Genus **Alasmidonta** Say.

- b². Shell with the hinge-teeth obsolete; only a mere vestige of the cardinal teeth remaining; ovisac of each water-tube subdivided into a number of compartments, each containing a well developed placentula, running crosswise to the gill; placentulae persistent till they are discharged.

Genus **Strophitus** Rafinesque.

- a². Sculpture of the beak generally double-looped, if concentric, not heavy; inner lamina of inner gills always free; ovisacs not subdivided.

- b¹. Shell rather solid, lateral hinge-teeth more or less imperfect; cardinal teeth present, but of peculiar shape, sculpture of the beak more or less double-looped.

Genus **Sympnnota** Lea.

- b². Shell thin; hinge edentulous, or with mere traces of cardinal teeth.

²See above p. 330, footnote. The European genus *Unio* Retzius, although similar in anatomical detail, differs in shape and color of shell, and chiefly in beak sculpture (wavy, zig-zag or double looped) and glochidia. The type species of *Elliptio* is *U. crassidens* Lamarck.

- c*¹. Sculpture of the beak concentric, not heavy; supra-anal about as long as the united part of the margin of the mantle, which separates it from the anal opening.

Genus *Anodontoides* Simpson.

- c*². Sculpture of the beak generally double-looped; supra-anal small, widely separated from the anal opening.

Genus *Anodonta* Lamarck.²⁴

3. Subfamily LAMPSILINÆ Ortmann.

Inner lamina of inner gills rarely more or less free from the abdominal sac, generally connected with it throughout; supra-anal opening separated from the anal, rarely entirely closed; branchial opening well defined; edge of the mantle in front of the branchial opening smooth to crenulated, or with peculiar papillæ or a flap; marsupium rarely formed by the whole outer gill, generally only by or within the posterior part of the outer gill; edge of marsupium, when charged, distending, and bulging out beyond the original edge of the gill, generally assuming a beaded appearance; water-tubes simple in the gravid female; glochidium semi-circular or semi-elliptic, without spine, rarely celt-shaped and with two spines; shell heavy or lighter, rounded, or oval, to elongate; color of epidermis rarely dull, mostly bright, with color markings; sculpture of the beak generally double-looped, but often obsolete, more rarely concentric; hinge generally complete, with well-developed teeth, which only in rare cases show a tendency to become reduced; sexual differences more or less noticeable in the shell, often very strongly expressed.

GENERA

- a*¹. Whole outer gill serving as marsupium, its edge thrown into a number of folds.

Genus *Ptychobranchus* Simpson.

- a*². Marsupium located in the posterior part of the outer gill, and projecting considerably beyond its original edge.

- b*¹. Inner edge of mantle in front of branchial opening smooth, crenulated, or with few and weak teeth, but without papillæ or flaps; male and female shell differing only slightly, or hardly at all.

- c*¹. Shell rounded, with surface sculpturings; marsupium consisting of comparatively few ovisacs, located near the centre of the outer gill.

- d*¹. A row of large knobs on each valve; marsupium projecting beyond the edge of the gill, not coiled up.

Genus *Obliquaria* Rafinesque.

- d*². Sculpture of the surface nodular; marsupium projecting immensely beyond the edge of the gill, and coiled up spirally.

Genus *Cyprogenia* Agassiz.

- c*². Shell rounded, oval, or compressed, without surface sculpture; marsupium large, kidney-shaped, occupying a large portion of the posterior part of the outer gill.

- d*¹. Shell solid, rounded, ovate or triangular, more or less swollen; if compressed, not winged.

²⁴European writers (See Thiele in Brauer, Suesswasserfauna Deutschlands, Heft 19, 1909, p. 32) recently use *Anodontites* Bruguière, 1792, for *Anodonta* Lamarck 1799. This is entirely wrong. The type of *Anodontites* is *A. crispata* Bruguière a South American shell, belonging to *Glabaris* Gray 1847. Of course, *Anodontites* has the priority over *Glabaris*, and should be used in its place.

e¹. Shell rounded or ovate, without distinct posterior ridge. Color of epidermis dull, without color-markings, or simply with rays. Glochidia normal in shape and size.

Genus *Obovaria* Rafinesque.

e². Shell ovate or triangular, with a distinct, and often sharp posterior ridge; epidermis painted with broken rays, forming a pattern of lunate, squarish, or arrow-shaped marks; glochidia (in one species at least) rather large and with gaping margins.

Genus *Plagiola* Rafinesque.

d². Shell not very solid, or thin, ovate, more or less compressed and winged along the dorsal margin (at least when young).

e¹. Glochidia of normal shape, but of unusually small size. Genus *Paraptera* gen. nov.²⁵

e². Glochidia celt-shaped, with two spines on each valve, with gaping margins.

Genus *Proptera* Rafinesque.

b². Inner edge of mantle in front of the branchial opening, chiefly in the female, differentiated by papillæ or flaps, and sometimes not parallel to the outer edge; male and female shells distinct, generally very markedly so.

c¹. Inner edge of mantle essentially parallel to the outer edge, with papillæ or flaps; shell ovate or elongate, the postbasal region of the female somewhat swollen and more rounded than in the male.

Genus *Lampsilis* Rafinesque.

c². Inner edge of mantle in the female in front of the branchial opening not parallel to the outer edge, but more or less remote from it, with papillæ; shell ovate or triangular, the postbasal region of the female very strongly inflated and projecting, giving to the whole shell an entirely different shape from that of the male.

Genus *Truncilla* Rafinesque.

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²⁵Type *P. gracilis* (Barnes).

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EXPLANATION OF PLATE LXXXVI.

Horizontal cross-sections through the gills of Unionidae, to show structure of water-tubes, ovisacs, and septa, in the males, sterile and gravid females.

All photographs taken with Bausch & Lomb 1 inch objective. None of the figures has been retouched.

Fig. 1. *Quadrula subrotunda* (Lea) *Male*.—Allegheny River, Kelly, Armstrong County, June 22, 1909. Cat. No. 61.4400. Specimen 199.

1a. *Left inner gill*. 1b. *Left outer gill*.

Fig. 2. *Quadrula subrotunda* (Lea) *Female, sterile*.—Allegheny River, Kelly, Armstrong County, Sept. 5, 1907. Cat. No. 61.3083. Specimen 5.

1a. *Left inner gill*. 2a. *Left outer gill*.

Fig. 3. *Quadrula subrotunda* (Lea) *Female, gravid (eggs)*.—Allegheny River, Kelly, Armstrong County, June 22, 1909. Cat. No. 61.4399. Specimen 7.

3a. *Right inner gill*. 3b. *Right outer gill*.

Fig. 4. *Quadrula tuberculata* (Barnes). *Female, sterile*. Mahoning River, Mahoningtown, Lawrence County, Aug. 4, 1908. Cat. No. 61.3574. Specimen 34.

4a. *Right inner gill*. 4b. *Right outer gill*.

Fig. 5. *Elliptio gibbosus* (Barnes) *Male*.—Little Beaver Creek, Enon Valley, Lawrence County, May 11, 1907. Cat. No. 61.2186. Specimen 54.

5a. *Left inner gill*. 5b. *Left outer gill*.

Fig. 6. *Elliptio gibbosus* Barnes. *Female, gravid (eggs)*. Allegheny River, Templeton, Armstrong County, Aug. 13, 1907. Cat. No. 61.2963. Specimen 56.

6a. *Left inner gill*. 6b. *Left outer gill*.

Fig. 7. *Strophitus edentulus* (Say) *Female, sterile*. Allegheny River, Templeton, Armstrong County, Aug. 4, 1909. Cat. No. 61.4150. Specimen 117.

7a. *Left inner gill*. 7b. *Left outer gill*.

Fig. 8. *Strophitus edentulus* (Say) *Female, gravid, young (eggs), beginning of period of gravidity*. Conococheague Creek, Greencastle, Franklin, County, Sept. 6, 1909. Cat. No. 61.4160. Specimen 112.

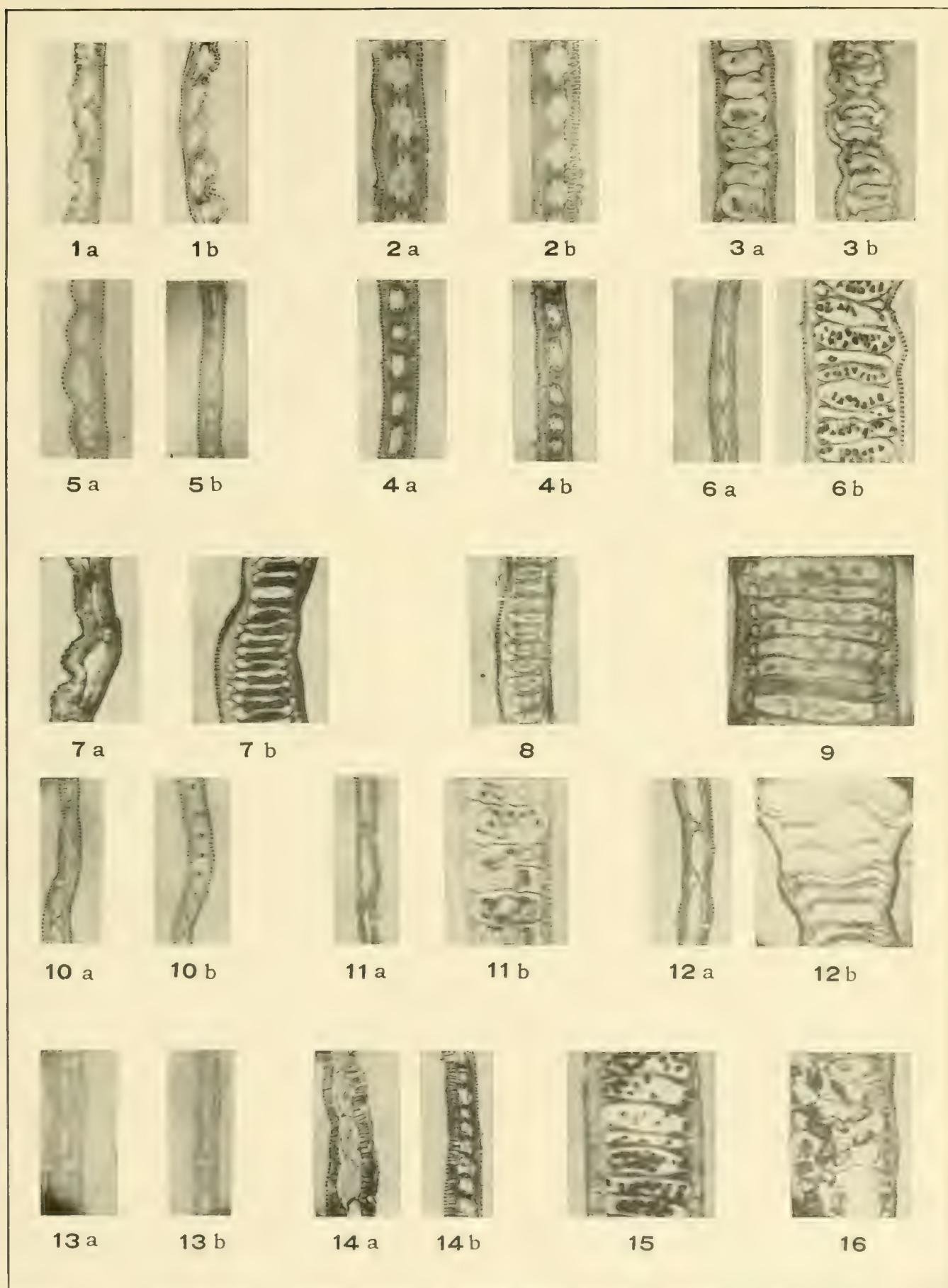
Left outer gill.

Fig. 9. *Strophitus edentulus* (Say) *Female, gravid (eggs), a little more advanced than fig. 8*. Cush-Cushion Creek, Green Township, Indiana County, July 11, 1908. Cat. No. 61.3627. Specimen 109.

Left outer gill.

Fig. 10. *Strophitus edentulus* (Say) *Female, sterile, very young (shell 17 mm. long)*. Crooked Creek, Rosston, Armstrong County, Aug. 3, 1909. Cat. No. 61.4148. Specimen 230.

10a. *Left inner gill*. 10b. *Left outer gill*.



SECTIONS OF GILLS

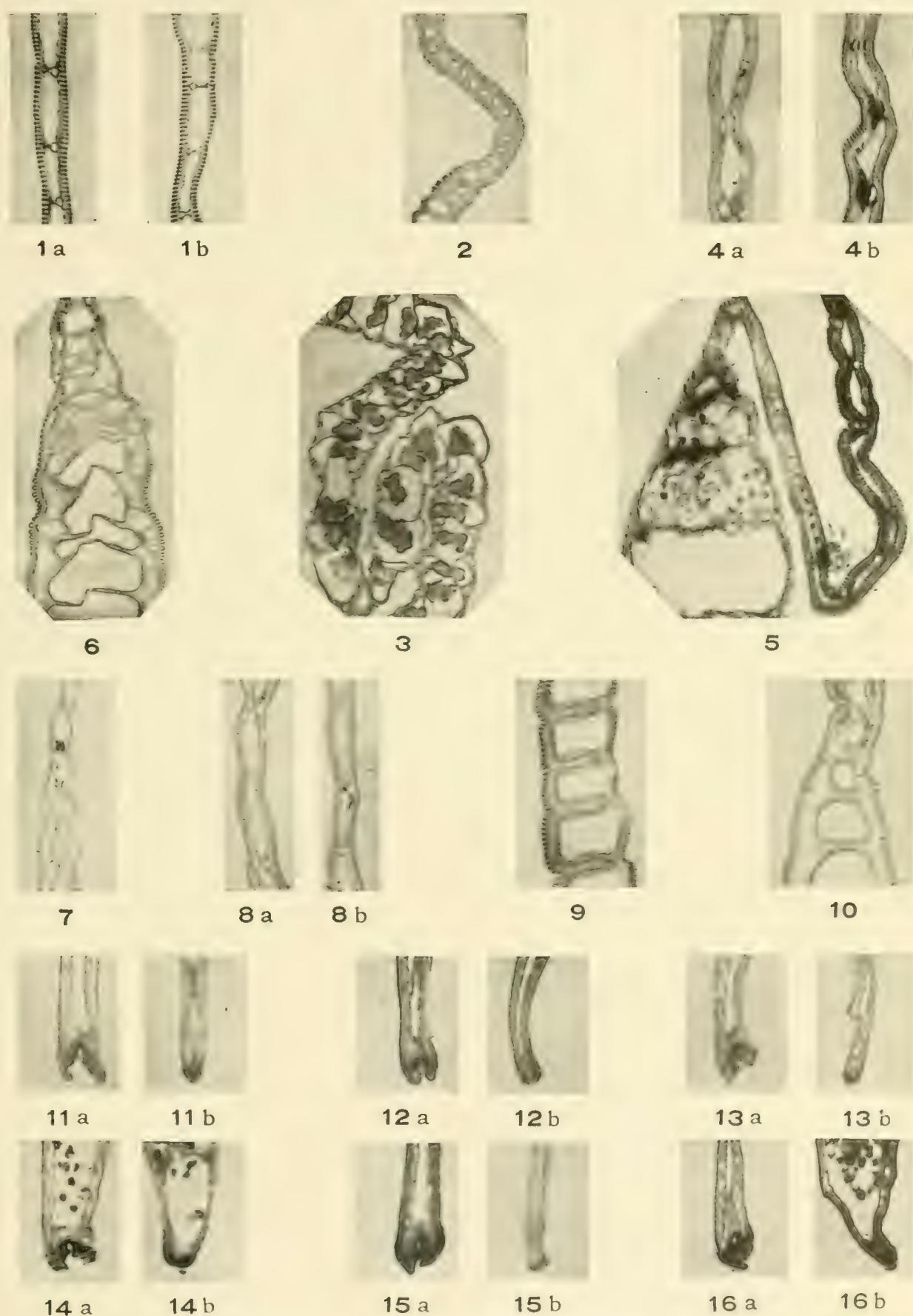
- Fig. 11. *Sympynota viridis* (Conrad) *Probably hermaphrodite, gravid, very young (shell 31 mm. long) (with eggs and young glochidia).* Great Tonoloway Creek, Thompson Township, Fulton County, Sept. 5, 1909. Cat. No. 61.4221. Specimen 235.
11a. *Left inner gill.* 11b. *Left outer gill.*
- Fig. 12. *Sympynota costata* (Rafinesque) *Female, gravid, discharging posteriorly (glochidia).* Ten Mile Creek, Amity, Washington County, April 22, 1908. Cat. No. 61.3303. Specimen 82.
12a. *Left inner gill.* 12b. *Left outer gill.*
- Fig. 13. *Anodonta grandis gigantea* (Lea) *Male, young (shell 37 mm. long).* Pond, Harmarville, Allegheny County, Oct. 10, 1908. Cat. No. 61.3668. Specimen 231.
13a. *Left inner gill.* 13b. *Left outer gill.*
- Fig. 14. *Anodonta grandis gigantea* (Lea) *Female, sterile, young (shell, 46 mm. long).* Pond, Harmarville, Allegheny County, Oct. 10, 1908. Cat. No. 61.3668. Specimen 236.
14a. *Right inner gill.* 14b. *Right outer gill.*
- Fig. 15. *Anodonta grandis* Say. *Female, gravid (eggs), beginning of gravidity.* Conneaut Lake, northeast shore, Crawford County, Aug. 8, 1908. Cat. No. 61.3657. Specimen 203.
Left outer gill.
- Fig. 16. *Anodonta grandis gigantea* (Lea) *Female, gravid (glochidia), fully charged.* Pond, Harmarville, Allegheny County, Oct. 10, 1908. Cat. No. 61.3668. Specimen 4.
Left outer gill (one lamina only).

EXPLANATION OF PLATE LXXXVII.

Horizontal (figs. 1–10) and *vertical* (figs 11–16) *cross-sections* through gills of *Najades*, to show structure of water-tubes, ovisacs, and septa, in the males, sterile and gravid females, and to show structure of the edge of the gills.

All photographs taken with Bausch & Lomb 1 inch objective. None has been re-touched.

- Fig. 1. *Ptychobranchus phaseolus* (Hildreth) *Male*. Loyalhanna River, Idlepark, Westmoreland County, Sept. 21, 1907. Cat. No. 61.3035. Specimen 119.
1a. *Left inner gill*. 1b. *Left outer gill*.
- Fig. 2. *Ptychobranchus phaseolus* (Hildreth) *Female, sterile*. Raccoon Creek, New Sheffield, Beaver County, June 30, 1908. Cat. No. 61.3275. Specimen 123.
Left outer gill.
- Fig. 3. *Ptychobranchus phaseolus* (Hildreth) *Female, gravid (eggs)*. Loyalhanna River, Idlepark, Westmoreland County, Sept. 21, 1907. Cat. No. 61.3035. Specimen 120.
Left outer gill.
- Fig. 4. *Plagiola securis* (Lea) *Male*. Allegheny River, Kelly, Armstrong County, Sept. 5, 1907. Cat. No. 61.3029. Specimen 127.
4a. *Left inner gill*. 4b. *Left outer gill*.
- Fig. 5. *Plagiola securis* (Lea) *Female, gravid (glochidia)*. Ohio River, Cooks Ferry, Beaver County, Sept. 10, 1908. Cat. No. 61.3565. Specimen 129.
Left outer gill.
- Fig. 6. *Paraptera gracilis* (Barnes) *Female, sterile*. Ohio River, Industry, Beaver County, Sept. 8, 1908. Cat. No. 61.3549. Specimen 137.
Left outer gill.
- Fig. 7. *Lampsilis iris* (Lea) *Female, sterile*. Presque Isle Bay, Lake Erie, Erie, Erie County, May 22, 1909. Cat. No. 61.4090. Specimen 144.
Left outer gill.
- Fig. 8. *Lampsilis recta* (Lamarck) *Male*. Cheat River, Cheat Haven, Fayette County, Sept. 16, 1907. Cat. No. 61.3020. Specimen 149.
8a. *Left inner gill*. 8b. *Left outer gill*.
- Fig. 9. *Lampsilis recta* (Lamarck) *Female, sterile*. Cheat River, Cheat Haven, Fayette County, July 10, 1908. Cat. No. 61.3509. Specimen 246.
Left outer gill.
- Fig. 10. *Lampsilis ventricosa* (Barnes) *Female, sterile*. Little Beaver Creek, Enon Valley, Lawrence County, May 11, 1907. Cat. No. 61.2144. Specimen 168.
Left outer gill.
- Fig. 11. *Margaritana margaritifera* (Linnaeus). Indian Run, Rene Mont, Schuylkill County, May 4, 1909. Cat. No. 61.4272. Specimen 200.



SECTIONS OF GILLS

11a. *Left inner gill.* 11b. *Left outer gill.*

Fig. 12. *Quadrula undulata* (Barnes) *Male.* Mahoning River, Mahoningtown, Lawrence County, Sept. 2, 1907. Cat. No. 61.3067. Specimen 17.

12a. *Right inner gill.* 12b. *Right outer gill.*

Fig. 13. *Quadrula undulata* (Barnes) *Female, sterile.* Mahoning River, Mahoningtown, Lawrence County, Sept. 2, 1907. Cat. No. 61.3067. Specimen 195.

13a. *Left inner gill.* 13b. *Left outer gill.*

Fig. 14. *Quadrula undulata* (Barnes) *Female, gravid (eggs).* Shenango River, Linesville, Crawford County, June 19, 1909. Cat. No. 61.4339. Specimen 16.

14a. *Right inner gill.* 14b. *Right outer gill.*

Fig. 15. *Pleurobema æsopus* (Green) *Male.* Allegheny River, Kelly, Armstrong County, Sept. 5, 1907. Cat. No. 61.3064. Specimen 194.

15a. *Left inner gill.* 15b. *Left outer gill.*

Fig. 16. *Pleurobema æsopus* (Green) *Female, gravid (eggs).* Allegheny River, Kelly, Armstrong County, June 22, 1909. Cat. No. 61.4333. Specimen 38.

16a. *Left inner gill.* 16b. *Left outer gill.*

EXPLANATION OF PLATE LXXXVIII.

Vertical (figs. 1–5, 10, 12–18, 20, 21) and *longitudinal* (figs. 6–9, 11, 19) *cross-sections* through the gills of *Unionidæ*, to show structure of ovisacs, septa, and edges of gills in males, sterile and gravid females.

All photographs taken with Bausch & Lomb 1 inch objective. None has been re-touched.

Fig. 1. *Elliptio gibbosus* (Barnes) *Female, gravid (eggs)*. Allegheny River, Templeton, Armstrong County, Aug. 13, 1907. Cat. No. 61.2963. Specimen 56 (Same as pl. LXXXVI, fig. 6).

Left outer gill.

Fig. 2. *Alasmidonta undulata* (Say) *Female, gravid (eggs), beginning of gravidity*. West Branch Mahantango Creek, Richfield, Juniata County, July 18, 1908. Cat. No. 61.3713. Specimen 75.

2a. Right inner gill. 2b. Right outer gill.

Fig. 3. *Alasmidonta undulata* (Say) *Female, gravid (glochidia) fully charged*. Schuylkill Canal, Manayunk, Philadelphia County, April 24, 1909. Cat. No. 61.4240. Specimen 206.

3a. Base of left outer gill. 3b. Edge of left outer gill.

Fig. 4. *Strophitus edentulus* (Say) *Female, sterile*. Allegheny River, Templeton, Armstrong County, Aug. 4, 1909. Cat. No. 61.4150. Specimen 117 (Same as Pl. LXXXVI, fig. 7).

Right outer gill.

Fig. 5. *Strophitus edentulus* (Say) *Female, gravid (glochidia), fully charged*. Newmans Branch, Wadsworth, Butler County, April 17, 1908. Cat. No. 61.3276. Specimen 201.

Left outer gill.

Fig. 6. *Strophitus edentulus* (Say) Same specimen as fig. 4.

Left outer gill.

Fig. 7. *Strophitus edentulus* (Say) *Female, gravid (eggs), beginning of gravidity*. Allegheny River, Templeton, Armstrong County, Aug. 4, 1909. Cat. No. 61.4150. Specimen 116.

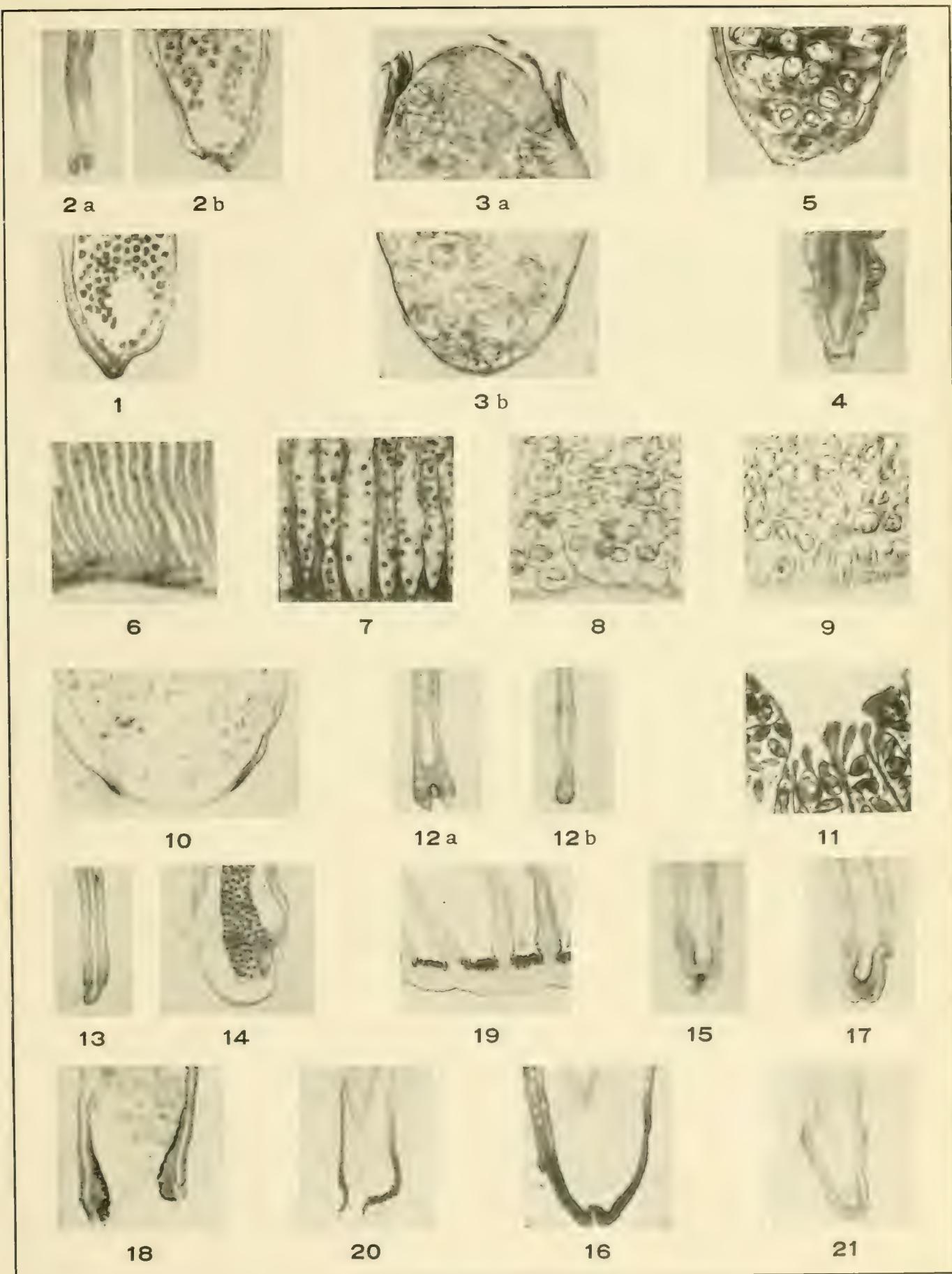
Left outer gill.

Fig. 8. *Strophitus edentulus* (Say) *Female, gravid (glochidia), more advanced*. Shenango River, Linesville, Crawford County, Oct. 10, 1907. Cat. No. 61.3118. Specimen 202.

Left outer gill.

Fig. 9. *Strophitus edentulus* (Say) Same specimen as fig. 5.

Left outer gill.



SECTIONS OF GILLS

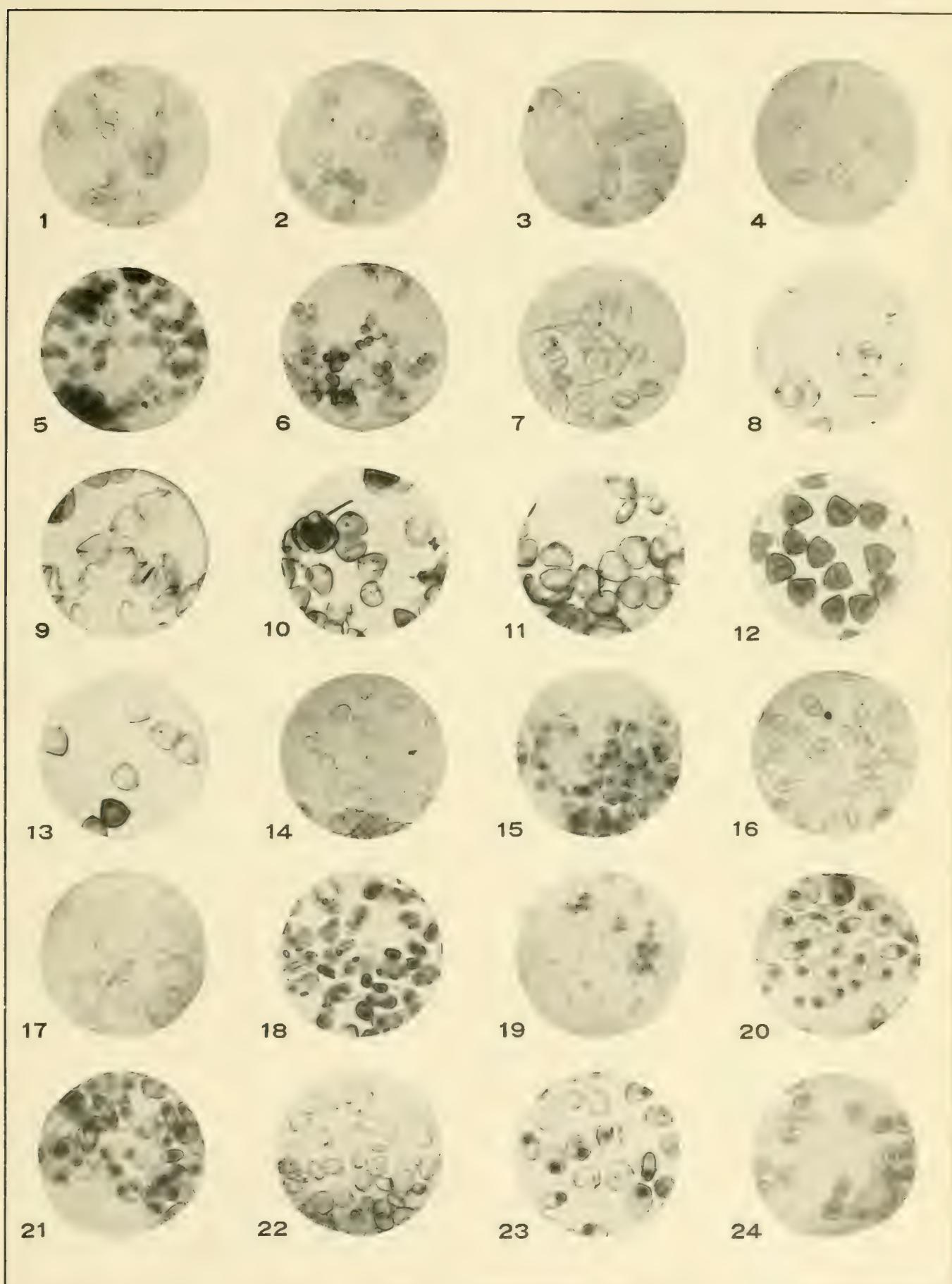
- Fig. 10. *Symplynota costata* (Rafinesque) Female, gravid (young glochidia). Loyalhanna River, Ligonier, Westmoreland County, Aug. 3, 1906. Cat. No. 61.1819. Specimen 205.
Left outer gill.
- Fig. 11. *Anodonta grandis gigantea* (Lea) Female, gravid (glochidia). Pond, Harmarville, Allegheny County, Oct. 10, 1908. Cat. No. 61.3668. Specimen 4 (Same as Pl. LXXXVI, fig. 16).
Posterior part of base of right outer gill.
- Fig. 12. *Ptychobranchus phaseolus* (Hildreth) Male. Neshannock Creek, Leesburg, Mercer County, Oct. 17, 1907. Cat. No. 61.3114. Specimen 183.
12a. *Left inner gill.* 12b. *Left outer gill.*
- Fig. 13. *Ptychobranchus phaseolus* (Hildreth) Female, sterile. Presque Isle Bay of Lake Erie, Erie, Erie County, May 22, 1909. Cat. No. 61.4123. Specimen 214.
Left outer gill.
- Fig. 14. *Ptychobranchus phaseolus* (Hildreth) Female, gravid (eggs). Mahoning River, Mahoningtown, Lawrence County, Sept. 2, 1907. Cat. No. 61.3032. Specimen 247.
Left outer gill.
- Fig. 15. *Obovaria ligamentina* (Lamarck) Female, sterile. Cheat River, Cheat Haven, Fayette County, Sept. 16, 1907. Cat. No. 61.3013. Specimen 156.
Right outer gill.
- Fig. 16. *Paraptera gracilis* (Barnes) Female, sterile, but just discharged. Ohio River, Industry, Beaver County, July 11, 1909. Cat. No. 61.4111. Specimen 210.
Left outer gill.
- Fig. 17. *Lampsilis luteola* (Lamarck) Female, sterile. Little Mahoning Creek, Goodville, Indiana County, May 25, 1905. Cat. No. 61.1760. Specimen 159.
Left outer gill.
- Fig. 18. *Lampsilis luteola* (Lamarck) Female, gravid, discharging glochidia. Ten-Mile Creek, Amity, Washington County, April 22, 1908. Cat. No. 61.3243. Specimen 207.
Left outer gill.
- Fig. 19. *Lampsilis cariosa* (Say) Female, sterile. Delaware River, Yardley, Bucks County, April 24, 1908. Cat. No. 61.3417. Specimen 166.
Left outer gill.
- Fig. 20. *Lampsilis multiradiata* (Lea) Female, gravid, discharging glochidia. Little Beaver Creek, Darlington, Beaver County, Aug. 9, 1907. Cat. No. 61.2921. Specimen 163.
Left outer gill.
- Fig. 21. *Truncilla perplexa rangiana* (Lea) Female, sterile. Allegheny River, Godfrey, Armstrong County, Aug. 10, 1909. Cat. No. 61.3978. Specimen 173.
Left outer gill.

EXPLANATION OF PLATE LXXXIX.

Glochidia of *Unionidæ*.

All photographs taken with Bausch & Lomb two-thirds inch objective. In figs. 1, 2, and 4, some of the outlines of the glochidia have been intensified.

- Fig. 1. *Quadrula subrotunda kirtlandiana* (Lea). Mahoning River, Mahoningtown, Lawrence County, Aug. 2, 1907. Cat. No. 61.2977. Specimen 9.
- Fig. 2. *Quadrula rubiginosa* (Lea). Crooked Creek, Rosston, Armstrong County, Aug. 3, 1909. Cat. No. 61.4366. Specimen 217.
- Fig. 3. *Quadrula undulata* (Barnes). Pymatuning Creek, Pymatuning Township, Mercer County, July 8, 1909. Cat. No. 61.4340. Specimen 15.
- Fig. 4. *Pleurobema obliquum coccineum* (Conrad). Slipperyrock Creek, Wurtemberg, Lawrence County, July 4, 1909. Cat. No. 61.4385. Specimen 19.
- Fig. 5. *Pleurobema clava* (Lamarek). Neshannock Creek, Eastbrook, Lawrence County, June 18, 1908. Cat. No. 61.3335. Specimen 40.
- Fig. 6. *Elliptio crassidens* (Lamarek). Allegheny River, Kelly, Armstrong County, June 22, 1909. Cat. No. 61.4297. Specimen 52.
- Fig. 7. *Elliptio gibbosus* (Barnes). Neshannock Creek, Eastbrook, Lawrence County, June 18, 1908. Cat. No. 61.3331. Specimen 57.
- Fig. 8. *Alasmidonta heterodon* (Lea). Schuylkill Canal, Manayunk, Philadelphia County, April 24, 1909. Cat. No. 61.4250. Specimen 70.
- Fig. 9. *Alasmidonta undulata* (Say). Crooked Creek, Tioga, Tioga County, Aug. 19, 1909. Cat. No. 61.4242. Specimen 76.
- Fig. 10. *Sympynota compressa* Lea. Conneaut Outlet, Conneaut Lake, Crawford County, May 14, 1908. Cat. No. 61.3297. Specimen 90.
- Fig. 11. *Sympynota complanata* (Barnes). Conneaut Outlet, Conneaut Lake, Crawford County, May 14, 1908. Cat. No. 61.3315. Specimen 80.
- Fig. 12. *Anodontoides ferussacianus* (Lea). Shenango River, Linesville, Crawford County, Oct. 10, 1907. Cat. No. 61.3127. Specimen 93.
- Fig. 13. *Anodonta imbecillis* (Say). Leboeuf Creek, Waterford, Erie County, Sept. 14, 1909. Cat. No. 61.4178. Specimen 102.
- Fig. 14. *Ptychobranchus phaseolus* (Hildreth). Slipperyrock Creek, Rose Point, Lawrence County, Oct. 23, 1907. Cat. No. 61.3116. Specimen 218.
- Fig. 15. *Obovaria circulus* (Lea). Crooked Creek, Creekside, Indiana County, May 27, 1908. Cat. No. 61.3269. Specimen 133.
- Fig. 16. *Obovaria ligamentina* (Lamarek). Allegheny River, Kelly, Armstrong County, Oct. 24, 1907. Specimen 157.
- Fig. 17. *Plagiola securis* (Lea). Ohio River, Industry, Beaver County, Sept. 23, 1908. Cat. No. 61.3567. Specimen 219.



- Fig. 18. *Proptera alata* (Say). Ohio River, Industry, Beaver County, Aug. 29, 1908. Cat. No. 61.3538. Specimen 141.
- Fig. 19. *Paraptera gracilis* (Barnes). Ohio River, Industry, Beaver County, July 11, 1909. Cat. No. 61.4111. Specimen 138.
- Fig. 20. *Lampsilis iris* (Lea). Conneaut Creek, West Springfield, Erie County, May 23, 1909. Cat. No. 61.4091. Specimen 145.
- Fig. 21. *Lampsilis recta* (Lamarck). Allegheny River, Godfrey, Armstrong County, July 23, 1907. Cat. No. 61.2935. Specimen 151.
- Fig. 22. *Lampsilis orbiculata* (Hildreth). Ohio River, Industry, Beaver County, Sept. 23, 1908. Cat. No. 61.3500. Specimen 154.
- Fig. 23. *Lampsilis ventricosa* (Barnes). Little Beaver Creek, Enon Valley, Lawrence County, May 11, 1907. Cat. No. 61.2144. Specimen 169.
- Fig. 24. *Truncilla triquetra* Rafinesque. Allegheny River, Kelly, Armstrong County, Sept. 27, 1907. Cat. No. 61.2985. Specimen 178.



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v. 1 Monograph of the naiades of Penns