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PHYLOGENY AND ONTOGENY OF NAIADES

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While the author of this paper was seeking data for a graduate thesis on Freshwater Mussels (Naiades) under the direction of the Department of Biology in the University of Missouri, it was his good fortune to be appointed for a few summers as a Scientific Assistant in doing field work for the benefit of the Pearl Button Industry under the Bureau of Fisheries. Some time was spent at the United States Fisheries Biological Station, Fairport, Iowa; however, most of the time was spent in making mussel surveys of the lakes and rivers of Missouri and adjoining states under the direction of the Fairport station. The result of these surveys were realized in several economic reports to the government Department of Commerce and in the author's graduate theses, "The Naiades of Missouri," an illustrated and descriptive catalogue of two hundred pages and twenty-nine plates, and reprinted from The American Midland Naturalist, Vol. 4, No.'s 1-10, 1915-1916.

In working out the Phylogeny of Naiades it is the author's belief, after several year's of intensive studies in field, library and laboratory, that the ultimate taxonomic system will be based far more upon larval characters and anatomical structures than upon shell characters, from the fact that the soft parts are more constant morphologically and less liable to parallelism and convergence. Yet we should not lose cognizance of the importance concerning shell characters. External factors may so shape the shell as to individualize it, but, under normal conditions, do not often destroy all traces of identification with some group. Since validity is so dependent upon the examination of the hard and soft parts of a large series of individuals it was felt that the species, as recorded in the author's catalogue for Missouri, were fairly settled within their genera, from the fact that extensive and intensive field studies made this possible. The ecologic facts secured in these field surveys were especially interesting. For example, in the three hundred mile survey of the Osage River, the largest tributary of the Missouri River in the interior of the state, it was found that the flat or compressed forms found at the headwaters, where the water was shallower and swifter, become more swollen and heavier shells further down the stream where the water was deeper and more sluggish. More accurate idea of the morphology (especially of soft parts as to color, form, etc.) was obtained while the specimens were fresh and uncontracted as examined afield.

For the world around the Phylogeny of Naiades naturally falls into two families, **Margaritanidae** and **Unionidae**. The latter falls into three definite sub-families, **Unioninae, Anodontinae** and **Lampsilinae.**

In the shell characters of Family I the structures of the inner and outer surfaces are not constant enough to be considered in the diagnosis; however, it may be said in a general way that the shell is narrowly elliptical, no sculpturing on disk, low beaks, epidermis black, so-named "Spectacle Case" in most species of this primitive group because of its general likeness of form. Most fossil forms, which come under Margaritanidae, can be easily identified because of this general shape.

So variable are the shell characters of Family II that a better diagnosis may be made for each of the sub-families. For the first **sub-family, Unioninae,** the shell is mostly heavy, hinge teeth complete and with no sex dimorphism; for the second **sub-family, Anodontinae,** the shell is mostly light and thin, hinge teeth lacking, with no sex dimorphism; and for the third **sub-family, Lampsilinae,** the shell is variable in thickness and weight, has well developed hinge teeth and a definite sex dimorphism. It has seen suggested that the shell characters of the first sub-group may be due to the fact that the species are fluviatile for the most part, that those of the second group are mostly lacustrine, while those of the third group are both fluviatile and lacustrine, since the swift current of rivers tends to building up a thicker heavier shell while pond and lake conditions tend to the opposite.

In the Naiad Phylogeny one very noticeable fact is seen in that all spineless post-embryos (technically called **glochidia**) are followed in the adult life by well developed cardinal and hinge teeth, while those glochidia which are spined, as seen in the Anodonta types, are followed in the adult forms by poorly developed hinge teeth, and, in most cases, by no teeth at all. As previously stated, the most reliable bases for classification are on anatomical characters. Also the glochidial characters, as well as the breeding habits, are much more constant than shell characters.

For Family I, **Margaritanidae,** we find no water tubes in gills, diaphragm incomplete, siphons suppressed, all four gills marsupial, postventral margin of mantle undifferentiated; glochidia very small, semicircular, ventral margin dentated; **tachytictic** (i. e., short period, or summer breeder).

For the animal of Family II we note that water tubes are present in the gills, diaphragm is complete, siphons not suppressed, marsupium formed by all four gills, or by two outer gills, or by the posterior ventral parts of the two outer gills alone. For the first group of this second family the postventral margin of the mantle is slightly crenulated and in the third group this part is very definitely differentiated by tentacles, flaps, etc. Also in the first group the glochidia are aproni-form, spineless and borne in conglutinates (*i. e.*, definitely formed masses); in the second group the glochidia are sub-triangular, spined and non-con-

glutinated—thus coinciding with the forms of the first group and hence showing atavism, or reversion to type, as characteristic of the principles of evolution.

The laws of evolution are also shown in a better adaptation for the survival of the embryos as seen in the following anatomical characters of the third sub-group, Lampsilinae:—

(1)—Mantle edge antero-ventrad to branchial opening of female with special structures, such as papillae, tentacles, flaps, etc.

(2)—Siphonal openings with a tendency to become tubular.

(3)—Marsupia mostly occupying the posterior part of outer gills with thinner ventral edges of ovisacs near the postero-ventral edge of mantle specialized with tentacular structures.

Those morphological adaptations are for better aeration of the embryos thus resulting in a minimum mortality. A greater mortality is discovered in the first two groups due to a lack of provision for a proper aeration of the early and late embryos; however, the second group, Anodontinae, have a better provision for survival of the embryos than the first group, Unioninae, by possessing water tubes in their gills, and larger palpi. The Anodonta type of glochidia may have an advantage over that of the Unio forms in the possession of spines on the ventral edges of their valves as well as long embryonic byssal threads which enable more readily to catch on passing fish hosts and encyst even on fins and scales.

The breeding seasons for these three sub-families also show better provisions for survival of the embryos in the second and third groups in that the first group, and also the first family, Margaritanidae, have a short breeding season during the summer (technically termed the tachytictic), while most of the species of the second and third groups have a long breeding season during the winter (or bradytictic). Of course there are some species which do not adhere to these general breeding habits, the most notable being **Megalonaias heros** which has been discovered to be breeding in late winter. Even **Cumberlandia monodonta**, type of Family I, Margaritanidae, has been found to produce two broods in one summer.

In order to more clearly define the Phylogeny of Naiades we would characterize the type species of two or three representative genera of each of the three sub-families of the second family.

Fusconaia undata, known by its trade name of "Pigtoe," is the most primitive of the Unionidae, having a thick, trigonal shell showing no true sex dimorphism; soft parts yellowish; marsupia formed by all four gills; conglutinates club-shaped, light red. This species was hidden

in synonomy for many years until Mr. Bryant Walker, a close student on Naiades, brought it to light through diligent study. Many varieties of this species occur according to its various ecologic conditions.

Megalonaias heros, known as "Giant Heros" because of the most ponderous shell of all mussels, will be characterized more in detail since it is taken as a type for an Ontogenetic study and can also be considered as a good intermediate type of the Unioninae.

Pleurobema Utterbackii may also be selected as a good intermediate type for this group. This species was a stranger found by the author on a government mussel survey in the White River of Southern Missouri. A good series of shells were sent to Mr. L. S. Frierson, another authority of mussels, especially for the Southwest of our country. He proved the novelty of the form, wrote up the first description and dedicated it to the author of this paper. Its shell is somewhat elliptical, beaks large and full, epidermis tan colored, gills long tapering posteriorly, siphonal openings blackish, suppressed. Gravid females are desired to make a complete description.

Uniomerus tetralasmus, known as "Pone Horn Shell," is the highest of the Unioninae. Being found in the same habitat of the second sub-family, **Anodontinae,** it is often confused with some members of that group because also of its similarity of shell, but can be distinguished by presence of hinge teeth. Its position is mainly due to its marsupia being confined to the outer gills and profusely crenated incurrent siphonal opening. It was the good fortune of the author to discover its glochidium and to write and illustrate it for the first time.

Symphynota costata, known on the market as "Squaw Foot," while not a type taken by students for this genus, yet it is a good representative of the lowest form of the second sub-family, Anodontinae. Its shell is most easily identified because of its sharp post-dorsal ridge with costal markings on this slope; marsupium is typically Anodontine and has one of the largest glochidia on record, being .38X.39mm.

Lastena suborbiculata may be taken as an intermediate form for Anodontinae. This is known locally as "Heel Splitter" and is very easily recognized by its very large suborbicular shell having about the same general shape and convexity of a dinner plate. As characteristic of most Anodontine species its supra-anal opening is wide and palpi long. Marsupia are confined to the outer gills and its glochidia are large, golden, spined and about as long as broad. The author also had the pleasure of discovering this glochidium, describing and illustrating it for the first time.

Strophitus edentulus is the highest type of this sub-group, **Anodontinae,** since its marsupia are confined to the outer gills, palps long,

mantle edge somewhat differentiated; glochidia large, length greater than height. This and **Lastena ohiensis** are the only species on record so far which do not normally possess a fish host for the metamorphosis of its larva, yet it is strange that these non-parasitic forms should have such a wide geographic distribution.

The lowest forms of Sub-Family III, Lampsilinae, fall into the Ellipsaria-Group. Marsupium most primitive in that the whole outer gill is occupied; yet advantage is secured for the aeration of the embryos in rendering the ventral edges thin by distention and in throwing the marsupia into folds thus increasing the surface for greater exposure to the water currents. A good type is **Ellipsaria clintonensis.**

The middle group of **Lampsilinae** may be termed **Obliquaria-Cyprogenia**. Number of ovisacs reduced, but greatly enlarged and elongated and placed at the great vantage point for oxygeneration of the embryos.

The highest forms of **Lampsilinae**,—as well as of all **Naiades**,—may be included in the Proptera-Lampsilis Group. In this division the best adaptation for the proper respiration of the embryos is secured by situating the numerous, dilated ovisacs in a more or less kidney-shaped marsupium near the incurrent opening where the postero-ventral margin of the mantle is set with papillae, flags, etc. The first members of this group have the mantle edge only slightly crenulate and lamellate while beyond the genus, **Proptera**, is the culmination of the modern structure in the arrangement of the inner edge with papillae or flaps close to, or remote from, the outer edge. The highest genus is Truncilla, good-types of which are **T. Curtis** and **T. Lefeveri.**

The relation of **Naiadgeography** to Phylogeny of the Freshwater mussels is very interesting especially as the author found it in his mussel survey of the state of Missouri. The zoogeography of the **Naiades** of that state and adjacent territory in relation to the restoration of the ancient geographic conditions of the Mississippi Valley is an interesting problem. With the Ozark Uplift in the south and the Missouri River, known as the "Old Muddy," flowing entirely across the center of the state as "The Great Faunal Barrier" we note distinct mussel faunae which coincide with the different physiographic provinces; yet these faunae, which distinctly show that they are primitive for North Missouri, intergraded for Central Missouri and modern for South Missouri, seem to occur as apparently contrary to geologic facts. The unique mussel faunae of that state are determined by the ecologic conditions of the physiographic features such as muddy, sluggish streams of the north, swift, clear streams of the south and mediocre streams for the central portion.

From the fact that the author found that primitive species, Cumberlandia monodonta, at several points in Central Missouri, its known

distribution was carried farther south and west of the Mississippi than ever recorded before. While the author was a resident on the west slope of the Rockies he noted that the mussel fauna there fairly well coincides with that as reported for the east coast of Asia. From this we might infer that some time in the remote past there were definite terrestrial connections with North America and Asia.

Megalonaias heros (Say), known as "Giant Heros" in trade parlance, was not chosen as a type for Ontogenetic study because it is most typical of all **Naiades**, but because he has given this form the most intensive study. From this study he has been able to discover such peculiar characters as to give it rank as a type of a new genus, **Megalonaias**. This creation of a new genus was only made after due deliberation with the leading authorities on **Naiades**. The following animal and shell characters have justified the elevation:—

(1)—A tendency of the inner laminae of the inner gills to become more or less united with the visceral mass.

(2)—The gravid marsupium, an enormously distended pad, colored purplish with reddish rusty splotches here and there parallel with the septa.

(3)—Thick, sole-shaped, subsolid conglutinates with rusty brown margins discharged more or less whole with glochidia lying all through the conglutinated mass.

(4)—A large, vital glochidium with post-ventral margin obliquely rounded.

(5)—Breeding season intermediate, or tachytictic with late season (i. e., bearing glochidia in late winter but sterile during summer).

(6)—Adult shell most ponderous of all **Naiades**.

(7)—Juvenile shell most sculptured of all **Naiades**.

The goal in the individual race-course (i. e., the ONTOGENY) of all forms of life is the reproductive cell; however, the logical point of start and finish is the mature life which marks the Etiology for the germ cell in a phenomenon we call death so that another ontogenetic life cycle may be perpetuated. Yet, in the last analysis, we scientists, who deal so much with the material and natural law, may lose sight of the spiritual and supernatural in the fact that the GREAT JEHOVAH (the "SELF-EXISTENT ONE") is the Alpha and Omega whether we consider Evolution in the life history of the individual, or even of all phyla.

Our type species, **M. heros**, has been claimed by some students as hermaphroditic, but as the author has found sperm within the gonads of the visceral mass without being accompanied by ova of those in-

dividuals that possess gills without the crowded septa of the female proves the sexes distinct and separate. Hence before the fertilization period spermatogenesis takes place in the gonads of the male and oogenesis of the gonads of the female.

It is a problem as to where, when and how fertilization may take place. It is inferred, however, that it may occur at the time of ovulation when the ova are enroute from the genital aperture to the openings of the ovisacs in the suprebranchial canals which are located at the top of the gills. Others think the fertilization may occur after the ova are deposited in the ovisacs of the marsupia. Since sterile ova are so often found in the ovisacs one might be led to think that the latter inference is more truly correct. Sperm masses discharged from the excurrent siphon of individuals kept in an aquarium and microscopically examined are found to be clinging together in globular forms as some Colonial Protophyta, such as Pandorina and Volvox. When the globular mass comes into contact with the ova the matrix ruptures and the individual sperm are freed. The object of the globular conglutination is for locomotion since the individual flagella, protruding from the matrix, just as seen in **Volvox globator,** all move in unison so that the movement is powerful and rapid.

Immediately after the fertillzation, as in all Mollusks, an unequal segmentation takes place. The Ovum, being holoblastic, i. e., without nutrient parts, all parts take place in the segmentation. Since unequal segmentation takes place in this pre-embryonis stage of development there is eventually a hollow ball formed. This is the blastula stage with its segmentation cavity surrounded by a single layered wall of micromeres (or small cells) and macromeres (or large cells) of equal number. This recapitulation of the Colonial Protozoon is very evident. Also the gastrula, formed by the invagination of the blastula, is an evident recapitulation of a simple **Porifera.**

All this pre-embryonic life takes place in early winter. All these so-called "eggs" of segmentation, blastulation and gastrulation are enveloped in jelly-like globules, just as in case of frogs' eggs. If gravid females bearing these early embryos are taken from their natural beds and roughly handled they will "abort" the eggs in broken conglutinates.

In late winter the ripe glochidia are formed and discharged in unbroken conglutinates. By laboratory tests the author has kept the glochidia of this species alive in cold, clear fresh water exactly thirty days (five times longer than the life of any other mature glochidia submitted to this watchglass test.) This unusual vitality of the larvae is an adaptation to its prolongation of breeding season into late winter when they are discharged into the ice-cold water and left to their fate, for it is the belief of the author that they are discharged as soon as

mature and may wait at least a month on the bottom of the stream until fish hosts start up stream to spawn or until the salamander host may come out of hibernation.

The parasitic life of the larva is an interesting one. As may be familiar with most of us, when this larva was first discovered it was thought to be a distinct form of an animal parasite and was called **Glochidium parasiticum**, but later, upon tracing its further development, it was found to be only a dependent phase in the life history of the mussel. However, the name, "glochidium," was still retained. As probably you may have observed the glochidium contracts its valves in such a snapping motion that when a passing fish attempts to swallow down the glochidial masses as food most of them may snap on the gill arches where they encyst. It is in this life of about four to six weeks that, in addition to securing food from the host, these so-called "hoboes" steal a ride for many miles from their original spawning beds.

As soon as this dependent life has run its course this post-embryo escapes from its cyst and falls upon the bottom of the stream as a tiny juvenile at first only about the size of a kernel of wheat. Some forms develop threads called byssi which attach to sticks and stones to prevent them being carried away by swift water currents. In case of **heros** juveniles no such byssal threads have been discovered. The author has had the rare opportunity to make much study of the juvenile shells of **M. heros** to find them most profusely sculptured with nodules, apiculations, corrugations, etc. Like children the juveniles are very active; however, the most sluggish of all Naiades is the adult as some individuals are known to remain in one position in a mussel bed for many months.