MORPHOLOGY OF THE GLOCHIDIUM AND JUVENILE OF THE MUSSEL ANODONTA IMBECILLIS[1]

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While the glochidia of Unionidae ordinarily pass through a stage of parasitism on a fish or other aquatic vertebrate, there has been considerable interest manifested in two species which have been reported normally to complete their metamorphosis within the body of the parent without any such period of parasitic existence. In the course of an experimental investigation upon the life cycle of one of these species, *Anodonta imbecillis*,[2] the writer has demonstrated that in the material studied there is no evidence of metamorphosis except following encystment upon the fins of certain species of fishes. Howard has stated (1914: 353–4) that he observed the juvenile of *Anodonta imbecillis* in the marsupia of the parent. Since he has called attention to the fact that they rather closely resemble the glochidia in shape and size, it has seemed worth while to bring together the results obtained from an intensive study of the larval and juvenile mussels of this species.

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THE LARVAL MUSSEL

The glochidia of *Anodonta imbecillis* were found in the marsupia of the mussels collected at various times of the year from small streams in the neighborhood of Urbana, Illinois. The larvae were also found to be given off by two specimens of *Anodonta imbecillis* taken from Lake Decatur, at Decatur, Illinois, in November (1926).

Type of Glochidia.—Members of the genus Anodonta belong to that division of mussels possessing the hooked type of glochidia. These are provided with a shell bearing a single stout hinged hook at the ventral edge of each triangular valve. Coker, Shira, Clark, and Howard (1921: 144) describe these hooks as provided with spines which undoubtedly assist the glochidium in retaining its hold upon the host. Further characterization of this type of glochidia shows them to be parasitic upon the fins and other exposed parts of fish but not usually on the gills. Whereas he

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[2] Baker (1927) created a new genus, Utterbackia, with *Anodonta imbecillis* as type. Evidences presented in an earlier paper (Tucker 1927) eliminate one of the principle characters for differentiating this genus from Anodonta. Under these circumstances, it seems desirable to use the older name until the exact status of Utterbackia is determined.

glochidial characteristics, with one exception, are said to be constant for the genus, Lefevre and Curtis (1910: 145) point out that the characteristically triangular shell outline in Anodonta is a distinguishing feature.

Size.—Lefevre and Curtis (1910: 145) declare the size of glochidia to be fairly constant for a given species. Surber (1912: 8) records the dimensions of different species of fresh-water mussels as distinguishing characteristics. He gives the measurements for *Anodonta imbecillis* as 0.319 mm. by 0.290 mm. The measurements of the glochidia of specimens here examined conform fairly closely to those given by Surber. The following table shows the measurements obtained, with a comparison of those from different places of collection.

TABLE I. Record of Measurements of Glochidial Shells of *Anodonta imbecillis*.

Place of Collection	Date of Collection	Extremes of Measurement in mm.		Most Frequent Size in mm.	
		Length	Depth	Length	Depth
Sidney, Illinois	8/28/18				
Specimen No. 1		0.296–0.320	0.280–0.304	0.304	0.288
Specimen No. 2		0.288–0.312	0.280–0.296	0.296	0.288
Homer, Illinois	10/28/15				
Specimen No. 1		0.296–0.312	0.288–0.304	0.304	0.296
Specimen No. 2		0.288–0.320	0.280–0.296	0.296	0.288
Decatur, Illinois	11/6/26				
Specimen No. 1		0.288–0.312	0.288–0.296	0.304	0.288
Specimen No. 2		0.296–0.320	0.288–0.304	0.312	0.296

Structure.—The glochidium of *Anodonta imbecillis* possesses two triangular valves joined by their bases at the hinge line. Lillie (1894: 69) has described the valves of the Anodonta glochidium as being "quite thick, strong, and brittle, and pierced by numerous fine pores." Coker, Shira, Clark, and Howard (1921: 143) found the two parts of the glochidial shell "much like the bowls of tiny spoons hinged together at the top." Each valve is provided at the apex by a strong hook which is joined to the valve by a hinge and possesses a number of minute teeth. The characteristic hooks with the teeth on the outer surfaces (Fig. 1, 2) are plainly evident from a microscopical examination of the larval shells.

Each valve is lined internally by a layer of cells comprising the larval mantle. These "large, flat, vacuolated cells" (Lillie 1894: 69) show clearly when stained with acid fuchsin (Fig. 2). In the fairly mature glochidium, a group of specialized cells marks the origin of the lateral pits, the entodermal sac, the ventral plate, and the stomodeal invagination. For the fully mature glochidium, Lillie has adequately described these developing cells. "Near the posterior angle of the valves are two ectodermal pits—the lateral pits. Between them, beneath the ectoderm is the entodermal

sac. Behind this lie the lateral wings of the mesoderm cells. The ventral plate occupies the whole of the posterior median region as far forward as the oral plate, which has now assumed the form of a stomodeal invagination. Just in front of the oral plate is the opening of the thread-gland, from which the long much tangled larval thread has been extruded." (Lillie 1894: 69).

The valves (Fig. 1) are united by a single, strong adductor muscle. The characteristic snapping or rapid closing of the valves of the living larva is brought about by the contraction of the muscle. This is usually followed quickly by the relaxation of the adductor, and the larva is seen with the valves gaping apart (Fig. 1).

The most definite structure to be found within the glochidium is the larval thread. This is regularly coiled (Fig. 2) in from three to four loops on the left mantle. The thread is of uniform makeup and stains readily with acid fuchsin. Some of the more mature glochidia show the larval threads extended (Fig. 1). They may be several times the length of the shell, an examination of stained material of ripe glochidia showing, in many cases, great coiled masses or mats of extruded larval threads. Lefevre and Curtis (1910: 151-152) confirm the descriptions of Schierholz and others as to the "tangling of the glochidia into masses by means of their extruded threads." The thread is apparently an aid in bringing about attachment to the host fish, since masses of the threads have been observed entangled on the fins and on other parts of the fish. Opportunity for attachment of the glochidia is thus extended over a much greater period of time than would be possible without the larval thread. The thread thus seems to have greater significance than frequently attributed to it. According to Lillie, it may be excretory in function (1894: 53). Coker, Shira, Clark, and Howard (1921: 143) report its presence but declare it of uncertain significance.

There are four paired tufts of sensory hairs (Fig. 2) borne by the larval mantle. These tufts are arranged in a very characteristic way. "Three pairs lie just beneath, and within the powerful hooks: these three form the angles of a right-angled triangle, the base of which is parallel to the transverse plane of the larva, the apex being directed anteriorly. The fourth pair lie on either side of the opening of the thread-gland." (Lillie 1894: 69).

The Juvenile

In the course of this investigation, glochidia became parasitic upon a green sunfish, *Apomotis cyanellus*, and actually underwent metamorphosis under controlled conditions. Juvenile mussels were recovered after a parasitic stage of from eighteen to twenty-two days.

Size of Juvenile.—The general external appearance of the juvenile mussel is very similar to that of the glochidium. There is only a slight increase in size due to a small shell growth. This consists of a "narrow rim around the edge of the glochidial shell." (Howard 1915). Table II. shows a comparison of the size of the glochidia and juveniles.

TABLE II. Comparison of the Size of Glochidia and Juveniles of *Anodonta imbecillis*

Glochidia		Juveniles	
Length	Depth	Length	Depth
0.304 mm.	0.288 mm.	0.307 mm.	0.300 mm.
0.296 mm.	0.288 mm.	0.304 mm.	0.296 mm.
0.304 mm.	0.296 mm.	0.312 mm.	0.304 mm.

Structure.—While the external appearance of the juvenile is very similar to that of the glochidium, there is considerable modification of internal structure. The characteristic protrusion of the juvenile foot presents one of the first evidences of this modification. In the living juvenile, the ciliated foot is readily observable, since the young mussel is usually active at first. The cilia can be plainly seen beating rhythmically as the foot is protruded. Figure 3 shows the foot partially extended. The cilia remain active until, at the limit of protrusion, the foot is flattened against the surface over which the juvenile is crawling, the cilia cease beating, and the body is drawn forward. As soon as the contraction of the foot commences, the cilia suddenly cease moving and stand out from the surface like the bristles of a brush absolutely motionless and rigid. Latter (1891: 157) offers no suggestion as to the "meaning or cause of this apparent rigidity other than that the pressure within the epithelial cells becomes so great that the cilia cannot assume any other position than one perpendicular to the surface, and forming a continuation of the long axis of the cells on which they are severally carried."

The newly developed structures within the young mussel (Fig. 4) are usually visible in outline through the semi-transparent shell. They are more readily observable, however, when the juvenile foot is extended and the valves gape apart. Instead of the single wide adductor muscle of the glochidium, there has resulted during the period of transformation the development of two muscles found at the anterior and posterior parts of the body as the anterior and posterior adductors (Fig. 4, 5, 6).

The mantle of the juvenile is a ciliated curtain lining the valve, its edges folding against those of the mantle of the opposite side so as to enclose the delicate internal structures when the valves are closed. When the valves are open the ciliated edges of the mantle (Fig. 3-6) are visible. From a ventral view of the juvenile with gaping shell, the proportionately large ciliated foot is evident, to each side of the base of which the gill papillae occur as small rounded ciliated outpocketings (Fig. 5, 6).

Within the living specimen, it is not possible to determine the definite structure of the digestive system. However, the general outline of the

visceral mass can be seen through the fleshy part of the base of the foot, and in two specimens a crystalline style has been seen revolving within. This was observed most clearly when the foot was fully protruded (Fig. 6) with the valves widely separated and the internal structure plainly visible. Since the juvenile upon liberation is capable of independent existence, it is to be expected that the essential organs should be laid down. Howard (1914) relates that "with the exception of the outer gills, all of the important organs of the animal have been laid down and have assumed something of their definite structure."

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Explanation of Plate X

All figures were drawn with a camera lucida

Fig. 1. End view of *Anodonta imbecillis* glochidia with valves partially opened.

Fig. 2. Front view of *Anodonta imbecillis* glochidia with valves widely opened.

Fig. 3. Dorsal view of *Anodonta imbecillis* juvenile.

Fig. 4. Antero-dorsal view of *Anodonta imbecillis* with foot partially extended.

Fig. 5. Ventral view of *Anodonta imbecillis* with valves partially opened.

Fig. 6. Ventral view of *Anodonta imbecillis* juvenile with foot extended.

Key to Abbreviations

a. a. = anterior adductor muscle
a. m. = larval adductor muscle
c. = cilia of juvenile mantle
c. s. = crystalline style
f. = juvenile foot
g. = gill papilla
h. = hook of valve
l. p. = lateral pit
l. t. = larval thread
m. = juvenile mantle
m. c. = cells of larval mantle
p. a. = posterior adductor muscle
s. h. = sensory hairs

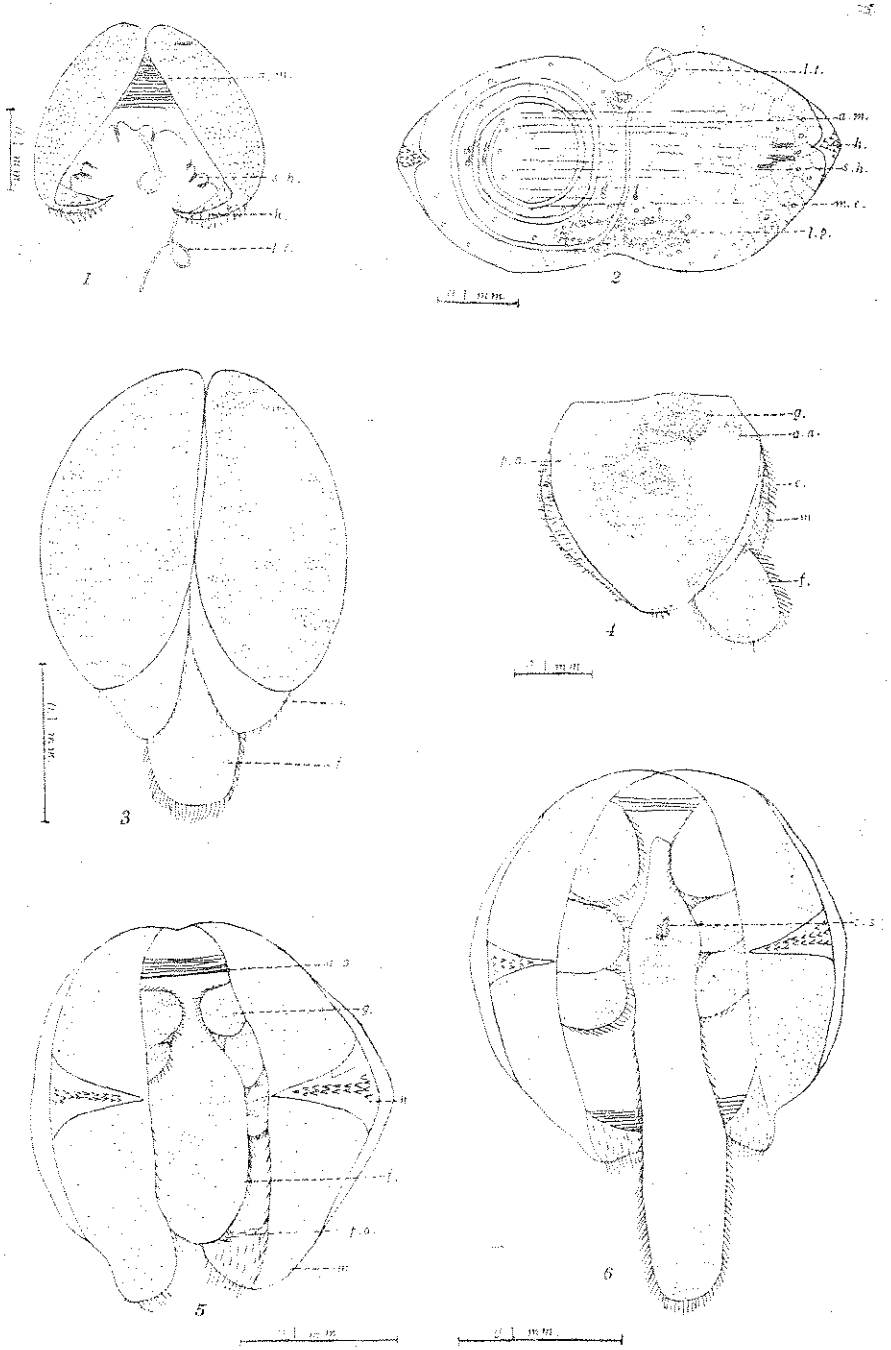

Plate X