SOME OBSERVATIONS ON THE LIFE HISTORY
OF STROPHITUS EDENTULUS

by

Earl Albert Martin, A.B.

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1. INTRODUCTION

Strophitus edentulus is a fresh water mussel which has been said to go thru its metamorphosis both as a parasite on fish (Howard 1914) and without parasitism (Lefevre and Curtis 1912). This condition in Strophitus is rendered more interesting by the fact that there is but one other exception to the parasitic habit among the fresh water mussels. This exception, Anodonta imbecillis (Say), is one of the hermaphroditic species and is not closely related to Strophitus. Since these two species are widely separated in structure, and since the same changes are occurring in each form, it is possible that we have here a case of convergent evolution, the investigation of which may throw some light on the nature of this most interesting adaptation of the fresh water mussels. In the following paper I have presented a review of the observations and experiments from which the above conclusions were drawn, together with some additional data which I have collected myself and a discussion of certain uncompleted and unpublished work which was placed in my hands.

2. THE LIFE HISTORY OF A TYPICAL FRESH WATER MUSSEL

The life history of a typical fresh water mussel such as Lampsilis anodontoides is as follows: The sexes are separate, the gonads being located in the dorsal region of the foot. When these are mature the genital products escape to the inner suprabranchial chamber. In the males the spermatozoa escape with the excurrent water, but in the females when the eggs reach the cloaca the current of water is reversed so that they are carried backward into

the outer suprabranchial chamber and drop down into the water-tubes. Fertilization may take place at any time after the eggs reach the suprabranchial chambers, the spermatozoa being carried in with the incurrent water, and passing thru the ostia of the gill lamellae. Shortly after the eggs drop into the water-tubes they are bound together with an agglutinating substance and the superficial water-tubes are formed. Development proceeds to a larval stage known as the glochidium. The glochidium is composed of two symmetrical valves held together by a huge central adductor muscle which is covered with a layer of embryonic mantle cells. Aside from the precociously developed shell, the only indication of the adult organs is a mass of darkly staining cells located near the posterior end (Fig. 1). When the glochidia are mature the adductor begins to contract spasmodically, and shortly after this the masses of glochidia are extruded thru the exhalent siphon of the parent. At this point the development stops unless they become attached to the fin or gill of a fish. In case this occurs the tissues of the fish, which come in contact with the glochidium hypertrophy, so that they soon inclose the glochidium within a cyst. Whether they derive nourishment from the fish or not is a disputed point, but at any rate the central adductor muscle soon disappears and the organs of the adult are formed; whereupon the cyst breaks, releasing the clam which is now ready to begin its life on the bottom.

3. DESCRIPTION OF STROPHITUS EDENTULUS

Strophitus edentulus is of medium size averaging about eight and one-half centimeters long by four and one-half centimeters wide. The males and females are not distinguished by differences in size or other external features. The adult shell has a slight pitch forward

in the umbone region. In the young mussels the color is light brown, but this changes to a darker hue with age. An internal feature of the shell which is often present and which is unique among the fresh water mussels of the Mississippi Valley is a pale orange tint exhibited by the nacre, but since in many cases the nacre is pearly white this is not a universal character of the species. Obviously, the characters enumerated above are not very definite and it is easy at first to confuse Strophitus with other species. With a little experience, however, one can soon learn to distinguish it by the conformation of the shell.

All the specimens examined came from the Upper Mississippi in the region of Fairport Iowa, in which locality it is not a common species, but one rather difficult to obtain.

4. METAMORPHOSIS WITHOUT PARASITISM

The account of the metamorphosis without parasitism given by Lefevre and Curtis is of a preliminary nature, and the completion of the study as the authors state (p. 173) was to have been undertaken by Miss Daisy Young, a graduate student at the University of Missouri. Miss Young, however, did not complete her studies and her notes and figures were turned over to the Department of Zoology. They were placed in the writer's hands for study and verification and in the hope that additional material would enable him to describe the development more completely and to reconcile the conflicting observations of the two published accounts referred to above.

The peculiar form and arrangement of the cord-like conglomerates in which the glochidia of Strophitus are embedded was described by the earlier investigators (Lea 1838, Sterki 1898, Ortman 1909),

but the first observations which showed aberrant development in this species were those of Lefevre and Curtis(1912),who in the course of work upon the mussels of the Upper Mississippi at La Crosse,Wisconsin during the Summer of 1908 were unable to secure infections with the glochidia,although repeated attempts were made in which "the fish were left in small dishes containing many cords for as long a time as 12 hours" (Lefevre and Curtis '12 p 173).This together with the peculiar structure of the marsupium,led these investigators to think that Strophitus might be a species which passed thru its metamorphosis without parasitism. In the autumn of the same year a single specimen of Strophitus was included in a shipment of mussels to the University of Missouri; and,as the species had previously attracted attention,this specimen was placed in one of the laboratory tanks under favorable conditions and kept under observation.It lived thru the winter and began discharging glochidia February 6.

The glochidia were imbedded in cords which varied in length from two to ten millimeters and were about one millimeter in diameter. The number of embryos in the larger cords varied from ten to twenty-four.Upon contact with the water the cords became slightly swollen and a small percentage of the embryos broke thru the egg membrane and the cord to the surface.Part of these remained attached to the cord by the larval thread,which originates at the anterior end of the embryo (Fig. 23) and is fused with the egg membrane at the other end;in other cases,however,the larval thread broke thus releasing the embryos from the cord.It was found that those which remained attached to the cord were still in the glochidial stage while those in which the thread broke and those which remained embedded within the cord were mostly young clams.The young clams possessed a well-

developed ciliated foot (plate VII) which they used effectively in crawling over the bottom of the dish. After the fourth day of exposure to the water the cords began to disintegrate and at the end of the fifth day both clams and glochidia had died.

Since the majority of the young clams were found within the cords it was thought that the cords might have a nutritive function. But experiments showed that the young clams and glochidia lived longer when they were separated from the cords. In one instance where a clam was kept for twelve days it had been extruded from the cord immediately after being discharged from the parent. Further evidence was obtained from a chemical analysis by Dr. J. A. Gibson of the University of Missouri, who found that the cords were composed of a chemical substance allied to conchiolin and which could not be utilized as food.

Taken as a whole the facts seem clearly to indicate that metamorphosis took place within the marsupium and that the cord does not have a nutritive function.

Miss Young's notes describe the reactions of the glochidia and young clams to various reagents. When treated with various concentrations of potassium nitrate, ammonium chloride, and sodium chloride the foot of the young clam would contract but no effect was produced upon the adductor muscles. Frog's blood was used with similar results and even strong hydrochloric acid failed to cause the clam to close. Similar experiments were performed upon the glochidia of Strophitus, which gave reactions very different from those typical for the glochidia of other species. Upon treatment with the above mentioned reagents a minute or more would elapse before the adductor would contract. Then after "winking" a few times they would slowly close, but never did they snap tightly together as other glochidia do.

From these experiments Miss Young concluded that it would be impossible to infect fish with any of the larval stages examined.

Since a large percentage of the embryos which had been extruded were glochidia, and since these would not infect fish it was important to find out whether they would develop outside the parent. In order to determine this a number of experiments were performed in which the glochidia were kept under conditions as nearly sterile as possible. Under such conditions the glochidia lived for several days but they did not undergo any change or growth during this time. At the end of three or four days the mantle cells began to disintegrate after which the embryos soon died. Accordingly it was concluded that these were immature glochidia which had been prematurely extruded from the parent.

As a check on the experiments mentioned above Miss Young repeated the experiments in infection already made by Lefevre and Curtis, attempting to infect fish with the young clams and glochidia. Four small sun-fish were placed in a jar with the glochidia and young clams and the exposure continued for more than an hour without results. Since these fish were readily infected by the glochidia of other clams, it seemed clear that these glochidia had lost their parasitic habit.

Besides these physiological studies Miss Young made a large number of preparations, both whole mounts and sections, illustrating the different stages. These have been studied and figured in the plates, part of the figures being drawn by Miss Young and part of them by myself.

Since it is important to show that these larvae which were the subject of study by Miss Young and by Lefevre and Curtis as shown

by their figure 45, possess the structures characteristic of the stage at which life on the bottom is begun in other species, a series of drawings from whole mounts showing the different stages in metamorphosis is given on plates I, II, and III. Figure 1 is a drawing of a glochidium in which the metamorphosis is just beginning. Protruding from the anterior end (ant) between the valves is the stump of the larval thread (lt). Crowded into a small space at the posterior end (post) are a few darkly staining cells (fc) which may be characterized as the "formative cells" of the embryo, since they produce a large part of the adult body. The remainder of the glochidium consists of a huge central adductor muscle (la Fig. 2) covered with the larval mantle (mc Figs. 1 and 2). Figures 8, 9, and 10 are transverse sections taken thru the stage shown in Figure 1. The section represented by Figure 8 passes thru the glochidium in the plane a-b and shows the beginning of the digestive tract (int). Figure 9 passes thru the plane b-c and shows the digestive tract giving off the liver diverticula (ld). Figure 10 passes thru the plane c-d, showing the larval thread gland (lt), the adductor muscle (la), and the larval mantle cells (mc).

In Figure 2 the mantle cells have been omitted in order that the adductor muscle (la) may be seen. It will be noticed that changes have taken place at the posterior end. The liver diverticulum (ld) is pushing out on either side, and posterior to this is a small protuberance (int) which forms the posterior region of the intestine. And on each side of the intestine is a layer of darkly staining cells (g) which mark the position of the developing gill buds.

Figure 3 is a later stage in which about half of the larval adductor (la) has been resorbed. The gill buds (g) may be seen on

each side, the intestine (int) now shows distinctly, and the foot (ft) is assuming its characteristic shape. Only half the mantle cells (mc) are represented in order that the muscle (la) may be shown on one side. A close study of the mantle cells (mc) shows them to have indistinct outlines and a reduced staining capacity which is evidence that they are being resorbed.

Figure 4 shows a further reduction in the size of the larval adductor (la), the remainder of which is taken over to form the anterior adductor (aa) of the adult. The posterior adductor (pa), however, is formed entirely of new tissue and may now be seen in the posterior region ventral to the intestine. Other features are the increased length of the intestine (int), the appearance of another pair of gill buds (g), and the addition of a layer of calcium carbonate (ns) to the glochidial shell.

Figure 5 does not show any further development but is interesting because it is still inclosed within the egg membrane (em). Note the origin of the larval thread (lt) at the anterior end of the embryo and its attachment to the egg membrane.

Figure 6 is the latest stage in development found in Miss Young's material. It is essentially the same as the specimen studied and described by Lefevre and Curtis (Fig. 45 Pl. XII). It will be noted that in addition to the structures shown above this clam possesses a large liver diverticulum (ld) on each side of the foot. The same stage is represented in anterior view by Figure 7. This stage has been studied further by a series of sections (Figs. 11, 12, 13, and 14) the planes of which are indicated on Figure 6. Figure 11 is a section taken thru the plane a-b. In the center of the figure lies the digestive tract (int) surrounded by the developing pericardium

(pc). On the extreme left is a part of the posterior adductor (pa) and between this and the intestine (int) is a spherical mass of cells which later forms the visceral ganglion (vg). Dorsal to these two structures lies the beginning of the kidneys (kd) with its thick glandular cells. On the ventral side the two gill buds (g) protrude into the mantle cavity, which is very large in this plane. Passing anteriorly to the plane b-c the relations change as shown by Figure 12. The gill buds (g) are now represented by two small ciliated patches and the foot (ft) now occupies the central part of the mantle cavity. Lying in the dorsal region of the foot (ft) are two small groups of darkly staining cells (pg) which form the pedal ganglia. Dorsal and lateral to these are the otocysts (o). The remaining part of the dorsal region is occupied by the digestive tract (int) which at this point is giving off the two liver diverticula (ld). The next section, Figure 13, passes thru the plane c-d and cuts the mouth region. The only points of interest here are a few strands of the anterior adductor (aa) and a ciliated region ventral to this which marks the mouth region. It will also be noted that the clam is still inclosed within the egg membrane (em). The last section of the series passes thru the plane d-e at the extreme anterior end and is represented by Figure 14. The only structures of interest is a few fibers of the anterior adductor (aa).

Following these is a series of figures (Pl. VII) drawn from the living specimens. These show a ciliated foot (ft) developed to a stage which is comparable with the foot of any young clam that has just dropped from the fish. The fact that they died at this period is no evidence that they were not fully developed, for it must be remembered that the young clams are always difficult to rear under

artificial conditions.

In nature they are dropped on the river bottom where there is plenty of food both in solution and in the form of unicellular organisms. Furthermore the inorganic salts in solution play a very important role, and as the water at the University of Missouri comes from deep wells, it differs very decidedly from river water with respect to this factor. Another difficulty which prevents the keeping of the young clam at this period is the rapid growth of bacteria and protozoa which soon foul the water. Therefore I think it is probable that the artificial conditions of the laboratory caused the young clams to die, and that had river conditions been supplied they would have lived.

From the above results, which I have organized and presented from Miss Young's notes, she drew the following conclusions, which are in agreement with the observations recorded by Lefevre and Curtis.

1. The glochidia of Strophitus do not infect fish.
2. The embryos pass thru their metamorphosis within the cords and before the extrusion from the marsupium of the parent clam.

Recently, the problem has been rendered more complicated by the discovery that Strophitus does infect certain fish, Dr. A. D. Howard of the U.S. Biological Station of Fairport Iowa having carried the glochidium thru its metamorphosis on fish, and finding no indication of metamorphosis without parasitism.

5. METAMORPHOSIS WITH PARASITISM

At the suggestion of Dr. Curtis I took up the investigation of this problem and have made observations covering a period of two years. Part of the work was done at the U.S. Biological Station

of Fairport Iowa, and part of it was done at the Zoological Laboratory of the University of Missouri.

One of the first problems which I had to solve was the collection of material. Strophitus is not only restricted in its distribution, but is also very thinly scattered over the bottom in the region where it is found. One may drag the "crow foot" or use the "shoulder rake" for a whole day on one of these beds and only get two or three Strophitus. For this reason it was necessary to rely entirely on the "Clammers" for the collection of the material. By making arrangements with several of these men I was able to secure all of their Strophitus and in this manner obtained sufficient material for my observations.

When the mussels were brought into the laboratory they were carefully pried open to ascertain whether or not they were gravid, and all such individuals were isolated and kept under observation. In most cases the gravid specimens died soon after being taken from the river. When placed in the water they would crawl about in the sand for a time, then begin discharging cords and in most cases die before the gills had been emptied of their glochidia. Those which were not gravid, however, readily adjusted themselves to laboratory conditions and lived into the next breeding season.

Since the center of interest in the investigation of this life history lies in the demonstration of the presence or absence of parasitism, most of the work was confined to the development following the glochidial stage. The plan of study was to ascertain the stage of development at the time the cords were discharged, determine whether the embryos developed any farther after their discharge from the parent, and to verify Howard's experiments by new infections.

In the above study and throughout the work whenever it seemed

necessary fixed and stained material has been examined in section or in whole mounts. In order to kill the glochidia expanded it is necessary to treat them with a narcotizing substance, since treatment with any fixative caused them to close. Even hot corrosive sublimate failed to kill them quickly enough. But when hydrochlorate of cocaine was slowly added to the water for a period of one or two hours they could be placed in the fixing solution without any contraction of the adductor.

A. Observations on Strophitus toward the close of the breeding season.

The Unionidae may be divided into two groups, the "summer breeders" and the "winter breeders". In the former case the period of gravidity extends over the summer months, while in the latter case ovulation takes place in August and the females carry ripe glochidia from October to the early summer. As Strophitus is one of the winter breeders, I was able to collect at Fairport, during the summer of 1914, material representing that part of the breeding season which is completed in the early summer, and also material which enabled me to follow the development in the early part of the next breeding season. Collecting was begun the first of July on which date I obtained four gravid Strophitus taken with the "crow foot". When some of the cords were removed and placed in water they behaved as had been described, becoming slightly swollen. The glochidia, however, behaved differently. Instead of lying inactive these glochidia kept up a continuous "winking" and within a short time most of them had broken thru both the egg membranes and the cords, quite a number of them remaining attached to the cord by means of their larval

threads. All the embryos were examined carefully to ascertain the stage of development and in all cases they were found to be typical glochidia, there being not the slightest indication of metamorphosis. The glochidia were then set aside in dishes in which the water was changed often in order to keep down the growth of microorganisms and to insure plenty of oxygen; but in spite of these precautions the larvae died within a few days without showing any signs of metamorphosis. This was repeated on several occasions at Fairport during the summer and also at Columbia in the fall of 1914 and in both the fall and spring of the years 1915 and 1916. In none of these experiments was there any growth after the glochidia had been discharged from the parent. Since Miss Young's notes and those made by Lefevre and Curtis at La Crosse in June 1908 record the same results, and since in my experiments at Fairport there was a very close approximation to river conditions, I think we may conclude that the glochidia of Strophitus do not develop after they have been discharged from the parent.

The next supply of gravid Strophitus was collected on July 13. In addition to performing the experiments described above I endeavored to infect a "crappie" (Pomoxis sparoides) with these glochidia and was successful. The fish was placed in a small jar which contained glochidia and in a short time a number of them had become attached to the gills where they produced hypertrophy of the tissues and became encysted in the normal manner. As this was the last gravid specimen obtained from the 1913-14 breeding season, further infection experiments at Fairport were impossible.

B. Observations on Strophitus at the beginning of the breeding season.

Between July 13 and August 7 eighty-five Strophitus were collected but none of these was gravid. They were put into a large tank thru which flowed filtered river water and were closely watched for the beginning of the 1914-15 breeding season. Toward the latter part of July I noticed that in some of the specimens the dorsal region of the foot had become swollen and found that it was caused by the rapidly developing gonads. On August 3 one of the males was observed discharging spermatozoa. The amount of discharge was extremely large; for the aquarium which was about $3 \times 2 \times 1\frac{1}{2}$ ft. was rendered milky within a short time. The particles which were being discharged looked too large for spermatozoa, and upon examination it was found that each particle consisted of hundreds of spermatozoa arranged in a hollow sphere with the heads pointing inward. (Fig. 21). Upon contact with the water the spheres disintegrated, presumably as a result of some change in the chemical environment and the mechanical effect of the vibrating tail. A few days later the same mussel discharged spermatozoa again in equal numbers. This gives some idea of the number of spermatozoa that must be produced when fertilization is effected by such a haphazard process.

On Aug. 8, the day following the last discharge of spermatozoa, I found a gravid female in one of the aquaria. Ovulation must have taken place only a day or two earlier because the embryos had developed no farther than the blastula stage. Figure 22 is a cross-section taken thru the outer gill of this specimen. It will be noted that the embryos (emb) fill the central part of the old water-tubes and that the superficial water-tubes have been formed.

These are made by the outgrowth and fusion of a vertical sheet of tissue which cuts off the outer sides of the old water-tubes. In the gravid gill, the respiratory current passes thru the ostia into these superficial water-tubes, which run up either side of the marsupium, then into the suprabranchial chamber; oxygen being furnished direct to the embryos by diffusion. Another feature to be noted is the conglutinating substance (con) which surrounds the embryos. This will later form the cords and is probably secreted by the walls of the water-tubes.

After Aug. 8 a large percentage of the females collected had ovulated. During the month of August the collections were as follows.

Aug. 11 ----- 6 Strophitus collected 1 gravid.

" 12 ----- 27 " " 7 "

" 20 ----- 29 " " 12 "

By the end of August the development of the larvae within the gravid females had reached a stage in which the glochidial shell was formed and the embryo was just ready to begin the invagination which forms the glochidium.

The next collections were made in October and the mussels were shipped to Columbia Missouri. When placed in the water they extruded ripe glochidia but contained no stages in metamorphosis, nor did any further development take place after they had been discharged from the parent. (Figs. 23 and 24).

After determining the stage of development the next step was to see if the glochidia would infect fish. Two cat-fish, two large sun-perch, and a number of small crappies were used in the experiment. In the case of the sun-perch and the cat-fish negative results were obtained; but in the case of the crappie the glochidia became encysted and passed thru their metamorphosis. (Figs. 25 to 29 inclusive).

At the end of twelve days the young clams were found crawling over the bottom of the dish. A study of the figures referred to above and of the sections (Plates XII, XIII, and XIV) shows them to possess all the structures of the juvenile at this period.

6. CONCLUSIONS

These results confirm those of Howard at Fairport and establish without doubt the parasitic habit of Strophitus. From the number of experiments that have been performed I think we may safely conclude that this is the usual method of development in this species. The reason Miss Young and Lefevre and Curtis did not get infections was due to the selection of the wrong kind of fish. At the time the first experiments were performed it was not known that there was a specificity in the parasitism. The work of Lefevre and Curtis did show that some species of fish were more susceptible than others to certain glochidia, but no further analysis was attempted. Howard in his work at Fairport conceived the idea that there might be different hosts for different species of mussels, and accordingly made an extended study of natural infections in the river. This in connection with some experimental work showed, comparable with that which so commonly occurs in other parasitic forms, specific hosts for certain of the mussels. It was found for example that the "gar" (Lepisosteus platostomus) was the natural host of Lampsilis anodontoides, and that the "channel cat" (Ictalurus punctatus) was the natural host of Quadrula pustulosa. This makes clear the negative results of Lefevre and Curtis and those of Miss Young. In the latter case it will be noted that the sun-perch was used, which is evidently not one of the natural hosts of Strophitus.

Therefore, the results only indicate a restriction in the parasitism and do not show that Strophitus has lost its parasitic habit.

In regard to metamorphosis without parasitism there can be no doubt as to the facts as shown by Figure 45 in Lefevre and Curtis and confirmed by the notes of Miss Young. Not one but many specimens were observed, as they were extruded during a period of almost eight weeks, and the material and figures show clearly the adult structures of the mussel. But the fact that I have examined fifty or more females containing ripe glochidia with no indications of metamorphosis shows that these conditions are of rare occurrence.

Upon a consideration of the observational and experimental data from all sources I think we may conclude: first, that the glochidia of Strophitus usually pass thru their metamorphosis on certain fishes; second, in a single case where the mussel was kept in the laboratory, they were observed to undergo metamorphosis without parasitism.

The above facts suggest the following question. Is this a form which is just beginning to change its habits from a parasitic to a non-parasitic existence? The case is not without a parallel in the Unionidae. Howard has discovered that Anodonta imbecilis completes its development without parasitism, metamorphosis taking place within the marsupium in the absence of any conglutinate substance such as the cords of Strophitus. Experiments with the glochidia failed to give infections on fish. The glochidia closed their valves upon the fins or gills of the fish and remained attached, but within a few days they dropped off without undergoing any change. Howard's paper does not state how many fish have been tried, and this may also be a case of restricted paras-

-itism. But leaving this out of account it would seem that Anodonta imbecillis which is a hermaphroditic species and is not closely related to Strophitus is abandoning its parasitic habit. The life cycle is being telescoped so that the whole development takes place within the parent. This may also be the direction in which Strophitus is moving. Assuming that it is, we have here a case of convergent evolution, and these two cases might be the first of a wide series of changes marking the the general evolutionary trend in the whole group.

Another possible explanation of the conflicting data is that some chemical substance present in the water was responsible for the metamorphosis without parasitism. Since the clam does not grow to any appreciable ^{extent} while on the fish, and since the larval structures are resorbed during metamorphosis, it may be that the relation between fish and glochidium is more a matter of stimulation than of nutrition, it may be that the tissues of the fish produce some substance which initiates the metamorphosis. If such a substance had been present in the aquarium where the single specimen from which glochidia and young mussels were obtained at Columbia in the Winter of 1909 it might have reached the embryos by diffusion thru the walls of the marsupium and thus caused the development which was recorded.

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8. KEY TO ABBREVIATIONS IN PLATES

1. aa ----- anterior adductor	
2. ant ---- anterior	
3. bs ----- byssus gland	
4. cd ----- cord	
5. con ---- conglomerate substance	
6. em ----- egg membrane	
7. emb ---- embryo	
8. fc ----- formative cells	25. pg ----- pedal ganglion
9. ft ----- foot	26. post --- posterior
10. g ----- gill buds	27. sen ---- sensory hairs
11. int ---- intestine	28. st ----- superficial water-tubes
12. kd ----- kidney	29. stom --- stomach
13. la ----- larval adductor	30. vg ----- visceral ganglion
14. ld ----- liver diverticulum	31. wt ----- water-tubes
15. lt ----- larval thread	
16. m ----- mantle	
17. mc ----- mantle cells	
18. mar ---- marsupium	
19. ns ----- new shell	
20. o ----- otocyst	
21. oes ---- oesophagus	
22. os ----- ostia	
23. pa ----- posterior adductor	
24. .pc ----- pericardium	

EXPLANATION OF PLATES

Figures 1 to 7 inclusive (Plates 1, 11, and 111.) are drawn from whole mounts of Strophitus embryos and illustrate metamorphosis without parasitism. Camera lucida, Leitz Oc.4 Obj.16.

PLATE 1

Figure 1. Glochidium of Strophitus edentulus ventral view, anterior end (ant) above. Showing the large cells of the larval mantle (mc), the larval thread (lt), the beginning of the intestine (int), and the formative cells (fc) which later give rise to the adult organs. The lines a-b, b-c, c-d indicate the planes of sections represented by figures 8, 9, and 10.

Figure 2. Orientation same as above. In this figure the microscope was focused at a lower level in order to show the larval adductor (la). It represents a stage in development just following that shown by figure 1. Note that the formative cells (fc) have assumed a definite arrangement which marks the liver diverticulum (ld) and the beginnings of the intestine (int). Lying on either side and lateral to the intestine is a row of rapidly dividing cells (g) which are the rudiments of the gills.

Figure 3. Orientation as above. At the anterior end the larval mantle cells (mc) are represented on the right side while on the left side the larval adductor (la) is shown at a lower focus. It will be noted that about half of the larval adductor has been resorbed, the foot (ft) has assumed its characteristic shape, the intestine (int) now shows plainly, and near the posterior end on

each side are seen the gill buds (g).

PLATE II

Figure 4. Young clam drawn from ventral view with valves slightly flexed. The larval adductor shows a further decrease in size and may now be called the anterior adductor (aa) of the young clam. Other changes are the increased length of the intestine (int) shown by the developing fold, the four gill buds (g) in place of two, and the posterior adductor muscle (pa) which has been formed ventral to the intestine (int). It will also be noted that a thin layer of calcium carbonate (ns) has been added to the glochidial shell.

Figure 5. Young clam still inclosed within the egg membrane (em). The larval thread (lt) originates at the anterior end of the embryo and becomes attached to the egg membrane (em) in that region. Other structures are similar to figure four.

Figure 6. This represents the latest stage of development reached by the specimens obtained by Miss Young in the absence of infection. The figure shows the anterior adductor (aa), the foot (ft), the liver diverticula (ld), the intestine (int), and the gill buds (g). The lines a-b, b-c, c-d, and d-e mark the plane of sections represented by figures 11, 12, 13, and 14.

PLATE III

Figure 7. Anterior view of stage similar to that shown in Figure 6. Note the well developed ciliated foot.

Figure 8. Cross section thru plane a-b of stage represented by figure 1. Showing intestine (int), the visceral ganglion (vg), and the

and the larval mantle cells (mc).

Camera, Leitz Oc.3 Obj.7.

PLATE IV

Figure 9. Thru plane b-c of stage represented by Figure 1. Showing the digestive tract giving off the liver diverticula (ld), a group of formative cells (fc), and the cells of the larval mantle (mc).

Camera, Leitz Oc.2 Obj.7.

Figure 10. Thru plane c-d of stage represented by Figure 1. Showing the larval thread gland (lt), the larval adductor (la), and the larval mantle cells (mc).

Camera, Leitz Oc.2 Obj.7.

PLATE V

Figure 11. Cross-section of young clam represented by Figure 6. Passing thru posterior end, plane marked by line a-b. The tube in the center is the intestine (int). Proceeding laterally on the left side the following structures appear in order; visceral ganglion (vg), kidney (kd), posterior adductor (pa), and gill buds (g).

Figure 12. Section anterior to Figure 11, thru plane b-c. Showing the digestive tract giving off the liver diverticula (ld), the pedal ganglia (pg), and the ciliated foot (ft).

PLATE VI

Figure 13. Cross-section thru plane c-d Figure 6. Note that the clam was still inclosed within the egg membrane (em). The anterior adductor (aa) is shown.

Figure 14. Cross-section thru extreme anterior end, plane d-e, Figure 6. The remains of the larval thread gland (lt) and the anterior adductor muscle (aa) are shown.

PLATE VII

Figures 15 to 20 inclusive are drawings from living Strophitus that had passed thru their metamorphosis without parasitism and were moving about upon the bottom. Note the well developed ciliated foot (ft) and the protruding mantle which is characteristic of the young clam in this stage of development. Camera, Leitz Oc.2 Oj.3.

PLATE VIII

Figure 21. Section thru a packet of Strophitus spermatozoa.

Figure 22. Cross-section thru the outer gill of a gravid Strophitus a few days after ovulation. The superficial water-tubes (st) have been formed thus inclosing the embryos in the central part of the old water-tubes (wt). The embryos are in the blastula stage and are surrounded by a conglomerate substance (con) which later forms the cords.

PLATE IX

Figure 23. Side view of glochidium just extruded from the cord showing sensory cells (sen), larval mantle cells (mc), larval thread (lt), egg membrane (em), and cord (cd).

Figure 24. Glochidium with larval thread (lt) and everted egg membrane (em) attached.

Figures 25 to 29 inclusive (Plates X and XI) are drawn from living specimens that had passed their metamorphosis on a fish (Pomoxis sparoides) and were actively crawling over the bottom.

Camera, Leitz Oc.4 Obj.16.

PLATE X

Figure 25. Side view of a young clam showing how the mantle (m) extends beyond the glochidial shell.

Figure 26. Dorsal view of young clam expanded, showing the ciliated foot.

Figure 27. Ventral view of young clam showing mantle (m), anterior adductor (aa), posterior adductor (pa), gills (g), and foot (ft).

PLATE XI

Figure 28. Drawn from contracted specimen, ventral and side view.

Figure 29. Same view as Figure 28 except clam is expanded. Showing anterior adductor (aa), posterior adductor (pa), the foot (ft), the byssus indentation (bs), the gill buds (g), and the mantle (m).

The figures in plates XII, XIII, and XIV are drawn from a series of sections of the stage represented by the previous drawings (Figs. 25 to 29 inclusive). Leitz projection apparatus, Oc.4 Obj.4.

PLATE XII

Figure 30. Taken thru extreme posterior end showing the intestine (int) and the posterior adductor (pa).

Figure 31. Anterior to Figure 30. Showing intestine (int), posterior region of the foot (ft), sections of gill buds (g),

and the adult mantle cells (m).

Figure 32. Section thru region where intestine (int) bends down into the foot (ft).

PLATE XIII

Figure 33. Section showing intestine (int) in the ventral region of the foot (ft). Also shows inner and outer epithelium of the mantle (m), and sections of the gill buds (g).

Figure 34. Section taken thru the central region of the foot (ft). Showing stomach (stom) occupying most of foot, a fold of intestine (int) ventral to stomach, a section of the kidneys (kd) in dorsal and lateral region, and sections of gill buds (g).

Figure 35. Section passing thru anterior region of the foot. Showing oesophagus (oes), and kidney (kd).

PLATE XIV

Figure 36. Section thru extreme anterior end showing anterior adductor (aa), and the anterior tip of the foot (ft). Space between dorsal part of foot and anterior adductor marks the position of the mouth.

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Fig 4

323

Fig 5

322

Fig 6

274

Fig 7

Drawn by E.A. Martin

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Fig 8

thru plane a-b fig. 1.

Drawn by M. S. Young

3164

Fig 11

Thru plane a-b fig 6

Drawn by Miss Young

386

Fig 12

Thru plane b-c fig 6

Drawn by Miss Young

346

Fig 13
thru plane c-d fig 6

Drawn by Miss Young

3146

Fig 14
thru plane d-e fig 6

Drawn by Miss Young 316a

Fig 15

Fig 16

Fig 17

Fig 18

Fig 19

Fig 20

Fig. 21.

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Fig. 22.

Fig 23

Fig 24

Fig. 25

Fig 26

Fig 27.

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Fig 29

Fig 30

Fig 31

Fig 32

Fig 33

Fig 34

Fig 35

Fig. 36

E.A. Martin

UNIVERSITY OF MISSOURI
COLUMBIA

ZOOLOGICAL LABORATORY

May 15th, 1916.

Dean Walter Miller,
University of Missouri.

My dear Dean Miller:- I have examined the thesis of
Mr. E A. Martin, which is herewith submitted, and find it
satisfactory.

Very truly yours,

W. C. Custer

Title:- "Some Observations on the Life History of
Strephitus edentulus"

UNIVERSITY OF MISSOURI
COLUMBIA

DEPARTMENT OF PHYSIOLOGY

May 19, 1916.

Dean Walter Miller,
Graduate School.

Dear Doctor Miller:-

I have read the thesis on
"Some Observations on the Life History of
Strophitus Edentulus" by Earl Albert Martin.
I consider the paper as maintaining a satis-
factory standard in partial fulfillment of
the requirements for Master's Degree.

Yours very truly,

CWG/O.

Charles W. Greene

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