Life History of Elliptio complanatus (Dillwyn, 1817)*

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INTRODUCTION

Although *Elliptio complanatus* is a very common fresh-water mussel, found generally through the northern Atlantic seaboard states, comparatively little information can be discovered in conchological literature on its life history or ecology. The reasons for this scarcity of substantial research on the mussel are its doubtful commercial value and the scarcity of investigators in the field. This mussel is not commercially valuable at present, but knowledge derived from a study of its life conditions may apply to other mussels which are economically important.

Investigation described in this dissertation was begun in the summer of 1941. In order to gain sufficient data for completing the study of the life cycle of *Elliptio complanatus*, this research was continued through the summer of 1946. As is often the case in solving a natural life cycle, the intensity of research was not dependent on the manipulator but on the development of the organism itself. Because of the ample facilities of the University of Michigan Biological Station, all of the basic phases of the life history of the mussel studied were investigated at the original site of experimentation.

The primary and almost sole objective, originally, was a study of the life cycle of *Elliptio complanatus*. However, little time had elapsed after initiation of the project before many interesting ecological problems had arisen. Those problems which are not directly associated with the life cycle will be discussed in a later paper.

APPARATUS AND METHODS

As a knowledge of certain physico-chemical features was essential for pursuance of the problems involved, certain determinations were made on all bodies of water connected with the research.

It might seem that a very exhaustive system of determinations would portray a more accurate impression of the problem at hand. However, some factors deemed necessary for a complete analysis of fresh water were judged to be superfluous in the study of the life-cycle. As a result, only certain significant physico-chemical conditions were determined.

The most important environmental factors tested were water temperatures, hydrogen ion concentration, free carbon dioxide, dissolved oxygen, dissolved carbonates and bicarbonates, and conductivity. In all cases the tests followed

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as closely as possible those delineated in *Standard Methods for the Analysis of Water and Sewage*.

Apparatus used for the collection of mussels for various purposes was, almost entirely, prepared from materials at hand. Those clams obtained from the lake used as the source of supply were secured during the summer months and could be easily gathered by hand. On windy days, they were collected with the aid of a glass-bottomed bucket. Because particles of clay, of which the lake bottom is largely composed, tended to obscure visibility the bucket was often discarded and the clams obtained merely by sense of touch.

During those months when the water was cold, hand-picking was impossible. Mussels obtained during fall and spring were secured by raking them from deeper water by means of a rake equipped with a screen apron. This method proved to be very laborious and slow but seemed to be the only solution. Coker (1919) suggests several methods for the collection of mussels, including the use of a modified rake.

For winter use, mussels were placed in concentrated groups in shallow water in the fall. Stakes were driven firmly into the bottom among the clam concentrations. After the ice had formed, the stakes remained as markers for locating the supply. When a supply was needed, a hole was cut in the ice and the clams were easily extracted from the bottom. This procedure was highly satisfactory. The clams were sluggish to the extent of being almost dormant during the winter, most of them moving little except to imbed in the bottom. Some remained until gathered in the same position which they had taken when dropped in the fall, entirely on the surface of the bottom.

Individual identification of the mussels was assured by first cleaning the shell and then filing the desired symbol on it by use of a three-cornered file. Several methods used by other workers in the field were considered but none seemed practical for marking the large numbers of clams used for studying yearly growth rate. Up to the present, erosion of the valves, even under the most adverse conditions, has been insufficient to destroy the identification marks or even seriously to affect their legibility.

Measurements of growth were taken for length, height, width and weight. Length, height and width were obtained by a simple instrument constructed from two pieces of maple flooring (Fig. 1). Maple was purposely selected because of several desirable inherent qualities. A portion of one piece was fitted into the other and permanently attached thereto. The remainder of the second piece was allowed to slide against the fixed portion thus making a simple caliper. An accurate rule, graduated to millimeters was attached to the fixed portion. Weight was obtained by means of a torsion balance equipped with a home-made carrier so that it could be taken into the field. The sides of the carrier acted as windbreaks when used on the lake-shore.

At various times it was necessary to store clams for future study. This was necessarily accomplished in anticipation of two types of investigation: (1) That for clams needed in the living state and (2) that for those studied after killing and preserving. The method for storage of living clams for winter study has already been discussed.

Clams needed for study during subsequent summer months were stored in large earthenware tubs in an aquarium shelter. Originally it was thought that a small constant flow of surface lake water would be desirable for the clams' well-being. However, due to the increased water temperature, lack of proper food, and perhaps other factors, mortality among the stored clams was high. It was found that the clams fared much better by having the water unchanged. This was due to the fact that water stored in suitable containers and protected from the sun during the day will experience a considerable drop in temperature during cool nights but will not regain as high a temperature during the following day, as does the surface water of a lake. The resulting cooler average temperature lowers the metabolic rate of the clams and, therefore, their oxygen consumption.
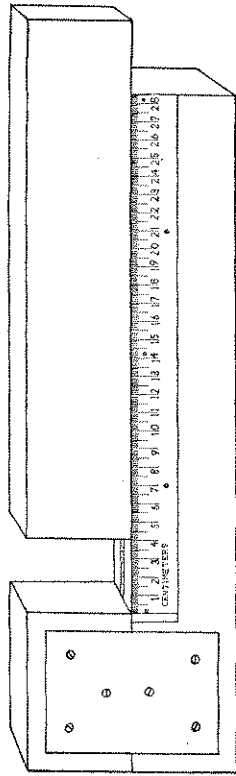

Fig. 1.—Caliper used for measuring clams. The smallest unit on the scale is one millimeter; the entire range is 285 millimeters.

Clams remaining on the site employed for winter storage were also used during the summer. However, on the advent of warmer water-temperatures, the clams tended to move from the shoal, where they had been placed, into deeper water and were thus too scattered and difficult to obtain for practical purposes, other than for incidental experimentation.

Cages, four feet square and covered with one-half inch mesh screen, were employed to a certain extent for storing live mussels but were quite unsatisfactory due to the effects of wave action.

As a complete history of summer development, particularly for gametogenesis, was desirable, clams in sufficient quantity were prepared periodically for winter study. These clams were killed and fixed by various methods which will be described later. Both those with the soft parts still in the valves and those removed from the valves were then stored in large-mouthed gallon jars.

Originally, floating cages for housing the experimental host fish were used in caring for the parasitic stages of the mussel but were later displaced by glass aquaria. The cages were arranged in linear series, with six individual cages composing a complete raft. The bottoms of the cages were constructed of zinc in order to allow careful examination of any bottom deposits. The sides and covers were of one-half inch mesh galvanized screen (Fig. 2).

Aquaria were of assorted sizes, varying from a capacity of one gallon, which were used as infecting chambers, to those of 10-gallon capacity for

containing the infected fish. The aquaria were of the usual type, with glass sides, steel frames and slate bottoms. The bottoms were made free of all irregularities so that any deposits could be secured easily.

Lake water was used exclusively during the determination of the fish host. It was pumped into the aquarium shelter where it was stored in a large overhead tank. From the tank the water ran continually as needed.

This study was conducted under the direction of Professor Frank E. Eggleton, of the Department of Zoology, University of Michigan. Invaluable aid, especially on taxonomy of the fresh-water pelecypods and bibliographical sources, was contributed by Dr. Henry van der Schalie, Curator of Mollusks at the University Museum of Zoology.
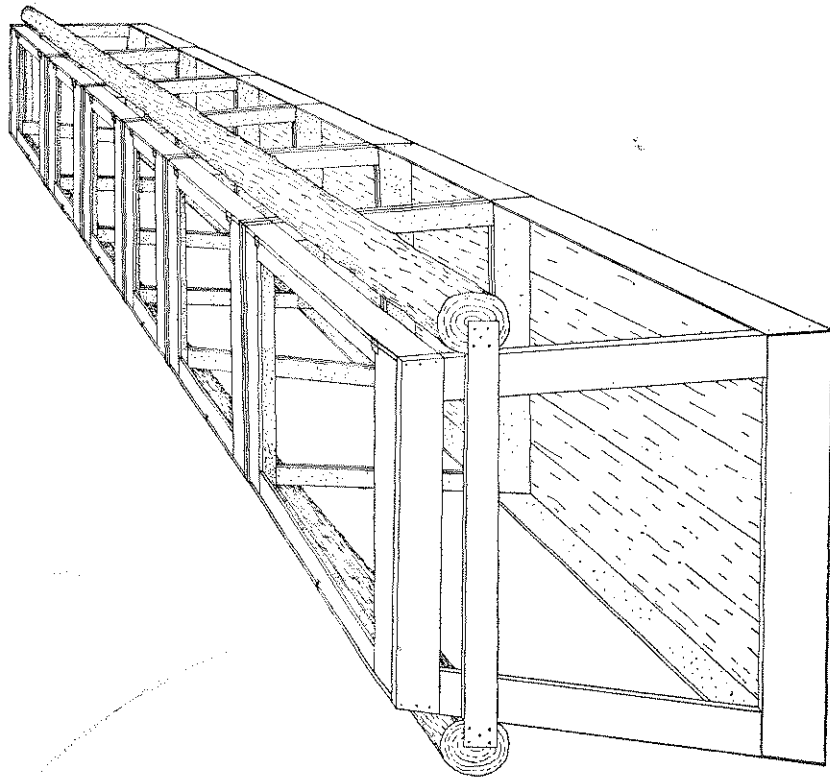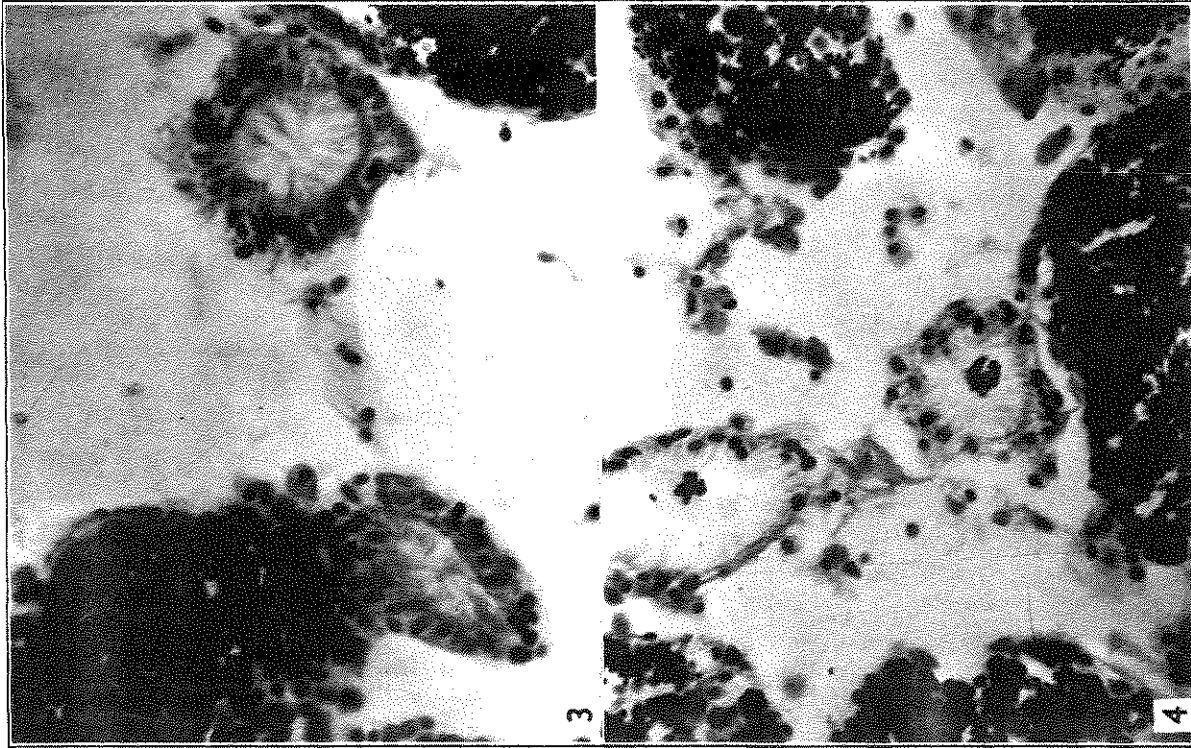

Fig. 2.—Floating raft for harboring parasitized host fish. The raft is both supported and floated by the attachment of two cedar poles, one on either side. The tops are removable and are screened to prevent the fish from escaping.

TECHNIQUE

The complete story of gametogenesis in *Elliptio complanatus*, and the subsequent phenomena concerned with fertilization and the clam's early embryology, is a complicated one. As a result, certain details, chiefly on gametogenesis, will be reported more in detail at a later time. However, all observations and results on gametogenesis described later in this paper are accurate and have been verified by several competent cytologists.

The basic stain used in all prepared slides for microscopic study was Heidenhain's iron-hematoxylin, which is specific for structures composed chiefly of chromatin. In various instances a counter-stain with eosin for cytoplasmic study proved profitable. Mallory's triple stain was also used. In general, however, the multiple stains often tend to be a hinderance because they mask underlying cells which can be easily studied when only the iron-hematoxylin stain is used.

GAMETOGENESIS AND FERTILIZATION

Fertilization occurs in the suprabranchial chambers of the female clam, as is customary among the various unionids. Viable spermatozoa, ejected into the water from the exhalent siphon by ciliary action and by the forcible closing of the valves of the male are able to swim considerable distances. Water movements also are probably significant in dispersing them. Eventually many of them reach the female. Here they are drawn into the mantle cavity through the inhalent siphon. After entering the ostia of the gills they are carried upward through the water tubes to the chief site of fertilization, the suprabranchial chambers.

Simultaneously with the above procedure the female reproductive cells have been propelled upward from the ovarian mass, through the various ciliated ducts, and thence into the suprabranchial chambers. At this time oögenesis has proceeded to the primary oöcyte stage. No further development occurs until a spermatozoon has penetrated the oöcyte.

As the immature ova are heavier than water they tend to drop into the water tubes. In *Elliptio complanatus*, only the outer gills serve thus as marsupia. Any of the ova which are not penetrated by spermatozoa in the suprabranchial chambers are very liable to meet sperm during their descent in the tubes. However, examination of the developing young in the marsupia has shown the presence of many unfertilized eggs in some specimens. This fact probably can be attributed, in these isolated cases, to a scarcity of spermatozoa at the time when the immature ova are in the proper location for penetration. Although impregnation is accomplished chiefly in the suprabranchial chambers, and to a certain extent in the water tubes, spermatozoa were observed in one instance in the ovarian ducts leading to the suprabranchial chambers. This would imply that sperm had been able to swim successfully against the influence of ciliary action in the ducts. Probably penetration could result. There is the possibility, however, that sperm had been forced into the ducts during the mechanical processes leading to the making of the slides.

Figs. 3, 4.—3. Testicular acini and sperm ducts from mussel killed November 2. Two ciliated sperm ducts, devoid of spermatozoa, may be observed. 4. Testicular acini and sperm ducts from mussel killed May 2. Most of the germ cells at this time, just prior to the reproductive period, are spermatozoa. A thin rim of spermatogonia and spermatocytes is evident. The sperm ducts contain spermatozoa which are moving toward a suprabranchial chamber.
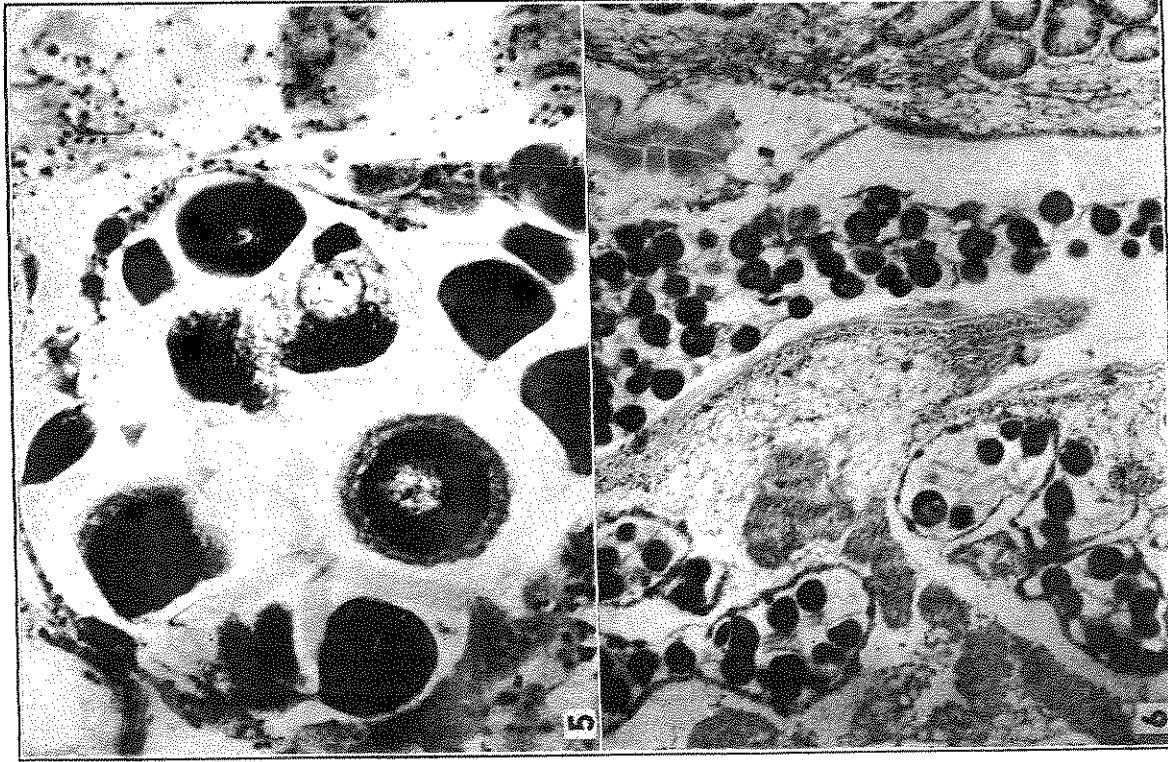
Many clams of both sexes were gathered and prepared for microscopic study during each week throughout the entire year. Also, specimens were often obtained at various times during subsequent years. The prepared mussels were then sectioned and examined microscopically. It was observed that, because environmental conditions vary on a specific date in successive years, only a close approximation concerning developmental stages to be expected could be predicted.

Examination of prepared slides showed that spermatozoa were present in the testicular acini throughout the year. The number of sperm present increased as the time of a new breeding season approached. For example, in the sections from clams killed in November the preponderance of reproductive cells was in stages prior to spermatozoa (Fig. 3). The sperm, if present, in a specific acinus usually occupied a position in the center at that time. In specimens examined which were killed on May 2, the greater portion of the cells were spermatozoa. Although no sperm were observed in the sperm ducts earlier in the male reproductive cycle, many ducts were filled in those killed on May 2 (Fig. 4). Some microscopic evidence from slides in the author's collection tends to show that the immature spermatozoa may spend more time imbedded in epithelial cells of the ducts which may act as sperm mother cells. However, this presumption must be verified and will be discussed in later papers. As the epithelium of all sperm ducts is ciliated, the journey of the spermatozoa to the suprabranchial chambers is thus facilitated.

Spermatozoa in *Elliptio complanatus* are viable throughout the year. This was proven by examining the fluid taken when mussels were vivisected. By inference it may be supposed that they are contained in the lumina of the testicular acini in the mature state until the time of breeding is at hand. Then, probably due to the environmental factors of increased water temperature and perhaps changed light conditions, certain physiological phenomena occur within the mussels, which cause ciliary action in the sperm ducts to be resumed.

Although there are individual differences between male clams, and climatic factors for different years may vary considerably, it may be said that spermatozoa begin entering open water in late April and continue to do so until the latter part of May, with a few isolated males shedding them as late as the middle of June. The period for maximum liberation of sperm is near the middle of May.

The germinative layer of the ovarian acini begins developing the female reproductive cells to the primary oöcyte stage much more rapidly than spermatozoa are developed during the reproductive cycle in the male. Within a few months the number of oöcytes is about as great as it is at the time of their liberation into the ovarian ducts. However, immediately after liberation only a very few primary oöcytes are contained in the lumina of the acini. Many may be observed in the process of taking on cytoplasmic material (Fig. 5). During this period they are attached firmly to the germinative layer of the acini by a definite stem. This stem persists for a short time after each oöcyte has gained full size and then the connection is broken. The area formerly occupied by the stem develops into a micropyle. At this time each oöcyte

Figs. 5, 6.—5. Ovarian acinus containing primary oöcytes during the process of increasing their cytoplasmic content. Several nuclei and stems are visible. A membrane which surrounds each reproductive cell is evident. 6. Ovarian acini during the passing of primary oöcytes into ovarian ducts. A duct is located at right center.

is surrounded by a thin membranous covering which can be observed when subjected to eosin stain. It is very irregular, loose-fitting and noncellular. Its function and origin are as yet unknown to the author.

Evidence as to the time when the primary oöcytes pass into the ovarian ducts was obtained by microscopic examination of prepared slides. It was observed that no reproductive cells appeared in considerable numbers until the middle of May (Fig. 6). Again, as with spermatogenesis, we may assume that there are probably random examples of female clams which reach the period for profitable reception of spermatozoa previous to early May and perhaps as late as the last week of May or early June.

The liberation of spermatozoa into lake water by the male may be said to cover an appreciably wider time-span than the period during which primary oöcytes are in favorable position for sperm penetration in the female. Roughly speaking, the time-span of oöcyte exposure lies midway within that of the liberation of spermatozoa. From the standpoint of productivity this situation is fortunate.

Immediately following penetration of the primary oöcyte by the sperm, through the micropyle, a definite fertilization membrane is laid down by the cell membrane of the oöcyte (Fig. 7). As mentioned earlier, the micropyle lies on the area formerly acting as a stem for attachment to the germinative layer of the ovarian acini. After penetration by the spermatozoon the fertilization membrane at this point develops into a transparent chimney-like structure. Immediately surrounding this area the membrane adheres tightly to the cell. At all other points the membrane appears as a neat, loosely-fitting, transparent sac.

Very soon after the appearance of the fertilization membrane a very small body arises and is pinched off the main cell. This is the first polar body and signifies the transformation of the primary oöcyte into the secondary oöcyte. The second polar body is closely affixed to the first. The male and female pronuclei then combine to form the zygote.

PREGLOCHIDIAL DEVELOPMENT

The early developmental stages were studied with the use of living material. The material was obtained by opening the marsupial gills of over twenty females which possessed embryos in all stages from zygotes to mature glochidia. Because of the immense amounts of yolk material no attempt has been made as yet to study the mitotic figures involved during the cleavage processes. Observations made follow closely the results obtained by Lillie (1895, 1897, 1898).

It was observed that no cleavages occur while the zygotes remain in the suprabranchial chambers. They quickly settle in the water tubes of the entire outer gill where all further preglochidial development takes place. In a short time, probably several hours, the fertilization membrane loses its distinctive shape, breaking free from the zygote at all points. The chimney-like structure which marked the micropyle also collapses at this time. The polar bodies quickly disintegrate.

In Elliptio complanatus the entire outer gills act as marsupia. This fact is supported by literature and has been verified by direct observation (Fig. 8). As the water tubes of the outer gills are in direct connection with the suprabranchial chambers each tube becomes more or less filled with young. However, the upper openings of the water tubes composing the inner gills merely open into the mantle cavity at the place where the gills join the visceral portion of the foot (Fig. 9). This means that any water circulating through the water tubes, after entering through ostia from the mantle cavity, must again enter that cavity.

There are two possible ways for water in the cavity to leave: (1) by escaping between the mantles at some point; and, (2) by passing through ostia into the water tubes of the outer gills.

There is no direct evidence to prove whether water does escape through the mantles. Because of the location of ciliary tracts on the surfaces lining the circuit taken by the water as it proceeds from the inhalent to the exhalent siphon, we may assume that the amount of water escaping by this means is probably negligible. What seems more logical is that ciliary action in the upper respiratory areas causes lowered water pressure there by beating water from the suprabranchial chambers through the exhalent siphon. The water in the mantle cavity, then, in order to equalize the water pressure above, is forced, by its greater pressure, to enter the ostia of the outer gills. From there it passes among the eggs and eventually to the suprabranchial chambers,
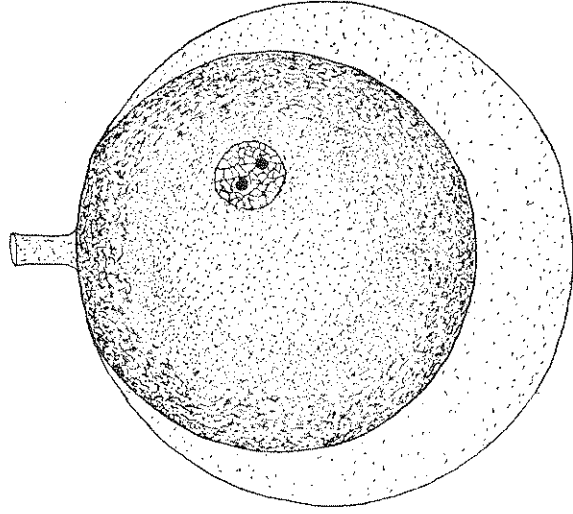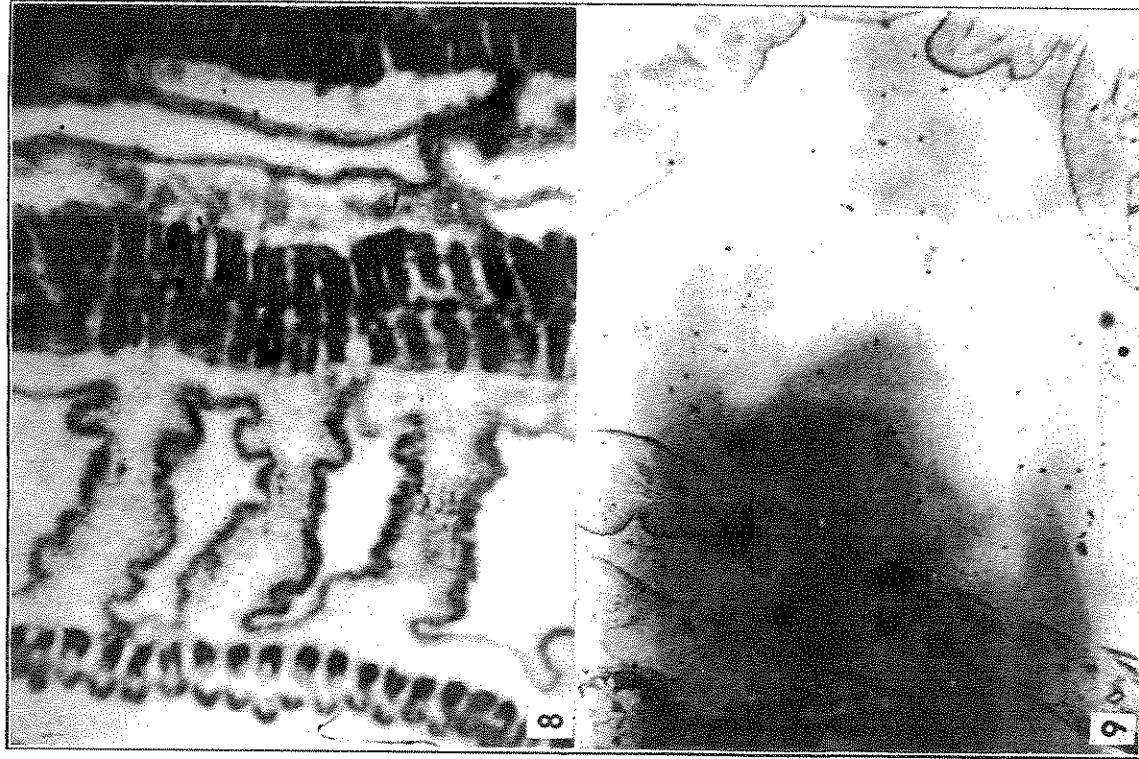

Fig. 7.—Zygote of Elliptio complanatus.

thus equalizing the pressure. This would tend to be beneficial for several reasons. It would insure oxygenation of the eggs and the elimination of any toxic or waste substances in their proximity. Added oxygenation would be afforded the parent. Finally, wastes from the excretory and digestive tracts would be flushed from the common postanal region as usual. So, it is to the advantage of the female mussel to allow no water to escape through the mantle, not only for the embryos' sake, but also for her own. A suspension of powdered carmine placed in the mantle cavity, does not reappear until it leaves by means of the exhalent siphon.

In from seven to ten hours the first cleavage has been completed. The two resultant cells are unequal in size, one being considerably larger than the other. From then on the cells cleave quite rapidly until the blastula stage is reached. The number of cells present in the blastula probably approximates one-hundred and fifty. The gastrula stage has not as yet been identified in the material at hand. However, Lillie (1895) has described it in detail.

The volume of the developing embryo changes little, or none, from the zygote to the glochidium. All food needed for development is contained in the original primary oöcyte, with the possible exception that dissolved organic material might be absorbed. The possibility that food materials are transferred from the lamellae or interlamellar junctions of the marsupial gills of the mother is very slight. No special organs for attachment, or any kind of special secreting cells, have been noticed in any of the gill structures. Furthermore, although there is no shell formed around the egg, the fertilization membrane persists until the glochidium is completely mature. This structure prohibits the passing of appreciable amounts of nutritive materials from marsupium to the young, especially as the water medium is continually in motion.

Organogenesis is completed in approximately two weeks. The original fertilization membrane still persists as a loosely fitting sac. It is even present after the glochidia are capable of opening and closing their valves. When mature glochidia are shed normally by the female, however, it has always been observed that the larval clams are entirely devoid of the membrane. How this membrane is lost is unknown.

It is not unusual to observe clams aborting their young. This is accomplished either by exuding the ovisacs in an intact state, or, as is habitual with some species, as fragments. Abortion is usually caused by various undesirable situations such as sudden changes in water temperature, rough handling, the presence of toxic substances in the water, and starvation. The tendency toward abortion is highly variable among the different species of clams.

The incidence of abortion among females of *Elliptio complanatus* is high as compared to most clams. The ovisacs are expelled in an intact condition, each ovisac retaining the shape of the extended water tube which it formerly occupied. During the period when embryonic development was in progress, clams were often brought from the supply lake to the laboratory in tubs, usually for the purpose of infecting fish. Invariably, after the clams had been removed from the tubs, the residue would contain great numbers of the

Figs. 8, 9.—8. Marsupial gill. The water tubes of the marsupial gill are square in appearance, while those of the inner gill are long and narrow. 9. Inner lamella of inner gill showing no attachment to the visceral portion of the foot.

aborted ovisacs. There seems to be no discrimination as to the degree of development of the young, as all stages are represented. This condition has been observed among members of *Elliptio complanatus* in their normal habitat.

GLOCHIDIAL STAGE

When the young of any clam are ready to be expelled from the marsupial gills of the female they may be termed mature glochidia. In some species of clams they are shed while the ovisac is still intact; in others, as individuals. Again, some species shed only mature glochidia, whereas, in others they are given off along with immature ones which perish. However, according to Ortmann (1911), this condition is quite unusual among clams. In any case the occurrence of a considerable number of undeveloped or unfertilized eggs in the marsupia is inevitable. These are liberated with the glochidia.

After much observation, it was concluded by the author that normally the glochidia of *Elliptio complanatus* are expelled from the exhalent siphon, not united in ovisacs but individually. A certain amount of mucous is secreted simultaneously, producing a cob-web-like structure in which strands of mucous are suspended from any projecting surfaces, with the active glochidia arranged at random wherever they happened to come in contact with it. This arrangement is a decided asset in securing a fish host. When glochidia are ejected into water which is devoid of projections they fall freely to the bottom. There is no evidence of a byssus on the glochidium of *Elliptio complanatus* (Fig. 10).

It is noticed that when a female spawns prematurely, due to some disturbing factor, the glochidia often emerge united as small fragments of the original ovisacs. Usually upon examination one finds that in such a mass there will be many representatives of earlier stages, as well as viable glochidia present in the structure. This may account for Ortmann's statement (1911) that the glochidia of *Elliptio complanatus* are shed as ovisacs. The examination of large numbers of aborted ovisacs has seldom shown any mature glochidia present, and these have always been retained in the egg membrane. Judging from the above observation, it seems that in *Elliptio complanatus* the embryos do not necessarily develop at an identical rate, but that those which are mature and held in the water tubes normally until most have reached that stage.

All factors being normal, the time required for the development of the young of *Elliptio complanatus* from fertilization to mature glochidia is roughly one month. Although generic differences are without doubt highly important, environmental conditions also definitely alter the time taken for development. Probably the most important influence is temperature. Both the time of fertilization and the length of the developmental period are affected by this factor. During the summer of 1945, the author opened a large number of clams, starting the procedure soon after the theoretical breeding period, and continuing far after the so-called normal spawning period had ended. He found only one female who had mature glochidia. The mean water temperature for that summer was considerably below average. The fate of the immature stages was never determined, although many probably were aborted in a still undeveloped condition.
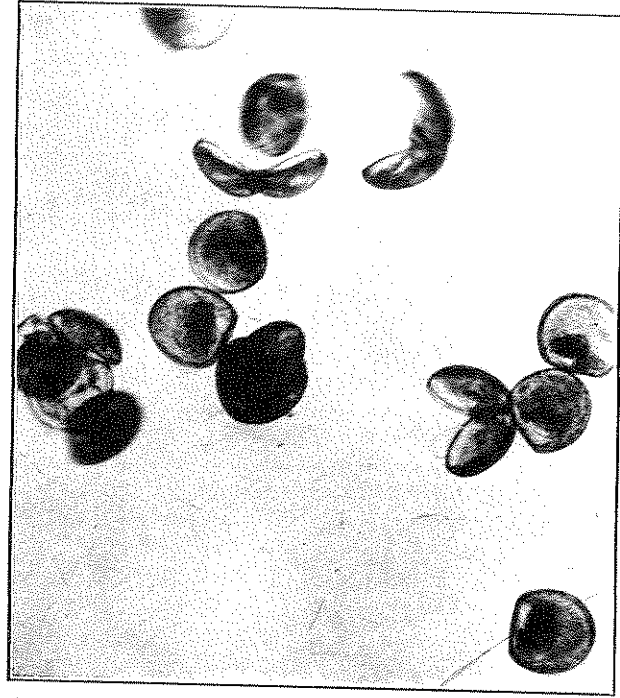
Fig. 10.—Glochidia of *Elliptio complanatus*.

During the summer of 1943, the following observations were made on the developmental stages of *Elliptio complanatus*. On June 30, out of sixteen experimental clams, both male and female, two females were in the process of shedding glochidia, and one possessed both glochidia and earlier stages. From July 4 to July 7, many clams were opened and approximately ninety per cent of the gravid females possessed either nearly mature or mature glochidia. On July 7, twenty-five were taken from shells and preserved for future study. Out of twelve females, three possessed glochidia and one possessed an earlier stage. On July 14, twenty-five more were preserved and no gravid ones were found. Each week, until August 3, twenty-five additional ones were preserved. No gravid clams were found in these groups. The mean temperature of the water from June 27 to July 7 was 22.5°C.

During the summer of 1944, the following results were obtained: On June 15, ten clams, both male and female, were preserved. Four females possessed very early developmental stages. From June 16 to June 19, the clams examined from the supply area in Douglas Lake possessed many very early stages. A considerable portion of those females gathered and placed in aquaria aborted their young within several hours.

On June 23, the first clam to shed viable glochidia was noticed. It had been collected that day from Ocqueoc Lake, in which *Elliptio complanatus* is native. From June 23 to June 29, the greater portion of female clams were shedding viable glochidia. On June 22, twenty clams chosen at random were

opened for preservation. Of these, five possessed mature glochidia and one possessed earlier stages. The rest of the females had spawned. On June 29, ten were opened and none were gravid.

Although during the summer, seventy additional clams were opened in the laboratory and preserved at intervals of three days, no others were found in the gravid state. However, on July 12, one with viable glochidia was discovered at Ocqueoc Lake after opening thirty-eight clams. The mean temperature of the water from June 27 to July 7, 1944, was 24.0°C.

The scarcity of mature glochidia during the summer of 1945 has been discussed in an earlier paragraph. The mean temperature of the water for the period of June 27 to July 7 for this latter summer was 20.9°C. Because this very unseasonable weather extended through most of the summer, the majority of the other aquatic animals, as well as the plants, was greatly retarded in development. The significance of unusual aquatic temperature conditions is great and is often overlooked.

From the preceding data, we notice that in 1943 there was evidence of spawning among Elliptio complanatus from June 30 to July 7, with one clam possessing immature stages on the latter date. In 1944, the first evidence of spawning was found on June 23 and the last, one shedding clam, was located with great difficulty on July 12. The majority had completed the process by June 29. Therefore, it is evident that the spawning season for Elliptio complanatus, in the Ocqueoc River system, extends from the middle of June to the middle of July, with very little shedding before or after this period. Incidental observations for several years support this statement.

The period of spawning mentioned above applies, in general, only to that portion of the range of Elliptio complanatus which lies from the St. Lawrence River Valley westward. Other writers have given data on the time of spawning elsewhere. Ortmann (1911) states that glochidia have been found as early as June 7, and discharging females on June 7 and 13, and on July 9 and 11. Conner (1907) states that the breeding season may extend to August. F. C. Baker (1928) mentions the breeding season as extending from the last of April to the middle of May, but does not mention when spawning comes. Lea (1863) found E. complanatus gravid in May. Probably all of the above data apply to the Atlantic seaboard, although specific localities are not reported.

Some observations were made on the tolerance of glochidia of Elliptio complanatus of certain adverse conditions. Sudden changes of temperature were lethal. The glochidia die after a few moments of dessication. On June 30, 1943, the mature glochidia of one clam were placed in a petri-dish filled with lake water. It was then placed in a refrigerator set to maintain a temperature of 4.5°C. They became active when re-examined on July 6. Again in 1944, another sample was placed in the same refrigerator on July 1. On July 3, they were used for infecting fish. The ability to withstand cold to the extent of remaining viable for several days may be common to other unionids. If so, this may prove valuable in the raising of clams which have economic importance.

PARASITIC STAGE OR METAMORPHOSIS

The glochidium is small in comparison with those of other mussels. It is hookless; its length is either slightly greater or equal to its height; and it is subovate in form (Fig. 10). It measures about 0.20 mm. in length and 0.19 mm. in height.

Glochidia must be ejected upward into the water by the female clam in order that they may meet their fish host. This is accomplished normally by water currents created by the action of cilia located on the walls of the respiratory tract. The siphons do not seem to be modified for attracting fish, as is the case among some mussels. The larval mussels of Elliptio complanatus may be observed as many tiny particles steadily flowing upward in the water from the exhalent siphon to a height of about seven inches. They are mixed with fine strands of mucous and waste materials. As mentioned before, if the substratum possesses projections of any type, the mucous becomes anchored thereto, and forms a cob-web-like structure on which glochidia become lodged. If no prominences are present, they slowly fall bottomward. Normally, the glochidia are now devoid of any enclosing sac.

At times the valves of the female close forcibly causing the glochidia to be ejected into the water to a greater height. This reflexive behavior is probably caused by the clam's reaction to ruptured egg membranes and mucous in the suprabranchial chambers, as well as the normal excretions.

Both the volume and velocity of the water escaping from the exhalent siphons of any unionid is often under-estimated by the casual observer. Invariably any clam of average size can create definite surface currents when located a foot or less under the surface of quiet water. In fact, during normal respiration a clam at this depth often may eject a stream which elevates that area of water directly above it higher than the surrounding water. One commonly notices clams squirting water into the air when their water cover has been removed suddenly. The mussel must depend on the water circulating through the valves for food-getting, excretion of all wastes, introduction of the sperm to the egg, and placing the glochidium in a position to contact a possible fish host.

During the first attempts at finding the possible fish host, or hosts, for Elliptio complanatus, floating cages were used to provide the necessary compartments for harboring the paratisized fish. The principle of utilizing floating rafts as used by Coker, Shira and Howard (Howard, 1922) in their experiments on the life cycle of Lampsilis siliquoidea on the Mississippi River was copied in modified form (Fig. 2). Six cages were placed in linear series and made into a raft by fastening a dried white cedar pole on either side which also added buoyancy. The bottom dimensions of the cage were four feet in length by three in width, while the top measured four feet in length by two and one-half in width, with the height two feet. All sides, as well as the movable top, of each cage were covered with one-half-inch mesh galvanized screen. The bottom was made of zinc sheeting and the sides possessed a three-inch barrier at the bottom to prevent the loss of young clams which might have otherwise escaped over the sides. The differences between

top and bottom dimensions also were designed to prevent loss of young as they dropped from the fish to the bottom. Two such rafts comprising a total of twelve cages were constructed.

At the same time, twenty-five aquaria ranging from two to ten gallons in capacity were set up in the aquarium shelter to act as housing for other infected fish, and as a safety measure in case the floating cages were unsatisfactory. As mentioned previously, they were cleaned of all foreign particles and the cement along the sides of the bottom was trimmed level with the glass. A constant supply of surface lake water from a supply tank was allowed to enter the aquaria as needed.

Three aquaria, each with a capacity of ten gallons, were first used as parasitizing chambers. As *Elliptio complanatus* does not show sexual dimorphism, about thirty clams of this species were placed in normal position in each chamber in the hope that several would begin to shed glochidia. They were placed there before any spawning of *Elliptio complanatus* had been noticed for that season.

The smaller species of fish to be used as possible hosts for the glochidia were netted. The larger ones were caught on hook and line. The barb of the hook was filed off and the fish caught were placed immediately in large tubs of lake water which were carried in the boat. No dry objects were allowed to touch them during transference to the tub. They were allowed to disengage themselves from the hook. If any captured fish had any encysted glochidia, or other foreign objects on either gills or fins, it was discarded. The gills and fins of the fish were examined under water with the aid of a hand-lens. Encysted glochidia appear as small light-colored tubercles. Once a glochidium is encysted it is very hard to identify.

As soon as spawning was in evidence, all available species of fish which occupied the same environment as *Elliptio complanatus* were exposed in small groups to the glochidia. Each species was represented by a minimum of six fish. As soon as suitable exposure had been experienced by the fish, they were placed in their respective compartments for study in anticipation of the possible dropping of immature mussels. The gills of all fish were examined before being placed in their containers to see that glochidia were present in suitable numbers on the gill filaments. This was done by placing the fish to be examined in a glass container full of water. The gills were gently opened and the filaments were then examined under a binocular dissecting microscope. Each species was assigned to a certain container. Clean, water-soaked sticks were placed as barriers in the cages of those fish which habitually quarrel with each other.

There is evidence that the fish experience an unfavorable reaction from the initial attachment of the glochidia. This is possible true when the glochidia of other species of mussels become attached to fish, especially among those types which possess hooks on the valves and attack both fins and gills. The glochidia of *Elliptio complanatus* are hookless and survive usually only on gill filaments. Within a few minutes after being inserted in the parasitiz-

ing chamber the fish, although quiet originally, would begin to dash blindly about the chamber for several moments. Then it would place its head as far as possible into a corner, or among the mussels, and from then on lie in a rigid condition until removed. Upon examining the gills microscopically, on exposed fish, it was discovered that a great portion of glochidia located on the gill filaments had pinched the arteries until the flow of blood was discontinued. This probably caused considerable physical discomfort to the fish. Any fish which died from over-infection did so with the gill-plates extended at the time of death. The chief cause of immediate death was asphyxiation. The amount of exposure which would not prove too harmful to the fish was never determined while the above method of infection was used, because the supply of glochidia could not be controlled. Usually two minutes were enough to cause suitable infection with little harm to the host. It has been discovered by other workers (Coker, Shira, Clark, and Howard, 1921) that certain fish can act as host to as many as 2,500 of their specific glochidia without lethal effects. Murphy (1942) found that 42 mm. average length rainbow trout (*Salmo gairdnerii*) could carry 600-1200 glochidia of *Margaritifera margaritifera falcata*) with 52 per cent mortality. No accurate data of this nature were obtained for the only species of fish which was proved to be the host for glochidia of *Elliptio complanatus*, but the author is positive that several hundred could be maintained without lethal effects upon the fish.

Although asphyxiation was the chief cause of immediate death, most of the deaths resulted from secondary infection caused by water mold (*Saprolegnia*). An attempt was made to combat this disease by several methods. The rafts were sunk to a depth of twenty feet where a temperature of about 15°C. was reached but where sufficient oxygen was present. However, the cooler temperature failed to keep them from dying. For example, out of sixty parasitized perch, thirteen remained. It was discovered that the parasitized fish fared much better in the aquaria, especially if the supply of running lake water was eliminated. The water temperature dropped to about 18°C. The reason for this improvement is still unknown, although *Saprolegnia* does not thrive at lower temperatures. There is also the possibility that it could not maintain itself without an outside supply and thus disappeared.

Table I shows a list of the fish infected and the results obtained from the parasitization. All fish except those deliberately killed and examined were kept even after all viable glochidia had disappeared. They were killed and examined periodically until the supply was exhausted.

It is evident that the yellow perch (Table I) is the only fish of the tested group which serves as the natural host. There is the possibility that some fish in the Ocqueoc River drainage system, which is not included in the list, may be an equally satisfactory host. Other unionids may have one or more fish hosts other than their specific one. Then there is the possibility that some fish, perhaps closely related to the perch, but foreign to the habitat studied, is acting as the host elsewhere, for example, on the Atlantic seaboard.

A check on the distribution of the yellow perch indicates that it has a general east coast range down to North Carolina, and that it cuts across the northern states from New England to northern Indiana and Illinois on to Wisconsin, Minnesota and Iowa. As this mussel covers oly part of the area occupied by the yellow perch, there is the chance that it will someday further extend its range.

TABLE I.—Experimental fish and results of parasitization by glochidia of *Elliptio complanatus*.

Number of fish	Species of fish	Period of glochidial attachment	Final condition of host
6	Largemouth black bass (*Huro salmoides*)	5 days	satisfactory
6	Northern smallmouth black bass (*Micropterus d. dolomieu*)	8 days	satisfactory 2 died during infection
20	Northern rock bass (*Ambloplites r. rupestris*)	2 days	satisfactory 1 died during infection
6	Northern logperch (*Percina caprodes semifasciata*)	5 days	1 died while parasitized
80	Yellow perch (*Perca flavescens*)	full term 18 days	59 died, 20 of parasitization
6	Common bluegill (*Lepomis m. macrochirus*)	1 hour	excellent
6	Great Lakes longear sunfish (*Lepomis megalotis peltastes*)	1 hour	excellent
6	Pumpkinseed (*Lepomis gibbosus*)	1 hour	excellent
6	Bluntnose minnow (*Hyborrhynchus notatus*)	3 hours	all died in 6 hours
6	Northern common shiner (*Notropis cornutus frontalis*)	unknown	all died while parasitized
6	Iowa darter (*Poecilichthys exilis*)	2 hours	4 died of parasitization
6	Johnny darter (*Boleosoma n. nigrum*)	1 hour	4 died of parasitization
160	Total		

The perch, although infected during a period of several days, all carried the glochidia about the same length of time: eighteen days. It was surprising to discover how closely the length of the parasitic stages coincided in various specimens. As a rule, one day elapsed between the time when young clams could not be found on the floor of a container to the time when the gills of the fish were quite bare. The fish were exposed to glochidia during the period from June 23 to 27, 1944.

The bottoms of all cages were examined daily throughout the summer, in addition to any experimentation of a nature similar to that described in the preceding paragraph. However, if it was discovered that any cage contained freshly dropped clams, its bottom, and the fish, were examined more frequently. The young were secured from the cages by means of a small suction pump, with a hose attached so that one could vacuum-sweep the bottom. The bottom materials were collected in buckets and the young were found in the laboratory by hand-sorting under a binocular microscope. The bottom materials in the aquaria were siphoned out by means of a rubber tube and then examined in the same manner as were those from the cages. The young discovered during each day were placed in separate containers for future study.

The 160 fish which were parasitized during the period from June 23 to 27, 1944, were distributed among the twenty-five aquaria and the twelve cages previously mentioned. On the morning of July 10, none of these experimental fish had yet shed any immature clams; but a considerable number of them had died by that time. Among the surviving hosts, all except the yellow perch had lost their glochidial infections.

As a safeguard, a special trip was made to Ocqueoc Lake and a determined search for gravid clams was conducted in that body of water. The thirty-eighth clam examined proved to have its gills distended with viable glochidia. The importance of this discovery, so far beyond the usual date for cessation of spawning, and the improbability of finding another gravid specimen prompted an immediate and hasty return to the laboratory.

It should be recorded, in passing, that the clam had been partially dissected in order to discover its condition, and that it had to be transported nearly fifty miles before its glochidia could be utilized for further experiments. Furthermore, in order to prevent loss of the glochidia, the mussel was carried back wrapped only in a moist cloth. Upon return to the laboratory, a fresh supply of approximately 100 yellow perch was secured from the lake as rapidly as they could be caught. All these fish were immediately exposed to the glochidia by the artificial method described in the succeeding paragraph. Twenty of the experimental fish were placed in aquaria, each of which eventually contained only two. The remaining perch were placed in tubs. The cages were used as containers for immature mussels which were to be left undisturbed. The keeping of parasitized fish in them was discontinued because *Saprolegnia* was uncontrollable in them, they were clumsy to manipulate, and they were too far from the laboratory. The parasitic stage again required about 18 days. The following year, 1945, the procedure was repeated with no difficulty, using the one available shedding clam as the source of all glochidia.

A new technique was used in parasitizing the perch with glochidia on July 12, 1944, and again in the succeeding year. A very small aquarium, barely longer than the largest fish, was used. It had been cleaned of all foreign material. The fish to be parasitized was then placed in the water. It was given sufficient time to become quiet. Then the purest possible concentration of glochidia, which had been obtained from an opened female clam ready to shed, were slowly and cautiously placed directly in front of the fish's mouth with a pipette. By this method, one could eventually estimate very closely the number of glochidia used for each fish. However, an attempt at a quantitative study was not made by the author at that time. Usually about one drop of water full of glochidia was used for each fish. Any glochidia falling to the bottom might later be taken in by the fish. The glochidia were usually viable even after lying on the bottom for at least a day. Murphy (1942) states that glochidia of *Margaritifera margaritifera falcata* remained alive for eleven days in a container. One decided advantage of this method over the former one is the fact that there is no danger of over-parasitizing the host, and, as a result, it can be left in the aquarium indefinitely.

Where glochidia are introduced artificially, one can ascertain the degree of their viability by jarring the container. They immediately begin to open and close their valves. It was also observed that they are highly sensitive to the materials which exude from torn fish tissue. A small amount of such material introduced on a scalpel blade causes them to perform the opening and closing reflex with great vigor.

The glochidia of *Elliptio complanatus*, as mentioned before, are hookless. That is why they are primarily found on the gills of the host. They often fasten to fins, and even scales, but none were observed to survive to maturity in such places. Tucker (1927) states that the hooked glochidium of *Anodonta imbecillis* usually fastens to the fins of the host fish. The hooked-type glochidial valve may cause considerable damage to the tissues of the gill filament. Microscopic examination showed that the successful attachments are made where the valves of *Elliptio complanatus* clamp onto a substantial piece of gill filament. Often an artery is blocked by the pressure. The epithelial tissue and stroma are mutilated by the edges of the valve. Arey (1932) states that the scar tissue which attempts to cover the wound, and which in doing so encases the glochidium, is not created by mitotic division and proliferation of the intact cells bordering the injury, but by their migration over the area to be covered. The time required for complete encystment was from two and one-half to three hours. Although rough and irregular when first completed, the cyst wall becomes smooth and thinner in a few days (Fig. 11).

The glochidium does not gain in size during the parasitic stage. This seems to indicate that the function of parasitism in *Elliptio complanatus* is not only to secure an easily available food supply during metamorphosis, but also to be in a position of safety during a time when it is unable to cope with a diverse and perhaps unfriendly environment. However, considerable growth must occur among certain species during the encystment period.

Murphy (1942) reports a 660 per cent increase in length of the encysted larvae of *Margaritifera margaritifera falcata* while in the rainbow trout. Tucker (1927), while working with *Anodonta imbecillis* in the green sunfish (*Apomotis cyanellus*), mentions "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)".

In the encysted glochidia, organogenesis is not completed until late in the parasitic stage. This is evidenced chiefly by the persistence of the single adductor muscle. However, during the last week metamorphosis proceeds rapidly, and, a day before being dropped, the young mussel can be seen moving about inside the cyst wall. Finally, both by movements of the valves and by normal disintegration of the cyst wall, the immature clam is ready to begin an independent life.

Fig. 11.—Encysted glochidia of *Elliptio complanatus* in gill filament of yellow perch. The cyst had been formed eight days.

DEVELOPMENT OF THE IMMATURE MUSSEL TO ADULTHOOD

The newly dropped immature clam possesses only the glochidial valves (Fig. 12). However, its internal anatomy is entirely altered. It now possesses very evident anterior and posterior adductor muscles and gills, which may be seen through the valves, a liver, and a very remarkable foot. The gills are in the form of papillae, with several on each side of the foot, the longest being located anteriorly. Howard (1922) and Tucker (1927) bear this out by their observations. Other structures found in the adult are not visible but are possibly present.

The foot of the young clam is extremely long and narrow, and can be

extended to a length equal to at least twice the height of the valves. The end of the foot is heavily ciliated and seems to possess adhesive qualities. When it is being extended, the cilia beat violently in a rhythmic manner; but, when at rest, the ciliary action ceases. Then, by contracting the foot, the body is dragged toward the ciliated portion. This procedure is repeated and the young clam moves with comparative ease. Howard (1922) states that an immature clam of this age possesses a bilobate foot. This was also observed in *Elliptio complanatus*, which accounts for its adhesiveness.

No final conclusion could be drawn as to the type of food which is eaten at this stage of development. The normal food of a free living clam (Allen, 1914, 1921; Churchill and Lewis, 1924), such as diatoms, protozoans, detritus, and other items, is perhaps half as large as the young clam. None of the common items of the adult's diet were seen to be ingested by the young. Water not only enters the inhalent siphon at this stage, but also along the full length of the ventral edges of the valves, which normally remain partly open. Some organisms, chiefly *Ceratium*, became partially enclosed by the open valves at various times, later to be forcibly ejected by water currents and the shutting of the valves. There is the possibility that the young of this species may utilize considerable quantities of bacteria and dissolved organic material at this stage. It must be remembered, in this connection, that the members of the subfamily Unioninae are considerably smaller, in the glochidial and post-glochidial stages, than are those of Anodontinae and Lampsilinae. This fact may account for the failure of the young of *Elliptio complanatus* to utilize the larger plankters as food.

In order to study growth increase, ten immature clams were selected and measured for length as soon as they were dropped. They were then isolated in finger-bowls supplied constantly with lake water, and were measured later at various times. It was hoped that they would be able to secure as much food with this arrangement as they would in nature. It is suspected, however, that this was not the case, as the intake pipe for the water supply was over a foot above the lake bottom. Table II shows the average measurements which signify increase in length.

By providing a constant supply of lake water, the immature mussels were kept alive beyond 35 days. Shortly after this period all died from the effects of being moved to a new location. Lefevre and Curtis (1910) were able to keep alive *Lampsilis ligamentina* and *subrostrata* for a period of six weeks.
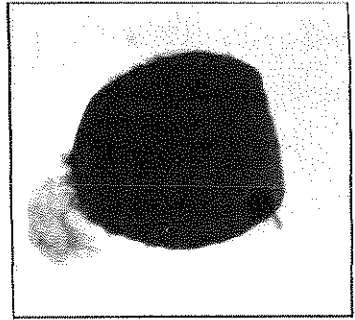
Fig. 12.—Immature mussel within one hour after dropping from the host fish. The foot is extended from the shell.

TABLE II.—Average lengths of the immature specimens of *Elliptio complanatus*.

Age in Days (when dropped)	0	7	13	21	35
Length in Millimeters	0.208	0.297	0.518	0.572	0.840

It is logical to believe that, if one were well enough acquainted with the habits of the yellow perch, he could locate the young clams quite easily. Since Ocqueoc Lake is a habitat in which *Elliptio complanatus* abounds, it was chosen as the site for finding the juvenile stages. A great portion of the shore line possesses an extremely narrow shelf which borders a very steep declivity. It was noticed that great numbers of perch inhabit the area of water near the upper limits of the inclined substratum. With this fact in mind, both Ekman and Peterson dredges were used in taking many bottom samples from what appeared to be ideal locations. As a matter of course, bottom samples were also secured from areas farther from shore, at a depth of about twenty-one feet, where the declivity had ceased. The samples were carefully screened, then taken to the laboratory, where they were hand-sorted. No evidence of juvenile clams of any growth stage were found. Indeed, no specimens less than 0.75 cm. in length have yet been found by the author. In the fall of 1945, one specimen which measured 0.75 cm. in length was discovered by screening bottom materials in shallow water where many adult clams were congregated. In all, only three specimens of this size have been located in nature during the time spent working on that phase of the problem. Also, very few can be found which are under four centimeters in length. During the same time only eight individuals of that size were collected. As *Elliptio complanatus* attains the length of about one centimeter during the first year, according to a study of the umbo of an adult, the one measuring one centimeter must have been dropped at the end of the summer during which it was found.

The rule seems to be that the availability of the mussels varies inversely with their size. This probably is true for any species of clams. It is the author's opinion that the scarcity of young stages is not hard to understand. The fresh-water mussel is a striking example of an animal which must produce many larvae in order to maintain the adult population. It has been stated that a female specimen of *Lampsilis gracilis*, 7.4 cm. in length, yielded 2,225,000 glochidia (Coker, Shira, Clark, and Howard, 1921). A great portion of these, perhaps all, are lost unless the fish host is present in considerable numbers at an opportune time. Of those which strike the fish, many attach in unfavorable positions, especially if they are of the hookless type. Of those which do attach satisfactorily, some are lost by faulty encystment. If the immature mussels drop upon an unsuitable bottom, which is liable to be the situation, they must die. If a favorable bottom is encountered, the young mussels must travel to that depth of water which is best suited for them.

There are many pitfalls along this path. However, if they do reach their permanent location, and can increase in size to the extent that they cannot easily be destroyed, they then live to a relatively old age encountering few hazards.

It has been found that the growth of a clam is not directly proportional to its age. After the third year, the amount of new shell material deposited each year in *Elliptio complanatus* diminishes. Isley (1914) supports this conclusion. After the twelfth year of age, the added amount is hardly noticeable (Fig. 13). This species adds the largest mass to its shell during the third growing season, and next largest, during its second year. Sexual maturity is reached at least as early as the end of the third growing season.

According to literature, *Elliptio complanatus* exhibits no sexual dimorphism. However, there is great variation among different examples of this species in regard to height of the marsupial ridge and body width. By using these features as criteria, the determination of sex was attempted. The soft
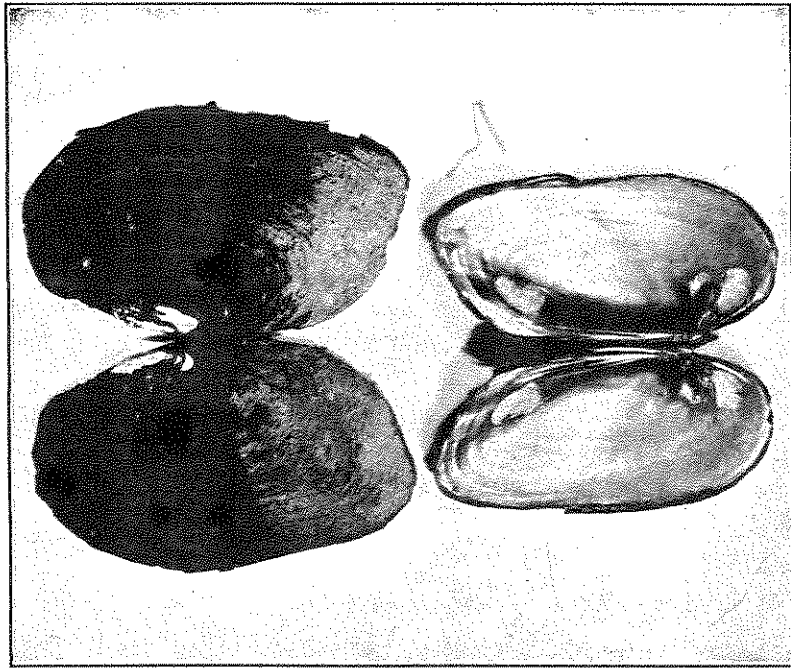
parts from 150 adults had been preserved previously for later microscopial examination for several purposes, one of which was a study of gonad tissue. The empty shells of these were used to establish the reliability of sex determination by valve characteristics. The author and several others, working separately, attempted to identify the shells as males and females. But, upon determining the sex definitely by microscopical examination of the gonad tissue, it was found that there was absolutely no correlation between the original designation from the shell characters and the true sex, proving that *Elliptio complanatus* shows no trace of sexual dimorphism, so far as shell characteristics are concerned. Incidentally, 78 were females, 71 were males, and one was hermaphroditic, with ovarian tissue predominating. According to literature this species is dioecious. The single hermaphrodite, therefore, was unusual.

GENERAL ECOLOGY

Elliptio complanatus does not discriminate between a lake and a not-too-rapid stream, judging from the data afforded by the habitats under observation. Ocqueoc Lake* may be termed a river-lake in that the Ocqueoc River flows into one end and out the other. The lake is about one-half mile wide at its widest point, and is about one and one-half miles in length. The current in the lake is not noticeable. *Elliptio complanatus* can be found any place on its periphery in varying numbers, other than on the short stretches where a muddy substratum is present. Most of those found in the lower river are either immediately where lake becomes river or within 100 feet downstream from this area. The water averages about four feet in depth within these boundaries. The river population of this mussel finally ceases about 200 feet from the outlet of the lake. This is probably due to the shallowness of the water and increased velocity of the current.

One interesting point observed was that three other common species, *Lampsilis siliquoidea, Anodonta grandis* and *Ligumia nasuta*, occupied the shelf above the declivity, whereas *Elliptio complanatus* was rarely found there. The first three were almost entirely absent from the whole face of the declivity, which usually extended from three or four to about six feet in depth. *Elliptio complanatus* was normally a resident there. The temperature varied considerably between the shelf and the upper part of the declivity.

The bottom where *Elliptio complanatus* is most abundant is composed chiefly of clay, mixed with marl and fine sand. The reason for this preference is not clear. The mussels are not plentiful on a sandy bottom. No shoreline which is predominantly composed of marl is present on the periphery of the lake. Therefore, it is not known whether the mussels live in this type of bottom. As stated before, they do not relish a mud bottom, probably because their heavy shells sink into the substratum. It is not unlikely that the habits of the perch themselves may determine in large measure the size of population in a bed. Stability of shoal seems essential, but to date there is very little

* Locus Key for Ocqueoc Lake, Presque Isle County, Michigan (Tier 36N, Range 3E, Section 30).

Fig. 13.—Valves of mature specimen of *Elliptio complanatus*.

experimental evidence as to the relative significance of the various specific components.

Elliptio complanatus lives at a depth relatively greater than most of the common mussels of northern Michigan. They seem to prefer a depth of 3-5 feet. Baker (1918) reports them at a depth of 5 feet in Oneida Lake. In the same lake he (1916) also reports them 2-3 feet on a hard sandy bottom. It seems probable that temperature of the water is, either directly or indirectly, an important factor in this distribution. The dispersal of mussels is somewhat stratified on the face of the declivity. Marked individuals, placed in relatively deep water in late summer or early fall, usually have returned to the selected stratum by the following spring. Those placed in water shallower than the optimum also migrate to the proper level in a very short time, usually in a matter of a few hours. Water warmer than about 24°C. usually will cause them to wander indiscriminately. Because they exhibit positive geotaxis, they eventually reach cooler water. When they reach a depth where the temperature is at, or near, their optimum the influence of geotaxis becomes less powerful than that of thermotaxis and they remain at the new level. Those thrown into deeper water migrate back up the slope to the optimum level because the combined influence of lower temperature and greater pressure is enough to overrule their positive geotaxis. Moffett (1943) found that certain species of mussels were greatly affected by wave action. This factor may also influence vertical distribution.

A vertical temperature series taken in the open water far from shore may show an epilimnion practically homothermous to a depth much below the level selected by the clams. However, a similar series of temperature determination taken at the same depths, but close to the surface of the bottom along the slope of the basin, will exhibit lower temperatures at much higher levels. This is especially true in a lake, such as Ocqueoc, where many small springs pour colder water into the lake along the face of the declivity. In Ocqueoc, these cold springs were much in evidence when clams were being collected along the declivity. Even in a lake where such springs are not known to be present, it has been shown that there is some difference between physico-chemical factors along the slope of the bottom and at the same levels out in the open lake but far from shore (Eggleton, 1931). Therefore, it is evident that the vertical temperature change occurring on the substratum occupied by mussels may be more pronounced than in the open water of that body of water.

TAXONOMY AND DISTRIBUTION

Elliptio complanatus (Dillwyn) 1817 is one of the most prominent species of the genus. Hass (Vid. Middel. Dansk Naturh. Foren., LXV, 1913, p. 54) revived the name *Unio violaceus* Spengler (1793). However, Walker (1918, p. 3) stated that *violaceus* failed to describe the species sufficiently. Also, according to the law of priority its first name was *Mya complanata* (Portland Catalogue, 1786, p. 100).

The synonymy for this mussel is very extensive. Simpson (1914, p. 651)

lists six complete pages of different names which have been associated with the species. *Mya complanata* was first used by Solander in an unpublished and undated manuscript. However *Mya* refers to a salt-water species. Dillwyn (1817) recognized Solander's unpublished article but used the name *Unio complanatus* in his catalogue; therefore, the official name, *Elliptio complanatus* (Dillwyn) 1817, is now recognized by most authorities.

The type locality listed by Simpson (1914), and by Ortmann and Walker (1922) is Maryland and New Jersey. As it is one of the most widely distributed mussels, there is extreme variation in its physical characteristics, especially in the shell. As a result, different attempts have been made to separate the species into several subgroups. Lea and several other American conchologists once decided simultaneously to combine all forms found north of Washington, D. C. under the name *Elliptio complanatus*. South of that location they began to apply specific names to the varieties. The diversity of these mussels was so great that eventually they had applied names to a large number of so-called varieties and still could see no relief from the task, as each new lot continued to show differences. The most recent concensus of opinion is that there probably is a typical *Elliptio complanatus* and that, because of genetic variations, one must also include the various intergrades from Florida to the west end of Lake Superior in the same group. One observation to be emphasized is that this genus contains probably more variations in shell characteristics than any other unionid (Matteson, 1948).

For clarity's sake the shell characteristics of a typical specimen as described by Simpson (1914) are listed below:

Shell generally rhomboid, inequilateral, subsolid to solid, convex; anterior end rounded; dorsal and basal lines nearly or quite parallel; dorsal slope obliquely truncated; posterior ridge well developed, single or double, ending behind at or near the base in a point or biangulation; beaks not much raised nor inflated, their sculpture consisting of strong ridges, which run nearly parallel with the growth lines and are carried back to the nucleus behind as delicate, radial lirae; surface with irregular growth lines, often nearly smooth in young or well developed shells, rough in old ones; epidermis tawny-green to greenish-brown, often rayed and rather smooth in young shells, becoming rough and dark in old ones; left valve with two ragged pseudocardinals and two nearly straight laterals; right valve with one pseudocardinal and often a small one above it with one lateral: beak cavities shallow; muscle scars large, impressed; nacre white, straw color, salmon or various shades of purple.

Length 105, height 55, diam. 33 mm.
Length 90, height 53, diam. 30 mm.
Length 60, height 33, diam. 21 mm.
Length 62, height 40, diam. 25 mm.

Baker (1928) also lists a similar description.

This mussel, which originated in Georgia or Alabama, gradually extended its range northward, east of the Appalachian Mountains. With the advent of the glacial epoch, the northernmost boundaries of its range were pushed southward. As the ice sheet receded, it returned as far north as Cape Breton Island. At the time when Lake Erie, as it is known today, was non-existent, this mussel was able to migrate up the Mohawk River valley to Lake Ontario

(Fig. 14). From there it proceeded through the now extinct Trent River to present day Georgian Bay. It then proceeded westward into Lake Superior (Walker, 1898). As has been mentioned before, the Ocqueoc River drainage system of the Lower Peninsula of Michigan, possesses it (Fig. 16,O.R.). Its distribution today, as plotted from records located in the Division of Mollusks, Museum of Zoology, of the University of Michigan, is limited to the St. Lawrence River, Lake Ontario, Georgian Bay, Ocqueoc River drainage system, the north shore of Lakes Huron and Michigan, Lake Superior and the Atlantic seaboard from Cape Breton Island to northern Florida (Fig. 15).
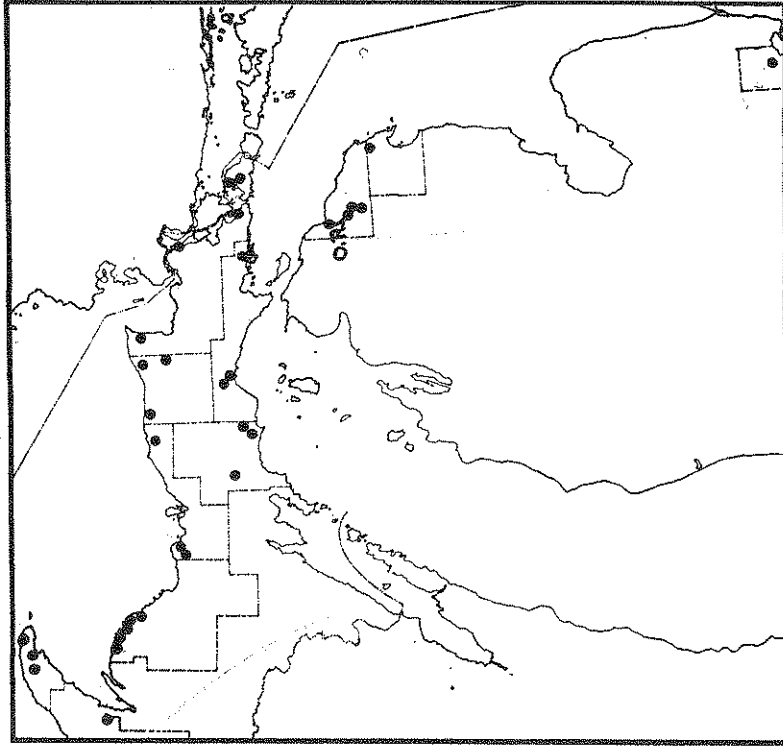

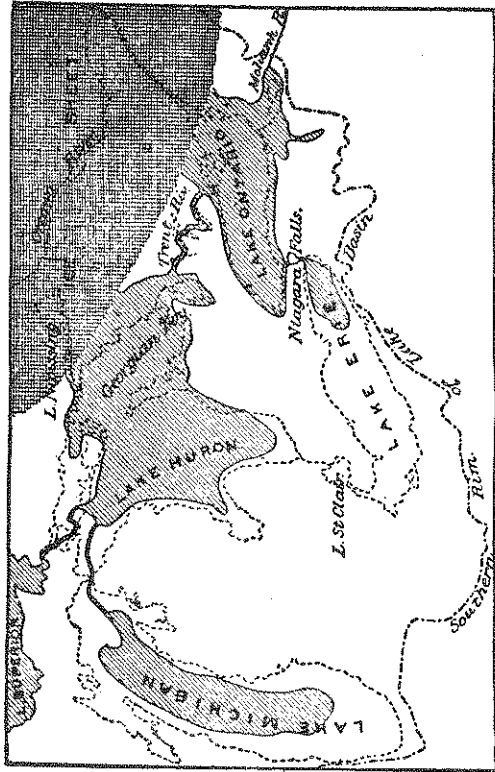Fig. 16.—Distribution of *Elliptio complanatus* in Michigan.

Fig. 14.—Great Lakes region at close of glacial epoch (after Walker).
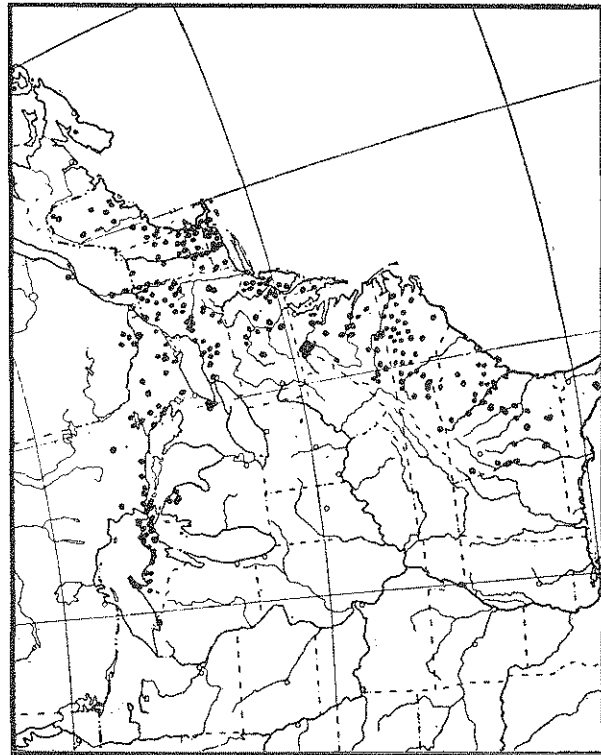

Fig. 15.—Distribution of *Elliptio complanatus*.

SUMMARY

1. The fact that mussels are quite dormant during the winter facilitated the establishment, under natural conditions, of a depot containing an ample winter supply.

2. Identification of individual experimental mussels was accomplished by filing a code symbol into the valves.

3. It was found that, if kept for considerable period of time in tubs, *Elliptio complanatus* fared better when the water was unchanged than when a constant supply of warmer lake water was flowing over them.

4. Glass aquaria were most practical for use in parasitizing the fish hosts and maintaining them after infection. The young mussels were most easily obtained from very clean aquaria.

5. Heidenhain's iron-hematoxylin proved to be most satisfactory for staining the tissues in which are represented the various stages of gametogenesis.

6. The ovarian acini contain comparatively few full-sized primary oöcytes in May, shortly after fertilization; but the number increases steadily until late fall when the maximum number is attained. These are stored until they are passed to the suprabranchial chambers in the following late April and May. The primary oöcytes require the penetration of spermatozoa for further development.

7. Spermatozoa are present in the male gonads at all times. However, the acini also contain germ cells in the earlier gametogenetic stages which follow the last reproductive period. As this period again approaches, the number of spermatozoa increases. The sperm ducts are almost devoid of spermatozoa in November, but are full in April and early May.

8. Fertilization occurs normally from late April to late May. This process takes place mainly in the suprabranchial chambers, but may occur in the upper limits of the ovarian ducts, or in the water tubes of the marsupial gills, or in both places.

9. In *Elliptio complanatus* the outer gills act as marsupia. The water tubes of the inner gills open into the mantle cavity, which prevents them from acting as marsupia.

10. The time required for development from the zygote to the glochidium is approximately one month, at least in the area where the study was made. Glochidia are shed normally from the middle of June to the middle of July. Environmental factors, chiefly temperature, are very important in determining the time of shedding.

11. Rough handling and sudden changes of temperature are the chief causes of abortion of ovisacs.

12. The glochidia are hookless and do not possess a byssus, but are often

suspended from a web-like mass of mucous secreted by the female clam.

13. The glochidial attachment of *Elliptio complanatus* is made on the gill filaments of the fish host.

14. The only one of the 12 species of fish, used in the experiments, which successfully harbored the glochidia of this mussel throughout its parasitic stage was the yellow perch (*Perca flavescens*). However, other fish possibly may act as suitable hosts in other portions of the range, or under other conditions.

15. The average duration of the parasitic stage is eighteen days.

16. Parasitism of the fish host is best accomplished in the laboratory by artificial means. The glochidia are relatively hardy and may be refrigerated until they are used.

17. Insufficient data were obtained to permit a conclusive statement concerned with the number of glochidia which would be lethal to the fish host. It was demonstrated, however, that a perch, 6 inches in length, showed no evidence of unfavorable effects from an infection of approximately 500 glochidia.

18. Death of the fish was prevented satisfactorily by lowering the water temperature to approximately 18°C.

19. The advantage of the parasitic stage does not lie only in the availability of a suitable food supply but in protection while metamorphosis of the glochidium occurs.

20. The immature *Elliptio complanatus*, upon leaving the fish, is shaped externally like the glochidium. At the time when the glochidium drops from the fish, no growth has been added to the valves. Subsequently shell material is added rapidly.

21. At the time of dropping, the foot is ciliated only on the tip, which is bilobate and adhesive.

22. The food of the young clam probably is composed chiefly of bacteria, detritus, very small protozoans, and, perhaps, dissolved organic materials.

23. *Elliptio complanatus* does not exhibit sexual dimorphism. Out of 150 adults examined microscopically, one hermaphroditic individual was discovered, with ovarian tissue predominating.

24. Either lakes or large slow-moving streams are suitable habitats for this mussel.

25. When occurring in the same body of water with *Lampsilis siliquoidea*, *Anodonta grandis*, and *Ligumia nasuta*, *Elliptio complanatus* is found in a zone beyond these three species, and in deeper water. It prefers a substratum composed chiefly of a mixture of clay and sand. It does not thrive on a muddy bottom.

26. Wave action is an important factor in preventing this mussel from occupying a shelf.

27. Physico-chemical analyses of the affected waters were limited to those factors which were thought to influence *Elliptio complanatus* most directly. These factors are temperature, pH, free carbon dioxide, dissolved oxygen, carbonates, bicarbonates and conductivity.

28. Because of its hardiness, the mussel has a very wide distribution. Certain morphological features of the shell are gradually changing, with the result that there is considerable variation in different parts of the range. Some authorities have attempted to establish definite sub-species for this mussel, but at present these are taxonomically unsound.

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