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PHASES IN THE PARASITISM OF THE UNIONIDAE

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There are few cases, probably, in which an animal parasite is itself an article of commerce. The large demand for mother of pearl in the industries has led to the artificial propagation of the fresh-water mussel, remarkable for its parasitic larval development. Although the parasitic stage is of comparatively short duration, it is an essential step in the life history. A thorough understanding of this as well as of other stages has been a prerequisite for successful propagation.†

The whole problem of mussel propagation has proved more complex than it was at first supposed to be. In early attempts (Lefevre and Curtis, 1912) at artificial infections of fish with the glochidia of mussels a susceptibility of certain groups was recognized, but the relation of one mussel as a specific parasite of a given fish or group of species was not recognized. The acquirement of this information made possible the propagation of more species of mussels, among them some of the most valuable commercial varieties. Another barrier to success was the subsequent post-parasitic stage in the mussel, called the juvenile, which on account of its minute size and vulnerability seldom survived. A method of bringing it through this critical period was required. Steps toward the attainment of the desired goal and a discussion of this phase of the life history have been made the special subject of other papers. In the progress of the investigations and the propagation of mussels opportunities for observation of the parasitic stages are continually presented which, while aiding the development of mussel culture, may likewise contribute features of interest to the parasitologist.‡

PREPARASITIC PERIOD: GLOCHIDIUM. MEANS OF INFECTION

The glochidium or parasitic larva developing from the egg within the modified gills or marsupium of the parent mussel is expelled, in the case of "summer breeders" (tachytictic forms), at least, soon after maturity. In the case of the winter breeders (bradytictic) the larvae after maturity (?) are retained for months over winter to be discharged

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† For full details regarding the progress of experiments in mussel culture reference may be made to recent summaries and bibliographies (Coker, Shira, Clark, and Howard, 1921; Howard, 1922).

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in the spring or summer. The two-valved form of the glochidium is adapted for attachment to a host. Among glochidia two general types are recognized, the hooked and the hookless; for the most part the hooked glochidia are larger and adapted for attachment to the exterior of fishes, as to fins, soft scaleless parts or even to the epidermis covering the scales, whereas the hookless type are smaller and become attached more readily to the minute lamellae or to the filaments of the host's gills.

The glochidia after extrusion from the parent mussel have been observed falling to the bottom in still water. In flowing water they may be carried in suspension for long distances, as shown by their occurrence in plankton catches (Kofoid, 1903, 1908). This transference seems to be due to their small size perhaps more than to specific gravity; as regards American species, so far as known, it is not due to any power of self-propulsion, notwithstanding early accounts frequently seen repeated in text books, of their locomotion through flopping of the valves after the manner of the scallop (Pecten); however, Japanese species are said to possess this power (Arey, 1921: 470, footnote). The mere presence in the water of the hookless type of glochidia, especially the smaller species, subjects fish to the chance of infection; this results from their ready transference by currents and coming in contact with the gills of fishes through the latter's respiratory movements.

The high percentage of infections and the heavy individual infections of some species indicate a more or less definite ecological relation between host and parasite (Coker, Shira, Clark and Howard, 1921). This relationship is supposed to exist between the river herring, *Pomolobus chrysochloris* Raf. and the niggerhead mussel, *Quadrula ebenus* Lea. Both are found in swift water habitats which would favor the carriage in suspension of the small glochidium of *Q. ebenus*. Other illustrations are the channel catfish, *Ictalurus punctatus* Raf., and the wartyback mussel, *Quadrula pustuolsa* Lea; the small mouthed black bass, *Micropterus dolomieu* Lacépède (not the sole host), and the mucket, *Lampsilis ligamentina* Lamarck. During the spawning * season (May) of the latter mussel, seine catches of the bass in Fox River have revealed a 90 per cent. infection. No doubt the spawning habits of the bass making their nests in the swift stony shallows brings them into closer association. The hooked glochidia seem less dependent upon the buoying action of currents. Their attachment in infections is usually upon fins, no doubt the result of near approach of the fish to the bottom where through the agitation produced by the fins they may be carried upward into contact with the host.

The presence of the "larval thread" (Lefevre and Curtis, 1912: 151) in hooked glochidia is thought by some to aid infection. The very

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* Spawning in this case signifying extrusion of the glochidia.

large hookless glochidia of *Quadrula heros* Say have been observed in nature more commonly in external infections upon the fins than upon the gills. This may be correlated with the presence of a thread gland in this species, also (Howard, 1914) with their large size. The hooked glochidia of *Alasmidonta marginata* Say may be an exception to the rule of external infection, having been found in many cases upon the gills, but upon more substantial parts as the gill rakers and rachises of the filaments rather than the lamellae. One aid to infection is doubtless the natural association of fish and mussels on mussel beds, localities favorable to both (Howard, 1914: 39; Coker, Shira, Clark and Howard, 1921). In the case of mussel-eating fish, and especially the fresh water drum, *Aplodinotus grunniens* Raf., the glochidia from the parent mussels consumed may infect the predator. In fact, the drum is found commonly to be heavily infected by the glochidia of the thin shelled and easily crushed species *Lampsilis gracilis* Barnes, and *L. laevissimus* Lea, inhabitants of quieter water which because of absence of current must be less effective in distribution of glochidia. A close habitat association is seen between the Salamander mussel *Hemilastena ambigua* Say and *Necturus maculosus* Raf., the mussel in spawning season, at least, living on the stream bed beneath flat rocks, a place frequented also by the salamander (Howard, 1915).

Evidence of special means of attraction between parasitic species and host has been secured (Coker, Shira, Clark and Howard, 1921: 85, 120). This consists in *Lampsilis ventricosa* Barnes in elaborately developed and brightly colored mantle lobes in the gravid female. "These lobes in their form and coloration including an eyespot, resemble small fish, and the motion of these in the current still further enhances the resemblance. The enlarged marsupia distended with glochidia lie close to these flaps, one on each side. It has been suggested that a fish darting at this tempting bait may cause the extrusion of the glochidia and then become infected."

Later observations reveal a similar development in the closely related *Lampsilis luteola* Lam. which here accompanies the highly specialized condition of the marsupium presented throughout the Lampsilinae. In mussels brought from Lake Pepin during May (1921) and placed in aquaria this phenomenon was especially well displayed and to a greatly varying degree. Its high development in some individuals seemed to warrant special attention. The mussels when observed were in a cement aquarium in running water at a temperature of 73 F. Although not imbedded in the mud as they would normally appear in nature, their position was considered especially favorable for showing photographically the detail of the structures (Fig. 1). The enlarged portion or mantle lobe is ventral to the incurrent siphonal opening. It consists of a narrow dorsal (with respect to the mussel) portion with tenninal eye-spot and broad ventral part with elaborately fimbriated edge, forming the tail of the simulated minnow (?). The coloration is striking. On a general ground color of reddish, are dark bluish or purplish bands with pencilings of black. The eye-spot is black with a light border. Extending out between the right and left mantle lobes in the region of the incurrent siphonal opening the light colored marsupia heavily distended with glochidia become visible. If undisturbed they are extended a full quarter of an inch beyond the mantle and a half inch beyond the shell.

Certain movements and reactions were noted. Regular undulations of two rapidly succeeding waves occurred lasting two seconds and each taking approximately a second to pass from the outer ventral lobe to the eye-spot. The interval between the undulations was timed and found to be somewhat uniform, as indicated by the following readings in seconds: 5, 5, 4, 5, 3, 5, 4, 4, 5, 4, 5, 5, 5, 4, 4, 4, 7, 4, 5, 4; average = 4.5 seconds. Withdrawal of the marsupium always followed the slightest disturbance of the water and invariably before the mantle lobes made any response. Motion of a small object like a pencil within the water at a distance of two inches caused retraction of the marsupium without visibly affecting the mantle lobes. No withdrawal followed light touching of the marsupium itself or the outer mantle lobe. Touching of the tentacles in the vicinity of the incurrent siphon promptly brought about the reaction. Considerable jar, as from a blow to the concrete tank, was not effective. Evidently the stimulus causing the reaction (withdrawal) was received through the tentacles. The question as to the function of these movements and reactions arises. The regular undulations suggest aid to respiration (for the enclosed young) but might also serve to attract a predatory fish as a possible host, suggested above.

The withdrawal of the marsupium and the closing of the valves, besides protecting the mussel, would cause extrusion of some glochidia with obvious advantage if in the presence of fish. It is significant perhaps that these two species (*Lampsilis ventricosa* and *L. luteola*) are predominately inhabitants of lakes or lacustrine portions of streams where dissemination by current action would be slight, and that the hosts of these mussels are predacious fish (chiefly members of the Centrarchidae and Percidae).

VICISSITUDES AND ENEMIES

With no known means of propulsion, dependent chiefly upon currents for transfer, the chances of the larva's finding the proper host must be exceedingly small (Lefevre and Curtis, 1912). Their tremendously prolific production contrasted with the relatively small number found as parasites bears witness to the great mortality occurring in nature at this stage. Falling to the bottom they become the prey of such observed enemies as the widely distributed *Chaetogaster diaphanus* (Fig. 2) and the Rhabdocoels (Fig. 4). Of the latter *Stenostoma giganteum* Higley has been identified, and there are no doubt other predatory forms. Unequipped, so far as known, for independent existence the duration of their effectiveness must be brief. The longest observed survival, in the authors' experience, was one week.

It is a common observation in experiments of the authors that the glochidia meet with resistence to attachment on the gills in the case of the gars (Lepisosteus Lacépède), through the copious production by the fish of a protective mucus. Similar means of resistance may be more common than is at present known. In practical propagation this can be obviated by changing the water which holds the fish.

According to Arey (1921), attachment is controlled by contact stimulus solely. This being the case, it is mere chance whether right or wrong host is secured; if the wrong host, destruction by desquamation, cytolysis or phagocytosis or other immunizing agent ensues (Howard, 1914; Reuling, 1919). Destruction also follows attachment to a natural host which has acquired immunity (Reuling, 1919) by having had successive previous infections. The precariousness of this period for the potential parasite is realized from a contemplation of the pitfalls enumerated. Artificial infection successfully bridges over this critical period. A measure of effectiveness of artificial infection is the high utilization of the glochidia from a given mussel. In artificial infection 100 per cent. of the fish are infected, utilizing as high as 50 per cent. of the glochidia supplied; in nature the records give as small as 3.5 per cent. of 674 fish examined (Surber, 1913), and these but lightly infected. It is common in propagation operations to put 2,500 glochidia on a medium sized fish which in nature would commonly have at the most, perhaps, 250.

PARASITIC PERIOD

The parasitic period begins with the implantation of the glochidium. Contact of the host's tissues with the sensory hairs inside the widely gaping valves of the glochidium (Arey, 1921) causes the valves to close vice-like upon the gill or epidermis of the fins or body surface. These tissues react by enclosing the glochidium in a cyst, the complete implantation usually occupying only a few hours. The demonstration by Arey of the effectiveness of a mechanical factor by employing a minute aluminum clamp in this process seems to disprove the previously accepted belief in a chemical agent based chiefly on the response of glochidia to certain ions.

The encystment varies with the species, the encapsulating tissue being more extensive in some than in others. In the case of fishes having gills with thin lamellae the cyst formation may involve several of these. Following encystment the parasite undergoes changes in the nature of a metamorphosis. This consists in a transformation from a comparatively simple glochidial larva to the more complex juvenile with most of the organs of the adult.* Having completed its metamorphosis the young mussel makes its escape, extrication apparently being initiated by its own activity with possible reaction by the host.

DEGREE OF PARASITISM

Three distinct types of parasitism have been observed in fresh-water mussels.

First, limited parasitism without growth.

Second, extended parasitism, or long continued demand upon the host, with more or less extended growth.

Third, abandoned parasitism, more or less complete loss of the parasitic habit.

The common relation between the parasitic mussel and its fish host is that of a limited parasitism (Fig. 5). The glochidium passes through a metamorphosis, making no external growth, and therefore probably receiving little sustenance from its host. The fresh-water mussels of commerce belong to this class.

Among some of the thinner shelled species of mussels the second type of parasitism prevails (Figs. 6 and 7). The parasite instead of leaving the host with the minute glochidial shell only, while still upon the fish, begins a growth which in some cases brings it to a size five times greater in linear dimensions than the glochidium. This is well illustrated by *Lampsilis laevissimus* Lea, *L. gracilis* Barnes, *Plagiola donaciformis* Lea, and *P. elegans* Lea (?) which all have small glochidia and have for a host the fresh-water drum, *Aplodinotus grunniens* Rafinesque. It has been suggested that this extra-glochidial growth is correlated with their small size, bringing them by compensatory growth to the size of other mussels when beginning the juvenile period. In the case of the large celt-shaped glochidia of *Lampsilis alata* Say and of *Lampsilis purpurata* Lamarck the growth on the host is limited to an extension sufficient only to give the form of the definitive shell (Howard, 1914). Evidence from the juvenile shell of *Lampsilis capax* Greene shows that it also belongs to this group, but its host (probably *A. grunniens*) has as yet not been reported. A single instance of such growth other than on the drum has been observed upon the mud cat,

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* Among recent contributions on this phase perhaps the most complete is that of Herbers (1913), which gives a complete review of the literature.

Leptops olivaris Raf.; the mussel has been provisionally identified as *Quadrula lachrymosa* Lea, which also possesses a small glochidium.

The third type is represented by *Anodonta imbecillis* Say, with possibly closely allied species and by members of the genus Strophitus (Simpson). In *Anodonta imbecillis* (Fig. 3) the glochidia at maturity possessing the hooks characteristic of their parasitic relatives, the other Anodontas, instead of attaching to a fish continue their development within the marsupium of the parent. On completing metamorphosis they leave the parent mussel without extra growth and take up an independent existence as rapidly growing juveniles.

A similar modification of normal parasitism has been reported for *Strophitus edentulus* Say from a single instance noted (Lefevre and Curtis, 1912). Howard (1914) followed through normal parasitic development of this species on different fish hosts. If both types of parasitic behavior exist in this species, as reported, it presents an instance of facultative parasitism, or a condition intermediate between the first and third types.

DURATION OF PARASITISM

The period of parasitism extends from the time of implantation of the glochidium to the time of escape of the young mussel from its host. The length of this period shows considerable variation and, since it is a matter of some importance in mussel culture, has received considerable attention. Investigations have ascribed the variations to the operation of various factors which may be enumerated as follows: (1) temperature, (2) species of mussel, (3) species of host, (4) condidition of host, (5) age of glochidia, (6) nutrition with reference to location; these will be considered seriatum. References to earlier literature may be found in Lefevre and Curtis (1912).

Temperature was early recognized as a factor in determining the length of the parasitic period. Schierholz and Harms maintained that the duration of this period varied inversely with the temperature of the water. Lefevre and Curtis (1912: 167) recognized the modifying influences of obscure factors. A later publication (Coker, Shira, Clark, and Howard, 1921: 150) stresses the possibility of the operation of factors other than temperature. In recent experiments by the authors, a method was employed which, as far as known, eliminated other factors. Gars (Lepisosteus Lacepede) infected with the glochidia of *L. anodontoides* Lea on June 22, 1921, were divided into two lots and kept in separate troughs at temperatures that differed by approximately 7.3 degrees, averaging 81.3 F. and 74 F., respectively (average of three daily temperatures for 18 and for 22 days, respectively). The lower temperature was obtained by conducting the water through an underground cistern. Those held at higher temperature completed the period of parasitism in less than 18 days, those at lower temperature in more than 22 days, a difference of 4 days, or 22 per cent. Such are the reactions under conditions of summer temperature.

On falling temperatures, as at the approach of winter, the encysted mussels remain upon the host until the following spring, when, with increase of temperature, they make their escape. Many observations on shedding have called attention to the possibility that retaining and shedding of glochidia may both be governed by more or less fixed points on the temperature scale. Data have been obtained which give some support to this view, and help to determine these temperatures. Further evidence is necessary to substantiate these findings.

TABLE 1.—WATER TEMPERATURES ACCOMPANYING THE SHEDDING AND THE RETAINMENT OF JUVENILES OF *LAMPSILIS LUTEOLA* LAM. BY THE LARGE-MOUTHED BLACK BASS, *MICROPTERUS SALMOIDES* LACEPÈDE

Date	Temp. Water, ° F.	Date	Temp. Water, ° F.
August 31, 1921*a*	77	November 28	39*d*
September 1	79	December 1	40
September 2	78	December 7	39
September 3	79	December 14	38
September 4	79	December 30	33
September 5	79	January 1, 1922	33
September 6	76	January 7	33
September 7	76	January 14	33
September 8	73	January 21	33
September 9	73	January 30	33
September 10	72	February 1	33
September 11	76	February 7	33
September 12	72	February 14	33
September 14	73	February 21	33
September 15*b*	75	February 28	33
September 29*c*	71	March 1	33
September 30	65	March 7	33
October 1	64	March 14	35
October 3	62	March 21	35
October 4	62	March 28	42
October 5	58	April 1	44
October 7	56	April 7	57
October 11	54	April 14	52
October 12	54	April 19	52
October 17	61	April 28	46
October 21	56	May 1	61
October 25	56	May 7	63
November 2	60	May 10	64*e*
November 7	50	May 12	67*f*

a Date of fourth infection; all during same season, 1921.
b Date on which fourth infection was completely shed; note temperature.
c Fish infected for fifth time.
d Lowering temperatures.
e Apparently shedding begun.
f Shedding very evident.

The data given in the following tables (1 and 2) were taken from experiments not otherwise falling within the province of this paper. The fish referred to in Table 1 had received successive infections; that of Table 2 received a single infection October 27, carrying the glochidia through the winter and yielding live juveniles in the spring. Table 1 shows dates and temperatures at periods of infection and shedding during September. A subsequent infection of the same fish shows retainment upon falling temperature. It will be noted that following September 29, the date of the second infection, the temperatures fell below 65 F.; shedding occurred the following spring upon the attainment of approximately this temperature.

Table 2, represents a single infection and shedding. During the period of retainment, at no time did the temperature go above 65 F. At this temperature in the spring shedding began. These observations seem to fix the "critical" temperature as near 65 F. Whether this temperature is "critical" for the metabolism of the host, or of the mussel, or of both, has not been determined.

In nature it is not uncommon for the mussel parasites to be carried over winter, and fall infections seem to be normal for certain species. This is true of *Obovaria ellipsis* Say on the sturgeons, Scaphirhynchus Heckel, of *Quadrula heros* Say, on various species of fish, and of *Hemilastena ambigua* Say, on the salamander, *Necturus maculosa* Raf. This wintering on the host doubtless has distinct advantages to the mussel, chief among which is the earlier start obtained and consequent escape from the ravages of enemies during the most critical period in the life history.

TABLE 2.—WATER TEMPERATURES ACCOMPANYING THE RETAINMENT AND THE SHEDDING OF JUVENILES OF *LAMPSILIS LIGAMENTINA* LAM. BY THE LARGE-MOUTHED BLACK BASS, *MICROPTERUS SALMOIDES* LACEPÈDE

Date	Temp. Water, ° F.	Date	Temp. Water, ° F.
October 27, 1920	48	November 17	45
October 28	48	December 20	39
October 29	47	December 22	38
October 30	50	January 3, 1921	39
October 31	51	January 21	38
November 1	42	February 13	38
November 2	42	April 15	55
November 3	43	April 18	49
November 4	46	April 20	51
November 5	48	April 21	55
November 6	46	April 26	60
November 7	45	April 28	60
November 8	46	May 8	60
November 9	46	May 13	62
November 10	41	May 16	61
November 11	35	May 17	61
November 12	32	May 18	65*b*
November 13	32	May 20	72*c*
November 14	33	May 21	73*d*
November 15	34	May 23	76*e*
November 16	43.3, 40*a*		

a Temperatures indoor trough and outdoor pond, respectively, for comparison; temperatures previous to this date from pond, after same from indoor trough in which fish host was held.
b, *c* Juveniles being shed.
d Found juveniles in trough.
e Juveniles mostly gone from fish.

Wintering over is apparently the normal condition in the extraglochidial parasitism of the mussels (list, p. 73) which parasitize the drum, *A. grunniens* Raf. If this is the case, glochidia are retained, in spite of summer temperatures, until spring of the following year.

A peculiar case of retention over winter and into summer (July 3) was observed. Gar fish were infected late in the fall with the yellow sand shell and their persistence after the "critical" temperature attracted attention; examination revealed the fact that all the mussels were dead. Two experiments of this sort are thought to indicate that the yellow sand shell is not normally carried over winter. The persistence of the dead parasites is added evidence that normal elimination is initiated by the parasite.

Harms noted a difference in length of parasitic period between Unio and Anodonta which he ascribed to the less advanced stage of development of the glochidium in Unio when leaving the parent mussel. Lillie (1895) working upon American species from the standpoint of embryology substantiated the above, finding greater development in Anodonta sp. than in Unio sp. (*complanata?*). He also seems to imply (p. 65) that development of the glochidium of Anodonta progresses during the winter while still in the brood pouch of the parent (see age of glochidium p. 78). These facts have a practical application in mussel propagation in that they point to the necessity of determining whether a glochidium is normally released in the fall or in the spring.*

The present authors have no specific data with reference to the European forms nor to the differences between hooked and hookless glochidia mentioned by Lefevre and Curtis. It is believed, however, that there is considerable variation in habit, at least, among both these large groups as suggested in the following examples.

The hooked glochidium of *Hemilastena ambigua* Say is normally a fall infecting species, having been observed both in artificial and natural infection to carry through, while *Anodonta imbecillis* has lost its parasitism. These instances indicate that all hooked glochidia are not like the Anodonta reported by Lillie. As between summer and winter breeders (both within the hookless group) it has been noted, as far as they have been compared, that the summer breeders have the shorter parasitic period. No extensive investigation of the groups, as a whole, has been made, but the difference was noted incidentally on several occasions when infections with the two groups of mussels corresponded closely in time.†

In later experiments when opportunity presented, this phenomenon was given closer attention. The following experiments demonstrate the difference quite clearly. Gars (*Lepisosteus platostomus* Rafinesque) were infected on July 12 (1918) with *Quadrula plicata* Say (a "summer breeder"). The same species of fish on July 13 were infected with

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* *Lampsilis anodontoides* is a doubtful case. Although infection upon a fish can be secured in the fall none thus far tried have survived the winter upon the host (see duration of parasitism p. 74).

† Some of the records pertaining to such observations were lost with the burning of the Fairport Laboratory in December, 1917.

Lampsilis fallaciosa Smith (a "winter breeder") and kept in the same pond. On July 23 the *Q. plicata* had all been shed, while the *L. fallaciosa* were still present in the full number, complete elimination not being observed until July 31. In the first case a period of parasitism of 11 days or less, in the second one of 4 to 7 days longer was indicated. In another experiment the period of parasitism for *L. anodontoides* on the gar was 21 days (July 7 to July 28, 1919); catfish infected with *Q. pustulosa* on July 18, 11 days later, under otherwise similar conditions, were also free of the parasites on July 28, or after a period of 10 days, less than one-half that required by *L. anodontoides*. A better test of this phenomenon would be a simultaneous infection of the same individual host by members of the two groups, for example, *Q. plicata* and *L. anodontoides* on the gar. Another example is the extended parasitism of all known species but one infecting the drum, *A. grunniens*, in which the greater development demands more time, namely, nine months or more as compared with two or three weeks for the one exception, *Plagiola securis* Lea.

Corwin (1920) finds a difference in the length of parasitism of the same mussel on different hosts. Mussels were shed 5 to 10 days earlier by the small-mouthed black bass, *Micropterus dolomieu* Lacépède, than by four other species infected at the same time. Our own observations give some indication of a shorter period for *Lepomis pallidus* Mitchill than for *Micropterus salmoides* Lacépède, when infected with *Lampsilis luteola* Lamarck.

Coker (1921: 150) has suggested that the vitality of the host may be a factor in affecting the length of the parasitic period. The only data bearing on this topic possessed by the present writers is the observation of mussels escaping from the gills of dead and dying hosts. These observations indicate that a moribund condition in the host hastens shedding when metamorphosis is well advanced.

Lampsilis luteola Lamarck is known to spawn out early in the summer (about July) in Lake Pepin; it is difficult to find gravid females at this time. Later in the summer a new brood of glochidia is produced. Corwin (1920) finds a difference in the results obtained from infections made with these two types of glochidia, which he calls "old" (carried by the parent over the winter and spring) and "new" (mature [?] ones of the current season). Since the two types may, during a short period, be obtained together, Corwin, carrying them in parallel experiments, found that the "old" glochidia completed the parasitic period in a shorter time than the "new." A difference of development in the "old" and "new" glochidia of one species is here suggested comparable to that seen in different species.

Considerable variation has been reported by a number of workers in the lengths of the parasitic period of "glochidia of the same species when infected upon the same fish" (Coker, Shira, Clark, and Howard, 1921). This has been explained as being due to differences in nutrition as governed by position on the body of the host. Glochidia on the sides of the gill filaments are thought to make their escape before those on the tips, the cause supposedly being the better vascular supply in the position of the former. This condition is commonly noted in infections. In some cases the differences may be striking; Lefevre and Curtis have observed variations of from 13 to 24 days, or almost 100 per cent. Since variation may be due to the death of the glochidia, a condition frequently seen in normal infections, careful discrimination is required in coming to conclusions as to the causes of such variation in time.

RACIAL AND INDIVIDUAL IMMUNITY

Certain species of mussels in their parasitism are restricted to a single species or genus of hosts. In others is found the opposite extreme in which almost any species of fish seems to meet the requirements. When a glochidium becomes attached to a species to which it is not adapted (non-host) it becomes encysted apparently in the normal manner, but is sloughed off within two or three days. Well known examples of restricted parasitism are that of the wartyback mussel, *Quadrula pustulosa* Lea, on the catfishes, Siluridae, the niggerhead, *Quadrula ebenus* Lea, on the river herring, *Pomolobus chrysochloris* Raf., and the yellow sandshell, *Lampsilis anodontoides* Lea, on the garpikes, Lepisosteus Lacépède. A striking example of adaptation is that of *Aplodinotus grunniens* Raf. which is the sole known carrier of eight or more species of mussels. The known species are as follows:

Lampsilis (*Proptera* Ort.) *alata* Say.
Lampsilis (*Proptera* Ort.) *purpurata* Lam.
Lampsilis (*Proptera* Ort.) *laevissima* Lea.
Lampsilis (*Proptera* Ort.) *capax* Green (probable).
Lampsilis (*Paraptera* Ort.) *gracilis* Barnes.
Plagiola donaciformis Lea.
Plagiola elegans Lea.
Plagiola securis Lea.

As many as three or four different species have been observed at one time upon a single individual (Figs. 6 and 7). Racial immunity is best illustrated and readily recognized in such cases of restricted parasitism. In such instances any species that will not carry a given species of mussel may be designated as racially immune. The mechanism of racial immunity is probably similar to that of individual immunity (Reuling, 1919). A previously unreported case of racial immunity is that of the orange spotted sunfish, *Lepomis humilis* Girard, toward the mussel *Lampsilis luteola* Lam. This was unexpected in view of the fact that all of the five species of the Centrarchidae previously tested had proved to be carriers of this mussel. An example of unrestricted parasitism is that of the hooked glochidium *Alasmidonta marginata* Say which was found in natural infections upon the following species of fish: *Moxostoma aureolum* Le Sueur, *Catostomus commersonii* Lacépède, *Catostomus nigricans* Le Sueur, *Ambloplites rupestus* Raf., *Chaenobryttus gulosus* Cuvier and Valenciennes. Another example is the large hookless glochidium of *Quadrula heros* Say reported as normally parasitizing as many as thirteen different species of fish (Coker, Shira, Clark, and Howard, 1921, Table 19).

When an individual fish has carried three or more broods of glochidia through the parasitic period it may not be further susceptible to infections from any species of mussel so far as known which means that attaching glochidia will be eliminated in a few days without metamorphosis. Such a condition in a fish may be termed individual immunity. The action has been described by Reuling (1919) as cytolytic, the parasite being first killed by a hemolysin and then eliminated by desquamation. The gross features of the process are similar to those of racial immunity described above.

SOURCES OF LOSS

In nature once the glochidium gains attachment to a suitable host the loss in numbers becomes, doubtless, relatively low. In the progress of experimental propagation of mussels, however, with the confinement of fish in small enclosures or in troughs losses are often very high, from diseases produced by Saprolegnia, *Bacillus columnaris,* Ichthyopthirius, and similar organisms. Methods for the treatment of these organisms have been devised. A certain amount of handling of the fish is necessary, during which abrasions to the skin become points of entrance for microorganisms of which *B. columnaris* is most virulent at the season when the greater number of experiments are conducted. Excessively heavy infections are often the source of loss.

Recent experiments conducted by the authors gave opportunity to test the effectiveness in artificial infection experiments of a mode of treatment for *Bacillus columnaris* devised by H. S. Davis (unpublished report) for general treatment of fish affected by this organism. The experiments mentioned involved the use particularly of the species *Micropterus salmoides* Lacépède and *Lepomis pallidus* Mitchill. The fish were introduced into experimental troughs on June 21 (1921). By the end of the fourth day 18 out of 95 fish had succumbed from the disease. Treatment with copper sulphate after the manner recommended by Davis * was begun on June 25 and repeated on June 30,

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* The fish were subjected for two to three minutes to a solution of copper sulphate, 1:1,000 dilution.

July 2, 6 and 9. Immediately following the first treatment marked improvement was noted; during the period between the first and second treatment only 4 out of 74 fish died; between the second and third, 4 out of 69. The results are striking in view of the fact that the disease had gained a foothold so that the treatment was therapeutic. It is a point of interest that the copper sulphate treatment had no apparent effect on the encysted glochidia, since the fish from which the highest production in juvenile mussels was obtained had been treated the full number of times. As a further means of ensuring sanitary conditions for fish retained as hosts in small enclosures care must be taken to remove all uneaten organic material, and to guard against the introduction of infective forms carried by the small fish supplied as food. In this connection it is worthy of note that feeding of fish was successfully dispensed with in the experiments referred to above.

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Explanation of Plate VII

Fig. 1.—A gravid female of *Lampsilis luteola* Lamarck, showing mantle lobe and extruded marsupium (light, regularly striated structure).

Fig. 2.—*Chaetogaster diaphanus* Gruithuisen, an observed predator upon mussel glochidia.

Fig. 3.—Juvenile of *Anodonta imbecillus* Say. Removed from the marsupium of the parent July 15. An illustration of abandoned parasitism. The foot and the gill papillae are visible, thus distinguishing it from a glochidium.

Fig. 4.—*Stenostoma giganteum* Higley. The specimen photographed has ingested 8 glochidia which are visible as lighter rounded areas.

Fig. 5.—*Lampsilis fallaciosa* Simpson on *Lepisosteus platostomus* Rafinesque (a natural infection). Illustrating limited parasitism, in which the parasite makes no external growth, with consequent slight demand upon the host.

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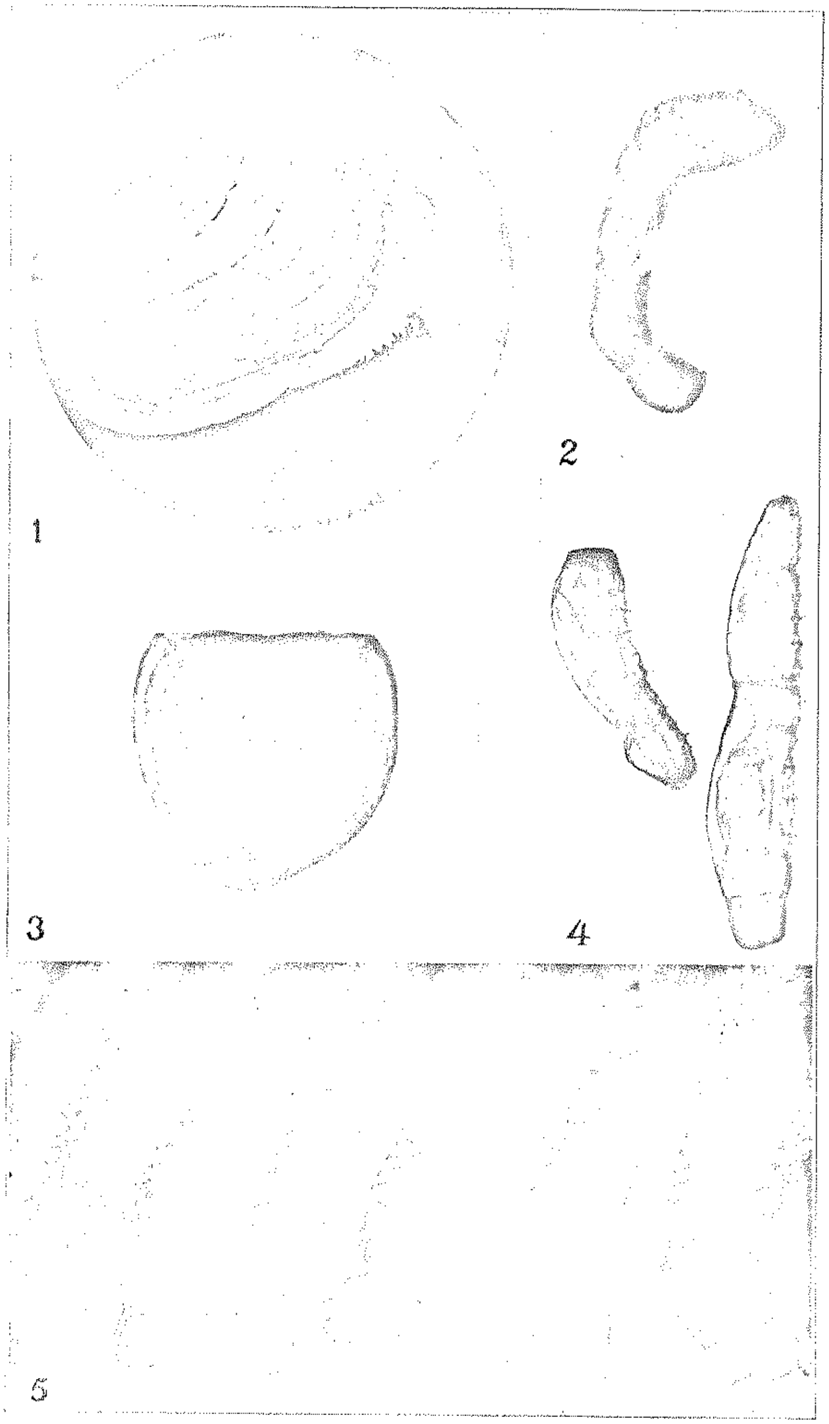

PLATE VII

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EXPLANATION OF PLATE VIII

Fig. 6.—*Lampsilis alata* Say, *L. laevissimus* Lea, and *L. gracilis* Barnes on *Aplodinotus grunniens* Rafinesque. Illustrating extended parasitism, in which there is growth and increased demand upon the host.

Fig. 7.—*Lampsilis laevissimus* Lea and *L. gracilis* Barnes on *Aplodinotus grunniens* Rafinesque. Illustrating extended parasitism. The lower encysted mussel is *L. laevissimus;* the celt-shaped glochidial shell is visible in dorsal view as a saddle upon the definitive shell.

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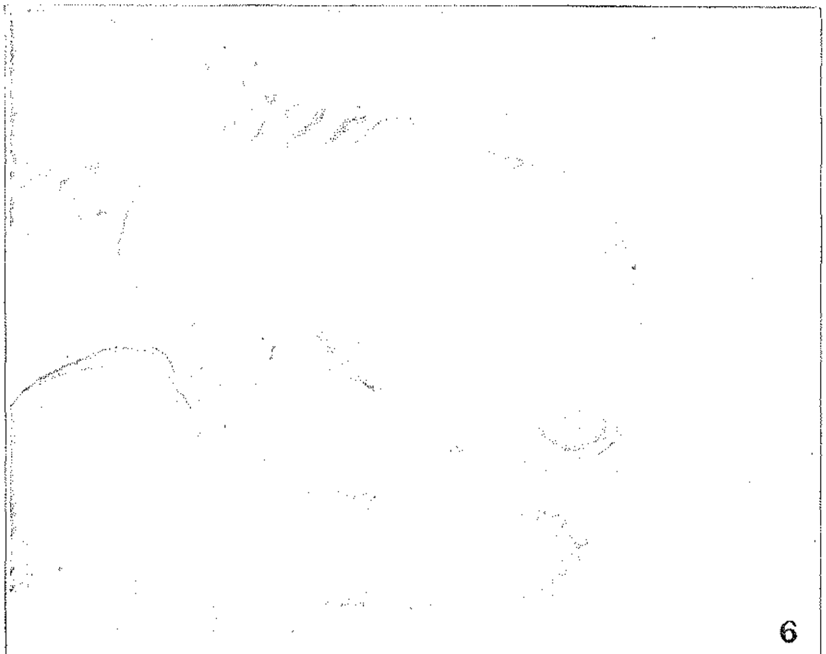

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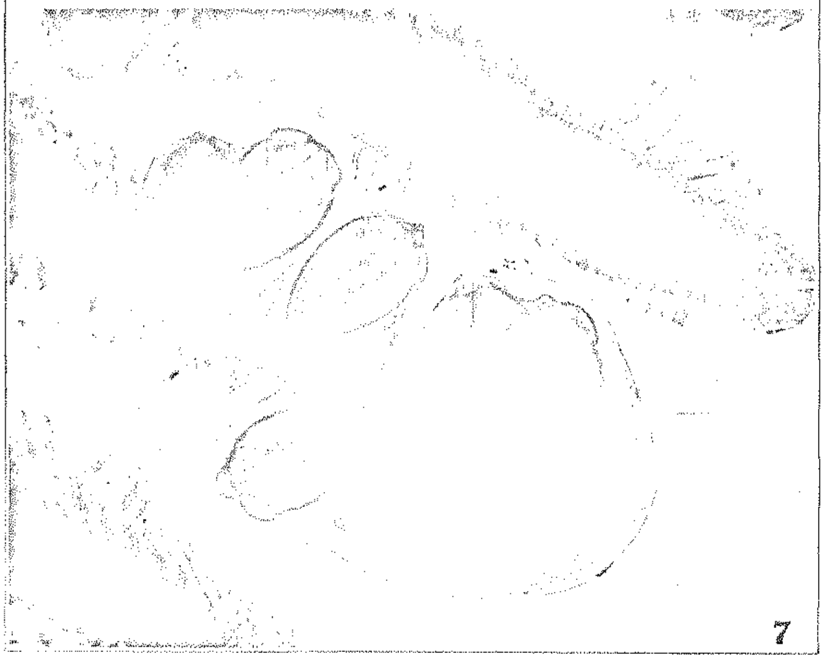

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PLATE VIII