NATURAL HISTORY AND PROPAGATION OF FRESH-WATER MUSSELS

By

R. E. Coker, *Assistant in Charge Scientific Inquiry*
A. F. Shira, *Lately Director Fisheries Biological Station, Fairport, Iowa*
H. W. Clark, *Scientific Assistant,* and
A. D. Howard, *Scientific Assistant*

CONTENTS.

NATURAL HISTORY AND PROPAGATION OF FRESH-WATER MUSSELS.

By

R. E. COKER, *Assistant in Charge Scientific Inquiry*,
A. F. SHIRA, *Lately Director Fisheries Biological Station, Fairport, Iowa*,
H. WALTON CLARK, *Scientific Assistant*, and
A. D. HOWARD, *Scientific Assistant*.

INTRODUCTION.

Adult fresh-water mussels are free-living but sedentary in habit. Though attached to nothing they remain for indefinite periods nearly as still as if their position were irrevocably fixed. They have powers of locomotion but only occasionally use them. A snail is expected to be in travel, however slow, in the search for food; but when a mussel is found in motion the observer is inclined to look for a special cause of this behavior.

If a living animal remains generally in one place without going after its food, it must have some effective mechanism for bringing food to itself, and it must also depend in part upon outside agencies to convey its food within reach. In the fresh-water mussel, the mechanism employed for food gathering consists of hundreds of thousands of active microscopic paddles covering the flaps that hang from the side of its body. These paddles are exceedingly minute and all within the shell; each is weak and ineffective alone, but the effect of their concurrent action is to keep a strong current of water passing into the mussel and out again. The water is filtered in passing, and the food, of course, consists of the fine materials suspended and perhaps in part dissolved in the water. The food in the water that lies within the influence of its currents is thus available to the mussels; the natural circulation of the outside water must do the rest.

A single animal that finds food brought within its reach might live the full period of its life in one spot, but all animals of a species can not live in the same spot. It is inevitable, therefore, that at some stage in the life history of such an animal as the fresh-water mussel, there must be a period of movement or of distribution by outside agencies. Through one of nature's nice adaptations, such a period of migration or distribution occurs in the life history of the mussel at the stage of infancy. Even then the mussel shifts the burden of its distribution upon fish, as will be more fully told in the section on life history. As inactive in youth as in old age, the fresh-water mussel, having taken passage upon a fish, may then travel extensively to find a new home far removed from the scene of its birth. Its living conveyance dispensed with, the mussel settles down to a relatively immobile existence.

Peculiarly victims of circumstance at all stages of existence, the fresh-water mussels under natural conditions yet throve abundantly and broadly in streams and lakes of this country and in those of other countries, but more especially in the Mississippi and Great Lakes drainages. For them, however, times changed with the discovery that their shells formed a good material for the manufacture of a universal necessity—buttons. Equal as they were to the vicissitudes of natural conditions, they were unable to withstand the unchecked ravages of commercial fishery. Thus there has arisen the necessity for measures of conservation—propagation and protection.

It is the purpose of the present report to present such an account of the structure and habits and relations of fresh-water mussels as will serve to diffuse knowledge of fresh-water mussels and interest in them, as may promote intelligent measures for their conservation and efficiency in propagation and as may stimulate investigation of the many problems presented by the behavior, distribution, and propagation of mussels. Directed as it is both to the layman and to the scientist, the report must labor under the disadvantage of embodying matter that may seem trite to the scientist and much that may seem overtechnical to the layman. As far as possible, however, the more technical data are omitted or embodied in tables which can be passed over by those who are not interested in the details.

The first part, on the natural history of mussels or the relation to their environments, embodies data from many sources, but more especially from the general experience of the several authors. In the second part is comprised perhaps the greatest measure of original data gained from experiments and investigations conducted at the U. S. Fisheries Biological Station, Fairport, Iowa, though there are incorporated also results of the published investigations of Lefevre and Curtis and of others. The third part, presenting a summarized account of the structure, does not pretend to offer new data, but rather to afford a background of knowledge of the mussel as a complex living animal with many functions and needs. It might have been placed first but that it seemed best to begin with the subjects which constitute the essential purpose of the paper.

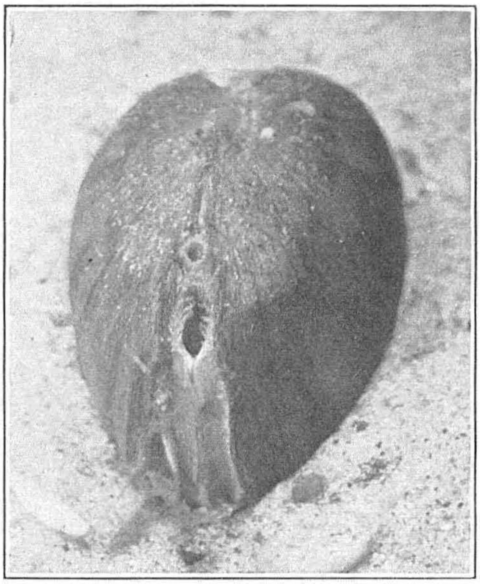


FIG. 1.—Rear view of yellow sand-shell in natural position in bottom under water, showing the two siphonal openings, the gaping shell, and the apposed margins of the mantle.

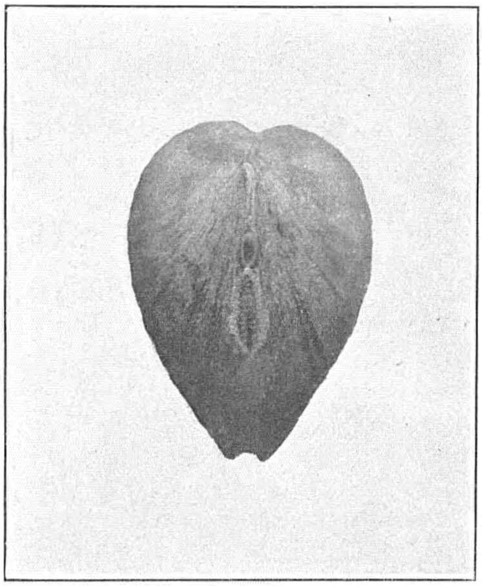


FIG. 2.—Rear view of *Anodonta corpulenta* showing siphonal openings. Note the very smooth margins of the upper exhalent opening and the fimbriae or "feelers" protecting the lower or inhalent opening.

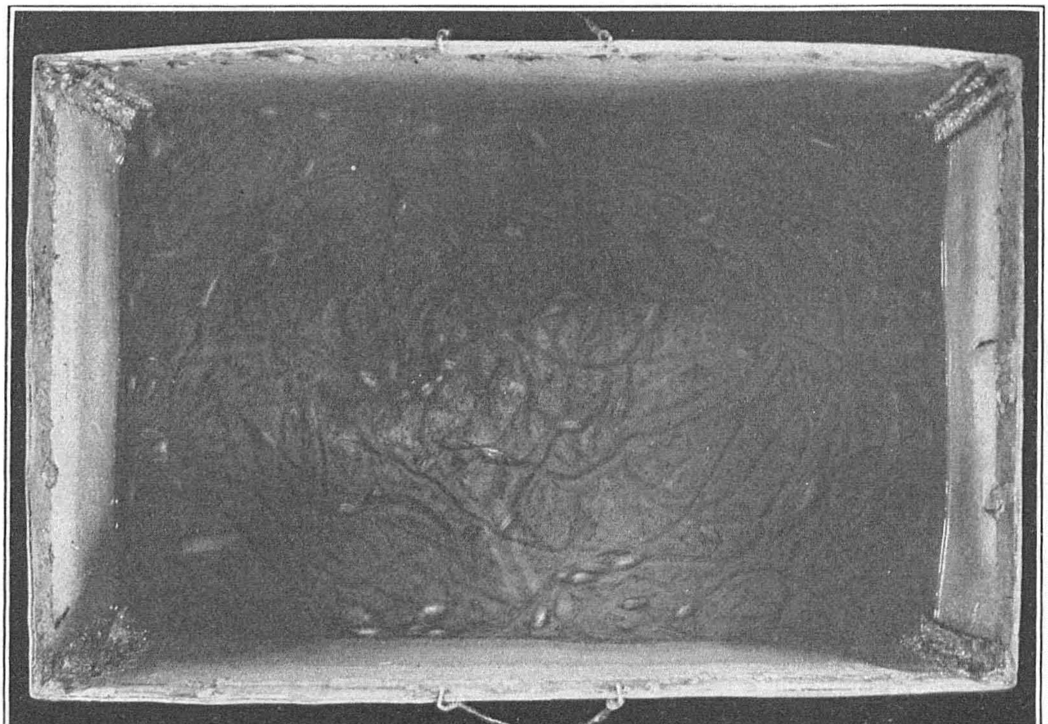


FIG. 3.—Tracks of young mussels in crate. Change in the conditions of the water had caused them to wander more than normally.

PART 1. NATURAL HISTORY OF FRESH-WATER MUSSELS.

HABITS.

CONDITIONS OF EXISTENCE.

A mussel, in natural position in a stream, is partly or almost entirely embedded in the sand, mud, or gravel of the bottom (Pl. V, fig. 1). Almost invariably it will be found to have an oblique position, the front end of the body being directed down into the bottom and in a direction with the flow of the current, while the hinder end of the shell is exposed and is directed upward and against the flow of the stream. Unless the mussel has been disturbed, the shell will be slightly gaping, with the edges of the mantle protruding through the opening and closing it everywhere except at the rear (upper) end where it is so arranged as to form two neat funnel-like openings. The upper opening is usually the smaller, and the edges of the mantle about it are smooth or crinkled. The lower opening is generally much longer, and the border of the mantle here is commonly adorned with a number of delicate feelers, or water testers as these may be called (Pl. V, figs. 1 and 2). The significance of the two openings can be easily ascertained if a small amount of some colored liquid, such as finely powdered carmine in water, is placed near to the openings in a mussel which has been allowed to remain undisturbed in a small aquarium or dish of water. The carmine may be seen to be expelled forcibly from the upper smaller opening, while, if placed near the lower opening, it will be drawn in. It becomes apparent that the water is continually drawn in through the lower (inhalent) opening and passed out through the upper (exhalent). In view of the functions of the gills and the mantle, described on page 174, it may be understood that this stream of water not only serves the purpose of respiration but also that, as it is strained through the minute pores in the surfaces of the gills, it must yield up the microscopic materials that serve as food for the mussel. The position of the mussel, directed against the flow of the river, not only insures a more effective resistance should the current of the river be excessively strong, but it perhaps gives the mussel greater advantage in collecting the food floating with the current. In lakes where no regular current prevails mussels may lie with their axes in any direction, but the oblique position in the bottom is virtually constant for those that are not in movement.

The advantages of rivers over lakes for the growth of mussels may readily be inferred. The mussel can draw in and strain only the water that is close about it, and in the quiet water of a lake or pond new supplies of food are brought to its vicinity only by the comparatively slow forces that cause the intermingling of the waters of the lake. In the steady current of a river, on the other hand, the same water is never strained twice by the same mussel and, besides, the action of the current tends to stir up the small organisms and nutritive sediment which abound in the surface scum of the bottom. Observations by Clark indicate that mussels in lakes feed more largely upon plankton than those in rivers, the latter of which contain in their stomachs chiefly detritus or finely divided nonliving organic materials. The rate of growth of mussels generally is much higher and the size attained is greater in rivers than in lakes. Other factors than currents, of course, enter into consideration, and these will be discussed in the appropriate places.

A chief condition of rich growth of mussels is a plentiful food supply, and not all rivers are alike in this regard. There are relatively fertile and relatively sterile rivers and lakes, and the fertility of streams is likely to correspond in a rather general way with the fertility of the lands from which the drainage is derived. Whatever materials suitable for the construction of plant tissues are brought into the waters are likely ultimately to be converted in great part into plant or animal life, and no little part of the plant life that is formed is likely to be converted ultimately into animal life.

A primary condition for the formation of thick shells of good quality is the presence in the water of suitable minerals, principally calcium, and all of the important mussel-bearing streams are those whose tributaries flow from regions of limestone or other calcareous deposits. Consequently it is the Mississippi Basin which largely supports the pearl-button industry, though shells of commercial value are also found in the Great Lakes and Gulf of Mexico drainages, and some in the Red River of the North. The streams of the Atlantic and Pacific slopes are almost or entirely barren of valuable shells.

Many factors, indeed, enter into the suitability of waters for mussels, and of the various species of mussels—more than 500 in the United States—each has its special requirements; some will thrive where others will not. Much remains to be learned concerning the relation of mussels to their environment, and the subject is particularly complex because of the great number of species involved; but it will be attempted to place the several phases of that subject in general review in a later section on habitat (p. 94). It is the purpose of this section to give such a general account of the habit of life and the conditions of existence as is necessary to establish the peculiar dependence of fresh-water mussels upon the immediate environment.

LOCOMOTION.

As regards their place of abode, fresh-water mussels are very largely creatures of circumstances. Since they are not frequently seen in motion it is probable that most of them spend their lives after the period of infancy very near to the place where they first settle down. Nevertheless they can and do move, and certain species, principally the more elongate forms, manifest a condition of restlessness at times.

All mussels are sensitive to some stimuli; a splash of the water near them, a touch on the edges of the mantle especially at the siphons, or the passing of a shadow over them, will cause the siphons to be withdrawn and the shell to be tightly closed. There are evidences to indicate that when the disturbance is severe, as when the mussel is taken entirely out of the water, or is exposed to the sun by an unusually low stage of water, or is affected by extreme cold, the withdrawal of the mantle is so extreme as to break the living connection with the edge of the shell, and thus to cause, when growth is resumed, an interruption line or plane in the shell which is present ever afterwards. (See p. 132.)

The reaction to evident stimuli consists merely in closing up; there are times, however, when a mussel is impelled to change its position. The movement may then be in a vertical direction, the mussel going down deeper into the bottom; rarely does it go completely beneath the surface of the bottom; more frequently the mussel moves horizontally, leaving a distinct path behind it, which reveals the direction and distance of travel. Locomotion is accomplished by thrusting the muscular foot forward into the bottom, expanding the outer end, and then contracting special muscles so as to draw the shell and body nearer to the end of the foot. Mussels that are most likely to travel in this way are the yellow sand-shell, black sand-shell, and slough sand-shell, species that are relatively long and narrow. Rotund forms, like most of the species of Quadrula, are less likely to migrate, but, of the Quadrulas, perhaps the most vagrant form is the very elongate rabbit's-foot, *Quadrula cylindrica.*[a] The pocketbook, *Lampsilis ventricosa*, and the pink heel-splitter, *Lampsilis alata*, are also fairly active. Juvenile mussels are more active than adults. (Pl. V, fig. 3.)

The causes of movements from one location to another are not known and the subject offers an interesting field of study. Change of pressure (depth), temperature, or more probably light may be the governing factor. Yellow sand-shells move up on the shoals or toward shallow water in times of flood, and return toward deeper water as the stage of water recedes. It is a matter of common report that after high-flood stages these mussels are sometimes found stranded in the swamps at some distance from the ordinary channel of a river, but the authenticity of such reports is not established. Headlee and Simonton (1904, p. 175) observed that fat muckets moved away from shore during periods of high-wave action.

Isley (1914) tagged and planted large numbers of mussels in comparatively shallow natural waters and after several months recovered a considerable percentage of them, finding very little evidence of migration. The Quadrulas placed in water over 3 feet deep remained approximately where planted; those placed in water as shallow as 1 foot moved to deeper water, which was easily reached. The species of Lampsilis used in the experiments showed more activity, but none were discovered which had moved more than a few yards. He concluded from his experiments and field observations that mussels, especially the Quadrulas (heavy-shelled mussels) and related species, were unable to help themselves if conditions became unfavorable, but that, on the other hand, their power to endure unfavorable conditions was remarkable.

From observations in Lake Maxinkuckee, Ind., Evermann and Clark (1918, p. 256) say:

> The mussels in shallow waters near the shore move into greater depths at the approach of cold weather in late autumn or early winter and bury themselves more deeply in the sand. This movement is rather irregular and was not observed every year. It was strikingly manifest in the late autumn of 1913, when at one of the piers off Long Point a large number of furrows was observed heading straight into deep water, with a mussel at the outer end of each. The return of the mussels to shore during spring and summer was not observed. [These were mostly *Lampsilis luteola*, the fat mucket.]

It is evident from the available data that the locomotion of fresh-water mussels can play little part in their distribution. Distribution is, in fact, effected principally during the period of parasitism on fish, when it is governed by the migrations of the hosts. When dropping from the fish, the little mussels are naturally subject to the force of the current, and some that fall in unfavorable environments may be carried to a more suitable place, while others falling upon good ground may drift into a less favor-

---

[a] Wilson and Clark (1914, pp. 35 and 59) have noted a particularly vagrant habit for *Quadrula cylindrica*.

able situation. Distribution by currents presumably has little practical effect, except, perhaps, in the case of such a thin-shelled species as *Anodonta imbecillis*.

DENSITY OF POPULATION.

Strange stories are heard of the density of mussels in beds. It has been said that the living mussels in certain beds were in a layer 2 feet deep. Such stories, persistent among clammers, are, of course, based upon faulty reasoning. A bed is gone over repeatedly with crowfoot bars, and with continuing success, but the fact is overlooked that the appliance takes mussels only at random. A layer of mussels is not moved at each drag. A particular bed in the Mississippi River, more than a quarter of a mile long and 100 yards wide, was insistently described as being uniformly 2 feet deep in mussels. Further inquiry elicited the information that the bed was virtually cleaned up in a season and that about a half dozen carloads of shells were obtained. A simple calculation showed that, had the bed been as described, at least 30 trains of 100 cars each would have been required to move the shells obtained. Other stories relate to such observations as the taking of mussels by suction dredges after excavating deep holes in the bottom, no consideration being given to the possibility of a mussel falling in with the caving sand from above.

In planting operations and in experiments involving the retention of mussels for considerable periods, if normal health and growth are desired it is important to know how closely mussels may be crowded. The following observations are therefore offered.

The place of densest mussel growth observed by the senior author in the Grand River, Mich., in 1909, yielded 52 living mussels of 6 species from a space 6 feet long by 3 feet wide, giving a density of about 3 mussels per square foot. Clark and Wilson (1912, p. 20) found a most favorable place for observations of density in the Feeder Canal, near Fort Wayne, Ind., which had been recently drained. The bottom of the canal had been abundantly populated with mussels and from 1 square meter they took 81 mussels of 8 species, or about 7½ per square foot. At the place of greatest observed density in the Clinch River, Tenn., J. F. Boepple took 66 mussels of 10 species from an area which he estimated to be 4 square feet; if his estimate was correct, the density was 16½ per square foot.

At all of these places mentioned, mussels occurred in such striking and unusual abundance as to suggest to experienced observers the desirability of making actual counts. It is fair to assume, then, that the natural occurrence of more than three or four mussels per square foot over any considerable area is unusual and that plantings of large mussels in greater density are warranted only where the conditions are shown to be particularly favorable.

Very small juveniles may safely be planted more closely. Howard reared for a season 217 juveniles in a floating crate 18 by 24 inches, but the rate of growth among them was very variable. (Pl. V, fig. 3.) In other rearing experiments at Fairport (conducted by F. H. Reuling) 2,006 juvenile sand-shells were obtained from a trough 14 feet long and 1 foot wide, a density of 143.3 per square foot. In another trough of the same size, 3,016 juvenile Lake Pepin muckets were reared, a density of 215.4 per square foot. It is not to be assumed, however, that the young mussels would have lived long and grown normally while crowded so closely as were these.

BREEDING.

The internal phenomena connected with reproduction are presented in connection with the discussion of life history (Part 2, p. 138ff). We have to do here only with the very few external manifestations which have been observed as related to the breeding activities.

The eggs are fertilized by sperm emitted into the water by males and taken in with the inhalent current of the female. In a few species the females, when about to spawn, are marked by a striking development of lurid colors and elongate flaps on the margin of the mantle about the inhalent orifice. In addition to the bright colors there are peculiar spasmodic movements of this part of the mantle. This peculiarity has been observed in a good many pocketbooks, *Lampsilis ventricosa*, in a few fat muckets, *Lampsilis luteola*, in some *L. radiata*, *L. orbiculata*, *L. higginsii*, and *L. ovata* (grandma), and in nearly all of the *L. multiradiata* which have come under observation. (See Clark and Wilson, 1912, p. 54; Wilson and Clark, 1912, pp. 13, 14; and Evermann and Clark, 1918, p. 284.) Ortmann (1911, p. 319) has described such flaps in *Lampsilis ventricosa* and *L. multiradiata*. He observes that when the gravid females are undisturbed the marsupia are pushed outward, so that they project out through the inhalent opening and even a little beyond the shell, as previously figured by Lea. The waving flaps lie alongside the marsupia, and he attributes to them a function in promoting a current of water over the marsupia. It seems more probable that these conspicuous flaps, which sometimes suggest the appearance of small fish, may serve as a lure to fish, bringing them into desirable proximity to spawners when the glochidia are ready for extrusion, thus rendering the fish liable to infection and so increasing the chance of survival of the glochidia. The following is quoted from Wilson and Clark (1912, pp. 13, 14):

> The mussels were thickly scattered everywhere, with especially dense beds along the shore. The small fish were again noticed playing about in the immediate vicinity of the spawning mussels.
>
> *L. ventricosus* has a habit of moving its bright-yellow siphon fringes, which are much enlarged during spawning, back and forth in the water. This undulatory motion seems to attract the small darters and minnows, particularly *Notropis blennius*, which could be seen darting in toward the fringes repeatedly. It also probably assists in furnishing fresh water for the respiration of the young mussels.
>
> At intervals during the undulations small numbers of glochidia are discharged from the brood chambers of the mussel and carried out of the excurrent aperture. These glochidia are of the hookless type, and must be taken into the mouth of the fish that is to carry them during their parasitic period. We can thus understand the advantage of attracting these fish and keeping them in the immediate vicinity during the discharge of the glochidia.

WINTER HABITS.

Very little is known of the habits of fresh-water mussels in winter. Observations of rate of growth indicate that growth practically ceases during the very cold months. (See Isely, 1914; and also p. 132.) Microscopic studies of sections of shell indicate that there are numerous slight interruptions and resumptions of growth, corresponding to each period of winter, and these are no doubt related to the fluctuations of temperature in fall and spring.

According to clammers, mussels cease to "bite" with the approach of cold weather. The observations of Evermann and Clark on the movement of certain mussels from the very shallow waters near the shore of Lake Maxinkuckee in late fall have been previously quoted (p. 83). They do not generally migrate or bury themselves, however, but simply become benumbed so that they respond very slowly if at all to such stimuli as the touch of the clammer's hook. Evermann and Clark (1918, p. 256) also observed that mussels are not altogether inactive in midwinter:

Occasional mussels were observed moving about in midwinter, even in rather deep waters. During the winter of 1900–1901, an example of *Lampsilis luteola*, in rather deep water in the vicinity of Winfield's, was observed to have moved about 18 inches in a few days. Its track could distinctly be seen through the clear ice.

FEEDING HABITS.

It has been previously noted that a mussel in normal condition on the bottom keeps a stream of water continually passing in through one of two siphonal openings and out through the other. The food is derived from this current as it passes through the gills. The manner in which the food is collected and taken to the mouth has been well described by Allen (1914, p. 128 ff) from studies conducted at the Indiana University Biological Station, Winona Lake, Ind.

The filaments of the gills are covered with cilia which intercept the particles contained in the water and prevent their passing through the gills with the water. They become entangled in mucus, and through the action of these cilia such particles are wafted toward the mouth in streams. If they are of a harmless nature or of food value, they are permitted to enter the alimentary tract. During the incubation of the glochidia, the female gives up a greater or less part of one or both of the gills for marsupial purposes. At this period these parts are of little use for respiration or for the collection of food.

Cilia similar to those of the gills line the entire branchial chamber, cover all organs which come into contact with the water, and also line the alimentary tract. They are, as is always true of cilia, in constant motion during life; they act independently of nervous control and in a single plane. Their concerted action is in the form of waves—resembling in appearance the passing of a breeze over a field of grain, or the movement of a bank of oars. The direction which these waves or streams take varies in the several organs. But all of the streams taken together are coordinated to accomplish a certain common end. * * *

The mouth of the Lamellibranch lies nearly as far as possible from the external openings, just behind the anterior adductor muscle. It is thus well protected from the entrance of harmful substances. It is flanked above and below by the thin narrow lips. The upper lip is continuous with the outer labial palp on each side, while the lower lip is prolonged into the inner right and left palps. Most of the ciliary currents of the contiguous faces of the palps and of the lips are directed forward to the mouth. The outer or noncontiguous faces of both palps and lips as well as the edge of the inner face of the lips bear cilia which are directed backward and away from the mouth. Thus particles which find their way between the palps are carried to the mouth. As will soon be seen, very little undesirable matter ever reaches the mouth or palps, but even here Wallengren (1905) has pointed out how selection and rejection may be made.

* * * The inner surface of the labial palps, except their outer margins, are made up of minute vertical ridges, or furrows. These constitute a quite complex mechanism for the sorting of material. * * *

Upon the ridges as elsewhere occurs a ciliated epithelium. But the ciliary currents are disposed in a unique manner. Upon the anterior slope of each ridge they are directed backward while those on the posterior slope lead forward. This seeming conflict is not such in fact, because only one set of cilia comes into action at a time. The position of the ridges determines which set shall function at a given moment. Thus the after slopes are ordinarily brought uppermost, the ciliary currents leading to the mouth are upon the surface, while the cilia which lead from the mouth lie somewhat underneath the ridges. So long as no adverse stimuli are received, particles which lie between the palps are thought to be passed on forward from one ridge to another, to the lips and mouth.

In the event that distasteful matter reaches the palps a reflex erection of the ridges brings uppermost the cilia leading backward and such material is returned from summit to summit to the edge of the palps and discharged into the mantle chamber. * * *

The entire epithelium touching the branchial chamber is abundantly supplied with glands which secrete a mucous substance. The mucus envelops and binds together in strands the material to be transported by the cilia. This is particularly true of those particles which are of a very distasteful nature. * * *

Observers have differed widely in their notions of the ability of the mussel to select its food. To me it is evident that there are, to summarize, four points where such choice is exercised:

(1) The labial palps, at the upper margin.
(2) The labial palps, on the furrowed surfaces.
(3) The mouth.
(4) The incurrent siphon.

As to the last, it is surrounded by a row of pointed, fleshy papillæ, having a resemblance to plant structures. These have two sensory functions—tactile and gustatory; for upon being disturbed mechanically they are withdrawn into the shell, while a continued teasing, or a strong chemical stimulus results in the closing of the shell.

Allen conducted experiments the results of which indicated that a mussel siphons a liter of water (about 1 quart) in approximately 42 minutes. From other observations he was led to infer that mussels pass food through the digestive system somewhat automatically or regardless of appetite, but that the secretion of digestive juices and the utilization of the food ingested may be controlled according to the needs of the mussel.

Allen gives a list of diatoms, desmids and other algæ, and miscellaneous food items, but without quantitative data or appraisal of the relative values of the different sorts of food and without reference to the presence of plant detritus in the stomachs. Seemingly he supposed, as did many others before him, that mussels subsisted almost exclusively upon living organisms. Data bearing on this question are presented in the following section.

FOOD OF MUSSELS.

SIGNIFICANCE OF THE PROBLEM.

The fact that the rate of growth of mussels seems so directly proportionate to the thickness of the shell (p. 129), or, speaking from a physiological point of view, to the mineral requirements of the mussel—for the shell is chiefly mineral—leads naturally to the supposition that the limiting factor of growth is not the organic food supply, but the mineral food supply. This is a rather startling inference, since we are accustomed to view animals in nature as engaged in a fierce competition for food, their numbers and the luxuriance of growth being proportioned to the abundance of food available; and the food we ordinarily think of is the organic (animal and vegetable) substance required rather than the mineral matter. Yet, if it could be assumed that the food requirements of a floater mussel are of the same nature as those of a pimple-back, then, since in the same body of water the floater with its shell of paperlike thickness may attain a length of 3½ inches in two seasons, while the pimple-back with thick shell may not in the same period attain a length of more than about an inch, the conclusion would seem probable that the thick-shelled species was restricted in growth, not for deficiency of organic food, but for lack of the materials necessary for the formation of shell. The assumption proposed, viz, that the food requirement of the different species is virtually identical, although plausible and substantiated by some evidence, can not be accepted as finally proved.

It becomes of importance to determine what is the food of fresh-water mussels, whether the requirements of different species are the same, whether there is serious competition for organic food between commercial and noncommercial species, and whether there is a sufficient food supply in water in which it is desired to promote an abundant growth of mussels.

Three bodies of evidence bearing upon some of these questions are presented in the following pages. One is a summary of the observations by H. Walton Clark, which have been published elsewhere in part; another is a table embodying the results of Shira's studies of the 60 juvenile mussels taken in Lake Pepin (Shira, unpublished manuscript); the third comprises previously unpublished observations made in 1916 by Franz Schrader,[a] formerly scientific assistant in the Bureau of Fisheries. The last will be given first since the studies were directed more particularly at the questions just presented.

OBSERVATIONS OF FRANZ SCHRADER ON FOOD OF MUSSELS.

SPECIES STUDIED.

Four species that were thought to be fairly representative were selected for investigation: The river mucket, *Lampsilis ligamentina,* the Lake Pepin mucket, *Lampsilis luteola,* the blue-point, *Quadrula plicata,* and the spike, *Unio gibbosus.* The first named is a typical river mussel, and one of the most important of all from the button manufacturer's point of view—considering the quantity and quality of the shells together. *Lampsilis luteola,* a shell of fine quality, is predominantly a mussel of standing bodies of water, and is found to comprise 31.5 per cent of the entire shell output of Lake Pepin. *Quadrula plicata,* also a good button shell, is evidently equally at home in stagnant and in flowing water. It is a member of a genus in general slow, ponderous, and heavy-shelled. Finally, *Unio gibbossus* is a form of little commercial importance because of its colored shell but is extremely common in some localities. Thus in Lake Pepin 13 per cent of the shells were found to be of this species, and it was thought that if competition for food played an important part in mussel ecology, the presence of this valueless form might be detrimental to the commercial species, especially when occurring in such numbers as in Lake Pepin.

FOOD CONTENT OF WATERS.

The first step taken was to make a careful examination of the water. For this purpose samples were taken from well-known mussel grounds. A water sampler operating by means of valves that are closed through releasing the catch by a string was used. The sample of water taken at from 2 to 4 inches from the bottom was treated with formalin and the contents allowed to settle in the usual way.

The solid matter thus obtained may be roughly divided into three groups: (1) Mineral matter; (2) organic remains predominantly from plants (detritus); (3) plankton, chiefly green algæ and diatoms. The proportions of these were extremely variable, varying not only with the season but also with changes in the river level. Plankton varied from less than 1 to more than 20 per cent. The remaining material comprised chiefly detritus, for, except after thaws or rains, the mineral matter seldom exceeded 5 per cent of the total of solids.

Regarding the plankton, it may be said that relatively few forms made up the greater bulk. Thus, among green algæ there were Scenedesmus, Selenastrum, Pediastrum, Cosmarium, and Volvox, the latter especially in the spring. In August greater

---

[a] Included with his consent.

or lesser fragments of various thread algæ, such as Spirogyra, increased in numbers until they outranked all others in importance. The list of diatoms showed these forms as important: Coscinodiscus, Synedra, Asterionella, and Navicula. In far smaller quantities but generally present were Gyrosigma, Tabellaria, Gomphonema, Epithemia, and a few others that are negligible for practical purposes.

In both quantitative and qualitative constitution no appreciable difference was noticed between samples from Lake Pepin and those from the Mississippi River at Homer, Minn.

FOOD DISCRIMINATION UNDER NORMAL CONDITIONS.

Having ascertained the materials available in the water as a possible source of food, the next step was to determine whether the different mussels showed a preference or dislike for any of these constituents. This necessitated an examination of the stomach and intestinal contents of naturally feeding mussels. In every case the constituents of the material obtained from the stomachs corresponded to those found in a free state in the water. This refers not only to the kind of material found but also to the percentages, which were discovered always to correspond, at least roughly, to those obtaining in the water at that period. Lastly, no difference was observed—in stomach or intestinal contents—among any of the four forms of mussels concerned. Thus, under normal conditions no discernible degree of discrimination is evinced.

UTILIZATION OF FOOD MATERIALS.

The question of the utilization of these materials was best solved by an examination of the feces. It was astonishing to note that only about one-half of the green algæ and diatoms were attacked to any degree by the digestive processes. In fact the green algæ, with their often delicate cell walls, on many occasions did not even lose color. It was the detritus that underwent the greatest changes. The vegetable origin of this material was easily discerned under the microscope before digestion had taken place, but in the feces, after digestion, the substance was found almost always to have undergone a radical change in appearance and in structure. It was evidently attacked by the digestive processes to a much greater degree than the plankton.

These observations point to a comparatively unimportant rôle as played by algæ and diatoms in the food of mussels. Not only are these forms present in very much smaller amounts than the dead-food materials but also they are not digested as well.

EXPERIMENTS IN FEEDING VEGETABLE MATTER.

Although under normal natural conditions no discrimination of food was observed, conditions might easily arise which would bring about a radical change in the constituents of this normal food supply. Feeding with different materials was tried, therefore, to determine any preference that the mussels might have.

The method used was to starve the mussels for four to five days and then feed them with the material under investigation. In this way the intestine was first cleared and the state of digestion of the fed material determined without any disturbing contamination from substances previously present in the intestine. As starved mussels may lose their sense of discrimination to a certain degree, an equal number of control mussels feeding and living in a tank with a flow of river water were always experimented on at the same time. The food was administered from a long pipette into the intaking siphon. It is unnecessary to go into the details here, but it may be mentioned that the utmost care had to be employed so as not to feed particles of food exceeding a certain size. A neglect of this caution invariably caused violent expulsion of the whole dose of food, no matter what it was.

THREAD ALGÆ.—These were accepted by all four species, but only in limited quantities by the mucket, *Lampsilis ligamentina.* An examination of feces confirmed the previous observations that green algæ are only very incompletely digested.

PALMELLALES.—These soft, slimy, green algæ gave no other result save that they seemed somewhat better digested by the blue-point mussel.

DETRITUS.—This was artificially prepared by immersing the leaves and soft stalks of plants that are generally found near the water in some water for a few days until nitrogenization had set in. They were then macerated with mortar and pestle and the resulting pulp strained through bolting cloth. All mussels took this artificial detritus readily, and the feces showed the characteristic features of digested detritus.

FRESH VEGETABLE MATERIAL.—This was not so readily taken.

VEGETABLE FAT.—Olive oil in the form of an emulsion was accepted by the Lake Pepin mucket and the river mucket. It was evidently thoroughly absorbed, as no traces could be found after digestion. The blue-point and the spike were not tried with this material.

EXPERIMENTS IN FEEDING ANIMAL MATTER.[a]

FISH MEAT (heart of the wall-eyed pike, *Stizostedion vitreum*).—Two out of three examples of the Lake Pepin mucket accepted this material readily, the third less so. The control mussels vacillated, occasionally taking very small quantities. The other three species evinced strong repulsion, expelling any of the substance taken in in from 1 to 15 seconds. Abnormal reddish feces.

TAILS OF TADPOLES (macerated).—These were refused or quickly expelled by the river mucket and the Lake Pepin mucket. The other mussels were not tried with this material.

BLOOD OF PICKEREL.—This was refused by all species, even when given in a state of high dilution.

ANIMAL FAT.—This was an emulsion of fat obtained from the sheepshead fish, *Aplodinotus grunniens.* Extremely small doses at long intervals were taken and evidently digested.

In all these cases the food material was generally readily taken (from 1 to 15 seconds) into the siphon. After a varying period of time (a few seconds), the length of time necessary for the substance fed to affect the taste organs, disagreeable food was always expelled again.

The experiments do not point to any undoubted conclusion regarding animal food, except that they seem to establish the fact that vegetable food is preferred to the animal substances employed. Probably, under normal conditions, small quantities of the latter are taken in with other substances, but it is hardly believed that it ever plays a large rôle.

GENERAL OBSERVATIONS.

Throughout the experiments it was noticed that the Lake Pepin mucket, *Lampsilis luteola,* was not so exact in its requirements as the river mucket, *Lampsilis ligamentina.* The latter was indeed the most delicate feeder of the four species, and the

---

[a] Allen (1914, p. 138) fed mussels upon living Paramecia with apparent success.

greatest care had to be taken in handling it, while just the opposite was true of its near relative, the Lake Pepin mucket, which fed readily on most of the experimental material and was not so fastidious regarding the physical state of the food; that is, the size of food particles and the amount given at one time. This may explain to a certain degree the success attending the culture of the latter species in ponds, but the question then arises why the river mucket is not crowded out everywhere by this mussel, since one species, judging from the shell structure, is as well adapted to live in moving water as the other. As was observed above, however, *Lampsilis luteola* is typically an inhabitant of water with little or no current, while *Lampsilis ligamentina* is a true river mussel. The available data of shell structure and feeding habit evidently offer no explanation.

The blue-point and the spike take a midway position as regards their feeding habits, although the former is perhaps less exacting than the latter.

Detritus undoubtedly forms the main bulk of the food of fresh-water mussels. Dissolved substances may also play a part (Churchill, 1915 and 1916), but their rôle is probably a comparatively unimportant one when compared with the solid food matter. This must be especially true of streams with relatively pure water, in which mussels have been found to thrive just as well or better than those carrying large quantities of dissolved matter.

In view of the universal presence of plants in or near waters productive of mussels there is little likelihood of a shortage of food, for detritus will always be forthcoming. There can be only a very little competition among mussels as far as food is concerned, and the noncommercial species are not objectionable from this standpoint.

OBSERVATIONS OF H. WALTON CLARK ON FOOD OF MUSSELS.[a]

In general it may be said that the food of fresh-water mussels, as indicated by their stomach contents, includes about everything obtainable and not positively harmful, organic or inorganic substances, living or dead matter, if not too large or too active for the mussels to take in. As the mussel has no means of mastication it can not use long objects such as filaments of algæ and the like.

In the course of general biological investigations and of mussel surveys opportunity was had to study the stomach contents of mussels from widely separated areas and under widely different conditions. One of the striking features of the case is that the size and apparent health of mussels bear no direct relation to the apparent nutritiveness of the material in the stomach. Thickness of shell is partly a matter of heredity; thick-shelled species of Lampsilis are found in fairly good currents where nutritious food material is scarce; thin-shelled Anodontas are usually found in quiet places where the food supply is rich. Moreover, generally speaking, Lampsilis of any species in a quiet lake where food in the form of plankton is abundant, are thinner shelled and smaller than those of rivers.

Although, generally speaking, thickness of shell seems to be almost always in inverse ratio to richness of food, that relation itself may be partly accidental. In mussels the secretion of shell is in relation to current or to mineral content of the water.

The stomach contents of some large heavy pocketbooks, *Lampsilis ventricosa*, from the mussel beds in Yellow River, Ind., where this species reaches maximum size,

[a] For additional data see Clark and Wilson (1912) and Evermann and Clark (1918).

consisted chiefly of the yellow mud of the river bottom, with organisms of any sort few and far between. In general, mud[a] is an abundant element in the stomachs of all mussels; so much so that the color and general appearance of the mass of the stomach contents of all river mussels examined was that of the bottom soil. In ponds full of diffused plankton algæ the plants may be present in sufficient quantities to at least fleck the "ground color" with a pronounced green or blue green. Studies of the stomach contents of the mussels in the reservoir of the Feeder Canal at Fort Wayne, in 1908, revealed the presence of many flagellates, such as Trachelomonas and Phacus, together with such minute plants as Scenedesmus, Pediastrum, Botryococcus, such diatoms as Gomphonema, Navicula, and the like, a few desmids (Cosmarium), fragments of *Ceratium hirundinella*, casts of the rotifer *Anuræa cochlearis*, and small fragments of confervoid algæ. In the main current of the St. Joseph, St. Mary, and Maumee Rivers there was much mud with about the same organisms scattered sparsely through it. A mucket, *Lampsilis ligamentina*, taken in the Auglaize River, contained what appeared to be bacteria. Mussels in Lake Amelia, near St. Paul, Minn., contained an abundance of that peculiar organism *Dinobryon sertularia*. The mussels of Lost Lake and Lake Maxinkuckee, Ind., contained enough plankton organisms of all the minuter sorts to give the stomach contents a greenish cast or to mottle it considerably with greenish flecks. Not to enter into too great detail, they contained such organisms as *Microcystis æruginosa*, *Pediastrum boryanum*, and *P. duplex*, *Cœlastrum microporum*, *Botryococcus braunii*, Scenedesmus, *Melosira crenulata*, *Coconema cymbiforme*, Navicula, *Epithemia argus*, Fragilaria, *Cocconeis pediculus*, and *Lyngbya æstuarii*. Melosira and Spirulina represented the longest filaments taken. *Anuræa cochlearis* was common but represented only by lorica, and Chydorus was the largest and most active organism taken.

Observations believed to be of both interest and importance were made in the Mississippi in the late summer and autumn of 1919. The river had remained high and swift until about the beginning of September, when it fell rapidly. With its fall the great body of marginal water lost the velocity of its flow, and great areas behind wing dams, lagoons, and mouths of sloughs became extensive areas of calm. In these a rich and varied plankton, consisting chiefly of holophytic sorts (Euglena, Pandorina, rotifers, Platydorina, and a bottom benthos of diatoms), rapidly developed in considerable quantities. The stomachs of the mussels in the bottom of these areas of calm contained numerous organisms of the plankton and benthos such as *Anuræa cochlearis*, Pandorina, Mycrocystis, Scenedesmus, Phacus, and various diatoms; the stomach contents bore general resemblance to those of the mussels of the Feeder Canal reservoir.

Opportunity was taken to examine the stomach contents of some young mussels which were obtained at the same time. In a slough sand-shell, *Lampsilis fallaciosa*, 19.1 mm. long, all that could be recognized was one colony of Clathrocystis. Another, 18.9 mm. long, contained chiefly brown, gritty mud in which were several *Scenedesmus caudatus*, *Phacus pleuronectes*, 1 Coscinodiscus, a few very minute Melosiras, and some rough spherical cysts. A third example, 19.6 mm. long, contained much brown flocculent organic mud, a large colony of Microcystis, 1 *Scenedesmus caudatus*, the diatom *Cyclotella compta*, and many of the green rough cysts.

The stomachs of some very small *Lampsilis anodontoides* and *L. luteola*, reared in troughs at Fairport and apparently thriving, contained only a fine brown flocculent

[a] The mud is probably mixed with much decomposing organic matter.

mud, with rarely an occasional diatom. A young *L. anodontoides* from Smiths Creek bar in the Mississippi contained fragments of diatom shells indicating that it had been feeding on them to an unusual extent. Although Pleurosigma covered the mud of that region, forming an almost unbroken brown scum, it is noteworthy that it was only rarely found in the stomachs of the young mussels, it being apparently too large to enter the mouth.

As regards the entire subject of mussel food and feeding there are some general observations it may be pertinent to make at this point.

At one time it was thought that extremely dense beds of mussels in the bottom of lakes might act as reducers of an excessive accumulation of plankton. They might indeed take care of many sunken and decaying plankton organisms, but under favorable conditions plankton can develop more rapidly than anything can eat it.

The finding of what appears to be bacteria in the stomachs of mussels of the Auglaize River and the observation made in tanks at the Biological Station at Fairport—that turbid water in which there were mussels cleared up rapidly, the mussels collecting the silt and other materials in suspension—raise the question as to whether mussel beds are not or can not be of use in the purification and sanitation of rivers. If oysters grown in polluted waters may harbor typhoid bacilli and so communicate the disease to those who eat them, there seems to be no good reason why mussels, which are not eaten, may not serve to arrest and devour those as well as other pathogenic organisms.

Since mussels are very inactive animals, the rate of metabolism may be expected to be low and the food requirements correspondingly small. The problem of obtaining nourishment for mussels is then one of the least of our troubles. Doubtless younger, more active mussels require a richer diet, and the first problem of mussel propagation, that of finding a suitable host, is fundamentally one of finding suitable nutrition for a creature remarkable for its fastidiousness in this regard. It may be that a critical problem is the finding of suitable nourishment for the first month or so of free life, but beyond this the only problem, so far as food supply is concerned, appears to be the avoidance of actually poisonous or harmful substances.

OBSERVATIONS OF A. F. SHIRA ON FOOD OF JUVENILE MUSSELS.

The following table (1) embodies a record of the stomach contents of 60 juvenile mussels, distributed among 6 species, taken in Lake Pepin during 1914. The material was studied with the use of a rafter counting cell, but since only a very small quantity of food could be obtained from each mussel the calculation of percentages can be only approximate.

TABLE 1.—FOOD OF SIX SPECIES OF JUVENILE MUSSELS TAKEN IN LAKE PEPIN, SEPTEMBER, OCTOBER, AND NOVEMBER, 1914.

Juveniles examined.		Length of juveniles (millimeters).			Percentage of food.			
Species.	Number.	Minimum.	Maximum.	Average.	Organic remains (principally vegetable matter).	Inorganic remains (silt, etc.).	Unicellular green algæ.	Diatoms.
Lampsilis luteola	12	5.0	15.4	9.5	89	6	3	2
Lampsilis ventricosa	10	4.8	13.4	8.8	90	5	3	2
Lampsilis alata	8	8.2	21.5	13.7	.96	1	2	1
Lampsilis gracilis	10	6.6	19.6	13.5	95	1	3	1
Quadrula plicata	8	6.4	11.0	7.4	96	Trace.	3	1
Anodonta imbecillis	12	6.2	19.5	12.7	91	4	3	2

HABITAT.

The pearly mussels, as inhabitants of fresh water, are found in diverse habitats, in lakes and in rivers, in shallow and in deeper waters, in cold and in warm waters, in mud, in sand, and among rocks. Yet they do not occur in all lakes and rivers, nor in all parts of the lakes and rivers in which they do live; and the several species of mussels, when living together, are not always found in the same relative abundance. It may, therefore, be supposed that fresh-water mussels, like other animals, are adapted rather definitely to particular conditions of environment; that some find congenial environment in still or sluggish water, while others thrive best in strong currents; that a mud bottom supports certain species, while a firmer soil is required by others.

Adult mussels in some cases thrive, or continue to live at least, in environments where the young would perish, for delicately balanced conditions are required by very young mussels of many species, and only where these conditions exist can a mussel bed originate or perpetuate itself. On the degree of stability of the conditions favorable to the growth of the young the permanency of the bed must depend, since, when replenishment fails, the bed can continue only as long as the life of the adult mussels it contains. As any mussel has rather limited powers of independent locomotion, the place where it lives (or prematurely dies) is probably, as a general rule, near where it falls when it drops from its fish host; yet the early juvenile can be carried by the current, and doubtless this means of transportation may sometimes aid the young mussel in finding a suitable habitat. An adult niggerhead mussel lived in apparently healthy condition in a balanced aquarium at the Fairport station for nearly nine months; yet in nature this species is found only in strong currents, the favored environment of its fish host, the river herring.

The relationship of fresh-water mussels to the environment may be treated with reference to body of water, bottom, depth, light, current, water content, vegetation, and animal associates.

BODY OF WATER.

The various geographic types of fresh water in which mussels occur are rivers, lakes, ponds, sloughs, swamps, marshes, and canals. In so far as distinctive conditions characterize these various types of waters, each may have its characteristic mussel fauna. It may be said in general, that wherever conditions suitable for a particular species of animal prevail, that species will be found, except as it may have been naturally excluded through features of geologic history or other factors governing the distribution of animals; in the case of fresh-water mussels, however, emphasis must be placed upon a qualification of this general statement. Though all conditions in a body of water may be otherwise suitable, mussels can not naturally occur where conditions do not permit the entry and survival of the species of fish which serve as hosts.

STREAMS.

Mussels have undoubtedly reached their greatest development, as to numbers, both of species and of individuals, in flowing water. From the commercial standpoint, also, the quality of shells from streams is almost invariably superior. In general, where other conditions are favorable to mussels, larger bodies of flowing water are more productive than the smaller. Brooks do not usually contain mussels. Morphologically, mussels adapted to life in strong currents are differentiated from those adapted to still water by

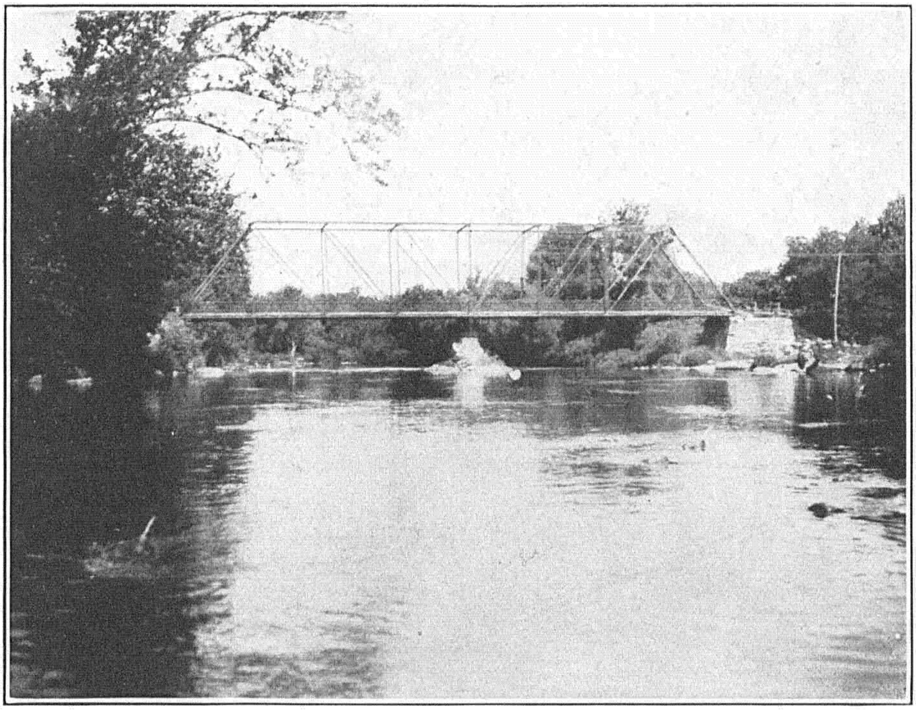


FIG. 1.—Upper waters of Grand River. Habitat of mussels in shallow swift water.

FIG. 2.—Upper waters of Grand River. Habitat of mussels in sluggish water.

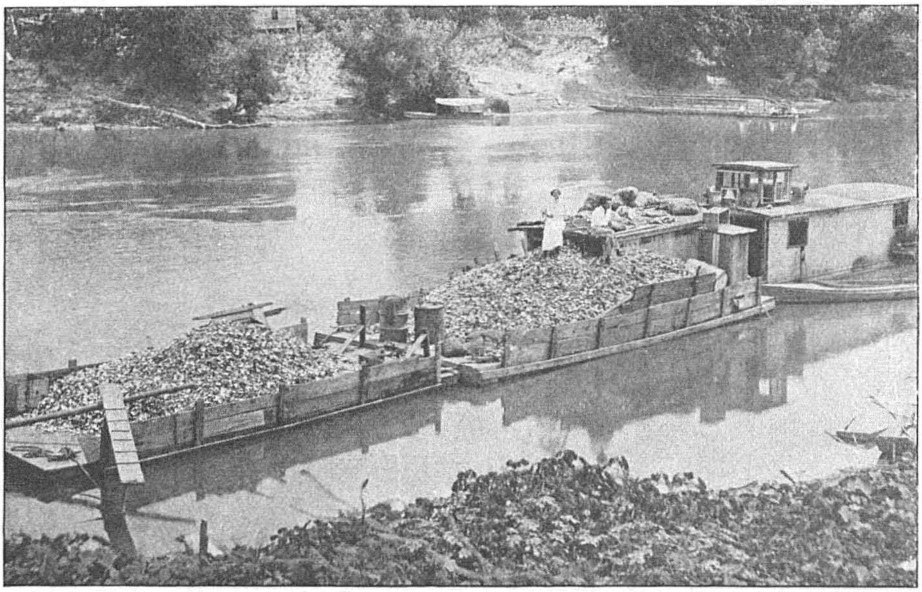


FIG. 1.—Black River, Ark., a very productive mussel stream.

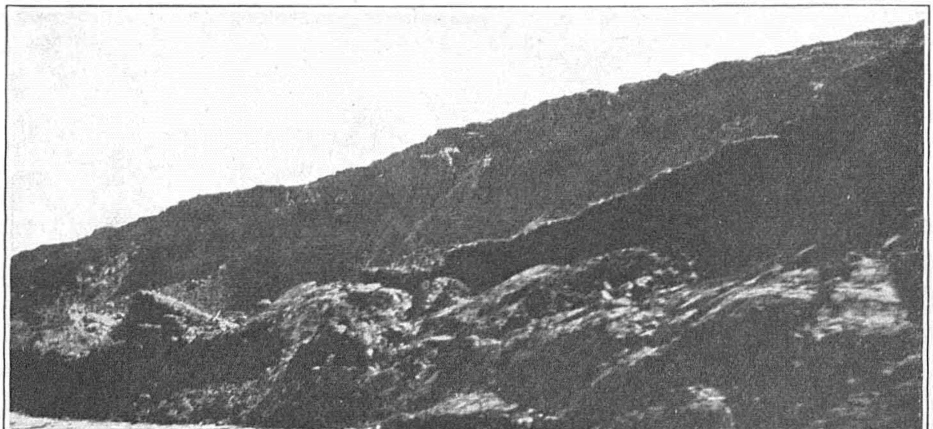


FIG. 2.—Red River, near Campti, La., a turbid stream with caving banks and shifting bottom, quite unfavorable for mussels.

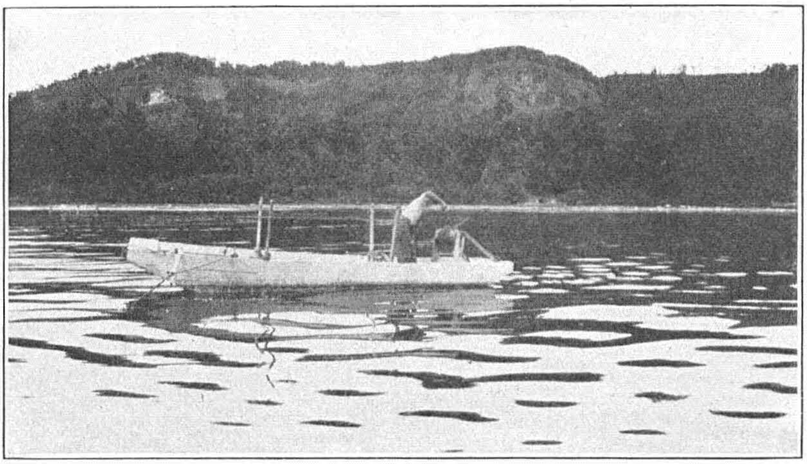


FIG. 1.—Lake Pepin, an expansion of the Mississippi River between Wisconsin and Minnesota, a favorable habitat for fresh-water mussels.

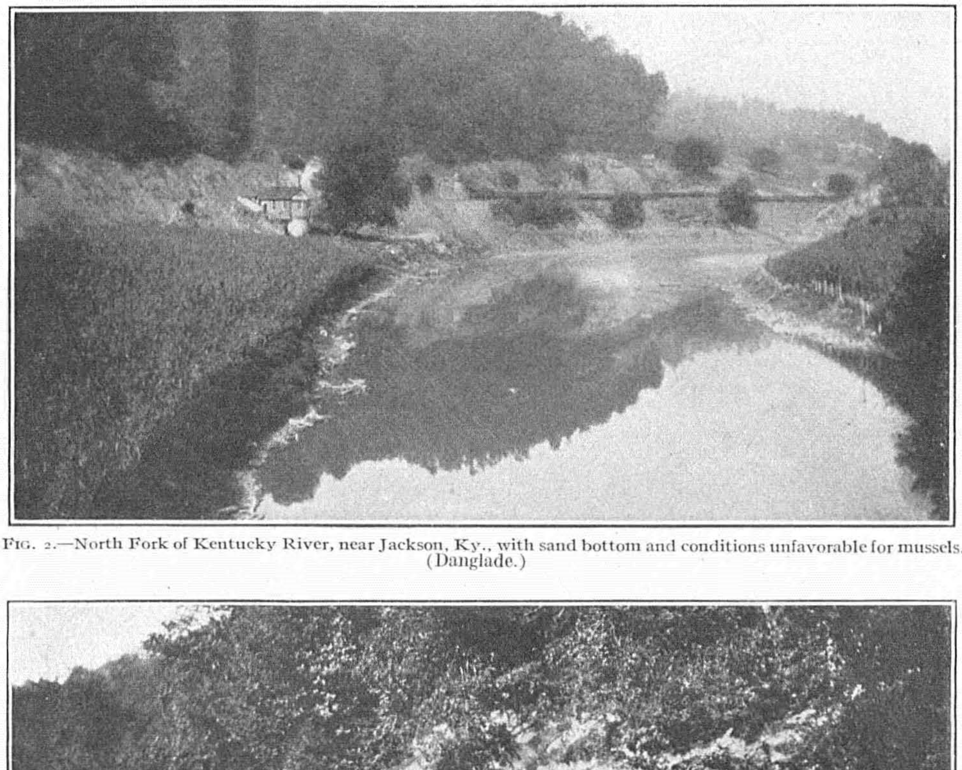


FIG. 2.—North Fork of Kentucky River, near Jackson, Ky., with sand bottom and conditions unfavorable for mussels. (Danglade.)

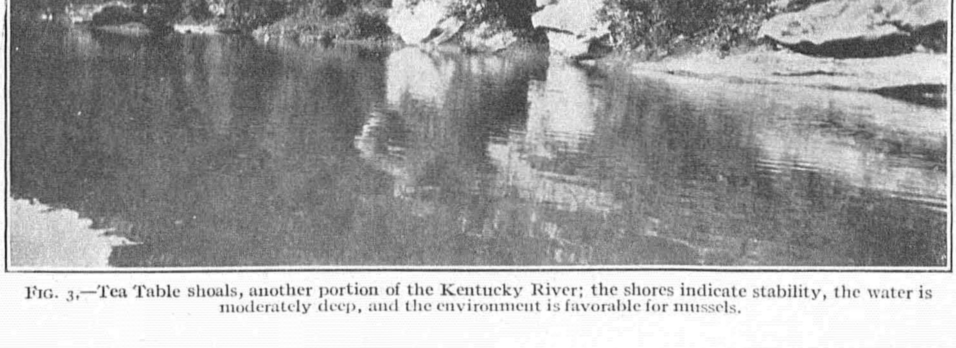


FIG. 3.—Tea Table shoals, another portion of the Kentucky River; the shores indicate stability, the water is moderately deep, and the environment is favorable for mussels.

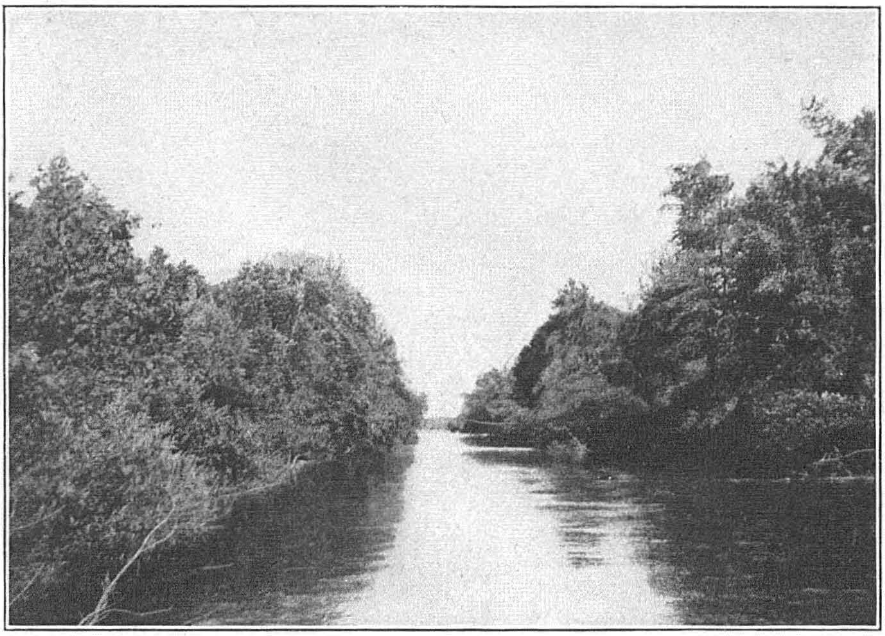


FIG. 1.—An undredged portion of the Kankakee River where valuable mussels flourish.

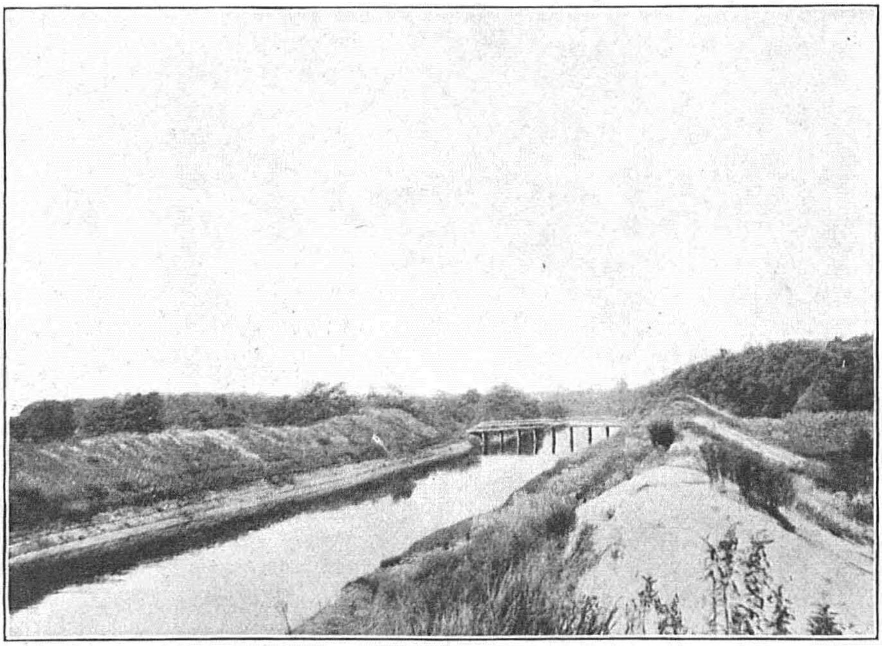


FIG. 2.—A dredged portion of the Kankakee River rendered (temporarily, at least) unfit for fresh-water mussels.

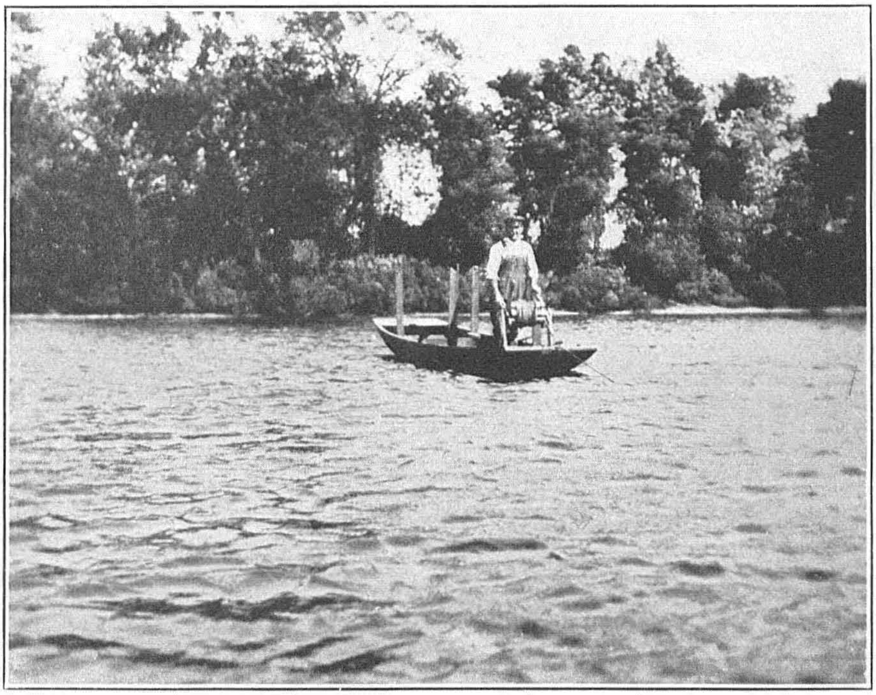


FIG. 1.—Lower portion of Grand River, Mich., where mussels thrive under natural conditions.

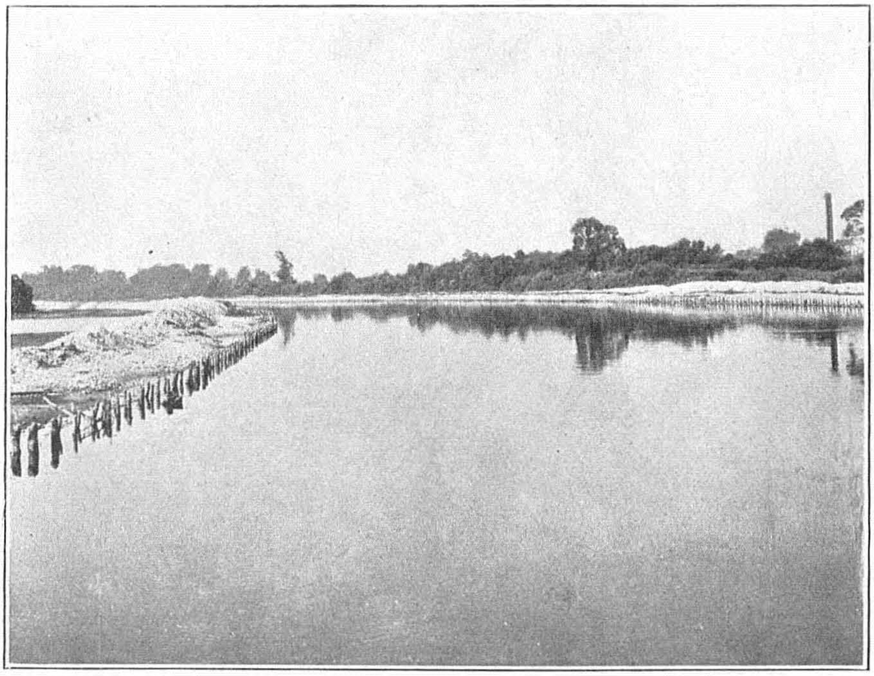


FIG. 2.—Lower portion of Grand River where conditions have been rendered unsuitable for mussels by canalization in interest of navigation.

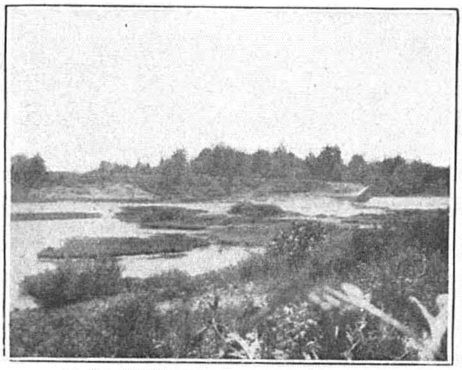


FIG. 1.—Auglaize River near Defiance, Ohio, showing islets and pools containing dense beds of mussels.

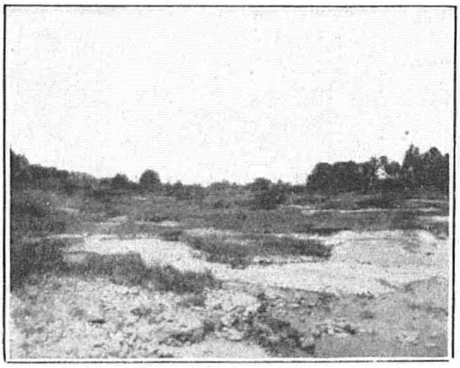


FIG. 2.—Maumee River, Defiance Ohio. The river bed a broad valley with limestone bottom, broken into numerous pools and channels with little islands —an excellent growth of fresh-water mussels.

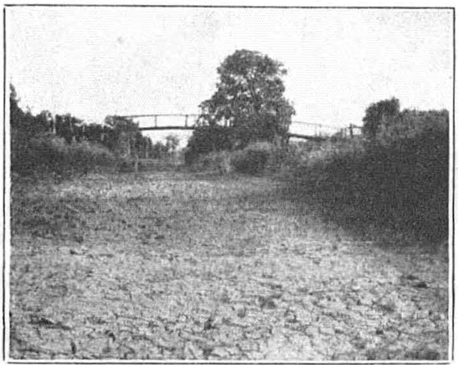


FIG. 3.—The draining of the Feeder Canal near Fort Wayne, Ind., revealed a remarkably dense population of fresh-water mussels.

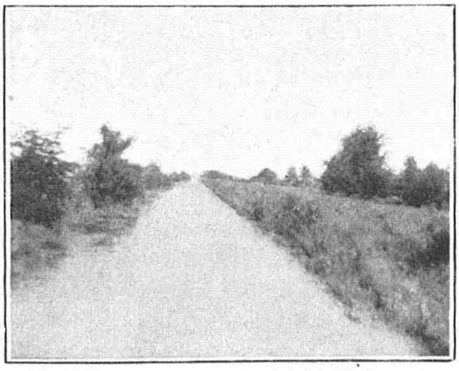


FIG. 4.—Parts of the Miami and Erie Canal afford excellent environments for mussels.

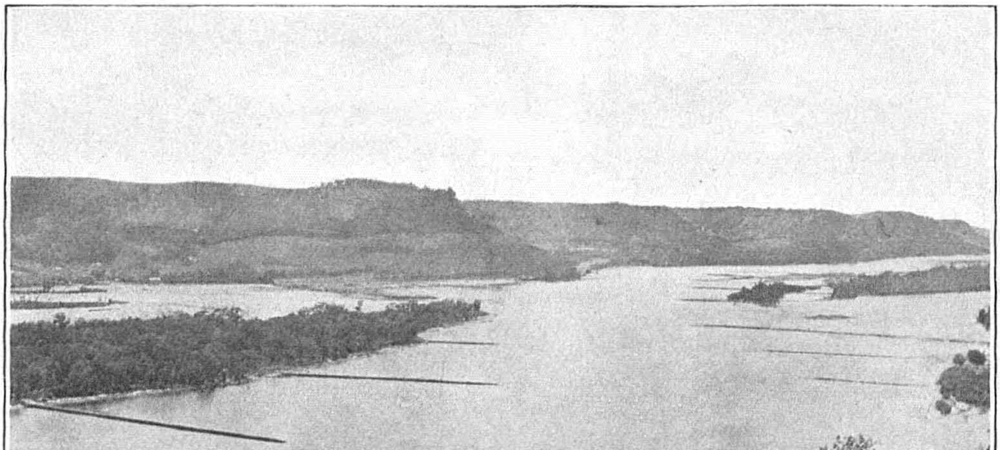


FIG. 5.—Construction of wing dams in the upper Mississippi River often renders conditions unfavorable for mussels that previously throve in such sections of the river.

the stronger development of the hinge teeth which aid in keeping the two valves of the shell in perfect apposition.

Since a river presents from source to mouth conditions of varying suitability for any form of animal life, there will usually be found in some measure a longitudinal succession of mussels. Shelford (1913, p. 122) gives a table showing the longitudinal sequence of eight species of mussels in the Calumet Deep River.

If one goes down a river from its headwaters, making collections of mussels at various points, many species may be found at each place, but some species first encountered may disappear before the upper waters are passed. Others appear here or there and perhaps disappear as one proceeds still farther down. The mussel fauna of the different sections of the stream are characteristic, although one or more species may be so adaptable as to live throughout the entire course of the stream.

This longitudinal succession of species is well illustrated by Table 2, which shows the distribution of mussels in the Grand River, Mich.

TABLE 2.—LONGITUDINAL DISTRIBUTION OF MUSSELS IN GRAND RIVER, MICH.[a]

Scientific name.	Common name.	Observations made at and below—							
		Outlets of headwater lakes.	Rives Junction.	Eaton Rapids.	Lansing.	Portland.	Ionia.	Lowell.	Grand Rapids.
1. Quadrula coccinea	"Flat niggerhead"	x	x	x	x	x	x	x	x
2. Strophitus edentulus	Squaw-foot	x	x	x	x	x	x	x	x
3. Anodonta grandis	Floater	x	x	x	x	x	x	x	x
4. Lampsilis ventricosa	Pocketbook	x	x	x		x	x	x	x
5. Quadrula rubiginosa	Flat niggerhead	x	x	x			x	x	x
6. Anodontoides ferussacianus	Small floater	x	x	x			x	x	x
7. Lampsilis iris	Rainbow-shell	x	x		x			x	x
8. Symphynota compressa		x	x	x		x			
9. Lampsilis luteola	Fat mucket	x	x	x					x
10. Alasmidonta calceola	Slipper-shell	x	x		x				
11. Unio gibbosus	Spike		x	x	x	x	x	x	x
12. Symphynota costata	Fluted shell		x	x	x	x	x	x	x
13. Lampsilis ellipsiformis			x	x	x	x	x	x	
14. Quadrula undulata	Three-ridge		x	x		x	x	x	x
15. Lampsilis ligamentina	Mucket			x	x	x	x	x	x
16. Alasmidonta marginata	Elk-toe			x	x			x	
17. Quadrula tuberculata	Flat purple pimple-back					x	x	x	x
18. Lampsilis recta	Black sand-shell					x	x		x
19. Lampsilis alata	Hatchet-back, pink heel-splitter							x	x
20. Quadrula pustulosa	White warty-back							x	x
21. Lampsilis gracilis	Paper-shell								x
22. Obliquaria reflexa	Three-horned warty-back								x
23. Obovaria ellipsis	Hickory-nut								x
24. Plagiola elegans	Deer-toe								x
25. Quadrula lachrymosa	Maple-leaf								x
26. Symphynota complanata	White heel-splitter								x
Total		10	14	14	10	12	13	16	22

[a] Observations by R. E. Coker in 1909.

SUMMARY OF TABLE.

Total species observed	26
Other species occurring above Portland	6
Species occurring throughout river	10
Species found only at or below Portland	10
Species not found below Grand Rapids	4
Species found only below Grand Rapids	6

It will be observed at once that a far greater number of species is found in the lower part of the stream. Thus, while only 10 of the 26 species observed in the river were found near the headwater lakes, 22 species were met in the section of the river between

Grand Rapids and the mouth at Grand Haven. It might be thought that this was due to the fact that there would be fewer obstacles to the passage of mussels downstream than to their distribution in an upstream direction. It seems sufficient, however, to assume that the unequal distribution is due rather to the greater variety of conditions of depth and of fish associates presented in the lower portion of the river. Shallow water only is found in the upper river, except as artificial pools have been formed in recent years by the construction of dams, while in the lower river deep water prevails in its channel and all lesser depths are found between the channel and the shores. The very breadth of the lower part of the river affords also a greater area for fish and mussels.

A difference of up-river and down-river habitat is presented by the distribution of two closely related species, the three-ridge, *Quadrula undulata*, and the blue-point, *Quadrula plicata;* the former, a more compressed and rougher form, is found in the more rapid waters of upstream habitats, while the latter, being thicker and less ridged, occurs in the deeper waters of the lower parts of a river system.[a] (See Clark and Wilson, 1912, and Wilson and Clark, 1912.)

In some rivers mussels are almost entirely lacking for long distances, as in the main course of the Missouri River for hundreds of miles above its mouth, where the absence of mussels is apparently due to the rapidly shifting bottom of sand. The Red River, with its heavy load of silt and its habit of suddenly cutting into its banks and changing its course, is manifestly unsuited for mussels, and examination of its bottom in many places by Isely (1914) and Howard revealed extremely few mussels (Pl. VII, fig. 2). There is also a virtual absence of mussels in the Mississippi River, except close alongshore, below the mouth of the Missouri River. Examination of the Musselshell River in Montana by J. B. Southall in 1919 revealed the presence in numbers of only a single species of mussel, and this a species (*Lampsilis luteola*) characteristic of lakes, which lived in the portions of the river deep enough to remain as isolated pools during the periods of dry weather. In the east fork of the Chicago River, Baker (1910) found only 3 species, and these were mussels characteristic of pond habitats, which were able to survive the dry seasons in the small ponds left isolated in the deeper parts of the river channel.

The James River, in North and South Dakota, though having very few fish, was found to possess a comparatively varied and abundant mussel fauna in the still waters between shallow riffles; but there was evidence that the mussels were derived from fish infected in other waters, that ascended the stream in times of flood (Coker and Southall, 1915).

The suitability of any section of a stream for the growth of mussels arises from a diversity of causes, including the nature of the rock or soil through which the stream is flowing, the character of the drainage waters entering the river at or above the section, the gradient of the stream bed with its effect upon depth and currents, and the species of fish which frequent the region.

Barriers in the course of a stream such as natural falls, or artificial dams, if impassable to fish, may have an effect upon the distribution of mussels. Wilson and Danglade (1914) found no mussels of the genus Quadrula above the Falls of St. Anthony in the Mississippi River, although several species of this genus are very common in the river

[a] Ortmann (1920) has definitely shown, for certain species, that: "(1) The more obese (swollen) form is found farther down in the large rivers, and passes gradually, in the upstream direction, into a less obese (compressed) form in the headwaters; (2) with the decrease in obesity often an increase in size (length) is correlated; (3) a few shells which have, in the larger rivers, a peculiar sculpture of large tubercles, lose these tubercles in the headwaters." He ascertains also that these laws do not apply to all species.

below that barrier. Wilson and Clark (1914) found only 4 species of mussels in the Cumberland River above the Cumberland Falls (one of these probably planted), while 19 species were taken in the pool immediately below the falls, but in this case the conditions prevailing in the river above the falls appeared distinctly unfavorable for fresh-water mussels. An impassable dam formed after mussels were generally distributed throughout a stream would have little significance with reference to the distribution of mussels the hosts of which subsequently thrived both above and below the dam. The effect, however, of a dam in changing a region of rapids into a pool, might cause the mussel fauna of swift waters to give place to a fauna of slack-water habitat.

Studies of rivers in cross section indicate that there may be quite definite distribution of life with reference to the banks. Shelford (1913) has discussed a horizontal arrangement of animals that is best illustrated in the cross sections of curves where there is a horizontal gradation in rate of current and in size of material in the bed of the stream. In the strong current only the coarsest materials are dropped, while the finest silt is deposited where the flow is most retarded. The depth of water is doubtless one factor governing the horizontal distribution of mussels, but the nature of the bottom material is of first importance. Howard (Survey of Andalusia Chute, Mississippi River, report in preparation) found in a branch of the Mississippi, following a comparatively straight course (not on rapids) and averaging 1,200 feet in width, that mussels were uniformly restricted to a border 200 feet from the shore line. (See table below.) Some mussels were found almost anywhere along this border, but occurring in beds at points where the channel touched the shore and where bottom conditions were favorable; depth seemed to be a minor factor as affecting the distribution.

The following table (3) indicates the results of a sample series of unit hauls taken at stated distances from the water's edge and so represents the distribution in a cross section of the river. It is not typical because of the narrowness of the bed on the left bank, but it illustrates in a general way the distribution found throughout the survey.

TABLE 3.—DISTRIBUTION OF MUSSELS IN ANDALUSIA CHUTE, MISSISSIPPI RIVER.

	From right bank.					Middle of river.	From left bank.				
Distance, in feet, from water's edge	35	85	100	200	300	400	300	200	110	60	20
Number of mussels per unit haul	13	3	0	0	0	0	0	0	0	12	32

Where there are rapids with bowlder or cobblestone bottom across a river of this size, it is known that mussels are not limited to such a border but are found at all points across the stream.

LAKES.

The mussels from some lakes are large and heavy-shelled, while in others they are small, thin-shelled, and stunted. These extremes represent the varied conditions which lakes present in respect to mussel life.

Lakes that have a free circulation of water seem to be favorable; such are those that are interposed in the course of a river. A favorable feature in such cases, no doubt, is the direct and free connection with streams that are well supplied with mussels. Examples are Lakes Pepin and Pokegama, Minn., and the former is noteworthy for the abundance of mussels produced. Though at first sight Lake Pepin might be considered no more than an expansion of the Mississippi River, further observation shows it to be a true lake in many of its characters, as in clearness of the water, depth, growth of vegetation, and virtual absence of current. In both of the lakes mentioned, a characteristic lacustrine species, the fat mucket, or Lake Pepin mucket, *Lampsilis luteola*, which is thin-shelled and worthless in ordinary inclosed lakes, attains so fine a commercial quality of shell as to appear almost as a distinct variety. Caddo Lake, La., which is interpolated in the course of a stream, possesses a rich mussel fauna and has been the scene of active pearl fishery (Shira, 1913). The small Rice Lake near La Crosse, Wis., which is, in effect, an expansion of a thoroughfare connecting the Black River, near its mouth, with the Mississippi River, also supports a varied and luxuriant mussel fauna. Where lakes are freely connected with rivers, as are those first mentioned, or as are others with short open outlets to the rivers, the lakes and rivers have many species of mussels in common.

In Lake Pepin, Shira (report in manuscript) found that the distribution of the mussels is confined wholly to the shore line and the flats within a maximum depth of 25 feet; no mussels at all were taken in the deep central part of the lake. In certain places the mussels were quite densely distributed, forming very well-defined beds, but as these beds were generally connected by areas of lesser population, a more or less continuous mussel bed was found to occur on each side of the lake. The largest and most extensive beds were located on a gravel bottom, or a mixture of gravel and sand. Several good though less extensive beds occurred on bottoms containing a considerable percentage of mud.

The upper end of the lake evidently serves as a settling basin for the silt poured in from the river proper, and for a distance of about 2 miles below the entrance of the river the lake is comparatively shallow with a soft oozy bottom. In this section of the lake very few mussels are found.

Shira records 32 species of mussels (report in manuscript). Ten of the most abundant species with the percentage of occurrence are given as follows:

	Per cent.
Fat mucket, *Lampsilis luteola*	31.5
Spike, *Unio gibbosus*	13.0
Blue-point, *Quadrula plicata*	12.7
Pig-toe, *Quadrula undata*	10.0
Pink heel-splitter, *Lampsilis alata*	8.3
Pocketbook, *Lampsilis ventricosa*	5.6
Slop-bucket, *Anodonta corpulenta*	5.5
Squaw-foot, *Strophitus edentulus*	4.3
White heel-splitter, *Symphynota complanata*	2.3
Black sand-shell, *Lampsilis recta*	1.4

In small lakes of considerable depth and without circulation, except as effected by winds and changes of temperature, animal life generally is absent or greatly restricted in the deeper portions, and mussels, when present, are confined to zones near the shores (Headlee and Simonton, 1904). Muttkowski (1918) in Lake Mendota found the optimum conditions for mussels at depths of 6 to 9 feet on sand bottom, but there was not an extensive mussel population in the lake as a whole.

The restriction of mussels to the border zones is indeed generally characteristic of the lakes of the Middle Western States, and even in this environment where the circulation effects of wave action may be felt, the mussels are stunted in growth. In their report on the mussel fauna of Lake Maxinkuckee, Evermann and Clark (1918, p. 251), summarize as follows the results of observations of mussels in lakes of Indiana and elsewhere:

Generally speaking, lakes and ponds are not so well suited to the growth and development of mussels as rivers are; the species of lake or pond mussels are comparatively few and the individuals usually somewhat dwarfed. Of about 84 species of mussels reported for the State of Indiana, only about 24 are found in lakes, and not all of these in any one lake, several of them but rarely in any. Of the 24 species occasionally found in Indiana lakes, but 5 are reported only in lakes, and only 3 or 4 of the species common to both lakes and rivers seem to prefer lakes.

Characteristic species of mussels of inclosed lakes of upper Central States are named in the following table (4), and it may be remarked that the fat mucket and the floater are easily predominant over all others.

TABLE 4.—CHARACTERISTIC MUSSELS OF LAKES OF UPPER CENTRAL STATES.

Species.	Michigan.[a]	Minnesota.[b]	Indiana.[c]
Fat mucket, Lampsilis luteola	x	x	x
Floater, Anodonta grandis	x	x	x
Pocketbook, Lampsilis ventricosa	x	x	x
Squaw-foot, Strophitus edentulus	x	x	x
Small floater, Anodontoides ferussacianus	....	x	x
......, Quadrula rubiginosa	x	....	x
Spike, Unio gibbosus	....	....	x
......, Lampsilis subrostrata	....	....	x
Rainbow-shell, Lampsilis iris	x	....	x
Slop-bucket, Anodonta corpulenta	....	x	....
Paper-shell, Anodonta imbecillis	....	x	....
Paper-shell, Anodonta pepiniana	....	x	....

[a] Coker, R. E. (unpublished notes).
[b] Wilson and Danglade (1914).
[c] Clark and Wilson (1912); Wilson and Clark (1912); and Evermann and Clark (1918).

While, as has been previously indicated, the plains streams, such as the Red River or the Missouri, with their ever-changing banks and bottoms and silt-laden currents, present conditions entirely unfavorable to mussels, yet the oxbow or cut-off lakes adjacent to them may offer favorable habitats for several species of mussels (Isely, 1914, and Howard, unpublished notes).

The sand shores of the Great Lakes to a depth of 8 feet are virtually barren of animal life (Shelford, 1918, p. 26). Fresh-water mussels are found in these lakes, chiefly, it appears, in the shallower bays, where they sometimes manifest a vigorous growth. They have not been used commercially to any extent, and probably few possess shells of a size and quality rendering them suitable for button manufacture.

In a biological examination of Lake Michigan in the Traverse Bay region, Ward (1896) encountered 9 species of mussels, all of species generally possessing relatively thin shells, while Reighard (1894) reported 20 species and subspecies from Lake St. Clair, of which the following 8 were described as abundant:

Pink heel-splitter, *Lampsilis alata* (Say).
Thin niggerhead, *Quadrula coccinea* (Conrad).
Spike, *Unio gibbosus* (Barnes).
Mucket, *Lampsilis ligamentina* (Lamarck).
...... *Lampsilis nasutus* (Say).
Black sand-shell, *Lampsilis recta* (Lamarck).
Pocketbook, *Lampsilis ventricosa* (Barnes).
Floater, *Anodonta grandis* (Say).

A more extensive list of mussels from Lake Erie and the Detroit River is given by Walker (1913), the list including 39 species of 15 genera. Since the great majority of the species named are those that normally possess thin and fragile shells, it may be supposed that the conditions in these waters are not favorable to the production of good shells. Certain species are mentioned, however, which, in other regions at least, possess shells of commercial quality. Principal among these are the following:

Maple-leaf, *Quadrula lachrymosa* (Lea).
Pimple-back, *Quadrula pustulosa* (Lea).
Pig-toe, *Quadrula undata* (Barnes).
Long solid, *Quadrula subrotunda* (Lea).
Hickory-nut, *Obovaria ellipsis* (Lea).
Black sand-shell, *Lampsilis recta sageri* (Conrad).

Clark, collecting on the shores of Lake Erie at Put in Bay, found dead shells all dwarfed in form but representing 14 species, of which the more common were as follows:

Three-ridge, *Quadrula undulata*.
Spike, *Unio gibbosus*.
Round hickory-nut, *Obovaria circulus*.
Paper-shell, *Lampsilis gracilis*.
Pink heel-splitter, *Lampsilis alata*.
Black sand-shell, *Lampsilis recta*.
Fat mucket, *Lampsilis luteola*.
Pocketbook, *Lampsilis ventricosa*.

PONDS, SLOUGHS, MARSHES, AND SWAMPS.

These types of environment are grouped together, since their mussel fauna is generally similar. The mussels are thin-shelled as a rule, since light weight is favorable for life in mud or soft bottoms and mass is not essential in the absence of current. Some possess narrow bodies and keel-like shells that fit them for locomotion through soft soil, and a few of the narrow-bodied species, where other conditions are suitable, have relatively heavy shells. Such are the pink heel-splitter, *Lampsilis alata*, and the white heel-splitter, *Symphynota complanata*.

The heavier mussels characteristic of rivers are sometimes found in sloughs, but in these the characters of flowing and still water are in a measure combined, since strong currents may prevail at seasons of high water. Sloughs, as parts of river systems and subject to being stocked from them, have mussel fauna to a certain extent related to that of the river; that is, the still-water species of the river are to be found in the sloughs. Marshes and swamps may have mussels at places where they contain pond or streamlike openings. In general the marsh and swamp environment is not favorable to mussels.

In ponds that are more or less isolated the thin-shelled mussels of the toothless type, as *Anodonta grandis* (floater) and *Anodontoides ferussacianus*, are characteristic. *Lampsilis parva*, one of the tiniest of fresh-water mussels, scarcely exceeding an inch in length, is sometimes found in such environments. A characteristic pond-dwelling species is the mussel *Unio tetralasmus*, which will survive in ponds that become dry in summer. Examples of this species of mussel have been found alive buried in the bottom three months after the water had disappeared on the surface (Isely, 1914, p. 18).

ARTIFICIAL PONDS AND CANALS.

Artificial ponds may present a favorable environment for many species of fresh-water mussels if the water supply is suitable, and some species are likely to become accidentally introduced with fish that are brought into the pond. The ponds of the Fisheries Biological Station at Fairport, Iowa, are supplied with water pumped from the Mississippi River. The first species of mussel to appear in the ponds was the large thin-shelled slop-bucket, *Anodonta corpulenta*, some examples of which had attained a length of 3 to 3½ inches when they were first discovered at the expiration of the second season of the pond, 17 months (May, 1910, to October, 1911) after the date of introducing water and fish into the newly excavated pond. Eighteen species which have been accidentally introduced are listed on page 165 below.

Few of these mussels are of commercial value, but it has been attempted to introduce several useful species by artificial infection upon fish, and success has been attained with the Lake Pepin mucket, a lacustrine mussel of high commercial value, which thrives well in the ponds and has attained a size and quality of shell suitable for commercial purposes at the age of 4½ years.

In canals mussels frequently thrive (Pl. XI, figs. 3 and 4). A mill race from a well-stocked stream seems to present a favorable environment for them. Clark and Wilson (1912, pp. 19–22) describe a luxuriant development of mussels in a canal at Fort Wayne, Ind., as follows:

> Toward the upper end of the canal, in a place where the bottom was 15 feet wide, the mussels were counted for a stretch of 10 feet along the canal bed and the following species noted: *Quadrula rubiginosa*, 11; *Q. cylindrica*, 1; *Q. undulata*, 86; *Anodonta grandis*, 6; *Ptychobranchus phaseolus*, 1; *Lampsilis ligamentina*, 5; *L. luteola*, 6. The width taken was the total width of the bottom of the canal and was considerably wider than the space occupied by the mussels.
>
> About a mile farther down the canal a space of 10 feet square was measured off in the bottom of the canal, and the following species were found: *Quadrula rubiginosa*, 6; *Q. undulata*, 60, all rather small; *Pleurobema clava*, 1; *Alasmidonta truncata*, 2; *Symphynota complanata*, 2; *S. costata*, 5; *Anodonta grandis*, 15; *Obovaria circulus*, 4; *Lampsilis ligamentina*, 5; *L. luteola*, 1; *L. ventricosa*, 4. This gave a little over one shell per square foot. In 1908, in a square meter of bottom near the Rod and Gun Club, the following species were noted: *Quadrula rubiginosa*, 9; *Q. undulata*, 36; *Symphynota complanata*, 1; *Anodonta grandis*, 17; *Obovaria circulus*, 11; *Lampsilis iris*, 2; *L. ligamentina*, 2; *L. luteola*, 3, giving a total of 81 per square meter. In addition to these shells there were many small Sphæriums, the ground being paved with them, 34 Campelomas, and 23 Pleuroceras. The square meter referred to above represents, as nearly as could be judged, an average number rather than either extreme.

It would appear from a general comparison of the aspect of mussels in lakes, ponds, and rivers that the effect of currents or circulation upon the growth of mussels is variable according to the relative proportions of organic and mineral foods present. In rivers, where the circulation of water is constant, mussels may grow to large size and possess thick shells, but when circulation is reduced, as in inclosed bodies of water, the mussels may be small and relatively thin-shelled, or they may attain a large size with thin shells (suggesting relative deficiency of mineral food), or else, with heavier shells, they may be dwarfed in size (suggesting a relative deficiency of organic food).

BOTTOM.

Most mussels are normally embedded in the bottom from one-half to three-quarters of their bulk.[a] That they may thus establish themselves, a firm but not impenetrable soil is required. The character of the bottom is, therefore, of especial significance to fresh-water mussels, though it has important relations to all bottom-dwelling animals. With regard to the bottom, consideration must be given both to its topography and to the materials of which it is composed. Major inequalities in topography, such as waterfalls and rapids, are discussed elsewhere. Minor inequalities are of importance because of the effects upon currents, sedimentation, light conditions, growth of food,

[a] The cases of deep embedding mentioned by Wilson and Danglade (1913), where they give a depth of 1 foot or more for living mussels in Shell River (p. 15), and the report of a fisherman of 2 to 3 feet at Lake Bemidji, seem to be cases of "digging in" because of drought. *Unio tetralasmus* (Isely, 1914) and *Quadrula plicata* (Howard, 1914) seem to have a remarkable power of resistance under these conditions.

and protective conditions; stability of soil is important for the establishment of the juveniles, for otherwise they will be overwhelmed. For some species objects for attachment, to which the byssus of the juvenile may be fastened, may also be necessary. Most of the varieties of bottom soil encountered are composed of one of the following materials, or of mixtures of two or more of them: Silt, mud, marl, clay, sand, gravel, pebbles, cobbles, bowlders, and ledge rock.

In rivers, sandy bottoms are regions of change comparable to sand-dune areas on land where immobile forms are killed. Sand bottoms occur extensively in many rivers and they may be veritable deserts. Rivers like the Missouri are devoid of mussels for hundreds of miles partly because of a preponderance of bottom of shifting sand. Mussels when found on sand bars in rivers are in transit seeking more stable conditions. Although comprising regions of instability in rivers where decided currents prevail, bottoms of sand may offer more favorable conditions in lakes where they furnish a permanent habitat for mussels.

A greater variety of bottoms favorable for mussels, as well as a more indiscriminate disposition of them, prevails in rivers than in the other bodies of water considered. In many lakes there is a more definite sorting of materials, leading especially to a segregation of the finest sediment in the deeper portions of the lake to form a bottom that is very soft and generally unsuitable for the Unionidæ; mussels possessing much mass would sink too deeply and have the gills too much clogged with silt to survive (Headlee and Simonton, 1904, p. 176). Where such conditions prevail the mussels are found near shore.

Headlee (1906, p. 315) summarizes observations and experiments in certain lakes of Indiana in the following words:

> The work of 1903 and 1904 shows conclusively that the mussels of Winona, Pike, and Center Lakes can not exist on the fine black mud bottom—they become choked with mud and apparently smother—and that the light-weight forms and the forms exposing great surface in proportion to weight can rest on top of comparatively soft mud and can, therefore, live farthest out on the deep-water edge of the bed. Because the mussels can not occupy any region where the pure black mud is present, they are confined by it to isolated beds and narrow bands of shore line.
>
> I believe that the whole evidence of the distributional and experimental work of 1903 and 1904 points clearly to the character of the bottom as the great basal influence in the distribution of mussels in small lakes generally.

The species he dealt with were the fat mucket, *Lampsilis luteola*, *Lampsilis subrostrata*, *Quadrula rubiginosa*, *Anodonta grandis*, and other small species with light shells. While his conclusion accords generally with the observations of the writers in other waters, the exclusion of mussels from mud bottoms can not be taken as an invariable rule. In the Grand River, at Grand Rapids, Mich., for example, one of the authors has observed such a heavy-shelled mussel as the three-ridge, *Quadrula undulata*, living in considerable numbers along with the light floater (Anodonta) in very soft mud. Also, in Mississippi Slough, in the Wisconsin lowlands along the Mississippi River opposite Homer, Minn., the blue-point, *Quadrula plicata*, the pimple-back, *Q. pustulosa*, and the pig-toe, *Q. undata*, have been found in considerable numbers on a soft-mud bottom along with the heel-splitters, *Symphynota complanata* and *Lampsilis alata*, and the slopbucket, *Anodonta corpulenta*.

Baker (1918, p. 117) gives a summary of results of studies of mussels with reference to bottom and depth in Oneida Lake, N. Y., in the following words:

The greatest number of individuals occurred on a clay or sandy-clay bottom. Twice as many mussels occurred in water deeper than 6 feet than within the 6-foot contour. These features are expressed in Table No. 27, the figures being averages per unit area of 9 square feet.

TABLE NO. 27.—AVERAGE NUMBER OF MUSSELS ON BOTTOM.

Bowlder and gravel bottom	6.14
Sand	6.39
Clay and sandy clay	13.00
Mud	10.26
Within 6-foot contour	7.84
Outside 6-foot contour	16.85

The above table shows that mussels are more abundant on the mud bottom in deep water (8 to 14 feet) than on sand, gravel, bowlder, or clay in shallow water (1 to 6 feet). These are the only studies of this character known to me.

In that lake one species, *Anodonta implicata*, is reported from one kind of bottom only, in sand between bowlders; while another species, *Lampsilis luteola* Lamarck, is said to be common on all varieties of bottom, except gravel (Baker, 1918, pp. 161, 162).

Muttkowski (1918) found that sand bottoms marked the favored environments of fresh-water mussels in Lake Mendota, Wis.

In Lake Pepin most of the adult mussels are found on a bottom of gravel or a mixture of gravel and sand. Bottoms composed largely of mud but made firm by a mixture of sand or gravel or both, yield a good supply of mussels; such areas are of much less extent in the lake than bottoms of gravel or gravel and sand. Of 1,397 juvenile mussels comprising 16 species collected in Lake Pepin in 1914, practically 95 per cent were taken on a sand bottom; about 4 per cent, principally *Anodonta imbecillis*, were found on a mud bottom; and the remaining 1 per cent on gravel or a mixture of sand, gravel, and mud (Shira, report in manuscript).

In ponds and sloughs there is less choice of bottoms than in lakes, and mud bottoms usually prevail; for such conditions *Lampsilis parva*, *Lampsilis subrostrata*, the light-shelled Anodontas, and similar species are especially adapted.

When we consider the relation between various mussel species and the bottom in rivers, we find the matter complicated by several considerations. This much, however, may be said definitely: No mussels can survive in a shifting bottom, nor upon a bottom of solid bare rock. Between the extremes, beginning with clean sand or soft miry silt and ending with coarse gravel and bowlders or stiff clay, there is a great variety of bottoms utilized to a greater or less extent as habitats for various species of mussels.

There are, of course, more or less definite relations between bottom and other features. Soft, muddy bottom is always associated with a current that is feeble at least near the bottom, or with the checking of the current; gravel bottom is usually associated with swift current; and clean sand or gravel is associated with clear water. Certain of the "mud-loving" mussels, such as the Anodontas, may be really lovers of quiet places and their association with mud rather an accident. Some of those supposed to be partial to sandy or gravelly bottom may simply prefer clear to turbid water. or may thrive best in a swift current.

Several species, including most of the Anodontas, *Symphynota complanata*, *Arcidens confragosus*, and others, are confined chiefly to one sort of bottom. A great many, however, seem indifferent to the character of the bottom, provided other conditions are favorable. Mussels may also apparently thrive where one would naturally think conditions unfavorable and where they might not survive if artificially planted. Thus in the crescent-shaped bayous along the Kankakee *Quadrula undulata*, and in sloughs of the Mississippi a closely related mussel, both heavy-shelled species, are found thriving on the top of deep, soft, silty mud which would not seem stiff enough to bear their weight.

In the Grand River, Mich., various species of mussels were found upon "clean" sand bottoms, but always sparsely. *Quadrula undulata* and *Lampsilis ellipsiformis* and *ventricosa* seemed best adapted to life in accumulations of drift. In sewage and waste-polluted waters at Lansing, Mich., *Lampsilis ligamentina*, *ventricosa*, and *ellipsiformis*, *Quadrula coccinea*, *Symphynota costata*, and *Alasmidonta marginata* were found in apparently healthy condition. The *Lampsilis ellipsiformis* obtained there, of especially large size, bore innumerable (but worthless) small pearls. (Coker, unpublished notes.)

In the Mississippi River near Fairport, Iowa, bottoms of unmixed mud and pure sand were found to be much less occupied by many of the species than mixtures of gravel and sand or of sand and mud, which supported both a far greater number of individuals and a somewhat greater variety of species. The preference for certain bottoms is most conspicuous when the proportion of the total catch of mussels found on the favored bottoms is viewed in connection with the proportions of these bottoms in the total area surveyed. Table 5 shows the total number of mussels taken from the different types of bottom in a survey of Andalusia Chute, Mississippi River (Howard, report in preparation):

TABLE 5.—MUSSELS COLLECTED IN SURVEY OF ANDALUSIA CHUTE, WITH REFERENCE TO CHARACTER OF BOTTOM.

Composition of bottom.	Approximate percentage of total area of bottom.	Number of mussels.	Number of species.
Mud	7	44	17
Mud and sand	4	158	20
Mud and ledge rock	½	17	7
Sand	71	87	23
Sand and gravel	9	289	28
Sand and pebbles	½	29	12
Gravel (pure)	2	5	3
Gravel, cobbles, and rock	2	34	14
Gravel and mud	1	....	....
Pebbles	1	....	....
Rock	2	....	....

The niggerhead mussel, *Quadrula ebenus*, in some streams, at least, is said to show a decided preference for firm bottoms, as of gravel or blue clay, but few observations have yet been made upon these mussels in streams having considerable areas of clay bottom. In the Grand River, Mich., the pink heel-splitter, *Lampsilis alata*, was found living in a ledge of very tough slippery blue clay (Coker, unpublished notes). So firm was the clay that a mussel could be extricated from it only by the exertion of considerable muscular effort. Several other species of mussel were in the vicinity, but none were embedded in the clay except one example of the three-ridge, *Quadrula undulata*, and that was in a spot where the clay was mixed with mud and was distinctly softer. Some spikes, *Unio gibbosus*, were found lying on the blue clay but not embedded; it seemed evident that they were unable to penetrate so tough a bottom.

The character of the soil has an effect upon the amount of materials carried in suspension in the water. If the amount is too great, as over soft mud or over extremely fine sand, under some conditions the mussel becomes smothered, or having no chance to feed, is starved. Too much decomposing organic matter in the soil is said to cause enough acidity to attack and erode the shell. For several reasons, therefore, areas of rapid silt deposition, or soft-mud bottoms, are quite unfavorable to mussels. Mussels are usually found in rivers in places where the bottom is swept clean by the current, even though in flood time the water may be heavily laden with silt in suspension.

The selection by some species of bottoms of gravel, pebbles, and bowlders as most favored habitats can readily be understood from the foregoing remarks; but there are still other favorable features of rough bottoms. The very stability of the larger-sized materials protects the bottom from washing, and may save the mussels from being smothered or carried away. It is of advantage to mussels to be surrounded by numerous other animals, especially by the smaller ones, which furnish attraction to fishes and thus promote the reproduction of the mussel. Many of these small animals live attached to stones, thus giving added value to gravelly and rocky bottom. In gravels, too, the youngest mussels may be protected through inaccessibility to enemies, and as they grow older the resemblance to small pieces of stone among which they lie may be the cause of escape from enemies. As previously indicated (p. 97), where bowlder rock or cobblestone bottoms occur in regions of rapids, mussels are commonly found abundantly and occur over the entire river.

The following table (6) embodies the experience of several observers regarding the preferences exhibited by 62 common species of fresh-water mussels for bottoms of different characters. In view of the intergradation of the several types of bottom and the almost unlimited variety of mixtures of sand, gravel, mud, and clay, the classification of the bottoms for the purpose of a table must of necessity be rough, and the characterization of mixed bottoms may in some cases be affected by the personal equation of the observer. Young mussels may have bottom requirements somewhat different from those of adults.

EXPLANATION OF TABLE 6.

The letters refer to the experience of the several observers (including the present authors and three previous writers), as follows: A, Baker (1898); B, Call (1900); C, Clark; D, Howard; E, Scammon (1906); F, Shira; G, Coker.

The use of large capitals indicates that, according to the observer whose letter is in large capitals, a certain type of bottom is preferred by the particular species of mussel. Wherever a small capital is used, the observer corresponding to the letter has indicated the type of bottom as favorable for the particular species of mussel, but not necessarily preferred to other favorable bottom.

The observations of Shira refer largely to lake conditions (Lake Pepin, Lake Pokegama, and Caddo Lake).

The observations of Coker refer primarily to shallow rivers (Grand River, Mich.).

The habitats indicated by Howard are based chiefly on the observed preferences of juvenile mussels in rivers, streams, ponds, and slues to the exclusion of true lakes.

TABLE 6.—HABITATS OF CERTAIN FRESH-WATER MUSSELS, CLASSIFIED ACCORDING TO CHARACTER OF BOTTOM.

Scientific name.	Common name.	Sand.	Sand and gravel.	Gravel.	Stones and rocks.	Mud and sand.	Mud and gravel.	Soft mud over firm bottom.	Mud.	Deep, soft mud.	Clay and sand.	Clay.
1. Alasmidonta calceola	Slipper-shell		D		G	D			A		C	
2. Alasmidonta marginata	Elk-toe	G	DG	BCG				C	A			
3. Anodonta corpulenta	Slop-bucket					F		C	FD	C		
4. Anodonta grandis	Floater					C		C	ABDE	C		
5. Anodonta imbecillis	Paper-shell	E				CF		C	AEF	D	C	
6. Anodonta suborbiculata	do								BE	CD		
7. Anodontoides ferussacianus.		G	GD			DGC	G		A		C	
8. Arcidens confragosus	Rock pocketbook			D		C			BD	C		
9. Cyprogenia irrorata	Fan-shell			C								
10. Dromus dromas	Dromedary mussel		C	C								
11. Hemilastena ambigua				BC	ABD				B			C
12. Lampsilis alata	Pink heel-splitter	F				DF		C	ABEF	C	C	G
13. Lampsilis anodontoides	Yellow sand-shell	EGD				DC		C	ABED			
14. Lampsilis capax	Pocketbook	C				D			D			
15. Lampsilis ellipsiformis		G		DG	GD				AE		C	
16. Lampsilis fallaciosa	Slough sand-shell	CF		DF		F		C	DF		C	C
17. Lampsilis glans				C				C				
18. Lampsilis gracilis	Paper-shell	EFG	F	D	D	F			ABDEF	C		G
19. Lampsilis higginsii	Higgin's eye	F	D	F							C	
20. Lampsilis iris	Rainbow-shell	AG	C	C	CG	DG		C	A			
21. Lampsilis lævissima	Paper-shell	EF				F		C	EF	CD		
22. Lampsilis ligamentina	Mucket	DGF	CFGD	CFG	DG		G	C	ABD		C	C
23. Lampsilis ligamentina gibba.	Southern mucket		C									
24. Lampsilis luteola	Fat mucket	CDFG	CF	DF				C	AEFD		C	
25. Lampsilis multiradiata		AC	C						A		C	
26. Lampsilis parva		D		D		D		C	ADEF			
27. Lampsilis purpurata	Purply	F	F			F				E		
28. Lampsilis recta	Black sand-shell	GF	D	EFG		F			AE		C	C
29. Lampsilis subrostrata		C							BED	C		C
30. Lampsilis ventricosa	Pocketbook	CFG	CGF	D	G	DF	G	C	DAE	D	C	
31. Margaritana monodonta	Spectacle-case	D	CD	BC	BD			C	BD			
32. Obliquaria reflexa	Three-horned warty-back.	BDFG	FD	BCDFE	BD	D		C	ABD		C	C
33. Obovaria ellipsis	Hickory-nut	CDFE	CFD	CDF		D	D	C	D		C	
34. Plagiola donaciformis		CFDE	CDF	CDF		D	DF		ADE			
35. Plagiola elegans	Deer-toe	CEGF	CDF	CF	D				ADEF			
36. Plagiola securis	Butterfly	BDEF	F	BDECF		D		C	B		C	
37. Pleurobema æsopus	Bullhead		D					C	D		C	
38. Ptychobranchus phaseolus.	Kidney-shell										C	
39. Quadrula coccinea	Flat niggerhead		CDG	EG	GD	G				A	C	
40. Quadrula cylindraca	Rabbit's foot		C	C								
41. Quadrula ebenus	Niggerhead		DF	FGD	D	D		C				
42. Quadrula granifera	Purple warty-back		F	F				C				
43. Quadrula heros	Washboard		DF			F		C	BDF			C
44. Quadrula lachrymosa	Maple-leaf	AEG	D	E	C	DF		C	ABFE		C	C
45. Quadrula metanevra	Monkey-face		DF	BDCEF	D	D	D	C	BD			
46. Quadrula obliqua	Ohio River pig-toe		C								C	
47. Quadrula plicata	Blue-point	F	DF	F		DF		C	AB	CE		
48. Quadrula pustulata	Pimple-back	CD		C		D		C	BF			
49. Quadrula pustulosa	do	FG	DF	CEF	D	F		C	ABFDE		C	
50. Quadrula rubiginosa		BGG	DG	B	BDG	DE	G	C	ABD		C	
51. Quadrula trapezoides	Bank-climber								FD			
52. Quadrula tuberculata	Purple warty-back	G		BC				C	ABF			
53. Quadrulata undata	Pig-toe	DF	DF	BDF	D	D		C	ABDF		C	
54. Quadrula undulata	Three-ridge	G	CG	G	G	D			AD	CG		G
55. Strophitus edentulus	Squaw-foot	CDGF	GDF	CDFG	G	DFG	G	C	ADEF		C	
56. Symphynota complanata	White heel-splitter	F	F	F		F		C	ABDEF	C		
57. Symphynota compressa			G							D	C	
58. Symphynota costata	Fluted shell	GF	CDGF	BCF	D	G			ADF		C	
59. Tritogonia tuberculata	Buckhorn	F	EF	DEF		F		C	BFDE		C	
60. Truncilla sulcata	Cat's paw		C								C	
61. Unio crassidens	Elephant's ear					F		C	BF		C	C
62. Unio gibbosus	Lady-finger	DFG	GF	DFGE	G	F	G		ADEF			

It appears from this and the following table that the preferred bottom for the majority of species is mud (but not deep, soft mud, to which type of bottom few species are adapted) and gravel, including sand and gravel. Sand ranks next and clay last; but few species of mussels exhibit a preference for sand or sandy clay, and only two are recorded (by one observer) as finding the most favorable environment in a bottom of clay unmixed with sand.

Table 6 may be simplified by reducing the types of bottom to four general classes, sand, gravel, mud, and clay, and by eliminating all but the leading commercial species. The results are indicated in Table 7 following:

TABLE 7.—PREFERRED HABITATS OF LEADING ECONOMIC FRESH-WATER MUSSELS, ACCORDING TO CHARACTER OF BOTTOM.

[X indicates preference as noted by majority and x by minority of observers.]

Scientific name.	Common name.	Sand.[a]	Gravel.[b]	Mud.[c]	Clay.[d]
Lampsilis anodontoides	Yellow sand-shell			X	
Lampsilis fallaciosa	Slough sand-shell			X	
Lampsilis recta	Black sand-shell	x	X	x	x
Lampsilis ligamentina	Mucket		X	x	x
Lampsilis ligamentina gibba	Southern mucket		X		
Lampsilis luteola	Fat mucket	X		x	
Lampsilis ventricosa	Pocketbook	X	x	X	
Obovaria ellipsis	Hickory-nut	X	x		
Plagiola securis	Butterfly		X	x	
Quadrula coccinea	Flat niggerhead		X	x	x
Quadrula ebenus	Niggerhead		X	x	
Quadrula heros	Washboard			X	x
Quadrula lachrymosa	Maple-leaf	x		X	
Quadrula metanevra	Monkey-face		X	x	
Quadrula obliqua	Ohio River pig-toe				X
Quadrula plicata	Blue-point		x	X	
Quadrula pustulosa	Pimple-back	x	x	X	
Quadrula rubiginosa		x		X	x
Quadrula undata	Pig-toe		x	X	
Quadrula undulata	Three-ridge		X	x	
Unio crassidens	Elephant's ear			X	
Unio gibbosus	Lady-finger		X	x	

[a] Sand alone.
[b] Including sand and gravel, mud and gravel, and rocks.
[c] Mud alone.
[d] Including sand and clay, mud and clay.

DEPTH.

The distribution of many animals of the water is known to be influenced by depth, the effect of which may be felt, among other ways, through pressure, light, temperature, dissolved gases, and freedom from wave action, or exposure thereto. In an indirect way, too, the effect of depth is experienced by any animal through the influence of these conditions upon food and enemies.

The increase of pressure is approximately 1 atmosphere for each 10 meters (33 feet) in depth, but fresh-water mussels are, so far as known, restricted to shallow waters where pressures must be insignificant. The Sphæriids are the only mollusks found below the 25-meter line in Lake Michigan (Shelford, 1913). Maury (1916, p. 32), (see Baker, 1918, p. 155), reporting the results of dredging in Cayuga Lake, N. Y., says: "These dredgings proved conclusively that Mollusca after 25 feet become very scarce. * * * In the greater depths no signs of Mollusca or of plants were found." In clear water minor depths do not markedly affect the light, but if the water is turbid, a common condition in the environment of fresh-water mussels, the penetration of light is very much diminished (see p. 114), and mussels if affected by light may, therefore, be expected to live at greater depths in clear lakes than in turbid streams. Temperature changes due to depth alone are so inconsiderable for shallow water as doubtless to have little effect upon the distribution of mussels, except where freezing to the bottom may occur.

The depth of water below which waves would reach them is apparently a factor in determining the habitat of many species of mussels in lakes (Headlee, 1906, p. 308—Winona Lake; Muttkowski, 1918—Lake Mendota). In large bodies of water like Lake Michigan the action of the waves is said to extend to 8 meters below the surface. The zone of wave action is a region in lakes comparable to the rapids and riffles of streams, where there is maximum circulation and aeration and a solid bottom suitable for such mussels as can withstand the violent action of waves and undertow currents. The species occupying this zone are given by Headlee for Winona Lake as the spike, *Unio gibbosus*, and the fat mucket, *L. luteola*. Baker (1916) says of this habitat in Oneida Lake:

> The shore may be free from vegetation. It receives the full force of the winds and waves from the open lake. The water is from 1 to 3 feet in depth and the bottom is heavily and thickly covered with stones and bowlders, many of the latter being of large size. Animal life is abundant, the clams living between the stones and on the sand between the stones.

The mussels he reported are as follows: *Elliptio complanatus*, common; *Lampsilis luteola*, rare; *Lampsilis radiata*, common; *Lampsilis iris*, rare; *Margaritana margaritifera*, rare; *Anodonta cataracta*, common; *Anodonta implicata*, common; *Anodonta grandis*, common; *Strophitus edentulus*, rare. Some of these are very thin shelled and doubtless survive the force of the waves only through the protection afforded by the large rocks. No doubt the thorough aeration of the water, resulting from wave action, is a favorable factor in this zone

On the shores of Lake Pepin one of the authors has often picked up live mussels that had been thrown up by heavy wave action. The mussels thus most frequently encountered were *Unio gibbosus*, *Lampsilis alata*, *Anodonta corpulenta*, *Strophitus edentulus*, *Lampsilis ventricosa*, and *Lampsilis luteola* in about the order named. They were usually immature examples. Occasionally after a storm had subsided one could see mussels that had not been entirely stranded on the beach near shore and in the act of making their way back again into deeper water. Headlee and Simonton (1904, p. 175) recorded similar observations.

While the data available are sufficient only to suggest how depth may affect the habitat selection of mussels, it is of interest to note some of the observations on this relation. A maximum depth of 22 feet for mussels in Winona Lake is given by Headlee (1906), who ascribes the control of distribution to bottom characters chiefly. Baker (1918) found that in Oneida Lake twice as many mussels occurred in water deeper than 6 feet as within the 6-foot contour. (See quotation, p. 103, above.) He records three species as limited to a depth of 1½ to 8 feet, three as living at varying depths between 1½ and 18 feet, and one subspecies as occurring only between 8 and 18 feet, the greatest depth which he explored. He reports an interesting case of bathymetric distribution of two races, *Lampsilis radiata*, occurring at 1½ to 3 feet, and a subspecies, *Lampsilis radiata oneidensis*, living only at 8 to 18 feet, the two forms showing a distinct difference in habitat. For Lake Mendota the optimum depth for mussels of the genera Anodonta and Lampsilis is given as from 2 to 3 meters (6 to 10 feet) (Muttkowski, 1918, p. 477); they were, however, found abundantly between 3 and 5 meters and rarely at greater depths than 7 meters (23 feet).

Wilson and Danglade (1914), in reporting a reconnoissance of mussel resources in Minnesota waters, give depths of the lakes, but without detailed data on the distribution of the mussels. In Lake Maxinkuckee, Evermann and Clark (1918, p. 255) say: "Mussels are to be found almost anywhere in water 2 to 5 or 6 feet deep where the bottom is more or less sandy or marly." Headlee (1906, p. 306) found that the mussel zone generally extended from the shore line to where the bottom changes from sand, gravel, or marl to very soft mud, a region in Winona Lake covered by from 4 inches to 9 feet of water. He did find, however, some mussels on sandy bottom in 22 feet of water. He made some experiments in retaining mussels at various depths and in a crate placed in 85 feet of water; only 1 of 10 specimens died in six days of exposure. After 12 days several specimens were found badly choked with mud.

In Lake Pepin mussels are plentifully found at depths ranging from 8 to 20 feet, but the majority are taken at depths ranging from 12 to 18 feet. Relative to the juvenile mussels, out of a total of 1,397 collected in 1914, 1,283, or 91.8 per cent, were taken at a depth of 3 to 8 feet; 2.6 per cent at 8 to 12 feet; 2.3 per cent at 12 to 16 feet; 0.4 per cent at 16 to 20 feet; and 2.9 per cent at 20 to 25 feet. *A. imbecillis* was the only juvenile found in any abundance at a depth greater than 15 feet, and 41 of the 79 individuals of this species collected were taken at 25 feet (Shira, report in manuscript).

A marked distribution with regard to depth has been observed in the artificial ponds at Fairport, Iowa. Here the species, *Lampsilis luteola*, is seldom found below a depth of 3 feet. When held in crates below this depth it does not thrive, although in its natural habitat, Lake Pepin, this species is abundant at a depth of 8 to 20 feet and has been taken at a depth of 25 feet.

In rivers and smaller streams mussels seem to be found commonly at lesser depths than in lakes, but unfortunately we have very few reports of observations in the deeper parts of large rivers. In the Illinois River, Danglade (1914) mentions a small bed 2 to 3 acres in extent above the mouth of Spoon River, where the bottom was of mud, the current about 2 miles per hour, and the depth of water 8 feet. At Chillicothe he found a good bed at a depth of 12 to 15 feet. The survey of Andalusia Chute, Mississippi River (Howard, report in preparation), carried on during relatively high-water stages in 1915, revealed no mussels in the deeper portion of the river over 12 feet in depth, and the greater number of mussels were found at depths less than 10 feet. Local informants at Madison, Ark., stated that the niggerhead, *Quadrula ebenus*, was found in water 20 to 50 feet deep; it was also said that in flood season it was captured from a depth of 75 feet. There has been no opportunity, however, to verify these statements.

With regard to a collection of 183 juveniles of the Quadrula group from 12 stations in the Mississippi River, Howard (1914, p. 34) reported depths from 0 to 8 feet. Wilson and Clark (1914) reported a rich find (19 species) in the Rock Castle River off the Cumberland, in water having a maximum depth of 1½ feet. In the Grand River, Mich., the senior author has found mussels (muckets, *Lampsilis ligamentina*, three-ridge, *Quadrula undulata*, and others) in conspicuous abundance in swift water less than a foot in depth. Boepple (Boepple and Coker, 1912) found mussels abundant and of fine commercial quality in water from 1 to 3 feet in depth in the Holston and Clinch Rivers of Tennessee. In Caddo Lake, Tex., Shira (1913) found an abundance of mussels in 4 to 8 inches of water, and in many places there was scarcely enough water to cover the shells. This lake was very shallow over large areas. In fact, mussels are frequently found in very shallow water where the conditions of the bed of the stream and other factors are favorable. In various parts of the country considerable commercial quantities of mussels are collected by hand from shallow waters. At one such place, Lyons, Mich., the mucket, *Lampsilis ligamentina* comprised 80 per cent of the collection, although the three-ridge, *Quadrula undulata*, the pocketbook, *Lampsilis ventricosa*, the spike, *Unio gibbosus*, and the black sand-shell, *Lampsilis recta*, were quite common. Among other species that were frequently found in very shallow water (1 to 2 feet in depth) in that stream were the following: *Lampsilis luteola, iris*, and *ellipsiformis, Quadrula coccinea* and *rubiginosa, Strophitus edentulus, Symphynota compressa* and *costata, Alasmidonta marginata, Anodontoides ferussacianus*, and *Anodonta grandis*. In fact, the only species that were not found in water less than 6 feet in depth in the Grand River were the three-horned warty-back, *Obliquaria reflexa*, the hickory-nut, *Obovaria ellipsis*, the deer-toe, *Plagiola elegans*, and the white heel-splitter, *Symphynota complanata*.

LIGHT.

The small floater, *Anodonta imbecillis* Say, in sunlight will draw in its siphons when a shadow passes over. Wenrick (1916) has demonstrated experimentally with measured illumination, that a fresh-water mussel, *Anodonta cataracta* Say, is very sensitive to decrease in intensity of light. Observations in the Washington laboratory indicate that the yellow sand-shell, *Lampsilis anodontoides*, will close when a black cloth is placed over the aquarium, but will open when exposed either to daylight or to the light of a bright electric lamp. These reactions may be for protection of the animal from approaching enemies, but it is probable also that the distribution of mussels is largely influenced by light conditions. Mussels are seldom found in vegetation which is dense enough to exclude the light to a great extent. This is especially true with regard to plants like the water lily which have floating leaves. Some relations to vegetation are brought out in a study of the habitats in Oneida Lake (Baker, 1916).

An exceptional case is reported by Wilson and Danglade (1914, p. 15) where the mussels were found in densest aggregation submerged deeply in the bottom and below a covering of vegetation. Their account is of sufficient interest to be quoted in full:

> The bottom of the river where these shells are obtained is covered with algæ and water weeds to the depth of 12 to 18 inches, and the thicker the vegetation the more plentiful the mussels beneath it. Two men were actively working the Shell River at Twin Lakes near Menahga at the time of our visit, and we watched them rake off the algæ and weeds and then dig into the underlying gravel and sand for the mussels. The latter are often buried to the depth of a foot or more. This is, at the least, a novel condition and one which, so far as is known, has not been reported from any other locality.

Certain species of mussels, the mucket, pocketbook, black sand-shell, and others are sometimes pink-nacred and sometimes white-nacred, and with the two former, at least, the outside covering of the shell has a reddish cast in pink-nacred examples. With such species it is a matter of common observation that pink-nacred shells and brightly colored exteriors are more frequently found in shallow clear water where the mussels are exposed to bright light.[a] Thus the black sand-shells of the upper part of the Grand River, Mich., have a deep purple nacre, while white shells of the same species predominate in the more turbid Mississippi. The spike, *Unio gibbosus*, is usually purple-nacred, but uncommon examples that are nearly white are found in turbid rivers. Clark

[a] Grier (1920a) presents the result of an extensive study of the nacreous color of mussels. He notes a tendency to lighter or bluish nacreous color in the lower portion of stream courses. He has evidence of some correlation between color and sex.

and Wilson (1912) describe the Maumee River as rather muddy most of the time, and it is interesting to find that they report that two-thirds of the spikes, *Unio gibbosus*, in that river were white-nacred and that the black sand-shells were usually white-nacred.

The reputed migration of certain mussels toward shore in time of flood may be an accommodation to light conditions associated with turbidity of water under such conditions. We have virtually no data on the distribution of mussels with respect to permanently shaded areas or with regard to the reactions to daily changes in light.

CURRENT.

The luxuriant development of certain mussels in streams where the current is strong, in contrast with their growth in sluggish portions of rivers and lakes, bears witness to the significance of current as a favorable factor of environment for fresh-water mussels. Current is a characteristic feature of streams, and the rate of flow is largely determined by the gradient of the channel. Currents producing a circulation of water occur also in lakes, where they are caused chiefly by wind and to a less extent by changes of temperature. In some lakes the circulation extends from top to bottom, but in small deep lakes only a partial surface circulation commonly prevails (Birge and Juday, 1911). Undertow currents are also developed where there is wave action, and under some conditions convection currents must exist in natural bodies of water, but we have little data on this.

Shelford (1913) emphasizes the relation of water animals to current as follows:

> The distribution of dissolved salts and gases is dependent upon the circulation of the water, as their diffusion is too slow to keep them evenly distributed. The water of streams has been found to be supersaturated with oxygen [citing Birge and Juday, 1911]. Oxygen is taken up by water near the surface. Nitrogen and carbon dioxide are produced especially near the bottom, and if the water did not circulate, they would be too abundant in some places and deficient in others for animals to live (p. 60). * * *
>
> The current in streams differs from that in lakes in that it is for the most part in one direction while the lake currents often alternate. There are backward flows and eddies at various points in streams in front of and behind every object encountered in the current. As we pass across a stream we find the current swiftest near the surface in the middle and least swift at the bottom near the sides (p. 61). * * *
>
> The factors of greatest importance in governing the distribution of animals in streams are current and kind of bottom. They influence carbon dioxide, light, oxygen content, vegetation, etc. (p. 66).

Since mussels are bottom dwellers and largely stationary in habit, one can appreciate how dependent they must be upon circulation of the water to bring renewed supplies of organic food, mineral matter in solution, and oxygen, and to remove the poisonous products of metabolism that are produced in their own bodies and in those of other organisms living about. Mussels, of course, cause by their respirative currents circulation of the water immediately about them, but this is not sufficient to prevent an early exhaustion of food supply unless broader currents prevail.

It must be emphasized, too, that flowing water carries more matter in suspension than still water. It has been seen (p. 91) that the food of mussels consists to a considerable extent of the finely divided solid matter; but such materials, however abundant on the bottom, are not available to the mussel until they are taken up in the water and carried to the mussel. The effects of the current, then, both in lifting solid matter from the bottom and in holding it in suspension play a foremost part in its relation to the welfare of mussels. The power of water to move solid matter on the bottom increases very rapidly with the rate of flow.

The capacity of water to move solid matter from a condition of rest on the bottom of a stream varies with the sixth power of the velocity of the stream. If the velocity is doubled, the increase in the force which is capable of putting the particle in motion is multiplied 64 times. (New York report of Metropolitan Sewerage Commission, 1912, p. 41.)

Fish frequent areas near the current but maintain themselves in eddies or in places where the current is relatively slack, as at the bottom and near the shores (Shelford, 1913). In view of the essential part that fish play in the distribution of mussels, the habits of the fish may be a very significant factor in the distribution of mussels with reference to current. It has been suggested by Evermann and Clark (1918, p. 252) that currents may promote the reproduction of mussels by making fertilization of the egg more certain and by decreasing the chance for inbreeding through the conveyance of sperm from mussels farther upstream. In still waters the chance for fertilization of eggs may be less favorable.

The relations of mussels to temperature have not been fully investigated, but it seems certain that flowing water must protect mussels from excessively high temperatures and thus permit many species to live in much shallower water in streams than in ponds or lakes.

The tendency of mussels to locate apart from the main channel and nearer the banks of the streams has previously been mentioned (p. 97). While this distribution may be partly due to the fact that there the full force of the current is avoided while many of its benefits are received, nevertheless it must not be overlooked that many species of mussels thrive in rapid shallow streams and that such regions of swift water in the Mississippi River, as the former "rapids" at Keokuk or the existing "rapids" above Davenport, have been among the most prolific mussel grounds of the entire river. In these circumstances, however, the rocky nature of the bottom affords the mussels protection against some effects of the current. Evidently the barrenness of the main channel in most cases is due rather to the nature of the bottom combined with the force of flow than to the strength of current alone.

On page 99 there have been listed the species of mussels which are characteristic of lakes and ponds, regions of comparatively still water. The more common mussels of rivers may be classified according to apparent adaptation to sluggish water, strong current, and rapids (Table 8). These general comments should be made: In a firm bottom, such as furnishes good anchorage, a mussel may dwell in a current swifter than is characteristic of its common habitats; where rocks furnish shelter, mussels below them may be in rather slow water despite the current around them; deep water may be fairly sluggish under a swift surface current.

EXPLANATION OF TABLE 8.

The symbols are those used in Table 6, C representing Clark; D, Howard; F, Shira; and G, Coker. The large capital denotes preference in the opinion of the observer, for a particular condition of current. The small capital denotes that the condition is favorable but not, so far as is known, preferred to other conditions. When no large capital occurs on a line, no preference is indicated; and when a particular letter appears in small capital throughout a line, the observer denoted by the letter has no evidence upon which to base an opinion of discrimination on the part of the particular mussel between the different conditions of current regarded as favorable.

TABLE 8.—CLASSIFICATION OF COMMON FRESH-WATER MUSSELS IN RELATION TO CURRENT.

Scientific name.	Common name.	Little or no current.	Fair or good current.	Strong or swift current.
1. Alasmidonta calceola	Slipper-shell		CG	
2. Alasmidonta marginata	Elk-toe		C	DG
3. Anodonta corpulenta	Slop-bucket	CDF	cf	
4. Anodonta grandis	Floater	CDF	cg	
5. Anodonta imbecillis	Paper-shell	cDF	cf	
6. Anodonta suborbiculata	do	CD		
7. Anodontoides ferussacianus		cg	Cg	g
8. Arcidens confragosus	Rock pocketbook	CDF		
9. Cyprogenia irrorata	Fan-shell			C
10. Dromus dromas	Dromedary mussel			C
11. Hemilastenia ambigua		D	Cd	
12. Lampsilis alata	Pink heel-splitter	cDFG	cf	
13. Lampsilis anodontoides	Yellow sand-shell	d	CDF	
14. Lampsilis capax	Fat pocketbook	cD	C	
15. Lampsilis ellipsiformis		cg	CG	D
16. Lampsilis fallaciosa	Slough sand-shell	DF	Cf	
17. Lampsilis glans		c	c	
18. Lampsilis gracilis	Paper-shell	CDFG	cdf	
19. Lampsilis higginsii	Higgin's eye		CDF	
20. Lampsilis iris	Rainbow-shell	cgD	CG	
21. Lampsilis lævissima	Paper-shell	CDF	f	
22. Lampsilis ligamentina	Mucket		CF	DG
23. Lampsilis ligamentina gibba	Southern mucket		C	c
24. Lampsilis luteola	Fat mucket	CDFG	cfg	
25. Lampsilis multiradiata			c	C
26. Lampsilis parva		CDF		
27. Lampsilis purpurata	Purply	cF	cf	
28. Lampsilis recta	Black sand-shell	f	CDFG	g
29. Lampsilis subrostrata		CD	c	
30. Lampsilis ventricosa	Pocketbook	cfgd	cdFG	g
31. Margaritana monodonta	Spectacle-case		CD	
32. Obliquaria reflexa	Three-horned warty-back	df	CFGd	d
33. Obovaria ellipsis	Hickory-nut		CDFG	
34. Plagiola donaciformis		df	CDF	
35. Plagiola elegans	Deer-toe	f	CFG	D
36. Plagiola securis	Butterfly	d	CDF	
37. Pleurobema æsopus	Bullhead		CDF	
38. Ptychobranchus phaseolus	Kidney-shell		C	
39. Quadrula coccinea	Flat niggerhead		CDg	dG
40. Quadrula cylindrica	Rabbit's-foot		CF	
41. Quadrula ebenus	Niggerhead		CFd	D
42. Quadrula granifera	Purple warty-back		Cd	D
43. Quadrula heros	Washboard	df	CDF	
44. Quadrula lachrymosa	Maple-leaf	DF	CFG	
45. Quadrula metanevra	Monkey-face	f	CDF	d
46. Quadrula obliqua	Ohio River pig-toe		C	
47. Quadrula plicata	Blue-point	cdf	CDF	
48. Quadrula pustulata	Pimple-back	cd	CDF	c
49. Quadrula pustulosa	do		CFGd	D
50. Quadrula rubiginosa		cg	CDG	dg
51. Quadrula trapezoides	Bank-climber	cF	cf	
52. Quadrula tuberculata	Purple warty-back		cg	cg
53. Quadrula undata	Pig-toe	Df	CFd	
54. Quadrula undulata	Three-ridge	cgD	CFGd	G
55. Strophitus edentulus	Squaw-foot	cgDF	cdg	
56. Symphynota complanata	White heel-splitter	cfg	CDF	
57. Symphynota compressa			g	g
58. Symphynota costata	Fluted shell		CF	d
59. Tritogonia tuberculata	Buckhorn	dfg	CFd	Dg
60. Truncilla sulcata	Cat's paw		C	
61. Unio crassidens	Elephant's ear		CDF	
62. Unio gibbosus	Lady-finger	cdgF	cdg	DG

WATER CONTENT.

The matter that is carried in all natural waters in varying quantities and proportions consists of suspended matter, both dead and living, minerals and other ordinarily solid substances in solution, and dissolved gases. All of these classes of substances are utilized by fresh-water mussels in one way or another, and the quantity of any of them in the water has a direct bearing upon the suitability of waters for mussels.

SUSPENDED MATTER.

The solids carried in suspension by water consist of mineral and organic substances. The particles of mineral matter brought in by surface drainage or derived from bottom and shores, apart from that which is in solution, range in size from coarse to very minute. The carrying power of the water varies with the sixth power of the velocity, although in the case of the most minutely divided substances other factors than rate of flow come into play.

Mussels are affected in various ways by the matter in suspension. It has been reported that some mussels stop feeding when the water is excessively turbid, as after a storm. In this way they would avoid taking into their stomachs large amounts of indigestible mineral. They have, however, the power of ejecting undesirable matter; this may enable them to continue feeding even though the water is moderately turbid In streams like the Mississippi, mussels could hardly survive without feeding during the long periods of turbidity that prevail. Excessive precipitation of silt may smother or even bury the mussel (Headlee and Simonton, 1904, p. 176). The turbidity of water over deeper beds materially restricts the amount of light reaching the mussel, and it is possible that this has an untoward effect. Data regarding the turbidity of several streams are given in Table 9, page 116. The turbidity of representative mussel-producing streams varies from 37 to 188, except that the Des Moines River at Keosauqua has a turbidity rating of 542—a striking exception. The Missouri and Red Rivers (non-productive) and portions of the Mississippi River which do not yield commercial mussels have turbidity ratings from 556 to 1,931.

Organic materials, both living and dead, are abundantly suspended in most natural waters, and form a large part of the food of mussels. (See p. 91.) The living bodies are the microscopic plants and animals which make up what is called the plankton. The dead organic materials are the remains or fragments of plants and animals in a state of decomposition, and such also form a part of the food supply.

Some of the plankton originates in the lake or stream in which the mussels are living. Another and perhaps the greater part is brought in by the tributary streams. Similar statements may be made regarding the dead organic matter, with the addition that some of this may be brought in by surface drainage from the bordering lands.

MINERALS IN SOLUTION.

To what extent mussels derive the mineral matter necessary for the sustenance of life and the formation of shells directly from the water or through the solid food consumed can not be said, but even that part which is derived from solid food must have been obtained by the smaller organism from the water or the soil. Churchill (1915 and 1916), from experiments conducted at the Fairport Station, has shown that fresh-water mussels possess the ability to make use of nutriment which is in solution in the water. While he demonstrated this for such nutritive substances as fat, protein, and starch, there are yet wanting, as he has pointed out, analyses of the natural water in which mussels live to prove that such organic substances are present in the waters in quantities sufficient to play an important part in the nutrition of mussels. There are, however, abundant analyses to prove the presence of dissolved minerals.

The requirements of mussels in mineral food may be ascertained by analysis of the soft bodies and shells. Such analysis shows that while the shell is about 95 per cent calcium carbonate, and 3½ per cent organic matter, it also contains other minerals in very small proportions, less than 1 per cent each, such as silica, manganese, iron, aluminum, and phosphoric acid. It does not follow that because these minerals, other than calcium, occur in minute proportions, they are any the less essential to the welfare of the mussel; iron forms a very small proportion of the human body, but man can not live without it. So these minerals may, then, be just as essential to the formation of good shell as calcium, but with the possible exception of manganese it is probable that all natural waters contain a sufficient quantity of the minerals to satisfy the needs of mussels. Nevertheless an interesting and important problem may be found in a comparative study of the mineral content of different waters which yield shells of diverse qualities. It is even possible that an excessive proportion of certain minerals in water tends to the formation of shells that are brittle, discolored, or otherwise inferior.

The sundried meats of mussels from the Mississippi River when analyzed have been found to contain, besides moisture (about 7.6 per cent), protein (calculated from nitrogen), 44 per cent; glycogen, about 9 per cent, ether extract (presumably fats), a little less than 3 per cent; and undetermined organic material, 13 per cent. The remainder is mineral matter (chiefly phosphoric acid), 9 per cent; calcium (calcium oxide), 8 per cent; silica, 3½ per cent; manganese, about one-half of 1 per cent; and such other minerals in small proportions as sodium, potassium, iron, and magnesium (Coker, 1919, p. 62, analysis by U. S. Bureau of Chemistry).

As previously indicated, nearly all natural waters, at least those fed largely with surface drainage, probably contain certain quantities of the required minerals, but it would be going beyond the bounds of present knowledge to say whether or not the abundant growth of mussels in certain streams and the variable qualities of shells produced in different streams are related to the proportions of minerals present other than calcium. Certain it is that a deficiency of lime is very unfavorable. The soft waters of the Atlantic slope support very few mussels and these are small in size and possess thin shells which are usually badly eroded. The thinness of the shells is associated with the deficiency of calcium in the water, and the erosion is an indirect result of the same cause, since the free carbonic acid, which attacks and consumes the shells wherever the protective horny covering has been broken by abrasion, would, in harder waters, be combined with the calcium in solution to form the bicarbonate.

Circulation, of course, plays a great part in making available to mussels the dissolved content of the water. It may be due not so much to low calcium content as to inadequate circulation that small lakes and ponds in States of the Middle West generally yield mussels with thin or dwarfed shells.

The waters of many streams of the United States have been subjected to analysis by the United States Geological Survey (Dole, 1909). The summarized analyses for several streams, or parts of streams, productive of mussel resources, and for 10 others that are not productive of commercial shells, are given in Table 9 below. It appears that, within broad limits, the variations in content of silica, iron, magnesium, sodium, and potassium are not significant as affecting productiveness (unless, as may be the case, the quality of the shell produced is affected). Particular attention may be directed to the columns of turbidity, calcium, carbonate radicle, and nitrate radicle. The nonproductive streams, or parts of streams, listed are generally either very high in turbidity or very low in calcium, bicarbonate, and nitrate. The Shenandoah, among nonproductive streams, is an interesting exception. So far as can be seen, its analysis conforms essentially to the standard of productiveness in mussels as revealed by streams of the Mississippi Basin. It is possible, then, that the Shenandoah, and perhaps a few other streams of the Atlantic or Pacific slopes, might support fresh-water mussels of commercial value should the proper species be introduced.

TABLE 9.—CONTENTS OF WATERS OF CERTAIN PRODUCTIVE MUSSEL STREAMS AND OTHER NONPRODUCTIVE STREAMS.[a]

	Turbidity.	Suspended matter.	Coefficient of fineness.	Total iron (Fe).	Silica (SiO_2).	Iron (Fe).	Calcium (Ca).	Magnesium (Mg).
PRODUCTIVE RIVERS.								
Wabash, Vincennes, Ind	172	193	1.20	....	13.0	0.24	61.0	22.0
Illinois, La Salle, Ill	159	136	.80	....	12.0	.21	50.0	22.0
Illinois, Kampsville, Ill	188	145	.80	....	12.0	.27	47.0	20.0
Fox, Ottawa, Ill	94	87	1.20	....	11.0	.20	60.0	32.0
Sangamon, Springfield, Ill	74	39	.80	....	16.0	.32	52.0	24.0
Cumberland, Nashville, Tenn	126	94	.74	....	20.0	.42	26.0	3.6
Cumberland, Kuttawa, Ky	176	165	.92	....	18.0	.30	28.0	4.3
Des Moines, Keosauqua, Iowa	542	642	1.09	....	22.0	.36	58.0	21.0
Grand, Grand Rapids, Mich	37	43	1.61	1.1	14.0	.07	56.0	19.0
Cedar, Cedar Rapids, Iowa	64	61	.97	....	14.0	.09	48.0	16.0
Maumee, Toledo, Ohio	143	112	.95	3.4	17.0	.27	57.0	16.0
Mississippi, Moline, Ill	117	106	.9	....	16.0	.39	33.0	13.0
Mississippi, Quincy, Ill	173	119	.8	....	18.0	.46	36.0	16.0
NONPRODUCTIVE RIVERS.								
James, Richmond, Va	90	71	.96	3.9	18.0	.5	14.0	3.0
Potomac, Cumberland, Md	28	29	1.59	3.0	8.2	.14	24.0	4.6
Wateree, Camden, S. C	259	214	.79	....	25.0	.28	6.3	1.8
Shenandoah, Millville, W. Va	31	39	1.64	.9	15.0	.08	32.0	8.2
Mississippi, Chester, Ill	858	634	....	.8	22.0	.39	44.0	16.0
Mississippi, Memphis, Tenn	556	519	.97	....	24.0	.61	36.0	12.0
Red, Shreveport, La	790	870	1.11	....	30.0	1.1	74.0	17.0
Missouri, Ruegg, Mo	1,931	1,890	1.02	....	29.0	.51	52.0	16.0
Savannah, Augusta, Ga	172	142	.77	....	23.0	.44	5.7	.8
Hudson, Hudson, N. Y	13	16	1.26	.7	11.0	.15	21.0	3.8
Cape Fear, Wilmington, N. C	73	21	.92	1.3	9.9	.78	5.0	1.5

	Sodium and potassium (Na+K).	Carbonate radicle (CO_3).	Bicarbonate radicle (HCO_3).	Sulphate radicle (SO_4).	Nitrate radicle (NO_3).	Chlorine (Cl).	Total dissolved solids.
PRODUCTIVE RIVERS.							
Wabash, Vincennes, Ind	25.0	0.0	230	55.0	6.4	36.0	336
Illinois, La Salle, Ill	16.0	....	203	50.0	6.6	13.0	278
Illinois, Kampsville, Ill	18.0	....	202	42.0	4.3	15.0	267
Fox, Ottawa, Ill	14.0	....	275	61.0	4.9	7.9	335
Sangamon, Springfield, Ill	16.0	....	247	37.0	3.4	7.5	276
Cumberland, Nashville, Tenn	9.6	.0	92	14.0	1.2	2.1	119
Cumberland, Kuttawa, Ky	7.8	.9	100	9.7	1.8	3.0	124
Des Moines, Keosauqua, Iowa	17.0	.0	216	71.0	3.3	4.8	312
Grand, Grand Rapids, Mich	10.0	8.5	214	33.0	2.3	7.7	258
Cedar, Cedar Rapids, Iowa	12.0	.0	209	30.0	3.1	3.4	228
Maumee, Toledo, Ohio	24.0	2.5	173	48.0	4.5	40.0	298
Mississippi, Moline, Ill	10.0	....	152	24.0	1.8	3.7	179
Mississippi, Quincy, Ill	11.0	....	175	25.0	2.2	4.4	203
NONPRODUCTIVE RIVERS.							
James, Richmond, Va	6.7	.0	60	7.1	.3	2.3	89
Potomac, Cumberland, Md	9.0	.0	36	58.0	.9	6.4	130
Wateree, Camden, S. C	8.4	.0	34	4.2	.4	2.8	73
Shenandoah, Millville, W. Va	6.7	1.3	132	6.2	2.6	3.0	140
Mississippi, Chester, Ill	21.0	....	174	56.0	2.7	9.8	269
Mississippi, Memphis, Tenn	19.0	.0	129	43.0	1.7	8.6	202
Red, Shreveport, La	90.0	4.6	135	140.0	.4	121.0	561
Missouri, Ruegg, Mo	36.0	.0	178	104.0	2.9	12.0	346
Savannah, Augusta, Ga	12.0	.0	30	6.0	.6	2.1	60
Hudson, Hudson, N. Y	7.9	.0	73	16.0	.8	4.0	108
Cape Fear, Wilmington, N. C	7.2	.0	25	3.2	.2	5.8	57

[a] After U. S. Geological Survey.

DISSOLVED GASES.

Air is inconspicuous, yet nothing is more important to man. Without it he dies; and his comfort, health, and normal development depend upon the purity of the air by which he is surrounded. This is because of the absolute necessity for oxygen, and the deleterious effect of too much carbonic-acid gas. The gases dissolved in water are as invisible as air, but the mussels are as dependent upon the free oxygen in solution in the water as man is dependent upon the oxygen of the air. The water of streams and lakes dissolves air at the surface from the atmosphere and derives it from the physiological action of plants in light. Cold water will hold more free oxygen than warm, but the absorption of oxygen at the surface is favored by increased evaporation, with warm dry air and the prevalence of winds (W. E. Adeney, in Report of the Metropolitan Sewerage Commission of New York, 1912, p. 81). Falls, rapids, and swift currents promote the absorption of oxygen, and circulation currents lead to its better distribution into the deeper parts and throughout the whole body of water. Even without the aid of circulation currents, a measure of distribution of oxygen dissolved at the surface is effected by diffusion and "streaming" of the gas within the water (W. E. Adeney, loc. cit., p. 82).

Carbon dioxide (CO_2), commonly called carbonic-acid gas, which is given off as a waste product of mussels and other animals, and which is also formed by the decomposition of animal and vegetable matter, is helpful in small quantities, but is poisonous to animals when present in too great quantities (Shelford, 1913, p. 59; 1918, pp. 39, 40; and 1919, p. 106). It is used up by green plants in sunlight and is also given off to the atmosphere at the surface of the water. The same conditions that are favorable to the absorption of oxygen are also favorable to the loss of CO_2.

Carbon dioxide is of especial significance sometimes because of its tendency to unite with calcium carbonate to form the bicarbonate, which is soluble in water. Since the shell of a fresh-water mussel is composed principally of calcium carbonate it is liable to be attacked by free carbon dioxide in the water and taken up into solution. The horny covering of the shell is a protection against the action of the gas, but if that becomes broken or worn off in spots, as frequently occurs, the shell is exposed to the destructive effect of the acid. This leads to little harm in hard waters where the CO_2 may unite with the calcium carbonate derived from rocks or soils, but in soft waters, or in any waters where there is an excess of gas over dissolved calcium, the shells are partially or completely destroyed by corrosion. On many rivers "baldhead" shells are commonly encountered, and sometimes the shells are full of pits or even eaten clean through in the older parts.

Nitrogen, though an important element in the composition of mussels, can not be used by them in the form of a gas, and its presence in water (unless in excess) is presumably a matter of indifference to them, just as the nitrogen which composes the bulk of the atmosphere is uninjurious to men and not directly utilized by them (Shelford, 1918, p. 36). Other gases found in water are ammonia, methane (CH_4) and other hydrocarbons, and hydrogen sulphide (H_2S), which are formed in certain processes of decomposition (Needham and Lloyd, 1916, p. 47). These are of importance only when occurring in sufficient quantity to be injurious.

Mussels and other animals grow more plentifully in regions of water where, with other conditions favorable, there is a proper gas content—abundant free oxygen and limited amounts of carbon dioxide. Such places are near zones of wave action in lakes and in rapids in streams, where the influence of green plants is felt, and where water circulation is good.

VEGETATION.

In many lakes and streams in protected locations rooted plants occur in more or less abundance. If this vegetation is of open character, not producing a heavy shade, it frequently harbors an extensive mussel fauna (Baker, 1916, pp. 94 and 95). This kind of habitat is especially favorable to many fishes,[a] and to this fact in part may be attributed the presence of mussels, since the young mussels upon leaving the fish, having small power of locomotion, will remain where they fall if the habitat is at all suitable. Since mussels are found in abundance where there is no vegetation, as in rivers like the Mississippi, and generally are conspicuously absent from dense growths, it would seem that the association with rooted plants is largely incidental. There is other direct evidence to indicate that mussels of such habitats are those that are parasites upon species of fish that have a preference for such an environment.

Shira's observations in Lake Pepin (unpublished manuscript) indicated a certain association of juvenile mussels and vegetation, since 94 per cent of the juvenile mussels taken in a survey conducted in 1914 were taken in situations where more or less vegetation was encountered. On the other hand, he found juveniles at as many stations without vegetation as with it. As the result of many observations he concluded that a dense growth of vegetation was distinctly unfavorable to the survival of young mussels, and he suggests that the association of juvenile mussels with vegetation may be partly due to the fact that environments marked by the presence of aquatic plants are attractive to fish. He also observed that a given area of bottom supportive of mussels might display a heavy growth of aquatic plants one year but be practically or entirely free of them in another year. The same author has observed relatively dense growths of vegetation on mussel beds in Lake Pokegama.

It has frequently been observed in lakes that mussels live abundantly in patches of Chara, a low-growing green plant usually containing a considerable proportion of calcium carbonate. In the Grand River, Mich., Coker noted that mussel collecting was invariably poor in the midst of abundant rooted plants. The principal species found in such localities were the floaters (*Anodonta grandis*), the fat mucket (*Lampsilis luteola*), and the pink heel-splitter (*Lampsilis alata*). The mucket (*Lampsilis ligamentina*), and other species were likely to be found in the vicinity of rooted aquatic plants.

As quoted on page 110, above, Wilson and Danglade (1914, p. 15) described the finding of mussels beneath layers of algæ and weeds in Minnesota streams.

It must be remarked that rooted plants are not the only ones that contribute to the oxygen supply and to the depletion of the carbon dioxide of the water. There are thread algæ and innumerable microscopic floating plants which play an important if not the most important part in oxygenation of the water, and these are widely distributed in all zones to which sunlight penetrates.

[a] "Little fishes and the greater number of mature fishes keep more or less closely to the shelter of shores and vegetation" (Needham and Lloyd, 1916, p. 23).

ANIMAL ASSOCIATES.

In the previous discussion of the Naiades in relation to the physical environment, there has been shown to be an adaptation by certain species to particular physiographic situations, as to pond, lake, river, swift or quiet water, hard or soft bottom, etc. In any habitat each mussel is in association with other mussels of the same or other species and with animals and plants of various classes, all more or less adapted to the same environment. Such an association of organisms forms a community, the members of which interact more or less upon one another and upon their environment. The consideration of these communities with reference to their members and to the environment often reveals important relations. Because of the mutual relations existing, a disturbance or destruction of any one element, by affecting a balanced condition, may cause a marked disturbance of the whole community. (See Shelford, 1913, p. 17.) Some of the relations between mussels and their associates may be described as competition, symbiosis and commensalism, parasitism, and preying. A description of a typical habitat with its inhabitants will illustrate the variety of life associated with mussels. For Oneida Lake, N. Y., Baker (1916, p. 94) gives an account of a particular sort of habitat which he designates the bulrush-waterwillow type, where there is not great exposure to waves, where the bottom is more or less covered with stones and bowlders, but with sandy spots here and there, where the depth varies from 1 to 4 feet, and where the vegetation consists of bulrushes, waterwillows, and pickerelweed.

The principal differences between this habitat and the bowlder type are the less exposed situation, the density of the vegetation, the deeper water, and the sandier bottom. Such a habitat is particularly favorable for black bass, sunfish, rock bass, and others, because of the hiding and breeding places provided by the thick vegetation, the attachment for eggs by the roots and stems of plants, and the excellent feeding ground, by the abundance of animal life, insect, crustacean, and molluscan. The largest number of molluscan species, 39, occur in this type of habitat, including upwards of 15 which are known to be eaten by bottom-feeding fish. [The following numbers of species are listed: Mussels, 11, including several species of Anodonta and Lampsilis; univalves, 16; crustaceans, 1 (crayfish); Sphæriids, 10; leeches, 5; insects, 4.]

A typical association of mussels and other species in Andalusia Chute, Mississippi River, near Fairport, Iowa, is as follows (Howard, unpublished notes):

Bottom—gravel, rock, and sand.

Water—depth 5½ to 7½ feet. Current at surface estimated 2 miles.

Haul—250 feet in length, with crowfoot drag 10 feet wide and with dredge 18 inches wide.

Distance from edge of water—20 feet.

Mussels—*Lampsilis gracilis*, 3; *Plagiola elegans*, 1; *P. donaciformis*, 3; *Quadrula ebenus*, 1; *Q. metanevra*, 3; *Q. pustulosa*, 1; *Q. undata*, 2; *Strophitus edentulus*, 1; and *Unio gibbosus*, 3. Total, 18.

Bivalve—*Musculium transversum* Say, 1.

Bryozoa—*Plumatella polymorpha* Kraepelin, 1 colony.

Snail—*Vivipara subpurpurea* Say, 36; *Pleurocera elevatum*, Say 1.

Flatworm—Planarian.

Leech—*Placobdella parasitica* Say.

Insects—Stonefly, Perla sp. (larvæ); mayfly, Chirotenetes, 1 (larva); Heptagenia, 14 (larvæ); Polymitarcys, 2; dragonfly, *Gomphus externus*, 5, Argia, 3 (larvæ), Neurocordulia, 1; caddisfly, Hydropsyche, 70 (larvæ); beetle, Parnids, 2 (adult).

Crustacea—Crayfish, Cambarus.

In communities of animals and plants, as the individuals increase in numbers there may develop the keen competition for food which has been designated as the struggle for existence of the animate world. Since mussels feed upon suspended matter, living or dead, which they filter from the water, and since water once filtered must be less richly supplied with food for other mussels, an actual competition for food undoubtedly exists. Clark and Wilson (1912, pp. 19–20) give an account of a measured area of 1 square meter (10.76 square feet) in which they counted 81 mussels and 57 other mollusks, making a total of 138 individuals, or about 13 per square foot; and there were present, of course, many other animals, some of which took the same kind of food as the mussels. This recorded determination of numbers per given area illustrates the possibilities of competition. As indicated on pages 91 and 93, above, a detrimental competition for organic food probably does not occur ordinarily with mussels.

Symbiosis and commensalism exist in such communities. A few supposed instances affecting mussels are afforded by small forms that live within the shells in the mantle cavity of the mussel where they receive food and protection. A small bristle worm, *Chætogaster limnæi*, frequently observed in the mantle cavity of mussels; is supposed by some to be merely a commensal, but it may be considered a predacious species since it has been seen with juvenile mussels within its digestive tract (Howard, paper read at meeting of American Fisheries Society, 1918). The leech, *Placobdella montifera*, enters living mussels, but is not known to feed upon them (Moore, 1912, p. 89).

Bryozoa and other sessile forms are found attached to the exposed portions of live-mussel shells. Doubtless there are many cases of commensalism to be revealed by closer study of mussels in their natural habitat.

An interesting symbiotic relation exists between a mussel and the bitterling, a small European fish, which lays eggs in the mantle cavity of a fresh-water mussel which in turn infects the fish with glochidia (Olt, 1893). A different relation, which shows some reciprocity, however, is that of the fresh-water drum (*Aplodinotus grunniens*) of the Mississippi Basin, that eats fresh-water mussels but pays for the privilege, in part at least, by nourishing the young of several species parasitically encysted on its gills. (Surber, 1913, p. 105, and Howard, 1914, pp. 37 and 40.) The same is true of other fish that eat mussels, as the catfishes.

Parasitism is a phenomenon of community relations, and it is of double significance in the case of mussels, because not only have the mussels parasites to prey upon them, but they with few exceptions depend for existence upon the opportunity to become parasites of fish or, in one case, of an amphibian. A rather close relationship of fish to the mussel community is essential, and there may be a particular interrelation of given species of fish and of mussels. Questions arise as to when and how this special and intimate relationship came about and to what extent the habits of host and mussel interlock in such cases as the gar pikes and the sand-shells (Howard, 1914a), the river herring and the niggerhead, the shovel-nose sturgeon and the hickory-nut, the catfishes and the warty-back, the mud puppy and the little salamander mussel. In the last-named case, the peculiar habit of the mussel which lives beneath flat stones conforms evidently to the habits of the host, for the mud puppy is well known to frequent such situations.

One feature of certain mussels that possibly serves to decoy fish is the elaborate development of the mantle flap in gravid females of the pocketbook mussel, *Lampsilis ventricosa*, and others. (See p. 85.) These flaps in their form and coloration, including an eyespot, resemble a 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. (See Wilson and Clark, 1912, pp. 13, 14.) The unwelcome members in the associations to which mussels belong are discussed in the following section on "Parasites and Enemies."

PARASITES AND ENEMIES.

PARASITES.

Long green algæ are occasionally found attached to the exposed tips of the shells of mussels, and these may cause some erosion of the shells. Marly concretions, composed of intermingled low algæ and lime often form knoblike lumps on shells in lakes.

Among the most common of mussel parasites are water mites which dwell in the gill cavity and lay their eggs within the flesh of the mussel, in the inner surface of the mantle, in the foot, or in the gills. These water mites, which belong to the genus Atax, vary in size and color and to some extent in shape (Wolcott, 1899). One is black with a white Y-like marking on its back; others may be reddish. The largest and most degenerate is of a honey color with white treelike markings, but because of its inconspicuous coloration it is often overlooked. The different species of Atax are hard to distinguish without special preparation and study. Under magnification these water mites look somewhat like spiders. Small pearls are sometimes formed about Atax eggs.

Leeches are occasionally seen on the inner surface of the mantle of some mussels, especially in Anodontas (floaters) in ponds. They probably feed on the mucus of the mussel.

A small organism closely resembling a minute leech in general shape and appearance is occasional in the axils of the gills of mussels in some lakes. This is *Cotylaspis insignis*, one of the trematodes or flukes (Leidy, 1904, p. 110). One mussel may harbor a dozen or more of these parasites. Rather similar to *Cotylaspis insignis* but considerably larger and pink instead of yellowish, is the trematode *Aspidogaster conchicola*. It is more complex than *Cotylaspis insignis* and is usually found in the pericardial cavity of the host mussels, although in severe infection it may overflow into other organs.

Distomids, both free and encysted, are found in mussels. The distomid occurs in almost any muscular part of the body but most frequently in the foot or along the edges of the mantle. Sometimes pearls are formed around distomid cysts. The free distomids are usually found on the mantle surface next to the shell; they are chiefly confined to the flesh along the hinge line but may extend lower down. They are often associated with small irregular pearls. Sporocysts of distomids are common, especially in some Quadrulas. Many distomid parasites of mussels appear to be harmless, but one, *Bucephalus polymorphus*, destroys their reproductive organs (Kelly, 1899, p. 407; Wilson and Clark, 1912, pp. 69, 70; Lefevre and Curtis, 1912, p. 121). An ascarid worm is occasionally found in the intestine of mussels.

A worm with peculiar hooks on its head was found encysted in the margin of the mantle of some mussels in a pond near Fairport, Iowa. It was probably a trematode but has been found only once and never identified.

An oligochæte worm, *Chætogaster limnæi*, is occasionally found in mussels. It is possibly a parasite of snails from which it now and then migrates to mussels. We have some reason to believe that it devours the other mussel parasites. The crystalline style, a long translucent gelatinous body which is formed by the mussel within its intestine, is often mistaken by clammers for a worm.

Certain protozoa, *Conchopthirus curtus* and *Conchopthirus anodontæ*, somewhat resembling in general appearance the slipper animalcule, Paramœcium, are occasionally met in the mucus of mussels. Attached protozoa, like Vorticella, are also occasionally found on the edge of the mantle.

Occasionally larval Atax migrate into the space between the mantle and shell and are covered by nacre, where they may form minute white tracks, or in some cases apparently small raised "blisters" or pimples (Clark and Gillette, 1911). One or perhaps several species of distomid causes a brick-red or purplish discoloration of the nacre, mostly in thin-shelled mussels (Anodonta and Strophitus) (Osborn, 1898; Kelly, 1899, p. 406; Wilson and Clark, 1912, p. 66). The marginal cyst distomid sometimes causes a steel-blue stain of the nacre near the margin (Wilson and Clark, 1912, p. 63).

ENEMIES.

Mussels have numerous enemies, among which may be mentioned the mink, the muskrat, the raccoon, water birds, turtles, fishes, hogs, and man.

Of the depredation of many of these we know little. Water birds probably kill but few mussels, and of fishes, catfish and the sheepshead, or fresh-water drum, are the most noteworthy. These probably feed mainly on the thinner-shelled species. Small mussels (*Lampsilis parva*) have been found in the intestines of the turtle, *Malaclemmys lesueurii*.

Besides man the muskrat is the most notorious enemy of mussels, and the shell piles left by them are often conspicuous objects along the shores of lakes and rivers. Conchologists sometimes rely upon the muskrat's shell piles to furnish them choice and rare shells. Evermann and Clark (1918, p. 284) found not a few examples of *Micromya fabalis* in muskrat shell piles on the banks of Lake Maxinkuckee, though collecting in the lake during several seasons failed to reveal a single living specimen. Clammers prospecting new rivers sometimes use the piles of shells left by the muskrat as aids indicating where to dredge for shells.

Direct observations of the work of muskrats in Lake Maxinkuckee, Ind., were made by Clark and reported in "The Unionidæ of Lake Maxinkuckee" (Evermann and Clark, 1918, pp. 261, 262), as follows:

> The greatest enemy of the lake mussels is the muskrat, and its depredations are for the most part confined to the mussels near shore. The muskrat does not usually begin its mussel diet until rather late in autumn, when much of the succulent vegetation upon which it feeds has been cut down by the frost. Some autumns, however, they begin much earlier than others; a scarcity of vegetation or an abundance of old muskrats may have much to do with this. The rodent usually chooses for its feeding grounds some object projecting out above the water, such as a pier or the top of a fallen tree. Near or under such objects one occasionally finds large piles of shells. The muskrat apparently has no especial preference for one species of mussel above another but naturally subsists most freely on the most abundant species. These shell piles are excellent places to search for the rarer shells of the lake.
>
> In the winter after the lake is frozen, great cracks in the ice extend out from shore in various directions, and this enables the muskrat to extend his depredations some distance from shore in defi-

nite limited directions. During the winter of 1904 a muskrat was observed feeding on mussels along the broad ice crack that extended from the end of Long Point northeastward across the lake. The muskrat was about 50 feet from the shore. It repeatedly dived from the edge of the ice crack and reappeared with a mussel in its mouth. Upon reaching the surface with its catch it sat down on its haunches on the edge of the crack and, holding the mussel in its front feet, pried the valves apart with its teeth and scooped or licked out the contents of the shell. Some of the larger mussels were too strong for it to open, and a part of these were left lying on the ice. The bottom of the lake near Long Point, and also over by Norris's, is well paved by shells that have been killed by muskrats. Muskrats do not seem to relish the gills of gravid mussels; these parts are occasionally found untouched where the animal had been feeding.

In spite of all these enemies mussels held their own and throve and flourished until the appearance of man upon the scene, when depletion of the mussel beds became noticeable. Man exterminates a good many mussel beds by sewage discharge, by drainage, through which sand is washed down over the beds, by dredging and construction of wing dams for navigation, by pearling, but, most of all, by exhaustive clamming for the shells.

CONDITIONS UNFAVORABLE FOR MUSSELS.

Since mussels are animals of generally sedentary habit, with limited powers of locomotion, they are more helpless to escape from unfavorable conditions of environment than are fish or other active creatures of the water. This relative helplessness does not characterize the adult mussel alone, but is even exaggerated for the young stages. From the time the larval mussel attaches itself to a fish until it is liberated it is entirely dependent upon the movements of its host for its future home; it may be dropped in a suitable environment or in a place wholly unfavorable to its survival. On the other hand, adult mussels of many species can endure unfavorable conditions for a considerable period of time. This is found to be especially true of several species of Quadrula.

NATURAL CONDITIONS.

Some natural conditions unfavorable to mussel life are shifting bottom, turbidity, sedimentation, floods, and droughts. These conditions pertain usually to streams rather than to lakes. They have received some consideration in various paragraphs of this section on "Habitat"; therefore it is only necessary to summarize them in this connection.

The paucity of mussels in the Missouri River, as well as in the greater part of the Red River and other streams of the plains, is no doubt due to its exceedingly shifting bottom. Similar conditions apply in lesser degree in the lower stretches of many streams. In fact, all rivers, for some distances above their mouths, are as a rule very deficient in mussels as compared with sections farther up where bottom and other conditions are more favorable. Shifting bottoms not only prevent mussels from securing a foothold, but may also entirely destroy established beds.

Interrelated with shifting bottom are turbidity and sedimentation. All three factors and the extent to which they may be operative are largely dependent upon flood conditions. In nearly all large rivers floods commonly plow new channels here and there in the stream bed, cut away banks to a greater or less extent, and build new shoals or change the form and dimensions of old ones. Such changes in navigable streams are familiar to pilots who find it necessary to ' learn the river" each season. Many of these changes must be catastrophic to mussels in certain localities.

Excessive turbidity with consequent increased sedimentation, when of considerable duration, is no doubt seriously unfavorable to the well-being of mussels. It has been stated that mussels do not feed during periods of high turbidity, but no definite data in support of this can be given. That mussels do not "bite" well on the crowfoot hooks during a rising stage of water is a condition recognized by clammers. Whether the fact that the shells are not generally open and the mussels feeding at this time is due to the turbidity, or to other changing conditions incidental to the rising water, can not be stated. If heavy deposits of sediment are unfavorable for adult mussels, they must be more directly harmful to the young during the early stages of independent life, for the tiny juveniles may be smothered by deposits that would have less disastrous effect upon larger mussels.

The effects of droughts are ordinarily felt but little by the mussels of the larger streams and lakes. The most unfavorable condition arises when, owing to a prolonged dry season, the water is lowered to such an extent that the mussels fall easy prey both to muskrats and to clammers and pearlers seeking them in the shallow water. Crows, too, are known to pluck out and kill Anodontas when the water over them becomes low and clear.

In the small streams, lakes, and sloughs, the mussels may be killed by the partial or complete drying up of the water. Certain species of mussels are, of course, more resistant to such condition than others. Isley (1914) states that live specimens of *Unio tetralasmus* were plowed up in a pond three months after it had become dry. The mussels had burrowed down to zones of moisture.

ARTIFICIAL CONDITIONS.

Among the conditions imposed by man that may be detrimental to mussel life in our streams may be mentioned the discharge of sewage, industrial wastes, dredging, and the building of wing dams. (See Pls. IX, X, and XI.)

Disposition of the sewage and wastes of large cities without harmful contamination of the rivers presents an issue of growing importance. Portions of streams just below important cities are sometimes veritable cesspools, unsuited to both mussel and fish life. The Illinois River for a considerable distance below its origin is greatly influenced by sewage pollution through the Des Plaines River and the drainage canal; from the head of the stream down to Starved Rock, 42 miles from the source, no mussels are found, and a normal variety and abundance of fishes is not present above Henry, 77 miles from its source (Forbes, 1913, p. 170; Forbes and Richardson, 1919, p. 148). Industrial wastes from pulp and paper mills, tanneries, gas plants, etc., are injurious to fishes, and no doubt harmful to mussels as well. Such unfavorable conditions as arise through the depletion of oxygen supply by the decomposition of sewage are partially or completely corrected by the intervention of rapids or waterfalls. (See Shelford, 1919, p. 111, and Baker, 1920.)

River improvement work, such as dredging and the building of wing dams, creates conditions more or less unfavorable for mussels. Hydraulic dredging may destroy mussels, either directly by pumping them up, or by shifting the river channel so that ensuing changes cause new sand bars to form and to bury previously existing beds. Wing dams constructed for improvement of the Mississippi River, built of rock and brush and projecting from the shore to the channel, have far-reaching effects upon the course of the current, upon sedimentation, and upon the formation of sand bars. The area between the dams may fill up with sand, so that eventually willows are growing where a mussel bed once flourished. Such changes have been observed in the Mississippi River near Fairport, Iowa, and at Homer, Minn.

The effect of the construction of dams directly across the channel of a river, as for water-power development, has been discussed on page 97.

Greater irregularity of stream flow resulting from the clearing of forests greatly influences the life of mussels. The drying up of ponds inhabited by mussels and the extreme low stages of water which allow clammers to obtain the mussels by wading, form disastrous conditions to which mussel beds are occasionally exposed. Extreme low stages of lakes and streams in summer may lead to mortality of mussels resulting from high temperature of the water and diminished oxygen supply. (See Strode, 1891; Sterki, 1892; Farrar, 1892.)

GROWTH AND FORMATION OF SHELL.

MEASUREMENTS OF GROWTH.

Methods of propagation, estimate of results, and measures for protection all depend in a considerable degree upon knowledge of the rate of growth of mussels. It is important to know how many years elapse before a mussel may attain a market size, as well as at what age it may be expected to begin breeding. Furthermore, these questions require answers for more than 40 economic species, even if consideration were not given to the more than 500 additional American species of fresh-water mussel. The rate of growth is not, however, easily ascertainable for most species.

Mussels of any species may be left under observation for a considerable period in tanks or troughs, but experiments indicate that normal growth does not occur under the conditions of life in tanks. Even large ponds do not offer the conditions required by many species. The data to be offered on this subject are derived principally from experiments conducted at the Fairport station. Further data on growth of mussels will be found in Isley's paper (1914).

Pocketbooks, *Lampsilis ventricosa*, reared in one of the ponds at the Fairport station attained a length of 41 to 47 mm. (1.6 to 1.85 inches) in two growing seasons, and about 65 mm. (2.56 inches) by August of the third season. Examples 45 to 47 mm. long (1.76 to 1.85 inches), and these evidently in the second year of free life, were measured and planted in the Mississippi River by Lefevre and Curtis in June, 1908, and recovered by the senior author of this paper in November, 1910, at the close of the fourth year of growth (Lefevre and Curtis, 1912, p. 180 ff). They had attained lengths of 81 to 85 mm. (3.18 to 3.35 inches). (See fig. 6, p. 133.)

It is evident, then, that pocketbook mussels under only ordinarily favorable conditions may attain a marketable size by the end of the fourth season of independent life (at 3½ years of age from date of infection). The observations reported in the following table (10) show that a nearly equal rate of growth applies to the Lake Pepin mucket, *Lampsilis luteola*.

TABLE 10.—AVERAGE LENGTH OF SIX EXAMPLES OF THE LAKE PEPIN MUCKET, LAMPSILIS LUTEOLA, REARED IN POND 3D AT FAIRPORT, IOWA.

Time of measurement.	Length.	
	Millimeters.	*Inches.*
Close of second growing season	43.4	1.71
Close of third growing season[a]	68.8	2.72
Close of fourth growing season	77.0	3.04
Close of fifth growing season	80.6	3.18
Close of sixth growing season	84.9	3.35

[a] The records of the original lot for the third year having been lost in the fire, there is substituted a corresponding record for the third year of mussels of another lot recorded in Pond 8D. The mussels in Pond 3D were from a fall infection and those in 8D from a spring infection; therefore the former are slightly older.

Another species of pocketbook, *Lampsilis* (*Proptera*) *capax*, had attained a length of 49 mm. (1.93 inches) at the end of the second season, indicating a slightly more rapid growth for this species than for *Lampsilis ventricosa*. Thinner-shelled species of the genus Lampsilis may grow more rapidly. Thus some examples of the paper-shell *Lampsilis* (*Proptera*) *lævissima*, known to be not over 16 months of age (in free life), had attained lengths of 78 to 81 mm. (over 3 inches). An example of the paper-shell, *Lampsilis* (*Paraptera*) *gracilis*, grew from 17.6 mm. (0.7 inch) to 107 mm. (4.2 inches) in 2 years 9 months and 18 days, the rate of growth averaging about 1⅓ inches per year.

The very thin-shelled mussels of the genus Anodonta grow even more rapidly. Examples of the floater or slop-bucket, *Anodonta corpulenta*, taken from a pond at the Fairport station 16 months after the ponds were constructed, varied in length from 66 to 88 mm. (2.59 to 3.46 inches). Examples of another paper-shell, *Anodonta suborbiculata*, taken at the same time from another pond of the same age, but which may have offered less favorable conditions, were 64 to 67 mm. in length (2.52 to 2.63 inches).

With regard to heavy-shelled mussels, such as the niggerhead, pimple-back, and blue-point, there is much less satisfactory evidence as to growth. They undoubtedly grow much more slowly than mussels possessing thin shells, yet the rates of growth secured in such experiments as have been conducted can hardly be assumed to be representative of the conditions prevailing in nature. The species are not well adapted to life in tanks or ponds, and there are few places where measured specimens can be placed in rivers with any assurance that they will remain undisturbed or may be recovered at a later time. In Lefevre and Curtis's experiments (1912) an example of the hickory-nut, *Obovaria ellipsis*, that was practically full-grown when first measured, gained 5 mm. (one-fifth of an inch, 0.197) in a little less than 2½ years. In the same period an example of *Quadrula solida*, somewhat less mature, gained 10 mm. (two-fifths of an inch, 0.394).

In the following table (11) there are indicated sizes, at the close of the second year, of certain mussels reared accidentally or intentionally in ponds at the Fairport station. The short-term breeders, at least, were a little less than 1½ years of age.

Since these are all mussels of river habit, it can not be assumed that the growth attained in ponds is representative of the rate of growth in a natural environment.

TABLE 11.—SIZES AT CLOSE OF SECOND YEAR OF CERTAIN MUSSELS REARED IN PONDS, FAIRPORT STATION, IOWA.

Scientific name.	Common name.	Length.	
		Millimeters.	*Inches.*
Lampsilis ligamentina	Mucket [a]	20.0	0.79
Lampsilis anodontoides	Yellow sand-shell [b]	41.0	1.62
Obliquaria reflexa	Three-horned warty-back	16.0	.63
Obovaria ellipsis	Hickory-nut	11.4	.45
Plagiola donaciformis		20.0	.79
Quadrula plicata	Blue-point	13.5	.53
Quadrula pustulosa	Pimple-back	24.2	.69
Quadrula undata	Pig-toe	15.8	.62

[a] Other observations indicate that the mucket grows more rapidly in streams.
[b] The yellow sand-shell was only 1 year and 3 months of age.

Some medium-sized examples of several species of Quadrula were placed, after measurement, in a crate which was anchored in the Mississippi River at Fairport, September 19, 1910. When the crate was recovered and the mussels remeasured, July 31 of the following year, very little growth was apparent in most of the specimens. The data for measurements of length in the several examples are given in the following table (12):

TABLE 12.—INCREASE IN LENGTH OF MUSSELS IN CAGE.

Scientific name.	Common name.	Length, Sept. 19, 1910.	Length, July 31, 1911.	Increase in length.
		Inches.	*Inches.*	*Inches.*
Quadrula ebenus	Niggerhead	1.92	1.98	0.06
Quadrula pustulosa	Pimple-back	1.74	1.85	.11
Quadrula metanevra	Monkey-face	1.70	1.86	.16
Quadrula plicata	Blue-point	2.80	3.02	.22
Quadrula undata	Pig-toe	1.41	1.74	.33

In another experiment 76 mussels, representing 19 species, principally the thick-shelled forms, were placed in a crate with nine compartments which was anchored in the river about 25 feet from shore. The crate was put out July 31, 1911, and recovered November 14, 1913, when 36 of the original mussels, representing 13 species, were found to be alive. These mussels generally manifested a higher rate of growth than marked some of the mussels used in the experiment just described, although the increase in size was disappointingly small. The period of time between the dates of measurements was 2 years 3 months and 14 days. The mussels were of medium size at the beginning of the experiment, so that the growth to be expected was that which would characterize the period of approaching maturity rather than that of early life. The mussels living at the close of the experiment, with the maximum and minimum gain in length and the average for the species (when more than two examples were available), are shown in the following table (13):

TABLE 13.—GROWTH OF 36 MUSSELS IN CRATE FROM JULY 31, 1911, TO NOV. 14, 1913.

Scientific name.	Common name.	Examples.	Increase in length.		
			Maximum.	Minimum.	Average.
		Number.	*Inches.*	*Inches.*	*Inches.*
Quadrula ebenus	Niggerhead	7	0.64	0.38	0.463
Quadrula pustulosa	Pimple-back	5	.50	.20	.376
Quadrula pustulata	do	1	.22		
Quadrula metanevra	Monkey-face	2	.46	.12	
Quadrula plicata	Blue-point	7	.80	.32	.517
Quadrula undata	Pig-toe	2	.49	.38	
Obovaria ellipsis	Hickory-nut	4	.72	.20	.455
Obliquaria reflexa	Three-horned warty-back	1	.18		
Tritogonia tuberculata	Buckhorn	1	.36		
Lampsilis ligamentina	Mucket	2	.84	.10	
Lampsilis recta	Black sand-shell	1	1.76		
Strophitus edentulus	Squaw-foot	2	.66	.56	
Unio gibbosus	Spike	1	.17		

It must be borne in mind that the conditions of life for mussels in an inclosed crate, and relatively closely crowded together, are probably not nearly so favorable for growth for the majority of mussels as are those of the natural river bottom, where the mussel has a fair chance to assume its desired position and secures the full benefit of the food-laden current. Doubtless the maximum rate of growth shown in the crate is more nearly normal than the average rate. Our impression is that thick-shelled mussels, such as the niggerheads, pig-toes, and pimple-backs, after they are half grown, increase in size ordinarily at the rate of a quarter of an inch a year or less. If this be true, it would require four years or more for a niggerhead mussel, under ordinarily favorable conditions, to increase from a length of 2 inches to a length of 3 inches. Assuming that the rate of growth is more rapid in early life, it may be inferred that niggerheads or pimple-backs 3 inches in length are 10 or 12 years of age. Additional experiments conducted under proper conditions are clearly wanted.

A marked contrast in rate of growth is thus afforded by the species of Quadrula (and others having generally similar character of shell), on the one hand, and those of Lampsilis, on the other. This was strikingly shown, in connection with the last experiment described, by two examples of the yellow sand-shell, *Lampsilis anodontoides*, which were not put into the crate but which must have found their way in by chance when still small enough to pass through the screen wire of ½-inch mesh. Although the crate was out only a little over two years, these two sand-shells were respectively 3.30 and 4.12 inches in length. Being elongate in form, they may have entered the crate when a little more than an inch in length.

Table 14 embodies the result of measurements of length and counts of rings on yellow sand-shells, *Lampsilis anodontoides*, from the St. Francis River, at Madison, Ark.

TABLE 14.—CLASSIFICATION OF 40 YELLOW SAND-SHELLS FROM ST. FRANCIS RIVER, ARK., ACCORDING TO LENGTH AND AGE.

Length in inches.	Number each length.	Age as indicated by interruption rings on surface of shell.					Length in inches.	Number each length.	Age as indicated by interruption rings on surface of shell.				
		Three years.	Four years.	Five years.	Six years.	Older.			Three years.	Four years.	Five years.	Six years.	Older.
3	1		[a] 1				4¼	6		5	1		
3⅛	1	1					4½	3		3			
3¼	1		[a] 1				4¾	9		2	5	1	1
3½	2		2				5	5			1	2	2
3¾	4	2	2										
4	8	1	6	1			Total	40	4	22	8	3	3

[a] Shell with stunted appearance.

The observations indicate that mussels of this species in the St. Francis River attain a length of 4 to 4½ inches in 4 years, that they may attain a length of 4 inches in 3 years, and that 6 years or more are ordinarily required to attain a length of 5 inches.

In summary, the rate of increase in length of fresh-water mussels varies from 1½ or 2 inches per year for paper-shells (as *Lampsilis lævissima*) to ¼ inch (a little more or a little less) per year for the niggerhead and related species, while an intermediate rate of ¾ or 1 inch per year characterizes the muckets and pocketbooks, and a slightly more rapid rate the sand-shells. In general the rate of growth is so directly proportioned (in inverse ratio) to the thickness of shell of the species as strongly to suggest that the limiting factor of growth ordinarily is not organic food, but the mineral content of the water (p. 87).

PRESENCE OF SO-CALLED GROWTH RINGS.

The ages of animals may not infrequently be determined, at least approximately, by the "rings of growth," on teeth, scales, scutes, or otoliths (ear stones), or other hard parts of the body. A similar criterion of age determination is of course commonly applied to trees. More recently the rings on the scutes of terrapin and those on the scales and otoliths of fish have been used for the same purpose.

This method of determining age is generally based upon the belief that the cessation or the slowing down of growth during the winter season may cause the formation of a distinguishable line or band on a concentrically growing structure. By counting the number of winter lines or bands the number of winters through which the animal has passed is ascertained, or by counting the number of zones between such rings, beginning with the center zone, the number of seasons of growth is discovered. It is one thing to know that such rings are formed in winter, but quite another thing to learn just how or why the rings are formed. It is also of primary importance to determine whether or not similar rings may be formed upon any other occasion than the occurrence of a season of winter. In the case of the fresh-water mussel shell, at least, these questions can be answered by observations and experiments. (Coker, unpublished notes.)

Some years ago when collecting mussels in lakes in southern Michigan it was observed that the shells of the fat muckets were all marked with several conspicuous rings which were approximately equally spaced on all the mussels of a bed. It seemed a natural inference that these dark rings represented winter periods and thus afforded a means of age determination. At another time, upon examination of mussels which had been measured and placed in crates in the river two years previously, it was observed that there were rings apparently corresponding to the two winters which had elapsed since the date of original measurement, but that there was also another ring which marked the exact size of the mussel when originally measured. (See text fig. 6.) Subsequent observations showed that whenever a mussel was measured and replaced in the water, a ring would be formed on the shell before growth in size was resumed.

These observations led to an effort by microscopic examination of sections of the shell to determine the significance of rings which apparently could be formed either by a season of cold weather or by the procedure of taking a mussel from the water, applying a caliper rule, and returning it to the water. To make clear what was learned from the study of the sections it is necessary first to explain briefly the mode of formation of shell which leads to growth in size.

MODE OF FORMATION OF SHELL.

The shell is composed of four distinct layers (text figs. 1, 2, and 3). The outer is the horny covering called the periostracum.[a] Immediately beneath this is a calcareous layer composed of prisms of calcium carbonate set vertically to the surface. This prismatic layer is very thin, though thicker than the periostracum, and is likely to remain

[a] The fact that the periostracum itself comprises 2 layers of separate origin, while very significant in some respects, is immaterial in this connection.

attached to the periostracum when that is peeled off. Beneath the prismatic layer and composing nearly the entire body of the shell is the nacreous or mother-of-pearl layer, which is made up of almost innumerable thin laminæ lying one upon the other and parallel to the inner surface of the shell. Through the nacre, intersecting its laminæ, passes a very thin fourth layer, the hypostracum,[a] secreted by the muscles (p. 172).

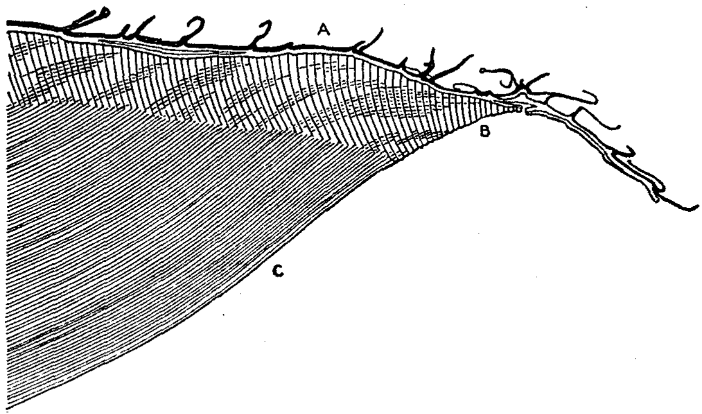


FIG. 1.—Diagrammatic and highly magnified camera lucida drawing of section of margin of fresh-water mussel shell, *Obovaria ellipsis* (Lea), showing arrangement of layers: *A*, epidermis (double layer); *B*, prismatic layer; and *C*, nacreous layer. Note the folds of epidermis which give the shell its "silky" appearance.

Growth of shell in thickness is accomplished by the laying down of successive laminæ, from the entire surface of the mantle. Layer after layer is added to the inner surface of the shell, each layer exceedingly thin and generally a little larger than the preceding. Ring after ring is added to the margin of the shell, but since growth is most pronounced in the posterior (rear) direction, less so in a ventral, and still less in the anterior (forward) direction the rings must be widest behind and narrowest in front. It will be noted that any mussel shell is marked with innumerable concentric lines. Superficially such lines suggest the annual rings seen on the section of the trunk of a tree, but the resemblance is entirely misleading. The shell is added to in layers, but a very great number of layers are made in a year. Pfund (1917) has, by refined physical methods, measured the thickness of the layers or laminæ and determined that the thickness in the examples he studied lies between 0.4 μ and 0.6 μ. Translating these terms into ordinary language, there are some 50,000 layers to an inch of thickness. A shell one-quarter of an inch thick would have 12,500 laminæ; and if such a shell were 8 years old, more than 1,500 laminæ would have been formed each year, on the average. The outcropping edges of these laminæ on the surface of a polished niggerhead shell have also been measured and found to be spaced at the rate of about 9,000 to the inch. Such lines are of course not visible to the naked eye, and therefore the fine rings in evidence on the surface of the shell can not represent these

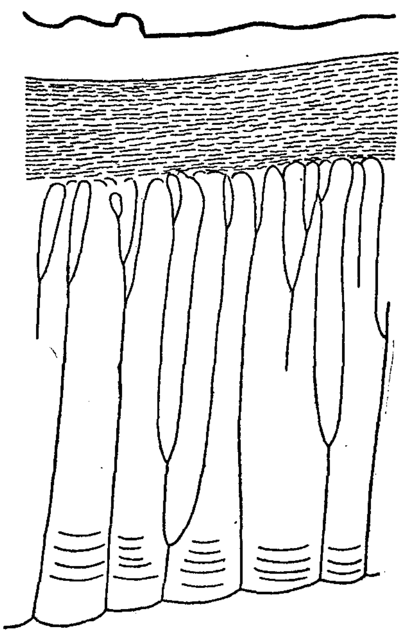


FIG. 2.—Section through double-layered periostracum and prismatic layer. Nacreous layer below not shown.

[a] Not shown in figures herewith.

laminæ but must have some other significance. They probably mean nothing more than slight and frequent but irregular retractions of the margin of the mantle during the process of shell formation, which have registered themselves in fine wrinkles on the surface of the shell as it is built. The more conspicuous rings that mark some shells still await our attention.

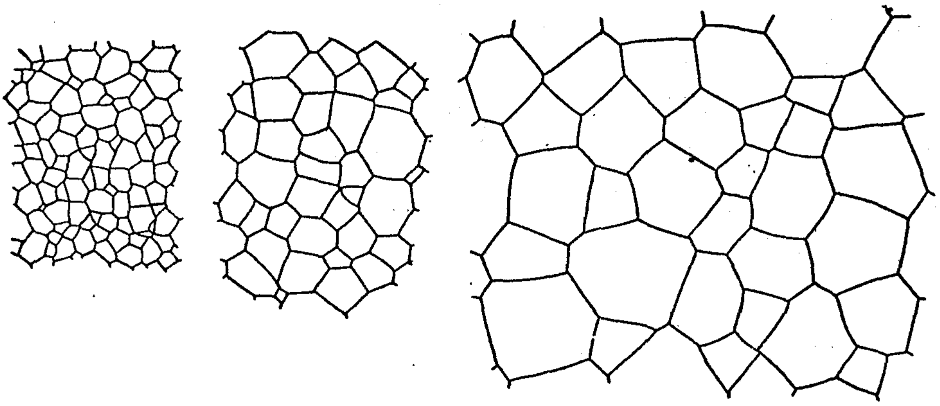


FIG. 3.—Sections through prismatic layer of *Quadrula ebenus*. The sections were made at different levels, the prisms being smaller and more numerous in the outer portion. × 300.

Growth of the shell in length and breadth is accomplished by the secretion of shell substance of the three layers by cells at or near the margin of the mantle. There are certain cells of a furrow in the margin of the mantle which form only periostracum, and there is a certain portion of the mantle near the margin which forms only prismatic shell substance, while the greater portion of the mantle surface normally forms only nacre. Now, the important point for our present consideration is this: If, from any cause, the margin of the mantle is made to withdraw within the shell to such an extent as to break its continuity with the thin and flexible margin of the shell, then, as the study of sections indicates, when the deposition of shell is resumed, the new layers

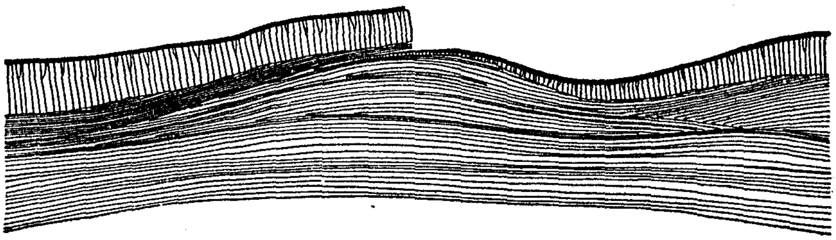


FIG. 4.—Section through the interruption ring on pocketbook mussel, caused by handling mussel in summer. Simple duplication.

of prismatic substance and periostracum are not continuous with the old, end to end, but are more or less overlapped by the old. In other words, growth does not begin again exactly where it left off, but a little distance back therefrom, and the cause of this is largely mechanical (text fig. 4). The amount of overlapping probably depends upon the degree of disturbance and the extent to which the mantle has withdrawn itself. The result is an unwonted duplication of layers. Counting inward from the outer surface we find not simply one series of periostracum, prismatic, and nacreous layers, but periostracum and prismatic layers, then periostracum and prismatic again, and finally the nacreous layer; the outer layers are doubled up.

SIGNIFICANCE OF RINGS.

In a case such as has just been described, where the outer layers are doubled up as a result of an extreme retraction of the mantle, the effect of seeing a second horny layer through the outer periostracum and the fairly translucent prismatic layer gives the appearance of a dark band on the shell. This is the so-called growth ring, which would be better termed duplication ring or interruption ring,[a] since its significance is simply that the continuity of the outer layers is interrupted and the break is repaired by overlapping. In other words, the periostracum and prismatic layers are "spliced" at this point. A duplication of layers should easily be observable on shells having fairly light-colored or translucent periostracum but not on shells having a very dark or opaque covering, and this is found to be the case. Growth rings or interruption rings are commonly seen on pocketbooks, fat muckets, yellow sand-shells, floaters, and other shells of light or only medium dark colors, while they are distinguishable with difficulty, if at all, on niggerheads, pimple-backs, blue-points, and other dark-colored shells.

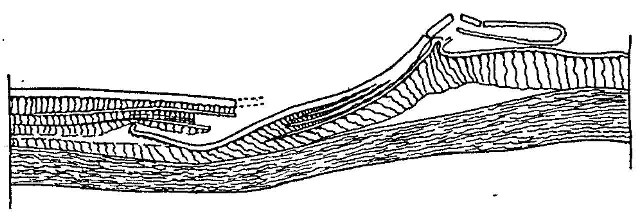


FIG. 5.—Section through interruption ring (winter ring) on shell of pocketbook, *Lampsilis ventricosa*, showing repeated duplications of periostracum and prismatic layers.

If the winter rings are formed in the same way, and the breaking of the continuity of the outer layers is due to the withdrawal of the mantle in cold weather, then it would be expected that several duplications would occur for a single winter. For cold weather does not ordinarily fall with one blow. Periods of cold and warm weather alternate for a time before winter sets fairly in, and again in the spring periods of low and high temperature alternate before winter is entirely passed. Such fluctuations of temperature are, of course, not so frequent or noticeable in the water as in the air, but they do occur. It might be expected that the mussel would react to the first sharp touch of winter by closure and a sharp withdrawal of the mantle but that the deposition of shell would be resumed after a time, while further interruptions and resumptions of growth would occur before the full effect of winter was experienced. Again in the spring there might be alternate interruptions and resumptions of growth. This, at least, is the story which seems to be told by a section through a winter ring when examined under the microscope. Text figure 5 shows such a section, where the alternation of periostracum and prismatic layers is repeated seven times, indicating six interruptions of growth. As virtually no increase in size occurs between the several interruptions, the duplicated or repeated layers are simply piled upon one another.

Interruption rings corresponding to seasons of winter differ from those corresponding to a single severe disturbance of the mussel during the normal period of growth in that the latter are rings of single duplication (text fig. 4), while the former show several repetitions (text fig. 5). The winter rings in shells that have been observed are, therefore, darker, though they may or may not be broader (text fig. 6).

[a] See Isely, 1914, p. 18.

ABNORMALITIES IN GROWTH OF SHELL.

Seriously malformed mussels are not infrequently found, and peculiar interest attaches to these because shellers generally entertain the belief that a mussel with deformed shell is most likely to contain a pearl. It seems possible that this belief is not without some foundation. Pearls probably occur more frequently in parasitized mussels, and many of the observed malformations are undoubtedly due to parasites.

A few distomids upon the mantle of Anodontas along or near the dorsal fold evidently cause rusty stains in the nacre, abnormal growths on the inner surface of the shell, deformities of the hinge teeth, and dark or poorly formed pearls. Another parasite which infests the reproductive organs may almost completely destroy the gonads of the female mussel, and in such case the female may develop a shell in the form of a male or in a form intermediate between that of the male and the female. There is evidence that parasites found encysted in the margin of the mantle may give rise to stains on the nacre at the margin of the shell, that others cause the not unfamiliar steely or leaden-colored margins of shells, while some produce a pitting of the inner surface of the shell.

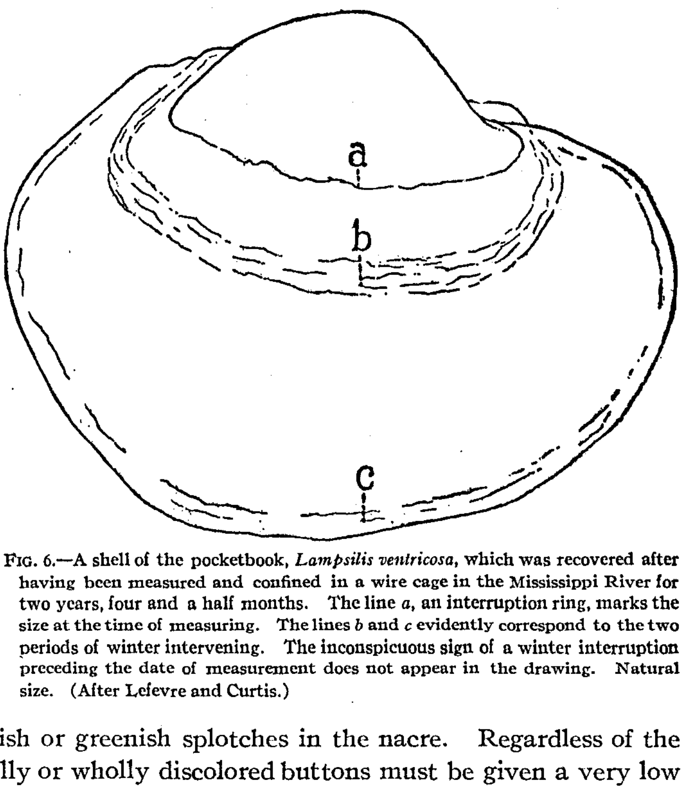
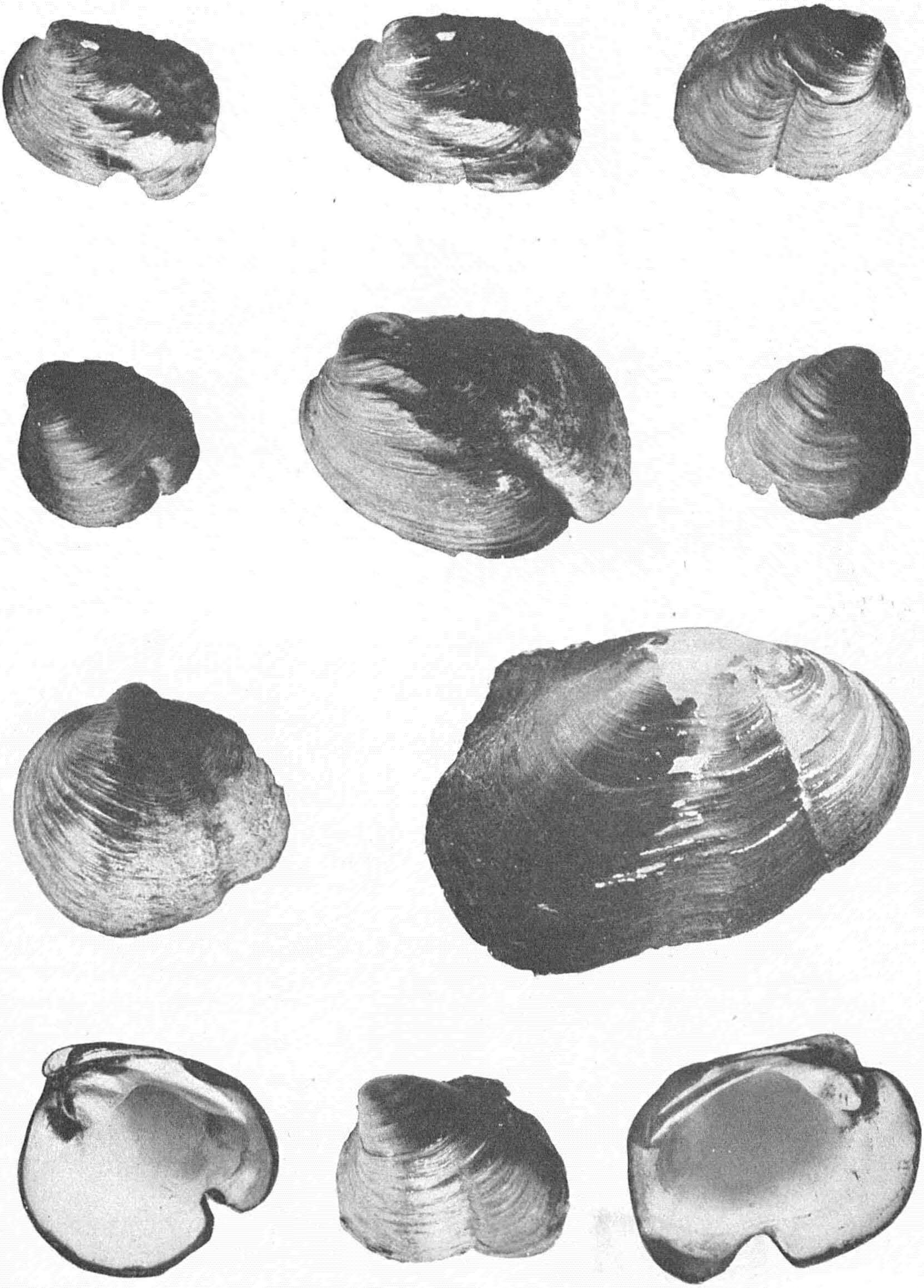


FIG. 6.—A shell of the pocketbook, *Lampsilis ventricosa*, which was recovered after having been measured and confined in a wire cage in the Mississippi River for two years, four and a half months. The line *a*, an interruption ring, marks the size at the time of measuring. The lines *b* and *c* evidently correspond to the two periods of winter intervening. The inconspicuous sign of a winter interruption preceding the date of measurement does not appear in the drawing. Natural size. (After Lefevre and Curtis.)

One of the most common and serious defects of otherwise valuable commercial shells is the presence of yellow and brown spots or bluish or greenish splotches in the nacre. Regardless of the texture of the shell, the partially or wholly discolored buttons must be given a very low grade. The spots are not always found upon the surface but may lie deep within the nacre, to be brought out in the finished button by the processes of shaping and polishing. Spotted shells are most common in certain rivers or parts of rivers, particularly where the current is sluggish as in partly inclosed sloughs. Some of these discolorations are often observed to be associated with a parasitized condition of the mussels, but it is not probable that the spots are always due to parasites. The U. S. Bureau of Standards, in connection with an investigation of the bleaching of discolored shells, has found that the dark-yellow and brown spots are mud fixed by the nitrogenous organic layer which binds together the calcium carbonate, and that the pale-yellow color is apparently due to an organic coloring matter in the organic layers. That bureau also reports that the color of the pink shells is due to an organic coloring which is not confined to the organic layer but permeates the whole shell.

A striking form of shell associated with the presence of parasites is that with abbreviated gaping anterior margins, the edges being much thickened and in appearance rolled outward. The explanation appears to be simply that the parasites check the peripheral growth of the forward portion of the mantle, or perhaps, as the result of irritation, keep the mantle more or less retracted in this portion. The shell being controlled in growth by that of the mantle, its forward extension is checked, while growth in thickness continues. Meantime the valves of the shell, growing normally in other directions, are gradually and naturally pushed apart as successive layers are added in the posterior portions. In consequence, after a time the valves of the shell cease to meet anteriorly when the posterior margins are apposed. The result is a shell of normal dimensions behind and below but abbreviated in front, where the edges are disproportionately thick and gaping.

A very familiar form of abnormality is shown by the shells in Plate XII. When a single shell of this type is first seen one is inclined to suppose that the deformity is the result of a mechanical injury; but when shells marked by almost identically the same abnormality are repeatedly found in various places and in different kinds of bottom, it becomes evident that the explanation of mechanical injury is not applicable. It is probable that a parasite checked the growth of the mantle at a particular point, so that, while growth of shell continued normally both before and behind, it was so retarded at that point that a permanently notched outline resulted. The subject of discolored and malformed shells is not introduced, however, with the object of definitely explaining them, but rather with a view to directing attention to the desirability of further investigations of the parasites of mussels, as well as of certain features of the environment of mussels, as regards their effects upon the form and quality of shells.



Illustrating a peculiar abnormality of not infrequent occurrence among fresh-water mussels.

[See text, page 139, and compare Plate XXI, fig. 1, showing marsupium occupying outer gills only. Figures after Lefevre and Curtis.]

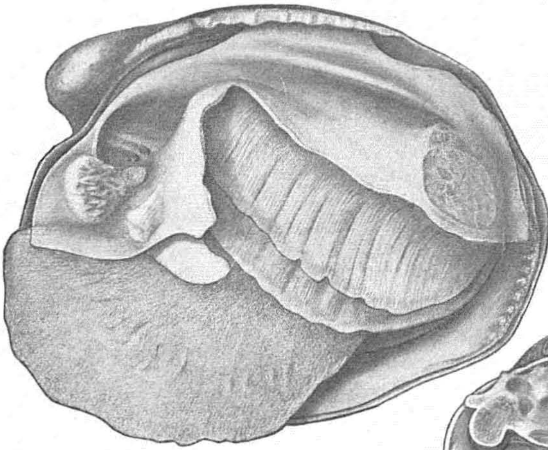


FIG. 1.—Niggerhead mussel, *Quadrula ebenus;* marsupium occupying all four gills.

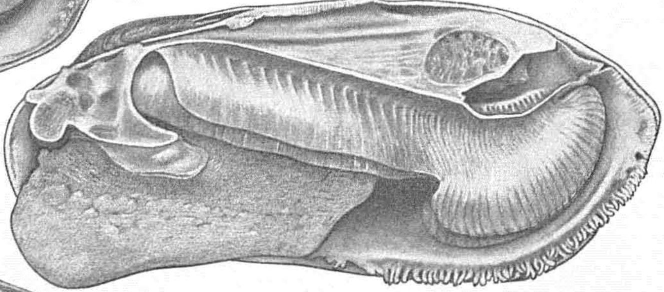


FIG. 2.—Black sand-shell, *Lampsilis recta;* marsupium occupying only posterior end of outer gills.

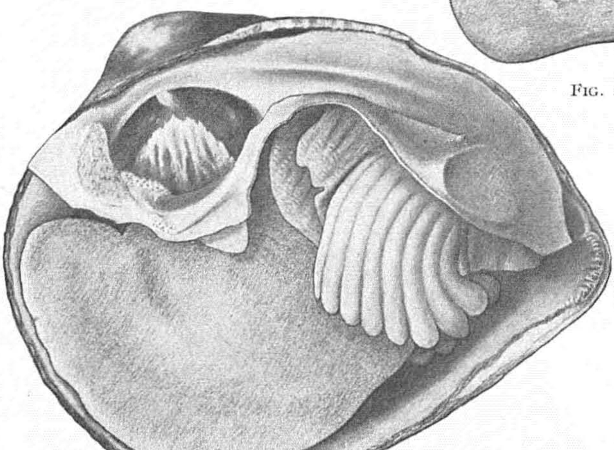


FIG. 3.—Three-horned warty-back, *Obliquaria reflexa;* marsupium occupying middle region of outer gills.

FIG. 4.—Dromedary mussel, *Dromus dromas;* marsupium occupying only lower border of outer gills. Anterior end of gill not included in marsupium but overhangs it.

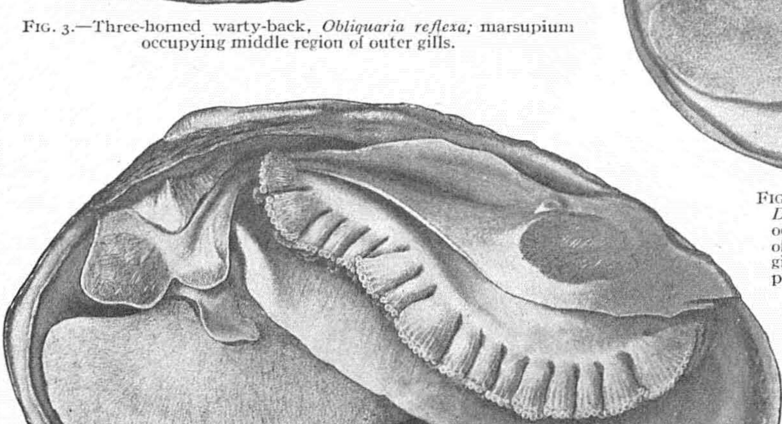


FIG. 5.—Kidney-shell, *Ptychobranchus phaseolus;* marsupium occupying entire lower border of outer gills and much folded.

PART 2. LIFE HISTORY AND PROPAGATION OF FRESH-WATER MUSSELS.

INTRODUCTION.

The life histories of fresh-water mussels present features in striking contrast to those of other familiar mollusks of our seas and rivers. The American oyster, the clam, the quahaug, and the sea mussel cast the eggs out to undergo development while floating in the water. The pearly mussels of rivers and lakes, on the contrary, deposit their eggs in marsupial pouches which are really modified portions of the gills, and there they are retained until an advanced stage of development is attained. This particular feature of breeding habit is not, however, unique to mussels. There are clams in coastal waters that incubate the eggs in the gills, and the common oyster of Europe displays a similar habit; but with all these the larvæ when released are prepared for independent life. Such is not the case with fresh-water mussels. When the larval mussels are discharged from the marsupial pouches, the mother has done all that she can for them, but they still want the services of a nurse or foster parent, as it were. Lacking the structure and appearance of young mussels, they display a peculiar form designated as glochidium, and (with few exceptions) they will not continue to live unless they become attached to some fish, upon which for a certain time they will remain in a condition of parasitism.

During the period of parasitic life the glochidium undergoes a change of internal reorganization, or metamorphosis, with or without growing in size. After the change is complete and a form somewhat similar to the adult is attained, the young mussel leaves the fish to enter upon its independent existence. At this time, or soon thereafter, some mussels, but not a great number, differ distinctly from the adult form in bearing a long, adhesive, and elastic thread, or byssus, by which they attach to plants, rocks, or other anchorage.

The life history, then, comprises the following five stages: (1) The fertilized and developing egg retained in the marsupial pouches of the mother mussel; (2) the glochidium, which, before liberation, is often retained for a considerable further period in the gills; (3) the stage of parasitism on fish (or water dogs); (4) the juvenile stage, which may or may not be marked by the possession of threads for attachment to foreign objects; and (5) the mussel stage, with the usual periods of adolescence and maturity.

Such in brief is the typical story of the life of a pearly mussel. And yet each species of mussel, and there are many, has its own characteristic story, which differs in more or less important respects from those of other species. One kind of mussel will pass through the stage of parasitism only upon a particular species of fish, while another kind acquires the aid of certain other fish. The diversity in life histories also manifests itself in such details as in the season of spawning, in the part of the gills in which the glochidia are carried, in the duration of the incubation period, in the matter of growth in size during parasitism, and in many other particulars. There are even some mussels which, like exceptions that prove the rule, undergo complete development without being parasites upon fish at any stage. It is advisable, therefore, to treat the several stages of life history at greater length and with such detail as is necessary to establish an understanding of the conditions necessary for the successful propagation of the various useful mussels and for the effective conservation of the mussel resources.

HISTORICAL NOTE.

It seems appropriate to remark that the considerable fund of knowledge which has been gained in very recent years regarding the diversified life histories of fresh-water mussels has been gained very largely as a result of scientific studies which have been stimulated by the practical need of conserving an economic resource, and which have been pursued preliminary to or in connection with the propagation of mussels as a measure of conservation. To put it in another way, the development of the fresh-water pearl-button industry has furnished an effective stimulus to biological studies of high scientific interest and importance, just as the application of science to studies of commercial mussels has rendered a distinct economic service.

As early as 1695 at least, the glochidium (see text fig. 8, p. 143) was observed in the gills of European mussels, and was understood to be the larval form of the mussel, although it was not then called a glochidium. Of the further stages of life history, science, as well as the public, remained in ignorance for a long time. So wide indeed was the gap of knowledge that it became possible for a scientific writer in 1797 to advance the theory that the little mollusks noted in the gill pouches were not young mussels, but were parasites of mussels constituting a genus and species of their own, which the investigator designated with the Latin name *Glochidium parasiticum.* This view, known as the Glochidium theory, though it never won full acceptance, was strongly supported, and an exhaustive inquiry and report upon the subject by a special committee of the Academy of Sciences in Paris, completed in 1828, failed to effect its decisive defeat. When, however, in 1832, Carus was fortunate in observing the passage of the eggs from the ovary of the mussel into the gill pouches, the false theory was definitely overthrown. The name glochidium, suggested though it was by an erroneous assumption, has persisted ever since, being now correctly understood to designate not a distinct animal but a typical stage in the development of the mussels.

It still remained to determine how and where this peculiar larva became transformed into the familiar adult mussel, and this important gap was abridged by Leydig, in 1866, when the glochidium was discovered in parasitic condition upon the fin of a fish.

The advance in knowledge of the life history of fresh-water mussels made in the ensuing decades was slow and inconspicuous, and textbooks, both American and foreign, continued to reproduce accounts based upon the inadequate observations of the life histories of European mussels. A period of distinct progress came with the extensive and admirable investigations conducted by Lefevre and Curtis (1910, 1910a, and 1912) in association with the Bureau of Fisheries during the years 1905 to 1911. These investigations served to reveal not only some of the distinctive features of the breeding habits and life histories of the American mussels as contrasted with the European species but also the great diversity existing among the many American species, in breeding season, period of incubation, and form of glochidia. The results of the investigations aggregated a mass of original observation on various phases of the propagation and life history of fresh-water mussels. Other investigations, notably Ortmann's (1911, 1912, etc.), have contributed materially to knowledge of the breeding characters and habits and the development of mussels, while Simpson (1899, 1900, 1914, etc.), Walker (1913, 1918, etc.), Ortmann (1911, 1912, 1913, etc.), and others have greatly extended our information regarding classification, distribution, and structure.

With the establishment of the Fisheries Biological Station at Fairport, Iowa, and the beginning of its scientific work in 1908, the studies pursued by the scientific staff of that station, in connection with the propagation of mussels, made still further advances. Chief among the results of the studies conducted at this station may be mentioned the discovery that particular species of mussels are restricted in parasitism to one or a few species of fish, the rearing of young mussels in quantity from artificial infections upon fish, the demonstration that the glochidia of certain species of mussels may grow materially in size during the period of life on the fish (being, therefore, true parasites), and the observation that one noncommercial species of fresh-water mussel normally completes its life history without a stage of parasitic life.[a]

Finally it should be remarked that one of the most difficult of all gaps to bridge was the rearing of young mussels after they leave the fish. Strange as it may seem, all attempts to keep alive and to rear the young mussels under conditions of control failed of result. Lefevre and Curtis (1912, pp. 182, 183) recorded the rearing from an artificial infection of a single young mussel which attained a size of 41 by 30 mm. In 1914, however, Howard was successful in rearing over 200 Lake Pepin muckets from an artificial infection, when the infected fish were retained in a small floating basket in the Mississippi River (Howard, 1915). These mussels attained a maximum size of 3.2 cm. in the first season; and in subsequent years many of them were reared to maturity, the glochidia developed from their eggs were infected upon fish, and a second generation was reared to an advanced stage. In that year (1914), too, Shira, using watch glasses and balanced aquaria, reared a few mussels from an artificial infection to a maximum size of 0.44 cm. in 291 days. In the same year, though from an experiment initiated by the senior author in the fall of 1913, young mussels were reared in a pond, from an artificial infection of fish liberated in the pond, to a maximum size in the first season of 3.5 cm. Some of these mussels at the age of 4 years had attained sizes suitable for commercial use in the manufacture of buttons. The same species, *Lampsilis luteola* (Lamarck), known as the Lake Pepin mucket, was used in all of these experiments. Subsequent experiments on a larger scale conducted both at Fairport and in Lake Pepin are mentioned on a later page.

AGE AT WHICH BREEDING BEGINS.

The age at which mussels begin to breed varies with the species. There is reason to believe that the paper-shell, *Lampsilis (Proptera) lævissima*, breeds in the same summer during which it leaves its host or when just 1 year of age from the egg. *Anodonta imbecillis* and *Plagiola donaciformis* apparently breed in the second summer. The smallest breeding Quadrula observed was a pig-toe, *Quadrula undata*, 30 mm. (about 1.2 inches) in length, and 4 or 5 years of age as evidenced by the interruption rings. The smallest washboard, *Quadrula heros*, observed in breeding condition was 91 mm. (3.58

[a] Lefevre and Curtis (1911) had previously observed and reported the fully developed juvenile mussels in the gills of *Strophitus edentulus*. Later, Howard (1914) while showing that the glochidia of that species will become parasitic on fish and undergo development under the usual conditions, discovered that another species, *Anodonta imbecillis*, normally develops without the aid of fish. (See p. 156, below.)

inches) in length and of an estimated age of 8 years. Females of the Lake Pepin mucket, *Lampsilis luteola*, reared at the U. S. Fisheries Biological Station, Fairport, Iowa, were found with mature glochidia in the third season of growth, a period of slightly more than two years after dropping from the fish. Undoubtedly not all species breed at such an early age, and it perhaps takes the heavier Quadrulas 6 or 8 years to reach the breeding age.

OVULATION AND FERTILIZATION.

With a few exceptions,[a] the sexes are separate in American species of fresh-water mussels. The discharge of eggs (ovulation) has been observed in some instances (Latter, 1891; Ortmann, 1911, p. 298; and Howard, 1914, p. 35). The eggs pass from the ovaries by way of the oviduct, through the small genital aperture into the cloaca and suprabranchial chambers, and then into the portions of the gills which are to serve as brood pouches. The sperm which has been thrown out into the water by one or more male mussels, doubtless those in the near vicinity of the female, is taken in by the female with the respiratory current, but whether the eggs are fertilized while on the way to the brood pouches or after reaching them is unknown, since the process of fertilization in nature has never been observed. We have no clue either as to the nature of the stimulus which may excite ovulation or as to how it may be timed so as to take place when a supply of living sperm is available in the water for the fertilization of the eggs. Certain it is that the eggs are usually fertilized, although in the brood pouches of any gravid mussel that may be examined there are found a good many eggs that have failed to develop, presumably because they have escaped fertilization.

The discharge of sperm in great quantities may not infrequently be observed when male mussels are retained in aquaria. The writers have observed in a large tank at the Fairport station a male mussel discharging sperm. During the process it traveled extensively over the bottom, leaving in the sand a long winding furrow which was filled with a white cloud of sperm. Perhaps the discharge of sperm and its introduction with the respiratory current into the female constitute the exciting cause of ovulation. Experiments are clearly wanted to determine this question. The arrangement of the eggs in the several chambers of the brood pouches varies according to the character of the pouch, and will therefore be more conveniently described in the following section.

BROOD POUCHES OR MARSUPIA.

The gills of mussels, as of other lamellibranch mollusks, are thin flaps that hang like curtains from each side of the body, a pair on each side. As explained in another place (p. 175) each gill, thin as it may appear, is really a double structure, or more correctly is a sheet folded upon itself just as a map, larger than the page of a book in which it is bound, is folded on itself. There is this difference; the map may be unfolded at will, but the gill may not, because the two sections are attached together by many parallel partitions which divide the narrow space between the sheets into a lot of long slender tubes. It is into these tubes that the eggs are deposited, and when filled with eggs or glochidia the several tubes are greatly distended (text fig. 7). The entire gills or the parts of the gills bearing the eggs then appear not as thin sheets but as thick

[a] The known exceptions are, occasionally, *Quadrula rubiginosa* and *pyramidata*, and *Lampsilis parva*, and, usually, *Anodonta imbecillis* and *henryana* (Sterki, 1898), and *Symphynota compressa* and *viridis* (Ortmann, 1911, p. 308).

pads. In this condition the marsupial pouches might be compared to pods filled with closely packed beans, the individual beans representing not single eggs but separate masses of eggs.

When the tubes of a mature female mussel are empty the gills may be as flat as those of the males, or they may appear as sacks with thin translucent walls. The latter condition generally characterizes the long-term breeders, in which the portions of the gill intended to receive the eggs are permanently enlarged.

The marsupia are conspicuously colored in some species, but in different species the coloration is not necessarily attributable to the same cause. In the niggerhead, *Quadrula ebenus*, the pig-toe, *Quadrula undata*, and other species, the bright-red appearance of the marsupia is due to the deeply colored eggs showing through the thin walls of the marsupia. In the yellow sand-shell, *Lampsilis anodontoides*, the pocketbook, *Lampsilis ventricosa*, and the Lake Pepin mucket, *Lampsilis luteola*, the pigment lying in the outer walls of the ovisacs takes the form of dark bands on the lower portion of the marsupium, the pigmentation becoming more dense and conspicuous when the mussels are gravid. In the young *Lampsilis ellipsiformis* that we have seen the pigmentation is more intense and more general, extending even to the upper portion of the marsupia, but there restricted to the partitions separating the ovisacs. The color in the black sand-shell, *Lampsilis recta*, and the Missouri niggerhead, *Obovaria ellipsis*, is white or cream, in contrast to the yellowish color of the remainder of the ovisacs.

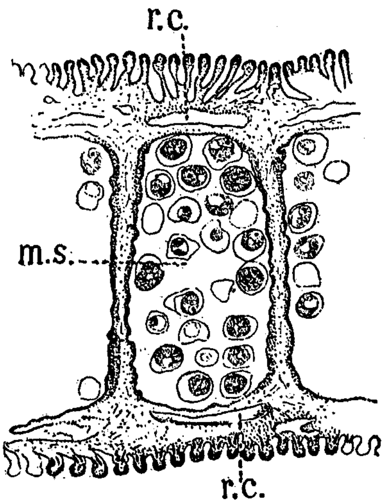


FIG. 7.—Horizontal section of a water tube of a gravid marsupium, showing respiratory canals (*r. c.*), and marsupial space (*m. s.*), containing glochidia. (After Lefevre and Curtis.)

The extent to which the gills are specialized or modified to receive and retain the eggs while they are developing into the glochidia has been largely utilized in the classification of mussels. All of the North American species belong to the groups in which the brood pouch or marsupium comprises either all four gills or only the outer gills. This group, in turn, is divided into the following seven divisions, according to the specializations involved (Simpson, 1900, p. 514):

1. Marsupium occupying all four gills, as in the niggerhead mussel, *Quadrula ebenus*, and perhaps all Quadrulas (Pl. XIII, fig. 1).
2. Marsupium occupying the entire outer gills, as in the heel-splitter, *Symphynota complanata* (Pl. XXI, fig. 1).
3. Marsupium occupying the entire outer gills, but differing from the second in that the egg masses lie transversely in the gills, as in the squaw-foot, *Strophitus edentulus*.
4. Marsupium occupying only the posterior end of the outer gills, as in the black sand-shell, *Lampsilis recta*, etc. (Pl. XIII, fig. 2).
5. Marsupium occupying a specialized portion in the middle region of the outer gills, as in the three-horned warty-back, *Obliquaria reflexa* (Pl. XIII, fig. 3).
6. Marsupium occupying the entire lower border of the outer gills in the form of peculiar folds, as in the kidney-shell, *Ptychobranchus phaseolus* (Pl. XIII, fig. 5).
7. Marsupium occupying the lower border only of the outer gills, but not folded, as in the dromedary mussel, *Dromus dromas* (Pl. XIII, fig. 4).

Most of the commercial species belong to the first and fourth types.

With such species as have all four gills, or the entire outer gills serving as marsupia, the sexes are scarcely, if at all, distinguishable from an examination of the shell; but when a distinct portion of the outer gill is used as a brood pouch there is usually a pronounced inflation of the shell over the region of the marsupia, so that the female mussel is clearly marked on the exterior. (See also Grier, 1920.)

It is to be remarked that the eggs packed into the water tubes or marsupial chambers do not usually remain free of each other, but become either attached together by their adhesive membranes or else embedded in a common mucilaginous substance. When the eggs or glochidia are removed from the gills they do not separate from one another unless fully ripe, but remain in large masses which conform to the shape of the tubes from which they have been removed[a] (Pl. XIV, figs. 8–11). It occurs frequently when gravid mussels are disturbed that the eggs, in whatever stage of development they may be, are aborted or discharged into the water. This not infrequently happens in aquaria, and doubtless may occur in nature. Abortion is presumed to be due to a deficiency of dissolved oxygen in the water; the mussel, beginning to suffocate, discharges the eggs in order to employ its gills more effectively for respiration.

SEASONS OF DEPOSITION OF EGGS.

We must distinguish with fresh-water mussels the seasons when eggs are matured, passed out of the body, and deposited in the marsupial pouches from the season when the developed glochidia are cast out into the water. The term "spawning season" might be misleading, because it is commonly used to refer to the occasion when the glochidia are discharged to the exterior, and this may be weeks, months, or sometimes nearly a year after the eggs are actually extruded from the reproductive organs and the young are launched into existence. In general, the deposition of eggs—the actual spawning process, scientifically speaking—occurs with the long-term breeding class (see below) in the latter part of the summer or early fall. In the short-term breeding class spawning usually takes place in June, July, or August, although in one or two species it is known to occur as early as April. One mussel, the washboard, deposits eggs only in the late summer and early fall, August to October.

It is the experience of the Fisheries Biological Station at Fairport that the spawning seasons of mussels fluctuate to some degree in different years, no doubt because the ripening of mussels is affected by varying conditions of water temperature. There are also, of course, some differences of breeding season corresponding to differing climatic conditions in more northern or more southern waters.

SEASONS OF INCUBATION OF EGGS.

Generally speaking, fresh-water mussels may be divided into two classes with respect to their breeding seasons—the long-term breeders and the short-term breeders.

In the case of the long-term breeders the eggs are fertilized during the middle or latter part of the summer and, passing into the brood pouches, develop into glochidia, which are usually matured by fall or early winter. The glochidia may pass the entire winter in the brood pouches, to be expelled during the following spring and early summer. As might be expected, there is some overlapping of successive breeding seasons; females

[a] Exceptions to this rule are noted by Ortmann (1911, p. 299). In such cases (the genera Anodonta, Anodontoides, Symphynota, and Alasmidonta) the eggs or glochidia are entirely separate from one another and flow out freely when the ovisac is opened.

that have discharged the glochidia quite early in the summer may already have the brood pouches filled with eggs for the next season, while other mussels of the same species are still retaining the glochidia developed from eggs of the past year. This fact is obviously favorable to the work of artificial propagation, rendering it possible to obtain glochidia of certain species of mussels at any time during the year. Thus in Lake Pepin, a widened portion of the Mississippi River between Minnesota and Wisconsin, where the Lake Pepin mucket or fat mucket is being propagated on a large scale by the Bureau, a sufficient number of gravid mussels can be obtained for carrying on the operations from the time they are commenced in May until they are terminated in October or November.

In the case of the short-term breeders the breeding activities are restricted to a season of about five months, from April to August, inclusive. The period of incubation for any individual mussel of this class is undoubtedly very much shorter, although temperature or other conditions may cause the period of incubation to be lengthened or shortened.

In Tables 15 and 16 there are listed the more common species of mussels with indication of the months in which females have been found with mature glochidia. The lack of a record of gravidity may, of course, be due in some cases not to an actual gap in the breeding season but to the want of opportunity for sufficient observation of the species during a particular month. (See also Ortmann, 1909; Lefevre and Curtis, 1912; and Utterback, 1916.)

The commercial and noncommercial species are grouped in different tables, not only because the records are more complete for the former but because those who are concerned with the conduct or regulation of the mussel fishery will be interested almost exclusively in the mussels of direct economic importance.

TABLE 15.—THE MORE IMPORTANT COMMERCIAL MUSSELS, WITH INDICATION OF MONTHS DURING WHICH FEMALES HAVE BEEN FOUND WITH MATURE GLOCHIDIA.

Scientific name.	Common name.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Cyprogenia irrorata	Fan-shell										(?)	x	
Dromus dromas	Dromedary mussel										x	x	
Lampsilis anodontoides	Yellow sand-shell	x	x	x	x	x	x	x	x	x	x	x	x
Lampsilis fallaciosa	Slough sand-shell				x	x	x	x	x	x	x	x	x
Lampsilis higginsii	Higgin's eye					x				x			
Lampsilis ligamentina	Mucket		x	x	x	x	x	x	x	x	x	x	x
Lampsilis luteola	Fat mucket	x	x	x	x	x	x	x	x	x	x	x	x
Lampsilis recta	Black sand-shell			x	x	x	x	x	x	x	x	x	x
Lampsilis ventricosa	Pocketbook	x	x	x	x	x	x	x	x	x	x	x	x
Obliquaria reflexa	Three-horned warty-back				x	x	x	x	x				
Obovaria ellipsis	Hickory-nut		x		x	x	x		x	x	x	x	x
Plagiola securis	Butterfly		x			x	x	x	x	x	x	x	
Pleurobema æsopus	Bullhead					x	x	x					
Ptychobranchus phaseolus	Kidney-shell								x	x	x	x	
Quadrula cylindrica	Rabbit's foot						x	x					
Quadrula ebenus	Niggerhead				x	x	x	x	x	x			
Quadrula heros	Washboard	x	x	x						x	x	x	x
Quadrula lachrymosa	Maple-leaf				x	x	x	x	x				
Quadrula metanevra	Monkey-face				x	x	x	x					
Quadrula obliqua	Ohio River pig-toe				x	x	x	x	x				
Quadrula perplicata	Round Lake					x	x	x					
Quadrula plicata	Blue-point					x	x	x	x				
Quadrula pustulata	Pimple-back						x	x					
Quadrula pustulosa	do						x	x	x				
Quadrula rubiginosa						x	x	x	x				
Quadrula solida						x	x						
Quadrula undata	Pig-toe						x	x	x	x			
Quadrula undulata	Three-ridge					x	x	x					
Symphynota complanata	White heel-splitter	x		x	x	x	x			x	x	x	x
Tritogonia tuberculata	Buckhorn				x	x	x						
Unio crassidens	Elephant's ear				x	x	x						
Unio gibbosus	Lady-finger					x	x	x	x				

TABLE 16.—SOME NONCOMMERCIAL MUSSELS, WITH INDICATION OF MONTHS DURING WHICH FEMALES HAVE BEEN FOUND WITH GLOCHIDIA.

Scientific name.	Common name.	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
Alasmidonta marginata	Elk-toe									x			
Anodonta cataracta												x	
Anodonta corpulenta	Slop-bucket	x			x						x	x	
Anodonta grandis	Floater	x	x	x						(?)			x
Anodonta imbecillis	Paper-shell	x	x	x		x	x	x	x	x	x	x	x
Anodonta implicata										x	x		
Anodonta stewartiana												x	
Anodonta suborbiculata	Paper-shell	x	x										x
Arcidens confragosus	Rock pocketbook	x								x		x	
Gonidea angulata							x						
Hemilastena ambigua										x	x		
Lampsilis alata	Pink heel-splitter	x	x	x		x	x	x	x	x	x	x	
Lampsilis borealis										x			
Lampsilis capax	Pocketbook						x	x	x	x			
Lampsilis gracilis	Paper-shell	x	x		x	x	x	x	x		x	x	x
Lampsilis iris	Rainbow-shell						x						
Lampsilis ellipsiformis						x	x						
Lampsilis lævissima	Paper-shell	x		x	x		x	x	x	x		x	
Lampsilis lienosa						x				x			
Lampsilis parva							x						
Lampsilis subrostrata							x			x			
Lampsilis texasensis						x							
Lampsilis ventricosa satura						x	x						
Plagiola donaciformis						x		x					
Plagiola elegans	Deer-toe					x		x					
Ptychobranchus phaseolus	Kidney-shell								x				
Quadrula cooperiana							x	x	x				
Quadrula granifera	Purple warty-back							x					
Strophitus edentulus	Squaw-foot			x	x	x	x		x	x	x	x	
Symphynota costata	Fluted shell									x	x		
Symphynota compressa										x			
Truncilla arcæformis	Sugar-spoon										x		
Truncilla capsæformis	Oyster mussel										x		
Unio tetralasmus						x							

It will be observed that, generally speaking, the several species of Quadrula and Unio, as well as *Pleurobema æsopus* (bullhead), *Tritogonia tuberculata* (buckhorn), and *Obliquaria reflexa* (three-horned warty-back) are short-term breeders, while the species of Lampsilis, as well as *Obovaria ellipsis* (hickory-nut), and *Symphynota complanata* (white heel-splitter), *Plagiola securis* (butterfly), and others are long-term breeders. Most interesting is the case of the washboard, *Quadrula heros*, which, from its taxonomic position, would be expected to have the short summer breeding season, but which at least simulates the long-term breeders. The glochidia become mature from early autumn to winter, apparently varying with the latitude, but so far as known are not held for a long period after maturity. They react like the short-term summer breeders when removed from the water in that they quickly abort the contained glochidia. It may be either that its relationship has been incorrectly appraised or that it represents a transition stage from the short-term to the long-term breeding class. Certainly it is the one species of mussel subjected to close study which has never been found to have either eggs or glochidia in its gills during the summer months.

Finally, it may be remarked that the terms "short-term" and "long-term," as applied to the breeding season, are perhaps inappropriate and misleading. So far as we know, in all species (except the washboard, in one respect) the development of the egg into the glochidium follows promptly on ovulation, occupies a period of a very few weeks, and occurs during warm weather. The short-term breeders are those which throw out the glochidia at once, while the long-term breeders carry them over until the following year. It seems to be a general rule that the short-term breeders pass through all phases of reproductive activity on a rising temperature, while the long-term breeders begin their breeding activities on falling temperatures of one season, but discharge the glochidia on rising temperatures of the following season.

Several experiments have shown that the glochidia taken from long-term breeders in the fall of the year may be successfully infected upon fish and that the young mussels will undergo development. It appears, however, that these "green" or newly formed glochidia require a longer period of parasitism than those which have been nursed by the parent through the winter season (Corwin, 1920).

The origin and purpose of the retention of glochidia during the winter season remains a mystery. This may be an instance of nature's remarkable adaptations, permitting the development of the egg to occur during the warmer months of summer, and the glochidia to be discharged for attachment upon fish in the spring when there is a general tendency toward an upstream movement of fishes. It is distinctly interesting to note that the long-term breeders (mucket, sand-shells, etc.), as a general rule are mussels of much more rapid growth than the short-term breeders (niggerhead, pimpleback, etc.), although the young of the former are delayed for nearly a year in becoming attached to fish and completing their metamorphosis.

It is important to point out one fact which is clearly established by data in Table 15, page 141. There is no month of the year in which a considerable number of commercial mussels are not gravid with glochidia. This fact deserves careful consideration in connection with measures of conservation, since it makes impracticable the protection of mussels by "closed seasons" of months based upon the times of breeding.

GLOCHIDIUM.

The larval mussel or glochidium, when completely developed and ready to emerge from the egg membrane and before attaching itself to a fish, has apparently an extremely simple organization. The soft mass of flesh possesses neither gills nor foot nor other developed organ characteristic of the adult mussel, but it bears a thin shell composed of two parts which are much like the bowls of tiny spoons hinged together at the top (text fig. 8). The two parts or valves of the shell can be drawn together by a single adductor muscle, but, when the muscle is relaxed, they gape widely apart as shown in the illustration. There are also on the inner surface of each side of the body several pairs of "sensory" cells with hairlike projections. It has been assumed that the cells were sensory in function, and recently L. B. Arey, working at the Fairport station, determined after detailed experiments upon several species of Lampsilis and Proptera that there is a well-developed sense of touch centralized in the hair cells. He regards the tactile response as entirely adequate to insure attachment of the glochidium.

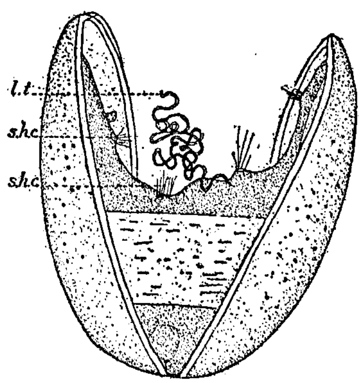


FIG. 8.—Glochidium of *Quadrula heros* with gaping valves, seen from a side view. The larval thread (*l. t.*) is seen between the valves. Inner and outer sensory hair cells (*s. h. c.*) are visible on each valve.

In at least three genera of American mussels (several species of Unio, Anodonta, and Quadrula) the glochidium possesses a peculiar larval thread of uncertain significance (text fig. 8). This thread, so generally mentioned in textbooks based upon studies of European mussels, is not found on the great majority of American species. We have observed it on glochidia of the following species: The washboard, *Quadrula heros*, the blue-point, *Q. plicata*, the pig-toe, *Q. undata*, the bullhead, *Pleurobema æsopus*, the spike, *Unio gibbosus*, the slop-bucket, *Anodonta corpulenta*, and the river pearl mussel, *Margaritana margaritifera*. The squaw-foot, *Strophitus edentulus*, has a modified larval thread (Lefevre and Curtis, 1912, p. 173).

That the structure of the glochidium is less simple than appears to the ordinary observer is shown by the fact that, in the fully developed glochidium, close microscopic study will reveal the rudiments of foot, mouth, intestine, heart, and other organs which will not, however, assume their destined form and functions until after the period of parasitism. The shell of the glochidium is firm but somewhat brittle owing to the carbonate of lime of which it is partly composed. If the lime is dissolved out with acid, the remaining shell, composed only of cuticle, preserves its general form, although it becomes wrinkled and collapsible.

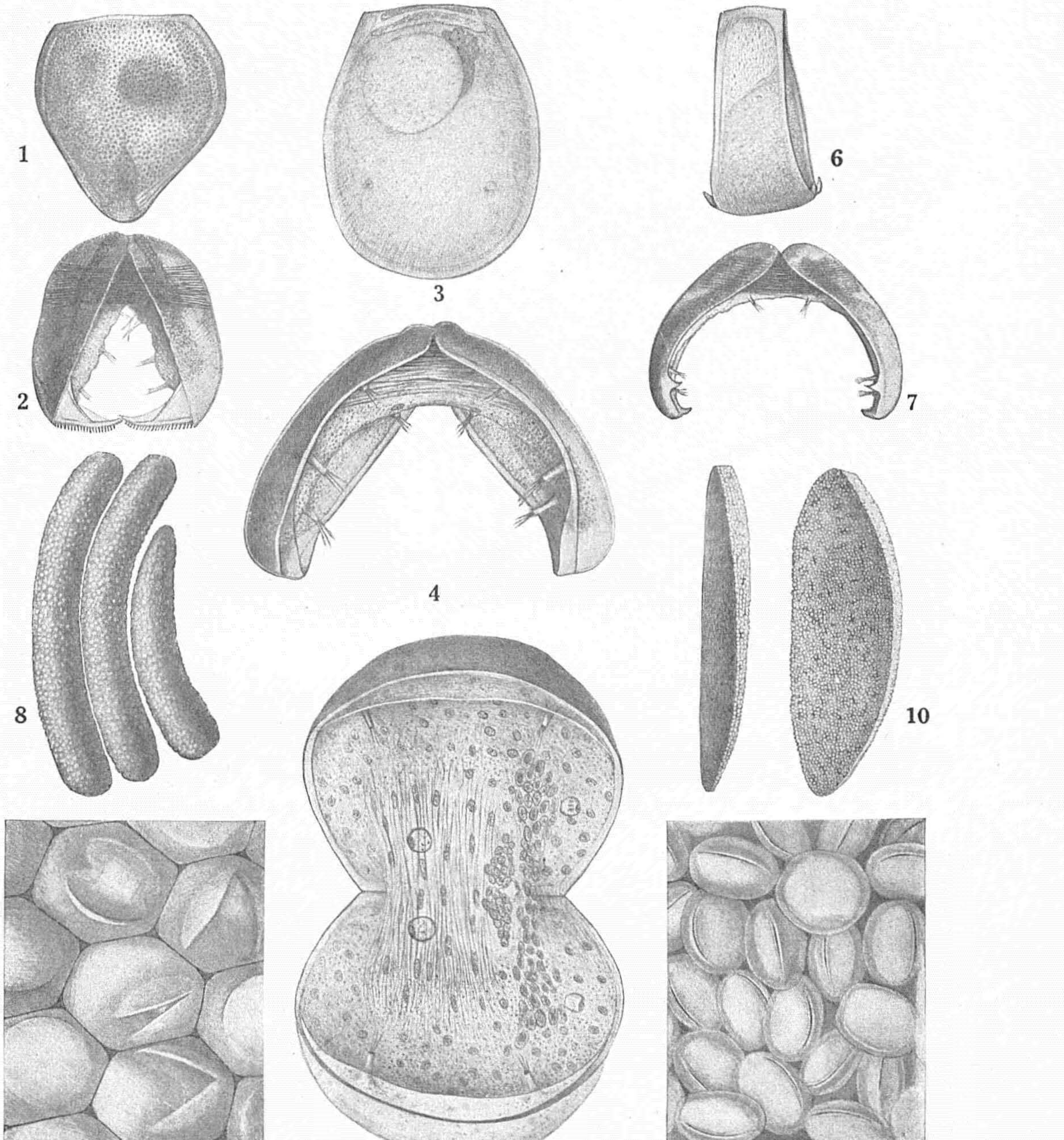
The number of glochidia borne in the brood pouches of a fully grown female mussel according to the counts and computations made by various observers, varies in the different species from about 75,000 to 3,000,000. An example of the paper-shell, *Lampsilis gracilis*, yielded by computation 2,225,000 glochidia. The mussel was 7.4 cm. (about 3 inches) in length. Several examples of the Lake Pepin mucket yielded glochidia in the following numbers, the length of the mussel being indicated in parentheses: (6.1 cm.) 79,000; (7 cm.) 74,000; (7.4 cm.) 125,000; (8.5 cm.) 129,000.

The glochidia of mussels are very diverse in size and form, although for any given species the dimensions and shape of the glochidium have been regarded as fairly constant (Surber, 1912 and 1915). Differences in sizes of glochidia within the species are noted by Ortmann (1912 and 1919)[a] and Howard (1914, p. 8). The matter requires investigation. As regards their form, glochidia are separable into three well-known types: (1) the "hooked" type, (2) the "hookless" or "apron" type, and (3) the "ax-head" type.

(1) The "hooked" type (Pl. XIV, figs. 1 and 2) possesses a rather long stout hinged hook at the ventral margin of each triangular or shield-shaped valve. These glochidia are usually larger than those of the other two types and the shell is considerably heavier. The hooks are provided with spines which no doubt assist the glochidium in retaining its hold upon the host. As all hooked glochidia generally (though not invariably) attach to the exterior and exposed parts of the fish, the fins and scales, the advantage of the heavier shell and stout hooks may readily be seen. This type of glochidium is possessed by mussels of the genera Anodonta, Strophitus, and Symphynota (floaters, squaw-foot, and white heel-splitter, etc.). (See also text figs. 9 and 12.)

(2) The shells of glochidia of the "hookless" type (Pl. XIV, figs. 3, 4, and 5), while lighter than those of the hooked type, are nevertheless of sufficient strength to withstand considerable rough handling. So far as we now know, all the glochidia of this type are gill parasites with the exception of the washboard, *Quadrula heros*, which has been successfully carried through the metamorphosis on both gills and fins. The hookless glochidia vary rather widely in shape and in size (text figs. 9 to 12); among the smallest is that of the spectacle-case, *Margaritana monodonta* (0.05 by 0.052 mm).; while one of the largest is that of the purple pimple-back, *Quadrula granifera* (0.290 by 0.355 mm.). Placed side by side, about 500 of the smallest or about 80 of the largest

[a] Ortmann gives many cases of small discrepancies between his measurements and those of others, based no doubt upon the different sources of material. In several cases he has observed differences in sizes of glochidia from different individuals. See papers in the Nautilus, Vol. XXVIII, 1914, and Vol. XXIX, 1915. In one instance he reports glochidia of two sizes from one individual (1912, p. 353). See also Surber, 1912, p. 4.



[Figures from Lefevre and Curtis, 1912.]

FIGS. 1 and 2.—Hooked glochidium of *Symphynota costata*.

FIGS. 3, 4, and 5.—Hookless glochidium of *Lampsilis subrostrata*.

FIGS. 6 and 7.—Ax-head glochidium of *Lampsilis* (*Proptera*) *alata*.

FIG. 8.—Conglutinates (masses of glochidia) from the three-horned warty-back, *Obliquaria reflexa*.

FIG. 9.—Portion of conglutinate of *Obliquaria reflexa*, magnified. Glochidia still within egg membranes which are closely pressed and adhering together.

FIG. 10.—Conglutinates (masses of glochidia) from the mucket, *Lampsilis ligamentina*.

FIG. 11.—Portion of conglutinate of *Lampsilis ligamentina* magnified. Glochidia inclosed in membranes are embedded in a mucilaginous matrix.

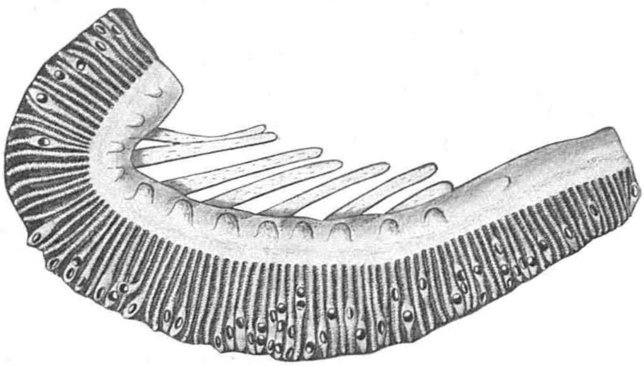


FIG. 1.—Gill of a black bass infected with glochidia of mucket, *Lampsilis ligamentina*.

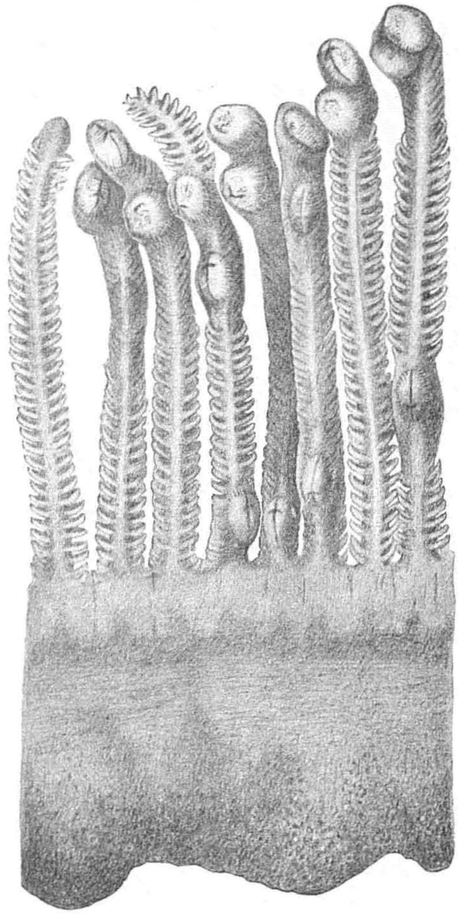


FIG. 2.—Part of fig. 1, enlarged.

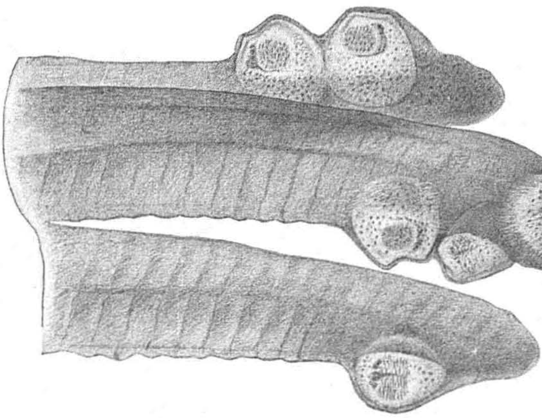


FIG. 3.—Three gill filaments of rock bass, with glochidia of mucket.

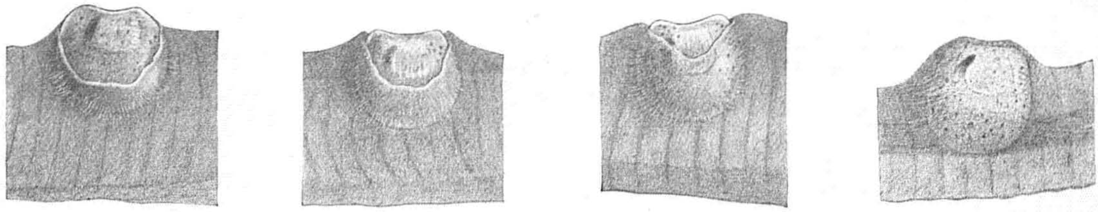


FIG. 4.—Stages in formation of cyst surrounding a glochidium of the mucket. Taken at 15 minutes, 30 minutes, 1 hour, and 3 hours, respectively, after infection.

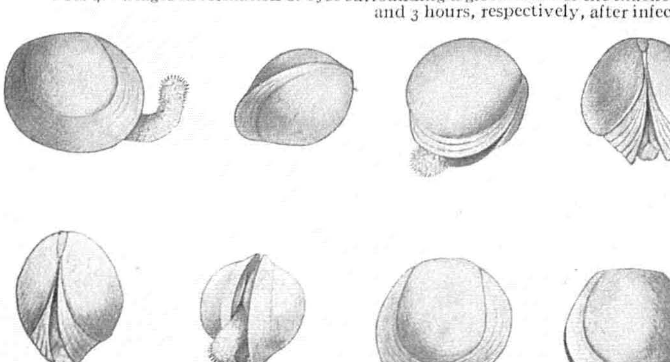


FIG. 5.—Young muckets, one week after liberation from the fish, showing new growth of shell, cilia on foot, and positions assumed in crawling. Enlarged.

FIG. 6.—Young Lake Pepin muckets at ages of 1, 2, 3, and 4 months, respectively. Natural size.

[Figs. 1–5 after Lefevre and Curtis.]

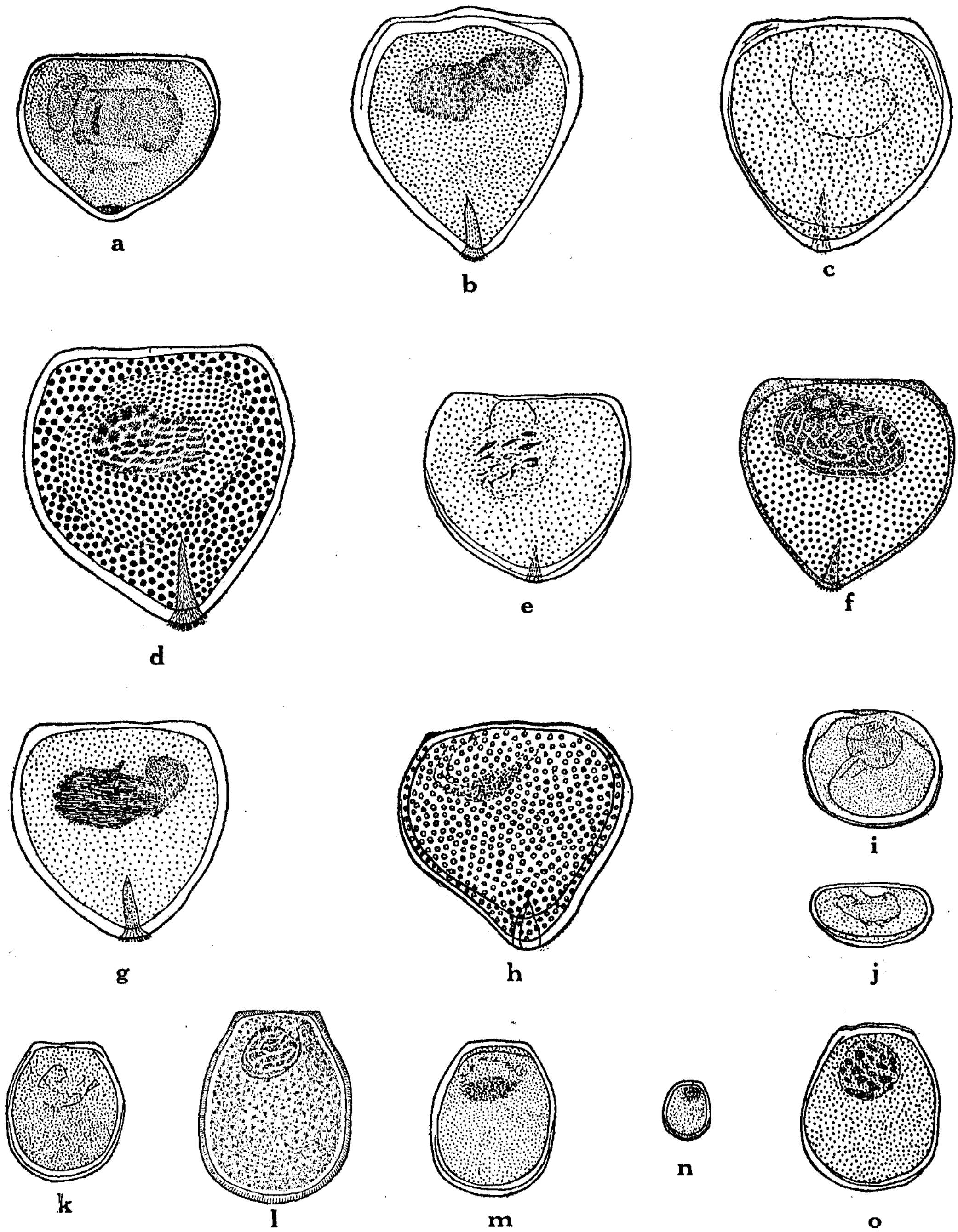


FIG. 9.—Glochidia of common fresh-water mussels. (After Surber, 1912 and 1915.)

a, Alasmidonta calceola.
b, Alasmidonta marginata.
c, Anodonta corpulenta.
d, Anodonta grandis.
e, Anodonta imbecillis.
f, Anodonta suborbiculata.
g, Anodontoides ferussacianus subcylindraceus.
h, Arcidens confragosus.
i, Cyprogenia irrorata.
j, Dromus dromas.
k, Lampsilis anodontoides.
l, Lampsilis breviculus brittsi.
m, Lampsilis fallaciosa.
n, Lampsilis gracilis.
o, Lampsilis higginsii.

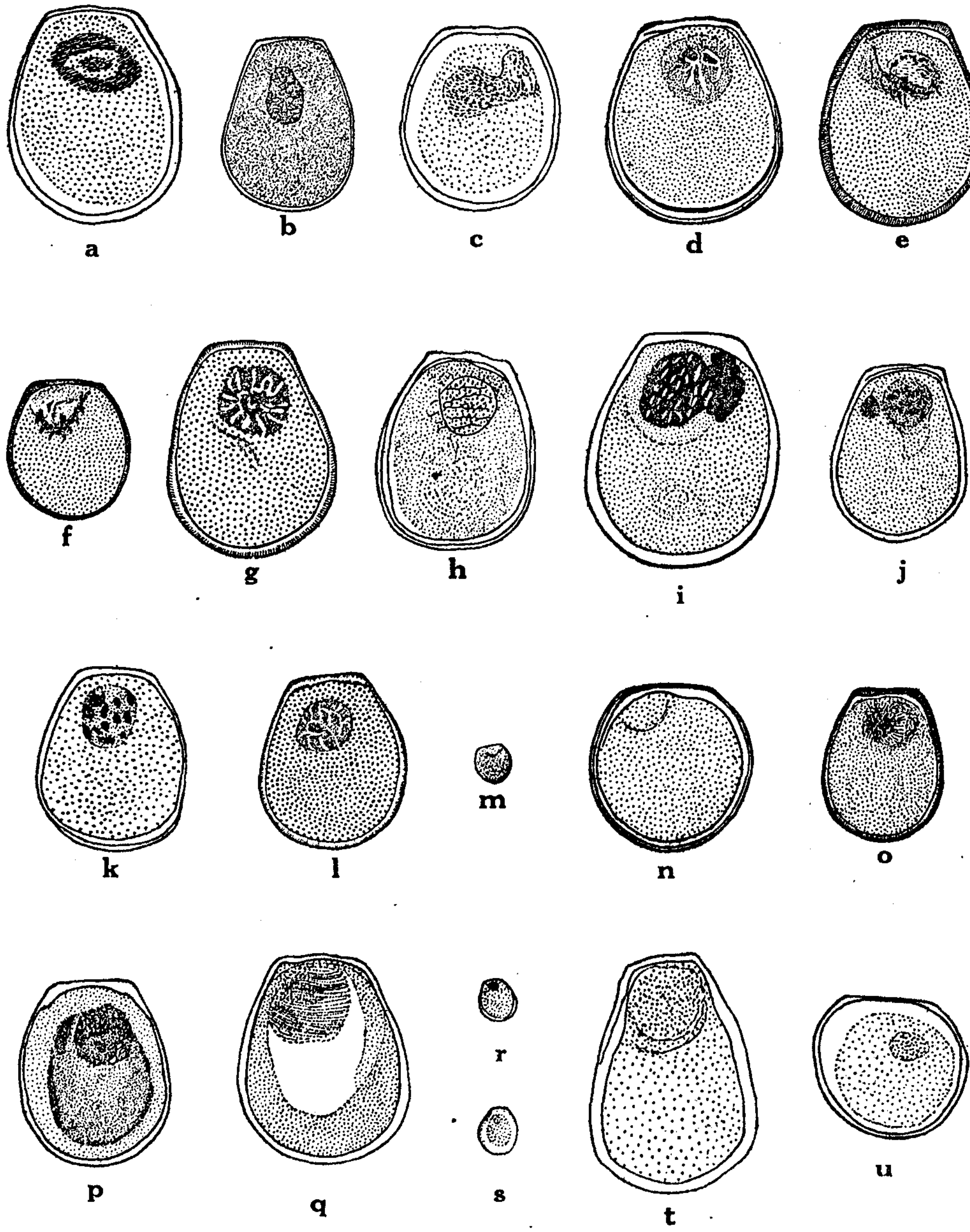


FIG. 10.—Glochidia of common fresh-water mussels. (After Surber, 1912 and 1915.)

a, Lampsilis iris.
b, Lampsilis lienosa unicostata.
c, Lampsilis ligamentina.
d, Lampsilis luteola.
e, Lampsilis multiradiata.
f, Lampsilis parva.
g, Lampsilis picta.
h, Lampsilis recta.
i, Lampsilis subrostrata.
j, Lampsilis trabalis.
k, Lampsilis ventricosa.
l, Lampsilis ventricosa satura.
m, Margaritana monodonta.
n, Obliquaria reflexa.
o, Obovaria circulus.
p, Obovaria ellipsis.
q, Obovaria retusa.
r, Plagiola donaciformis.
s, Plagiola elegans.
t, Plagiola securis.
u, Pleurobema æsopus.

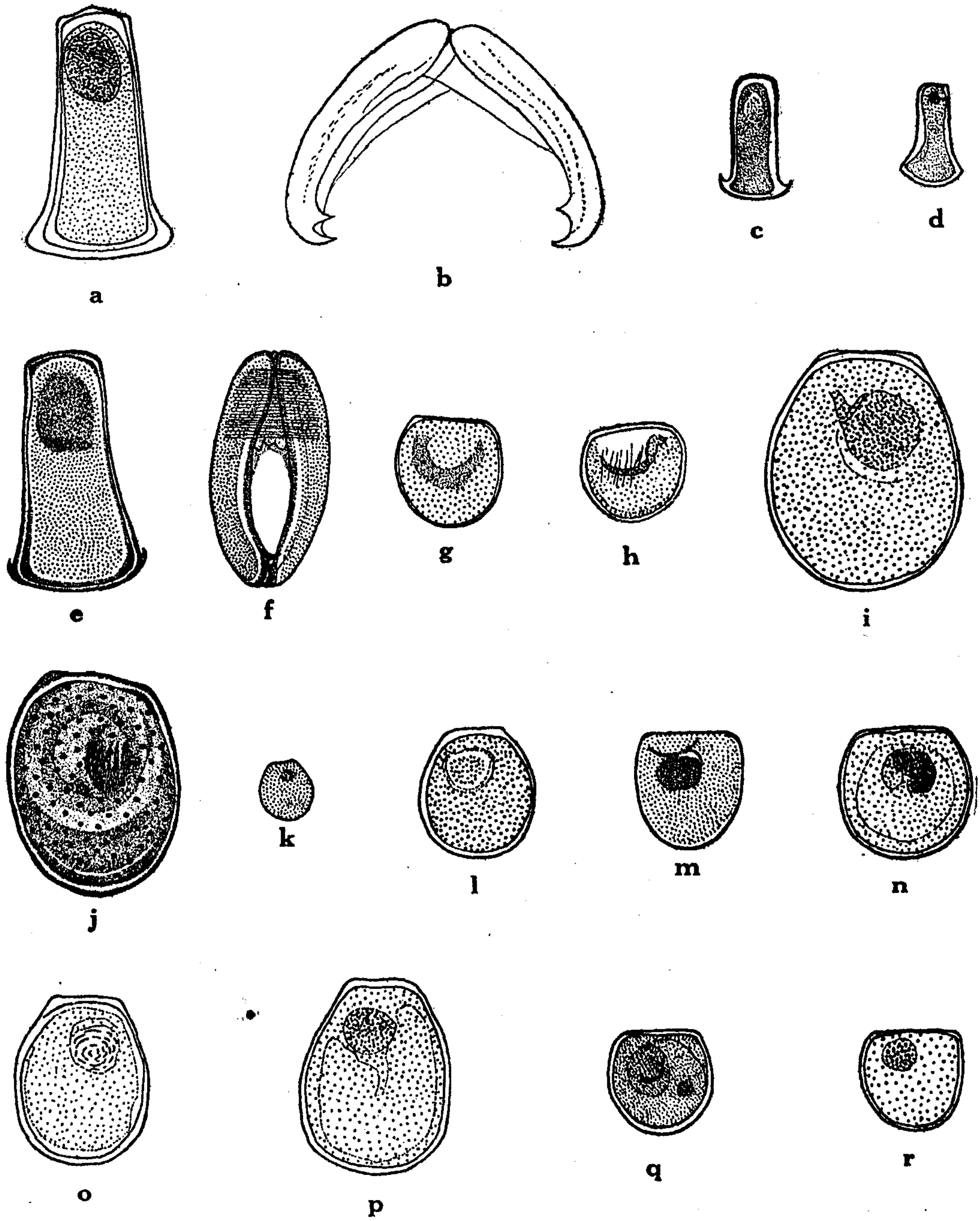


FIG. 11.—Glochidia of common fresh-water mussels. (After Surber, 1912 and 1915.)

a and *b*, *Proptera alata*.
c, *Proptera capax*.
d, *Proptera laevissima*.
e and *f*, *Proptera purpurata*.
g, *Quadrula coccinea*.
h, *Quadrula ebenus*.
i, *Quadrula granifera*.
j, *Quadrula heros*.
k, *Quadrula lachrymosa*.
l, *Quadrula metanevra*.
m, *Quadrula obliqua*.
n, *Quadrula plicata*.
o, *Quadrula pustulata*.
p, *Quadrula pustulosa*.
q, *Quadrula solida*.
r, *Quadrula undata*.

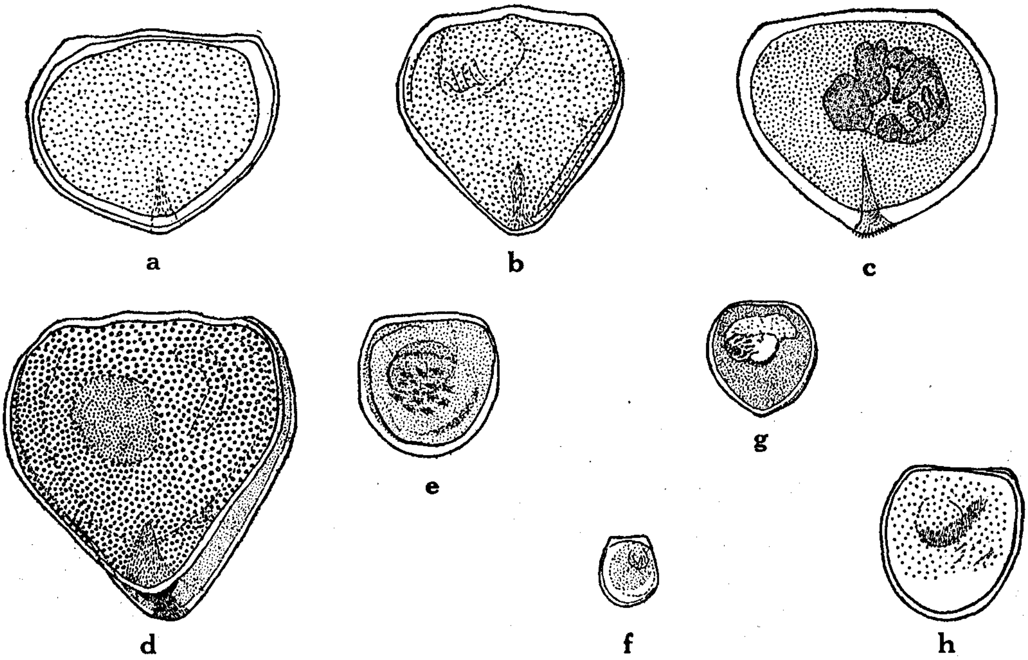


FIG. 12.—Glochidia of common fresh-water mussels. (After Surber, 1912 and 1915.)

a, Strophitus edentulus.
b, Symphynota complanata.
c, Symphynota compressa.
d, Symphynota costata.
e, Truncilla sulcata.
f, Tritogonia tuberculata.
g, Unio crassidens.
h, Unio gibbosus.

would make a line 1 inch in length. Hookless glochidia are possessed by practically all of the more important commercial mussels; in fact, as far as we know, this type of glochidium characterizes all the genera and species not mentioned in the paragraphs immediately preceding and following.

(3) The "ax-head" type (Pl. XIV, figs. 6 and 7) is considered more closely related to the hookless than to the hooked type, although glochidia of this type, except those of a single species, *Lampsilis* (*Proptera*) *lævissima* (Coker and Surber, 1911), possess four hooklike prongs, one at each lower corner of the shell. These pointed projections of the shell are not comparable to the pivoted hooks of glochidia of the hooked type. The ax-head type of glochidium occurs with the following species: *Lampsilis* (*Proptera*) *alata, lævissima, purpurata,* and *capax.* (See also text fig. 11, a to f.)

When the glochidia are fully developed they are ready to break out from the egg membrane and to be liberated from the gills of the mussel, although as previously indicated many species of mussels retain the developed glochidia in their gills for many months. A characteristic feature of the mature and healthy glochidium is the active snapping together and opening of the shell. This action can be stimulated by adding a drop of fish blood or a few grains of salt to the water in which the glochidia are held.

STAGE OF PARASITISM.

After the fully matured glochidium has been expelled from the brood pouch of the mother, its continued development is dependent upon its coming in contact with the gills or fins of a suitable fish host and attaching to them. If it fails to make this attach-

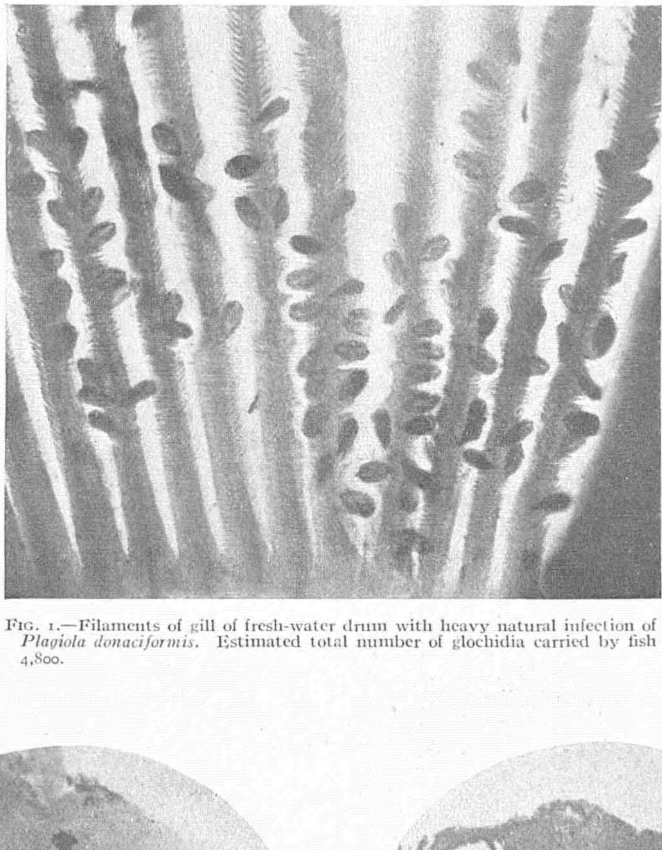


FIG. 1.—Filaments of gill of fresh-water drum with heavy natural infection of *Plagiola donaciformis*. Estimated total number of glochidia carried by fish 4,800.

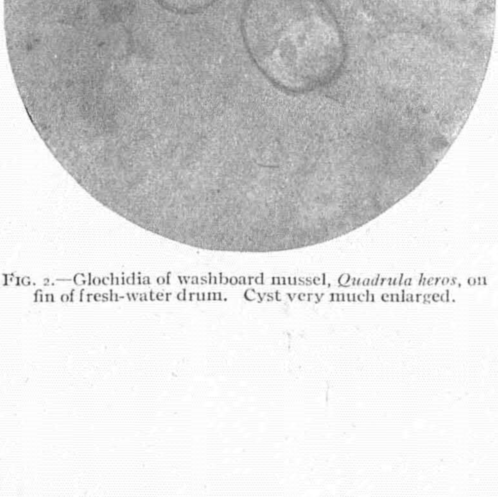


FIG. 2.—Glochidia of washboard mussel, *Quadrula heros*, on fin of fresh-water drum. Cyst very much enlarged.

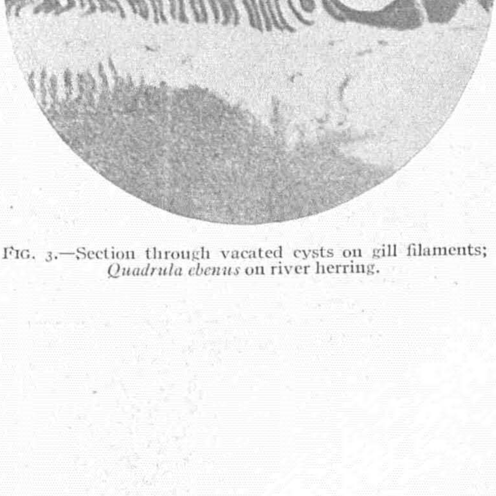


FIG. 3.—Section through vacated cysts on gill filaments; *Quadrula ebenus* on river herring.

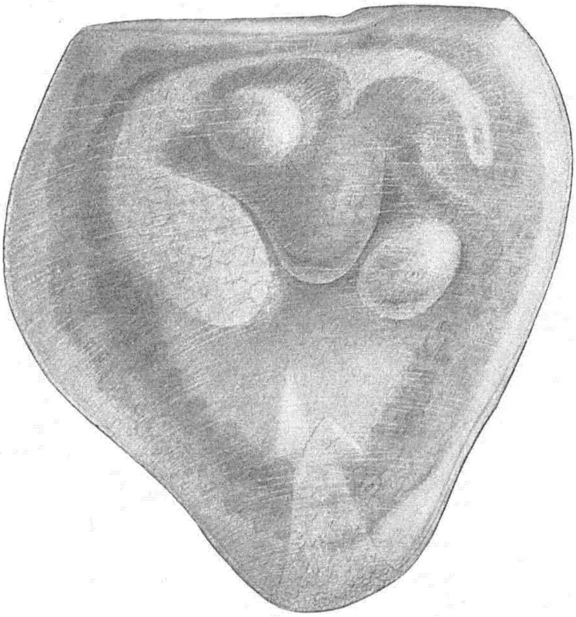


FIG. 1.—Glochidium of *Symphynota costata* in process of transformation during stage of parasitism. (Lefevre and Curtis.)

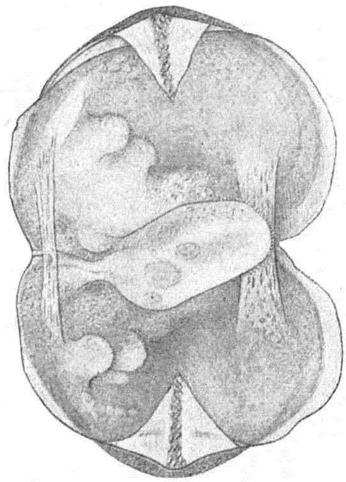


FIG. 2.—A young mussel, *Symphynota costata*, six days after completing the stage of parasitism. (Lefevre and Curtis.)

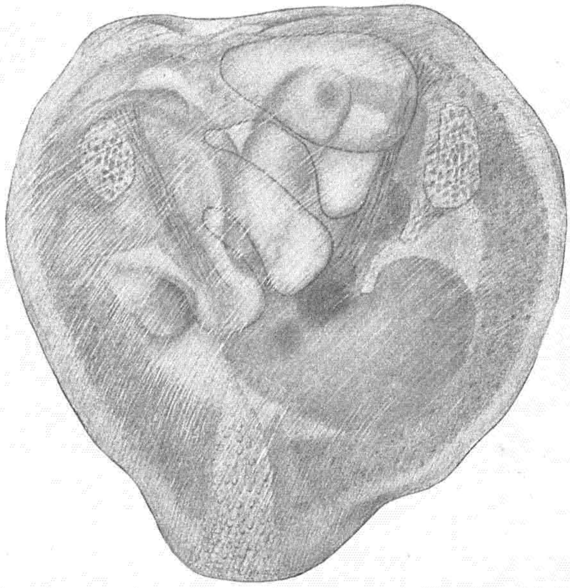


FIG. 3.—A young squaw-foot mussel, *Strophitus edentulus*, which had completed metamorphosis without parasitism; showing two adductor mussels, foot, gills, and rudiments of other organs of adult mussel. (Lefevre and Curtis.)

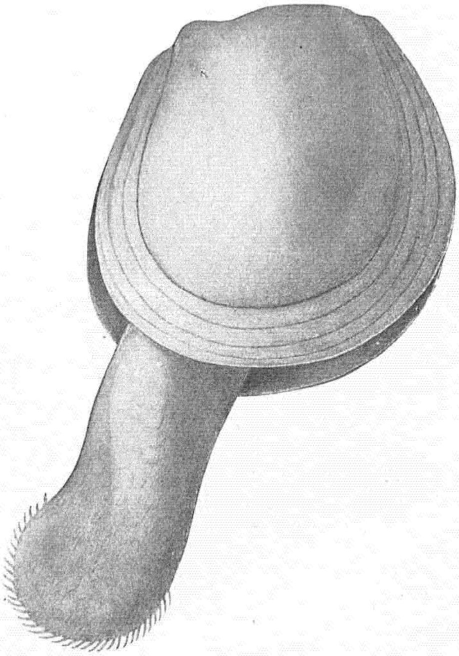


FIG. 4.—A young mucket, *Lampsilis ligamentina*, a week after the close of the parasitic period. (Lefevre and Curtis.)

ment it will die within a few days' time. In other words, the glochidium must pass the life of a virtual parasite on the fish while undergoing its metamorphosis into the free-living juvenile stage. In the light of our present knowledge, this is true of all the fresh-water mussels (Unionidæ) except the squaw-foot, *Strophitus edentulus*, and one of the small floaters, *Anodonta imbecillis*. The former species may complete its metamorphosis either with or without parasitism (Lefevre and Curtis, 1911 and 1912, p. 171; and Howard, 1914, p. 44), while the latter, as it appears, never endures a condition of parasitism (Howard, 1914, p. 44).

On coming in contact with the gill filament or fin of the fish the glochidium attaches itself by firmly clamping its valves to the tissue of the host. A certain portion of the tissue of the fish thus becomes inclosed within the mantle space of the glochidium, and this quickly disintegrates and is taken into the cells of the glochidium and consumed as food (Lefevre and Curtis, 1912, p. 169). Within a very short time the tissue of the fish commences to grow over the glochidium, presumably in an effort to heal the slight wound caused by the "bite" of the glochidium, or perhaps as the result of a positive stimulus imparted by the glochidium. L. B. Arey (report in preparation) successfully induced encystment by attaching to the filaments of excised gills of fish minute metallic clamps the size of glochidia or smaller. The growth of tissue continues until the larval mussel is completely inclosed within a protective covering known as the cyst (Pl. XVI, fig. 2). The several stages of encystment are clearly represented in the series of figures reproduced from Lefevre and Curtis (1912) (Pl. XV, fig. 4), and the process may be completed within 24 or 36 hours. The appearance of a gill bearing a considerable number of glochidia is shown by figure 1 of Plate XV, while figure 2 is an enlarged view of a few of the gill filaments of a black bass carrying glochidia of the mucket.

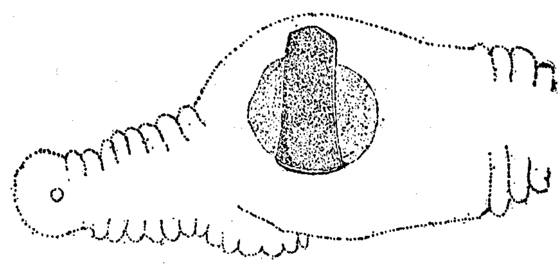


FIG. 13.—Glochidium of pink heel-splitter, *Lampsilis (Proptera) alata*, in condition of parasitism on gill of sheepshead, showing growth of the juvenile mussel beyond the bounds of the glochidial shell.

It is not our purpose to go in detail into the changes which occur in the glochidium during the period of its parasitism. They are principally changes of internal structure which scarcely affect the external appearance. Nevertheless, at the conclusion of parasitic life the young mussel is a very different sort of an organism from the simply organized glochidium which has been described on page 143. Generally it has not increased in size, but the single muscle which held the valves of the glochidial shell together has given place to two adductor muscles as in the adult; the mouth and the intestine are formed, the gills and foot are represented by rudiments which are prepared to function. The larval mussel is, in fact, ready to begin its independent life and to take care of itself. All of the changes which occur during parasitism require the expenditure of energy and the use of body-building material, and as the glochidium enters upon the parasitic life with no considerable store of food material, it is reasonable to assume that it derives at least a small amount of nutritive material from the fish. Since no growth in size generally occurs, the drain upon the fish therefore must be comparatively slight. There are, however, a few species (none of the commercial mussels, so far as we know) in which, during the period of metamorphosis, the larval mussel grows to a comparatively large size (text fig. 13), and, in such cases, the mussel must be generously nourished by the fish. (See Coker and Surber, 1911.)

The duration of the parasitic period varies greatly with the season of the year during which it occurs, and with other conditions which are not fully understood. The results of some recent experiments indicate that glochidia of long-term breeders have a relatively long infection period when they are infected upon fish shortly after maturing and a relatively short period when infected after they have remained in the marsupial pouches over winter; that is, young glochidia complete metamorphosis in parasitism more slowly than old glochidia. The temperature of the water seems to be one of the factors governing the duration of the parasitic period, and doubtless the vitality of the host fish is another; but there is diversity even among glochidia of the same species when infected on the same fish. Lefevre and Curtis (1912, p. 168), for example, show under such circumstances variations from 9 to 13 days, and even from 13 to 24 days. The following instances (Table 17) from records at the Fairport station are illustrative:

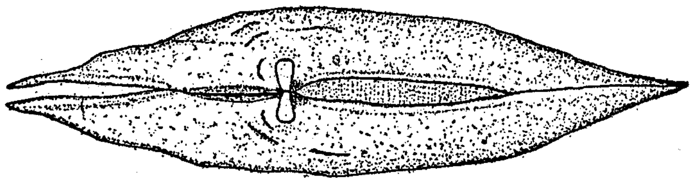


FIG. 14.—A dorsal view of a juvenile pink heel-splitter showing glochidial shell still visible. (×18).

TABLE 17.—INFECTIONS SHOWING DURATION OF PARASITIC PERIOD.

Species of mussel.	Species of fish.	Date of infection.	Duration of infection in days.	Average water temperature during period.
Lampsilis anodontoides	Lepisosteus osseus	June 5, 1919	13	
Do	do	June 20, 1919	12	
Do	do	July 3, 1919	11	
Do	do	July 9, 1919	13	
Do	do	July 23, 1919	12	
Lampsilis luteola	Micropterus salmoides	June 5, 1919	13	
Do	do	June 20, 1919	13	
Do	do	July 14, 1919	10	
Do	do	do	11	
Do	do	do	12	
Do	do	July 25, 1919	10	
Do	do	do	12	
Do	do	do	12	
Do	do	Aug. 21, 1919	12	
Do	do	do	11	
Do	do	Aug. 22, 1919	10	
Lampsilis ligamentina	do	June 5, 1919	15	
Do	do	June 30, 1919	13	
Do	do	do	14	
Lampsilis luteola	Micropterus dolomieu	July 2, 1914	19	
Do	Stizostedion vitreum	do	20	
Do	Perca flavescens	Aug. 18, 1914	68	
Do	do	Sept. 26, 1914	(a)	
Do	Stizostedion vitreum	Sept. 16, 1914	(a)	
Quadrula pustulosa	Ameiurus melas	Aug. 21, 1912	6 to 8	75.1
Do	Ictalurus punctatus	July 7, 1912	9 to 11	78.1
Do	do	Aug. 4, 1912	11 to 12	75.5
Quadrula plicata	Lepisosteus platostomus	July 12, 1918	11	76.5
Lampsilis fallaciosa	do	July 13, 1918	14 to 18	78.3
Lampsilis anodontoides	do	July 7, 1919	14 to 21	74.6
Quadrula heros	Aplodinotus grunniens	Oct. 7, 1912	193	43.3 ca.

[a] Still carrying infection, Apr. 14, 1915.

In about one week after attachment, as a rule, the wall of the cyst begins to assume a looser texture, the intercellular spaces becoming infiltrated with lymph, and from this time on to the end of the parasitic period there is little further change in its structure.

Before liberation of the young mussel, the valves open from time to time and the foot is extended. By the movements of the latter the cyst is eventually ruptured, its walls gradually slough away, and the mussel thus freed falls to the bottom (Lefevre and Curtis, 1912, p. 171).

Before taking up the history of the mussels in independent juvenile life, we must discuss the very significant facts which have been discovered concerning the special relation between mussel species and fish species, and refer also to the rare instances known of mussels which complete their development without the aid of fish.

HOSTS OF FRESH-WATER MUSSELS.

As has previously been indicated in a general way, mussels do not attach to fish indiscriminately, but for each species there is a restricted choice of hosts. Some are more catholic in their tastes than others, yet for any mussel there is a limited number of species of fish upon which it will attach and complete its metamorphosis. The Lake Pepin mucket has nine known hosts, while the niggerhead has apparently but one; the yellow sand-shell is restricted to gars, and the pimple-back to catfishes. It is, of course, employing language in a loose sense to refer to this selection of hosts in terms of taste or choice; it is a matter of physiological reaction. When fish and glochidia are artificially brought together, glochidia will sometimes attach to the wrong fish, but in such cases they soon drop off, or even if partial or complete encystment ensues, the glochidium does not develop normally and after a time cyst and glochidium are sloughed off and lost. It seems evident, then, that successful encystment and development depend upon appropriate reactions on the part of both glochidium and fish, and that failure ensues upon the lack of a favorable reaction on the part of either parasite or host. The reaction may depend in part upon the condition of the individual glochidium or fish, but primarily it depends upon the species of mussel and the species of fish.

It is evident that the artificial propagation of mussels can not be conducted successfully and economically unless we have accurate knowledge of what species of fish serve as hosts for the several species of mussels. Such knowledge has been gained by following two methods of inquiry, the observational and the experimental.

By the observational method, fish taken in the rivers are subjected to careful examination for the presence of glochidia on the gills or fins. Preliminary to and attendant on such studies, glochidia have been taken from as many species of mussels as could be found in gravid condition, these have been studied with the microscope, measured, and figured, so that in most cases the species of mussel can be identified in the glochidium stage as well as in the adult. (See text figs. 9 to 12.) This method of determining the natural hosts is exceedingly laborious. Infection in nature is a matter of chance, and only a small proportion of fish bear infections. If it were otherwise, artificial propagation might not be necessary. One must, therefore, examine large numbers of fish from different localities and at different seasons, and even then the glochidia of some species may not be encountered, or they may not be found upon all the hosts to which they are adapted. During the calendar year 1913, for example, 3,671 fish of 46 species were examined for natural infections principally during the warmer months from April to October. Of these, 324, or 8.9 per cent, were found to be infected with glochidia of some species, but only 104 of these, or less than 3 per cent, were infected with glochidia of commercial species of mussels. The fishes infected with commercial mussels belonged to 12 species, and the glochidia represented 20 species. The average number of glochidia of a given species on infected fish ran from 1 to 416, with a mean of 125.[a]

[a] In August, 1912, 5 examples of the river herring were taken and found to bear glochidia of niggerhead mussels in numbers ranging from 1,895 to 3,740 per fish (Surber, 1913, p. 110). Similarly, heavy infections are frequently found on the fresh-water drum, but the glochidia are not usually those of commercial mussels.

The experimental method is simpler in some respects. It consists in submitting various species of fish to infection with the glochidia of a given species of mussel and observing whether or not the glochidia attach. Since glochidia will sometimes attach to fish which are not their natural hosts, it is necessary to hold the fish under observation until the mussels have completed the metamorphosis and dropped off. It is, however, impracticable to have on hand all the species of fish at the particular time when the glochidia of a given species of mussel may be available. Furthermore, the failure of an artificial infection to go through successfully on fish held in confinement may be due, not to the want of a natural affinity between mussel and fish, but to the fact that the fish does not retain its full vitality in close confinement, or to some other defect in the experimental conditions. Neither of the two methods for the study of infections may, then, be relied upon exclusively for the determination of the natural hosts of fresh-water mussels. On the contrary, it has been found necessary to carry on the two lines of study hand in hand, according to the plan which was adopted at the beginning of the scientific work of the station. In this way, though our knowledge of the hosts of mussels is as yet incomplete, there has been obtained a considerable body of information most of which is summarized in the following table (18),[a] listing 17 species of mussel and 30 hosts (29 fishes and 1 amphibian), and indicating those which serve as hosts for each species of mussel.

EXPLANATION OF TABLE 18.

N. Found on the gills in natural infection.
Nf. Found on the fins in natural infection.
n. Record of natural infection but of doubtful significance.
A. Carried through on gills after artificial infection.
Af. Carried through on fins after artificial infection.
a. Results of artificial infection unsatisfactory or not uniform.
o. Tested and found unsuitable.
T. Tested; development occurred; host perhaps suitable, but experiment not carried to conclusion.

TABLE 18.—COMMERCIAL MUSSELS AND THEIR HOSTS.

Mussels. Scientific name.	Mussels. Common name.	A. melas, bullhead.	A. nebulosus, bullhead.	A. calvus, bowfin.	A. chrysypa, eel.	A. grunniens, sheepshead.	D. cepedianum, gizzard shad.	E. lucius, pike.	E. gibbosus, red-ear sunfish.	H. tergisus, mooneye.	I. punctatus, spotted cat.	L. osseus, long-nosed gar.	L. platostomus, short-nosed gar.	L. tristœchus, alligator gar.	L. cyanellus, blue-spotted sunfish.	L. euryorus, sunfish.
Lampsilis anodontoides	Yellow sand-shell	o	o	a		o					o	AN	A	A	no	
Lampsilis fallaciosa	Slough sand-shell										o		NA			o
Lampsilis higginsii	Higgin's eye					n										
Lampsilis ligamentina	Mucket	o	o	o	n	o		a			o		a		N	
Lampsilis luteola	Fat mucket	o	o			o				o	o		o			
Lampsilis recta	Black sand-shell				n						o				a	
Lampsilis ventricosa	Pocketbook															
Obovaria ellipsis	Missouri niggerhead					o					o					
Plagiola securis	Butterfly					NA									n	
Quadrula ebenus	Niggerhead	o	o	o		o	a			o	o				o	
Quadrula heros	Washboard	A	A		N	AfNf	Nf				Af				A	
Quadrula metanevra	Monkey-face														N	
Quadrula plicata	Blue-point	a	a					N	N		o		A			A
Quadrula pustulata	Warty-back										N					
Quadrula pustulosa	do	NA	A								AN		o			
Quadrula solida																
Quadrula undata	Pig-toe															

[a] A great many data regarding the hosts of noncommercial species of mussels had been accumulated, but unfortunately most of the records applying to such species were destroyed with the burning of the laboratory in December, 1917.

TABLE 18.—COMMERCIAL MUSSELS AND THEIR HOSTS—Continued.

Mussels: Scientific name.	Mussels: Common name.	L. humilis, orange-spotted sunfish.	L. pallidus, bluegill.	L. olivaris, yellow cat.	M. dolomieu, small-mouth black bass.	M. salmoides, large-mouth black bass.	N. maculosus, mud puppy.	P. chrysochloris, river herring.	P. flavescens, yellow perch.	P. annularis, white crappie.	P. sparoides, black crappie.	R. chrysops, striped bass.	S. platorhynchus, sand sturgeon.	S. gyrinus, mad Tom.	S. canadense, sauger.	S. vitreum, walleye.
Lampsilis anodontoides	Yellow sand-shell	n	o			na			o	no	no	a	o		o	
Lampsilis fallaciosa	Slough sand-shell			o		o				n	o		n			
Lampsilis higginsii	Higgin's eye														N	
Lampsilis ligamentina	Mucket		aN		N	AN			AN	NA	A	AN	o	n	A	
Lampsilis luteola	Fat mucket		NA	o	A	A			AN	A	A	A	o	n	A	NA
Lampsilis recta	Black sand-shell		aN							N						
Lampsilis ventricosa	Pocketbook		A		A	A			A	AN					N	
Obovaria ellipsis	Missouri niggerhead		o			o			o	o	o		NA			
Plagiola securis	Butterfly		o			o				o	o					
Quadrula ebenus	Niggerhead		o	o		o		TN	o	o	o		o			
Quadrula heros	Washboard		NA	AN		o	n	n		NA	A	N		Nf		
Quadrula metanevra	Monkey-face		on			o									N	
Quadrula plicata	Blue-point		a	o		AN			A	Nf AN	A	n			N	
Quadrula pustulata	Warty-back			n						n						
Quadrula pustulosa	do		o	an		o				on	o		n			
Quadrula solida			N													
Quadrula undata	Pig-toe									n	n					

It will be observed that the number of hosts corresponding to a particular species of mussel (as so far determined) varies from one to thirteen. It is of interest to give the number of known hosts for each species of fresh-water mussel, as determined both by observation of natural infections and by the experimental method, and this is done in Table 19.

TABLE 19.—NUMBER OF SPECIES OF FISH KNOWN TO SERVE AS HOSTS FOR CERTAIN SPECIES OF MUSSELS.

Mussels: Scientific name.	Mussels: Common name.	Natural infection.	Artificial infection.	Common.	Total.
Lampsilis anodontoides	Yellow sand-shell	1	3	1	3
Lampsilis fallaciosa	Slough sand-shell	1	1	1	1
Lampsilis higginsii	Higgin's eye	1	0	0	1
Lampsilis ligamentina	Mucket	7	6	4	9
Lampsilis luteola	Fat mucket	3	9	3	9
Lampsilis recta	Black sand-shell	2	0	0	2
Lampsilis ventricosa	Pocketbook	2	5	1	6
Obovaria ellipsis	Missouri niggerhead	1	1	1	1
Plagiola securis	Butterfly	1	1	1	1
Quadrula ebenus	Niggerhead	1	1	1	1
Quadrula heros	Washboard	8	9	4	13
Quadrula metanevra	Monkey-face	2	0	0	2
Quadrula plicata	Blue-point	5	6	2	9
Quadrula pustulata	Warty-back	1	0	0	1
Quadrula pustulosa	do	2	3	2	3
Quadrula solida		1	0	0	1
Quadrula undata	Pig-toe	(?)	0	0	(?)

Table 20 lists the common species of fish showing the number of species of mussels which each fish has been observed to carry as parasites. The greatest number is six, for the bluegill, *Lepomis pallidus*, the white crappie, *Pomoxis annularis*, and the sauger, *Stizostedion canadense*.

TABLE 20.—NUMBER OF SPECIES OF COMMERCIAL MUSSELS KNOWN TO BE CARRIED AS PARASITES BY CERTAIN FISHES.

Fishes.		Natural infection.	Artificial infection.	Common.	Total.
Scientific name.	Common name.				
Ameiurus melas	Bullhead	1	2	1	2
Ameiurus nebulosus	.....do	0	2	0	2
Anguilla chrysypa	Eel	1	0	0	1
Aplodinotus grunniens	Sheepshead	2	2	2	2
Dorosoma cepedianum	Gizzard shad	1	0	0	1
Esox lucius	Pike	1	0	0	1
Eupomotis gibbosus	Red-ear sunfish	1	0	0	1
Ictalurus punctatus	Spotted cat	2	2	1	3
Lepisosteus osseus	Long-nosed gar	1	1	1	1
Lepisosteus platostomus	Short-nosed gar	1	3	1	3
Lepisosteus tristœchus	Alligator gar	0	1	0	1
Lepomis cyanellus	Blue-spotted sunfish	2	1	0	3
Lepomis euryorus	Sunfish	0	1	0	1
Lepomis humilis	Orange-spotted sunfish	(?)	0	0	(?)
Lepomis pallidus	Bluegill	5	3	2	6
Leptops olivaris	Yellow cat	1	1	1	1
Micropterus dolomieu	Smallmouth black bass	1	2	0	3
Micropterus salmoides	Largemouth black bass	2	4	2	4
Necturus maculosus [a]	Mud puppy	(?)	0	0	(?)
Pomolobus chrysochloris	River herring	1	1	1	1
Perca flavescens	Yellow perch	2	4	2	4
Pomoxis annularis	White crappie	5	5	4	6
Pomoxis sparoides	Black crappie	0	4	0	4
Roccus chrysops	Striped bass	2	2	1	3
Scaphirhynchus platorhynchus	Sand sturgeon	1	1	1	1
Schilbeodes gyrinus	Mad Tom	1	0	0	1
Stizostedion canadense	Sauger	4	2	0	6
Stizostedion vitreum	Wall-eye	1	1	1	1

[a] An amphibian.

It is necessary to point to some significant practical conclusions from the data presented. Since mussels are "choice" as to their hosts, the chances for the successful attachment of glochidia in nature are greatly diminished. The glochidia when discharged from a parent mussel are lost if no fish are at hand to receive them or if the fish that pass are not of one of the very limited number of species which are useful to the glochidia of that particular mussel.

There must necessarily be some definite ecologic relation between the mussel and the fish. The bottom that is inhabited by the hickory-nut mussel must be one that is frequented by the sand sturgeon during the breeding season of that mussel. Again, if one were looking for the river herring, it would be reasonable to expect to find them, during June at least, in places where niggerhead beds are known to exist. It is evident that no species of mussel could exist unless its host were of such habit as to be at the right places at the right times in a sufficient number of cases to permit first, of the infection occurring, and second, of the young dropping where they can survive.

What the factors are that bring mussels and fish into proper association we can not say. In the case of one species of mussel (the pocketbook) at least, it is known that the gravid mussel protrudes from its shell a portion of its mantle as a long brightly marked flap that waves in the water, assuming the appearance of an insect larva or other attractive bait (p. 85). Again we have the sheepshead fish (fresh-water drum) which is known to feed upon small mollusks, mussels, and the sphæriids and univalves that live on mussel beds, and which thus exposes itself to easy infection; sheepshead, indeed, are almost invariably found to be loaded with glochidia. The behavior of the pocketbook is believed to be exceptional, and the sheepshead is one of a very few species of fish known to feed directly upon mussels. It is certain, however, that the fresh-water mussel beds harbor quantities of other small animal life, such as insect larvæ, snails, and worms, and are gardens for the food of fishes (p. 119); in this, probably, lies the principal clue to the association of fish and mussels.

Finally, an economic consideration should be emphasized. The conservation of the fishes is as important to the preservation of the fresh-water mussel resources and the industries dependent upon them as is the propagation and protection of mussels. The disappearance, or the radical diminution in number, of certain species of fish would result in the complete or virtual disappearance of corresponding species of mussel. On the other hand, if the growth of mussels in more or less dense beds produces conditions which are favorable to the growth of fish food, and observations do so indicate, then the disappearance of the fresh-water mussels would result in the diminution of the food supply for fishes, and the conservation of mussels is important for the preservation of our resources in fish.

PARASITISM AND IMMUNITY.

It is worth while to inquire as to the effect of the glochidia upon fish. Are they parasites in the same sense as tapeworms or round worms? Do they sap the vitality of the fish, and are they accordingly to be regarded as in the nature of a disease? While the relation of the glochidium to the fish can not be fully stated in the present stage of investigation, it can be said that the principal effect upon the fish, at first, at least, is the slight laceration of the gills caused by the attachment of the glochidium. The fish quickly heals over this wound to inclose the glochidium and form a small cyst, and after that there is in nearly all cases no evidence of further irritation or of material detriment to the surrounding tissues, except as the cyst and glochidium are sloughed off at the expiration of the proper period.

The fish feels the attachment of the glochidia; it shows that by the flirting movements which are made as infection begins, and it is known that excessive infections of young fish, at least, may cause the gills to become so lacerated and inflamed as to produce the death of the fish (Lefevre and Curtis, 1912, p. 165). The use of small fish is avoided in experiments and operations conducted at Fairport, and as care is taken to avoid excessive infections it can be said that of thousands of fish artificially infected and kept under observation in experimental work at that place there has been no case of death or evidently diminished vitality with evidence to implicate the glochidia as cause.

After the microscopic lesion of the gill is healed over, which usually occurs in the course of a day, the commercial species of mussels generally make little demand upon the fish. No doubt they derive some nourishment from the fish, but this must be very slight, since the young mussels, after spending two or three weeks in undergoing metamorphosis, are found to be of the same size as before they attached to the fish.[a] The demands upon the energies of the fish caused by the glochidia are probably not greater than those arising from a few extra movements.

It has recently been learned that some fish acquire a certain immunity to glochidia, thus being protected against too frequent repetition of infections. Reuling (1919) has

[a] The mussels which grow in size while in parasitism (p. 149) are not commercial species.

found that some of the very large bass, having doubtless experienced some previous natural infections, become immune after one heavy artificial infection, while small bass, without previous infections presumably, require two or three artificial infections before showing immunity. When immunity is acquired, the fish can not be successfully infected with glochidia of any species of mussel. The period of duration of immunity is not known.

An earlier significant discovery had been made by C. B. Wilson (1916, p. 341). His observations and experiments showed that the fish which are most susceptible to glochidia are those which are subject to parasite copepods (fish lice); that there is a definite connection or fellowship of copepods and mussel parasites, so that knowing the species of mussel for which a given species of fish serves as host, one may often predict what species of copepod fish of that species will carry; and finally, that the presence of glochidia on an individual fish renders that fish practically or completely immune to the attacks of the fish lice, and vice versa. These conclusions may be stated in another way: While glochidia and copepods have essentially identical taste in fish hosts, the presence of the one is antagonistic to the other.

These observations indicate that artificial infection of fish with glochidia may have a positively beneficial effect upon the fish in giving it protection against a class of parasites which are pernicious in effect; for copepods are relatively large parasites which sap the vitality of fish and have been known to cause serious mortalities.

The case of the sheepshead or fresh-water drum, *Aplodinotus grunniens*, may be significant. Sheepshead are found to be almost invariably loaded with glochidia upon the gills, carrying infections which would be regarded as highly excessive if caused artificially (Pl. XVI, fig. 1). They are, no doubt, greatly exposed to infection in consequence of the habit of feeding upon molluscs, which they are well fitted to crush with their strong grinding teeth. By carrying successfully glochidia, which they secure while devouring the parent mussel, they are aiding in the propagation of the mussel which may serve them as food. Indeed, the sheepshead unwittingly engages in growing its own food supply. Now, of the fish which have been examined in numbers, the sheepshead is the one species of fish (besides those of the sucker family, which carry neither glochidia nor copepoda) which has never been found to have copepods on the gills. Its immunity from copepods is now easily understood, and it may be presumed that this immunity is worth the cost of almost continually carrying heavy infections of glochidia.

METAMORPHOSIS WITHOUT PARASITISM.

So generally, almost universally indeed, are fresh-water mussels dependent upon fish for the completion of their development, that peculiar interest attaches to the two exceptions which have so far been encountered. Lefevre and Curtis (1911) discovered that glochidia of one species, the squaw-foot, *Strophitus edentulus* Rafinesque, may undergo metamorphosis into the juvenile stage without the aid of the fish (Pl. XVII, fig. 3). In this mussel, as in others, the eggs when deposited in the gills are packed in a formless mucilaginous matrix, but in the course of the development of the glochidia, the matrix becomes changed into the form of many cylindrical cords, in each of which a few glochidia are embedded. There is evidently in this case a special provision for the nourishment of the embryo from materials supplied by the mother, so that metamorphosis of the glochidium is accomplished at the expense of the parent rather than of a fish. Howard (1915) subsequently found that the glochidia of this species could be made to attach to fish and would undergo metamorphosis in the usual way on this fish. He also discovered that the glochidia of another species, a small floater, *Anodonta imbecillis*, developed into the juvenile mussel within the gills of the parent, and that they would not remain attached to fish.

It is significant that there are just a few species of mussels which diverge in two directions from the general rule that fresh-water mussels undergo metamorphosis only in parasitism and without evident growth in size during the process. On the one hand, we have the cases just cited of change of form accomplished without parasitism, and on the other the instances mentioned on page 149 of two or three species in which the larval mussel increases many times in growth while still encysted upon the fish. The tendency manifested by two species is toward independence of fishes or other hosts, while the tendency revealed by a few others is toward a much greater dependence upon fishes. The vast majority of species, including all the mussels having shells of commercial value, occupy the middle ground of limited dependence upon fish; they must live upon the fish, but they require little from them. The hope has been cherished that in time a means would be found of supplying artificially to the glochidia of the common species of useful mussels the food materials and other conditions necessary for the metamorphosis. so that it might become possible to rear mussels without the use of fish. So far, however, failure has marked every attempt to accomplish this purpose.

JUVENILE STAGE.

At the close of the period of parasite life, the young mussel is no longer a glochidium, and while it possesses the rudiments of the principal organs of the adult, it has yet to undergo many changes of structure—or better perhaps, a progressive development in structure—before it fully assumes the adult form and manner of life (Pl. XV, figs. 5 and 6; Pl. XVII, fig. 4). To the intermediate stages, or series of stages, between parasitism and the development of functional sex organs the term juvenile may properly be applied. The siphons or respiratory tubes, the labial palps, outer gills, and sex glands are among the conspicuous features of structure acquired during this stage.

With many and probably most of the common species of mussels, the early juvenile mussel is no larger than the glochidium—in the case of the Lake Pepin mucket slightly less than one one-hundredth inch in length and slightly more than one one-hundredth inch in height. Its thin mussel shell underlies the glochidial shell, and is scarcely visible until after several days of growth. The most conspicuous feature of the young mussel at this time is the foot, which may be protruded from the shell as a relatively long, slender, and active organ of locomotion. The following description applies primarily to the Lake Pepin mucket: The foot is somewhat cleft at the apex to give a bilobed appearance and it is clothed with cilia or minute living paddles, which are in rapid motion while the foot is extended. The foot has also the power of adhesion to surfaces as smooth as glass; by means of it the young mussel can move about rapidly or effect temporary attachments to foreign objects. It is not long before the peculiar characters of the juvenile foot are lost, for during the first month of independent life this organ becomes changed into the characteristic form of the foot of the adult mussel.

At a very early stage a special organ of attachment is formed in some species, especially among the Lampsilinæ (Sterki, 1891, 1891a; Frierson, 1903, 1905; and Lefevre and Curtis, 1912). This is the byssus, a sticky hyaline thread produced by a byssus gland formed in the middle line of the rear portion of the lower side of the foot. In the washboard, *Quadrula heros*, a very few days after leaving the fish there is apparent a tough mucuslike secretion by means of which the juvenile mussel may anchor itself. The byssus may serve to anchor the mussel by attachment to foreign objects, but its function needs to be more definitely ascertained. Juvenile mussels are sometimes captured in considerable numbers, owing to the sticky thread becoming attached or entangled on the crowfoot hooks or lines or on aquatic vegetation drawn into the boat. While such observations suggest the function of keeping the mussel from being carried away by the current, nevertheless the organ is well developed in young Lake Pepin muckets which are observed to bury themselves deeply in the bottom. The byssus is retained a varying length of time in different species and in different individuals of the same species. The byssus has been seen in young muckets, *Lampsilis ligamentina*, late in the second year of free life and rarely in adults of *Plagiola donaciformis*. The species of mussel observed with byssus are listed below.

SPECIES OF MUSSELS THE JUVENILES OF WHICH ARE KNOWN TO HAVE A BYSSUS.

Lampsilis alata, pink heel-splitter.
L. anodontoides, yellow sand-shell.
L. capax, pocketbook.
L. ellipsiformis.
L. fallaciosa, slough sand-shell.
L. gracilis, paper-shell.
L. iris, rainbow-shell.
L. lævissima, paper-shell.
L. ligamentina, mucket.
L. luteola, Lake Pepin mucket.
L. recta, black sand-shell.
L. ventricosa, pocketbook.
Obovaria ellipsis, hickory-nut.
Plagiola donaciformis.
P. elegans, deer-toe.
Quadrula ebenus, niggerhead.
Q. plicata, blue-point.

The shell formed during the first month (more or less) of development possesses certain peculiar characteristics—besides having a relatively low lime content and being transparent, it bears on its surface certain relatively high ridges, knobs, etc. (Pl. XX). The cause or the meaning of these nicely formed ridges is unknown, but the pattern of sculpture of the early juvenile shell is characteristic for the species. Though all the remainder of the shell be perfectly smooth, the "umbonal sculpture," as it is called, can be made out in well preserved adult shells of most species, and their markings are given significance in the classification of mussels.

We need not concern ourselves here with the details of development of the internal organs, except to say that a considerable elaboration of structure must ensue before the mussel is prepared to assume its culminating function—the reproduction of its kind. The first act of breeding marks the close of the juvenile period, and this occurs in the Lake Pepin mucket two years after the beginning of the juvenile stage, or early in the third summer of life counting from the deposition of the egg in the gill of the mother. In some species of mussels, those of small adult size, or those possessing very thin shells, sexual maturity comes at an earlier age, but in most species of mussels it undoubtedly occurs later. (See p. 137.)

The maximum sizes, at various ages, attained by Lake Pepin muckets under observation, are shown in the following table:

TABLE 21.—MAXIMUM SIZE OF YOUNG LAKE PEPIN MUCKETS AT VARIOUS AGES.

Age.	Length.		Age.	Length.	
	Millimeters.	*Inches.*		*Millimeters.*	*Inches.*
Beginning of juvenile stage	0.25	0.01	68 days	13.0	0.51
15 days	.5	.02	5 months	32.3	1.27
38 days	4.2	.17	End of second growing season	58.3	2.30

This species displays perhaps the most rapid growth of any commercial mussel, although it is surpassed in this respect by some of the noncommercial floaters and paper-shells. The maximum size attained in the second year by mussels of several other species reared at the Fairport station is given in Table 22.

TABLE 22.—SIZE AND AGE OF MUSSELS REARED AT FAIRPORT STATION.

Species.	Length.		Approximate age.	Remarks.
	Millimeters.	*Inches.*	*Years.*	
Lampsilis ligamentina, mucket	20.0	0.79	2	Accidentally reared.
Lampsilis anodontoides, yellow sand-shell	41.0	1.62	1¼	Intentionally reared.
Obliquaria reflexa, three-horned warty-back	16.0	.63	2	Accidentally reared.
Plagiola donaciformis	20.0	.79	2	Do.
Quadrula plicata, blue-point	13.5	.53	2	Do.
Quadrula undata, pig-toe	15.8	.63	2	Do.
Obovaria ellipsis, hickory-nut	11.4	.45	2	Do.

Much remains to be learned regarding the habits and habitats of the juvenile mussels of many species. The study is somewhat difficult, because mussels in the juvenile stage are usually hard to find. This is the experience of all collectors, although rich finds of larval mussels are occasionally made in particular locations (Howard, 1914, pp. 34 and 47). In 1914 Shira collected 1,394 juveniles representing 16 species in Lake Pepin, and 92.9 per cent were taken upon sand bottom where there was scattering vegetation. This figure can not, however, be taken as an index of preference for that particular sort of habitat, since 86.2 per cent were taken at one station. Isely (1911, p. 78) made a collection of 32 juveniles comprising 9 species, 6 of which were represented in the Lake Pepin collections, but Isely's specimens were all taken in fairly swift water, 1 to 2 feet deep, and from a bottom of coarse gravel. In rearing young mussels, principally Lake Pepin muckets, in ponds at Fairport, the best success has been attained on prepared bottom of sand; yet when Howard reared Lake Pepin muckets in a crate floating in the river, silt accumulated to a considerable depth, and the juvenile mussels were sometimes found deeply submerged in the soft mud; nevertheless, more than 200 young mussels survived the season in a very small crate, and excellent growth was made.

After the byssus is shed the young mussels often bury themselves in the bottom more deeply than do adults. They are inclined to travel considerably at this stage, but the rate of movement and the distances covered are less than might be thought from observation of the conspicuous and apparently fresh tracks behind the young mussels. It has been found that the tracks will retain the appearance of freshness for several days; hence the trail which one might at first suppose to have been made in a few hours may represent a journey covering a considerable period of time. Clark observed a young mussel which made forward movement every 10 seconds, each movement being followed by a brief rest period. A young hickory-nut mussel was observed to travel 0.1 meter (about 4 inches) in 29 minutes. The rate of travel of sand-shells is much more rapid.

Because of their small size and delicate shell the early juvenile mussels are doubtless the prey of numerous enemies. Turbellarian and chætopod worms are known to devour them. No doubt they are sometimes eaten by fish and aquatic animals, such as are accounted enemies of larger mussels, yet there has been found little evidence of serious depredations upon young mussels by such animals. Perhaps the most serious natural mortality among juvenile mussels occurs from falling upon unfavorable bottoms or from the effects of currents, especially in times of flood, which may draw the relatively helpless mussels into environments in which they have small chance for survival. It may be expected, too, that the repeated dragging of crowfoot bars over favorable mussel bottoms works damage to juveniles both by injuries directly inflicted and by pulling them from the bottom and exposing them to the action of currents from which they had previously found protection.

ARTIFICIAL PROPAGATION.

PRINCIPLE OF OPERATION.

As the previous account of the life history of fresh-water mussels has shown, the mussel not only deposits great numbers of eggs but nurtures them in brood pouches within the protection of her shell. There is not, as in fish, a great wastage of eggs and larvæ in the very earliest stage of development. There exists, therefore, no necessity for artificial aid to effect fertilization; that is, to bring the male and female reproductive elements together. Nature's own provisions have adequately provided for the bringing of enormous numbers of each generation of offspring to the glochidium stage. It is after this stage is attained that the greatest mortality occurs; the great abundance of glochidia produced by each female is, indeed, evidence that enormous losses are to occur subsequently, and observation indicates that the critical stages are, first, when the glochidia are liberated from the parent to await a host, and, second, when the juvenile mussels are dropped from the fish that serves as host.

The artificial propagation of mussels as now practiced aims to carry the young mussels through the first great crisis. Its object is to insure to a large number of glochidia the opportunity to effect attachment to a suitable fish. Under present conditions the operations can be conducted extensively and economically only in the field. The procedure in brief is to take fish in the immediate vicinity of the places to be stocked, infect them with glochidia of the desired species of mussels, and liberate them immediately. Artificial propagation, then, as applied to fresh-water mussels, is a very different sort of operation from that employed in the propagation of fish, although it is no less directly adapted to the conditions and needs of the objects to be propagated.

METHODS.

In each field the operations are conducted under the immediate direction of a qualified person who may be either a permanent or temporary employee of the Bureau working under the Fairport station. The fishing crew is comprised of three or four local fishermen, or laborers, temporarily employed.

The equipment for seining and handling the fish consists of a motor boat, one or two flat-bottomed rowboats, seines or other nets, including small dip nets, tanks, buckets, etc. The motor boat is used to cover the various fishing grounds as rapidly as possible to distribute the infected fishes, and to move the outfit from place to place as it becomes advisable or necessary to extend the field of operations. The rowboat is employed in the actual work of seining and handling the fish. If the fish are taken in very large numbers it is convenient to have one or two tanks, similar to the ordinary 4-foot galvanized stock tanks and equipped with handles. Under ordinary conditions, tubs serve very well, especially if the fish have to be transported by hand for some distance, as is the case when the fish are taken in rescue work from land-locked ponds or lakes. At times, when the field of operations is at some distance from a place where living and sleeping accommodations can be secured, a camping outfit, or a house boat, is used for quartering the crew. The head of the party must be provided with a dissecting microscope, a magnifying hand lens, and simple dissecting instruments.

Before an infection can be made, it is first necessary to obtain a supply of glochidia of the desired species of mussels. In localities where commercial shelling is actively practiced this can be done by visiting the shellers' boats and examining the catch for freshly-taken gravid mussels. If it is desired to use the glochidia at once, the brood pouches are immediately cut from the females and placed in water; but if it is desired to use them over a period of several days, the gravid shells are purchased and the glochidia removed as needed. In locations where shells are scarce, or where little or no commercial shelling is done, it is sometimes necessary to hire a sheller to procure the mussels.

The fish are next sought by means of seines or nets, and when secured are sorted and transferred to the tanks or tubs; the fish that are not required for purposes of mussel propagation are immediately liberated in suitable waters. When the containers are comfortably filled with fish, overcrowding being avoided, the brood pouches of one or more mussels, as necessary, are cut out and opened with scissors or scalpel and the glochidia are teased out in a small pail or other container from which they are poured into the tanks with the fish. Figures 1 to 4, Plate XVIII, show the seining and infection operations in the field.

The experienced operator can usually tell at a glance whether or not the glochidia are sufficiently ripe for infection. If they freely separate when removed from the brood pouches and placed in a dish of water, it is usually a sign that a sufficient degree of ripeness has been obtained. If, however, they adhere in a conglutinate mass and can be separated only with difficulty, it is certain indication that they are unsuitable for infection; examination with a hand lens in such case will show also that the glochidia are still inclosed in the egg membrane, thus revealing their immaturity. If the glochidia are fully developed, one can readily determine if they are alive and active by dropping a few particles of salt or a couple of drops of fish blood into a small dish containing some of the glochidia. It is a sign of maturity and vitality if the valves begin to snap together as the salt or blood diffuses through the water.

After being removed from the brood pouches the life of the glochidia is usually rather short, but it is possible to keep them alive a day or two if the water in which they are retained is changed at frequent intervals and not permitted to become too warm.

The operator is guided by his experience as to the quantity of glochidia to be placed with a given lot of fish and as to the length of the infection period. The water may be stirred from time to time in order to keep the glochidia in somewhat even suspension, but in most cases the movements of the fish themselves insure a circulation of the water and a general distribution of the glochidia. At intervals individual fish are taken by hand or small dip net, and the gills examined with a lens; when, in the opinion of the operator, a sufficient degree of infection has occurred, the fish are placed at once in open waters, or transferred to other containers for conveyance to a place suitable for their liberation. The rapidity with which infection takes place depends upon a variety of conditions, such as temperatures of water, kind and size of fish, and activity of glochidia. Ordinarily a period of from 5 to 25 minutes is sufficient to insure an optimum infection. The infection time is usually shorter in warm water than in cold. As basis for approximate computation of the number of glochidia planted, several average-sized specimens of each species of fish infected are killed and the gills removed for subsequent counts of the glochidia attached. The counting is done by the foreman with the aid of a microscope and usually in the evening after the close of the field operations of the day. The number of glochidia per fish of each species having been determined by the count of representative examples, and the numbers of fish of the species being known, the entire number of glochidia planted on a given lot of fish is easily computed. The data in detail are promptly recorded on form cards provided for the purpose. The count of total glochidia planted is of course only approximate, but the method of count and computation described is as accurate as the conditions of operation permit, and it is as precise as the methods of count generally practiced in fish-cultural operations. In the long run, the actual errors on one side and the other must approximately balance.

That degree of infection which employs the fish to best advantage in mussel propagation, without doing appreciable injury to the host, is termed the "optimum infection." It varies with the species of mussel and with the kind and the size of the fish. Table 23 gives illustrative instances.

TABLE 23.—OPTIMUM INFECTION FOR CERTAIN SPECIES OF MUSSEL ON SEVERAL SPECIES OF FISH.

Species of mussel.		Fish host.		Number of glochidia on fish.
Scientific name.	Common name.	Species.	Size in inches.	
Lampsilis luteola	Lake Pepin mucket	Black bass	8	2,000
Do	do	White bass	8	2,000
Do	do	Wall-eyed pike	8	2,500
Do	do	Bluegill	5	500
Do	do	Crappie	5	400
Do	do	Yellow perch	6	1,500
Lampsilis anodontoides	Yellow sand-shell	Gar	16	2,000
Lampsilis ligamentina	Mucket	Black bass	8	2,000
Lampsilis pustulosa	Pimple-back	Channel catfish	14	1,200

Incidental to the field work in mussel propagation, valuable results are frequently gained in the reclamation of fish from the overflowed lands bordering the various rivers. All fishes rescued in connection with propagation work, whether suitable or unsuitable for infection, are liberated in the open waters, and under such circumstances the value of the fish thus saved in large measure recompenses for the cost of the mussel propagation work.

The operations of mussel propagation as just described serve to carry the young mussels through the most critical stage of the life history—to give to thousands the

FIG. 1.—Seining fish from overflow water for infection with glochidia of mussels.

FIG. 2.—Seining fish in Lake Pepin for mussel propagation.

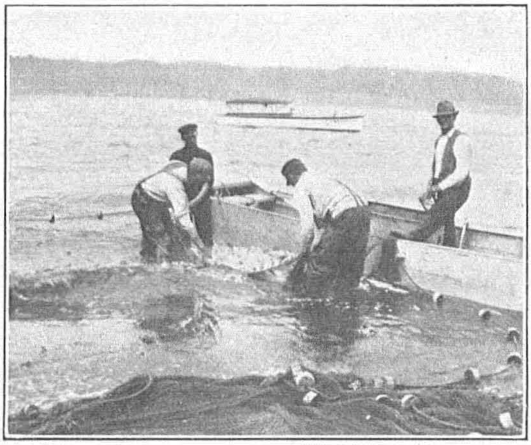


FIG. 3.—Transferring fish to infection tank. Foreman in boat is pouring the glochidia from a can into the tank.

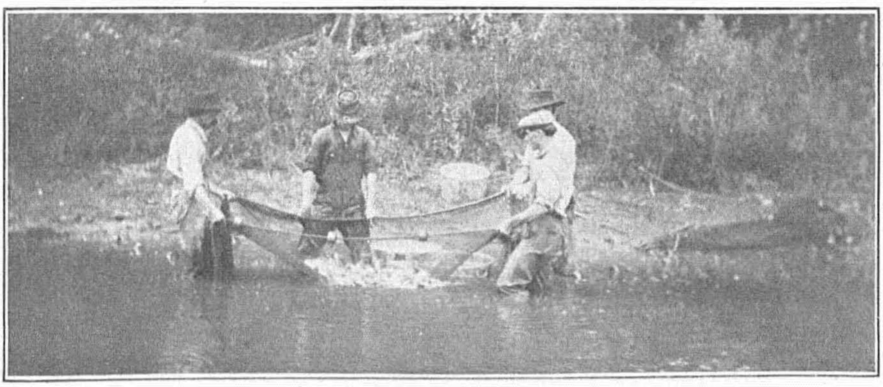


FIG. 4.—Sorting the fish for infection with glochidia.

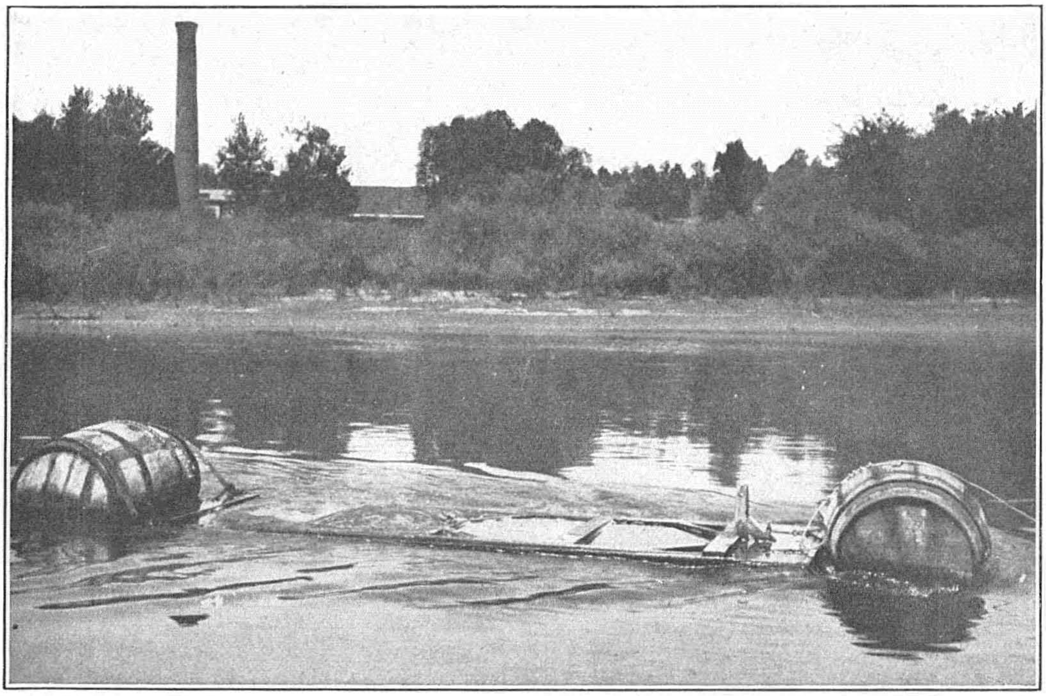


FIG. 1.—A floating crate containing four baskets in which fish infected with glochidia were placed and young mussels reared. (Compare Pl. V, fig. 3.)

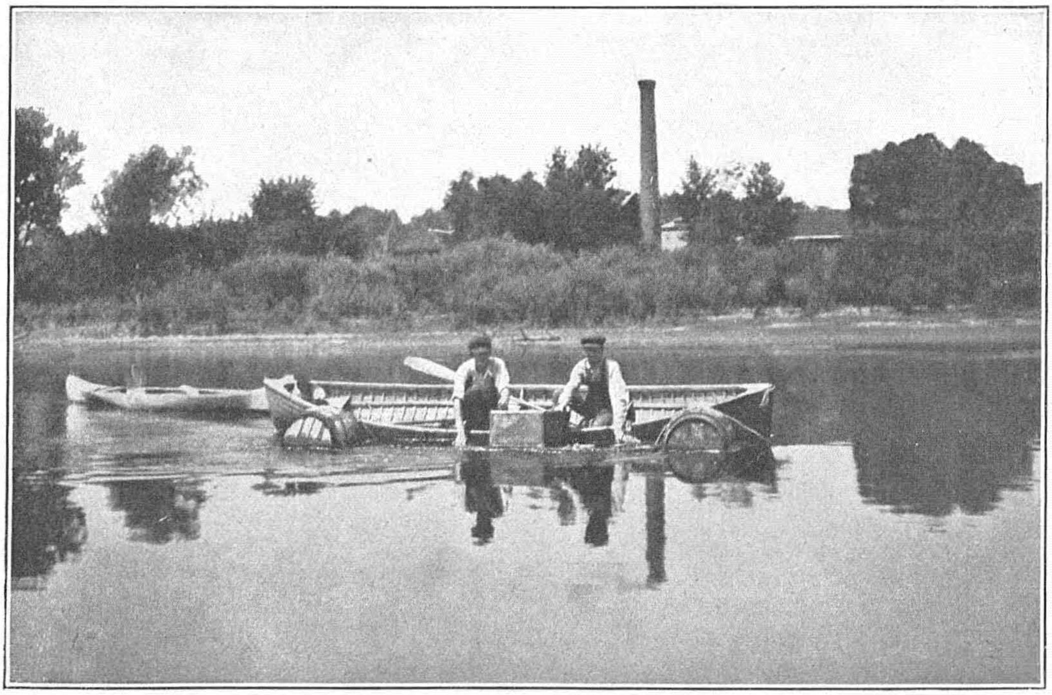


FIG. 2.—Lifting one of the baskets from the crate for examination and cleaning.

chance of life that would ordinarily fall only to dozens. As previously pointed out (p. 151), an extensive series of observations of fish reveals the fact that but few are naturally infected with mussels and these usually in slight degree. The chance that a large proportion of the glochidia discharged by any mussel will become attached to a proper host is slight, and it is only because nature is prodigal in the production of glochidia that the various species of mussels can maintain their numbers under natural conditions. With the disturbance of natural conditions by the active pursuit of a commercial shell fishery, nature's fair balance is destroyed, and some compensatory artificial aid to the propagation of mussels is rendered necessary.

It is not presumed that all the vicissitudes of mussel life are removed by the bringing together of fish and mussel. Nature undoubtedly exacts heavy tolls at other stages. Many of the young mussels on being liberated from the fish will fall in unfavorable environments and meet an early death, while those that survive the earliest stage of independent life may still be subjected to numerous enemies throughout the juvenile period at least. Nevertheless, glochidia of certain species can be planted in such large numbers and at such slight cost that, after making due allowance for an extraordinary subsequent loss, substantial returns can be expected. That such results do obtain is indicated both by experiments to be later described (p. 166) and by common experience

MUSSEL CULTURE.

The rearing of young mussels in tanks, in ponds, or (if under conditions of control) in the river, may properly be termed "mussel culture," as distinguished from "mussel propagation," which, as we have seen, consists in bringing about the attachment of glochidia to fish and liberating the fish in public waters. For several years experiments in mussel culture have been carried on by the Bureau of Fisheries at Fairport and elsewhere, with a view both to securing information regarding the life history of mussels and to testing experimentally the possibilities of culture as a public measure of conservation or as a field for private enterprise. At first little success attended these efforts. It was found that the mussels could readily be carried through the parasitic stage, but that soon after leaving the fish hosts they perished. Apparently there was something inimical to the young mussels in the artificial conditions of aquaria, tanks, or ponds, although these might be supplied with running water derived from the natural habitat of mussels.

The first reported rearing of mussels under control was accomplished with the Lake Pepin mucket in a crate floating in the Mississippi River (Howard, 1915). Experiments initiated by the senior author in the ponds at Fairport, Iowa, about the same time were also successful with the same species. Subsequently broods of the Lake Pepin mucket have been reared from year to year by various methods. Less consistent results have been obtained with the following river mussels: The pocketbook, *Lampsilis ventricosa*, the pimple-back, *Quadrula pustulosa*, and until recently the yellow sand-shell, *Lampsilis anodontoides*, and the mucket, *Lampsilis ligamentina*. Apparently the conditions required for rearing the Lake Pepin mucket are less difficult to meet under control than is the case with the other species mentioned. The reason is, doubtless, that *Lampsilis luteola*, being a lake-dwelling species as well as an inhabitant of rivers, is adapted to more varied conditions.

The methods employed in rearing mussels may be designated as follows: (1) The floating crate with closed bottom (chiefly used in rivers); (2) the floating crate with open bottom (chiefly used in ponds); (3) the bottom crate; (4) pen with wooden or box bottom; (5) concrete ponds; (6) earth ponds; (7) troughs of sheet metal, wood, or concrete tanks, and aquaria.

(1) The floating crate with closed bottom was devised to meet the special conditions of a large river where the level is subject to considerable change, where excessive turbidity frequently prevails, and where there is a decided current. To prevent the washing away of the microscopic mussels, while permitting the passage of water and food through the crate, the crates are constructed of fine-meshed (100 mesh to the inch) wire cloth on a wooden frame. The form of the crates and the manner of using them may be understood from the illustrations (Pl. XIX, figs. 1 and 2). They are described in more detail in a forthcoming paper by A. D. Howard. A plant of young mussels is obtained by placing infected fish in the crate and removing them after they are freed of the mussels. The results with the floating crate have been quite satisfactory with the Lake Pepin mucket, and a few yellow sand-shells have also been obtained in them. Other river mussels have failed to develop beyond early stages. Good results with river mussels would be expected, but it is found that even with the crate floating in the river, the conditions within it are not those of the natural habitat of the mussel on the clean current-swept bottom of the river. No one has yet devised a container to employ under such conditions that would fully answer the requirements.

(2) The floating crate with open bottom has been used in artificial earth ponds. The bottom is actually closed to fish, though open to juvenile mussels, since it is made of coarse-mesh wire cloth (1½-inch mesh). The infected fish are kept inclosed until freed of glochidia, which fall through the wire to the bottom of the pond. To obtain the mussels when developed, the water is temporarily drawn from the pond. Good results have been obtained with the Lake Pepin mucket only.

(3) The bottom crate has been used in studies of growth of larger mussels, by Lefevre and Curtis (1912, p. 180), Coker, and others, and in experiments in pearl culture by Herrick (Coker, 1913). It has recently been adapted for the purpose of retaining infected fish and securing plants of early postparasitic stages of mussels. The crate rests on the bottom of the pond. It may have either a solid bottom or one of screen wire which, of course, sinks a little way into the mud covering the bottom of the pond.

(4) The pen of galvanized netting with wooden floor is adapted to quiet water without current. The pen, having walls of wire cloth that extend from the bottom to a safe distance above the surface of the water, allows the fish to seek their own range of depth and permits the mussels that fall from the fish to remain close to the bottom of the pond or lake, as is natural for them. The mussels are collected by raising the wooden bottom at the end of the growing season. Excellent results have been obtained in Lake Pepin with the Lake Pepin mucket. In the most successful experiment more than 11,000 living young were secured in one crop in a pen 12 feet square. These were liberated from 79 fish which had been artificially infected (Corwin, 1920).

(5) Concrete ponds having vertical sides have been planted in the usual way and the fish removed with a seine after the mussels have been shed. Some 50 examples of a river-inhabiting species, the pimple-back, *Quadrula pustulosa*, were reared to the age of 4 years in one experiment, but other trials with this species have failed. The usual consistent results have been secured with the Lake Pepin mucket.

(6) Earth ponds with devices for control of depth and water supply have been stocked with mussels by introducing infected fish. As a rule the fish are not removed

until the end of the season when the pond is drawn. The Lake Pepin mucket in considerable numbers have been reared in earth ponds. A few pocketbook mussels, *L. ventricosa*, were obtained after a recorded plant in a pond of modified type, having earth bottom but wooden sides. Mussels of several other species have been found in ponds from accidental plantings. The sporadic occurrences of young mussels in the first ponds and in the reservoir constructed at the Biological Station at Fairport, Iowa, are of interest as showing how, through parasitism upon fish, many species of mussel will quickly invade new waters. It is significant that none of the species which have introduced themselves abundantly into these ponds are commercially valuable. Apparently the commercially useless mussels are more easily and abundantly distributed by natural means than the useful ones. A list of the species noted, with additional data, is comprised in the following table (cf. Pl. XX):

Table 24.—Mussels Recorded from Ponds at the Fairport Station.

Scientific name.	Common name.	Number or frequency.	Length in millimeters.
Anodonta corpulenta Cooper	Floater	Abundant	60–90
Anodonta suborbiculata Say [a]	Paper-shell	3	67.4
Anodonta imbecillis Say	do	Abundant	2–48
Arcidens confragosus Say [a]	Rock pocketbook	7	39–49
Lampsilis ligamentina Lam	Mucket	7	6–20
Lampsilis (Proptera) alata Say	Pink heel-splitter	2	69.5
Lampsilis (Proptera) capax Green	Pocketbook	2	49.5
Lampsilis (Proptera) lævissima Lea	Paper-shell	Abundant	27–90
Lampsilis subrostrata Say [a]		do	8.48
Lampsilis gracilis Barnes	Paper-shell	do	9.1–71
Lampsilis parva Barnes [a]		do	5.7–27
Obliquaria reflexa Rafinesque	Three-horned warty-back	1	16
Plagiola donaciformis Lea	Deer-toe	Abundant	2.6–20
Quadrula plicata Say	Blue-point	1	13.5
Quadrula undata Barnes	Pig-toe	1	15.8
Strophitus edentulus Say [a]	Squaw-foot	1	62.1
Symphynota complanata Barnes	White heel-splitter	26	64–91
Obovaria ellipsis Lea	Hickory-nut	1	11.4

[a] Uncommon in the river.

(7) Experiments have also been made with various containers of small dimensions which are usually supplied with running water. Such are the glass aquarium and the tank or trough which may be made of wood, concrete, or sheet metal. Of these the one most used for experimental rearing of mussels at Fairport, Iowa, has been the trough of sheet metal painted with asphaltum. A special arrangement for water supply is employed. The water is not taken directly from the main reservoir, but is drawn from the surface of a pond containing vegetation; in some cases it is also strained through cloth. In this way water is obtained that is very clear and probably free to a large extent from such small animals of the bottom as would prey upon the young mussels. The Lake Pepin mucket, the river mucket, and the yellow sand-shell have been reared through the first year in such troughs. The experiments are of such importance as to merit detailed description. The following account is based upon a report of F. H. Reuling, who first assisted in the experiments and later was charged with their conduct. (See also Reuling, 1919.)

The experiments were conducted in a series of eight galvanized iron troughs, placed at a sufficiently low level to receive a gravity supply of water from pond 1D. This pond was supplied by gravity from the reservoir which received its supply direct from the Mississippi River through the pumping plant. The water in pond 1D remained comparatively clear throughout the season, and this was one of the primary considerations in locating the troughs. The troughs were 12 feet long, 1 foot wide, and 8 inches deep, painted with asphaltum, and each had its independent inflow from a common screened supply pipe in the pond. The bottom of each trough was covered with fine sand to a depth of about one-half inch.

Records were kept of the progress of the larval mussels through the process of development, and when they had reached that stage when they were ready to drop from the fish, counts on the fish gave a close approximation of the number dropped in the trough.

The results of the experiments the first season were quite meager, as only 7 young of the Lake Pepin mucket, *Lampsilis luteola*, varying from 6 mm. to 17.8 mm. in length, and 4 of the mucket, *L. ligamentina*, with an average length of 2.6 mm., were reared. However, in case of the mucket the results were very encouraging, as it marked the first instance of juveniles of this species being artificially reared to this size.

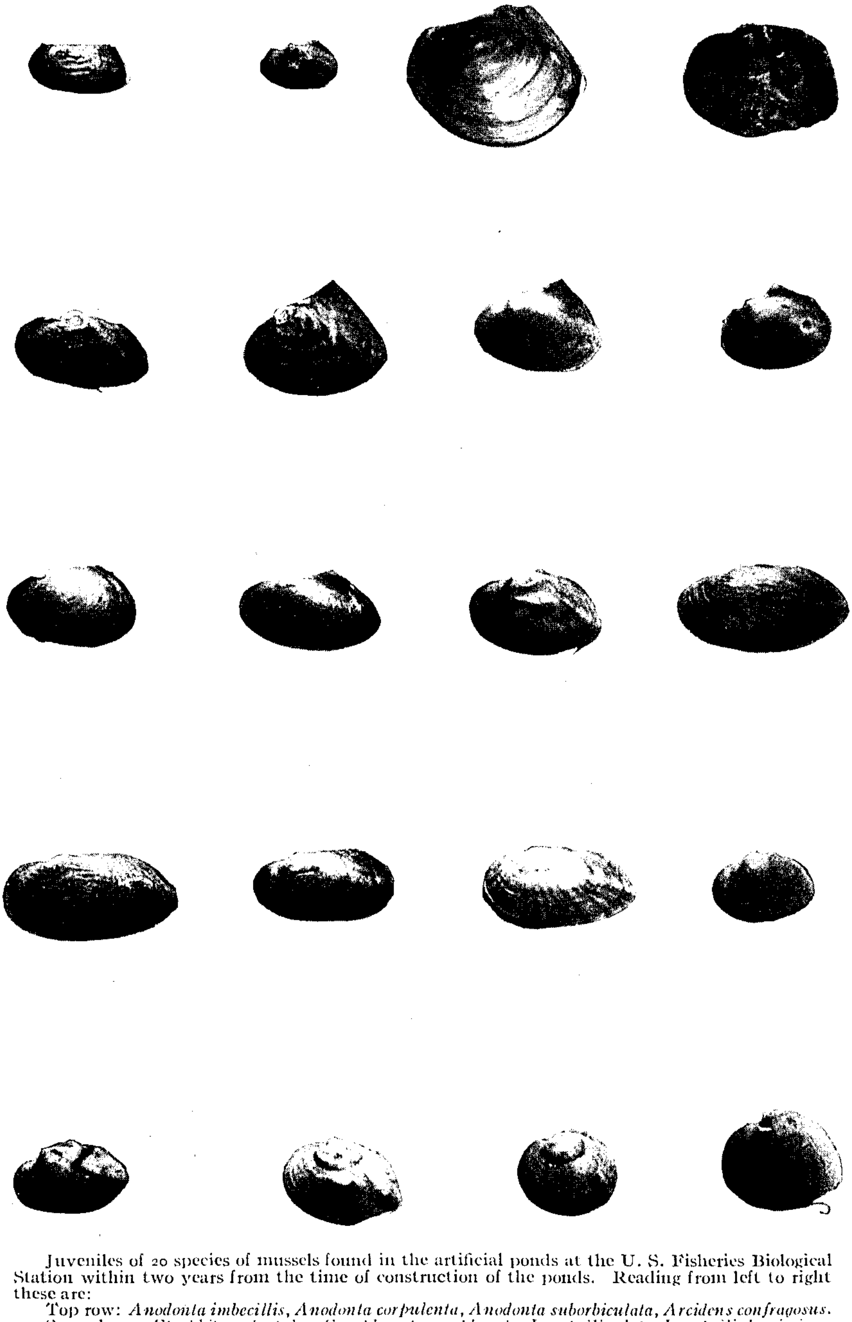
During the season of 1918 greater results were obtained with the Lake Pepin mucket, the young mussels being successfully reared in four troughs. In one trough a count of 746 was obtained. The experiments with *ligamentina* yielded negative results, though a lack of glochidia for infection greatly handicapped the work with this species.

The results in 1919 were still more gratifying. Young Lake Pepin muckets were obtained in each of five troughs planted with this species. In one trough 2,008 were counted at the end of the season, these little mussels varying in length from 9 mm. to 17.5 mm., the growth comparing very favorably with that made by the young of this species in their natural habitat. In a trough devoted to the river mucket, *L. ligamentina*, a total of 565 were reared. These little mussels varied in length from 5 mm. to 8.5 mm. In a trough planted with the yellow sand-shell a count of 2,006 was obtained at the end of the season, the young mussels varying in length from 5.5 mm. to 12 mm. The result of this experiment is highly interesting, in that it is the first record of the artificial rearing of this very valuable species in any quantity.

The 746 young *luteola* reared during the summer of 1918 were carried over the winter in a shallow crate bottom 5 feet square and 8 inches deep, submerged in one of the earth ponds. During the summer of 1919 an inventory of the crate bottom gave a count of 238 young mussels, a survival percentage of about 32 per cent.

The method of artificial rearing of young mussels, as detailed above, denotes a distinct departure from the methods previously used and gives the operator complete control of conditions throughout. The results of the experiments have been such as to justify the employment of the method on a much larger scale in future, and plans are under way for materially increasing the facilities and equipment. Certain phases of the work need further study and amplification. Additional information on the possible enemies of the young mussels in the troughs is needed; a study of their food should be made; it should be learned if artificial feeding is practicable; and further experiments should be made to determine the most favorable bottom material for the troughs, whether fine sand alone, or sand with a slight admixture of silt, etc. The present indications are that fine sand is the most desirable bottom material.

In summary of the topic of the culture of fresh-water mussels, it may be stated that the results of many experiments conducted under diverse conditions demonstrate that the valuable Lake Pepin mucket can be reared in quantities, under conditions of control. Sufficient success has been attained with other species to warrant confidence that, with them also, methods of securing constant results will be found.



Juveniles of 20 species of mussels found in the artificial ponds at the U. S. Fisheries Biological Station within two years from the time of construction of the ponds. Reading from left to right these are:

Top row: *Anodonta imbecillis, Anodonta corpulenta, Anodonta suborbiculata, Arcidens confragosus.*
Second row: *Strophitus edentulus, Symphynota complanata, Lampsilis alata, Lampsilis laevissima.*
Third row: *Lampsilis capax, Lampsilis gracilis, Lampsilis ventricosa, Lampsilis luteola.*
Fourth row: *Lampsilis subrostrata, Lampsilis parva, Lampsilis ligamentina, Obovaria ellipsis.*
Fifth row: *Plagiola donaciformis, Obliquaria reflexa, Quadrula plicata, Quadrula undata.*
All reproduced natural size excepting the two right-hand figures in top row which are reduced one-half. (Photographed by J. B. Southall.)

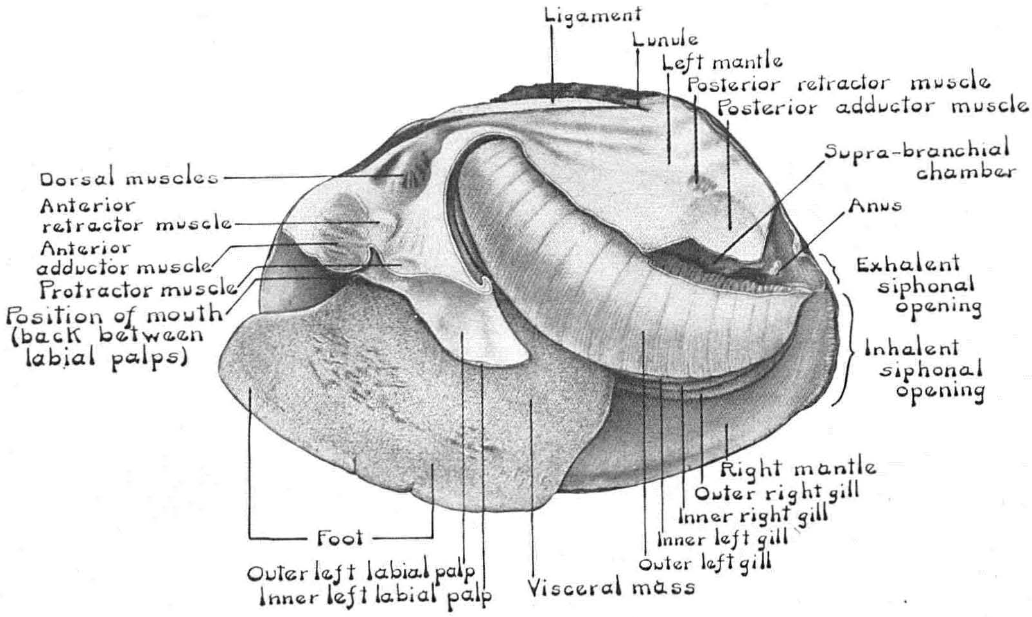


FIG. 1.—The structure of a fresh-water mussel. (Based upon drawing of white heel-splitter, *Symphynota complanata*, from Lefevre and Curtis, 1912.)

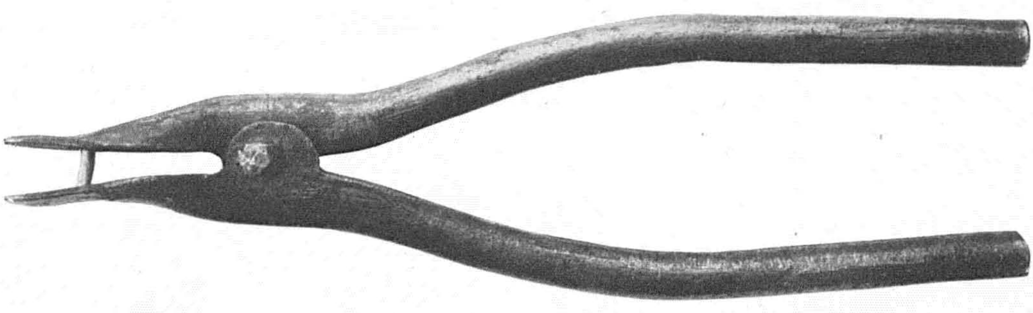


FIG. 2.—A tool which, if employed with care, may be used for partially opening living mussels for examination of conditions within the shell.

PART 3. STRUCTURE OF FRESH-WATER MUSSELS.

INTRODUCTION.

A general description of the structure of fresh-water mussels may assist those without special knowledge of the anatomy of mussels to follow intelligently the account of the natural history, propagation, and development which it has been the primary purpose of this report to give. It may also serve as a helpful introduction to persons with limited technical knowledge who wish to make original observations or experiments concerning the habits and growth of mussels. It has been the special purpose of the authors to point out the more conspicuous gaps in our knowledge of the behavior of mussels and their relations to the environment. Many of these gaps can readily be bridged by any who will take the trouble to observe painstakingly and repeatedly the conditions under which fresh-water mussels live in the streams, lakes, or ponds in one's own neighborhood. The species subjected to observation or experiment should of course be definitely known, but identifications of species can always be obtained of Government agencies or from independent specialists in the study of mollusks.

In most localities some species of mussels are easily obtainable and observable in nature or in aquaria. In rivers of the Atlantic States, generally, the common mussel is the *Unio complanatus*. The more familiar forms in lakes and alongshore in streams of the Mississippi Valley and the Great Lakes drainage are the fat mucket *Lampsilis luteola*,[a] and some of the floaters of the genus Anodonta. Closely related to the fat mucket is the mucket, *Lampsilis ligamentina*, which is common in the Mississippi and its tributaries as well as in many streams discharging into the Great Lakes. As a representative type in the simplicity of its form and of the sculpture and markings of its shell, the mucket serves as the basis of the following general description, except as explicit qualifications are made. With more or less modification, the account may be applied to whatever species is most readily available. The functions of the organs described will generally be briefly indicated.

Let it be understood first that a living mussel is commonly partly embedded in the bottom, with the forward end directed obliquely downward and the rear end upward. The "mouth" as understood by fishermen is in reality the double siphonal opening in the hinder part of the mussel; the true mouth, through which food is taken into the body, is a very small and scarcely discernible opening in the part of the soft body which is farthest away from the exposed end of the mussel.

The fresh-water mussels differ markedly in structure from the oyster or the pearl oysters which pertain to a different order of lamellibranchs. They are likewise far removed from the sea mussels, which lie in a third order. Their nearer relatives are the sea clams and the small Cyrenians of the rivers; the sea clams and the little clams (Cyrenians) of the rivers are more closely allied to each other than to fresh-water mussels. The pearly fresh-water mussels or Naiades comprise two great families,

[a] The best commercial type of the mussels of this species is also known as the "Lake Pepin mucket."

the Unionidæ, with which the present paper is concerned, and the Mutelidæ of South America and Africa. The Mutelidæ differ from the Unionidæ in some particulars of structure, especially in the form of teeth on the shell and in the form of larva, which is a *lasidium*, instead of a glochidium such as has been described above.

THE SHELL.

The shell is composed of two parts very similar in exterior aspect, but generally differing from each other in interior form. Each portion is called a valve, and the two valves are hinged together.

EXTERNAL FEATURES.

In form the shell is roughly elliptical, evenly rounded in front, but more or less angular behind. The lower or ventral margin is generally evenly rounded, but may be arched inward just behind the middle, especially in shells of females. The dorsal or hinge margin is rather straight except for the rounded prominence on each valve just in front of the middle of the back; this knob, or arched portion of each valve, is called the umbo. Where the umbones of opposite valves approximate each other they are more or less elevated above the surrounding shell surface to form the beaks. The beaks in many species, though not in the mucket, are beautifully sculptured with coarse or fine ridges in the form of single or double loops. With the river mucket, beak sculpture is entirely wanting, while it can be seen clearly in *Symphynota complanata* (Pl. XX, 2d row, 2d fig.). Almost every species, if good specimens are available, show some form of beak sculpture;[a] commonly, however, in older specimens the beaks are so much eroded that the ridges are hardly, if at all, apparent.

In some streams scarcely a single example can be found with the beaks preserved; in other waters erosion occurs less commonly and the beak markings can be observed even in some of the large examples.

In some cases the resting periods of winter have left distinct marks by color or otherwise on the shell, so that rings or zones corresponding to the growth of each year are recognizable. The rings of annual growth are not, however, generally recognizable on shells having a dark-colored exterior surface. It is also observed that such rings may result from other causes than the interruption of growth by the severity of winter. (See p. 132.)

A conspicuous feature of the shell is the prominent ridge, which extends from the beaks backward and downward to the posterior ventral angle of the shell. A somewhat similar ridge characterizes almost every species of mussels.

The exterior color of the shell is a most variable character. Generally speaking, the body color is a greenish straw, relieved by narrow green rays, very narrow on the beaks and widening out toward the lower margin. These rays are a nearly constant character in the mucket, but vary in number, in width, in brightness of color, and in being continuous or interrupted. The periostracum, or horny covering, of shells growing in clear streams is generally much more brightly rayed than that of those in turbid

[a] The beak sculpture of young specimens is a very important diagnostic character or means of distinguishing species which may closely resemble each other in general form. Compare the yellow and the slough sand-shells, *Lampsilis anodontoides* and *Lampsilis fallaciosa*, or the pocketbooks, *Lampsilis ventricosa* and *Lampsilis (Proptera) capax*, which are occasionally distinguished by this feature alone. The beak is, of course, the beginning of the shell—the oldest portion.

ones. Young shells are more brightly rayed than old, the rays generally fading somewhat or wholly disappearing with age. In different localities, and even in the same bed, the colors are various, the shells may be nearly uniformly straw-colored or largely green; again, a red or rusty-brown color may predominate. The red color without is commonly associated with a pink nacre within. The shell may be smooth and glossy or roughened by fine lines; a silky appearance may be caused by innumerable fine laminæ or folds projecting out from the surface of the periostracum. The silky surface is characteristic of some species, as the hickory-nut, *Obovaria ellipsis*.

Looking now at the top or hinge of the shell there is seen just back of the beaks a long, narrow, tough, leathery, elastic band, the ligament, an important part of the hinge mechanism. Just in front of the beak is a small region between the shell valves, which is occupied by a similar horny material. This is called the anterior lunule, but in the mucket it is scarcely developed, being about one-half inch long and very narrow in a specimen of 3 inches total length. A posterior lunule may be found just back of the ligament. The compressed form of the shell is noticeable in this view. Roughly speaking, the thickness of a mucket from side to side is about one-third of the length, while the width—or height, more correctly—is about two-thirds of the length.

INTERNAL FEATURES.

The interior surface of the shell is smooth, white, and lustrous, and usually somewhat iridescent in the extreme posterior portion. In color it is white or pinkish in the mucket, but in other species it may be salmon or purple. Often the proper color is obscured by yellow, greenish, rusty, or salmon-colored stains, resulting from disease, injury, or inclusion of mud in the nacre. The body of the shell is mainly calcareous, being composed chiefly of a compound of calcium of somewhat the same chemical composition as marble or limestone, but differing in physical structure from either. An account of the structure of shell is given in another place (p. 129).

The conspicuous features of the interior aspect of the shell are the general concavity of each valve; the deeper beak cavities; the dorsal margin roughened by ridges or protuberances known as the "teeth;" two rounded, impressed, and roughened surfaces, one near each end, the adductor muscle cicatrices; and a curved impressed line parallel to the margin of the shell, extending between the two scars just mentioned. This last is the pallial line and marks the attachment of certain muscles of the mantle.

The two valves, it is noted, are practically identical except for the teeth, which instead of being equal in the two valves, correspond to each other in such a way that the teeth of one valve fit into the spaces between the teeth of the opposite valve. The two valves are thereby interlocked so that they can not slide over each other. Heavier teeth characterize the mussels that are adapted to live in strong currents, while weak teeth or the total lack of them mark the species that must live in quiet waters. The teeth in each valve are of two forms; at the anterior or front end are the stout, rough, and somewhat conical cardinal or pseudocardinal teeth; while behind these, and more or less separated from them, are long, narrow, bladelike ridges, the lateral teeth. On the right valve there is one lateral tooth which exactly fits into the deep narrow furrow between the two slenderer lateral teeth of the left valve. The two valves are practically exact mirror images of each other except for the teeth; accordingly, in species such as the

Anodontas, which are without teeth, the bilateral symmetry is complete. In some marine bivalves the two shells are essentially different, as in the oyster, where one is concave while the other is flattened and smaller.

The ligament is composed of two parts; the dark outer layer is inelastic and continuous with the periostracum of the shell; while the inner part, comprising the bulk of the ligament, is elastic and bears somewhat inappropriately the name of cartilage. The elastic cartilage is confined between the inelastic layer above and the firm hinge of the shell below. It is compressed when the shell is closed. The natural or relaxed condition of the shell is, therefore, open; that is to say, with the valves separated below by about one-half inch. Consequently, the shell is kept closed in life only by an exertion on the part of the animal. This is accomplished by means of two stout bands of muscle fibers, constituting the anterior and posterior adductor muscles, which extend from one valve to the other near each end of the shell. These are firmly attached to the shell at each end, the places of attachment being the conspicuous rounded impressions previously noticed.

The hinge mechanism is completed by the lunule previously referred to. This is a thin horny covering occupying the space between the valves in front of the beak. Unlike the ligament behind, it is stretched when the shell is open. The lunule doubtless has no especial significance except to serve as a protective covering and to make a firm union of the two valves.

Besides the two adductor impressions and the pallial line, some smaller muscle impressions are apparent. Such are those of the muscles which draw back the foot, or the anterior and posterior retractor muscles. These are small impressions, two in each valve, just above the big adductor impressions and in this mussel (*Lampsilis ligamentina*) confluent with the latter. The impression of the protractor, or the muscle which aids in protruding the foot, is usually quite distinct and just beneath the anterior adductor impression. Deep in the beak cavity and on the under surface of the cardinal teeth, or the bridge between cardinal and lateral teeth, are small pits which are the points of attachment of numerous small muscles that serve to elevate the foot. These last are the dorsal muscle scars referred to in systematic descriptions. (See Pl. XXI, fig. 1.)

DIVERSITY IN FORM.

Many modifications of the above description would have to be made for other species of mussels. The shell may be pear-shaped as in the niggerhead (*Quadrula ebenus*), or nearly circular as in *Quadrula circulus;* it may be very much inflated as in *Lampsilis capax* or in *L. ventricosa* (the pocketbook), or exceedingly compressed as in *Symphynota compressa*. In some the shell is not only greatly flattened from side to side but also extends upward in wings before and behind the beaks. Such species are given locally such descriptive names as pancakes, hatchet-backs (*Lampsilis alata*), or heel-splitters (*Symphynota complanata*). Some shells are proportionately very heavy, while others, included mostly in the genus Anodonta, the paper-shells or floaters, are so thin as to be useless for any present economic purpose. The Anodontas, adapted to live in lakes or close alongshore in streams, are further characterized by the entire absence of teeth.

Variations in thickness or in uniformity of thickness are important from the standpoint of the button makers, and so also are variations in the surface sculpture. Some forms are covered with protuberances or knobs in regular or irregular pattern, thus acquiring such common names as warty-backs or pimple-backs; while others have strong ridges running obliquely across the shell, as the three-ridge, *Quadrula undulata*, the blue-point, *Q. plicata*, and the washboard, *Quadrula heros*. One species, *Unio spinosus*, of Alabama, bears long sharp spines on the shell. Diversity of interior color has previously been alluded to. No satisfactory explanation of the colors of nacre has yet been offered. Certain species are almost always white-nacred, as the pimple-back, maple-leaf, and niggerhead. Others are white or pink, examples of the two colors living side by side. Some species have usually a deep purple or salmon nacre, but white-nacred shells of the same species may predominate in particular streams.

Variations in external color are conspicuous in any collection of shells even from the same mussel bed. Along with shells of uniform color, light or dark, we find shells of glossy surface and brilliantly rayed; the rays may be continuous or variously interrupted, sometimes composed of small zigzag markings forming striking and fantastic patterns. In short, the differences in form and color of shell are unlimited and could not be described, even within the limits of a systematic monograph.

THE SOFT BODY.

For observation of the body the mussel may be carefully opened by severing the adductor muscles close to one valve, preferably the left, and gently freeing the soft mantle from the shell as the knife blade is passed from one end of the shell to the other. Removing or bending back the upper (left) valve, the body of the mussel is seen to be almost completely enveloped in a thin mantle corresponding to the interior of the shell in form and size (Pl. XXI, fig. 1).

FORM AND FUNCTIONS OF THE MANTLE.

The mantle is composed of right and left sheets entirely free from each other except along the back where the two sheets are continuous not only with each other but with the body as well. The mantle is, in fact, a double fold from the back of the mussel draped over the body and lining the shell. A thin wing or dorsal extension of the mantle covers entirely the surfaces of the cardinal and lateral teeth and underlies the ligament.

The mantle is not of uniform character throughout but shows a broad border thicker than the central portion and somewhat muscular. This border along its inner line is attached to the shell through many fine muscle fibers, the attachment of which forms the pallial line on the shell. The border is muscular and, therefore, contractile; the lower or right mantle, which has not been separated from the shell, will have its edge contracted away somewhat from the margin of the valve; generally there is apparent a thin film of horny material which connects the edge of the mantle with the extreme edge of the shell. It is not infrequently the case that in separating the surface of the mantle from the shell a delicate transparent membrane is distinguishable, some parts of which adhere to the mantle and some parts to the shell. Unless, therefore, a rupture has occurred, the mantle normally is actually continuous at the margin with the outer surface of the shell, and probably organically but delicately connected to the inner surface of the shell over its entire surface.

The relations of the mantle as observed will have greater significance from a statement of its functions. Besides supplementing the gills in respiration and serving along its border as a sensory organ, a chief function of the mantle is the formation of shell. The extreme edge of the mantle secretes the horny covering of the shell, as also the ligaments and lunule, while the remaining mantle surface secretes the calcareous shell. For our purpose, accordingly, the mantle is a most significant organ. Diseases or other influences affecting the mantle frequently show effects in the shape, color, or quality of the shell, and it is in the mantle, probably, that all free pearls are produced. The mantle is not, however, the only portion of the mussel capable of forming shell. The two adductor muscles pass entirely through the mantle, having direct attachment to the shell. While the shell becomes thicker in other parts by the superposition of layer after layer of calcareous material from the surface of the mantle, the thickening of the shell against the muscles is in some measure, apparently, a function of the muscles themselves. It is not surprising, therefore, that these muscles also give rise to a large number of pearl formations, baroques, and slugs, but not, ordinarily, good pearls. No other parts commonly give origin to pearls, although it is reported that pearls have been found within the body. Baroque pearls and slugs are frequently found in the tissue just beneath the hinge line, but this is actually a part of the mantle.

The shell substance formed by the muscles is called hypostracum, and is largely horny in nature. Since each muscle occupies a nearly constant relative position regardless of the size to which the mussel attains, it is evident that in any adult individual the muscle traveled in the course of life history from the back to its latest position; the hypostracum, therefore, does not occupy a single spot but is a tapering vein passing through the nacre from the beak to the position of the muscle at any given time. Similarly the hypostracum of the pallial line is the margin of a thin stratum of like substance which extends from the beak or beginning of the shell and divides the nacre into two portions (p. 130).

The mantle has other functions of great importance. When the muscles are relaxed and the shell is gaping, the opening between the valves of the shell is largely closed by the apposed margins of the mantle. Nothing can enter between the valves of the shell without affecting the highly sensitive border of the mantle and thus giving warning to the animal, which may then contract its muscles and close the shell instantly. The nerves of the margin of the mantle are not only sensitive to tactile stimuli, but apparently are also connected with organs of something like visual function, so that the animal may close or open its shell under the influence of shadows or bright light.

It is the margins of the mantle that surround and form the two siphonal openings at the hinder end of the shell, through one of which water and food pass into the shell, while through the other water passes out, conveying the waste products. The lower of these two openings particularly is protected by projections of the mantle, in the form of papillæ or fimbriæ, which, being very sensitive, give warning of any objectionable character or content of the water.

OTHER CONSPICUOUS ORGANS.

Without disturbing the upper mantle two internal organs are distinctly evident. The heart is recognized by its throbbing action. It lies at the back just below the lateral teeth of the hinge and in front of the posterior adductor muscle. The rate of beating varies in different species and under different conditions but is generally under 20 pulsations per minute. The heart will continue to beat a long time after the shell has been opened. Near the anterior adductor is a greenish mass of tissue, the so-called liver or digestive gland, surrounding the white stomach. Through the transparent tissue, covering the chamber inclosing the heart, another portion of the alimentary tube is generally distinguishable. This is the rectum or hinder portion of the intestine which passes directly through the heart to discharge just above the posterior adductor muscle. The brownish tissue beneath the heart represents the organ of Bojanus, as it is called, with functions corresponding to a kidney.

To distinguish other organs the mantle must be folded back. The muscular mass of plowshare form and brownish white in color, constituting the anteroventral border of the body, is the foot. Several curtainlike flaps are conspicuous. Toward the forward end are two large earlike flaps, the labial palpi or lipfolds. They are easily torn in folding the mantle back, but if in good condition, it may seen that each of these palps is continuous, around the front end of the body, with the palp of the opposite side. Immediately in front of the body they are very narrow and lie one above and the other just below an exceedingly small opening, the mouth, which can be seen only by very careful examination.

The other two folds are much larger and rounded below. These are the gills, which extend from the anterior third of the body to the extreme posterior end. The inner is slightly the larger. The outer gill is connected above and on the outside to the mantle. Folding this one back, it is seen that it is attached also to the inner gill above. The inner gill on the inner side is attached to the body and, behind the body, to the inner gill of the opposite side. In many species the inner gill is partially free from the body. These gills, though thin, are really basketlike structures, containing chambers within, as will be described below.

INTERNAL STRUCTURE.

It is not the province of this paper to enter minutely into the internal anatomy. But the following epitomized statement of the structure of the animal is given to serve as a key to the understanding of the functions of the organism as a whole.

The digestive system comprises the mouth, with a short tube or gullet, leading from the mouth to the stomach; the dark brown digestive gland, or so-called liver, which surrounds the stomach; and the intestine, which is a long tube that leads downward from the stomach and coils upon itself behind the foot in a complex way, before bending upward to approach the back and extend posteriorly straight through the heart as the rectum, which opens just above the posterior adductor muscle. A long, slender flexible gelatinous rod, the crystalline style, is frequently found in the intestine; it serves a function in separating food from foreign particles and comprises a store of enzymes or ferments for use in the processes of digestion (Nelson, 1918).

The excretory system comprises a functional kidney with a bladder which discharges into the cavity surrounding the heart.

The circulatory system includes, as in higher animals, heart, blood, arteries, and veins. The blood of a mussel is colorless but maintains a regular circulation from the heart through certain arteries to many smaller vessels ramifying all through the body, returning by a main vein to the kidneys, thence to the gills and back through other veins to the heart to begin its course anew. The blood, however, which passes from the arteries to the mantle, returns, not through the kidneys or the gills, but directly to the heart.

The mantle and the gills constitute the chief respiratory organs, where the blood is aerated. The significance of the mode of circulation is evident. The venous blood returning from the body laden with waste products passes first to the kidney, thence to the gills to be cleared of impurities and freshened with oxygen, after which it returns to the heart in purified condition. The blood returning from the mantle requires no further purification or oxygenation before entering the heart.

Without a distinct brain, the body of the mussel is coordinated through a nervous system, consisting of three pairs of nerve centers, which are connected together by nerve cords. Two of these centers or ganglia lie one on each side of the gullet near the mouth, a second pair is in the foot, while the third lies just beneath the posterior adductor muscle. From these ganglia fine nerves are sent off to supply the various tissues and organs.

Though eyes and ears are not present, sensory organs are not entirely wanting. A small organ near the ganglia beneath the posterior adductor is supposed to serve to test the purity of the water. Another, the otocyst, is sometimes found near the ganglia in the foot and possibly serves as a balancing organ, by means of which the mussel may feel whether it is in horizontal or vertical position. Sensory cells are found along the border of the mantle, especially near the posterior openings for the passage of water. (See p. 87.)

The organs of reproduction comprise a large part of the body mass above the foot. The ova or semen are discharged through small openings on each side of the body into the chamber above the gills. In the case of the male the sperms are thence passed out with the respiratory (exhalent) current and set free in the water. They may be drawn into the female with the water of the inhalent current, to fertilize the ova perhaps as they are passed down from the suprabranchial chamber into the tubes in the gills where incubation takes place. In some species the reproductive tissue is brightly colored—orange, pink, or red.

STRUCTURE AND FUNCTIONS OF THE GILLS.

The gills, as the name would suggest, are primarily breathing organs. Nevertheless, they have an equal if not a greater function in food gathering, and, furthermore, in fresh-water mussels and in some other lamellibranchs, the gills have acquired a third office which is of coordinate importance with the other two. We have seen that the incubation of the egg takes place in the water tubes of the gills, a part or all of which may be filled with embryo mussels. The respiratory function of the gills of the female mussel must be greatly reduced during the period of incubation, and this condition is made possible by the fact that the mantle of the mussel plays an equal rôle with the gills in respiration. In becoming adapted to this function of protection and perhaps nourishment of the eggs and young, the gills of the female have undergone varied modifications in different species. In consequence, when gravid females can be examined, the gills of different mussels are often found to be more strikingly distinct than is the external form or any other obvious character. This is especially true when microscopic study of the structure of the gills can be made.

Whether or not, therefore, these differences are a true guide to relationships, the gills become one of the most convenient organs for distinguishing genera or species and serve as the most important basis of modern classification.

Some knowledge of the anatomy of the gills is necessary for proper comprehension of the life process of mussels in breathing, feeding, and reproduction.

The gills consist, as we have seen, of two platelike bodies on each side between the visceral mass and the mantle. We have thus a right and a left inner gill and a right and a left outer gill. Seen from the surface, each gill presents a delicate double striation, being marked by faint lines running parallel with the long axis and by more pronounced lines running at right angles to the long axis of the organ. Moreover, each gill is double, being formed of two similar plates, the inner and outer lamellæ united with one another below as well as before and behind but free at the top or dorsally. The gill has thus the form of a long and extremely narrow bag open above. Its cavity is subdivided by vertical bars of tissue, the interlamellar junctions, which extend between the two lamellæ and divide the intervening space into distinct compartments or water tubes, closed below but freely open along the dorsal edge of the gill. The vertical striation of the gill is due to the fact that each lamella is made up of a number of close-set gill filaments; the longitudinal striation, to the circumstance that these filaments are connected by horizontal bars, the interfilamentar junctions. At the thin free, or ventral, edge of the gill the filaments of the two lamellæ are continuous with one another, so that each gill has actually a single set of V-shaped filaments, the outer limbs of which go to form the outer lamella, their inner limbs the inner lamella. Between the filaments, and bounded above and below by the interfilamentar junctions, are minute apertures or ostia, which lead from the mantle cavity through a more or less irregular series of cavities into the interior of the water tubes. (After Parker and Haswell.)

The gills, then, which appear as thin plates, are really comparable to long baskets greatly flattened from side to side, the interior of the basket being subdivided into a series of deep tubes, all in one row. The surface of the basket, which is perforated by many pores visible only with a microscope, is covered with very minute paddles like fine flat hairs. The concerted action of these little paddles, called cilia, keeps driving the water from without the gill through the minute pores into the water tubes. Through these tubes the water passes upward into a chamber above the water tubes, called the suprabranchial chamber, and thence backward and finally out of the shell.

Since the cilia are habitually driving the water through the surface of the gills into the water tubes, it follows that there must be a regular stream of water entering the mantle chamber from without through the open valves, as well as an outgoing stream passing out from the chamber above the gills. These two streams are known as the inhalent current and the exhalent current, respectively. If a mussel is observed in undisturbed condition on the bottom of an aquarium (Pl. V, figs. 1 and 2), the two openings between the edges of the mantle are readily seen and the currents may easily be observed by introducing with a pipette into the water near each opening a little colored water. The coloring matter placed near the lower inhalent current is drawn into the shell, but that placed near the upper opening is driven forcibly away. The two pronounced currents, or rather two aspects of the same current, are, it may be repeated, formed entirely by the minute paddles surrounding the innumerable pores of the gill surfaces.

The gills themselves are living strainers in the course of this current, and as the water passes through them the material which serves as food is filtered out to be passed on to the mouth; at the same time, the blood in the minute vessels and spaces within the gill filaments and partitions is being purified and recharged with oxygen. The matter strained from the water becomes clotted with mucus and is driven along by the cilia over the surface of the gills to the labial palpi, where it is taken up and if suitable for food is passed on to the mouth, for the surfaces of the palpi as well as of the gills are covered by cilia or minute paddles, the combined action of which forms a wonderful mechanism for conveying the food from any point of the gill surface into the funnel-shaped mouth. The detailed working of this mechanism and the places and means of "switching off" undesirable matter form too complex a subject to be treated in this paper. (See Allen, 1914, and Kellogg, 1915.)

The course of the water is better understood after observing the mode of attachment of the gills. The outer lamella of the outer gill is attached to the mantle throughout its entire length, while its inner lamella and the outer lamella of the inner gill are attached together to the body. There is thus above each gill a small suprabranchial chamber just above the water tubes. Behind the body or visceral mass, however, the inner lamella of the right and left inner gills are attached together, and there is, therefore, a single large chamber above the four gills—the cloaca or exhalent chamber. The water, after passing through the pores of the gill surface, makes its course up the water tubes and backward by the suprabranchial chamber into the cloaca, to be passed thence out of the shell.[a]

It will be understood that the eggs and young borne in the water tubes of the gills, which become marsupial pockets, are most favorably located for respiration, being situated, as it were, in the respiratory current of the mother. There is, among the various species of the Unionidæ, great variation in the extent to which the gills are employed as marsupia (p. 139). In certain species the water tubes of all four gills are filled with eggs, in others only those of the outer gills receive the eggs, while in still others a portion of each outer gill is set apart as a marsupium. This may be the posterior half, the posterior third, or a few water tubes in the middle.

It is largely because of the great significance of the gills with their remarkably diverse functions of food collection, respiration, and gestation that the modifications both in the external form and in the histologic structure of the gills are important and serve so well as a basis of classification. Generally speaking, species in which all four gills serve as marsupia are considered lower or more primitive forms. Those in which the marsupia are most highly specialized are regarded as most highly developed.

---

[a] The effect of the gills in filtering the water is made clear when one fills two jars with turbid river water after placing in each sufficient sand for a mussel to become embedded. If one or two mussels are placed in one of these jars, the water will become clear in a comparatively short time.

BIBLIOGRAPHY.[a]

ADENEY, W. E.

1912. *See* New York (City). Report Metropolitan Sewerage Commission of New York. New York.

ALLEN, W. R.

1914. The food and feeding habits of fresh-water mussels. Biological Bulletin, Marine Biological Laboratory, Woods Hole, Mass., Vol. XXVII, No. 3, pp. 127–146, 3 pls. Lancaster.

BAKER, FRANK COLLINS.

1898. The Mollusca of the Chicago area. The Pelecypoda. The Chicago Academy of Sciences, Bulletin III, Part I of the Natural History Survey, pp. 9–130, pls. 1–27. Chicago.

1910. The ecology of the Skokie Marsh Area, with special reference to the Mollusca. Bulletin, Illinois State Laboratory of Natural History, Vol. VIII, Art. IV, pp. 441–499, pls. VI–XXV. Urbana.

1916. The relation of mollusks to fish in Oneida Lake. Technical Publication No. 4, New York State College of Forestry, Syracuse University, Vol. XVI, No. 21, pp. 1–366, figs. 1–50. Syracuse.

1918. The productivity of invertebrate fish food on the bottom of Oneida Lake with special reference to mollusks. Technical Publication No. 9, New York State College of Forestry, Syracuse University, Vol. XVIII, No. 2, pp. 1–253, figs. 1–44, 2 pls. Syracuse.

1920. Animal life and sewage in the Genesee River, New York. The American Naturalist, Vol. LIV, pp. 152–161. New York.

BIRGE, E. A., and JUDAY, C.

1911. The inland lakes of Wisconsin. The dissolved gases of the water and their biological significance. Wisconsin Geological and Natural History Survey, Bulletin No. XXII, Scientific Series No. 7, 259 pages. Madison.

BOEPPLE, J. F., and COKER, R. E.

1912. Mussel resources of the Holston and Clinch Rivers of eastern Tennessee. U. S. Bureau of Fisheries Document 765, 13 pages. Washington.

CALL, RICHARD E.

1900. A descriptive illustrated catalogue of the Mollusca of Indiana. Twenty-fourth Annual Report, Department of Geology, State of Indiana, pp. 335–535, pls. 1–78. Indianapolis.

CHURCHILL, E. P., Jr.

1915. The absorption of fat by fresh-water mussels. Biological Bulletin, Marine Biological Laboratory, Woods Hole, Mass., Vol. XXIX, No. 1, pp. 68–86, 3 pls. Lancaster.

1916. The absorption of nutriment from solution by fresh-water mussels. Journal of Experimental Zoology, Vol. XXI, No. 3, pp. 403–429. Baltimore.

CLARK, H. WALTON, and GILLETTE, GEORGE H.

1911. Some observations made on Little River, near Wichita, Kans., with reference to the Unionidæ. Proceedings, Biological Society of Washington, Vol. XXIV, pp. 63–68. Washington.

CLARK, H. WALTON, and WILSON, CHARLES B.

1912. The mussel fauna of the Maumee River. U. S. Bureau of Fisheries Document 757, 72 pages, 2 pls. Washington.

COKER, ROBERT E.

1913. Demonstration of Dr. Herrick's free pearls of forced production. Transactions, American Fisheries Society, 1912, pp. 71–74. Washington.

1919. Fresh-water mussels and mussel industries of the United States. Bulletin, U. S. Bureau of Fisheries, Vol. XXXVI, 1917–18, pp. 13–89, pls. I–XLVI. Washington.

[a] Including only publications cited.

COKER, ROBERT E., and SOUTHALL, JOHN B.
1915. Mussel resources in tributaries of upper Missouri River. [With description of shell found in the James River, Huron, S. Dak., July 27, 1913.] Appendix IV, Report, U. S. Commissioner of Fisheries, 1914, 17 pages, 1 pl., 1 fig. Washington.

COKER, ROBERT E., and SURBER, THADDEUS.
1911. A note on the metamorphosis of the mussel *Lampsilis lævissimus*. Biological Bulletin, Marine Biological Laboratory, Woods Hole, Mass., Vol. XX, No. 3, pp. 179-182, 1 pl. Lancaster.

CORWIN, R. S.
1920. Raising fresh-water mussels in enclosures. Transactions, American Fisheries Society, Vol. XLIX, No. 2, pp. 81-84. Columbus.

DANGLADE, ERNEST.
1914. The mussel resources of the Illinois River. Appendix VI, Report, U. S. Commissioner of Fisheries, 1913, 48 pages, 5 pls., 2 figs., 1 map. Washington.

DOLE, R. B.
1909. The quality of surface waters in the United States. Part 1. Analyses of waters east of the one hundredth meridian. U. S. Geological Survey Water-Supply Paper 236, 142 pages, 1 map. Washington.

EVERMANN, BARTON WARREN, and CLARK, HOWARD WALTON.
1918. The Unionidæ of Lake Maxinkuckee. Proceedings, Indiana Academy of Science, 1917, pp. 251-285. Indianapolis.

FARRER, W. J.
1892. Mortality in mussels at Orange, Va. The Nautilus, Vol. V, p. 141. Philadelphia.

FORBES, STEPHEN A.
1913. Biological and chemical conditions on the upper Illinois River. Proceedings, Fifth Meeting, Illinois Water Supply Association, Urbana, Ill., pp. 161-170.

FORBES, STEPHEN A., and RICHARDSON, ROBERT EARLE.
1919. Some recent changes in Illinois River biology. Bulletin, Department of Registration and Education, Division of the Natural History Survey of Illinois, Vol. XIII, Art. VI, pp. 139-156. Urbana.

FRIERSON, L. S.
1903. Observations on the byssus of Unionidæ. The Nautilus, Vol. XVII, pp. 76-77. Boston.
1905. Notes on young Unionidæ. The Nautilus, Vol. XIX, pp. 49-50. Boston.

GRIER, N. M.
1920. Sexual dimorphism and some of its correlations in the shells of certain species of Najades. The American Midland Naturalist, Vol. VI, No. 8, pp. 165-172. Notre Dame.
1920a. Variation in the nacreous color of certain species of Naiades inhabiting the upper Ohio drainage and their corresponding ones in Lake Erie. American Midland Naturalist, Vol. 6, pp. 211-243. Notre Dame.

HEADLEE, THOMAS J.
1906. Ecological notes on the mussels of Winona, Pike, and Center Lakes of Kosciusko County, Indiana. Biological Bulletin, Marine Biological Laboratory, Woods Hole, Mass., Vol. XI, No. 6, pp. 305-318, 1 pl. Lancaster.

HEADLEE, T. J., and SIMONTON, JAMES.
1904. Ecological notes on the mussels of Winona Lake. Proceedings, Indiana Academy of Science, 1903, pp. 173-179. Indianapolis.

HOWARD, A. D.
1914. Experiments in propagation of fresh-water mussels of the Quadrula group. Appendix IV, Report, U. S. Commissioner of Fisheries, 1913, 52 pages, 6 pls. Washington.
1914a. Some cases of narrowly restricted parasitism among commercial species of fresh-water mussels. Transactions, American Fisheries Society, Vol. XLIV, No. 1, pp. 41-44. New York.
1915. Some exceptional cases of breeding among the Unionidæ. The Nautilus, Vol. XXIX, pp. 4-11. Boston.

ISELY, FREDERICK B.
1911. Preliminary note on the ecology of the early juvenile life of the Unionidæ. Biological Bulletin, Marine Biological Laboratory, Woods Hole, Mass., Vol. XX, No. 2, pp. 77–80. Lancaster.
1914. Experimental study of the growth and migration of fresh-water mussels. Appendix III, Report, U. S. Commissioner of Fisheries, 1913, 24 pages, 3 pls. Washington.
KELLOGG, J. L.
1915. Ciliary mechanisms of Lamellibranchs with descriptions of anatomy. Journal of Morphology, Vol. XXVI, No. 4, pp. 625–701, 72 figs. Philadelphia.
KELLY, H. M.
1899. A statistical study of the parasites of the Unionidæ. Bulletin, Illinois State Laboratory of Natural History, Vol. V, Art. VIII. Urbana.
LATTER, O. H.
1891. Notes on Anodon and Unio. Proceedings, Zoological Society of London, pp. 52–59. London.
LEFEVRE, GEORGE, and CURTIS, WINTERTON C.
1910. Experiments in the artificial propagation of fresh-water mussels. Bulletin, U. S. Bureau of Fisheries, Vol. XXVIII, 1908, pp. 615–626. Washington.
1910a. Reproduction and parasitism in the Unionidæ. Journal of Experimental Zoology, Vol. IX, No. 1, pp. 79–115, 1 fig., 5 pls. Baltimore.
1911. Metamorphosis without parasitism in the Unionidæ. Science, Vol. XXXIII, pp. 863–865. New York.
1912. Studies on the reproduction and artificial propagation of fresh-water mussels. Bulletin, U. S. Bureau of Fisheries, Vol. XXX, 1910, pp. 105–201, pls. VI–XVII. Washington.
LEIDY, JOSEPH.
1904. Researches in helminthology and parasitology, by Joseph Leidy, M. D., LL. D. (Arranged and edited by Joseph Leidy, jr.) Smithsonian Miscellaneous Collections, Vol. XLVI, Art. III, pp. 1–281. Washington.
MAURY, C. J.
1916. Fresh-water shells from central and western New York. The Nautilus, Vol. XXX, pp. 28–33. Boston.
MOORE, J. P.
1912. Classification of the leeches of Minnesota. Geological and Natural History Survey of Minnesota, Zoological Series No. V, Part III, pp. 65–128. Minneapolis.
MUTTKOWSKI, R. A.
1918. The fauna of Lake Mendota. Transactions, Wisconsin Academy of Sciences, Arts, and Letters, Vol. XIX, Part I, pp. 374–482. Madison.
NEEDHAM, JAMES G., and LLOYD, J. T.
1916. The life of inland waters. 438 pages. Comstock Publishing Company, Ithaca.
NELSON, THURLOW C.
1918. On the origin, nature, and function of the crystalline style of Lamellibranchs. Journal of Morphology, Vol. XXXI, No. 1, pp. 53–111. Philadelphia.
NEW YORK (CITY). Report of the Metropolitan Sewerage Commission of New York.
1912. Present sanitary condition of New York Harbor and the degree of cleanness which is necessary and sufficient for water. 457 pages. (Adeney, p. 80.) New York.
OLT, A.
1893. Lebensweise und Entwicklung des Bitterlings. Zeitschrift für wissenschaftliche Zoologie. Band 55, pp. 543–575 (1 pl.). Leipzig.
ORTMANN, A. E.
1909. The breeding season of Unionidæ in Pennsylvania. The Nautilus, Vol. XXII, No. 9, pp. 91–95, and No. 10, pp. 99–103. Boston.
1911. A monograph of the Najades of Pennsylvania. Memoirs, Carnegie Museum, Vol. IV, No. 6, pp. 279–347, pls. 86–89. Pittsburgh.
1912. Notes upon the families and genera of the Najades. Annals, Carnegie Museum, Vol. VIII, No. 2, pp. 222–365. Pittsburgh.
1913. The Alleghenian divide, and its influence upon the fresh-water fauna. Proceedings, American Philosophical Society, Vol. LII, No. 210, pp. 287–390, pls. XII–XIV. Philadelphia.

ORTMANN, A. E.—Continued.

1919. A monograph of the Naiades of Pennsylvania. Part III. Systematic account of the genera and species. Memoirs, Carnegie Museum, Vol. VIII, No. 1, 384 pp., 21 pls. Pittsburgh.

1920. Correlation of shape and station in fresh-water mussels (Naiades). Proceedings, American Philosophical Society, 1920, Vol. LIX, pp. 269–312. Philadelphia.

OSBORN, HENRY LESLIE.

1898. Observations on the anatomy of a species of Platyaspis found parasitic on the Unionidæ of Lake Chautauqua. Zoological Bulletin, Vol. II, No. 2, pp. 55–67. Boston.

PFUND, A. H.

1917. The colors of mother of pearl. Journal of the Franklin Institute, April, 1917, pp. 453–464. Illustrated. Philadelphia.

REIGHARD, J. E.

1894. A biological examination of Lake St. Clair. Bulletin, Michigan Fish Commission, No. 4, pp. 1–60. Lansing.

REULING, F. H.

1919. Acquired immunity to an animal parasite. Journal of Infectious Diseases, Vol. XXIV, No. 4, pp. 337–346. Chicago.

SCAMMON, R. E.

1906. The Unionidæ of Kansas. Part I. The Kansas University Science Bulletin, Vol. III, No. 9 (whole series, Vol. XIII, No. 9), pp. 279–373, pls. 62–85. Lawrence.

SHELFORD, VICTOR E.

1913. Animal communities in temperate America. Bulletin 5, Geographic Society of Chicago, 362 pages, 306 figs. Chicago.

1918. Conditions of existence. Ward and Whipple's Fresh-water Biology, Chapter II, pp. 21–60. New York.

1919. Fortunes in wastes and fortunes in fish. The Scientific Monthly, August, 1919, pp. 97–124. New York.

SHIRA, AUSTIN F.

1913. The mussel fisheries of Caddo Lake and the Cypress and Sulphur Rivers of Texas and Louisiana. U. S. Bureau of Fisheries Economic Circular No. 6, 10 pages. Washington.

SIMPSON, CHARLES TORREY.

1899. The pearly fresh-water mussels of the United States; their habits, enemies, and diseases, with suggestions for their protection. Bulletin, U. S. Bureau of Fisheries, Vol. XVIII, 1898, pp. 279–288. Washington.

1900. Synopsis of the Naiades, or pearly fresh-water mussels. Proceedings, U. S. National Museum, Vol. XXII, No. 1205, pp. 501–1004, Pl. XVIII. Washington.

1914. A descriptive catalogue of the Naiades, or pearly fresh-water mussels. In 3 parts, 1540 pp. Bryant Walker, Detroit, Mich. [Ann Arbor Press, Ann Arbor, Mich.]

STERKI, V.

1891. A byssus in Unio. The Nautilus, Vol. V, pp. 73–74. Philadelphia.

1891a. On the byssus of Unionidæ, II. Idem., pp. 90–91.

1892. A few observations concerning death of fresh-water Mollusca. Idem., pp. 135–136.

STRODE, W. S.

1891. Destruction of *Anodonta corpulenta* Cpr. at Thompson's Lake, Illinois. The Nautilus, Vol. V, pp. 89–90. Philadelphia.

SURBER, THADDEUS.

1912. Identification of the glochidia of fresh-water mussels. U. S. Bureau of Fisheries Document 771, 10 pp., 3 pls. Washington.

1913. Notes on the natural hosts of fresh-water mussels. Bulletin, U. S. Bureau of Fisheries, Vol. XXXII, 1912, pp. 101–116, pls. XXIX–XXXI. Washington.

1915. Identification of the glochidia of fresh-water mussels. Appendix V, Report U. S. Commissioner of Fisheries, 1914, 9 pages, 1 pl. Washington.

UTTERBACK, W. I.

1916. Breeding record of Missouri mussels. The Nautilus, Vol. XXX, No. 2, pp. 13–21. Boston.

WALKER, BRYANT.
1913. The Unione fauna of the Great Lakes. *Reprinted from* The Nautilus, Vol. XXVII (June, July, August, and September), 20 pages, 5 figs. Boston.
1918. A synopsis of the classification of the fresh-water Mollusca of North America, north of Mexico, and a catalogue of the more recently described species, with notes. University of Michigan Museum of Zoology, Miscellaneous Publications No. 6, pts. I and II, 213 pages, 233 figs. Ann Arbor.
WARD, HENRY B.
1896. A biological examination of Lake Michigan in the Traverse Bay Region. Bulletin, Michigan Fish Commission, No. 6, pp. 1–71. Lansing.
WARD, HENRY B., and WHIPPLE, GEORGE C.
1918. Fresh-water biology, first edition, 1111 pages. John Wiley Sons (Inc.). New York.
WENRICK, D. H.
1916. Notes on the reaction of bivalve mollusks to changes in light intensity: Image formation in Pecten. Journal of Animal Behavior, Vol. 6, No. 4, pp. 297–418. Boston.
WILSON, CHARLES BRANCH.
1916. Copepod parasites of fresh-water fishes and their economic relations to mussel glochidia. Bulletin, U. S. Bureau of Fisheries, Vol. XXXIV, 1914, pp. 331–374, pls. LX–LXXIV. Washington.
WILSON, CHARLES B., and CLARK, H. WALTON.
1912. The mussel fauna of the Kankakee Basin. U. S. Bureau of Fisheries Document 758, 52 pages, 2 figs., 1 pl. Washington.
1914. The mussels of the Cumberland River and its tributaries. U. S. Bureau of Fisheries Document 781, 63 pages, 1 pl. Washington.
WILSON, CHARLES BRANCH, and DANGLADE, ERNEST.
1914. The mussel fauna of central and northern Minnesota. Appendix V, Report, U. S. Commissioner of Fisheries, 1913, 26 pages, 1 map. Washington.
WOLCOTT, ROBERT H.
1899. On the North American species of the genus Atax (Fabr.) Bruz. Transactions, American Microscopical Society, Vol. XX, pp. 193–258. Buffalo.