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BIOLOGICAL BULLETIN

THE FOOD AND FEEDING HABITS OF FRESHWATER MUSSELS.[1]

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THE FEEDING HABITS OF MUSSELS.

CONTENTS.

INTRODUCTORY.

With the increasing commercial demand for mussels and the rapidly diminishing supply we shall have need for all the available information concerning their life history. Lefevre and Curtis ('12) have done a great deal toward solving the problems which beset artificial glochidial infection. Much may still be learned concerning the practicability of artificial feeding, the nature of their enemies and of their diseases.[2]

[1] This paper is the result of observations made at the Indiana University Biological Station, at Winona Lake, Indiana, under the direction of Prof. Will Scott. It forms contribution No. 130 of the Zoölogical Laboratory of Indiana University.

[2] An important obstacle to their successful cultivation is offered by the pollution of streams. Searches which I made on several occasions in a certain section of the Mississinewa river, into which oil and salt water from oil wells, and sewage from a paper mill are poured, failed to produce a single living mussel, although there was an abundance of empty shells. At this point, during the dry season, great schools of fish take refuge in the shallow tributaries which are freer from pollution.

The mussel, regardless of its considerable size, depends entirely for food on the microscopic organisms floating in the water, and offering little resistance to capture. That this diet is sufficient, is probably due to the comparatively inactive life of the animal. Energy is further economized by a partial combination of the functions of respiration and food-getting in the same organ—the gill.

The Cilia and their Action.

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, as Field ('09) has said, 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 coördinated to accomplish a certain common end. So vigorous and powerful are the cilia that, when an organ or portion of one is removed and placed upon a smooth surface for study, the whole mass is moved by their action slowly and steadily in a direction opposite to that in which they are directed. Small parts will even climb the side of a watch glass. McAlpine ('88) found that seven twelfths by weight of the soft part of the animal may thus be moved by ciliary action. As long as the part so removed is kept in water their activity continues, even for several days. In one instance McAlpine kept the cilia of marine clams living for eight days after their removal from the animal. This illustrates the fact that, while the cilia generate considerable power, they accomplish it upon a minimum of metabolism.

The general character of the feeding habits of mussels has been known for nearly a century. Fragmentary bits of information on the various phases of the subject are to be found in the Molluscan literature, particularly that concerning marine forms, to whose study economic interest has added impetus.

Scope and Nature of Investigation.

It has been the purpose of this investigation to determine for fresh water forms, (1) what their food is, (2) how food material reaches the alimentary tract. (For the most part there is great similarity to the marine lamellibrancha in these two particulars, but there are a few essential differences.) (3) Incidental to the above a few observations concerning digestion.

Material.

In the work upon the nature of the food, lake-dwelling mussels were used altogether. In the other studies river forms were also used. Besides one or two unidentified species, the following were employed:

Lampsilis luteolus Lamarck
Lampsilis subrostratus Say
Quadrula rubiginosa Lea
Lampsilis alatus Say
Lampsilis rectus Lamarck
Unio gibbosus Barnes
Lampsilis ligamentinus Lamarck
Anodonta grandis Say

Being by far the most numerous at Winona Lake, *L. luteolus* was used for the greater part of the work.

Anatomy, and Previous Work on the Function of the Cilia.

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 (Figs. 3 and 5). The outer or non-contiguous faces of both palps and lips (Fig. 4) 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 ('05) has pointed out how selection and rejection may be made.

As shown diagrammatically in Fig. 4, 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. In cross section (lengthwise of the labial palps) they appear as in Fig. 5.

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 (Fig. 5, *p*) while those on the posterior slope lead forward (Fig. 5, *a*). 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. Their normal position seems to be that seen in the two ridges on the right in Fig. 5, a somewhat reclining one, overlapping one another toward the anterior. Thus the after slopes (*a*) are ordinarily brought uppermost, the ciliary currents leading to the mouth are upon the surface, while the cilia (*p*) which lead from the mouth lie somehwat 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 (Fig. 5, *I*) brings uppermost the cilia leading backward (*p*) and such material is returned from summit to summit to the edge of the palps and discharged into the mantle chamber.

It is extremely difficult to observe the cilia which lie at the bottoms of the furrows (*mf*). Wallengren (*l.c.*) ascribes to them the duty of carrying lengthwise of the furrow to the lower margin of the palps the minute particles that may fall between the ridges. But Siebert ('13) thinks they lead in the opposite direction.

In the event that any particles get past the palps they may still be rejected at the mouth. A strong compression of the lips will force them outward to the edge of the lips, where they encounter the cilia directed backward (Figs. 3 and 4, lower margin) and are carried to the edge of the palps and dropped into the mantle chamber.

The outer surfaces of the palps and lips have as their function the removal of particles from the mantle chamber (Fig. 4).

McAlpine's (*l.c.*) observations upon the movements of detached parts led him to conclude that the palps and gills have nothing to do with feeding, and that they are concerned only with carrying away foreign material. But Wallengren's (*l.c.*) conclusions are based upon far more careful and logical experiments, and Siebert's (*l.c.*) recent paper on the epithelium of Anodonta is of a confirmatory nature.

Observations.

The ciliary currents may be observed quite readily on a mussel from which the shell and mantle of one side have been removed, or on detached parts, which, as stated, continue to exhibit ciliary activity for a long time. Small quantities of carmine, indigo, or other nearly neutral coloring matter may be dropped upon the part to be studied, and their behavior noted. Care must be exercised in the amount of water used. The less water the better, within limits, for in a large amount of water currents may obscure the action of the cilia. The surface of the organ must be level in order to offset gravitational disturbance. A small piece of any ciliated organ, when placed in a watch glass with water and a very little color, will show under low power both the cilia and their currents in great detail.

The Ciliary Streams.

The figures will show more clearly than description the course of the streams of material collected from the water. All the material gathered by both gills and by the dorsal part of the body epithelium and mantle must finally reach one of the three adjacent points—(1) the mantle just above the palps, (2) the body wall just opposite the first point, or (3) a point on the edge of the inner gill just above the labial palps. All these are within easy reach of the palps (Figs. 1, 2, 4, and 6).

No one, to my knowledge, has succeeded in inducing a mussel to behave normally, after the shock of removing parts of the shell and mantle in order to observe the palps at work. But I have repeatedly obtained the reactions which occur. When the palps lie in contact with either body, mantle, or gill, their collections of material pass between the palps and mouthward. Otherwise such material is carried on down by the several structures and discarded. The fact that the upper margins of the labial palps adhere to each other and form a trough (Figs. 4 and 6) makes it possible to reach at least two of the three sources of supply simultaneously.

Since we have the mechanism for such a method, and since the reactions, though fragmentary and under abnormal conditions, are of a confirmatory nature, we may safely infer that the labial palps do actually accept or refuse food, either through reflex stimuli or in response to volition.

The Function of the Mucus.

The entire epithelium touching the branchial chamber is abundantly supplied with glands which secrete a mucous substance (Siebert, *l.c.*). 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. That this secretion is dependent on local reflexes is quite evident from the fact that it may be stimulated in an organ entirely severed.

It is this collection of food in a film of mucus, which makes possible the mechanism of the furrowed surface of the labial palps. If each particle were manipulated independently, it would tend to eddy back and forward between the opposing streams of cilia, and considerable confusion might result. But a strand of material spans the summits of several ridges, and while touching cilia that lead in both directions, it obeys the ciliary streams which lie uppermost and exert the greater force upon it.

Conclusions on the Function of the Ciliary Currents.

The surfaces of the gills and of the upper part of the mantle, and the contiguous faces of the labial palps, in fact, nearly all the upper parts of the mantle chamber, have for their general purpose the carrying of food to the mouth. The lower part of the mantle chamber, upon which the heavier fragments are likely to fall, are concerned principally with removing undesirable matter from the animal.

The Selection and Rejection of Food Particles.

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, or perhaps only the siphons.

It is true that some material of no food value finds its way into the alimentary canal. But the quantity is far smaller than if no selection were made, and is of a harmless nature. All distinctly injurious substances are rigidly excluded.

That which has been rejected at the mouth, palps, or gill accumulates upon the lower posterior margin of the mantle or body wall, along with the collections made by these parts themselves, and is here massed in clots of mucus. When this has attained considerable size the animal ejects it with a rapid current of water, set in motion by a quick contraction of the adductor muscles and closing of the shell (Figs. 1 and 2, *r*).

The Rate of Siphoning.

An effort was made to determine the rate at which water is siphoned through the mussel. If this can be done it will contribute to several quantitative studies relative to the feeding habits, and that of the effect of temperature and other conditions upon the activity of the cilia.

But it is very difficult to attach apparatus for making measurements to the siphons of the animal. Intimate contact must be made to avoid leakage and a high per cent. of error. Such contact irritates the mussel, so that it does not behave normally.

In only one mussel did I succeed in obtaining what seemed a normal circulation of water, when under this annoyance. This was done by placing a short piece of soft rubber tubing in the excurrent siphon. Into the end of this was thrust a calibrated glass tube, having a capacity of 2 c.c. between two given marks. The point of a pipette containing neutral coloring matter was thrust into the rubber just outside the siphon. The mussel with this simple apparatus was put into an aquarium near the lake, where the water could be changed frequently and the lake conditions maintained. A touch upon the pipette released a drop of coloring matter into the tube, where it encountered the stream flowing from the excurrent siphon.

This individual was a *L. luteolus* weighing 200 grams with the mantle chamber filled. It required five seconds for the pigment to pass between the two marks upon the tube, whenever the incurrent siphon was opened fully. The reading was repeated a number of times at intervals, with the same result.

While these are but meager results, they give at least an idea of the volume of water siphoned. At the above rate there are siphoned 24 c.c. per minute, 1,440 c.c. per hour, or 34,560 c.c. per day. To filter a liter of water would require 42 minutes.

Digestion.

Digestion fluctuates more in the case of mussels than does their feeding. That is, the animal continues to feed regardless of appetite; but the degree with which the food so ingested is really made use of seems to depend upon the relation of supply and demand. At times nearly all the intestinal contents are found to be at least partially digested; while again much material is found, even in the rectum, in perfect preservation, and often the fæces themselves contain forms which are apparently unaffected. Hence we may conclude that appetite fulfills its function by the control of the secretion of the digestive juices, without the voluntary regulation of the food supply.

The Crystalline Style.

The literature on the lamellibranchs is particularly rich in speculations concerning the function of the crystalline style; but I cannot forbear adding a word here parenthetically on the subject, by calling attention to the excellent work done by Mitra ('01) upon it. He reviews all the previous theories and repeats the experiments, extends them, and brings physiology, chemistry, and comparative morphology to bear upon the matter, so that there seems to be no way of escaping his conclusion that the style is a digestive ferment which converts starch into sugar. The previous hypothesis of Gegenbaur, that it is a secretion of enteric epithelium, he holds to be true, but says that this does not account for its existence. Against Balfour's notion that the style is a rudiment of a radular sac he brings six weighty proofs, and dismisses with two objections each the theories of Claus and Sedgwick, that it is an excretion product and a reserve of nutriment, respectively.

In two minor particulars my observations do not agree with those of Mitra. (1) In an experiment upon the renewal of the style he concludes that it appears and disappears *periodically*. But from the description of his experiment we find that the water and food supply were renewed at regular intervals, whence the periodicity. In a similar experiment of my own the crystalline style was found to disappear only with the lack of food, and to be regenerated only when food was supplied, regardless of time. Then too, as long as the food supply is abundant the style is never wanting. In all mussels freshly removed from the lake it was found to exist. In all mussel freshly removed from the lake it was found to exist. In these matters the work of Haseloff ('88) also confirms my point.

Hence the food supply must be a factor in its secretion. As it is dissolved when food is lacking, and as it is a proteid, why is not Sedgwick's theory as to its being a reserve food supply also true?

(2) The presence in the core of the crystalline style of cells similar to those found in the liver epithelium leads Mitra to conclude that the liver is the probable origin of the structure. This also does not seem well substantiated, especially in species where the style is found in a diverticulum. No channel for the passage of a secretion from the liver to the seat of the style has been discovered, and the ciliation of the stomach and intestine forbids their aiding in its transmission.

Since the publication of the above paper Grave ('03) has suggested in his work on the oyster that the crystalline style may perform the duty of preventing coarse particles from passing through the digestive canal. In fresh water mussels I can see but one way in which the style may attend to that function—by digesting the said particles. There are at least two objections to this explanation for fresh water mussels (1) As we have seen, the animal is well protected against the entrance of such particles. (2) In case they were admitted to the stomach but kept out of the intestine, they would accumulate in the stomach, for it is not equipped with either a muscular or a ciliary system by which these could be expelled through the mouth. Then too, the mouth is no larg r than the intestine and no more capable of receiving them. The largest body I have seen in the alimentary tract was a fragment of *Oscillatoria* (or similar form) measuring 1.5 mm. in length.

Food Materials.

No one but Zacharias ('07) seems to have undertaken a detailed examination of the contents of the alimentary tract of the freshwater forms, so I give the results of a purely qualitative examination. In marine mussels it is said that the food consists almost altogether of minute plant forms, and of these almost all are Diatomaceæ. In the mussels which I examined I found a somewhat different condition. In the first place there is a little higher proportion of animal food present. Living animals are found but rarely, and most of these are apparently living transiently upon the contents of the tract. But the mussel does not refuse minute dead animals or small fragments of sloughed and decaying animal tissue. In many cases bits of material seemingly the carapaces of small crustacea are found to resist digestion throughout the alimentary canal. However most of the animal matter consists of shapeless unidentifiable fragments.

In order to determine the ability of mussels to capture and digest living animals, a few were kept without food for several days, then a rich culture of *Paramecium* was added. This was found to be of sufficient nutrient value to regenerate the crystalline style in part. The digestive tract was seen to be filled again with half assimilated material. Few living *Paramecia* were discovered beyond the stomach, thus corroborating Vogt and Jung's statement ('94) that digestion is nearly completed in that organ.

In the second place, the plant material does not consist so largely of diatoms, there being probably as many other algal forms. Very few desmids were observed, in fact only three genera which I could identify with certainty. But Winona Lake does not produce many desmids, and it is not probable that they are discriminated against where they exist more abundantly.

The following is a list of genera recognized. There were several more which I could not identify.

Diatomaceæ.	Other Algæ.
Amphora	*Anabæna*
Arachnoidiscus	*Aphanocapsa*
Cocconeis	*Cœlastrum*[1]
Cocconema	*Cylindrocapsa*
Coscinodiscus	*Eudorina*[1]
Craspedodiscus	*Glœocystis*
Cymbella	*Leptothrix*
Epithemia	*Lyngbya*
Fragilaria	*Merismopedia*[1]
Gomphonema	*Œdogonium*[1]
Melosira	*Oscillatoria*
Navicula	*Pandorina*[1]
Pleurosigma	*Pediastrum*[1]
Surirella	*Protococcus*

Synedra
Triceratium
DESMIDACEÆ.
Closterium
Netrium
Staurastrum[1]
Rhaphidium
Scenedesmus
Spirogyra
Tetraspora
Ulothrix
Vaucheria

MISCELLANEOUS CONTENTS.

Inorganic fragments,
Plant and animal debris,
Mold,
Ova and spermatozoa
Of other animals,
Of the same individual or species,
(The sperm living and in motion),
Spores and swarm spores.

The posterior half of the mussel shell, the part protruding above the substratum, is usually very richly encrusted with diatoms and other algae. This may serve as a private garden, and particles dislodged by the passage of the animal along the bottom thus be brought into the incurrent siphon.

In addition to the very valuable assistance which I have received from Prof. Scott, I wish to acknowledge by indebtedness to the John Crerar Library of Chicago, through which I was able to procure several useful references, and to Profs. C. H. Eigenmann and W. C. Curtis, who have made indispensible critical suggestions.

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[1] Also noted by Zacharias (*l. c.*).

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EXPLANATION OF PLATE I.

The arrows indicate the directions of the ciliary currents.

The arrows which follow the margins of the inner gills show the *direction of* ciliary currents in the troughs which form their under edges (*Fig. 7, tr*).

x x x x x x indicates the line which divides mouthward-flowing streams from those leading posteriorly.

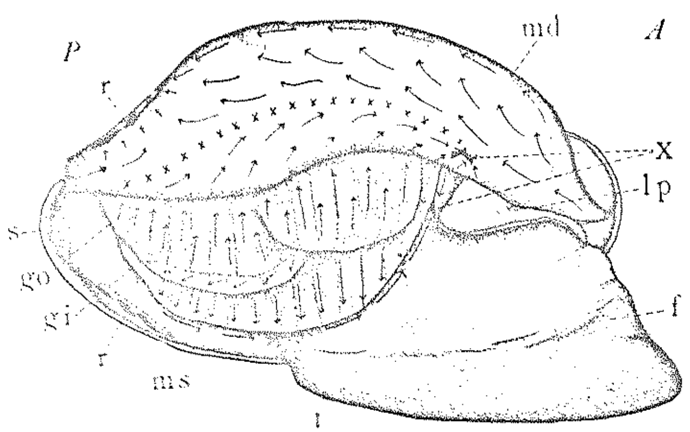
In all except Figs. 6 and 7 the left side is *posterior* and the right anterior.

FIG. 1. (Adapted from Wallengren.) The organs concerned with food-getting; the right shell removed and mantle folded back; showing ciliary streams of mantle and gills.

FIG. 2. (Adapted from Wallengren.) As in Fig. 1; mantle gills and palps of right side folded back; showing ciliary streams of inner gill and body wall.

Abbreviations.

A, anterior.
f, foot.
gi, inner gill.
go, outer gill.
lp, labial palps.
md, right mantle.
ms, left mantle.
P, posterior.
r, mucous accumulations of refuse material.
s, siphon.
X, point of convergence of ciliary currents near labial palps.



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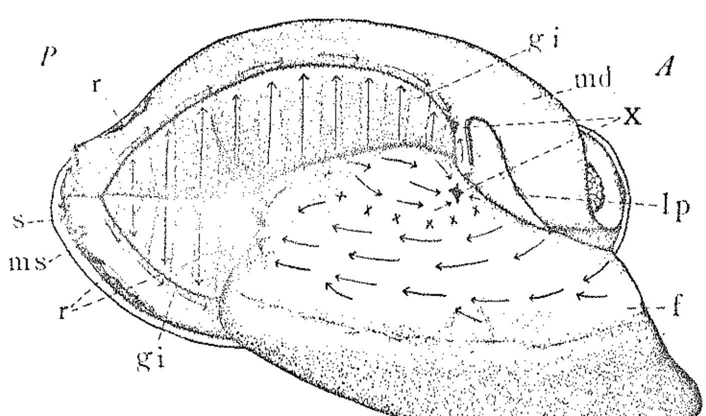

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EXPLANATION OF PLATE II.

FIG. 3. The inner labial palp; outer palp removed; normal ciliary streams of furrowed surface.

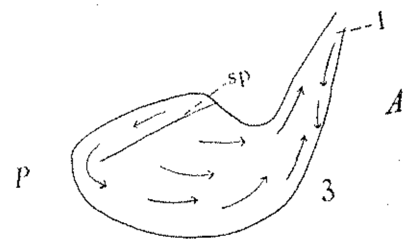
FIG. 4*a*. (Slightly diagrammatic. See Fig. 4*b*.) The left labial palps, adjacent mantle surface, and end of gills; right mantle, gills and palps, and whole body removed; showing point (*X*) where streams of food from gills and mantle converge at the labial palps.

Broken arrows indicate the ciliary currents of the mantle; solid arrows those of the gills; and barbed arrows those of the palps. Where the broken arrows are seen upon the gills they are meant to apply to the mantle just beneath.

FIG. 4*b*. Key to Fig. 4*a*; all organs removed except left mantle, gills and palps; the area within double lines has been enlarged as Fig. 4*a*.

Abbreviations.

A, anterior,
aa, anterior adductor muscle,
fs, furrowed surface of labial palps,
gi, inner gill,
go, outer gill,
l, lips
lp, labial palps,
lv, liver,
ma, unfurrowed margin of palps,
ms, left mantle,
P, posterior,
pa, posterior adductor muscle,
r, mucous accumulations of refuse material,
sc, suprabranchial chamber,
se, excurrent siphon,
si, incurrent siphon,
sp, line of attachment of the palps to each other,
X, point of convergence of ciliary currents near labial palps.



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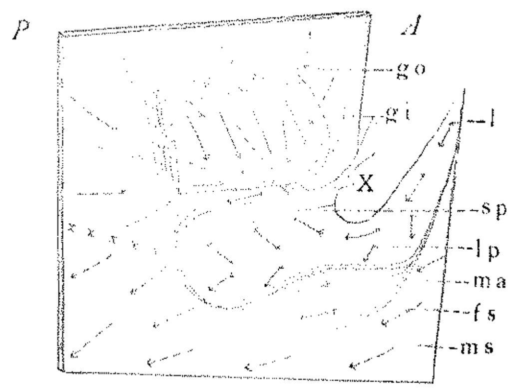

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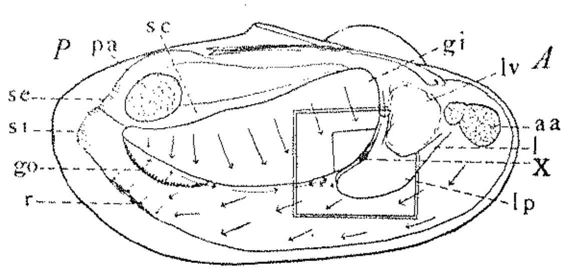

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EXPLANATION OF PLATE III.

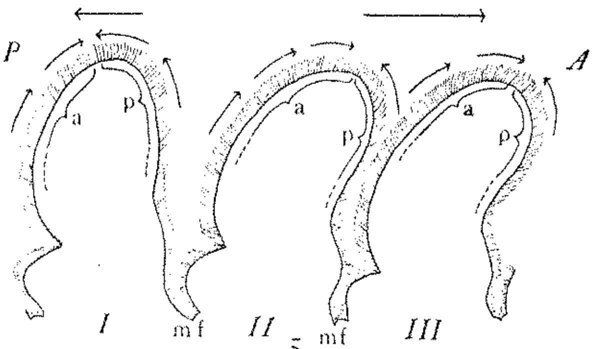
FIG. 5. Cross section of ridges on contiguous surfaces of labial palps (Fig. 4*a*, *fs*) showing their several positions. While *a* is uppermost (as in *II* and *III*) material is carried mouthward; when *p* is raised by the erection of the ridge (as in *I*) the stream is reversed toward the posterior, and the cilia *a* no longer function.

FIG. 6. (Slightly diagrammatic.) Cross section of the ciliated organs concerned with food collecting; showing how the labial palps (*lp*) by occupying several positions in the mantle chamber, may or may not receive the material collected at *X*. As a matter of fact, the palps can span almost the entire width of the mantle chamber at this point, but the width is exaggerated here to show details with greater clearness.

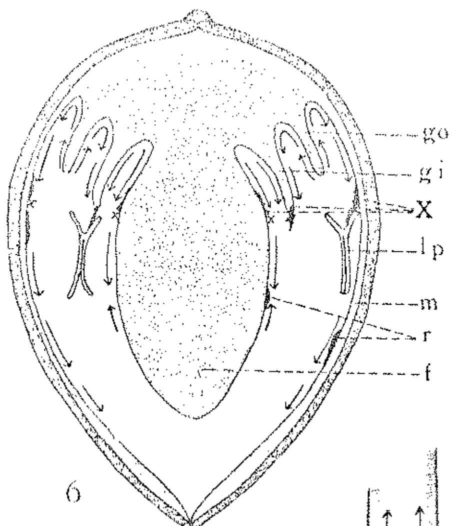
FIG. 7. (After Posner.) Cross section of the edge of inner gill; showing the groove (*tr*) by which material is transported toward the palps.

Abbreviations.

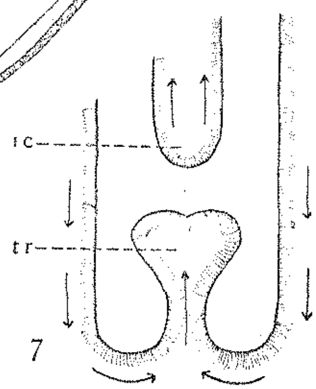
I, ridge erected; current reversed,
II–III, normal position of ridges,
A, anterior,
a, cilia directed anteriorly,
f, foot,
gi, inner gill,
go, outer gill,
ic, interlamellar chamber,
lp, labial palps,
m, mantle.
mf, cilia at bottom of furrows,
P, posterior,
p, cilia directed posteriorly,
r, mucous accumulations of refuse material,
tr, trough at margin of inner gill,
X, points of convergence of ciliary currents near labial palps.



5



6



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