CHAPTER VI

THE LABIAL PALPS

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ANATOMY

The four soft flaps which lie at the anterodorsal side of the body under the mantle hood are the labial palps. Their triangular members are attached by their broad bases to the visceral mass and have slightly curved margins which extend ventrally to the point where they touch the free edges of the gills (fig. 104).

The two pairs of palps, one on each side, are joined together into a single unit which serves primarily for final sorting of food particles and for the delivery of food to the mouth. Each pair consists of one external and one internal palp (r.i.p.; r.o.p.). The two external palps join together above the mouth (m.) where they form the upper lip (u.l.); the two internal palps are united below the mouth into a lower lip (l.l.). As a result of this arrangement the mouth is an irregularly shaped, narrow, curved slit. Both lips are arched; the lower one is shorter, and its edge is thicker than that of the upper lip.

At the central junction of the two internal palps there is a median gutter which leads to the center of the lower lip. The two lateral gutters (l.g.) formed on each side where the external palp meets its opposing internal member are the principal paths by which the food is conveyed to the corners of the mouth (fig. 104). The surface is smooth along the outer part of the external palps and on the inner palps along the median plane, where the palps meet; along the lateral gutters, both have a striated appearance due to numerous ridges and grooves which empty into the corresponding gutter. This arrangement is significant for an effective sorting of food.

HISTOLOGY

Each labial palp consists of a layer of connective tissue covered on both sides by columnar ciliated epithelium set on a basement membrane. These are made of large vesicular cells of the type found in the mantle (fig. 105, c.c.). Within the body of a palp there are many blood vessels and blood spaces or sinuses. These spaces are splits or interstices between the connective tissue cells and have no lining or wall. The longitudinal and transverse muscle fibers are numerous but not as well developed as they are in the mantle.

The smooth sides of the palps are covered with small epithelial cells, about 5 to 6μ long, with minute cilia not exceeding 3μ in length. Awati and Rai (1931) maintain that in *O. cucullata* only some of the epithelial cells of this surface are ciliated. They suggest that the ciliated cells have sensory function but present no evidence to support this view. The absence of cilia on some of the cells of this layer may be due to their destruction during the processing of tissue.

In *C. virginica* the epithelium of the smooth surface of the palp consists of almost cubical cells with relatively large nuclei and small cilia (fig. 105, c.ep.). Cell boundaries are indistinct, the cells themselves are crowded and compressed, and there is a very thin and transparent cuticle on the periphery. In the subepithelial layer large eosinophilic cells (e.c.) and mucous cells (m.c.) are very abundant. The mucous cells are frequently pear-shaped, but their appearance varies, depending on the amount of secretion they contain. Their length is between 25 and 30 μ. Wherever the secretion of mucus is least, the outer surface of the palp is slightly ruffled, as shown on the right side of figure 106, representing a longitudinal section of the palp viewed at low magnification.

The inner or ridged surfaces of the palps present a different picture. The entire surface is folded into deep ridges and grooves. In figure 106 the ridges are about 0.3 mm. high along the central axis. The ciliated cells of the ridged surface are slender, cylindrical, and tightly packed, with small, round nuclei. They form a layer varying from 40 to 60 μ in thickness. The difference in

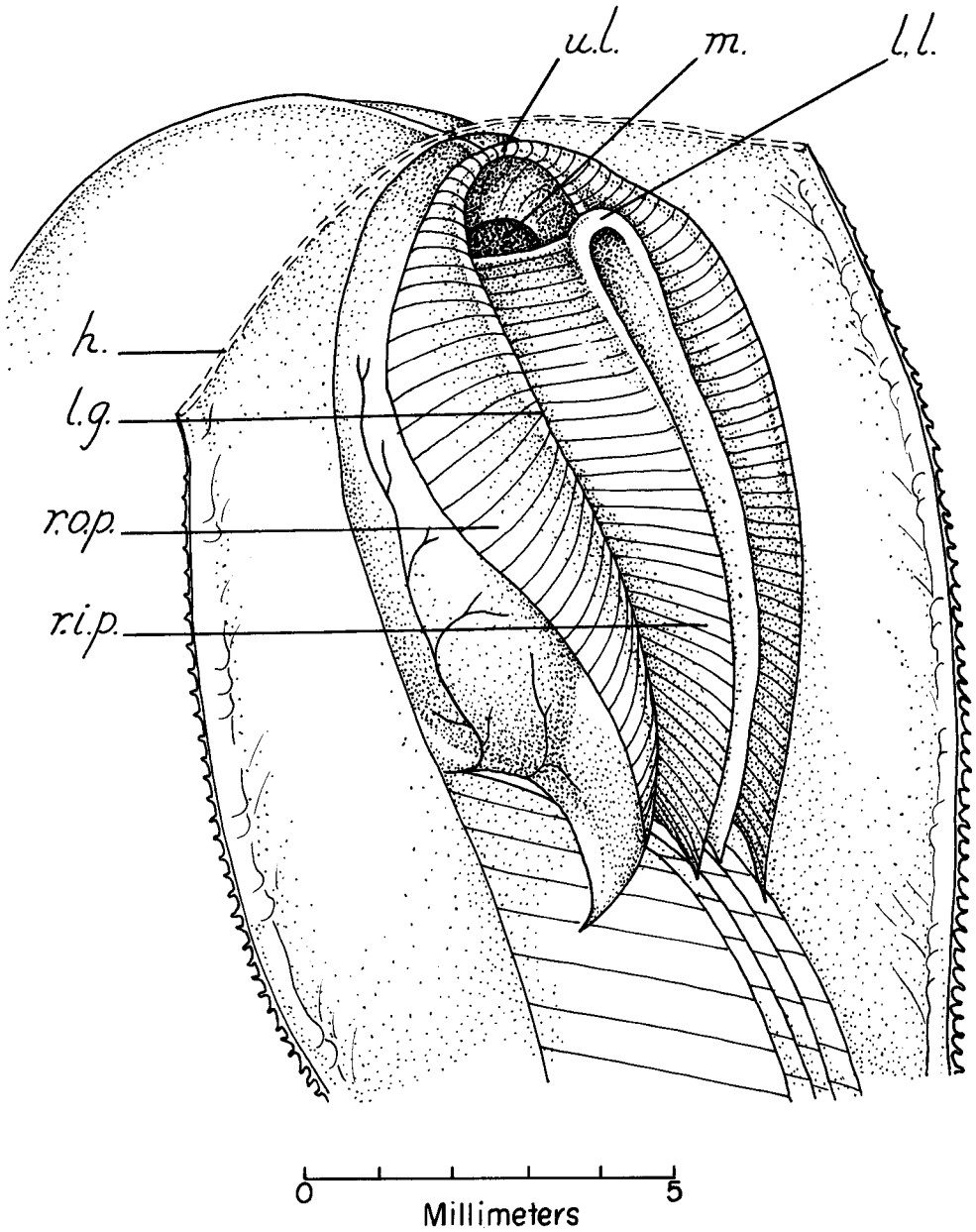

FIGURE 104.—Labial palps of *C. virginica*. The mantle hood is cut off at the middle, and the sides are pulled aside to expose the lips and the mouth. Drawn from life. h.—hood; l.g.—lateral gutter; l.l.—lower lip; m.—mouth; r.i.p.—right inner palp; r.o.p.—right outer palp; u.l.—upper lip.

the shape and size of the cells of the two sides of the palp is clearly seen in this figure.

Thin and transparent cuticle covers the epithelium of the ridged surfaces. The cilia are robust, ranging in length from 8 μ in the grooves to 20 μ on the tips of the ridges, with the longest cilia found near the free edge of the palps. Mucous cells are present but are less abundant than on the smooth side.

The ridges themselves are set at an acute angle to the surface of the palp and recline toward its free edge. There is a noticeable difference in the epithelium of the two sides of the same ridge. The cells lining the sides which face the mouth (lower sides of ridges in figure 106) have longer cilia, and the entire epithelium is slightly ruffled. On the opposite sides the ciliated cells are uniform and have smaller cilia. This difference appears on a tangential section of the palp shown in figure 107.

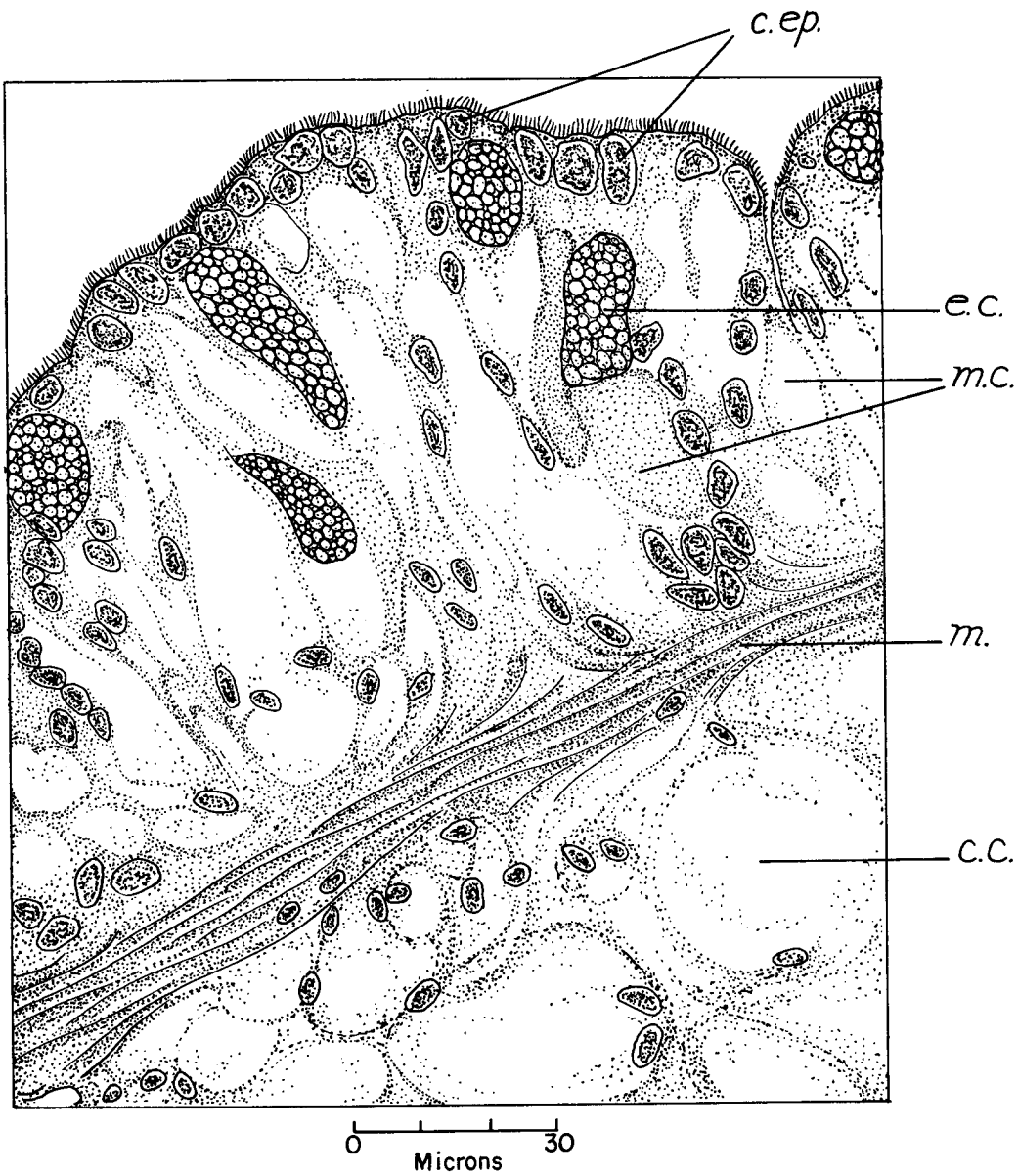

FIGURE 105.—Cross section of the smooth side of labial palp of *C. virginica*. c.ep.—cubical ciliated epithelium; e.c.—large eosinophilic cell; m.c.—mucous cell; m.—muscle fibers; c.c.—vesicular cells of connective tissue. Note the the infiltration of subepithelial layer by mucus and invasion of blood cells. Bouin, hematoxylin-eosin.

The epithelium rests on a thin basal membrane consisting of connective tissue fibers and muscles. The core of the ridge is made of delicate connective tissue with occasional large vesicular cells containing eosinophilic granules. The description of microscopical structure of the palps given above is in agreement with the observations made on various bivalves by previous workers (Leenhardt, 1926; List, 1902; Siebert, 1913; Thiele, 1886; and Wallengren, 1905a, 1905b).

The palps are well supplied with blood delivered through the anterior aorta, pallial artery, and short tentacular artery. The velar artery branches off from the short tentacular artery and runs the entire length of the palp, giving off numerous ramifications. According to Schwaneke's observation (1913) on *Anodonta*, the blood from the palp is returned to the heart by the way of the mantle.

The palps are innervated by the nerve emerging from the cerebral ganglion and entering the anterior end of the junction between the paired

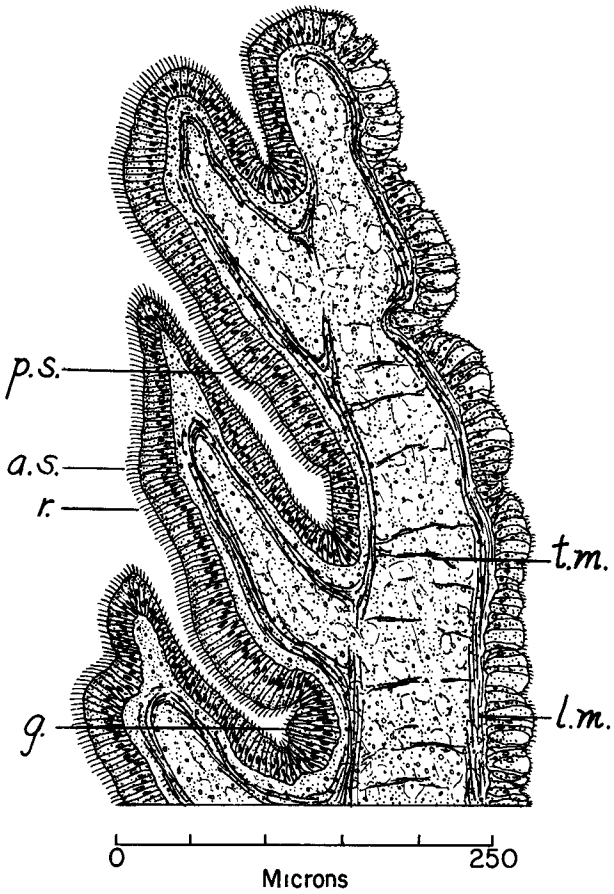

FIGURE 106.—Longitudinal section of a portion of the right external palp. The right (smooth) side is only slightly ruffled. The left side is folded and forms deep ridges and grooves. Bouin, hematoxylin-eosin. a.s.—anterior slope of the ridge; g.—grooves; l.m.—longitudinal muscles; p.s.—posterior slope of the ridge; r.—ridge covered with ciliated epithelium; t.m.—transverse muscles.

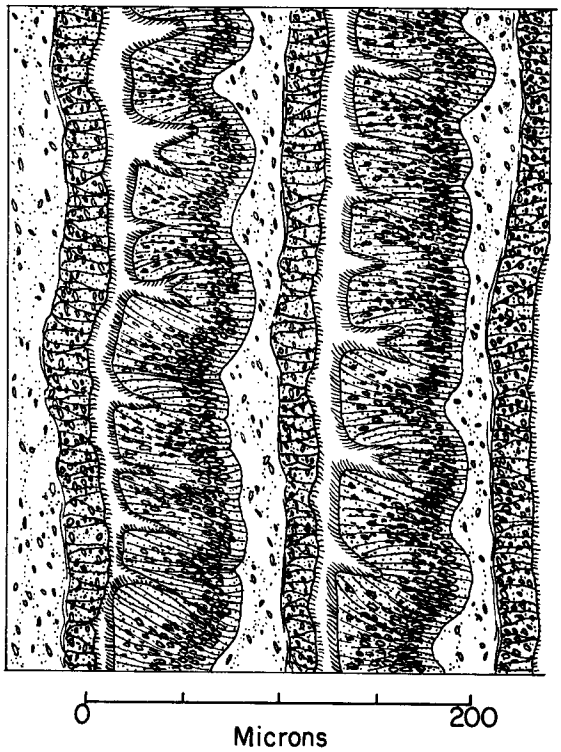

FIGURE 107.—Tangential section of the inner surface of labial palp of *C. virginica* made through two and a half ridges. The ruffled sides of the ridges are directed anteriorly toward the mouth. Bouin, hematoxylin-eosin.

lobes. A nerve net was described in the palps of *Anodonta* (Matthews, 1928). I was not able to demonstrate its presence in the oyster palps.

DIRECTION OF CILIARY CURRENTS

The most conspicous features of the palps are the abundance of mucous cells on their smooth sides and the powerful ciliated layer covering the ridges of the inner sides. The idea that labial palps of bivalves represent a sorting apparatus was clearly stated by Coupin (1893), who observed that in *Mytilus*, *Cardium*, and *Pholas* the more voluminous particles are discarded by the palps while the finest ones are delivered to the mouth. He concluded that the principal function of the palps of *Pholas* is to prevent the bulky material from reaching the digestive tract.

The sorting of food is accomplished by a complex system of ciliary currents along the surfaces of the palps. With reference to *C. virginica*, Kellogg (1915) states that the smooth sides of the two internal palps facing each other direct the food particles backward to the tips of the palps. This statement is only partially correct.

In describing the feeding habits of fresh-water mussels Allen (1914) noticed that the ridges of the inner surfaces of the palps normally overlap one another in a reclining position. This is also the usual position of the ridges in *C. virginica* (figs. 106 and 108). On the anterior slope of each ridge (fig. 106, a.s.) the currents are directed toward the free end of the palp; the currents of the posterior slope (p.s.) lead toward the mouth. Thus the final direction of the movement of a particle along the surface of the palp depends on the position of the ridges. Allen thinks that, as long as no adverse stimuli are received, the particles which lie between the palps pass on forward

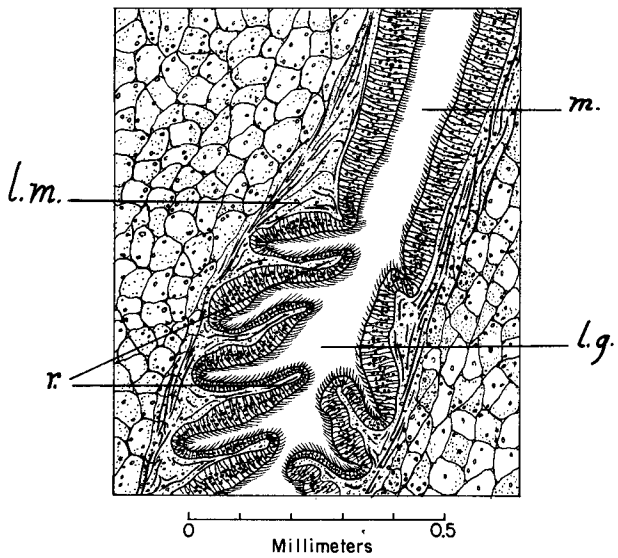

FIGURE 108.—Longitudinal section of the palps along the lateral groove at the place of entrance to the mouth. l.g.—lateral groove; l.m.—longitudinal muscles; m.—mouth; r.—ridges of the inner sides of palps. Bouin, hematoxylin-eosin.

from one ridge to another and eventually reach the mouth. In case of irritation the reflex erection of the ridges brings uppermost the cilia leading backward, and the particles on the surface of the palp are pushed from summit to summit to the edge of the palps and discarded. It is not clear from Allen's description whether his explanation is based on observations or on an assumption that the ridges are capable of changing their position in response to stimulation.

During observations of the feeding of an oyster spat less than 3 mm. long and attached to a glass slide, Nelson (1923) found that the filaments of the palps narcotized in magnesium sulfate solution lose their power of erection with the result that large masses of material passing over the filaments accumulated near the mouth and blocked it. This effect may have been caused by the inhibition of ciliary motion as well as by the suppression of muscular contraction.

The "filaments" of the palps of the spat observed by Nelson undoubtedly correspond to the ridges of the inner surfaces of the palps of adult oysters. The theory of sorting out of the material advanced by Allen and accepted by Nelson implies that the change in the direction of movement of the particles toward the mouth or away from it is controlled by the erection of the ridges. With a microscope I examined the palps of oysters intact except for the removal of one valve and was not able to observe changes in the position of the ridges. Similarly, no erection of ridges was noticed on the excised palps which were kept in sea water and examined with high power. The ciliary currents remained, as a rule, undisturbed for many hours.

Yonge (1926) states that in *O. edulis* "there are no muscles within the folds such as could cause it to contract downwards." This statement cannot be confirmed by my observations on *C. virginica.* In the palps of the American osyter the longitudinal muscles are clearly visible (figs. 106 and 108, l.m.). They extend along both sides of a ridge from its base to the very tip. The contraction of muscle fibers on one side of the ridge presumably may change the position of the ridge and make it stand at right angles to the surface of the palp. There is no evidence that this actually happens.

Churchill and Lewis (1924) arrived at the conclusion that in fresh-water mussels the cilia covering the upper portions of the ridge beat forward (toward the mouth) while in the deeper part of the groove between the ridges they beat in the opposite direction. They also make a generalization that "the palps appear to be a mechanism for reducing the quantity of material to an amount that can be handled by the mouth." According to these authors the two sides of the palps perform distinctly different functions. In fresh-water mussels the ciliary currents along the outer (smooth) surfaces remove the particles from the mantle chamber, while on the ridged surfaces the currents are directed toward the mouth.

The currents along the labial palps of *C. virginica* are, however, more complex and somewhat different from those described for fresh-water mussels. To observe these currents I removed one valve, dissected the mantle hood, and pushed apart its sides to expose the entire surface of the palps. I placed the oyster in sea water in a shallow tray and observed it with a low-power microscope under strong illumination directed at an angle of about 20 degrees to the surface. Suspensions of colloidal carbon or finely powdered willemite in sea water were used to flood the surface, and the distribution of the brilliantly fluorescent willemite particles was observed under ultraviolet light. A series of pencil diagrams outlining the positions of the palps were prepared in advance and were used to mark the direction

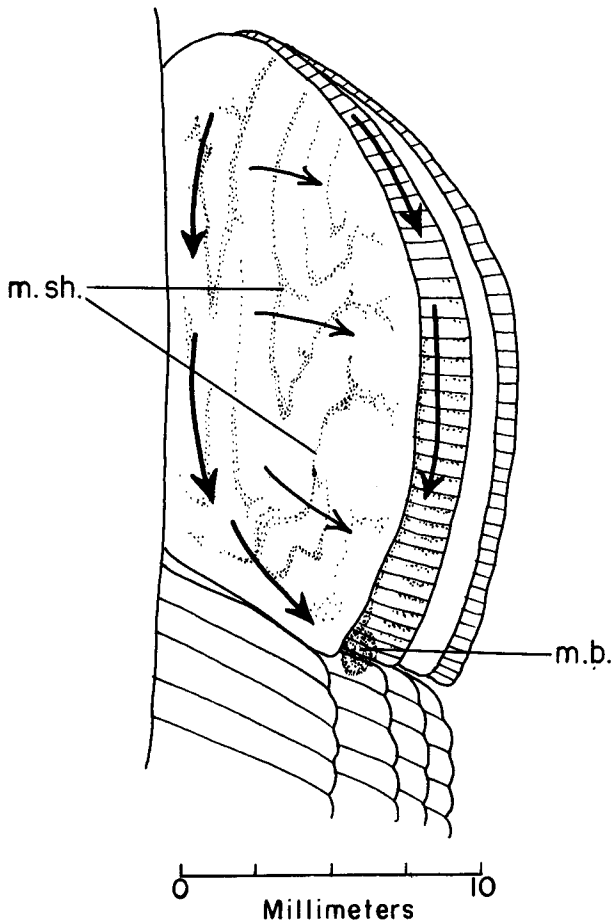

FIGURE 109.—Ciliary currents along the outer surface of the right external palp of *C. virginica*. Dark streaks (dotted areas) represent the distribution of mucus strands with black particles entangled in them 2 or 3 minutes after the surface was flooded with suspension of colloidal carbon. Large arrows indicate the direction of principal currents; small arrows show the secondary currents directed toward the free edge of the palp. The material entangled in a slimy ball (m.b.) is discarded at the corner of the palp. m.sh.—mucus sheet. Drawn from life.

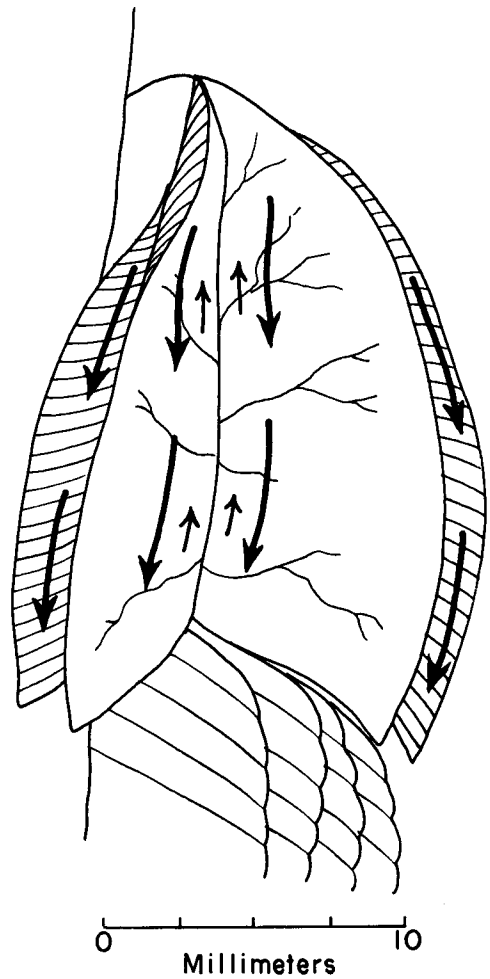

FIGURE 110.—Principal ciliary currents along the smooth surfaces of internal palps, *C. virginica*. Small arrows indicate the weak countercurrent directed toward the mouth at the bottom of the central gutter. Drawn from life.

of principal currents as they were observed immediately upon the addition of the suspended material. Figures 109 through 112 summarize the results of many observations on several large oysters.

The palps are usually totally covered with a sheet of mucus, but the secretion of the mucus is greatest on the outer surfaces of the external palps. Numerous mucous glands under the surface epithelium (fig. 105) are easily stimulated by the slightest irritation and begin to discharge large amounts of mucus as soon as their surface is flooded with water containing suspended particles. Figure 109 shows the two systems of currents, both directed away from the mouth. A strong current along the base and an equally powerful current along the free edge run toward the lower free corner of the palp. Weaker currents (small arrows) are directed across the surface from the base of the palp to its free edge where the particles cleared from the area are picked up by the strong ciliary current at the periphery and are carried to the corner of the palp touching the edge of the gill (m.). Here a strong eddy is formed, probably as a result of combined downward currents of the palp and of the ciliary epithelium of the gills. The particles discarded from the palps rotate in this area until a fairly large ball measuring about 0.5 cm. is formed and

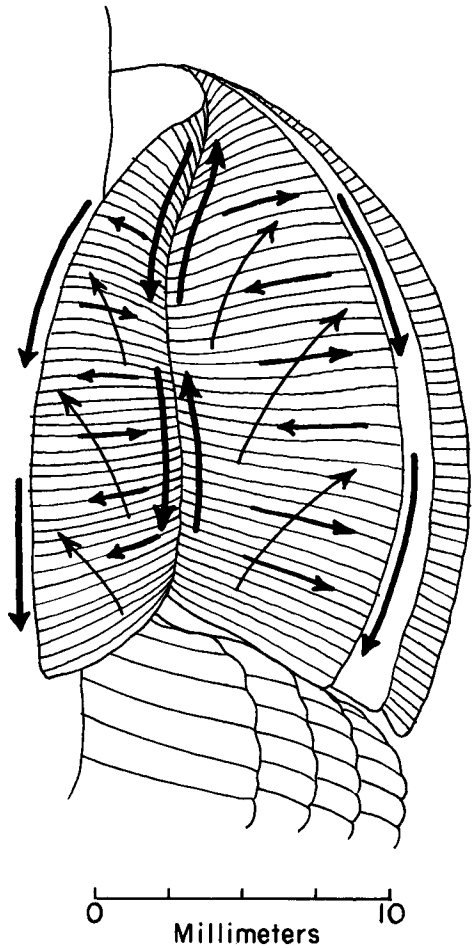

FIGURE 111.—System of currents along the ridged surfaces of the palps, *C. virginica*. Currents along the edges of the palps and at the bottom of lateral gutter are shown in heavy long arrows. The current and countercurrent along the ridges are shown by short arrows. Long narrow arrows denote the movements of particles across the palp toward its free edge. Drawn from life.

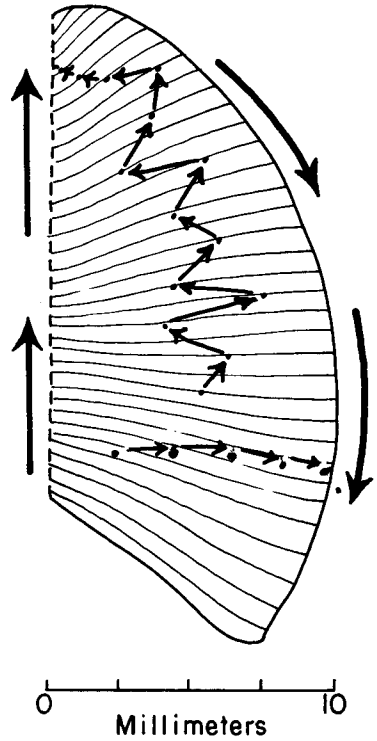

FIGURE 112.—The paths of two particles across the ridged surface of a palp (small arrows), *C. virginica*. Small particle at the lower part of the diagram fell between the two ridges into the furrow and was carried away by the current along the edge. A slightly large particle (upper half of drawing) settled on the top of a ridge and was kicked from one crest to another until it reached the bottom current of the lateral gutter and was pushed toward the mouth. Drawn from life.

the mass is dropped to the surface of the mantle and discarded through the principal discharge area (fig. 90). The currents along the smooth surfaces of the two internal palps (fig. 110) are directed primarily away from the mouth and toward the free edges along the entire length of the palps. There is a much weaker countercurrent along the central gutter. The material brought by this current reaches the lower lip and may be pushed into the mouth (fig. 113). Some of the particles which reach the rounded rim of the lower lip drop back to the surface of the palp and are carried away by the principal currents.

The system of currents on the ridged surfaces of the palps is very complex (fig. 111). There are two major and opposing currents along the lateral groove. The bottom current runs toward the mouth; at a slightly higher level (heavy long arrows) the currents run in the opposite direction. Equally strong currents directed away from the mouth run along the free edge of the palps.

There are at least three major currents along the inner surfaces of the palps: (a) from the base across the palp to the edge, (b) in an opposite direction from the edge to the base (fig. 111, short heavy arrows), and (c) slightly weaker currents from the central part of the palps at about 45 degrees to the edge (long slender arrows).

A particle moving along the ridged surface of the palp may follow a very irregular path. Figure 112 diagrams the route of two particles which both were pushed away from the surface. One particle (upper part of fig. 112) settled on the edge of a ridge and was pushed by the uppermost cilia from the top of one ridge to the others until it reached

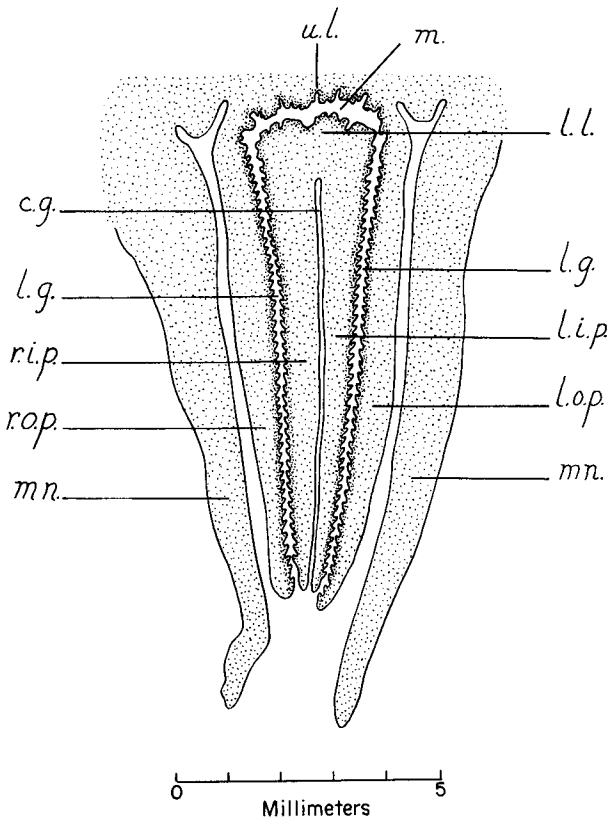

FIGURE 113.—Tangential section across the mouth and palps. Semidiagrammatic. c.g.—central gutter; l.g.—lateral gutter; l.l.—lower lip; l.i.p.—left inner palp; l.o.p.—left outer palp; m.—mouth; mn.—mantle; r.i.p.—right inner palp; r.o.p.—right outer palp; u.l.—upper lip. Formalin and hematoxylin.

the base and was carried toward the mouth. Another particle (lower part of fig. 112) fell into the furrow; several times it was kicked over two or three ridges, but it always fell to the bottom of a furrow and finally was carried toward the edge of the palp and discarded (heavy arrow). Frequently the medium-sized particles entangled in mucus are caught in an eddy between the ridges and begin to rotate in a turbulent current. Additional particles are entangled, and as the ball grows it is kicked out and caught by the current along the edge. There was no evidence of the reversal of ciliary motion and the pattern of currents described above was maintained throughout the periods of observations.

An effective sorting mechanism, which prevents all but the smallest particles from reaching the mouth, is provided by the system of ciliary movement. The main supply of food is delivered by the lateral gutters (fig. 113), which lead directly into the corners of the mouth. Only a small amount of food reaches the mouth via the central gutter where it must be pushed over the edge of the lower lip. Observations of the ciliary motion of the palps give one the impression that the number of food particles delivered to the mouth constitutes only a small fraction of the total quantity which reaches the palps. It appears that the principal function of the palps is to eliminate a large part of food gathered in feeding and allow only a very small portion of it to reach the digestive tract. The system of currents and countercurrents observed in the palps of *C. virginica* is much more complex than that described by Yonge (1926) for the palps of O. *edulis*.

Mucus plays an important role in the sorting of food. The discharge of mucus is directly proportional to the amount of particles which settle on the surface of the palps. The sheet of mucus is pulled over the ridges of the palps by the action of the more powerful cilia at the tops of the ridges. The smaller cilia of the grooves may not be in direct contact with the mucus sheet above them and beat in a different direction. Only the smallest particles, free of mucus, are moved directly by the cilia.

A study of the ciliary currents of the palps suggests that the food-sorting mechanism of the oyster is designed for continuous feeding in water containing a low concentration of minute food organisms. Under such conditions only a limited amount of mucus is used for sorting out the suitable forms. The question of whether the oyster is capable of selecting its food on some other basis than size has not yet been adequately studied.

REACTION TO STIMULI

The palps respond both to mechanical stimulation and to the chemical stimulation of weak acids, solutions of mineral salts, etc. If a weak mechanical stimulus is applied to the edge of the palp, the affected portion contracts, making a shallow indentation which is proportional in size to the intensity of the stimulus. Strong mechanical stimulus or application of such irritating solutions as weak hydrochloric acid, ethyl alcohol, adrenaline, etc., provoke general contraction of the palps and gradual curling up of their edges. The external palps bend to the outside, while the internal palps curl in the opposite direction and seal the access to the central gutter (fig. 114). Autonomous responses of the labial palps of *Ano-*

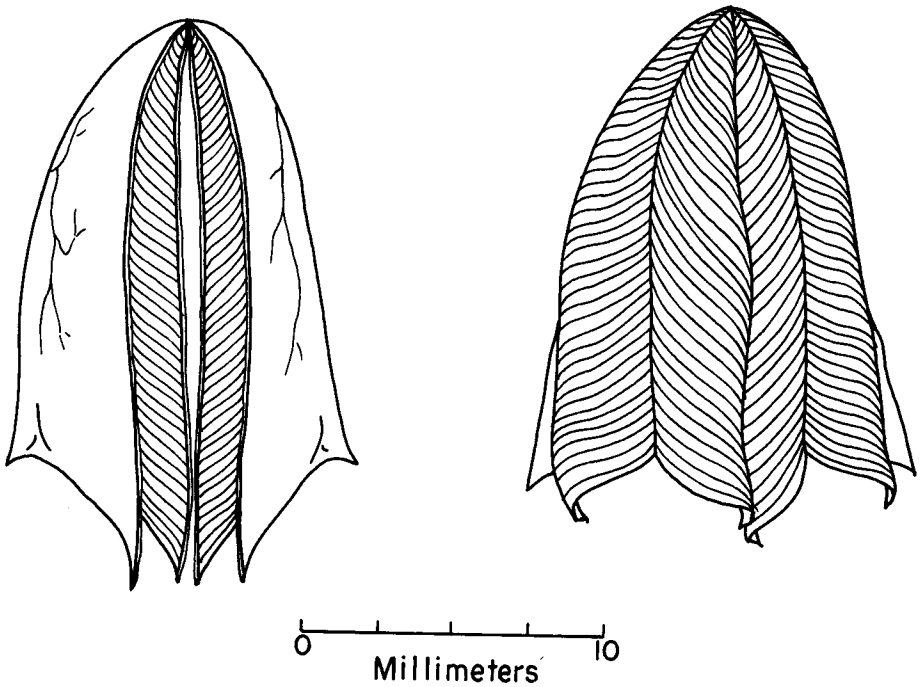

FIGURE 114.—Labial palps. Left—normal position. Right—position taken after mechanical stimulation. Drawn from life. Slightly enlarged.

donta were studied by Cobb (1918), who found that curling can be evoked by a jet of warm water (54° C.), a beam of sunlight, faradic current, and by a number of chemicals. His conclusion that chemical stimulation is more effective than are the mechanical stimuli in provoking a response could not be verified. While it is easy to determine the effectiveness of various concentrations of chemicals or to register the response to mechanical stimuli, a direct comparison between the intensities of chemical vs. mechanical stimulation is impossible without having a common standard for reference.

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