Notes on Nucula.

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With 5 Figures in the Text.

THESE notes record the result of work done at the Plymouth Laboratory during the summer of 1926. They deal chiefly with the feeding habits of Nucula, a Protobranch possessing the type of feeding mechanism characteristic of that order, and not found in any other Lamellibranch. During the course of my work I found Vlès' interesting paper on the sense organ of Nucula. After studying the organ, I arrived at a different interpretation of its function from that reached by Vlès.

I owe very much to the kindness of the Director and other members of the staff of the Laboratory, and am also indebted to Professor H. G. Cannon for friendly advice.

Three species of Nucula, common in the vicinity of Plymouth, were used, namely, *N. nucleus*, *N. radiata*, and *N. nitida*. Much important work has been done on *Nucula nucleus*, the most common European species, as well as on *Nucula proxima* and *Nucula delphinodonta*, which live on the American side of the Atlantic. Of course, many characters are common to these species, but not all.

The material used was dredged in 20 to 30 fathoms off Plymouth by the research steamer "*Salpa*," *N. nucleus* being the most abundant species. The Nucula were kept alive in a small glass dish with a little of the mud that was collected with them. A current of water from the general aquarium supply was provided, and the animals remained quite healthy during the two and a half months of my stay at the Laboratory. They were observed alive and dissected under a binocular microscope and some serial sections were cut after feeding with ferrous saccharate.

THE FEEDING APPARATUS.

In Lamellibranchs the labial palp is the most important feeding organ, its function being to select food material, to reject unnecessary substances, to make the food into suitable masses, and, finally, to conduct these to the mouth. The gill is an almost equally important feeding organ, being primarily a collector of food material, the collection being carried out in different ways and with different degrees of exactness according to the structure of the gill.

In Protobranchs, however, there is almost no co-operation between gill and palp.

The chief characteristic of the group is the primitive character of the gill, which is simple in structure, imperfect both as a selecting organ and a sieve for food-material, and possesses a very small surface area. Hence the palp is the sole organ of feeding in Protobranchs, and neither the high degree of specialisation in its structure nor the differentiation in function is surprising.

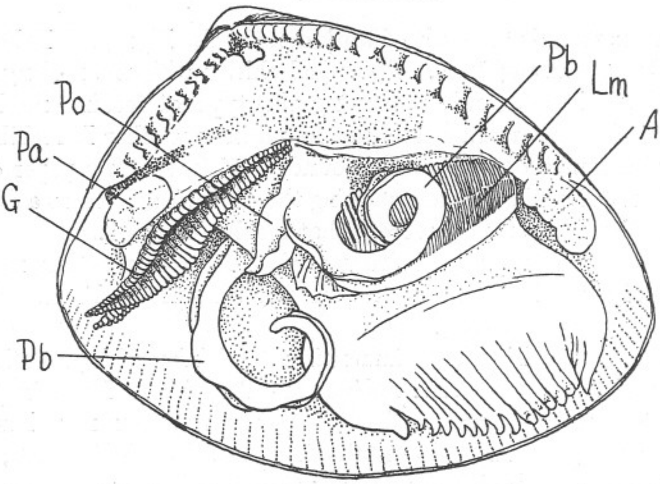

FIG. 1.—*Nucula nucleus*, alive; shell and mantle removed on right side. ×12. *Aa.*: Anterior adductor muscle. *G.*: Gill. *Lm.*: Palp-lamella. *Pa.*: Posterior adductor muscle. *Pb.*: Palp-proboscis. *Po.*: Palp-pouch.

The palp of Protobranchs consists of three different parts, the most important being the palp-proboscis, as I propose to call it, which is the food-collecting organ in all Protobranchs, but not in any other Lamellibranchs (Fig. 1, Pb.). Next comes the palp-lamella, corresponding to the labial palp of other bivalves, but a far larger organ resembling the gill (Fig. 1, Lm.). There is no palp-lamella in Solenomya. Finally, we have the palp-pouch, which is found only in Nucula (Fig. 1, Po.). These three structures form the complete feeding apparatus in Protobranchs, but the second and the third are sometimes lacking and only the proboscis is found in all species of the group.

I suggest this nomenclature, based on the form of the organ, to avoid confusion from the different names given by preceding authors. The *proboscis* has been called the " tentacular appendage of the labial palp "

(Mitsukuri, 1881), "appendice postérieur des palpes" (Pelseneer, 1891), "ventral palp-appendage" (Drew, 1901), "palp-appendage" (Morse in Solenomya, 1913; Kellog in Yoldia, 1915). The *pouch* has been called "hood-like appendage" (Mitsukuri), "appendice dorsal des palpes" or "capuchon" (Pelseneer), "dorsal palp-appendage" (Drew); and the *lamella*, "labial palp" (Mitsukuri), "palp" (Pelseneer), "labial palp" (Drew), "anterior palp" (Kellog in Yoldia).

The proboscis and the pouch are not really appendages of the palp at all; they seem to me to be feeding organs of equal or even greater importance.

Structure of the Feeding Apparatus.

A. *Palp-proboscis*.

This is a strong, muscular and contractile organ, the true form of which is difficult to determine in preserved specimens, for it always shrinks into a spiral and looks like a broad thick band with corrugated ridges on both margins. This appearance is, however, quite unnatural, and is due to extreme contraction.

In the living animal, the proboscis is very sensitive and active, and its size is very variable. At times it becomes very long, slender, and translucent, with an especially active tip, which is strangely similar to the trunk of the Proboscidea. The proboscis searches around in all directions outside the shell, and even over the shell surface itself, creeping up nearly halfway to the umbo (Fig. 2, a). I have seen this natural movement in a few specimens of *Nucula nitida* only, which had been kept in the Laboratory in a small aquarium for some weeks in the way described above. Probably they were very hungry. The proboscis is very flexible, moving around freely in all directions and becoming narrower or broader as may be necessary (Fig. 2, b, c). Food material is picked up by the tip, and travels swiftly and smoothly along the floor of the groove towards the base of the proboscis.

Writing of *Nucula proxima* the late Professor E. S. Morse aptly said: "Without seeing the behaviour of these appendages (he refers to the proboscis) it is difficult to appreciate the remarkable action of these feeding organs. The graceful movements of these beautiful and translucent appendages, exceeding in diameter the length of the shell, sweeping rapidly the bottom of the dish in which they are confined, or even turned back and feeding on the surface of the shell, are a most curious and interesting sight." This description differs only in one point from what I have seen in *Nucula nitida,* namely, that the size of the proboscis is less in *N. nitida* than in *N. proxima* (Morse, 1919, p. 147, Fig. 3). The exact length or even the length relative to the size of the animal is very difficult to ascertain, for the organ is only fully extended when the animal is alive. It is then extremely active, but the slightest shock causes it immediately to retract within the shell. I have several times tried to narcotise the animal, but it is very difficult to preserve it with the proboscis fully extended. From what I have seen it may be longer than the length of the shell by $\frac{1}{3}$ or $\frac{1}{4}$.

A proboscis lies under the mantle on each side, and almost in the centre of the body. The point of attachment is external to the postero-dorsal corner of the outer palp-lamella (Fig. 1, Lm., Pb.). In origin it must be only an outgrowth of the larval palp, as in *Nucula delphinodonta* (Drew,

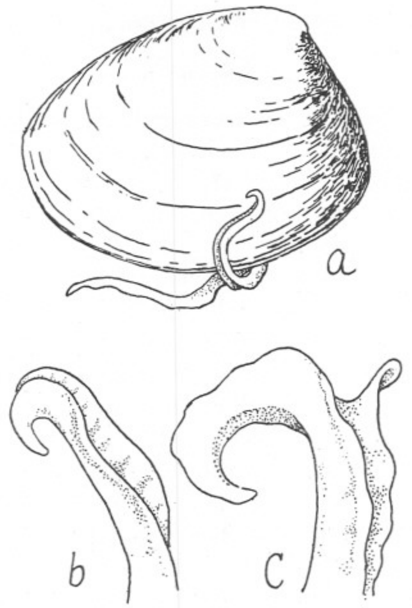

FIG. 2.—*a*, *Nucula nitida*, showing natural movement of palp-proboscis. *b* and *c*, ends of proboscis. All magnified.

Pl. 25, Figs. 54–57), but both in size and in function it is a very important organ in the adult.

In section the proboscis is V-shaped, as in *N. delphinodonta* (Drew, Pl. 25, Fig. 66), and the concave surface of its proximal part faces in a postero-dorsal direction. This surface and both its margins are covered by a single layer of high, columnar epithelial cells, with oblong nuclei and provided with long cilia, interspersed with secretory cells. The outer convex surface is also covered with a single layer of columnar cells, not as high as those of the inner surface, without cilia but accompanied by many secretory cells. Most of the space inside the epithelium is occupied by muscle fibres and large blood-lacunæ. At the bottom of the concave surface a single large bundle of nerve fibres runs just beneath the epithelium. At the point of attachment the longitudinal muscle bundles are united to the posterior retractor of the foot.

B. *Palp-pouch.*

This is the special organ which is found only in species of Nucula, and not in other Protobranchs. The pouch is a safety-cover or bridge for the food material, whilst it is being transmitted from the proboscis to the groove of the lamellæ. It is attached to the body just behind the proboscis and hangs down from the postero-dorsal corner of the lamella. It is a spoon-shaped organ, with the tip downwards and the concave surface looking forwards. Its margin is irregular and pointed at the end. Sections show that its structure is very simple, being bell-shaped with a thin layer of homogeneous connective tissue with spherical nuclei lying under the epithelium. The latter consists of a single layer of cubical cells with spherical nuclei, which, on the concave surface, carry short cilia. The posterior or convex surface is without cilia and has fewer secretory cells than the ciliated anterior surface, though the epithelial cells are arranged more densely. At the margin the thickness increases slightly and the tissue is impregnated with a chitinous substance with scattered nuclei, which looks very similar to cartilaginous tissue of higher animals. At the extreme edge this substance is thick and dense, but it gradually fades away and merges into normal connective tissue. The edge is tinged with a slightly yellowish colour.

In its natural position the pouch bridges over and establishes continuity between the two neighbouring organs, the proboscis and the lamella. The concave surface covers over the inner half of the proximal part of the proboscis and the extreme postero-dorsal margin of the outer palp-lamella ; in other words, the outer margin of the pouch is inserted into the groove of the proboscis, while its inner margin is inserted between the two lamellæ. The pouch moves very slightly, not actively except at its margin, which waves to and fro.

C. *Palp-lamellæ.*

This part of the palp corresponds to the labial palp of other bivalves, but is far more important and more differentiated than in them, because the gill is so primitive and so little developed as a primary selecting organ for food material. There are two lamellæ on each side covering the upper dorsal part of the foot which contains the stomach and many important visceral organs. These palp-lamellæ are much larger than in other Lamellibranchs, extending from the centre to the extreme anterior part of the body, a very small slit remaining between them and the anterior adductor muscle. At its anterior end each lamella becomes continuous with the corresponding lamella of the opposite side, just above and below the mouth, the lamellæ thus forming as it were a roof above and a floor beneath the mouth. The width of the lamellæ decreases gradually towards the anterior end. On each side of the body the outer and the inner lamella become continuous dorsally, except in the region of the mouth, thus forming a longitudinal groove, the whole being suspended from the body wall by a common thin membrane, which consists of a single layer of epithelium on each surface with a small quantity of connective tissue between. The margins of the lamellæ in their postero-ventral parts contain chitinous substance, which gradually changes to normal connective tissue in the dorsal and anterior parts ; a few ridges in the posterior regions also contain some chitinous substance.

In both lamellæ the outer surfaces are covered with a single layer of cubical or rather squamous epithelial cells, with inconspicuous short cilia on the outer lamella, and devoid of them on the inner lamella, except on its ventral portion ; whilst on the inner surfaces, which face each other, the cells of the single layer of epithelium are high columnar cells with long cilia.

These inner surfaces of the lamellæ are not smooth, but are profusely covered with ridges, those on the upper half being broad and high, those on the lower half narrow, low, and insignificant, the two kinds of ridges uniting in the middle line and forming a knob at the end of the higher ridges (Fig. 4, p. 637). These structures are very conspicuous through the thin wall of the lamella, and make the lamella look striated on the outer surface, although this surface is really quite smooth. The ventral margins of all the lamellæ are smooth and without ridges.

Between the two epithelial surfaces the space is narrow and occupied by connective tissue. Beneath the dorsal groove formed where the two lamellæ meet there is a large nerve cord and a spacious blood-lacuna immediately under the epithelium.

As regards the finer structure of the lamellar ridges, I think there are three different parts on the surface of each. The distinction is clearest in the posterior ridges, since the ridges gradually diminish in size towards the anterior end of the lamella. The ridges bend naturally forwards or towards the oral side, and consequently the posterior surface is somewhat broader than the anterior. The upper portion of the ridge (Fig. 3, A) is covered with strongly ciliated high columnar cells with oblong nuclei. This portion is very strongly developed in the posterior and dorsal part of the lamella, being broad in section and containing a large mass of connective tissue. The posterior surface of the middle portion (Fig. 3, B) is covered by the highest columnar cells, with very slender oblong nuclei, and there is a mass of finely granulated cytoplasm at the base of the long cilia. The lowest portion of the ridge (Fig. 3, C) forms a semicircular groove with the neighbouring ridge on each side. It is covered by a layer of epithelial cells, with bulky spherical nuclei and very long cilia. The cytoplasm of these cells is hyaline near the surface, having probably a very dense and homogeneous consistency. On the oral side of this part of the ridge there is one large knob formed by a mass of cells with spherical nuclei and many secretory cells.

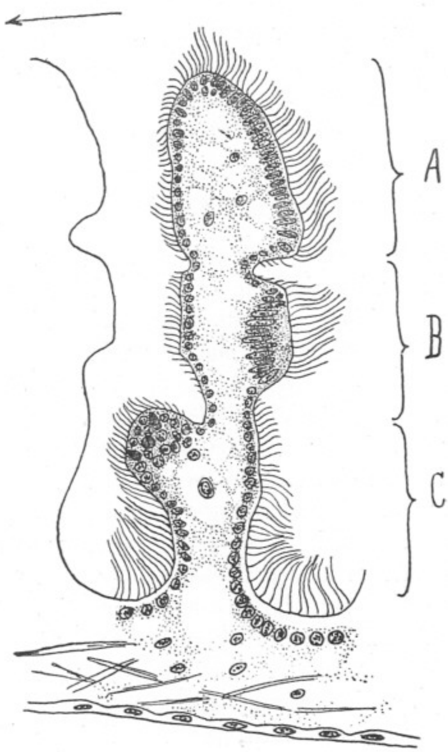

FIG. 3.—Diagrammatic sketch of lamellar ridge, in transverse section. Arrow shows oral or anterior direction.

The oral surface of the ridge is not provided with long cilia, except in its lowest portion which forms a groove with the next ridge. Many spaces were seen in the subepithelial connective tissue which seemed to be blood-lacunæ, the largest of them being in the basal portion.

There are no recognisable muscle fibres in the ridge, these being found only below the epithelium of the outer surface of the lamella.

I have already explained that the ridges on the dorsal side of the middle line of the lamella are much higher than those lying ventrally to that line

Considering these ridges in more detail, it may be noted that if one single ridge is followed from its dorsal to its ventral end, the three portions, which I have called parts A, B, and C, do not decrease in the same ratio, but, at the point where the ridges cut the middle line of the lamella, part C suddenly disappears and the ridges in the ventral portion of the lamella consist of the two other parts only. The ridges therefore become suddenly very low and narrow, with shallow grooves lacking long cilia between them. On the other hand, part C is well developed on the upper half of the lamella, and there is a deep furrow with long cilia between neighbouring ridges, the furrow gradually becoming shallower towards the ventral half. There is a conspicuous and sudden disappearance of part C in the middle of the lamella, forming a knob-like prominence followed ventrally by a lowering of the ridge.

The Function of the Feeding Apparatus.

In order to study the function of this mechanism I have made use of starch grains stained with tincture of iodine, by means of which it is possible to follow the ciliary currents in the living Nucula. I have also cut sections of animals which had been fed with ferrous saccharate one hour or half an hour before fixation, for the purpose of determining the real orientation of food material in these organs.

I have already described the function of the proboscis in the living animals. From further observations with the binocular microscope on living specimens, the shell and mantle of which had been removed on one side, it has been possible to follow completely the system of ciliary currents (Fig. 4). When any particles are put on the inner concave surface they are carried very rapidly by the beating of the cilia to the bottom of the central furrow. Having collected there they travel still more rapidly to the proximal end of the organ, being moved along by the strong cilia which occupy the centre of the furrow. They then enter the pocket-like pouch, the cilia lining which change their direction and carry them to the posterior end of the lamellæ. Most of the particles which arrive at this point are swept into the central groove of the lamellæ by the strong ciliary current and carried along the groove to the mouth. But those particles which do not reach the groove fall by gravity or for some other reason on to the other part of the lamellæ and are moved along by the ciliary current of the ridges.

Speaking generally, the size of the ridges is large posteriorly and gradually diminishes towards the mouth. The action of the ciliated ridges is probably more powerful in the posterior half of the lamellæ, and the coarser particles may be rejected here where they first strike the ridges.

As already explained each of the ridges consists of three different parts on the dorsal half of the lamella, and it appears to me that the function of each part is different. The distal part A (Fig. 3), with strong cilia which normally beat towards the ventral margin of the palp, removes material which is too large or not wanted. The second part B, the posterior surface of which is covered with very high columnar epithelial cells with long cilia, that are perhaps sensory cells, is in my view the place where the material collected is selected and sorted, being in part filtered by the ciliary sieve. The proximal part C is the most important organ of transport, where the already selected food material is pushed rapidly towards the central furrow by the powerful cilia which beat in exactly the opposite direction to those of part A. On the anterior face

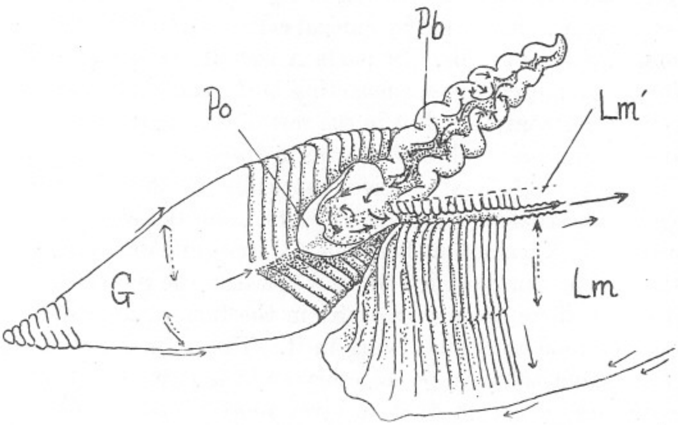

FIG. 4.—Diagrammatic sketch of palp-feeding mechanism of *Nucula nucleus*, ventral view, showing direction of ciliary current on right side; outer right lamella almost removed (*Lm′*). Broken arrows show ciliary currents in deeper zones. *G.*: Gill. *Lm.*: Palp-lamella. *Pb.*: Palp-proboscis. *Po.*: Palp-pouch.

of the ridges of part C are the large knob-like protuberances, which constitute the main secretory organs, the secretion from which consolidates the food material into masses of a size suitable for propulsion by the powerful ciliary movement.

There are thus on the whole two main currents running in opposite directions on the inner surface of each lamella, these currents being produced by ciliary action taking place at different levels on the ridges. First there is a superficial current due to the cilia of part A, by means of which unnecessary material is swept to the ventral margin of the lamella, while, secondly, in the deeper zone, the selected food substance travels to the dorsal side of the lamella, finally reaching the central lateral furrow between the two lamellæ, which is the main route to the mouth.

On the ventral edge of the lamella there are also ciliary currents which convey all particles to the posterior end of the lamella, where they fall into the mantle cavity and are soon expelled outside the shell.

Before leaving this part of the subject it will be useful to compare the lamellar ridges of the palp of Nucula with those found in other Lamellibranchs. In the common mussel (*Mytilus edulis*), which is provided with one of the most active and complicated labial palps, and has been the subject of many investigations (List, 1902 ; Wallengren, 1905, etc.), the ridges of the palp are differentiated as in Nucula into three parts. Part A is here also strongly ciliated, and covered by columnar epithelium interspersed with goblet cells. Part B is considerably larger than in Nucula, but is equally covered by very high columnar cells. Part C differs more from the corresponding part in Nucula, the furrow is very deep, especially anteriorly, the knob-like protrusion being high up on the ridge, and it is also very narrow. It is lined by cubical cells with short cilia, interspersed with many secretory cells. In parts A and B the sub-epithelial tissue contains many muscle fibres connecting both surfaces, which mostly run obliquely or horizontally. But in the rest of the organ only " vesicular " cells are found, muscle fibres being quite absent.

By a study of these structures, especially by cutting sections after feeding, I found that the functions of parts A and B were exactly the same in Mytilus as in Nucula, but that of part C was quite different. I conclude that there is no transmission of food towards the mouth by the latter part, because there are no long cilia in the furrow, nor could I find in sections any food substance lying in it. The main function of part C in Mytilus seems to me to be secretory and the part has no concern with food conveyance, except that it gives more room for the contractile activities of neighbouring parts.

According to Wallengren (1905, pp. 49–53) the work of sorting the food materials is completed by the co-operation of the different zones of ciliated epithelium, which beat in different directions with the changes of inclination of every individual ridge.

In many cases the ridges bend forward and their inclination becomes very oblique to the plane of the main surface of the labial palp, in which state the furrows between the ridges almost cease to function. But when the ridges are erect and perpendicular to the plane of the whole palp, almost all material falls into the furrows, and is conveyed to the margin of the palp, where it is rejected.

In Mya (Yonge, 1923, pp. 28–32) this furrow is very important for rejecting materials which are superfluous or rather heavy and unsuitable for food. These fall directly into the furrow and are removed by the same ciliary current that Wallengren described in Mytilus. The ridges in Mya are different in form from those in Mytilus, being short and broad, with part B not conspicuously developed. Changes in inclination and alterations in shape of the ridges are therefore quite difficult; the ridges remain almost stationary, and all the furrows are open the whole time.

In Mya, therefore, the furrows are important and provide the only method of rejecting unsuitable material, whereas in Mytilus, according to Wallengren, the method is different, the greater part of the rejection taking place in the higher zone of the ridges, and not in the bottom of the furrows. My observations support Wallengren's view, and I consider that the function of part C in Mytilus is quite different from what it is in Nucula.

Parts A and B are exceedingly active and contractile; sometimes the ridges are very broad and short, and then by the contraction of the muscles they become tall and slender. Under the binocular microscope a peristaltic depression of the ridges can be seen running from one end of the lamella to the other and forming a temporary groove between neighbouring high ridges. This motion occurs normally on the palp surface, the food particles rolling into this temporary groove, which travels rhythmically forwards in the direction of the mouth by the contraction of each neighbouring ridge. The change of inclination of the ridges, as Wallengren (1905) described it, is not so conspicuous. The change of ridge form is the consequence of muscular activity, which is controlled by nerve centres connected with the sensory epithelium of the surface of the ridge.

The transmission of food material to the mouth is not performed by part C, as in Nucula, but by part B, which with the corresponding part of the next ridge makes a tubular channel lined with long cilia, which convey the food particles, cemented together into one mass by mucus secreted by part C, in a forward direction. This fact was established by sections made after feeding, which always showed the food material formed into a mass in part B, present as separate particles in part A, and entirely absent from part C.

There is therefore this essential difference in manner of functioning between the palp-lamellæ of Nucula and Mytilus, notwithstanding their general similarity of form.

I have already said that the *gill* of Nucula is very defective as an organ for the collection of food, but probably it is not entirely inoperative, for there is the capacity of making a slit-like opening between the pouch and the inner lamella, by the movement of these organs, and particles can then stream from the posterior part of the pouch into the space between the lamellæ.

But although there is no real connection between the gill and palp organs, the gill has its own system of ciliary currents on its surface. These are indicated in Fig. 4. There are two opposite ciliary currents in each gill surface, a superficial one sweeping towards the margins of the gill, and a deeper interfilamentar current directed towards the central groove or depression. In this central groove and along both the gill margins particles travel rapidly in a forward direction.

But almost all particles on the gill fall into the mantle cavity, without getting on to the lamellæ of the palp, and by the action of the surface cilia of the foot and mantle they are collected at the mid-dorsal margin of the mantle, from which point they are expelled by an outgoing current produced by a movement of the foot, passing out from the shell just behind where the foot protrudes.

Several authors have suggested that the palp acts as a respiratory organ, for it seems to them to be too extensive for a feeding organ, and, on the other hand, the gill has such a small surface area. But this is not really so, as the lamella has quite a different histological structure to the gill, and one which is very similar to that of the alimentary canal. It seems to me more reasonable to regard the lamella as a pure feeding organ, its function being, like that of the intestine, the conveyance of food.

The Cephalic Sense Organ.

The sense organ of *Nucula nucleus,* which is innervated directly from the cephalic ganglion, was described by a French biologist in a preliminary note (Vlès, 1905), and no further account has, as far as I have seen, been published.

Walter Stempell (1899, Figs. 25 and 26) had already described the same organ in *Solemya togata,* and called it " adorale Sinnesorgan." He writes : " Ihre physiologische funktion dürfte in einer Prüfung des Wasserbestehen, welches mit der Nahrung zusammen der Mundöffnung zuströmt," and its function therefore according to his view resembles that of Thiele's (1887, 1889) " neues Sinnesorgan," or abdominal sense organ. Vlès' interpretation of the organ in Nucula is the same. It is strange that Stempell did not find this organ during the whole of his anatomical research on the Nuculidæ (Stempell, 1898).

Thea Clasing (1923) has described in Mytilus a tubular organ near the mouth and the cephalic ganglion, and almost in the same position as Vlès' organ in Nucula. He considered it to be a sensory organ for the perception of currents or of the pressure of the surrounding water. Its structure is, however, quite different from that of the cephalic sense organ of Nucula.

While I was investigating the feeding process in Nucula, I found this organ in *N. nucleus* and in two other species. It is situated very near to the mouth and to the point of attachment of the lamella, just below the cephalic ganglion. In section it appears as a remarkably differentiated part of the epithelium, consisting of two layers of cells in contrast to the single layer of cells in the rest of the epithelium (Fig. 5). Owing to its thickness it protrudes beyond the neighbouring epithelium, but there are one or two concave depressions on its surface denoting slight invagination. Superficially it is covered by a thick and structureless layer without nuclei, which seems to be of a very dense and homogeneous character, closely resembling the cornea of the eyes of other

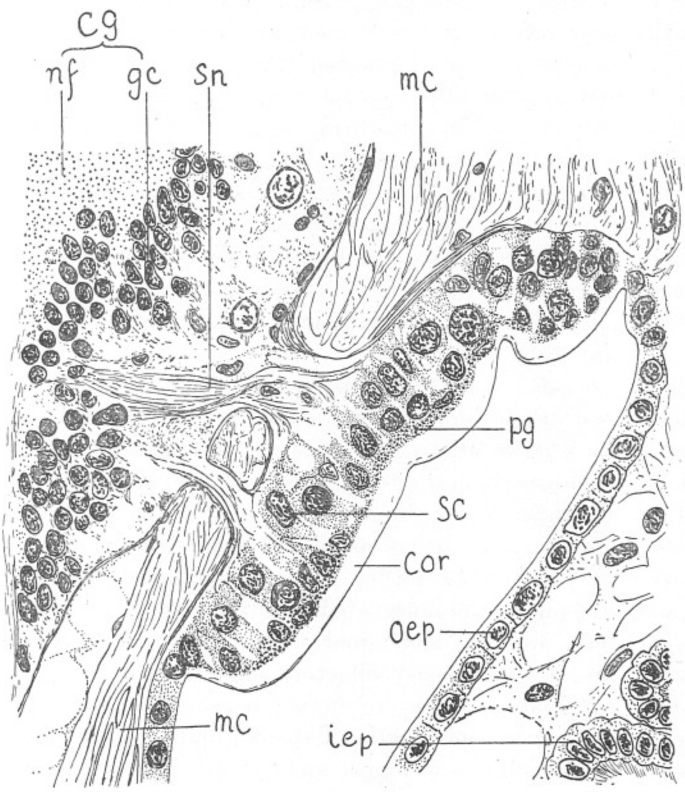

FIG. 5.—Cephalic sense organ in *Nucula nucleus*. *Cg.*: Cerebral ganglion. *Cor.*: Cornea. *Gc.*: Ganglion cells. *iep.*: Inner epithelium of lamella. *mc.*: Muscle. *nf.*: Nervous fibres. *oep.*: Outer epithelium of lamella. *pg.*: Pigment. *sc.*: Sensory cell. *sn.*: Sensory nerve.

invertebrates, and I propose to call it cornea (Cor. in Fig. 5). Its surface is clearly devoid of cilia.

Immediately below the cornea I found a single layer of cells with inconspicuous nuclei, which resembled normal epithelium, except that it contained pigment granules, but not in considerable amount (Pg. in Fig. 5).

The third or basal layer is the important sensory part of the organ, which is innervated on its proximal side. The cytoplasm has fine granules of several different kinds, and a large spherical nucleus (Sc., Fig. 5), and it sometimes appears vacuolated. Probably its finer structure could be made out with higher magnification.

All the nerve fibres which come from these sensory cells collect into one large nerve bundle, sometimes with one or more minor bundles, all of which pass directly into the cephalic ganglion, breaking through the muscles of the retractor pedes (Fig. 5, Sn.). The cephalic ganglion (Fig. 5, Cg.) is the most anterior and most conspicuous ganglion in Nucula, and really consists of two ganglia connected by a short commissure just above the mouth and in front of the œsophagus. In section it is a spherical mass with a fibrous part in the centre, surrounded by ganglion cells and covered by a thin membrane, which also extends around the basal part of the sense organ (Fig. 5, Gc., nf.). The sense organ has an exactly similar structure in the other two species.

As regards its function, from its histological structure and anatomical relations Vlès considered it to be an olfactory organ analogous to Hancock's organ in Gastropods, especially in Cephalaspides (a group including Bulla, Aplysia, etc.).

Hancock's organ is a real olfactory organ, which is regarded as quite homologous with the rhinophores on the tentacles. The latter are found in Gastropods, whereas Hancock's organ only occurs in burrowing forms in which tentacles are almost or quite absent (Plate, 1924).

In Lamellibranchs the osphradium and also abdominal sense organs are very common, both being sometimes found in the same animal. They are both innervated from the visceral ganglion, whereas Hancock's organ and rhinophores are innervated from the cephalic ganglion. Both the osphradium and the abdominal sense organs are concerned with respiration and are not purely olfactory organs. They have therefore been called by Plate, "respiro-receptor" organs (or "atmungs-geruchorgane"). Most of the opisthobranchiate and nudibranchiate gastropods possess both true olfactory organs and respiro-olfactory organs at the same time. It seems quite correct that these two classes of organs have different functions, the former (rhinophores, Hancock's organ) are more highly differentiated and are purely olfactory, the latter (osphradium, abdominal sense organs) are more primitive in structure, and are used to test the purity of the water before it is allowed to pass over the gill.

There is no Lamellibranch which possesses a real, independent olfactory organ. Probably the palp plays this rôle.

As already described by Pelseneer (1891, p. 167, Pl. VII, Fig. 11, III), Nucula possesses an osphradium in the neighbourhood of the gills, situated on the surface of the retractor muscle of the foot and directly innervated from the visceral ganglion. Its structure is quite different from that of the cephalic sense organ, for it consists of a single layer of large, cubical epithelial cells with long cilia, but without the thick transparent covering layer found in that organ.

For these several reasons I do not regard the cephalic organ as an olfactory organ, but as a visual organ or the remnant of a larval eye. Its structure, as I have described it, is particularly characteristic of a visual organ, that is to say, its invaginate form, the existence of a transparent external layer, the presence of pigment and of sensory layers. As a visual organ it is, however, very incomplete in structure ; for example, the pigment is so poorly developed that it shows only faintly. It is probably, therefore, only the remnant of a larval sense organ, for eyes would be very useful in the larva, before the palp-lamellæ are developed or whilst these lamellæ and the shell are all quite transparent. It is true that in the excellent description by Drew of the development of *Nucula delphinodonta* there is no mention of an eye, but the reason for this may well be that the larval stage of that species is spent almost entirely in the brood-sac. It is to be hoped that this point will be cleared up in the future by a study of the development of *Nucula nucleus*.

The visual organs of Lamellibranchs fall into two categories: (1) cephalic eyes and (2) pallial and siphonal eyes. The former are primitive in structure, but are the original eyes of the group mollusca ; the latter are very highly differentiated, but have developed secondarily in the group.

These cephalic eyes are only found in the more primitive groups of Lamellibranchs, such as Mytilidæ, Arcidæ, Avicula, Anomia, all belonging to the order Filibranchia. They are well known, especially in Mytilus (Pelseneer, 1900 ; List, 1902 ; Field, 1922 ; Clasing, 1923), being situated at the anterior ends of the animals, for example on the anterior margin of the inner gill lamella in Mytilus, and innervated directly from the cephalic ganglion. Their structure is of a very simple type, with a slight invagination, an imperfect lens or without a lens, and pigment cells interspersed amongst sensory cells or lying above them.

The cephalic sense organ is similar in Nucula, but it is very simple compared with the eye of Mytilus, and resembles somewhat the cephalic eye in Patella, which is the most primitive one amongst the Gastropods.

It seems to me to be most rational to regard this cephalic sense organ of Nucula as a visual organ, in the first place because of its structure, and, secondly, from phylogenetic considerations, for the Protobranchs are very closely related to the Filibranchs.

The Movement of the Foot.

I agree entirely with Drew, who described the foot of *N. delphinodonta* as being not a creeping, but only a burrowing organ.

All three species of Nucula with which I experimented burrowed immediately when mud was present, travelling very swiftly under it.

When, however, the animals were put in a glass dish without mud, they always remained quite helpless, notwithstanding full activity of the foot. The thrusting out and retraction of the foot accomplished only a slight shifting of the shell, turning it in different directions. The flat surface of the foot-sole never reached the smooth substratum at all.

But I once saw a small mollusc creeping very rapidly among some Nucula immediately after their collection, and at first I thought that it also was a young Nucula. It crept to the extreme edge of the glass dish and even hung down from the surface of the water by its foot. Afterwards I found that it was quite a different species, notwithstanding its great resemblance to a young Nucula. It was some species belonging to the genus Mactra or its relatives, and I am afraid that it was in this way that Forbes and Hanley were deceived when they described a swiftly creeping habit in *Nucula nucleus* (p. 217).

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