The 'Posterior Lobes' of *Nephtys*: Observations on three New England Species

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With one plate (fig. 2)

SUMMARY

The disposition of the prostomial mucus-glands in *Nephtys picta*, *N. incisa*, and *N. bucera* provides additional evidence that the posterior lobes, which are attached to the supra-oesophageal ganglion of species such as *N. californiensis* and *N. caeca*, have been formed by the posterior migration of prostomial epidermal mucus-cells. In *N. picta* there are few mucus-cells in the prostomium. In *N. incisa* there are many, and some at the sides of the prostomium occur in clumps and project into the prostomial cavity. In *N. bucera* there are numerous mucus-cells, but they are massed at the sides of the prostomium and open to the exterior over a narrow zone. The cell-bodies are in intimate contact with the sides of the supra-oesophageal ganglion and lie within the membranes investing the brain. Subsequent evolution of the prostomial mucus-glands has led to the accumulation of their cell-bodies in the posterior part of the supra-oesophageal ganglion in the form of posterior lobes.

SOME species of *Nephtys*, particularly those from the north-east Pacific, but including the common circumpolar species *N. caeca*, have a pair of long lobes attached to the posterior margin of the supra-oesophageal ganglion. These lobes are filled with mucus-cells, the long necks of which run in a tract on each side of the ganglion and open to the exterior in the lateral walls of the prostomium by way of conspicuous lateral organs. The cells in the posterior lobes and the lateral tracts of cell processes are all enclosed within the sheath that invests the ganglion, and they and the lateral organs are separated from the ganglion-cells only by a layer of neuroglial tissue. In other species these lobes are missing and mucus-cells are confined to the lateral walls of the prostomium, more or less in the position occupied by the lateral organs in the former species, and have no connexion with the supra-oesophageal ganglion at all.

In all species of *Nephtys*, whether they have posterior lobes or not, there is a mass of mucus-cells in the middle of the anterior edge of the prostomium. These generally open to the exterior on the ventral surface, and there may be other mucus-cells in the lateral walls of the anterior part of the prostomium. However, in one species, *N. longosetosa*, while most of the mucus-cells in the medial group open to the exterior ventrally, and most of those in the lateral walls open to the side, a few cells in the medial group open to the side by way of long necks, forming a small lateral organ in the anterior part of the prostomium. In some other species, most obviously in *N. californiensis*, most of the cells in the medial group open to the exterior by way of long necks which

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run to the lateral walls of the prostomium, forming a large anterior lateral organ on each side, which completely replaces the small mucus-cells in the epidermis at the sides of the prostomium, and which adjoins a similar posterior lateral organ associated with the posterior lobes. Anterior and posterior prostomial mucus-cell systems vary independently, and in *N. cornuta* there are well-developed anterior lateral organs, but no posterior lobes and, therefore, no posterior lateral organs.

When describing the mucus-gland system of *Nephtys* (Clark, 1955), I suggested that mucus-glands in the lateral walls of the anterior part of the prostomium had migrated into the medial mass, retaining their connexion with the lateral walls of the prostomium. *N. hombergi* is an example of a species with a complete separation of the lateral and medial mucus-cells, *N. longosetosa* represents an intermediate stage in which a few cells from the lateral walls have migrated into the medial group, and *N. californiensis* an extreme case in which all the mucus-cells opening to the lateral walls of the prostomium lie in the medial group. By analogy, I argued that the mucus-cells in the lateral walls of the posterior part of the prostomium must have hypertrophied and migrated back into the brain capsule, but retained their connexion with the prostomial walls so that they opened to the exterior by way of the lateral tracts and the lateral organs. The chief weakness in this interpretation lay in the absence of any intermediate steps in the process. The mucus-cells were found in the lateral prostomial walls or in the posterior lobes, but never half-way between the two in any species I had examined.

Recently I have had the opportunity of examining specimens of *N. bucera*, kindly sent to me by Dr. Marion Pettibone from various localities in Maine and New Hampshire, and I have re-examined specimens of *N. incisa* and *N. picta* from Massachusetts. This material has provided additional evidence about the evolution of posterior lobes in *Nephtys* and has provided the intermediate stages which were previously missing.

Material and Methods

Specimens of *N. bucera* Ehlers, *N. incisa* Malmgren, and *N. picta* Ehlers were fixed whole in Bouin's fluid. Frontal and transverse sections have been cut at 10μ and stained with paraldehyde fuchsin (Clark, 1955), Altmann's fuchsin and methyl green picrate (Gabe, 1947), Heidenhain's iron haematoxylin, or by Holmes's silver impregnation technique (Nicol, 1948).

Observations

None of the three species possesses posterior lobes, and the mucus-cells in the anterior medial group open to the exterior ventrally. There are thus no lateral organs and we are concerned solely with the arrangement of the mucus-cells in the lateral walls of the prostomium, particularly those in the posterior part of it that are in the neighbourhood of the supra-oesophageal ganglion.

The supra-oesophageal ganglion of *N. picta* lies mainly in the first body segment and only a small part of it is in the prostomium (fig. 1). The nuchal

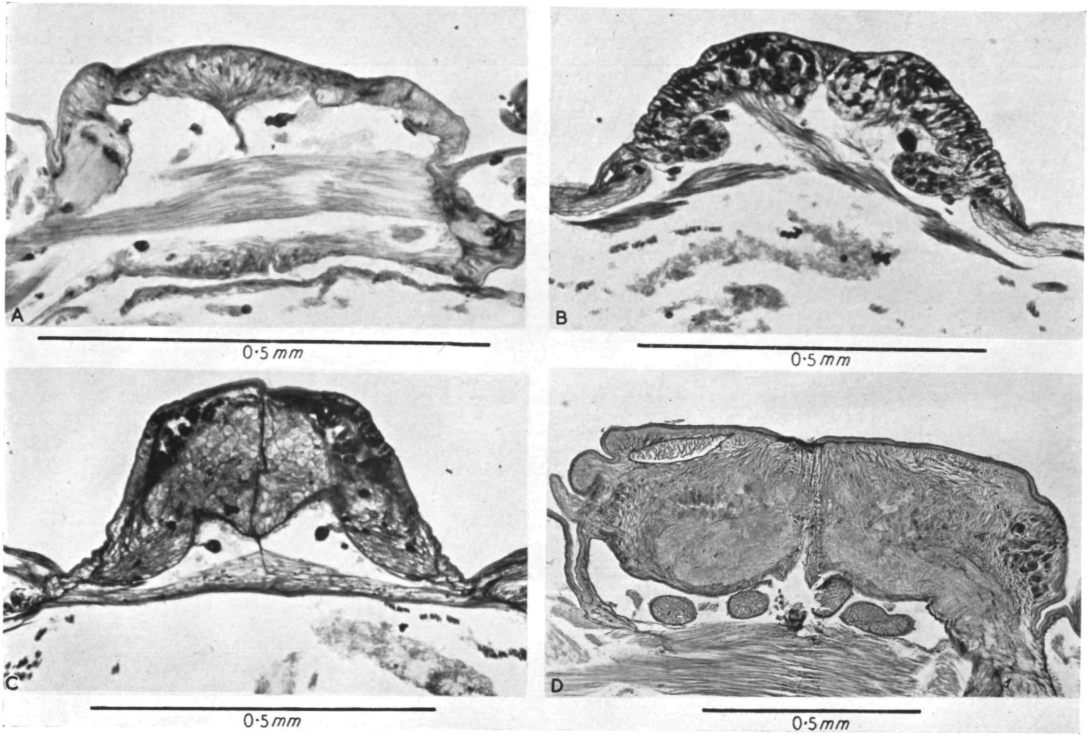

FIG. 2
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organs, which mark the posterior limit of the prostomium, are at the level of the most anterior ganglion-cells in the brain. While the ganglion is attached to the dorsal surface of the prostomium, it makes no contact with the sides of it, although the circum-oesophageal connectives in front of the brain do so.

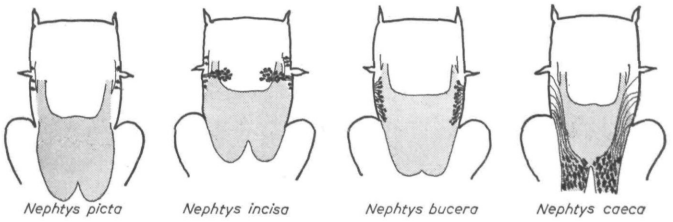

FIG. 1. Evolution of prostomial mucus-glands in the Nephtyidae. In *N. picta* there are only a few mucus-cells in the prostomial walls and these have no contact with the ganglion. In *N. incisa* there are more mucus-cells, and clumps of them project into the prostomial cavity. In *N. bucera* the mucus-cells are in contact with the ganglion, are enclosed within the ganglionic membranes, and are massed at the sides of the ganglion. In *N. caeca* there are far more mucus-cells, these have migrated into the posterior part of the ganglion but open to the exterior in the sides of the prostomium. Supra-oesophageal ganglion stippled, mucus-cells black.

They run in the sub-epidermal basement membrane. Compared with most other species of *Nephtys*, there are few mucus-cells in the prostomial epidermis and those that there are, are in the lateral walls and have no contact with any part of the nervous system (fig. 2, A).

The brain of *N. incisa* occupies a more anterior position than that of *N. picta* and most of it lies in the prostomium, so that the nuchal organs are near the back of the brain. As is the case in all species of *Nephtys* in which the brain is largely prostomial, it is attached not only to the dorsal part of the prostomium, but also to the sides of it. The circum-oesophageal connectives, as usual, run forwards and downwards from the brain in the sub-epidermal basement membrane of the prostomial walls. There are numerous mucus-cells in the prostomial walls (figs. 1; 2, C), most of which lie in the base of the epidermis and have narrow necks running directly to the cuticle through which they open by fine pores. There appear to be more and larger mucus-cells than can be accommodated in a single layer of epidermal cells, and a number of them are arranged in clumps at the sides of the prostomium and project into the prostomial cavity (fig. 2, B). These clumps of mucus-cells lie dorsal

FIG. 2 (plate). A, transverse section of the prostomium of *N. picta*, cut a little anterior to the supra-oesophageal ganglion. Bouin, paraldehyde fuchsin. B, transverse section of the prostomium of *N. incisa*, cut a little anterior to the supra-oesophageal ganglion, showing a clump of mucus-cells projecting from the epidermis into the prostomial cavity on each side. Bouin, paraldehyde fuchsin. C, transverse section of the prostomium of *N. incisa*, including the anterior part of the supra-oesophageal ganglion. Numerous dark-staining mucus-cells occur in the epidermis. Bouin, paraldehyde fuchsin. D, slightly oblique transverse section of the prostomium of *N. bucera*, showing massed mucus-cells at the right-hand side of the supra-oesophageal ganglion. Bouin, paraldehyde fuchsin.

to the circum-oesophageal connectives and occur only anterior to the supra-oesophageal ganglion, so that they do not form any connexion with the nervous system.

The walls of the prostomium of *N. bucera* are curious in that a thickened ridge of epidermis runs along the middle of each side and the prostomial mucus-cells are concentrated in it almost to the exclusion of other epidermal elements. The mucus-cells are large and have long, narrow, and slightly coiled necks. The cuticle along the line of the two ridges is peppered with the pores through which these mucus-cells open to the exterior. Massed mucus-cells occur at the sides of the prostomium from the level of the posterior antennae almost to the nuchal organs. The supra-oesophageal ganglion of *N. bucera*, like that of *N. incisa*, occupies a relatively anterior position and is largely prostomial. It extends from side to side of the prostomium and is in intimate contact with some of the prostomial mucus-glands (figs. 1; 2 D). The latter extend anterior to the brain and lie dorsal to the circum-oesophageal connectives, but in the posterior part of the prostomium they lie within the membranes investing the ganglion (extensions of the sub-epidermal basement membrane) and are separated from the lateral groups of nerve-cells only by a barrier of neuroglial fibres. Some of these penetrate between the mucus-cells and there appears also to be a number of connective tissue elements in the zone between the ganglion proper and the cuticle; ordinary, structural epidermal cells are missing from this region of the prostomium.

Discussion

The disposition and form of the mucus-cells in the prostomium of *N. incisa* and *N. bucera* suggest how posterior lobes may have evolved from purely epidermal mucus-cells. The function of the mucus is unknown, but evidently there is a need for it to be released in copious quantities at the sides of the prostomium in some species. *N. picta* is exceptional because it has very few mucus-cells in the prostomium, but in other species there is either a considerable number of them in the prostomial walls or else they fill the posterior lobes and open to the exterior by way of the lateral organs at the sides of the prostomium. An incipient hypertrophy of the prostomial mucus-gland system may be seen in *N. incisa*, in which mucus-cells are particularly numerous in the entire prostomial epidermis and, further, groups of them bulge inwards into the prostomial cavity, so permitting a greater number of mucus-cells than can be accommodated in the epidermis to open to the exterior. In *N. bucera* the arrangement of the prostomial mucus-cells is more specialized. These cells are restricted to ridges at the sides of the prostomium and there are relatively few elsewhere on the prostomial epidermis. The cells have long, narrow necks and so, although there are many of them, they open to the exterior over a narrow zone running along the sides of the prostomium.

This concentration of mucus-cells brings them inevitably into contact with the supra-oesophageal ganglion. The brain of *Nephtys* is epidermal (Clark, 1958), as are the mucus-cells, and in the posterior half of the prostomium it

replaces the ordinary epidermal cells. There is thus no ganglionic sheath which, in *N. bucera*, might separate the lateral mucus-cells from the ganglion; both are invested by the sub-epidermal basement membrane and the mucus-cells are separated from the nerve-cells only by neuroglial tissue. Once this stage of organization has been reached, further development of the mucus-gland system must be influenced by the presence of the ganglion. The only way in which a substantial increase in the number and size of the mucus-cells can be achieved is by their migration in a posterior direction so that they can expand into the body cavity, retaining their connexion with the prostomial walls by long ducts. In *N. incisa*, to be sure, the mucus-cells have extended into the prostomial cavity, but there is space for only very limited development in that direction. In all the species that have a highly developed mucus-gland system, the extension of these cells has been into the body cavity. The mucus-cells of *N. bucera* have long, coiled necks and those of the more posterior cells run forwards, suggesting that even in this species there has been some posterior migration of the cell-bodies. A further migration in a posterior direction must inevitably result in the cells eventually lying in the posterior part of the ganglion (see fig. 1, p. 507). This is the situation in *N. californiensis* and *N. caeca*, and in *N. californiensis* there are a few mucus-cells occupying a lateral position in the lateral tract of ducts that runs from the cell-bodies in the posterior lobes to the lateral walls of the prostomium (Clark, 1955).

No further information about the function of the mucus-gland system has been discovered since the original description of the posterior lobes. The factors which must be taken into account in any explanation of their function are now clearer. In *N. picta*, a species which appears to be primitive in several respects (Clark, 1957), there are virtually no prostomial mucus-glands. In *N. incisa* there are many, but they are dispersed over the whole prostomial epidermis though the larger clumps of glands open laterally. In *N. bucera* the mucus-cells are concentrated and open in a narrow zone along the sides of the prostomium. In *N. californiensis*, *N. caeca*, and many other species, the mucus-gland system is enormously developed but the cells still open to the exterior along the sides of the prostomium, and in a few species (e.g. *N. californiensis* and *N. caecoides*) this copious supply of mucus at the sides of the prostomium is supplemented by the discharge from mucus-cells in the anterior median part of the prostomium. In *N. cirrosa* the mucus-cells of the posterior lobes appear to have been highly modified and reduced in number, and it may be supposed that in this species they serve a different function.

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