

The Gross Morphology of the Anterior Nervous System of *Nephtys*

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SUMMARY

The supra-oesophageal ganglion of *Nephtys* varies considerably in its size and gross morphology from one species to another. The ganglion is relatively larger in small species and then extends into the anterior body segments. It is epidermal and in contact with the cuticle in the prostomium, sub-epidermal in the anterior segments. In a number of species a pair of conspicuous posterior lobes to the ganglion has been developed. There is a tendency, particularly in the smaller worms, for the ganglion to be bifurcated at its posterior, and sometimes also at its anterior margin. The sensory nerves are as follows: tegumentary nerves, extremely variable in number and disposition, arising from the front of the ganglion; two pairs of antennary nerves arising immediately above the roots of the circum-oesophageal connectives, but generally distinct from them; and a pair of anterior optic 'nerves' supplying the paired, single-celled photoreceptors. The only other nerves arising from the ganglion are the nuchal nerves which arise from it opposite the nuchal organs, whatever the position of the brain. Since the latter may barely protrude into the prostomium, these nerves emerge from the anterior part of the brain in some species, instead of near the posterior end of the ganglion. The circum-oesophageal connectives are extremely long because the sub-oesophageal ganglion lies in the fifth segment. In their passage through the lateral lips of the mouth and along the sides of the gular membrane, they give off three pairs of stomatogastric nerves and the segmental nerves of the first two segments. The third and fourth segmental nerves arise from the front of the sub-oesophageal ganglion, those of the fifth segment from the back of the ganglion. The stomatogastric nervous system is also described. The entire nervous system shows little specialization compared with that of most other errant polychaetes.

INTRODUCTION

THE supra-oesophageal ganglion of *Nephtys* varies considerably from one species to another. This is surprising in a family of polychaetes which otherwise shows great uniformity of structure, and the variability is not restricted to the gross anatomy of the brain; there are considerable and important differences in its fine structure between species. Some of the reasons for this variation have already been discussed (Clark, 1957) and I propose to give an account of the fine structure of the ganglion in a later paper. At present I am concerned with the gross anatomy of the supra-oesophageal ganglion and its variation in the Nephtyidae. The variability does not extend to other parts of the nervous system, but as existing accounts of these parts are unsatisfactory in several respects, a description of them is also included.

The literature includes seven accounts of the anatomy of the nervous system of *Nephtys*, by Delle Chiaje (1825), Quatrefages (1850), Ehlers (1864-8), Claparède (1868), Pruvot (1885), Schack (1886), and de Saint-Joseph (1894). All deal with *N. caeca*, *N. cirrosa*, and *N. hombergi*. Of these accounts, that [Quarterly Journal of Microscopical Science, Vol. 99, part 2, pp. 205-220, June 1958.]

by Pruvot is the most ambitious. Mistakes occur in all these studies and in none of them is a comparative account of the nervous system attempted. Even where there are gross differences in the morphology of the nervous system between these three species, the authors do not agree in their observation, far less in their interpretation. Quatrefages described a chain of seven ganglia anterior to the supra-oesophageal ganglion and lying between the circum-oesophageal connectives in the prostomium. Later authors corrected this error and concluded that Quatrefages had mistaken a mass of connective tissue or muscle for ganglia. In fact the mass is glandular. There was also a difference of opinion between Quatrefages and de Saint-Joseph, on the one hand, and Ehlers and Schack, on the other, as to whether or not posterior lobes were attached to the supra-oesophageal ganglion of *N. caeca*. This apparently arose from a misidentification of the worms, for the lobes occur in *N. caeca*, but not in *N. hombergi* and a number of other species. The question has been resolved in favour of the German authors (Clark, 1955). Pruvot and de Saint-Joseph concluded that the sub-oesophageal ganglion lay in the fourth segment (in fact it is in the fifth) and as a result incorrectly described the innervation of the first four segments. Thus, although there is much that is correct and valuable in them, these seven accounts are too full of discrepancies and error to be reliable or to inspire confidence.

MATERIAL AND METHODS

The species of *Nephtys* which have been used in this study are: *N. buccera* Ehlers, *N. caeca* (Fabricius), *N. caecoides* Hartman, *N. californiensis* Hartman, *N. cirrosa* Ehlers, *N. cornuta* Berkeley and Berkeley, *N. ferruginea* Hartman, *N. glabra* Hartman, *N. hombergi* Audouin and Edwards, *N. incisa* Malmgren, *N. longosetosa* Oersted, *N. magellanica* Hartman, *N. parva* Clark and Jones, *N. picta* Ehlers, *N. punctata* Hartman, *N. rickettsi* Hartman, and *N. squamosa* Hartman. The structure of the nervous system has been elucidated by dissection and by the examination of serial frontal, sagittal, and transverse sections of material fixed in Bouin's or Helly's fluids, and stained with paraldehyde fuchsin, Mallory triple stain, Azan, and Heidenhain's iron haematoxylin.

THE EPIDERMAL NATURE OF THE NERVOUS SYSTEM

The nervous system of all species of *Nephtys* is to varying degrees epidermal, that is to say, its embryological epidermal origin is manifest in the adult and, as in a number of the more primitive polychaetes, parts of the nervous system are not clearly separated from the epidermis. This is most evident in the supra-oesophageal ganglion. It is bounded laterally and ventrally by a connective-tissue sheath which is continuous with the epidermal basement membrane, and the dorsal surface of the ganglion is in contact with the prostomial cuticle. In most species part of the ganglion extends into the anterior body segments, and in them the ganglion is suspended beneath the epidermis and is completely invested by its sheath (fig. 10, p. 217); only that part of the ganglion which lies in the prostomium is in contact with the cuticle (fig. 8, A,

p. 215). Probably the whole ganglion was originally prostomial and epidermal, but in the course of evolution of these worms it has tended to extend into the anterior segments as a sac beneath the epidermis (Clark, 1957, fig. 3). The epidermal cells of the prostomial wall stop abruptly at the sides of the ganglion, and the cells in the dorsal part of the ganglion which replace them appear to be modified neuroglial cells. Goblet or coiled mucus-cells, which are scattered in the prostomial epidermis, do not occur in the ganglion.

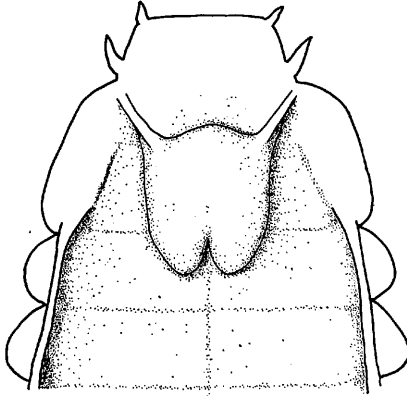


FIG. 1. Supra-oesophageal ganglion of *N. incisa*, ventral view.

Other parts of the nervous system, namely the ventral nerve-cord and sub-oesophageal ganglion, the segmental nerves, the stomatogastric nervous system, and the prostomial nerves, are all intimately connected with the epidermis, but never to the extent of replacing it as the supra-oesophageal ganglion does. All these structures lie in the sub-epidermal basement membrane and are separated from the cuticle by a layer of quite typical epidermal cells which differ in no way from those in other parts of the body-wall.

THE SUPRA-OESOPHAGEAL GANGLION

The supra-oesophageal ganglion of *N. incisa* (fig. 1) is subject to the fewest of the modifications discussed below and it will serve best for a description of the architecture of that organ. It lies in the posterior half of the prostomium and is as long as broad, with a slight bifucation in its posterior margin. Only the posterior tips of it project into the first segment, and from the foregoing discussion it will be clear that almost the entire ganglion is in contact with the prostomial cuticle. Only the extreme posterior tips are suspended beneath the epidermis. There is a groove in the ventral surface of the ganglion and the dorsal blood-vessel runs along it, bifurcating in the middle part of the ganglion, the two branches diverging and passing ventrally and having no further

contact with the brain (Clark, 1956a). The sheath investing the ganglion is thickened in this ventral groove and in the anterior part of it is drawn out into a process for the attachment of the prostomial muscles (as in fig. 8, A, B). A series of thick fibres traverses the ganglion in the mid-line and runs dorso-ventrally from the cuticle to the sheath investing the brain (as in fig. 8, B). They correspond with the insertion of the muscles on the other side of the

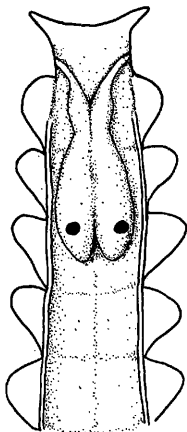


FIG. 2. Supra-oesophageal ganglion of *N. cornuta*, ventral view.

sheath and presumably prevent too great distortion of the ganglion when the muscles are contracted. The fibres do not form a continuous sheet bisecting the brain, but are arranged in several groups with spaces between to permit neural inter-connexions.

In accordance with von Haller's rule, the relative volume of the supra-oesophageal ganglion of *Nephtys* varies inversely with the size of the species (Clark, 1957). In all species the ganglion is of approximately the same width as the prostomium and differences in the relative volume of the brain are accounted for by an increase in its length. In small species the relatively long ganglion cannot be accommodated entirely within the prostomium and it extends backwards into the anterior body segments, so much so that in the two very small species *N. cornuta* and *N. parva* it extends into the third body segment (figs. 2, 3).

In nearly all species, whatever the relative size of the ganglion, it tends to lie mainly in the first body segment rather than in the prostomium. Thus, it is unusual to find more than a small part of the ganglion in the prostomium itself and, as a rule, most of it, unlike that of *N. incisa*, is sub-epidermal. The fact that not more than a small part of the ganglion lies in the prostomium has some influence on the relationship between the brain and the dorsal blood-vessel and the prostomial muscles, since these bear a fixed topographical relationship to the prostomium rather than to the supra-oesophageal ganglion. In those species in which the ganglion is mainly in the prostomium, the prostomial muscles are attached to the anterior half of the brain, but if the ganglion does not protrude far into the prostomium, the muscles are, of course, attached only to the anterior margin of it. In the same way, the dorsal blood-vessel which bifurcates half-way along, or even near the posterior part of the ganglion of those species with a largely prostomial brain, runs undivided along the whole length of the ganglion in species in which it occupies a more posterior position.

A source of variation in the morphology of the ganglion, quite unrelated to the size of the worm or its brain, is the presence of posterior lobes in some species (figs. 3, 4, 6). Except in *N. cirrosa*, these structures 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 (Clark, 1955).

The entire mucus-gland system is enclosed within the sheath which invests the ganglion and is separated from the nervous tissue by a barrier of neuroglial cells. The lobes may be very long and occupy a much greater volume than the ganglion itself. Thus in *N. caecoides* they extend from the posterior margin of the supra-oesophageal ganglion in the first segment, to the fifteenth segment; in *N. caeca* only to the fifth segment. Posterior lobes are missing from

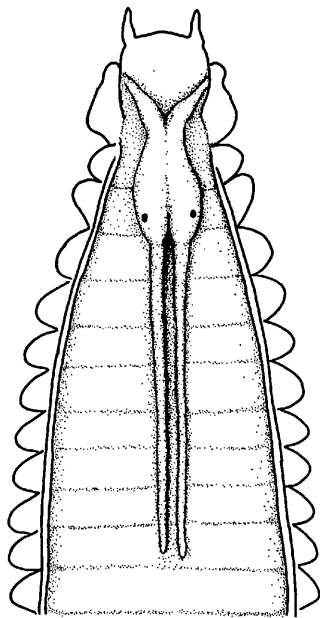


FIG. 3. Supra-oesophageal ganglion of *N. parva*, ventral view.

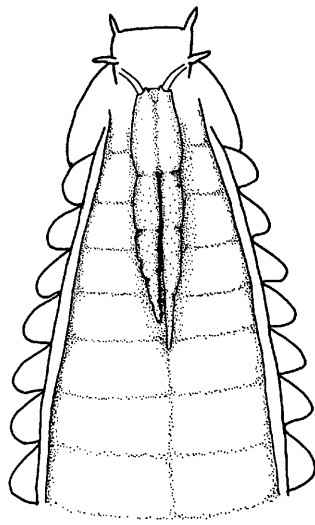


FIG. 4. Supra-oesophageal ganglion of *N. ferruginea*, ventral view.

the brains of the following species; *N. cornuta*, *N. hombergi*, *N. incisa*, *N. picta*, and *N. squamosa*, although the posterior margin of the ganglion is often slightly bifurcated, giving the spurious impression of small posterior lobes. *N. cirrosa* also has posterior lobes, though they are of a somewhat different nature from those in other species. In them, the mucus-cells appear to have been modified and more or less incorporated within the nervous system (Clark, 1956b).

There is considerable interspecific variation in the shape of the ganglion, particularly among the small-sized species, quite apart from differences in relative size and the occurrence or degree of development of the posterior

lobes. In worms larger than *N. incisa*, the ganglion is shorter than broad, roughly trapezoidal, and generally with only a slight bifurcation in its posterior margin and none in the anterior (e.g. *N. caeca*, *N. caecoides*, *N. californiensis*, *N. punctata*, *N. rickettsi*, all of which possess posterior lobes (fig. 6; see Clark, 1955, fig. 1)). In *N. hombergi* (fig. 7), a species which lacks posterior lobes, the posterior bifurcation is more obvious. In the small worms, however, the ganglion is elongated, extending into the anterior body segments and therefore largely sub-epidermal, and it has a very different appearance because of a tendency for it to be deeply bifurcated. Indeed, in the two smallest species, *N. cornuta* and *N. parva* (figs. 2, 3), the ganglion is deeply bifurcated at both anterior and posterior margins and has a pronounced ventral longitudinal groove in it so that it appears to be almost a double structure. The supra-oesophageal ganglion of *N. ferruginea* (fig. 4) has some peculiarities not shown by that of other species. It is barrel-shaped and much longer than that of *N. picta*, a species of comparable size. This is because the lateral tract of ducts from the cells in the posterior lobes of *N. ferruginea* is extremely well developed and occupies much of the cross-sectional area of the ganglion (fig. 8, b), while *N. picta* lacks posterior lobes and the lateral tracts of ducts. The volume of the truly ganglionic material (nerve-cells and neuroglia) is the same in both species, so the nervous part of the ganglion of *N. ferruginea* is elongated to compensate for its reduced cross-sectional area. A further peculiarity of the ganglion of *N. ferruginea* is that the circum-oesophageal connectives emerge from cup-shaped depressions at the antero-lateral corners of the ganglion and have a ventral flange covering the point of emergence of the connectives. This ornamentation of the anterior end of the ganglion does not occur in any other species, and I am at a loss to explain its occurrence in this one.

THE CIRCUM-OESOPHAGEAL CONNECTIVES

The circum-oesophageal connectives leave the supra-oesophageal ganglion at its antero-lateral corners, or, in the case of some small species, anteriorly. Macroscopically, they appear to emerge as single structures, not double as they are shown in Pruvot's (1885) illustration, though, in fact, they have a double origin in the supra-oesophageal ganglion and the two tracts of fibres retain their identity along the whole length of the connectives and into the sub-oesophageal ganglion. A short distance in front of the supra-oesophageal ganglion the connectives turn and run ventrally to the ventral surface of the prostomium, meeting it at the point where the lateral lips of the mouth are fused with it. The connectives then run posteriorly in the edges of the lips, giving off three stomatogastric nerves and the segmental nerves of the first segment. In the third segment the connectives leave the lateral lips and run in the ventral body-wall on each side of the gular membrane, converging on the sub-oesophageal ganglion in the fifth segment. In their passage through segments II, III, and IV the connectives are accompanied by the circum-oral blood-vessels, and, like them, are not subjected to tension when the proboscis

is everted, because the lateral lips are thrust aside and the gular membrane is stretched as the large pharynx passes through these segments; the body-wall in which the blood-vessels and nerves run is unaffected (Clark, 1956a).

THE SUB-OESOPHAGEAL GANGLION

The ganglia of the ventral nerve-chain of *Nephtys* are merely slight swellings on the nerve-cord. They are intersegmental in position, the greater part of each ganglion lying in the anterior part of the segment it principally innervates. The sub-oesophageal ganglion is a little larger than the other anterior ganglia, but otherwise not distinguished from them. It lies at the posterior end of the gular membrane, in the fifth segment, and the circum-oesophageal connectives are therefore a good deal longer than is usual in polychaetes. The connectives enter the ganglion at its antero-lateral corners. Immediately below and behind the point of entry of the connectives, the segmental nerves of the third and fourth segments emerge from the ganglion. The sub-oesophageal ganglion, like the connectives and the segmental nerves, lies in the sub-epidermal basement membrane, which is appropriately extended to accommodate the bulky ventral nerve-cord.

THE NERVES OF THE SUPRA-OESOPHAGEAL GANGLION

The sensory apparatus of the prostomium of *Nephtys* is somewhat reduced, though apart from the absence of palps, it is comparable to that of most other errant polychaetes in that there are two pairs of antennae, two pairs of photo-receptors, and a pair of nuchal organs. In addition, there are numerous cuticular sensory hairs, mainly on the dorsal surface of the prostomium. The sensory nerves of all these structures enter the supra-oesophageal ganglion.

The tegumentary nerves. The single-celled receptors of the dorsal surface of the prostomium and, in part, those in the antennae, are innervated by a series of tegumentary nerves which arise from the extreme dorsal part of the supra-oesophageal ganglion and emerge from its anterior margin. These nerves are extremely variable in their arrangement, not only from one species to another, but also between individuals of the same species, and even in a single worm the arrangement of these nerves may differ in right and left halves of the prostomium. As many as eight tegumentary nerves may arise from the ganglion, or there may be only two. In the former case one nerve on each side is larger than the others and innervates the greater part of the prostomium. Often there are anastomoses between the branches of the nerves. Some examples of the arrangement of the tegumentary nerves in different species are given in figs. 5, 6, and 7. Fig. 6 shows a specimen of *N. caeca* in which the innervation of the right and left sides of the prostomium is different.

The antennal nerves. The first antennae lie at the antero-lateral corners of the prostomium, the second about half-way along its sides. Two pairs of

antennal nerves arise in the dorsal part of the supra-oesophageal ganglion and emerge immediately above the roots of the circum-oesophageal con-

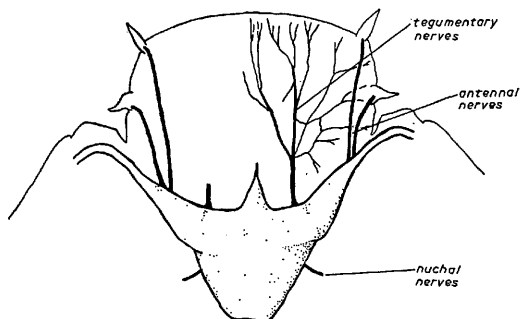


FIG. 5. Supra-oesophageal ganglion and cephalic nerves of *N. bucera*, ventral view. Only the root of the tegumentary nerve of the left side is shown.

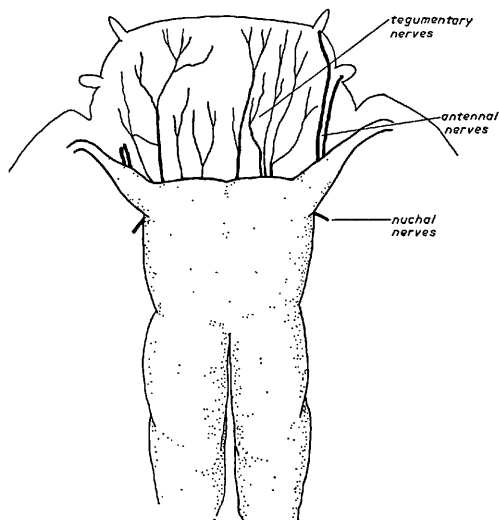


FIG. 6. Supra-oesophageal ganglion and cephalic nerves of *N. caeca*, ventral view. Only the roots of the antennary nerves of the left side are shown.

nectives. These nerves have a separate origin in the ganglion and, in most species, remain quite distinct from the connectives. The nerves run in the lateral walls of the prostomium to their respective antennae, where they

break up into a number of fine branches. In *N. hombergi* (fig. 7) the second antennal nerve is in a slightly more lateral position than it is in other species and it runs in the connective for a short distance, emerging from it near the base of its appropriate antenna. It is also unusual in that it innervates a small area of the prostomial wall as well as the antennal sense organs.

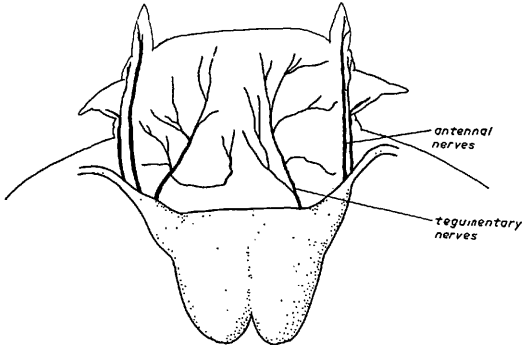


FIG. 7. Supra-oesophageal ganglion and cephalic nerves of *N. hombergi*, ventral view.

The optic nerves. The posterior photoreceptors with their pigment cups are embedded in the supra-oesophageal ganglion and there are no external nerves. These receptors have not been identified (though they are probably present) in *N. incisa* or *N. squamosa*, but otherwise they have been found in all species and always have the same structure. The anterior photoreceptors, consisting of a pair of sensory cells on each side, without pigment cups, lie just anterior to the roots of the circum-oesophageal connectives in the epidermis of the dorsal surface of the prostomium. Axons from these receptors enter the ganglion a little lateral to the connectives. The anterior receptors bear a constant relationship to the brain and are never far from its anterior margin, so that they may lie at the level of the nuchal organs (in *N. picta*) or farther forwards (as in *N. caeca*), depending upon the position of the ganglion in the prostomium. Anterior receptors appear to be missing from *N. punctata* and *N. rickettsi*. The structure and functioning of these photoreceptors have been described in more detail elsewhere (Clark, 1956c).

The nuchal nerves. The paired nuchal organs of *Nephtys* are small, spherical structures between 10 and 50 μ in diameter, depending upon the size of the species, and lying at the postero-lateral margins of the prostomium. They are eversible and are generally found everted in preserved specimens. Each is provided with a retractor muscle which is inserted in the base of the prostomial wall where it joins the wall of the first segment, and where the diagonal prostomial muscles are also inserted. In *N. incisa* the nuchal nerve consists of a small bundle of fibres which crosses the short intervening distance

between the organ and the dorso-lateral part of the ganglion. In this species, in which the ganglion is almost entirely prostomial, the nuchal organs are almost at the same level as the nuchal centres in the ganglion. For the sake of comparison with other species, it should be noted that at this level the dorsal blood-vessel is attached to the ventral surface of the brain, and the central neuropile in the ganglion forms a single, compact mass. In some species the ganglion is elongated and in most it is shifted backwards into the anterior body segments; in either case the posterior part of the ganglion, in which the nuchal centres are situated, lies some distance behind the nuchal organs. In fact, *N. incisa* is the only species in which the nuchal centres and organs are close together. It might have been expected that the posterior shifting of the ganglion would have resulted in an elongation of the nuchal nerve. This is not so. In all species of *Nephtys* the nuchal nerve emerges from the brain at the level of the nuchal organs, even though this may result in the nerve leaving the ganglion at its anterior edge. Fig. 8, A-C shows cross-sections of the prostomium of *N. cirrosa*, *N. ferruginea*, and *N. cornuta* at the level of the nuchal organs. In the first two species the section passes anterior to the dorsal blood-vessel and through the region where the prostomial muscles are attached to the base of the ganglion. In both, the neuropile is divided up to form the roots of the circum-oesophageal connectives and in *N. ferruginea* these nerve-bundles are at the sides of the ganglion immediately before they emerge from the brain. In *N. cornuta* a section through the nuchal organs is actually anterior to the ganglion and the nerves enter the neuroglial tissue that lies on top of the roots of the connectives in this species. In a species such as *N. ferruginea*, which possesses posterior lobes, the nuchal organs lie at the posterior ends of the lateral organs, where the mucus-cells contained in the posterior lobes open to the exterior. The nuchal nerves enter the ganglion dorsal to the lateral tracts of ducts running from the posterior lobes to the lateral organs.

THE STOMATOGASTRIC NERVOUS SYSTEM

The proboscis of *Nephtys* consists of a thin-walled buccal region and a very muscular pharynx. When the proboscis is everted, the buccal region forms a sheath around the protruded pharynx. The buccal sheath is attached to the body-wall beneath the prostomium, to the lateral lips of the mouth, and, ventrally, to the anterior end of the folded gular membrane. At the anterior end of the pharynx, that is at the tip of the everted proboscis, there are 22 large papillae arranged in two vertical rows of 11 each, which are provided with muscles so that they may be drawn back. The sub-terminal papillae, which are used as diagnostic features in nephtyid taxonomy, are merely evaginations of the buccal sheath and are not movable. The opening of the pharynx is a vertical slit which is bounded top and bottom by two strong ligaments (fig. 9, C). Although the opening is a dorso-ventral slit, the cavity of the pharynx is cross-shaped (fig. 9, D).

Three stomatogastric nerves arise from the circum-oesophageal connectives

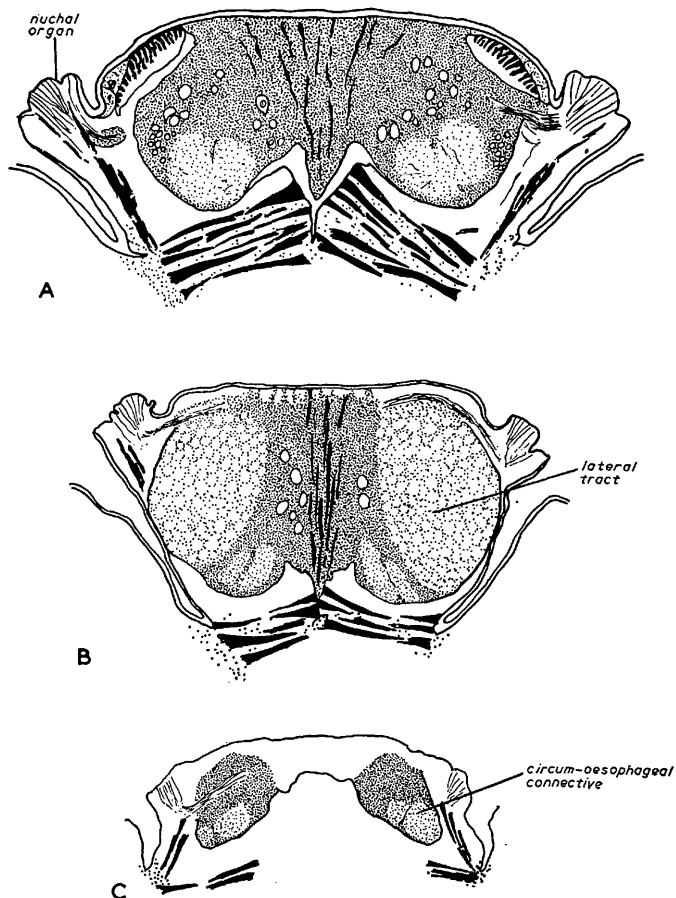


FIG. 8. A, transverse section through the prostomium of *N. cirrosa* at the level of the nuchal organs, showing the nuchal nerve entering the ganglion. B, a similar section through the prostomium of *N. ferruginea*. The nuchal nerves run to the ganglion over the top of the lateral tracts of ducts from the posterior lobes. C, a similar section through the prostomium of *N. cornuta*. The nuchal nerves enter the neuroglia, which lies above the roots of the circum-oesophageal connectives and anterior to the ganglion proper. Dense stipple, neuroglia; light stipple, neuropile and circum-oesophageal connectives.

on each side in their passage through the lateral lips of the mouth (figs. 9, A; 10). The third, most ventral, stomatogastric nerve gives off a fine side branch,

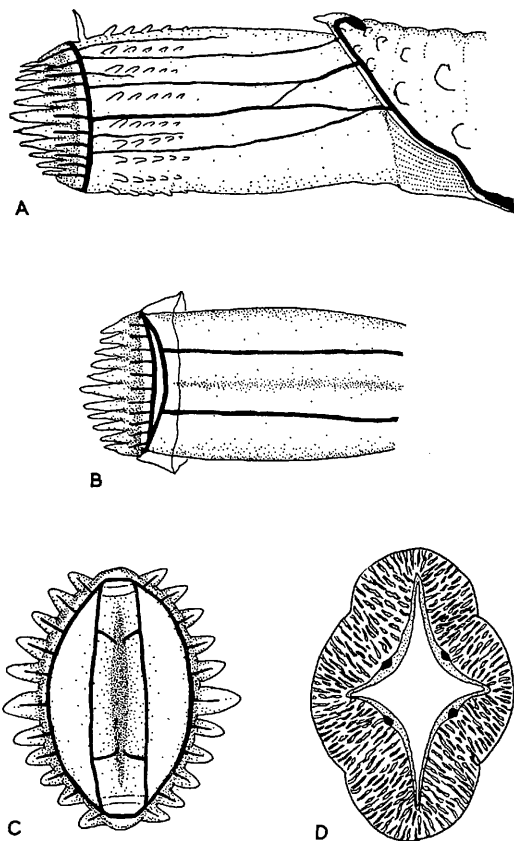


FIG. 9. A, buccal part of the stomatogastric nervous system of *N. hombergi*. B, pharyngeal part of the stomatogastric nervous system of *N. hombergi*. C, oral view of the proboscis of *N. bucera* to show the double stomatogastric nerve-ring at the anterior end of the pharynx. D, transverse section through the pharynx of *N. glabra* to show the position of the four pharyngeal stomatogastric nerves.

and these four pairs of nerves run along the buccal sheath to a nerve-ring at the base of the terminal proboscidal papillae. The second and third stomatogastric nerves are the most substantial, the first and fourth are fine. There is

a large anastomosis between the second and third nerves, and, in most species, a fine one between the first and second. A number of fine nerves arise from the terminal ring-nerve and run back along the buccal sheath, though they do not form a connexion with the circum-oesophageal connectives. Twenty-two nerves arise from the ring and enter the terminal papillae. In addition to the nerve-ring at the base of the papillae, there is a second ring near the anterior end of the pharynx (fig. 9, B, C). This is joined to the terminal ring

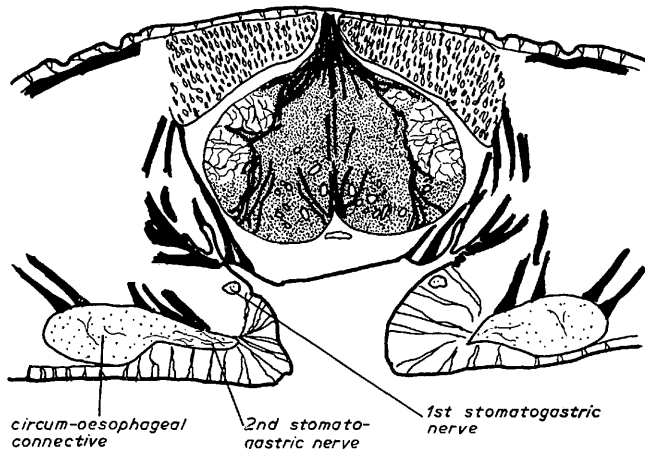


FIG. 10. Transverse section through the first segment of *N. californiensis* to show the origin of the second stomatogastric nerve from the left circum-oesophageal connective. The first pair of stomatogastric nerves lies in a more dorsal and internal position in the lateral lips.

on each side, dorsally and ventrally, so that only a single nerve runs above and below the ligaments at the top and bottom of the pharyngeal opening. Four nerves arise from the pharyngeal ring and run back along the four main muscle-blocks composing the pharynx. They lie at the base of the epithelium lining the pharynx (fig. 9, D).

THE SEGMENTAL NERVOUS SYSTEM

Since the sub-oesophageal ganglion lies in the fifth segment, some modification of the segmental nerves of the first four segments must be expected. The most conspicuous segmental nerve is the parapodial nerve, which leaves the posterior part of the ventral ganglion in typical segments and runs to a podial ganglion at the base of the appropriate parapodium. From this ganglion a series of nerves innervate the noto- and neuropodia and the rest of the parapodium. The parapodia of the fifth segment are innervated in the usual way by nerves arising from the posterior part of the sub-oesophageal

ganglion (fig. 11). The parapodial nerves of the third and fourth segments arise from the anterior part of the sub-oesophageal ganglion immediately behind the circum-oesophageal connectives. In both cases, the segmental nerves follow the connectives and branch off at the appropriate level to supply the parapodia and body-wall of their respective segments. These nerves clearly arise in the sub-oesophageal ganglion, although they become closely associated

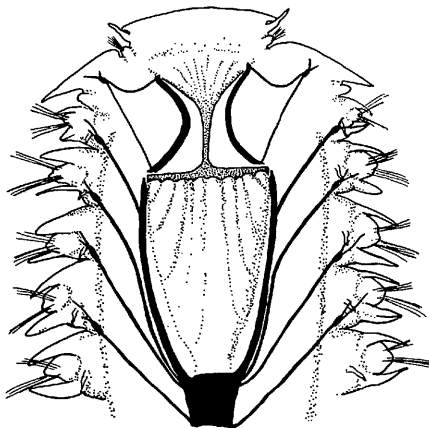


FIG. 11. Ventral view of the anterior nervous system of *N. buccera* to show the path of the circum-oesophageal connectives and the innervation of the first five segments.

with the circum-oesophageal connectives. The segmental nerves of the first two segments, however, arise from the connectives themselves and have no obvious connexion with the sub-oesophageal ganglion, although presumably their innervation is ultimately from that source. Two widely spaced nerves arise from the circum-oesophageal connectives in their passage through the lateral lips and converge on the podial ganglion at the base of the first segment. The parapodial nerve of the second segment is single and arises from the connectives at the point where they leave the lateral lips and enter the ventral body-wall, i.e. at the anterior end of the gular membrane. This agrees with the description given by Pruvot (1885), except that he omitted the segmental nerves of the second segment and concluded that the sub-oesophageal ganglion lay in the fourth instead of the fifth segment.

DISCUSSION

Although the general pattern of the nervous system of *Nephtys* resembles that of other errant polychaetes, it is useless to discuss homologies of the nerves at this stage because differences in the point of emergence of nerves from the central nervous system do not necessarily indicate differences in the

arrangement of the ganglionic centres from which they come. The variable position of the second antennal nerves and, still more, of the nuchal nerves of *Nephtys* are cases in point; they do not reflect a variation in the disposition of the antennal or nuchal nuclei within the brain.

The supra-oesophageal ganglion appears to be much less specialized than that of eunicids and aphroditids, for example, in which the development of an elaborate prostomial sensory system is associated with large and complicated supra-oesophageal ganglia (Hanström, 1928). Superficially, the nervous system of *Nephtys* bears a closer relationship with that of the nereids or phyllodocids, though in both these families there is a more elaborate prostomial sensory apparatus than in *Nephtys*. In these two families, two or more of the anterior segments are fused to form a peristomium and their ventral ganglia are also fused, and the segmental nerves come into a close association with each other. A rather similar disturbance of the nervous system of the anterior segments occurs in *Nephtys*, though for different reasons. The proboscis is much greater in diameter than the anterior segments through which it passes. The first four segments are particularly small and are provided with a ventral gusset in the form of a folded gular membrane, which is stretched when the proboscis is everted. The sub-oesophageal ganglion lies at the posterior margin of the gular membrane, and the circum-oesophageal connectives, which run along the sides of the membrane, are consequently remarkably long. As we have seen, the innervation of the third, fourth, and fifth segments, and possibly of the first and second also, is from the sub-oesophageal ganglion which, as in the nereids and phyllodocids, must be a composite structure formed from several ventral ganglia. Unlike these families, however, the segmental nerves of *Nephtys* are not affected by these modifications and do not come into any special, close relationship with each other.

The chief sources of variation in the gross structure of the anterior nervous system are the occurrence of posterior lobes and the great size range of species of this genus. The extreme variability of the tegumentary nerves of the prostomium is a reflection of the lack of discrete sense organs and is unimportant. The chief characteristic of the nervous system of these worms is its lack of specialization coupled with a reduced or primitive sensory system.

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