SOME STAGES IN THE EVOLUTION OF THE NERVOUS SYSTEM AND THE FORE-GUT OF THE POLYCHAET

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INTRODUCTION

As polychaets are primitive among the annelids, so are the Errantia among the polychaets; and the Eunicimorpha among the Errantia. Though the Amphinomorpha, since the work of Storch (1913), have by many been placed at the base, the Eunicimorpha are in many respects the most primitive. This is seen in the brain with its extended form and marked subdivisions, and in the stomodeum with its fold form and the very small amount of its protrusibility. This paper, at its first inception in 1926 (!), was suggested by the characters of *Eunice* (*Leodice*) as given by Heider (1925, see p. 61).

The Amphinomorpha also are primitive; especially (as is generally supposed) in their tetraneury, in their brain (except for the hind-brain), in the absence of specialization in the buccal segments, and in the small protrusibility of the pharynx. But they seem less primitive than Eunicimorpha: in their brain, both by its greater concentration and the enormous development of the "hind" or nuchal brain; and in their stomodeum, both by its cylindrical form and greater protrusibility.

The great antiquity of the Eunicimorpha is indicated by the annelid jaws (scolecodonts) which have long been known. They are abundant in Paleozoic rocks; and great numbers of species have recently been described, especially by E. R. Eller, from various horizons between the Middle Ordovician and the Upper Devonian. Practically all those described up to the present belong to the Eunicimorpha (e.g., Eller, 1945). Sometimes the denticles of both the "upper" and "lower" jaw series are found in their natural association (Lange, 1947). The claims made in this paper, however, give them a very much greater antiquity than the Ordovician.

Indications of evolution are best seen in these most primitive forms; but all the errant forms furnish evidence in varying degrees. The specialized "sedentary" families are naturally less satisfactory for this study and need not be considered, but their ancestors doubtless experienced the same evolution.

For the presentation of the theories given below, it is not necessary to discuss the origin of segmentation. The evolution pictured followed the acquirement of segmentation, and points back to a ringed worm more primitive than any now existing. Moreover, it preceded the acquirement of the trochophore larval stage.

The brain with its complement of sense organs and appendages, the stomodeum, and the visceral nervous system are all markedly compound in errant polychaets; and it is the chief purpose of this paper to claim that their structures are connected in origin.

THE BRAIN OF EUNICE

The brain by its form, especially in *Eunice,* suggests an origin in a complex and lengthy aggregation. Hatschek, 1891, and Racovitza, 1894, were the first to divide the brain into fore-brain, mid-brain, and hind-brain. Heider (1925, figs. 7, 12, 13, 15, 16) does the same; and he determined minutely the external features of the neuropil mass (see figs. 1, 3, 4, and 5, p. 6).

These three "brains" are here claimed to constitute three distinct *categories* of nervous matter.

The *fore-brain.* This separates itself from the rest by its position, form, structure, the senses it serves, and the gap above and behind it (through which pass muscles of the mouth-lips, the so-called "palps" of many authors). It is suggested here that this was the *primary* brain, and as an archicerebrum may well have had a complicated history of its own. It receives the ventral root of the perioesophageal commissure; and gives origin to the two pairs of stomatogastric nerves and to nerves of the mouth-lips.

The *mid-brain.* This, the main brain, innervates the prostomial appendages and the eyes. It is clearly subdivided into *three* successive sections diminishing rearwards—an anterior, middle, and posterior. The *anterior* receives the dorsal branch of the perioesophageal commissure, and innervates the anterolateral antennae; the *middle* innervates the single pair of eyes and the posterolateral antennae; the *posterior* innervates the median antenna and the posterior eyes when present. Heider, like Pruvot, instituted only two divisions: the last two here instituted forming his posterior division; but in his figures (loc. cit., figs. 12 and 13; see also figs. 3, 4, and 5 accompanying this paper) they are very clearly distinguishable from one another.

The antennae are comparable with the tentacular cirri of the second buccal segment and with the cirri of the normal body segments. The eyes too may well be homologous with the pigment spots on the body segments above the parapodia and gills. Each of these three subdivisions of the mid-brain is below claimed to originate in a separate pair of body ganglia added to the brain at *different* times, and to be the only parts which have homologues in the ventral chain.

The *hind-brain* is much smaller, having only a small fraction of the volume of even the smallest (the posterior) division of the mid-brain. It consists of two separate ganglia: these innervate the nuchal organs, which have no counterpart elsewhere in *Eunice.*

These three "brains," the fore, mid, and hind, thus constitute three distinct categories, distinct not only in character, but also, it is believed, in their origins and their histories as explained below.

HISTORY OF OPINION REGARDING THE CONSTITUTION OF THE BRAIN IN POLYCHAETS

As the theory here submitted differs so fundamentally from all previously presented, a short sketch of the diverse opinions regarding the origin and significance of the brain was written, but is withheld in order to shorten this paper. The views of the various authors beginning with Pruvot in 1885 (see list of references, p. 33) are extremely varied; they are summarized in table 1. The theory of

TABLE 1.—Summary of opinions regarding the significance of the brain *

Brain divisions first suggested by Hatschek	Fore-brain or stomatogastric lobes	Mid-brain or antennal brain			Hind-brain or nuchal brain
		Anterolateral antennae	Posterolateral antennae	Median antenna	
Pruvot, 1885	Seg. I with mouth lips and palps	Seg. 2		Seg. 3	
Hatschek, 1891		Seg. I			
Racovitza, 1896 / Holmgren, 1916		Nonsegmental brain			
Nilsson, 1911-1912	Seg. I		Seg. 2		Seg. 3
Lameere, 1925 / Binard and Jeener, 1928	Seg. I	Seg. 3	Seg. 2	Seg. I	
Hanström, 1927, 1928	Seg. I, added in some only	Nonsegmental brain			
Söderström, 1920		Nonsegmental brain			Outside the brain
Gustafson, 1930	? Seg. I after	The nonsegmental brain			Added to the brain
Raw, present paper	Ancient brain A — GAP	BIII — Gap	BII — Gap	BI	C

* Since this paper was finished and submitted for publication, papers by Laura M. Henry (1947, 1948) have appeared, discussing the segmentation of the anterior region of the body in Oligochaeta, Polychaeta, Onychophora and Arthropoda. Her outlook is quite different from that presented here. Her principle, derived from Hanström and G. F. Ferris, is the stability of the nervous system in the Annulata. She takes the oligochaet brain as the most primitive; though, having lost all eyes and antennae, it must be degenerate. She regards *Nereis* as presenting the simplest nervous system—"a basic type from which the other forms can be derived." According to her the polychaet brain is a unit: the visceral nervous system belongs to it, and it innervates her "segment I" which is represented *by the jaws only*; her "segment II" (the first apparent segment of the extended proboscis) is innervated by the connective ganglion. The prostomium "belongs either to the third or fourth body segment." In one respect she agrees with views expressed here, viz, that the proboscis represents segments; but in most other respects her conclusions are widely different.

the present writer, expressed cryptically on the last line, is developed below.

## SIGNIFICANCE OF THE DIVISIONS OF THE BRAIN IN PRIMITIVE POLYCHAETS

The *fore-brain*. Both the morphological position and the importance assigned to the fore-brain vary greatly. By Pruvot and by Nilsson it was regarded as the *first* of three head segments (though the other two of these supposed segments given by the one are different from those given by the other). Hanström, on the other hand, is in the opposite camp, regarding it as the sole *addition* to the brain. To Hatschek, Racovitza, Binard and Jeener, and Söderström it was perhaps of little significance.

But in primitive polychaets, as already remarked, it is separated from the mid-brain by an extensive muscle gap and may exhibit large size as in *Eunice* and *Euphrosyne*. In polychaets generally it gives issue to a pair of stomatogastric nerves, and in primitive forms it innervates the mouth-lips which evidently preceded antennal palps in the palpal function. This strongly suggests its great antiquity as an element of the brain. If, however, the stomatogastric lobes of the Amphinomidae and Euphrosynidae were the exact equivalent of the fore-brain of *Eunice,* as Gustafson seems to claim, there is a significant difference between them; for the ventral root of the perioesophageal connective enters the fore-brain in *Eunice,* but does not enter the stomatogastric lobes in these other families. This great discordance does not seem to have been remarked by Gustafson, and needs explanation. The equivalent in Amphinomidae of the fore-brain must also include the part which receives the ventral root of the perioesophageal connectives.

The characters and relationships of the fore-brain, therefore, quite justify one in assigning it to a different category from that of the adjoining mid-brain; and the fact that in the most primitive polychaets it innervates the organs which function as palps, suggests that it is the primal brain.

The *hind-brain*. The significance of the hind-brain is clarified by the discoveries of Söderström. It again falls in quite a different category from that of the mid-brain, as is indicated by its innervation of the nuchal organs alone. The fact, too, that in the Amphinomidae and Euphrosynidae these organs extend over several segments of the body, and that the hind-brain in them is so developed as to suggest the incorporation in it of several pairs of nuchal ganglia, suggests that the hind-brain is the *latest* addition to the brain. This is also
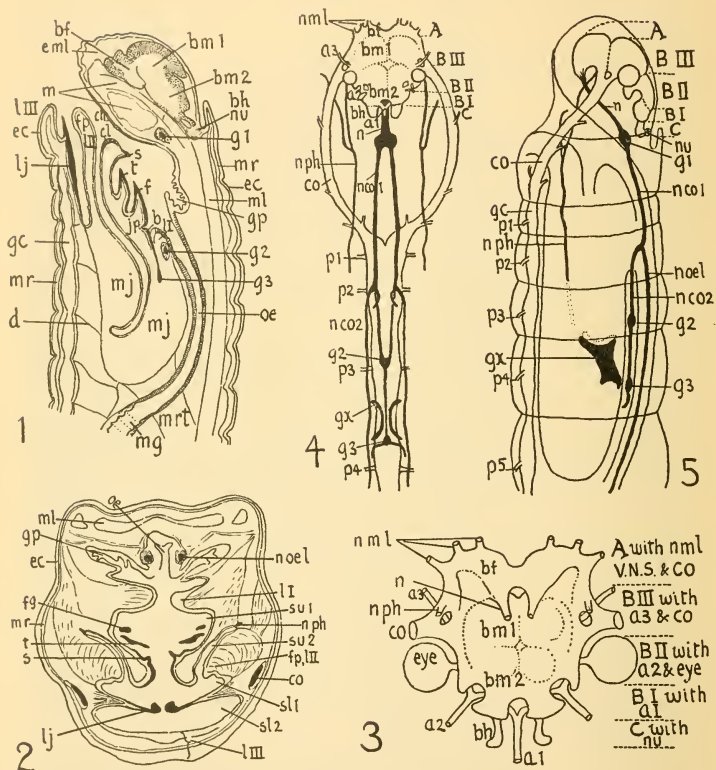
Figs. 1 to 5.—All the figures are traced from Heider's; and the present author's interpretation is added on the right side of figures 3, 4, and 5.

Fig. 1.—(After Heider's fig. 7.) Diagrammatic longitudinal vertical section through the anterior part of *Eunice punctata*. The oesophagus and the median plane ganglia are shown in median section; but the brain and the jaw sacs are represented as cut at one side of the median. × 12.

Fig. 2.—(After Heider's fig. 10.) Oblique cross section from the third segment behind the peristome on the dorsum forward to the lower lip. × 20.

Fig. 3.—(After Heider's fig. 13.) Brain of *Eunice punctata*, ventral aspect. Ca. × 20.

Fig. 4.—(After Heider's fig. 15.) Dorsal view of the brain and the anterior parts of the central nervous system and visceral nervous system of *Eunice punctata*. Ca. × 10.

Fig. 5.—(After Heider's fig. 16.) Side view of the same. Ca. × 15.

ABBREVIATIONS USED ON FIGURES 1-5

The central nervous system is in outline, the visceral nervous system is in black in figs. 4 and 5.

a_1, nerve of the posterior single antenna. | a_2, nerve of the posterior pair of antennae. | a_3, nerve of the anterior part of antennae.

b, bearer. | bf, fore-brain. | bm_1, anterior section of mid-brain. | bm_2, Heider's hind section of mid-brain. | bh, hind-brain.

ch, chitin thickening on the base of the prostomium. | cl, callus on the jaw-pad. | co, buccal commissure.

d, dissepiment. | ec, ectoderm. | eml, epithelium of the mouth-lips.

f, fang. fp, fore pad $= l\ II$.

g_1, supra-oesophageal ganglion of visceral nervous system. | g_2, infra-oesaophageal ganglion of visceral nervous system. | g_3, hindmost oesophageal ganglion. | gc, ventral ganglion chain. | gx, x-form ganglion body. | gp, glandular pouch.

jp, upper jaw pad. | $l\ II$, lips of pharyngo-oesophageal rift. | $l\ III$, lips bounding the upper jaw sacs. | $l\ III$, lip bounding the lower jaw sacs, the lower lip. | lj, lower jaw.

m, muscles of the prostomium. | mg, beginning of mid gut. | mj, muscles of the jaw sac. | ml, dorsal longitudinal muscle. | mr, ring muscle layer. | mrt, retractor of the jaw sac.

n, oesophageal visceral nerve or nerves (from the fore brain). | $n\ co\ 1$, oesophageal visceral commissure, anterior part. | $n\ co\ 2$, ditto, posterior part; in figure 4 it is the inner pair joining in g_2; the outer pair is $n\ oc\ l$, following. | $n\ oc\ l$, lateral oesophageal nerve. | $n\ ph$, pharyngeal visceral nerve | nu, nuchal organ.

oe, oesophagus. | p_1 to p_5, podial nerve roots.

s, saw-plate. | sl_1, sl_2, sacs of the lower jaw. | su_1, su_2, sacs of the "upper" jaw. | t, "tooth."

The present author's views as to the evolution of the brain and of the gut are suggested by the order of the capital letters A, B, C (respectively fore-, mid-, and hind-brain), and the Roman figures I, II, and III for the three successive invaginations and the three different ganglion pairs in the mid-brain. The original brain was the fore-brain and the corresponding gut the mid-gut. The first addition to the gut was the oesophagus—I, after which B I was added to the brain. The second addition was the upper jaw series of sacs with their armature—II, after which B II was added to the brain. The third addition was the lower jaw sacs with their armature—III, after which B III was added to the brain; which then incorporated also the hind-brain—C. The sequence of lower lips resulting from the successive invaginations are still represented by $l\ I$, $l\ II$, and $l\ III$, the present lower lip. The concomitant evolution of the visceral nervous system need not be repeated here.

suggested by the fact that "both Kleinenberg (1886) and Meyer (1901) have shown that the ganglia of the hind-brain are marked off from the ganglia of the nuchal organ and incorporated in the brain" (Gustafson, 1930, p. 339). The same writer supposes that it will be the same in other polychaets.

The *mid-brain*. The most primitive form of mid-brain seems to be exhibited by *Eunice,* where its extension in a plane and its strong suggestion of segmentation into three successive and well-defined divisions, which can be called mid-brain III, II, and I, can be regarded in that light. Hanström (1927, p. 592; 1928, pp. 259, 260), it is true, is very dogmatic in his expression of the opposite view; but the facts are against him. The anterior and largest pair, mid-brain III, innervate the anterolateral antennae ("palps" of authors), and receive the dorsal branch of the perioesophageal connectives. The middle pair, mid-brain II, innervate the posterolateral antennae and the eyes. The posterior and much the smallest pair, mid-brain I, innervate the median antenna, which, contrary to the view of Binard and Jeener, is best regarded as a coalescence of two; when two pairs of eyes are present, as in some eunicids, the posterior smaller pair may with confidence be assigned to this brain division.

In the other primitive brains, those of *Euphrosyne* and of Amphinomidae the mid-brain is still extended in a plane, and its parts have the same topographical relations to one another, but the subdivision into three pairs is not immediately apparent. The identity, however, of the succession of nerves with similar topographical relations strongly suggests a composition of the same three divisions III, II, and I.

The antennae compare so closely in *Eunice* with the pair of tentacular cirri on the second body segment and with the dorsal cirri on the other body segments, as is the case also in the Amphinomidae and in many other families, that it is quite natural to homologize them. The eyes again associated with mid-brain II and I can be regarded with great probability as serially homologous with the pigment spots on the body segments of *Eunice*.

From the comparisons below instituted with the visceral nervous system, the writer believes that the three divisions of the mid-brain represent three segmental body ganglia which have been added to the fore-brain at *three* different times—I, the posterior, first; III, the anterior, last—and that they do not belong to adjoining segments of the ancestor.

The supposed origin of these parts by the secondary subdivision of a unit brain—Hanström's "fore-brain," consisting of our mid-

and hind-brain—into four divisions, grouped above in two categories (Hanström, 1928, pp. 259, 260), and the grading of the three divisions of our mid-brain by posteriorly diminishing size is very difficult to imagine; whereas on the theory detailed below it follows quite naturally.

THE STOMODEUM IN EUNICE AND OTHER POLYCHAETS

At the outset in this paper the Eunicimorpha have been claimed as primitive, but it may be thought by some that in respect of their stomodeum they are less primitive than some others. Hempelmann (1934, *in* Kükenthal and Krumbach, Handb. Zool., vol. 2, 7, p. 161, Annelida Polychaeta systematic section) divides the Polychaeta Errantia into—(1) suborder Amphinomorpha with tetraneury; and (2) suborder Nereimorpha with dineury, of which the first family described is the Aphroditidae and the last the Eunicidae. From this one might think that he regarded the Aphroditidae as the most primintive and the Eunicidae as the most specialized. When, however, we note that the systematic part is a translation of Fauvel in Fauvel's order, except for the extraction of the Amphinomidae and its elevation into a suborder, we may conclude perhaps that the order was without significance for Hempelmann.

The stomodeum of the Eunicimorpha is unique among errant polychaets—in its form, its armature, and its very slight protrusibility. Its form is remarkable, consisting of the pharynx subdivided into four successive sacs separated by foldings of the pharynx wall, followed by the cylindrical "oesophagus." All the sacs, and the oesophagus as well, extensively communicate with one another by rifts in the midline. The armature, too, is remarkable and of great variety within the suborder; but by comparisons between the various types the courses of evolution can be clearly seen. The denticles are arranged within and on the ventral sides of two of the sacs in all forms, constituting respectively an upper jaw series of pairs of denticles and a lower jaw with a single (chisel and crusher) pair. The evolution of the armature could form a separate paper. In *Eunice* only the lower jaw chisels and the upper jaw fangs are protruded. The primitive symmetrical pairing of the denticles, well seen in *Stauronereis* (*Staurocephalus*), has been lost in the Eunicidae, s.s.

In the Amphinomorpha the stomodeum, though very different, presents the nearest approach to that of the Eunicimorpha in the very small amount of its protrusion and in the fact that this is largely limited to the ventral side, recalling the condition in *Eunice* where

only the ventral lower jaw and fangs are protruded. In the Nerei-morpha (as restricted by the exclusion of these) the pharynx is cylindrical and is often far protrusible, reaching its greatest length and protrusibility in the Glyceridae and the Goniadidae, which because of their unique conical, secondarily annulated prostomium, might well constitute a suborder, the Glycerimorpha. This long, cylindrical, far protrusible proboscis the writer regards as a high specialization.

THE STOMATOGASTRIC NERVOUS SYSTEM IN POLYCHAETS

A visceral nervous system has been known since the time of Stannius (1831), who investigated that of *Amphinome rostrata* and showed that the stomatogastric nerves issued both from the brain and from the first ganglia on the perioesophageal connectives. Pruvot (1885) showed that such a system occurs generally in the polychaets, the nerves issuing in different cases either only from the brain as in *Eunice,* or both from the brain and from the oesophageal connective as in *Nephthys* and *Phyllodoce,* or only from the perioesophageal ring as in *Ophelia.* A double origin has also been shown by Rodhe (1887) for the Aphroditidae (Polynoe), viz, from the brain and from the first perioesophageal ganglion. In *Nereis* according to Hamaker (1898) and Holmgren (1916) the innervation is from the brain and from the suboesophageal ganglion. The visceral nervous system of *Eunice,* described in considerable detail by Heider, and that of *Hermione* described by Bernert, are faily closely comparable with one another. In all cases there are two pairs of stomatogastric nerves, one pair of which arises in the fore-brain near the midline. It therefore is probable that all are inherited from the primitive polychaet.

So far as the writer is aware the origin of the visceral nervous system has not been determined or even deduced. Heider remarked upon its individuality in opposition to the remaining part of the nervous system; and he concluded that it had a separate origin.

INTERRELATIONS OF THE STOMODEUM, THE VISCERAL NERVOUS SYSTEM, AND THE BRAIN IN THE ANCESTRY OF EUNICE

The purpose of this paper is to show how closely related, in the writer's view, are the stomodeum, the visceral nervous system, and the brain; and how strongly a parallel evolution of all three is suggested by the anatomy of *Eunice.*

The compound stomodeal system (of oesophagus and pharynx)

and the visceral nervous system are closely associated with one another. Throughout their common extension the visceral nerves and ganglia are in the stomodeal hypodermis. And it is suggested that these two systems are also connected in origin; indeed, that the visceral nervous system is a direct result of the stomodeal invagination; that before the invagination commenced, the present visceral nervous system would not exist, and the brain would consist only of fore-brain!

The *stomodeum* is very complex and the invagination that gave rise to it must have been very complex, probably much more so than we can realize (see Heider, 1925, figs. 5 to 10; also figs. 1 and 2 in this paper, p. 6). Though so complex, it divides itself quite naturally into three divisions: (1) the oesophagus; (2) the sacs associated with the upper jaw armature; and (3) the sacs associated with the lower jaw armature. Three successive invaginations or series of invaginations appear therefore to be represented, which must have been separated by long halts, and probably imply changes of feeding. The first is represented by the oesophagus; and this would seem to have very long antedated the other two, represented by the upper jaw series and the lower jaw series of pharyngeal sacs, which were separated by a shorter interval. At each of these later invaginations, the new was not merely an extension of the old, but a new structure lying ventrad of the old (fig. 1).

The first or oesophageal invagination was probably a protracted process; it is represented by the long oesophagus, commencing in front of the mid-gut and bounded by the lips of the pharyngo-oesophageal rift (*l I,* figs. 1 and 2), which, but without the rift, may represent the lower lip at the end of that stage.

The second or upper jaw series was also probably a long process: its effects were to produce the main cavity of the pharyngeal sac with the upper jaw sac above it, and bounded below by the "fore-pad," which again, but without its rift, may represent the lower lip of that stage. It contains the so-called "upper jaw" apparatus, the different elements of which—the bearers, fangs, saw-plates, and "rub plates"— are here interpreted as representing several pairs of appendages! In the more primitive eunicid, *Cirrobranchia parthenopeia,* seven such pairs of appendages might seem to be indicated; but comparisons throughout the suborder show that it is impossible to judge of the number involved, and this is not surprising when it is realized that the evolution of the stomodeum took place very long before Cambrian time and probably over 1,000 million years ago.

The third or lower jaw invagination adds a further pair of pockets

to the pharyngeal sacs. It contains the "lower jaw" plates, here interpreted as representing another pair of appendages added to the mouth armature; and it is bounded by a new, the present, lower lip (*l III*).

Each of these pharyngeal invaginations has produced a two-fold sac, each sac being partly subdivided by the pair of pads, which can be likened to parapodia, on which the pair or pairs of denticles are situated. Besides the rifts between these pads, the parting between the upper jaw sacs and the lower jaw sacs, as also that between the upper jaw sac and the oesophagus, are markedly bifid. This suggests that with the evolution of each new sac the previous lower lip became bifid owing to the necessity for through-communication through the sacs to the oesophagus.

The *visceral nervous system* and its distribution, as suggested above, are explicable as direct results of the invaginations, which not only involved ordinary ectoderm and pairs of appendages, but also the "central" nervous system, which was still continuous with the ectoderm. It may not be possible to assign to each invagination its exact contribution to the visceral nervous system; on the other hand this is clearly subdivisible into an oesophageal and a pharyngeal section.

At this early stage, too, the main nerve cords from the brain were in a more primitive position than now obtains; for, judging from the parts of the visceral system both on the oesophagus and the jaw sac, they were ventrolateral, not midventral, in position; and, that this was still the case after the evolution of the polychaet, is suggested by the far-separated ganglion chains of Serpulae and of some arthropods.

Seeing that each invagination was rearward in direction, its effect on the nerve chains, when it involved them, was to *pull them back into a pair of loops open in front;* and their anterior connections, i.e., with the brain, were enormously stretched, in contrast with their posterior connection, i.e., with the continuing nerve cords. An effect of this is to be seen in the fact that the oesophageal visceral nerve cords from the fore-brain are quite free from the hypodermis, until, in the supra-oesophageal visceral ganglion, they reach the oesophagus. The stretch has pulled them free, as it has also the fore-brain.

The open loop in the nerve cords, *after each invagination* that involved them, seems to have been closed by the *advance of the foremost of the unaffected ganglia to the brain.* Such a change might be aided by the existence of a hypodermal nerve net.

It is not to be expected that the whole history will now be trace-

able, for nature in such an unimaginable time would simplify a
system complicated by repeated invaginations. And in any case a
more detailed knowledge of the visceral nervous system is needed
than is furnished by Heider, if we are to trace the history as com-
pletely as is still possible. The development of these interrelations is
illustrated by table 2, stages 1 to 10, pp. 14-15.

The effect of the most ancient, the *oesophageal invagination,* on the
disposition of the nervous system is to be seen in the oesophageal
nervous system; but it is perhaps difficult to interpret. Heider de-
scribed a considerable system, all of which, excepting the connection
with the brain, lies in the oesophageal hypodermis (Heider, 1925, pp.
77 and 78). From the posterior lappets of the fore-brain the visceral
oesophageal nerves ($n,$ fig. 3), freed from the hypodermis, and soon
apposed to one another, extend to the supra-oesophageal visceral
ganglion (figs. 4 and 5, g_1); thence the separated pair of nerves
continue rearward (figs. 4 and 5; $n \, co \, 1$), and both then branch,
one branch of each ($n \, oe \, l,$ figs. 4 and 5) continuing presumably for
the length of the oesophagus in the side pads (fig. 2), the other
($n \, co \, 2,$ figs. 4 and 5) continuing rearward to join its fellow in the
infra-oesophageal visceral ganglion ($g_2,$ figs. 1, 4, and 5). According
to Heider the visceral oesophageal ring, thus completed, has the
character of a long-stretched ganglion. From the infra-oesophageal
visceral ganglion a single cord in the ventral wall of the oesophagus
extends rearward to a terminal ganglion g_3 (at the level of the 4th
podial nerves). From this a pair of nerves go to the sides of the
upper jaw sac, and so join up with the pharyngeal system.

The oesophageal visceral nerve ring mimics the oesophageal central
nerve ring; but the union of the visceral nerves in the midventral line
of the oesophagus calls for explanation, in view of the evidence for
the lateral position of the nerve cords at that early period. Might it
be due to mechanical drag imposed by the upper jaw sac invagina-
tion?

The oesophageal visceral nervous system is much more com-
plex than our ideal oesophageal loop; but some redistribution may
well have taken place, since the time when the oesophagus was the
whole of the fore-gut. If appendages were present, and were in-
vaginated, as is probable, they have disappeared, having been super-
seded by those of the jaw sacs. The narrowness of the visceral
oesophageal ring in contrast with the great width of the correspond-
ing ring of the central nervous system can be attributed to the total
absence of oesophageal appendages in contrast with the size and the
action of those of the pharynx.

TABLE 2 (with stages 1 to 10).—*Supposed stages in the evolution of the central and visceral nervous systems of the polychaet*
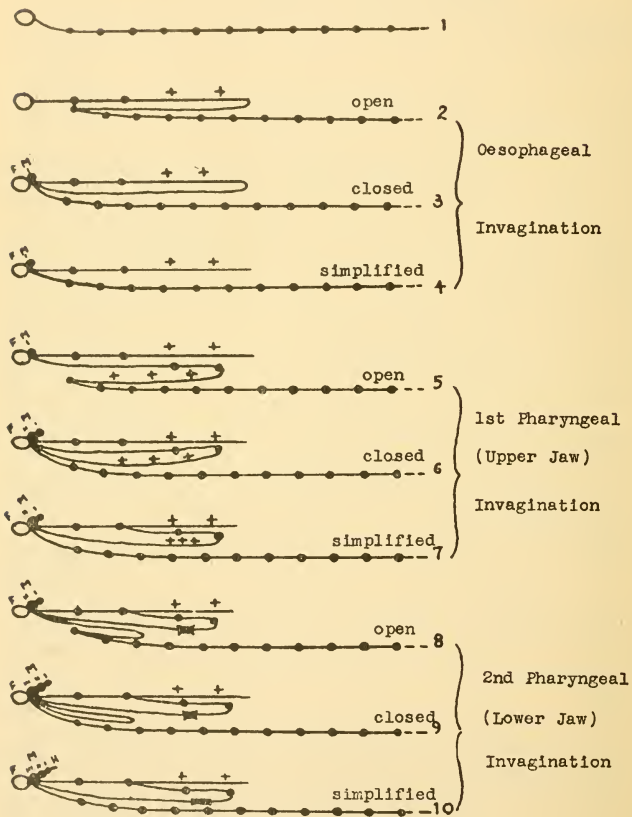
Stages 1 to 10 of table 2

Stages.

1. Brain and left ventrolateral nerve cord of the annelid ancestor of the polychaet. (The nerve cord was possibly not ganglionated at this stage. The podial-longitudinal and the nuchal nerves are omitted.)

2. The *oesophageal invagination* has produced open nerve loops, along which lie an unknown number of ganglia.

3. These oesophageal nerve loops have been closed by the advance of their terminal ganglia to the brain to form mid-brain I.

4. The oesophageal nerve loops have been simplified as suggested by the present visceral oesophageal nerves.

5. The *1st pharyngeal* or *upper jaw invagination* has produced open nerve loops, along which lie a considerable number of ganglia.

6. These upper jaw nerve loops have been closed by the advance of their terminal ganglia to the brain to form mid-brain II, which has pushed I to the rear.

7. The upper jaw nerve loops have been shortened by a coalescence with the visceral oesophageal cord.

8. The *2nd pharyngeal* or *lower jaw invagination* has produced an open nerve loop without, however, involving any ganglia.

9. These loops have been closed by the advance of their terminal ganglia to the brain to form mid-brain III, which has pushed II and I to the rear. (In this way I has been pushed up to the 1st nuchal ganglia which will join it as hind-brain.)

10. These nerve loops have aborted and the hind-brain is added.

The contrast between the oesophagus and the upper jaw sac could hardly be greater; and one can conclude that the interval between these invaginations was an enormous period of time. In this interval the open loops in the nerve chains would be closed; and the fore-brain would receive its most ancient addition. Judging from the structure of the brain this is now the posterior section of the mid-brain (mid-brain I); its small size (quite out of proportion with II and III) suggests its great antiquity. It would carry with it, too, a pair of cirri and a pair of eyes. At this time it would lie immediately behind the fore-brain (table 2, stages 3 and 4). The process just envisaged would have two advantages for the animal: first, the visceral nerves, as they had become, would thus constitute a system of their own, apart from the "central" nerve cords, according with their contrasting functions; and, second, the segmental ganglia behind the new effective mouth acquired again direct connection with the brain, thus rehabitating the "central" or rather the ventrolateral nerve cords, as they then were.

The *first pharyngeal invagination,* comprising the compound upper jaw sac subdivided by the jaw pads, appears to be mainly responsible for the pharyngeal part of the visceral nervous system. The second pharyngeal invagination, the lower jaw sac, appears to have added only the anterior part of the pharyngeal nerves, as explained below, p. 18. The upper jaw sac, together with its bounding bifid lips above and below (*l l* and *l ll*, fig. 2) is highly muscular; and, except for the muscles extending from it, it is bounded laterally by the body cavity. One of its great functions is its eversibility, allowing the fangs to be shot out to seize prey. This is largely effected by extroversion of the main long sac beneath the jaw pad.

Heider was unable to trace the nervous system throughout; but he believed his detached parts to be continuous, as suggested in his figure 16 (see also fig. 5, accompanying this paper). Except for the connections with the brain, all lie in the hypodermis of the jaw sac, and are lateral in position, from which we can infer that the nerve cords were still lateral and in the hypodermis. The nerves connecting with the oesophageal section have already been mentioned. Supposed to be connected with these are the pair of main nervous centers in the pharynx—Heider's "X-form bodies" (figs. 4 and 5; *g.x*). In plan these are irregularly quadrangular, with concave sides and horn-like angles, and they lie over the muscular posterior bases of the jaw pads, on either side of the dividing rift and with their convexities directed toward one another. Each consists of a nerve-fiber mass covered with a layer of small ganglion cells.

Heider, after satisfying himself as to the nervous character of the bodies, suggests that they are motor centers for the muscles of the jaw pads; and though he could not trace connections, he suggests that their posterior horns may connect with the nerves from the terminal visceral oesophageal ganglion g_3, and that their anterior ventral horns connect with the two visceral pharyngeal cords.

We can agree with Heider that the function of this pair of nerve centers is connected with the muscles of the jaw pads; but we can go further and suggest, on the theory here advanced, that each X-form nerve center is due to coalescence of the ganglia (lateral at that time) of the segments, the appendages of which are represented by the upper jaw apparatus, and the highly modified muscles of which are represented by the muscles of the jaw sacs. There is close coordination of the appendages, and there is union of the ganglia serving them.

The two pharyngeal cords of the visceral nervous system arise from the sides of the fore-brain via the anterior roots of the oesophageal commissures, and extend rearward to the side wall of the pharynx. They are traced by Heider as far back as opposite the second ventral ganglion and podial nerves. Their course is along the deepest (farthest sideways) part of the main sac, ventrad of the lateral bases of the jaw pads, and closely clinging to the hypodermis.

If Heider's supposed connections are correct we have here a nerve course from the fore-brain rearward to the main visceral nerve center in the pharynx, forming one side only of a visceral loop, the other side of which is to be found only in the oesophageal section. If at one time the ancestor of *Eunice* had separate oesophageal and pharyngeal nerve loops, their adjoining halves forming an opposite loop have disappeared. But if connection between the outside halves was effected, the connection of the inside halves with the brain would be redundant. Such a connection might be caused by the sharp folding of the hypodermis which the stomodeum exhibits, or might arise when the lip between the two invaginations became bifid.

On the general theory applied above to the oesophageal invagination, the evolution of the upper jaw sac was followed by the advance of the foremost unaffected segmental pair of ganglia to join the brain, thus completing the previously open pharyngeal loop. This is represented by the *middle pair* of the three mid-brain "ganglia," numbered II (the second in size and the second in antiquity) of the additions to the brain. It appears to have *arrived* like its predecessor *behind the fore-brain,* and to have *pushed the previous addition to the rear;* for the anterior section of the "mid-brain," considered below, was

the last to arrive, as indicated by the fact that it bears the visceral pharyngeal nerves and the roots of the oesophageal commissures, and further, they all *three* diminish in size from front to rear. Each of the three parts of the mid-brain carried with it to the head a pair of cirri, and the first two also a pair of eyes; for each segment in *Eunice* generally bears a pigment spot with the structure of an eye just above each appendage. The cirri survive as the antennae of the prostomium, but usually in *Eunice* one pair only of the eyes survives, belonging to mid-brain II. These eyes must have superseded earlier eyes innervated by the fore-brain. When a second pair of eyes exists, these are a posterior pair and belong to mid-brain I. The union of the pair of cirri belonging to this last into the median antenna may be connected, first, with the relegation of the brain division serving it to so posterior a position and, second, with its small size as compared with mid-brain II and III (see table 2, stages 5 to 7).

The *second pharyngeal* or *lower jaw invagination* comprises the two sacs beneath the "fore-pads." The upper of these sacs is bounded on its ventral side by the lower jaw pair of plates, there implanted. The median edges of these are free and thickened, forming a pair of crushers, between which the two sacs are in communication; whereas the anterior edges are sharp and form a pair of chisels. Not improbably the infolds bearing these plates may represent the highly modified parapodia of a single segment, opposed to one another by the invagination.

No ganglia or considerable nerves are associated with them, attributable to this invagination; and hence its ganglion pair is probably the one which, with its pair of cirri, subsequently advanced to the brain. Perhaps by this time the nerve cords were more ready to free themselves from the hypodermis. Probably the nerve cords were still lateral in position, or at least not closely approximated in the ventral line as now. On our theory the ganglia of the lower jaw segment were the last of the ganglia from the central nerve cords to join the brain, forming mid-brain III, the largest as well as the last of these additions. Like their predecessors, they in their turn addressed themselves to, and arrived behind, the fore-brain, for they alone of the mid-brain divisions receive the oesophageal connectives; and they, too, pushed their predecessors to the rear. Again, they brought to the fore-brain not only the central nerve cords which in this case persist as the oesophageal connectives with their *two* roots, but also the ends of a new loop of the visceral nervous system which persist as the pharyngeal nerves, reaching the brain with the ventral roots of the oesophageal connectives. As before, the other end of this loop has been short-circuited and has disappeared.

Mid-brain III, the anterior section, does not carry an eye in polychaets. Perhaps it is because by this time the eyes of the head were so much more efficient than the segmental eyes of the trunk that the pair belonging to the lower jaw segment has aborted. On the other hand, it should be noted that the present first body segment is without an eye-spot, so the abortion may have been effected earlier.

It will be agreed that the presence of five (the equivalent of six) similar antennae, as is still seen in the Eunicidae and the Amphinomidae, is the primitive condition in the polychaet. The development of so great a number by nature on *part* of a unit brain, such as is conceived either by Racovitza or by Hanström, is extremely improbable, if not indeed unimaginable; whereas, on the theory here advanced, it follows quite naturally.

The parallel evolution of the mid-brain, the stomodeum, and the visceral nervous system have now, it is hoped, been read at least in outline.

COMPLETION OF THE BRAIN

The mid-brain has now been evolved and added to the fore-brain. Arguments have already been advanced for the addition of the hind-brain or nuchal brain last of all. Its incorporation is probably to be attributed to the rearward extension of the brain due to the successive additions of mid-brains I, II and III, which brought mid-brain I to aggregated ganglia of the nuchal organs. This suggests that the incorporation of the hind-brain and of mid-brain III took place at the same time. This completed the basic plan of the polychaet brain. Söderström, however, who first claimed that it was an addition from the body, claimed also that for this reason it could not form part of the prostomium. But had he espoused the theory here advanced, on the same principle the whole of the mid-brain would have to go. Gustafson, though he accepted the first claim of Söderström, retained the nuchal brain as part of the brain and presumably of the prostomium. On the theory here presented there is still greater reason to accept the hind-brain as an integral part of the brain and of the prostomium. This question is further discussed below (p. 25).

SUMMARY OF THE AUTHOR'S THEORY

Now that the intimate relationships between these three systems of the brain, the stomodeum, and the visceral nervous system have been deduced and outlined, it is advisable to picture in greater detail the modus operandi of these supposed changes which are illustrated by table 2, stages 1 to 10.

As discussed below, we can hypothecate for the primitive annelid the presence of three pairs of longitudinal nerve cords represented now by the nuchal nerves, the podial longitudinal nerves, and the ventral nerve cords. Their positions in the primitive annelid, if symmetrical, would be dorsolateral, lateral, and ventrolateral respectively. As the annelid was already segmented, we can call these nerve cords the nuchal, podial, and ventral *chains*.

In the primitive annelid (table 2, stage 1) the *primal brain,* represented by the present fore-brain, must already have constituted the dominant nerve center of the body; and, judging from the structure of the brain of the polychaet and especially the eunicid, it must have *retained its dominance till the brain was completed.* The *original* anterior ends of the ventrolateral nerve cords or "ventral chains" issuing from the primal brain are represented *now* by the *visceral oesophageal cords,* not by the perioesophageal connectives. The invaginations may all have been brought about by the animal finding it useful to employ appendages within its alimentary tract and therefore invaginating them. Further, as its habits changed and the appendages improved, this was effected three times over. This mode of origin seems especially probable in the two pharyngeal invaginations where we still have the armature in each case; and if it is accepted for them, it can with great probability be hypothecated also for the oesophageal invagination where all armature is absent.[1] The effects of the stomodeal invaginations upon the primal ventral chains may ultimately be read in detail; but if the podial chains were also involved, we cannot at present cite effects due to them.

The *oesophageal invagination* (table 2, stages 2 to 4). The oesophageal nerve loops produced by this (fig. 2) are perhaps represented now only by the oesophageal cords extending from the brain to the supra-oesophageal ganglion (g_1) of the visceral nervous system, the upper half of the ganglionlike circumoesophageal ring (*n co 1*) and the continuations rearward in the main lateral pads of the oesophagus (*n oe l,* figs. 4 and 5, Heider, 1925, pp. 86-88). Unknown primal "ganglia" along the last are suggested by a few plus signs. The loops were closed by the advance of the foremost pair of uninvaginated ganglia to the brain (fore-brain) to form *mid-brain I,* bringing with them the ventral sides of the oesophageal loops and the ventral chains (table 2, stage 3). The nerves were brought up to, and appropriated by, the fore-brain, whereas the mid-brain I presided over a pair of

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[1] But the idea was first suggested to the author by the characters of certain trilobites, where several pairs of appendages seem to be entirely hidden within the alimentary tract.

antennae and a pair of eyes. For after the invagination the parapodia of this segment may well have become restricted to a pair of dorsal cirri—"tentacular cirri"—as in the first body segment of *Eunice*, associated with a pair of eyes, present on all the other body segments; and both cirri and eyes advanced to the prostomium with their ganglia. The oesophageal loops, though represented in stage 4 as simplified, may perhaps have continued in existence until the simplification of the first pharyngeal, stage 7.

The *1st pharyngeal invagination* (stages 5 to 7). The pair of nerve loops due to this (stage 5) are apparently represented by the lower half of the oesophageal ring and the cords joining g_2, g_3, and the X-form body, together with part of the pharyngeal cords (*n ph* of figs. 4 and 5). The unknown primal ganglia along it are again suggested by a few plus signs.

The loop was closed (stage 6) by the advance of the foremost uninvaginated ganglia to the brain to form mid-brain II, which also carried with it pharyngeal cords of the visceral nervous system and the ventral chains. But, as after the oesophageal invagination, it was to the fore-brain that they came, entering between this and mid-brain I and pushing the latter to the rear. As yet, there was no fusion between those brain parts. Again the fore-brain appropriated these added nerves, which arrived outside of the previous system. Mid-brain II again, like I, had to preside over the pair of antennae (the previous "tentacular cirri") and the pair of eyes, which had advanced with these ganglia.

After this stage came a simplification of this 1st pharyngeal visceral nerve loop, and not improbably of both the oesophageal and 1st pharyngeal loops together (stage 7). If two complete loops still existed, much was redundant, and the dorsal side of the first pharyngeal seems to have joined the dorsal side of the oesophageal; whereas other parts aborted.

The *2nd pharyngeal invagination*. This, the lower jaw invagination (stage 8), may be expected to have produced small nerve loops. No ganglia are associated with the lower jaw, so no ventral ganglion pair was involved. The invagination was probably due to the use by the mouth of the previously foremost pair of extra-stomodeal appendages, the dorsal cirri of which at the same time functioned as tentacular cirri! These appendages are represented by the lower jaw plates and pads.

The new visceral nerve loop was closed by the advance of the foremost pair of ventral-chain ganglia to the brain, in the same way as before, to form mid-brain III (stage 9). With them to the prosto-

mium traveled the tentacular cirri of the time to form the antero-
lateral tentacles. No eyes accompanied this third pair of cirri; and it
has been mentioned that eye-spots have been lost from the first body
segment (that with tentacular cirri) in *Eunice punctata*.

The added ganglia, following the established rule, addressed them-
selves to the fore-brain, as had their predecessors, whom they in turn
forced to the rear. They trailed again the ventral cords and by
applying themselves to the fore-brain caused the double roots of the
oesophageal connectives. They brought also with them new visceral
nerves—the present fore-brain roots of the pharyngeal visceral cords.
It is significant that these arise from the ventral roots of the oesopha-
geal connectives—both were brought together, and at the time of the
addition of mid-brain III.

How exactly the simplification of this visceral system was effected
may not be clear; but the three courses of stage 9 imply redundancy,
and one course alone seems to have survived, namely, the most
ventral, because this alone would be associated in origin with the
new oesophageal connectives.

One other change and the basic plan of the brain was completed:
mid-brain I had now been pushed so far to the rear that it has
approached the nuchal ganglia and these also have added themselves
in stage 10 to constitute the hind-brain. With this the brain of the
ancestral polychaet has been evolved. The stomodeum is completed,
and this has involved the completion of the brain.

LIMITS AND SIGNIFICANCE OF THE PROSTOMIUM OF THE POLYCHAET

Regarding the extent of the prostomium, there has been much
difference of opinion: it has indeed been a subject of keen contro-
versy. But there is perhaps no need to recall here the numerous
divergent views. Considering the great antiquity of the polychaets,
it is not surprising that the head should present great variety, and
suggest different opinions. The ideal prostomium, the prototype, is
the *region in front of the mouth in the common ancestor of the group;*
and this may be expected to be indicated by what the most primitive
polychaets have in common there. By previous writers this seems
generally to have been equated with the prostomium of the hypo-
thetical primitive annelid; but this is opposed by the claims advanced
in this paper.

As to its nature and origin, two markedly contrasted conceptions
have been held: (1) that in its origin it was segmental in some way
or other; (2) that it was a unit, and unsegmented (see table 1,

p. 4). Söderström, who held the latter view, sought in effect to change its definition into *the unsegmented anterior region of the body;* and he cast scorn on all who had not the same "prostomium idea." Such a definition is, however, quite unjustifiable.

The conclusion of Binard and Jeener, supported also by Gustafson and accepted by the present writer, is that the primitive appendages of the head comprise an anterior pair of antennae, modified in some forms into palps; a second pair, never so modified; and a median antenna. These are innervated by successive parts of the mid-brain. The morphological order of these appendages was naturally of less importance to those who regarded the prostomium as a unit, than to those who thought of it as segmented. The earlier writers, previous to Lameere, all placed them in their order of position—the anterior pair first, the median antenna last. Lameere reversed the order, and was supported by Binard and Jeener. Hanström seems to have accepted the reversal, but did not accept Lameere's theory. Gustafson was apparently in doubt, and perhaps for that reason numbered them chaotically. The present theory erected in entire ignorance of that of Lameere, also reverses the order, but for an entirely different reason; moreover, whereas according to Lameere the sequence of the three "pairs" was already developed in the *coelenterate* ancestor, on the present theory the three pairs of ganglia that innervated them (as well as the antennae themselves) were picked at random, so to speak, by nature out of a long sequence of postcephalic segments during the evolution of the polychaet, and carried forward to the head. Besides five antennae, the prostomium bears also two pairs of eyes. Even those who have recognized segmentation in the prostomium have not regarded the eyes as segmental; but the author claims that they belong with the intermediate antennae and the median antenna, and are thus segmental in origin (pp. 16, 18, 21, and 22).

Previous to the researches of Söderström on the Spionidae the prostomium was always considered to include also the whole of the compact mass of nervous matter constituting the brain. He, however, homologizing the nuchal organs with the dorsal, segmental, chemical sense organs of the Spionidae, which extend through the whole body, claimed that the hind-brain and nuchal organs must therefore be excluded from the prostomium. On the other hand, all the most primitive polychaets have a hind-brain closely associated with the remainder, and possess also these nuchal organs; hence there is every reason to credit the ancestral polychaet with a hind-brain and nuchal organs, and therefore to include these parts in the prostomium. And just as the nuchal organs have their homologues on the

postcephalic segments of the Spionidae, so the antennae have theirs in the dorsal cirri of the body segments, and the eyes have theirs in the postcephalic eye-spots. The principle on which Söderström would exclude the hind-brain is invalid, and is reducible to an absurdity. On the theory here advanced it would also exclude the whole of the mid-brain, the antennae, and the eyes. Furthermore, reason has above been given for the incorporation of the hind-brain at the same time as mid-brain III. Again, on the theory advanced by Hanström it would exclude the fore-brain and the mouth-lips! The principle is wrong: Söderström did not allow for any evolution within the annelid. We must get back to the primitive idea, and define the prostomium as *all that region in front of the mouth inherited in that position from the primitive polychaet.* On the theory here advanced this includes: (1) the fore-brain and the representative of the "mouth-lips," inherited from the head of the more primitive annelid, together with the following parts acquired in order by the prostomium during the evolution of the head of the polychaet: (2) the hind section of the mid-brain (mid-brain I) with the median antenna (due to coalescence of a pair), and a pair of eyes (the posterior pair); and long afterward (3) the middle section of the mid-brain (mid-brain II) with the second pair of antennae, and the anterior pair of eyes; and again long afterward (4) the anterior section of the mid-brain (mid-brain III) with another pair, the anterior, of antennae; and also (5) the hind-brain with the nuchal organs; these two brain parts (mid-brain III and the hind-brain) being probably acquired nearer the same time.

Gustafson, who is doubtful whether to accept the theory of Hanström that the stomatogastric lobes (or fore-brain) have been added from the ventral chain, is doubtful therefore whether to regard the mouth-lips, which they innervate, as part of the prostomium. Nothing better illustrates the enormous contrast between the present theory and that. What Hanström regards as the last addition is here claimed as the original nucleus.

Many may be surprised at the inclusion here of the hind-brain after Söderström's important and significant work; but it will be clear that the same principle, which would exclude it, would exclude also the whole of the mid-brain and all the cephalic tentacles and eyes.

It will thus be seen that the theory here advanced presents a new conception of the prostomium. It is not the representative in modern forms of the head of the primitive annelid, but the result of the long evolution from this of the head of the polychaet. It is not a unit as so many have supposed, but an aggregate, acquired only in the

course of unimaginable time. It is not due merely to the cephalization of additional anterior segments of the body as many have supposed, but is largely due to the advance to the brain of three pairs of segmental body ganglia at three far separated times, and, at the same times also, advance to the head of three segmental pairs of cirri and two segmental pairs of eyes, to become the cephalic sense organs. Incidentally this aggregation caused the brain to incorporate also the hind-brain innervating the nuchal organs, which are therefore just as much parts of the prostomium as are the other cephalic sense organs and the mid-brain.

Further, this great *aggregation of the brain* and the cephalic sense organs, which built up the polychaet prostomium, is claimed here as *incidental to the evolution of the stomodeum,* which again is referred to changes in the mode of feeding.

MORPHOLOGICAL SIGNIFICANCE OF THE HIND-BRAIN

The nuchal organs are quite dorsal in position. This is seen very clearly in the Spionidae which in some forms retain them completely; and it is indicated also by their position in the errant polychaets. But in these it is only in the tetraneural Amphinomidae and Euphrosynidae that extensive development of the nuchal organs occurs. Here development of the caruncle is accompanied both by great enlargement of the hind-brain (presumably by the addition of their ganglia), and by tetraneury; and again the nuchal organs are quite dorsad of these nerves. These relationships suggest that the ancestor of the polychaet, before the evolution of its brain, stomodeum, and visceral nervous system was characterized by *sexneury* having: (1) a pair of ventral nerve cords (still persisting as the ventral nerve cords of the central nervous system), (2) a pair of lateral or podial nerve cords (still retained only in the tetraneural families above mentioned), and (3) a pair of dorsal or nuchal nerve cords (still retained by the Spionidae, greatly developed and cephalized by the tetraneural families, and greatly reduced subsequently in other families).

The mode of evolution of the polychaet detailed above—by three ventral invaginations (two great and one small)—would involve, also, as these took place, the contraction and packing together of the dorsal parts of the ventrally invaginated segments and, therefore, of the nuchal ganglia. The tetraneural families, as they retained their podial longitudinal nerves, took advantage also of this, and have incorporated the nuchal organs into the caruncle, and the nuchal ganglia into the brain.

MORPHOLOGICAL SIGNIFICANCE AND RELATIONSHIPS OF THE PERISTOME

On our theory *the peristome is not a somite* but marks the site of a succession of breaks, causing a gap in an originally continuous sequence of ganglia, the remainder of which form the ventral nerve cord. Further, in the course of evolution the peristome has been extensively exchanged three times over. The missing members are believed to be partly distributed along the visceral nervous system, and partly coalesced with the brain. The magnitude of this "gap" furnishes a complete explanation of the hitherto mysterious fact— that the nervous system arises from two distinct rudiments, one giving rise to the brain, the other to the ventral chain—a fact which has been noted by numerous workers from Salensky (1882) and Goette (1882) onward. The visceral ganglia are thus brought into the succession of those of the central nervous system, in opposition to the generally accepted view of their separate origin. With more detailed knowledge of the visceral nervous system it may be possible to determine in large degree the succession of the various ganglia which can be recognized.

In the brain, besides the fore-brain and hind-brain we have an association of three pairs of comparable ganglia, sending out comparable pairs of nerves, and innervating comparable organs; and according to this theory they were added to the brain at three different times. Further, they were selected by nature in the course of evolution from a considerable length of the primitive ventrolateral nerve cords, including probably well over a dozen pairs of ganglia. The order, too, of the upbuild of the brain on this theory is quite different from that on any other. The contrast between this plan and the others that have been advanced could hardly be greater, whether we compare it with that of Pruvot, or Racovitza, Nilsson, Lameere, or Hanström. The reason for this is that it connects the three systems— the brain, the visceral nervous system, and the stomodeum. It is curious that the order of the elements of the mid-brain happens to be the same as on Lameere's theory; but the significance is entirely different. It may be remarked that there is much to be said in favor of Lameere's theory as a mode of origin of the annelid; not, however, of the polychaet but of its distant ancestor.

Should our theory prove correct, Racovitza will have builded wiser than he knew, though quite other than what he meant; for the primal brain was his fore-brain, to this was added his mid-brain, and to this the hind-brain.

But the evolution of the head and brain envisaged here is entirely

different from that of Racovitza. In his view the peristome did not differ fundamentally from a normal segment (1896, p. 154); the head of the ancestor *became* the head of the polychaet; the parts were already there, including the primal elements of the cerebral nervous system—the "aire palpaire," "aire sincipitale," and "aire nucale." Only further development of these was needed: that of the sense organs on them into palps, antennae, eyes, and nuchal organs; that of the areas themselves into the fore-, mid-, and hind-brains. Before this evolution in the polychaet there were no comparable sensory organs (1896, p. 161). On the contrary, according to the theory here presented, the ancestor was already furnished with eyes and parapodia throughout the body, and possibly also some form of appendages and eyes on the head, which already possessed a brain and bore also an early stage of the mouth-lips. The 4 (or more) pairs of ganglia, too, which initiated the mid- and hind-brains were already functioning in their own postcephalic segments. But whatever sense organs that primitive annelid had on its head, except for the mouth-lips these organs were superseded in the evolution of the polychaet by previously postcephalic eyes and antennae; while its brain was to be extensively supplemented and partially superseded. A fundamental difference between the two views is that Racovitza in evolving the polychaet brain thought he was evolving that of the primitive annelid, whereas on the here offered theory no primitive annelids survive.

APPLICATION OF THE AUTHOR'S THEORY TO POLYCHAETS IN GENERAL

Very close comparisons are now possible between the different families of errant polychaets in regard to the prostomium and its appendages and eyes, the brain, the stomodeum, and the central and visceral nervous system; and, to judge from the results of past research, the suggestions of close affinity are not likely to be diminished in the future. In the accompanying table typical representative sub-orders and families are tabulated in regard to their brain, sense organs, stomodeum, and buccal segments; in it, too, the homologies are indicated, and characterized as succinctly as possible. The agreement in brain and sense organs is extremely close; and even in the stomodeum, though the characteristics vary so much, a series of stages can be seen between the Eunicimorph through the Amphinomorph to even the Glycerimorph.

In table 3 the order of development of the different sections of the stomodeum is to some extent indicated by the letters a, b, c; and the order of incorporation of the divisions of the brain by A; BI, BII, BIII; C.

So close are these comparisons that one can have little doubt but that all derive from the same ancestral stock; and if the fundamental plan of the brain above detailed be accepted, it will be agreed that the closest approach to this ancestral stock is to be found in the Eunicimorpha. The evolution which has been traced, if it be substantially true, is therefore that of the ancestral polychaet. It can all be assigned to very far back in pre-Cambrian time, effected say before 1,000 million years ago. Of this the writer feels confident; because, as he hopes to show, the arthropods, some of the classes of which were evolved long before Cambrian time, were derived from a *particular family* of polychaet still extant!

If the above given conclusions as to the character and origin of the original polychaet brain be accepted, its further evolution can with some confidence be pictured. The separate ganglia of the two sides of the brain united in the midline, consolidation was effected, and enormous development has ensued—development which can be read by detailed comparisons of the brains of the various polychaets. The fore-brain, hitherto dominant, has lost its old eminence even in the Eunicidae; and in other families is often greatly reduced. The mid-brain has undergone great development, and perhaps in all forms has become the chief nervous center. And whereas, as is here assumed, the palpal function in the primitive polychaet was seated in the mouth-lips, and served by the fore-brain, now only in the Eunicidae and Amphinomidae is this the case. In some others it is apparently seated in the proboscis and is still served by the fore-brain: in yet others (viz, the Aphroditidae, Chrysopetalidae, Hesinoidae, Syllidae, and Nereidae) the function has been transferred to the anterior pair of antennae, transformed into palps, and is served mainly by the mid-brain. This is indeed the case even in a family of the Eunicimorpha—the Stauronereidae (Staurocephalidae). The degrees of development of the brain are extremely varied; and the new structures include neurone courses, nerves, commissures (transverse in considerable number, and also longitudinal), the true brain ganglia, and in the highest forms the corpora pedunculata. In the Amphinomorpha extra pairs of nuchal ganglia have joined the hind-brain and this has here become much the most voluminous division of the brain. With different modes of life very different lines of evolution were followed. All other suborders seem to have changed more than did the eunicid. Here the brain is still relatively primitive, exhibiting its primitive subdivisions still extended in a plane. In contrast, in the aphroditid it is compact, folded over between front and rear and very highly developed. On the other hand, in some

errant families and perhaps in all the sedentaries it has degenerated.

Regarding the stomodeum, if, as is above suggested, the much-folded form exhibited by the Eunicimorph is the most primitive type, the different errant polychaets present us with suggestions of the stages of evolution between this relatively nonprotrusible folded type and the extremely protrusible cylindrical type of say the Glyceri-morpha. Such an evolution one might expect to be accompanied by great changes in the visceral nervous system, and probably also in the brain.

To trace the evolution of any form and the deployment within the class, it will be of great advantage to have a starting point, a basic plan, which is all that the present paper can claim to attempt. Were zoologists to attempt to work out by ontogeny and by comparative anatomy the many courses of evolution within the class, the common starting point would soon be apparent.

TABLE 3.—*Comparison of supposed homologues of the morphological entities of the head region of typical errant polychaets (pelagic families omitted)*

Divisions of head region	Prostomium: front and venter	Prostomium: dorsum			Prostomium: rear	Stomodeum	Stomodeum	Peristome	Accessory buccal segments
Corresponding brain divisions	A Fore-brain in-nervating pri-marily the an-terior lips	BIII Anterior mid-brain innerv-ating a pair of tentacles	BII Median mid-brain innervat-ing a pair of eyes	BI Posterior mid-brain innervating the median tentacle (a coalesced pair) and a pair of eyes	C Hind-brain inner-vating the nuchal organs	Divisions and char-acter:	Armor of pharynx		
POLYCHAET suborders and families									
EUNICEMORPHA Stauronereidae (Stauronereidi-idae Dorville-idae) Staunoreis (Staurocepha-lus)	Anterior lips with no defined organs	Greatly devel-oped as "palps"	Tentacles — Large eyes	Median tentacle vestigial (*S. rubra* Grube, *S. melanops* Verrill) or absent — Small eyes or ab-sent	One pair of nuchal furrows, each sub-divided into 2 pits	Very limited pro-trusion (c) lower jaw sack; (b) upper jaw sack, bilater-ally symmet-rical (a) long oesopha-gus	(c) pair of plates, toothed at free edge (b) 2 or more se-ries of very nu-merous teeth on each side, all paired. Bilateral sym-metry	Rather large — No appendages	1 segment — No appendages
EUNICIDAE (Leodicidae)	Pair of anterior mouth-lips, so-called "palps"	Outside ten-tacles (palps of Gustafson)	Intermediate tentacles — Eyes	Median tentacle — Eyes rare	One pair under front of peristome	Very limited pro-trusion (c) lower jaw sack; (b) upper jaw sack, with bi-laterally un-symmetrical armor (a) long oesopha-gus	(c) pair of plates *left* side (b) 2 rub plates 3 saw plates fang, carrier *right* side 2 rub plates 2 saw plates fang, carrier Symmetry lost	Very large — No appendages	1 segment — One pair of tentac-ular cirri or none
AMPHINOMORPHA Amphinomidae	Lateral and an-terior mouth-lips (palpophor lobe of Racovitza)	Ventrolateral tentacles (sty-lode of Racovitza)	Intermediate tentacles — Large eyes (or absent)	Median tentacle — Small eyes (or ab-sent)	Supreme develop-ment into caruncle extending over an-terior segments, served by several ganglia of the hind brain	Proboscis with moderate protru-sion (c) eversible sheath, continu-ous dorsad with the phar-ynx, but ven-trad reaching it far to rear (b) pharynx with papillae { a. glandular b. muscular (a) oesophagus or ventricle, strongly, pli-cated, allowing protrusion	No jaws or teeth, but with papillae Bilateral symmetry	Peristome little differentiated, and bearing parapodia. Primitively, as *Paramphinome* the mouth is surrounded by the peristome and has the first ventral ganglia with their commissure behind it. But within the family the mouth opening has suffered great increase of size and rearward migration; and usually the second ventral commissure is the first behind it, the first being ap-parently broken.	None

(30)

TABLE 3—*Continued*

Polychaet suborders and families	Fore-brain	Mid-brain III	Mid-brain II	Mid-brain I	Hind-brain	Stomodeum	Armour	Peristome	Accessory buccal segments
NEREIMORPHA Phyllodocidae	No defined organs	Tentacles	Tentacles / Eyes	Median tentacle (or absent) / Eyes (or absent)	Primitive nuchal organs	Protrusible proboscis (c) eversible protrusible sheath (b) protrusible pharynx in 2 sections (a) ventricle often with 2 caeca	(c) with papillae and sometimes paragnaths Almost cylindrical symmetry	Peristome with one or two pairs of tentacular cirri	One or two other segments may bear only tentacular cirri
Nephthydidae	No defined organs	Tentacles (anterior)	Tentacles (posterior) / Eyes	Absent / Absent	Present (according to Pruvot, 1885)	Short protrusible proboscis (c) eversible sheath (b) pharynx in two stages (a) ventricle	(c) papillae in longitudinal series, and adjoining pharynx (b) 2 short horny jaws or none Bilateral symmetry	Peristome fused with next segment No cirri	with next segment
Nereidae	No defined organs	Large palps each with 2 "joints"	Tentacles / Large eyes	Absent / Smaller eyes	Nuchal organs	Strong protrusible proboscis (c) eversible muscular sheath (b) pharynx with massive muscles (a) oesophagus or ventricle with 2 caeca	(c) with papillae and with teeth (paragnaths) (b) jaws in front, transverse, and muscle ridges behind Bilateral symmetry	Peristome coalesced with next segment, each bearing 2 pairs (dorsal and ventral) of tentacular cirri. They may bear parapodia with setae	
Hesionidae	No defined organs	Palps 2-jointed (absent only in *Hesione*)	Tentacles (or absent) / Eyes	Median tentacle (or absent) / Eyes	Primitive nuchal organs	Strong, very extensible, protrusible proboscis (c) eversible sheath (b) muscular pharynx (a) ventricle, with a pair of caeca	(b) with papillae, and with or without horny jaws Bilateral almost cylindrical symmetry	Peristome with 2 pairs of tentacular cirri, with a bundle of bristles at base of each	0-3 segments without setae may be separate, or coalesced with the peristome, each with 2 pairs of tentacular cirri

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TABLE 3—Continued

Polychaet suborders and families	Fore-brain	Mid-brain III	Mid-brain II	Mid-brain I	Hind-brain	Stomodeum	Armour	Peristome	Accessory buccal segments
Syllidae	No defined organs	Greatly developed palps, much jointed	Tentacles / Eyes	Median tentacle / Eyes (2 extra pairs may be present drawn from rear)	Nuchal organ present according to Spengel, 1881	Long protrusible proboscis (c) eversible sheath (b) protrusible cylindrical pharynx followed by (a₂) barrel-form proventricle (a₁) postventricle ventricle with or without a pair of caeca	(b) with 1 dorsal tooth or several, and with papillae. Bilateral, almost cylindrical symmetry	Peristome with 1 or 2 pairs of tentacular cirri but no setae	None
APHRODITIDAE Polynoinae	No defined organs	Long palps	Tentacles (or absent) / Eyes	Median tentacle (or absent) / Eyes	Nuchal organ	Cylindrical protrusible proboscis (c) eversible sheath (b) protrusible pharynx (a) ventricle	(b) with a circle of papillae and a pair of dorsal and a pair of ventral jaws of bilateral symmetry	Peristome with 2 pairs of tentacular cirri with setae at the base	Ventral cirrus of next segment very long
GLYCERIMORPHA Glyceridae	Extremely modified, represented by the venter of the conical secondarily annulated prostomium. (Hanström, 1927)	Lower tentacles at end of prostomium	Upper tentacles at end of prostomium / No eyes or usually absent	Absent	Nuchal organ	Long cylindrical or clavate far-protrusible proboscis (c) eversible sheath (b) muscular protrusible pharynx (a) ventricle	(c) covered with papillae. (b) with 4 jaws or 2 jaws and numerous paragnaths. Almost cylindrical symmetry	Peristome with no appendages	None

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CONCLUSION

Both in their complexly folded stomodeum and in their brain the Eunicimorpha are claimed as the most primitive of polychaets. Their study suggests the characters of the ancestral annelid and the subsequent evolution of the complexities of the stomodeum, the brain, and the visceral nervous system of the polychaet.

In brief, on this view, the ancestors of the polychaet, in connection with their successive modes of feeding, transferred not only the external skin, but also the nerves and ganglia of the central nervous system, which at that time were lateral in position, and also the appendages associated with those ganglia, up the alimentary tract in the formation of the stomodeum. As a primary result they have originated (or greatly added to) their visceral nervous system; and as a secondary result have complicated their brain. The dominating factors were the invaginations; and the structure of the eunicid shows that these took place three times over. (An analogous process took place yet again in the evolution of arthropods, as the writer hopes to show.)

Most of the fundamental ideas expressed in this paper are already summarized on pp. 19 to 27.

Though the evolution here claimed is so great and so widespread, it is not believed to be beyond the capacities of variation and natural selection to effect.

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