On the Relation of the Arthropod Head to the Annelid Prostomium.

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THE question of the segmentation of the Arthropod head, and of the homology of the preoral region in Arthropods and Annelids, has for long excited the interest of naturalists, giving rise to much discussion, and leading investigators to the discovery of many important facts. The present paper, written at the suggestion of Professor E. Ray Lankester, does not claim to be a contribution to our knowledge of the problems involved, nor an exhaustive history of the subject; it aims neither at originality nor completeness, but is merely an attempt to give a plain account of the questions at issue, and the advance that has been made towards answering them, for the benefit of those who have not devoted special attention to the subject.

If we wish to compare the preoral region of an Arthropod with that of an Annelid, it is necessary first of all clearly to understand the relation of the prostomium and the peristomium, or buccal segment, to each other, and to the other segments of the body of an Annelid worm.

It was Professor Huxley who first introduced the word prostomium in his 'Lectures on General Natural History,' published in 1856 (5). "The body of the Polynoë," says Huxley, "is composed of a series of twenty-six 'somites,' terminated anteriorly by a 'segment,' the prestomium[1] (Kopf-lappen, Grube), and posteriorly by another, the pygi-

[1] The modified form prostomium was introduced by Lankester (8).

dium, which may or may not represent single somites." The first somite with parapodia, chætæ, and acicula he calls the "peristomium."

FIG. 1.

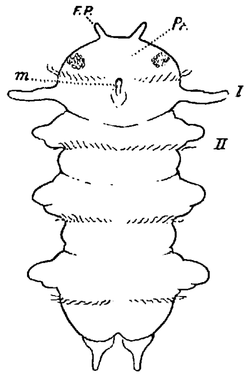


FIG. 2.

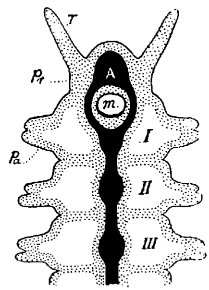


FIG. 1.—Ventral view of a young Nereis.

FIG. 2.—Diagrammatic plan of the anterior segments of the Polychæta. The nervous system is represented in black, the mesoblastic tissues are dotted, the cœlomic cavities are left white. *F. P.* Frontal process. *m.* Mouth. *Pa.* Parapodium. *Pr.* Prostomium. *T.* Tentacle. A. Archicerebrum. The Roman numbers refer to the segments.

The prostomium (Kopflappen, lobe céphalique), then, is a median anterior process lying above and in front of the mouth. It may be small and insignificant, as in most Oligochætes, or it may be large and of great physiological importance, as in many Polychætes. The prostomium may be long and produced into a moveable process (Stylaria), or distinctly annulated (Glycera). In the Polychæta it contains the brain or supra-œsophageal ganglion, and often bears specialised organs of sense, such as dorsal tentacles and eyes, and ventral palps. In the Oligochæta, on the other hand, the brain recedes from the prostomium (except Æolosoma) into the first, second, or third segment; whilst in some forms the prostomium is quite rudimentary (Diacheta), in others it extends backwards dorsally (as marked by a groove) to the hinder limit of the peristomium (Lumbricus).

In the Amphinomids it grows backwards over several segments.[1]

The peristomial segment, to which the prostomium is attached, is almost always considerably modified in connection with the mouth, and may even be sharply marked off from the posterior segments. It is often called the cephalic segment (Kopf segment, segment céphalique, buccal segment, head segment, &c.). The peristomium and prostomium together constitute the head in Oligochætes and some Polychætes. In many Polychætes, however, several anterior segments may become so modified as to contribute to the formation of the head.

Having thus briefly reviewed the structure and relations of the prostomium in the Chætopoda, we must proceed to a more accurate study of its homology.

The prostomium can be one of three things: (1) a modified or reduced segment; (2) an incipient segment, growing on the anterior surface of the peristomium; (3) not a segment at all, but a structure of different and special nature.

Before attempting to prove that the last interpretation is the true one, it must be clearly established what we mean by a true segment or metamere, and then how such a metamere differs radically from the prostomium.

It is comparatively easy to give a serviceable definition of a typical segment: it is a region more or less distinctly marked off from the rest of the body by transverse grooves, surrounding the alimentary canal, containing a special cœlomic cavity (more or less completely separated off from the cœlom of adjoining segments by means of transverse septa), a pair of nephridia and of peritoneal funnels communicating with the exterior, a pair of ganglionic enlargements of the ventral

[1] An excellent discussion of the structure and morphology of the prostomium and brain of the Polychæta has lately been given by M. Racovitza (**14**).

longitudinal nerve-cords, and (in Polychætes and Arthropods) a pair of appendages. But we know very well that such fully equipped segments are rarely found in nature. Intersegmental grooves frequently disappear (head and thorax of Arthropods); there are segments without cœlomic cavity (the thoracic segments of insects, for instance); and again, there are segments with neither peritoneal funnels nor nephridia (most Arthropod and Chætopod anterior segments). Some metameres have no ventral nerve-cord (the first two segments of Lumbricus, the posterior abdominal segments of many insects); appendages are often absent.

It is clear, then, that the examination of adult structure will help us little in deciding whether a debatable region represents a true segment or not, though a careful comparison with allied types may often be of use. Embryology is our best guide in these cases, and generally furnishes a decisive answer. We find, as a matter of fact, that the segments, which lack in the adult those structures most essential, possess them at some time during early development, and lose them at a later period. Yet here, again, it must be admitted that undoubted metameres may have lost even during development one or more of the structures characteristic of true segments (for instance, no distinct cœlomic cavity is known to occur in some of the anterior segments of many Crustacea). We cannot, therefore, assert that a given region is not a metamere because it does not possess this or that character. The only dogmatic statement we are justified in making is, that when a region exhibits during development a sufficient number of the essential structures of a typical segment, it may be assumed to be a true metamere.[1] What is "sufficient" has to be decided in each case. It should be added that one positive fact outweighs many negative ones; the known presence of a certain characteristic of a segment in a certain region of an Arthropod, for instance, is of far greater importance than its ascertained absence in numerous other cases. A good example of this

[1] Theories as to the origin of metameric segmentation do not concern us here; at any rate, I do not propose to include them in this discussion.

kind is offered to us in the case of the loss of the limbs in snakes. The argument which might be urged—that the ancestors of the Ophidia were legless, since no obvious vestiges of limbs are seen in by far the greater number of snakes at any time in their development—is entirely disproved by the few instances, such as the Python and Tortrix, in which such vestigial hind limbs are known to occur.

Segments may be suppressed, either temporarily in the young, as in the zoœa larva; or, on the contrary, in the adult,—as, for instance, the first abdominal segment in Arachnida. On the other hand, neglecting the special cases of reproduction by fission, new segments are never intercalated between old ones, except in the normal process of growth at the tail end of the animal. This brings us indeed to one of the most important characters of the segmentation of Annelids and Arthropods, namely, that new segments, during the development of an individual, are invariably added between the last segment or telson, and the one immediately in front of it. All apparent exceptions to this rule, often called the law of Milne-Edwards, seem to be due to retardation in development, as in the case of the zoœa already mentioned.

At the risk of wearying the reader, it has been necessary to indulge in these commonplace and well-known remarks for the sake of clearing the ground. We may now return to the discussion of the morphology of the peristomium in Annelids.

Careful modern researches (Vejdovsky, Wilson, &c.) have shown that in Oligochætes the peristomium exhibits the essential characters of a true segment. It develops as a region surrounding the mouth, in which are formed a pair of mesoblastic somites which become hollowed out to form the cœlom; a ganglionic thickening is produced ventrally, which soon fuses with that of the succeeding segment; a nephridium (head kidney) is developed. In the Polychætes, on the other hand, where the head in the larva is so often enlarged to a disc-like shape, it is generally more difficult to trace the origin of the cœlom in the peristomium, as indeed also in the segments behind it. In some cases, at all events, it has been shown that a pair of somites are formed in the peristomium, become hollowed out, and even give rise to peritoneal funnels (E. Meyer, **11**). Nephridia are almost invariably developed in this segment. In Polychætes, moreover, a pair of lateral appendages are often developed, although they generally

FIG. 3.

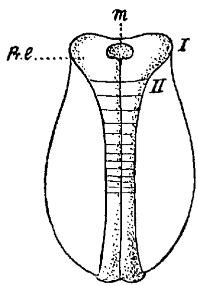


FIG. 4.

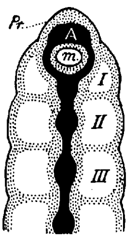


FIG. 3.—Ventral view of an embryo of Allolobophora putra (after Vejdovsky).

FIG. 4.—Diagrammatic plan of the anterior segments of the Oligochæta. *Pr. l.* Procephalic lobe; other letters as in Figs. 1 and 2.

become highly modified. In fact, it becomes evident, when we examine the development and the adult structure of the peristomium in the various groups of the Annelids, that it is really a metamere strictly comparable to the posterior segments, even when much modified owing to its position at the anterior end of the animal.

The prostomium, on the contrary, presents none of the characters essential to a segment. It never surrounds the alimentary canal; it never possesses a pair of mesoblastic somites.[1] The cavity which it contains is primitively of the

[1] Considerable confusion has been introduced into this question, apparently by the misunderstanding of Kleinenberg's results (**6**). The terms "cephalic germinal streak," "head segment," "head cavity," "cephalic zoonite," used by that author all seem to refer to the peristomium (not prostomium). Describing the development of the first pair of somites, he says, "The

nature of a blood-space, most clearly seen in trochosphere larvæ, where it is much enlarged. Although later in development in both Oligochæta and Polychæta, the prostomial cavity becomes confluent with the cœlom of the peristomium. It is only cœlomic by virtue of this connection.[1] No nephridia are developed in the prostomium, and on its upper surface is formed the primitive brain or supra-œsophageal ganglion. This brain may develop from the first as a single median structure, or may originate from several centres connected with the organs of sense, which subsequently become fused (Kleinenberg, Racovitza). We see that not only does the prostomium in Annelids differ from a metamere in size and shape, but it never at any time during its development exhibits the characters of a true segment. It therefore cannot be considered as a reduced or vestigial metamere. Can it be considered as an incipient segment? Obviously not, except on the very strongest evidence, since such a fact as the growth of a new segment in front of the first metamere would be opposed to the rule which is known to hold good for Annelid segmentation (Milne-Edwards' law). Such evidence is entirely wanting.

The only other opinion that can be held is that the pro-

splanchnic layer of the cephalic ring, which at first covers only the upper side of the buccal fossa and œsophagus with a thick layer of mesoderm, extends gradually its lateral parts towards the central [ventral?] surface, and embraces the ingestive aperture completely." And again, "The anterior end of the head segment becomes more and more prominent, and is transformed into a cylindrical process, the upper lip, a kind of proboscis" = prostomium?

[1] As Vejdovsky says (p. 320, 16), "die Kopfhöhle [peristomial cœlom] sowohl von Rhynchelmis als der Lumbriciden weicht also genetisch nicht von Leibeshöhle der nachfolgenden Segmente als. Sie wächst erst nachträglich zum sog. Præstomium aus, welches letztere daher nicht als Kopf, sondern als ein Kopf-fortsatz oder Kopflappen aufzufassen ist. Dafür sprechen zuerst die embryologischen Thatsachen bei Lumbriciden, wo der Mund am vorderen Körperende terminal nach aussen mündet, und erst nachträglich durch den sich verlängernden Kopflappen von der Rückenseite verdeckt wird. Dies allerdings erst sehr spät, nachdem das Kopfganglion längst angelegt ist und sich somit nicht im Praestomium bilden kann, wie unlängst von einer Seite behauptet wurde." With regard to the latter fact, the brain nevertheless arises from the prostomial region, although the prostomium may be retarded in development.

stomium, being neither a reduced nor an incipient segment, is a special region not of segmental value. Further, we may take two views of this question: the first, and the one generally held, is that the prostomium represents the region lying in front of the mouth of the primitive unsegmented ancestor; the second is that the prostomium is a new growth from the first segment, or region surrounding a terminal mouth in the primitive ancestor.[1] According to the first, the prostomium is a region of great morphological and phylogenic importance. According to the second, a more recent addition of relatively little significance. A comparison of the merits of these two views would land us in the midst of theories into which there is no need to enter here; it is sufficient for our present purpose to have shown that the prostomium is not a true segment.

In the Arthropoda we find a region in front of the mouth of varying size, bearing as a rule antennæ and well-developed sense-organs, and containing the brain. A certain number of segments behind bear appendages connected with and modified in relation to the mouth. These, together with the preoral region, constitute the "head." Long ago the evidence of comparative anatomy and embryology convinced naturalists that the head of Arthropods, both in front and behind the mouth, is composed of several metameres, more or less fused together. It is with the preoral region that we are most directly concerned in our comparison with the Annelid.

How do true segments come to lie in a preoral position? is one of the first questions we have to answer. If the first

[1] Such a supposition would lead us, perhaps, to somewhat modify our conception of the peristomium (first segment) as being merely a metamere, since it would have the property of producing an anterior prostomial outgrowth (and brain). It must be remembered, however, that, in the cases of reproduction by fission, other and posterior segments possess the same power. Lankester has assumed that theoretically every segment should develop a prostomium, and is only as it were withheld from this completion of itself by a "longitudinal cohesion or integration." "In most Annulosa this longitudinal cohesion counteracts entirely the opposing tendency to produce a head and to separate" (8).

segment behind the mouth in Arthropods represent the peristomium in Annelids, then those between it and the anterior extremity must be new metameres—a supposition which, if true, would contradict the general law of segmentation and the evidence of ontogeny.[1] Professor Lankester in 1873 argued that these preoral segments must originally have been post-oral, and that they have since moved forwards in front of the mouth—or, in other words, that the mouth has shifted backwards.[2] This fertile suggestion is supported by the facts observed in the ontogeny of Arthropods generally; and even in the Polychæta there is often a tendency for the primitively post-oral segments to shift forwards in front of the mouth, as in many Amphinomids and in Aphrodite. Lankester's explanation has been generally adopted, the only difference of opinion being as to how many of the "head segments" are true metameres, and therefore of post-oral origin.

Of the highest importance in connection with this problem is the study of the structure and development of the brain. It is well known that the Arthropod brain presents the appearance, either in the embryonic or adult state, of being formed of several segments. Here again the suggestion made

[1] Segments develop from before backwards. Although the sequence of the differentiation of the anterior segments of Arthropods may be somewhat obscured by what is almost certainly secondary modification and retardation (cheliceral segment in Arachnids), yet we never find the germ bands, after the first segment has been formed, growing forwards beyond it to give rise to new segments in front.

[2] "The segmentation of the prostomial axis in Arthropoda and some Annelids, which has an appearance of being a zooid segmentation comparable to that of the metastomial axis, on account of the identity in the character of the appendages with those of the metastomial axis, has yet to be explained. It may be suggested that it is due to a distinct breaking up of this axis like the posterior one into zooid segments or zoonites; there is much against this supposition (see 'Trans. Linn. Soc.,' 1869, "On Chætogaster and Æolosoma"). Much more likely, it seems, is the explanation that the oral aperture shifts position, and that the ophthalmic segment alone in Arthropoda represents the prostomium, the antennary and antennular segments being aboriginally metastomial, and only prostomial by later adaptational shifting of the oral aperture" (9).

by Lankester in 1881, that the ganglia of primitively post-oral metameres have shifted forwards, to fuse with the primitive Annelidan brain, the archicerebrum, to form a syncerebrum of compound structure, has been amply supported by the facts of comparative anatomy and embryology.[1] But this suggestion must not be pushed too far; not every lobe, not every epidermic invagination or centre of proliferation in the embryo must be taken for a metameric ganglionic mass. We know, as already mentioned, that the unsegmented archicerebrum of Annelids may be much lobed and differentiated, and may even arise from several separate centres in the prostomium itself. An apparent "neuromere" can only be accepted as of metameric value when the interpretation is supported by evidence derived from other parts, such as the mesoblastic somites and the appendages.

Let us now examine the various groups of Arthropods.

The Peripatoida (figs. 5 and 6).

In Peripatus, the most worm-like Arthropod, we find a head bearing a pair of antennæ and eyes, and two pairs of more posterior appendages modified in relation to the mouth—the mandibles and oral papillæ.

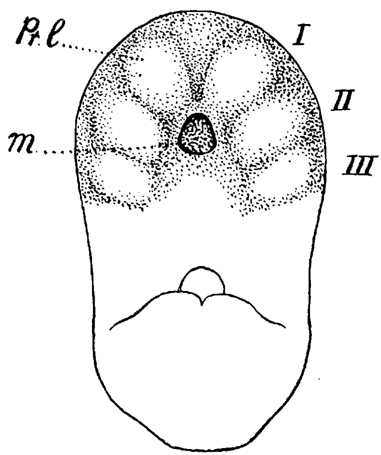
A study of the development has shown that the head of Peripatus is formed of three segments. All observers are agreed that the posterior two, to which the oral papillæ and mandibles belong, are genuine metameres; but some doubt exists as to the nature of the preoral segment bearing the eyes and antennæ, many writers having compared the antennæ to the prostomial tentacles of Annelids. Von Kennel and Sedg-

[1] "In the Chætopoda, the pre-œsophageal ganglion appears always to remain a pure archicerebrum. But in Crustacea (and possibly also all other Arthropoda, though there is a case to be considered for Peripatus and for the Hexapoda and Myriapoda, on the supposition that their antennæ are not the equivalents of Crustacean antennæ, but of the processes of the cephalic lobe of Chætopoda) the pre-œsophageal ganglion is a syncerebrum, consisting of the archicerebrum and of the ganglion masses appropriate to the first and second pair of appendages, which were originally post-oral, but have assumed a preoral position whilst carrying their ganglion masses up to the archicerebrnm to fuse with it."—E. Ray Lankester (10).

wick do not express a definite opinion on this point, but they show most conclusively that in its development the preoral segment resembles a true metamere. It has paired mesoblastic somites, developed post-orally as the first of the series which shift forwards in front of the mouth. As in the posterior segments, each of these somites becomes hollowed out to form the cœlom, from the wall of which is developed a rudimentary "nephridium" (peritoneal funnel). "It presents exactly the same relations as do the nephridia of posterior somites," says Mr. Sedgwick (**15**), and adds, "The first somite, therefore, behaves exactly as do the posterior somites."

As pointed out by Professors Korschelt and Heider, in their excellent text-book of embryology (**7**), it can now hardly be

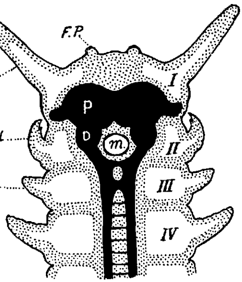
FIG. 5.



Ventral view of an embryo of Peripatus capensis (after Balfour). *Pr. l.* Procephalic lobe. *m.* Mouth.

doubted that the antennæ of Peripatus were primitively post-oral, and that the segment to which they belong is therefore homologous with the first segment or peristomium of Annelids. Heider has further suggested that the two small processes found in front of the head, near the median line in the embryo, represent the prostomial tentacles.

Fig. 6.



Diagrammatic plan of the anterior segments of the Peripatoidea. *Ant.* Antenna. *Md.* Mandible. *O. P.* Oral papilla. P. Protocerebrum. D. Deutocerebrum. Other letters as in Figs. 1 and 2.

The study of the development of the brain in Peripatus confirms the conclusions derived from that of the mesoblastic structures. It is formed by the fusion of two pairs of ganglionic masses derived from the first two segments. Whether the archicerebrum is still to be distinguished, perhaps in the median anterior region, in connection with the pair of small processes mentioned above, is a question which remains to be solved, and requires a renewed investigation.

The first and largest segment of the brain, which supplies the eyes and antennæ, is developed from the ectoderm of the large procephalic lobes (first metamere). The process is aided by the formation of a crescentic pit, a fold of the surface on either side. The second segment of the brain supplying the mandibles is smaller. The oral papillæ are innervated from the ventral nerve-cord.

We conclude, then, that in Peripatus the first segment has become much enlarged in development, and that the mouth has shifted behind it. The first pair of ganglia have attained a great size, and differentiation in connection with their anterior position and relation to the sense-organs. The prostomium is insignificant, and the archicerebrum no longer clearly distinguishable. The antennæ are not prostomial tentacles, but outgrowths of the first metamere.

The Myriapoda.

Unfortunately the development of the Myriapods is very imperfectly known; but, according to the account we have of Julus (Heathcote, 1), it resembles exactly that of Peripatus as regards the segmentation of the head. In the adult there are three pairs of cephalic appendages—the antennæ, the mandibles, and the labial plate (fused maxillæ). The last two pairs belong to undoubted metameres. The first pair, the preoral antennæ, are developed on the large procephalic lobes, which give rise to the main segment of the brain (cerebral grooves are formed here also). As in Peripatus, the antennary segment contains the first pair of mesoblastic somites.

The Hexapoda (figs. 7 and 8).

Four pairs of appendages are borne on the adult insect's head. A study of its development shows that, in reality, it is composed of six regions. Of these the three posterior, belonging to the labium, maxillæ, and mandibles, are universally considered to represent true metameres. The next, counting from behind forwards, the recently discovered premandibular segment (Wheeler, 18), although possessing in the earlier stages a distinct pair of cœlomic somites and cavities, and in some cases rudimentary appendages, becomes reduced, and disappears in the adult. The next anterior segment, bearing the antennæ, was for long considered to be not only preoral in position, but prostomial in origin. Here, again, embryology shows that, like the posterior segments, it has a special pair of mesoblastic somites, with well-developed cœlomic cavities (as a rule).[1] Moreover, since in the early

[1] "The deutocerebrum [antennary segment] in all the Orthoptera which I

stages of development the antennary segment, together with its appendages, is distinctly post-oral in position, most authors are now agreed that it is a true metamere of primitively post-oral origin.

FIG. 7.

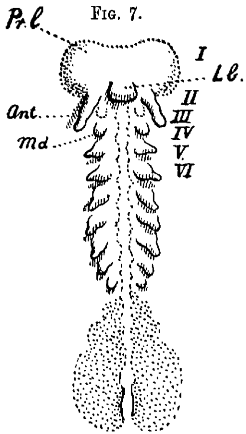


FIG. 8.

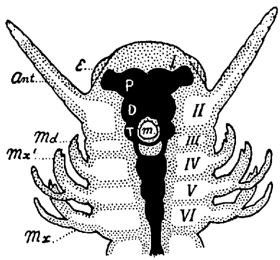


FIG. 7.—Ventral view of an embryo of Anurida maritima (after Wheeler).

FIG. 8.—Diagrammatic plan of the anterior segments of the Hexapoda (the numbering of the segments is doubtful, as explained in the text). *Ant.* Antennæ. *E.* Eye. *Lb.* Labrum. *Md.* Mandible. *Mx.* Maxilla. *Pr. l.* Procephalic lobe. P. Protocerebrum. D. Deutocerebrum. T. Tritocerebrum. Other letters as in Figs. 1 and 2.

We now come to the first serious difficulty in the interpretation of the Arthropod head. In front of the antennary segment, in the embryo Hexapod, extend the large procephalic

have examined is provided with a pair of true mesodermic somites and with a pair of appendages, the antennæ. Each mesodermic somite sends a hollow diverticulum into an antenna."—Wheeler (18).

"Das Cœlomsäckchenpaar des Antennensegments wor bei den von mir untersuchten Embryonen stets in typischer Weise ausgebildet."—R. Heymons (3).

lobes, from which region are developed the anterior segment of the brain, the optic ganglia, and the eyes. Three views may be maintained with regard to the homology of the procephalic lobes: (1) they represent the prostomium of Annelids; (2) they are merely the specialised anterior region of the antennary segment, due to its secondary subdivision; (3) they represent a true metamere, and the first.

In answer to the first suggestion, it may be said that they would be a strangely large rudiment (anlage) for a prostomium;[1] that they are differentiated before the posterior segments; that, although in the Insecta no special cœlomic cavities have been found as yet to develop in this region, they are known to occur in the similar procephalic lobes of some Myriapods and Arachnids; that in their development they strikingly resemble in general shape, position, and in their markedly bilobed character the first segment of Peripatus (antennary); and finally, that they give rise to the same and largest segment of the brain, which includes the optic centres.

The same arguments may be used to refute the second view, though perhaps not quite so convincingly. On the other hand, it must be remembered that embryologists are all agreed in considering the antennary segment of insects as complete in itself, and therefore as not including the procephalic lobes.

The third view, that the lobes represent the first metamere, remains as the most probable. It has recently been held, if I understand him rightly, by Heymons (3).

Viallanes[2] has shown, by his very careful researches on the structure of the adult brain (17), that it consists in insects of three segments. This conclusion is thoroughly supported by embryological evidence. The first or protocerebrum, includ-

[1] The procephalic lobes are also distinctly paired. The rudiment of an Annelid prostomium is unpaired (except Rhynchelmis, Vejdovsky).

[2] Although Viallanes speaks of these segments as belonging to three "zoonites," he draws a distinction between the first as preoral, and the second and third as originally post-oral. Such a view is difficult to reconcile with what we know of Peripatus.

ing the optic centres, corresponds to the first segment in Peripatus. The second or deutocerebrum, supplying the antennæ, corresponds to the mandibular segment; whilst the third, or tritocerebrum, represents the segment in Peripatus which supplies the oral papillæ.

It would appear, then, that in the Hexapoda the prostomium and archicerebrum have not been plainly distinguished;[1] that the large ophthalmic segment represents the primitive peristomium, or first metamere, which has shifted in front of the mouth together with the antennary or second metamere.

The Arachnida (figs. 9 and 10).

In the Arachnids the head appears to be formed of two segments—the anterior represented by the procephalic lobes in the embryo, and the posterior by the segment bearing the cheliceræ. The syncerebrum is formed by ganglionic masses from these two regions.

Concerning the metameric nature of the cheliceral segment there can be no doubt. It is primitively distinctly post-oral in position, and contains a pair of mesoblastic somites with cœlomic cavities extending into the appendages. These are innervated by a pair of primitively ventral post-oral ganglia, which subsequently move forward and dorsally to form the second and posterior segment of the syncerebrum.

The procephalic lobes, on the other hand, offer almost the same difficulties of interpretation as in Hexapoda. As a rule, they are separated from the cheliceral segment only after the appearance of several more posterior segments. No distinct appendages are produced. This large "procephalic" region,

[1] Mr. Wheeler says "it is extremely improbable that so highly important a structure as the Annelid brain should have completely disappeared in the Arthropods" (18). This no doubt is quite true; yet it must not be taken for granted that in the remote Annelidan ancestor of the Arthropoda the brain was as important and fully differentiated an organ as in certain modern Polychætes; and anyhow it must be admitted as a fact that some of the functions of such an archicerebrum have come to be shared, if not usurped, by the ganglia of posterior metameres.

which in certain forms occupies a peristomial position in the embryo, bears the same relation to the brain as the first seg-

FIG. 9.

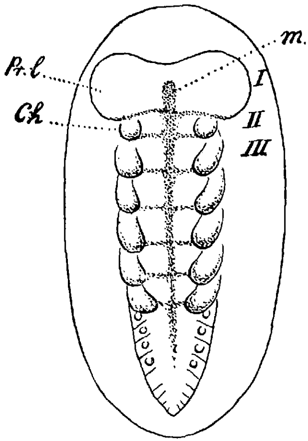


FIG. 10.

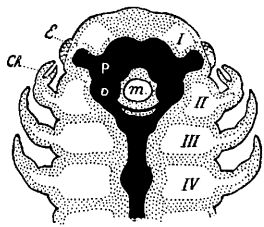


FIG. 9.—Ventral view of an embryo of Agelena labyrinthica (after Balfour).

FIG. 10.—Diagrammatic plan of the anterior segments of the Arachnida. *Ch.* Chelicera. *E.* Eye. *Pr. l.* Procephalic lobe. P. Protocerebrum. D. Deutocerebrum. Other letters as in Figs. 1 and 2.

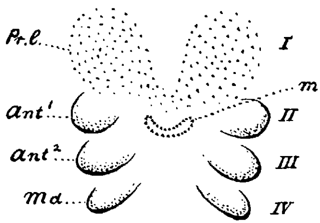
ment in Peripatus and insects, giving rise to the large protocerebrum including the optic centres. Mesoblastic somites are present, containing in scorpions and spiders (according to Balfour, Metschnikoff, Kowalevsky and Schulgin, Laurie, and Schimkewitsch) a pair of distinct cœlomic cavities. In Limulus and some scorpions (according to Kingsley, Kishinouie, and Brauer) the cœlom of the procephalic region is formed by the forward extension of the cavities of the cheliceral segment. It is unnecessary to repeat the arguments concerning the homology of the procephalic lobes already used in the case of the Hexapoda; one may add that the presence of a cœlomic cavity in the case of the Arachnida somewhat strengthens the evidence in favour of this region representing the primitive peristomial metamere.

The Crustacea (figs. 11 and 12).

The Crustacean head is composed of six regions. The last three are obviously true metameres, post-oral in position, and innervated from ganglia on the ventral nerve-cord; they bear the two pairs of maxillæ and the mandibles.

The next two regions, as we go forwards, are preoral in position, carrying the two pairs of antennæ, but are now almost universally considered to be metameres of primitively post-oral origin which have shifted in front of the mouth. In the lower Crustacea (Apus, &c.) the second pair of an-

FIG. 11.



Ventral view of an embryo of Astacus fluviatilis (after Reichenbach). *Ant.*¹ and *Ant.*² First and second antennæ. *Md.* Mandibles. *Pr. l.* Procephalic lobe.

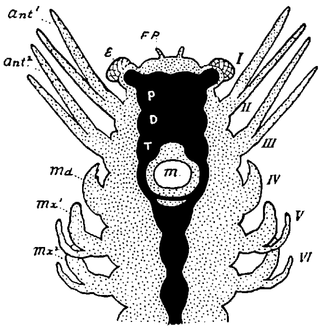
tennæ are still innervated from the œsophageal commissures (Pelseneer, **13**). In the higher forms the brain supplies both pairs. These two segments assume the preoral position during development, and their ganglia fuse with those of the most anterior region to form the deuto- and trito-cerebrum of the adult brain.

There remains in front the sixth region, which bears the large paired compound eyes. Ever since Milne-Edwards, in

1834, put forth the view that the stalked eyes of Crustacea represented a pair of metameric appendages, observers have been divided into two camps; some supporting this theory (Huxley, Reichenbach, Nussbaum, &c.), others opposing it. The latter maintain that the eyes, whether stalked or sessile, are merely prostomial sense-organs.

In the embryo we find, in this region, two large procephalic lobes from which are developed the eyes and optic centres and the anterior segment of the brain, corresponding to the pro-

FIG. 12.



Diagrammatic plan of the anterior segments of the Crustacea. *Ant.*[1] and *Ant.*[2] First and second antennæ. *E.* Eye. *F. P.* Frontal process. *Md.* Mandible. *Mx.*[1] and *Mx.*[2] First and second maxillæ. *Pr. l.* Procephalic lobe. P. Protocerebrum. D. Deutocerebrum. T. Tritocerebrum. Other letters as in Figs. 1 and 2.

tocerebrum of other Arthropods (Viallanes). Unfortunately, no definite evidence has been obtained with regard to the metameric nature of this region from the study of the mesoblast, since no distinct somites or cœlomic cavities have been traced with certainty in the anterior segments of most Crustacea. It is evident, however, that although the procephalic lobes may represent the first metamere, the stalked eyes need not necessarily be its true metameric appendages. Nevertheless some evidence for this interpretation is afforded by the cases brought forward by A. Milne-Edwards of a Palinurus (12), and by Hofer (4) of an Astacus, in which the eye-stalk on one side was produced into a jointed flagellum; also by some recent experiments of Dr. Herbst, who, having cut off the eyes of Palæmon, finds that jointed antenna-like appendages are regenerated in their stead (2).

The prostomium itself may have to be sought for in the median anterior region in front of the procephalic lobes. It has been suggested that the median eye and little frontal processes of the Nauplius larva represent prostomial sense-organs, and it is possible that the anterior region of the brain in connection with these represents the archicerebrum.

In the foregoing pages the view that the procephalic lobes are homologous throughout the Arthropoda, and represent the peristomial segment of Annelids, has been consistently favoured, not because this interpretation can be considered as firmly established, but from a conviction that the best way of presenting the problem is to uphold a definite theory. Thus both the weakness and the strength of the position become clearer. It is quite plain, however, that much evidence is still needed bearing especially on the presence of distinct mesoblastic somites in the procephalic region in several groups, and on the possibility of distinguishing the true prostomium and archicerebrum in the Arthropoda.

ANNELIDA.	PERIPATOIDEA.	INSECTA.	ARACHNIDA.	CRUSTACEA.
Prostomium with or without tentacles. Archicerebrum.	? Frontal processes?	?	?	? Frontal processes?
Segment 1 or Peristomium.	Procephalic lobes, antennæ, protocerebrum.	Procephalic lobes, protocerebrum.	Procephalic lobes, protocerebrum.	Procephalic lobes, protocerebrum.
Segment 2.	Mandibles, deutocerebrum.	Antennæ, deutocerebrum.	Cheliceræ, deutocerebrum.	First antennæ, deutocerebrum.
Segment 3.	Oral papilla.	Rudimentary appendage, tritocerebrum.	Trunk segment.	Second antennæ, tritocerebrum.
Segment 4.	Trunk segment.	Mandibles.	Ditto.	Mandibles.
Segment 5.	Ditto.	First maxillæ.	Ditto.	First maxillæ.
Segment 6.	Ditto.	Second maxillæ.	Ditto.	Second maxillæ.

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