

THE PROBLEM OF THE VERTEBRATE HEAD.

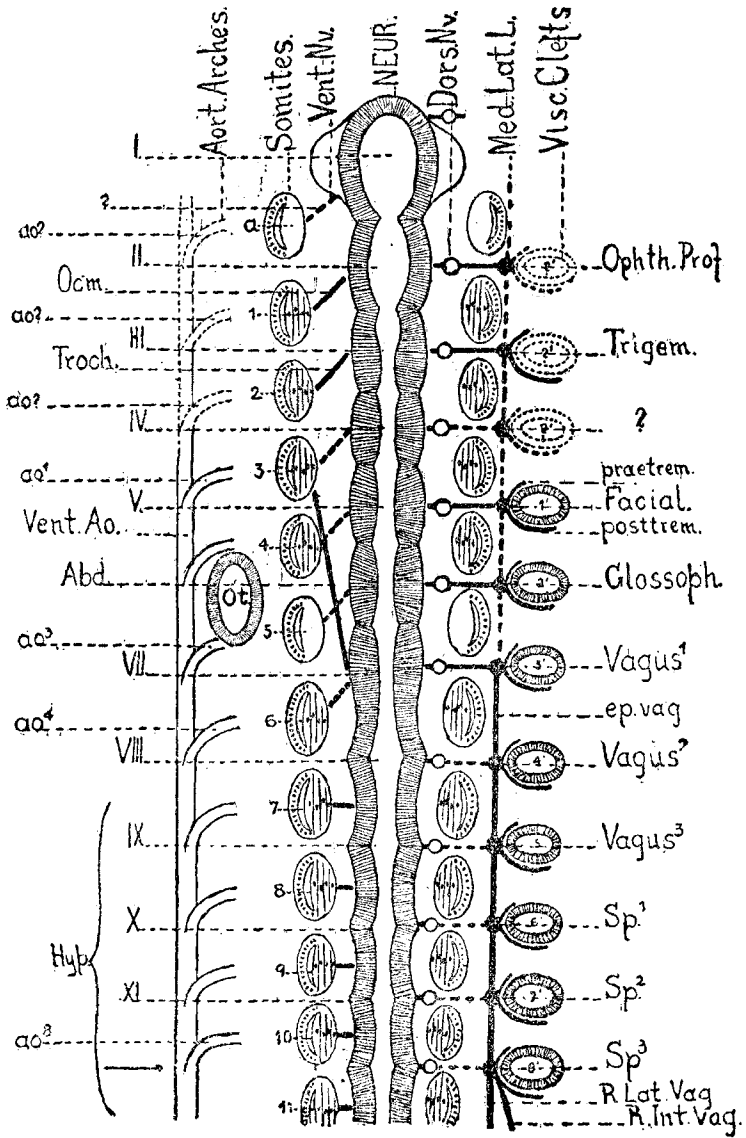
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Two of the most important morphological conceptions of the nineteenth century are attributed to the poet Goethe—one, that a flower is a modified branch and its organs metamorphosed leaves—the other, that the head and trunk of vertebrated animals were once composed of like segments which by slow adaptive change have become to a considerable degree unlike. After a century of probation no morphologist of today questions the truth of the former conception. The truth of the latter, however, is still debated and the attempt to compare a head segment with a trunk segment in vertebrates constitutes what is now known as the "head problem."

Since neither head nor trunk can be regarded as *primitive* in their present condition, probably a more correct statement of the problem would be as follows; Was the vertebrate head like the trunk, primitively segmented; if so, were these segments serially homologous with those of the trunk; and how many have entered into the composition of the head? So far as I am aware, no one doubts that the vertebrate head is segmented. That it is so, is indeed clearly evinced by such serially repeated organs as neuromeres or segments of the central nervous system, nerves both dorsal and ventral, somites, visceral clefts, visceral arches and aortic arches.

But while the great majority of the morphologists who have expressed an opinion on the question have concluded that Goethe's conception is true and that head segments are serially homologous with trunk segments, a few have been led during recent years to regard the head, or at least its anterior or preotic part, as one *sui generis*. This conclusion has been reached partly by the recognition of the considerable differences between head and trunk metameres and the organs of which they are composed—differences which seem too great to be merely differences in the degree of specialization and partly also by the



conflicting evidence and conclusions, both as to composition and number of cephalic segments, of those who have advocated the prevalent morphological opinion. Of the differences stated by them I shall speak later. The confusion in, and, as must be admitted, generally unsatisfactory condition of the literature bearing on the head problem, is in my judgment attributable in great part to the fact that the observations of investigators have been confined often to a single species, often to a single organ system, while their conclusions deduced from such limited observations have applied to the *phylogenesis of the entire vertebrate head!* That such methods are inadequate for the solution of such a difficult problem seems in view of the many divergent opinions too obvious to need insistence here, and I venture to predict that some time, if not now, it will seem strange that a morphologist should assume, or seek to demonstrate that the serial parts of any single organ system, whether neuromeres, or nerves, or somites or visceral arches, or epibranchial "sense organs," or what not, are the *essential* criteria of head segments. In my opinion, *phylogenetic conclusions concerning the metamerism of the head based upon the study of a single animal or a single organ system need to be "controlled" and confirmed by the study of other organ systems in the same animal.* The solution of no problem requires a broader knowledge of comparative embryological and anatomical facts.

Fig. 1. Diagrammatic representation of the cephalic metameres in Selachii, showing the component organ systems and their relations to one another.

I-XI, cephalic neuromeres (segments of the central nervous system); *a*, Miss Platt's "anterior" somite; *1-12*, van Wijhe's first to twelfth somites; *1-8*, first to eighth visceral clefts; *abd.*, abducens; *ao¹⁻⁸*, aortic arches, first to eighth; *ch.*, chorda; *dors. nv.*, dorsal nerve; *ep. vag.*, epibranchial portion of vagus nerve; *fac.*, facialis nerve; *glossoph. (gls.)*, glossopharyngeus nerve; *hyp.*, hypophysis; *m.*, mouth; *med. lat l.*, mediolateral line; *neur. (n.)*, neuromere; *ocm.*, oculomotorius; *olf.*, olfactorius; *ophth. prof. (pl.)*, ophthalmicus profundus nerve; *ot.*, otic capsule (ear); *postrem.*, postretrematic branch; *praetrem.*, praetrematic branch; *r. lat. vag.*, ramus lateralis vagi; *r. int. vag.*, ramus intestinalis vagi; *som.*, somites (van Wijhe's): *sp.^{1,3}*, spinal ganglia first to third; *trach.*, trochlearis; *vent. ao*, ventral aorta; *vent. nv.*, ventral nerve; *visc. clefts*, visceral clefts; *vag.^{1,3}*, vagus ganglia first to third (dorso-lateral series); *visc.³* third visceral arch. The arrow marks the posterior termination of the cranium in *Squalus*. All neuromeres anterior to this point are included in the cranium.

Holding this view, I have recently¹ made an attempt to solve the head problem, and while my observations were made primarily upon the nervous system in Selachian embryos, my theoretical conclusions have been controlled by the study of the actual relations of other organ systems and also by the study of embryos of all other classes of vertebrates except Reptiles. Whether or not I have come nearer a solution of the head problem than have many of my predecessors, depends, I am convinced, on whether or not I have adhered with greater fidelity than they to the principle above enunciated. I regard my results as in great part a confirmation of those of van Wijhe ('82) and valuable as such.

First, as regards the *nature* of cephalic metameres, I conclude with the majority of investigators that they are serially homologous with trunk metameres, although the homology is today but partial. To my mind, the differences which have been considered as objections to this view by certain morphologists, such for example as the fact that (*a*) visceral elefts and arches are confined to the head region (Gegenbaur); that (*b*) excretory organs are confined to the trunk region; that (*c*) there are no somites in the head, at least in its pre-otic portion, (Kastschenko, Rabl, Froriep); that cephalic nerves and spinal nerves cannot be compared by reason of the fact that (*d*) cephalic dorsal nerves receive cellular material from the skin, while spinal dorsal nerves do not; that (*e*) cephalic dorsal nerves are mixed, while spinal dorsal nerves are sensor in function; that (*f*) cephalic dorsal nerves extend lateral, and spinal dorsal nerves median, to the somites; that (*g*)—at least some—cephalic dorsal nerves have component sensor fibers which innervate lateral line organs, while in spinal nerves these are wanting; that (*h*) in one and the same occipital metamere there can be found (1) a cephalic dorsal nerve, (2) a spinal dorsal nerve, and (3) a spinal ventral nerve and that therefore spinal and cephalic

¹ NEAL, H. V., '98. The Segmentation of the Nervous System in *Squalus acanthias*—A contribution to the Morphology of the Vertebrate Head. Bull. Mus. Comp. Zool. Harvard Univ., Vol. 31, No. 7, pp. 145-294, with nine plates.

dorsal nerves cannot be of the same kind; and other less important differences by no means outweigh the evidence of similarity of head and trunk segments.

As a matter of fact some of the differences alleged above do not actually exist. Many, it is noted, apply to the nerves, and these have seemed so great that even Gegenbaur, the early champion of the present morphological conception of the vertebrate head states ('87) that he is no longer able to consider cephalic and spinal nerves as homodynamous. With our present knowledge, however, that in *Amphioxus* two kinds of nerves, viz. dorsal mixed nerves whose motor fibers innervate splanchnic musculature, and ventral motor nerves which innervate somatic musculature, are found in each segment of the body except the first; that in *Craniota* both of these kinds of nerves appear in the head as well as in the trunk; that a pair is to be found in each trunk metamere (in *Petromyzon* unconnected as in *Amphioxus*), and in some head metameres, I am unable to regard the actual differences between cephalic and spinal nerves as fundamental in character.¹

The differences which appear are, in my judgment, to be expected in the case of the nervous organs in such highly differentiated structures as head and trunk. Furthermore, the fact that the bounds of head and trunk in the vertebrate series are not definitely fixed; that they are variable; that there is an unbroken continuity throughout head and trunk of such essential components of metameres as neuromeres, nerves, somites, visceral arches, visceral clefts, and aortic arches, is evidence sufficient to warrant the general belief in the serial homology of the segments in these two regions. So far as I can see, no objections to this view apply to the pre-otic region which are not equally applicable to the post-otic region. If the segments in the one region are serially homologous with trunk metameres, those in the other region are also. I shall be obliged to refer the

¹ The evidence both histological (Lenhossék, Kölliker, Ramón y Cajal) and physiological (Steinach and Wisner) given in the last decade, seems to establish conclusively the fact (rendered *a priori* probable by the evidence from *Amphioxus*) that spinal dorsal nerves are like cephalic dorsal nerves mixed in function.

reader for further grounds for my conclusions concerning the nature of head segments to the more extended paper referred to above.

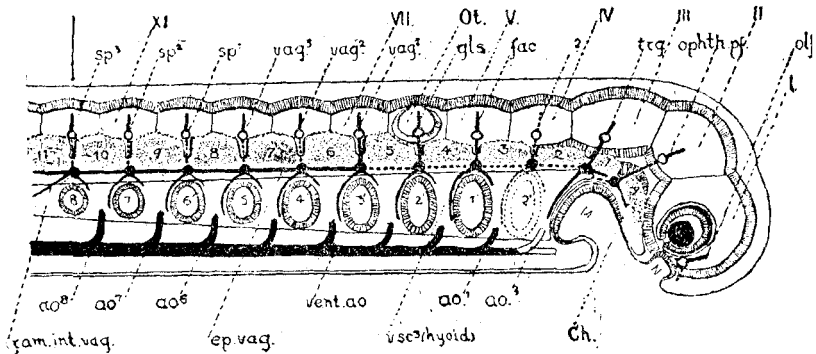


Fig. 2. Diagram of Selachian head, showing the cephalic metameres and their components, lateral aspect, based upon the study of *Squalus acanthias*. Upon the basis of the results of Kupffer, Miss Platt and others a distinction is made in the representation of dorsal nerves between dorso-lateral and medio-lateral (epibranchial) ganglia.

Secondly, as regards *number* and *composition* of cephalic metameres my conclusions have been summarized in Figs. 1 and 2. There are in vertebrates five pre-otic, one otic and (in *Squalus*) five post-otic cephalic metameres. The number of post-otic segments whose vertebral components fuse into the occipital region of the cranium of vertebrates is variable. The estimate of the number of pre-otic segments is based chiefly upon the evidences that in this region of *Squalus* embryos neuromeres and somites *numerically correspond*, and are in some cases connected by motor nerves. For a more extended presentation of this evidence I again refer to the longer paper ('98). Briefly summarized, the composition of cephalic metameres from the first to the last is as follows:

METAMERE I. *Neuromere*, neuromere I (primary forebrain vesicle); *dorsal nerve*, olfactory (motor component lacking—in correlation with the want of splanchnic musculature); *ventral nerve*, absent in correlation with the absence of somatic muscu-

lature ; somite, "anterior" (Miss Platt's); *visceral cleft* and *arch*, hypothetical ; *aortic arch*, hypothetical.

METAMERE II. *Neuromere*, neuromere II (primary mid-brain vesicle) ; *dorsal nerve*, ophthalmicus profundus (motor fibers absent in *Squalus*, but present in some vertebrates); *ventral nerve*, oculomotorius; *somite* van Wijhe's 1st; *visceral arch* and *cleft*, hypothetical ; *aortic arch*, hypothetical.

METAMERE III. *Neuromere*, neuromere III (Hinterhirn) ; *dorsal nerve*, trigeminus ; *ventral nerve*, trochlearis ; *somite*, van Wijhe's 2nd ; *visceral arch*, first (mandibular); *visceral cleft*, (bounding anteriorly the ventral portion of the segment) usurped by mouth ; *aortic arch*, first (mandibular).

METAMERE IV. *Neuromere*, neuromere IV ; *dorsal nerve*, hypothetical (absence correlated with the absence of a visceral arch) ; *somite*, van Wijhe's 3rd ; *ventral nerve*, abducens ; *visceral cleft* and *arch*, hypothetical ; *aortic arch*, hypothetical.

METAMERE V. *Neuromere*, neuromere V ; *dorsal nerve*, facialis (the acusticus a specialized sensor branch); *ventral nerve*, abducens ; *somite*, van Wijhe's 4th (which together with the 3rd forms in *Torpedo* the m. rectus posterior, Sewertzoff—rudimentary in *Squalus*); *visceral cleft*, first (hypobranchial, spiraculum); *visceral arch*, second (hyoid); *aortic arch*, second (hyoid).

METAMERE VI. *Neuromere*, neuromere VI ; *dorsal nerve*, glossopharyngeus ; *ventral nerve*, abducens ; *somite*, van Wijhe's 5th (myotome absent in *Squalus*; forms first myotome of the lateral trunk musculature in *Petromyzon*); *visceral cleft*, 2nd visceral (1st branchial) ; *visceral arch*, third (1st branchial) ; *aortic arch*, third.

METAMERE VII. *Neuromere*, neuromere VII (the last of the neuromeres having a lateral thickening. See Fig. 1); *dorsal nerve*, vagus¹ ; *ventral nerve*, abducens ; *somite*, van Wijhe's 6th (myotome rudimentary in *Squalus*); *visceral cleft*, third (second branchial) ; *visceral arch*, fourth ; *aortic arch*, fourth.

METAMERE VIII. *Neuromere*, neuromere VIII ; *dorsal nerve*, vagus² ; *ventral nerve*, hypoglossus (anterior root, rudi-

mentary); *somite*, van Wijhe's 7th (myotome, first myotome of lateral trunk musculature in *Squalus*); *visceral cleft*, fourth; *visceral arch*, fifth; *aortic arch*, fifth.

METAMERE IX. *Neuromere*, neuromere IX; *dorsal nerve*, rudimentary (unites with vagus in *Squalus*); *ventral nerve*, hypoglossus, second root; *somite*, van Wijhe's 8th (forms first segment of hypoglossus musculature); *visceral cleft*, fifth; *visceral arch*, sixth; *aortic arch*, sixth.

METAMERE X. *Neuromere*, neuromere X; *dorsal nerve*, first spinal (represented by a rudimentary ganglion in *Squalus* embryos); *ventral nerve*, hypoglossus; *visceral cleft*, sixth; *visceral arch*, seventh; *aortic arch*, seventh.

METAMERE XI. *Neuromere*, neuromere XI; *dorsal nerve*, second spinal (rudimentary ganglion in *Squalus* embryos); *ventral nerve*, hypoglossus; *somite*, van Wijhe's 9th; *visceral cleft*, seventh; *visceral arch*, eighth; *aortic arch*, eighth.

LIST OF SOME OF THE MORE IMPORTANT PAPERS BEARING ON THE
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'78. A Monograph on the Development of Elasmobranch Fishes. London, XI + 295 pp. 20 plates.

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'85. The System of Branchial Sense Organs and their Associated Ganglia in Ichthyopsida. A Contribution to the Ancestral History of Vertebrates. *Quart. Jour. Micr. Sci.*, Vol. 26, pp. 95-156, Plates 8-10.

DOHRN, A.

'75. Der Ursprung der Wirbelthiere und das Princip des Functionswechsels. *Genealogische Skizzen*. Leipzig, XV + 87 pp.

FRORIEP, A.

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FUERBRINGER, M.

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HOFFMANN, C. K.

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MARSHALL, A. M.

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PLATT, J. B.

'91. A Contribution to the Morphology of the Vertebrate Head, based on a Study of *Acanthias vulgaris*. Journ. Morph., Vol. 5, pp. 79-112, Pls. 4-6.

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'82. Ueber die Mesodermsegmente und die Entwicklung des Nerven der Selachierkopfes. Nat. Verh. d. K. Akad. Wissensch. Amsterdam, Deel 22, 50 pp., 5 Taf., 1883. Also separate, Amsterdam, 1882, 50 pp., 5 Taf.