Primitive Segmentation of the Vertebrate Brain.

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With Plate XXVIII.

In 1828 Von Baer (26) observed various symmetrical folds in the hind-brain of the Chick, but only recently has their segmental value been appreciated. Much later they were seen by Remak (23) and Dursy (5), the former pointing out their intimate relation to the cranial nerves. In 1875 Dohrn (6) showed the segmental relations of these folds to the mesoblastic somites, and compared them to the segmentation of an insect. In 1876 Foster and Balfour (7), and a year later Mihalkovics (20), inclined to consider them as the purely mechanical results of mesoblastic pressure; but later histological investigation of their structure seems to render such a position untenable. However, Balfour (2) says, in speaking of these constrictions in the hind-brain in the Chick, "The sides become marked by a series of transverse constrictions, dividing it into lobes which are somewhat indefinite in number. The first of these remains permanent, and its roof gives rise to the cerebellum. It is uncertain whether the other constrictions have any morphological importance. More or less similar constrictions are present in Teleostei. In Elasmobranchii the medulla presents on its inner face at a late period a series of lobes corresponding to the roots of the vagus and glosso-pharyngeal nerves, and it is possible that the earlier constrictions may potentially correspond to so many nerve-roots." Quite recently, Béraneck (4, *a*) in Amphibia, and Kupffer (16, *a*) in Teleostean and Cyclostome fishes, have observed and treated these folds as having segmental value, the latter enumerating eight segments or metameres in the hind- and mid-brains, and noting their resemblance to similar structures in the spinal cord. In a later paper Béraneck (4, *b*) gives details of the neuromeres (replis médullaires) in the Chick, assigning to each a segmental value. His observations of the nerve relations to them are substantially those given by Orr (21), except in regard to the fifth, which he considers, as does Miss Platt (22), to be derived from the first and second of the hind brain neuromeres, and the result of two primitively independent nerve trunks. Moreover he does not agree with the later investigators in homologising neuromeres and myelomeres, i. e. similar constrictions in brain and cord. In 1887 Orr (21), while investigating the embryology of the Lizard, figured and described six folds in the hind-brain, five of them of equal size; the sixth, from which the tenth nerve arose, somewhat larger. In describing them he used the name "neuromeres," a word somewhat differently applied by Ahlborn (1). Orr has observed—

(1) That each neuromere is separated from the adjacent one on either side of it by an external dorso-ventral constriction and an internal dorso-ventral ridge, each having between these limits a semicircular or half-oval appearance:

(2) That these constrictions or neuromeres are perfectly regular and opposite on both walls of the brain:

(3) That the elongated cells of which they are composed are situated radially to the inner curved surface of each neuromere, and that their nuclei are generally nearer the outer, approaching the inner surface only toward the apex of the ridge:

(4) That the cells are confined to their respective neuromeres, so that one structure does not insensibly pass into the next succeeding, but is separated from it by a more or less

sharp line of demarcation, along which the cells of both are much crowded together:

(5) That from the crest of each neuromere, i. e. the external convex surface, arises a mass of cells constituting the roots of the cranial nerves proper to that region. From the first the fifth, from the second the sixth, and from the third the seventh and eighth. Opposite to the fourth appears the auditory vesicle. From the fifth neuromere the ninth, and from the sixth (which he observed not so clearly as the others) the tenth nerve arises. Orr observed no neuromeres in the mid-brain, but described it as an unsegmented sweep of brain wall which was nearly equal in extent to three of the hind-brain neuromeres. In the fore-brain he has described two, similar to those in the medulla, save that they give off no nerves. Behind the origin of the tenth nerve he found no constrictions.

I have given these points at length because they formed the incentive and the basis of the work immediately afterward taken up in this direction, and because they resulted from the first definite and systematic investigation of these extraordinary appearances.

In 1888 McClure (19) undertook the investigation of these neuromeres with a view to demonstrating the neuromeric segmentation of the neural tube throughout its whole extent. By sections of early stages of Amphibian, Reptilian, and Avian forms, he corroborated the observations of Orr, except for the origin of the abducens nerve, and added the following points:

(1) That the fore-brain neuromeres conform in every detail of structure with a typical hind brain neuromere:

(2) That the lateral walls of the spinal cord are divided into segments, which, while less distinct, are histogenetically similar to those of the medulla, and, in fact, are continuous with them and the transition gradual. Thus in both regions they must have held similar relations to the mesoblastic somites:

(3) That from the dorsal surface of the segments of the spinal cord, or "myelomeres," as McClure has named them, the roots of the spinal nerves take their origin in the same

manner as that described by Orr for those of the medulla, or encephalomeres:

(4) That all these segmentations, whether giving origin to nerves or not, rapidly and early degenerate.

Since the preparation of this paper one has been published by Miss Platt (22) bearing upon the subject. She has developed the relation of the neuromeres to the protovertebræ, but falls into the error of confounding with the neuromeric segmentation, the so-called vesicular segmentation. She differs from Béraneck, Orr, McClure, and myself as to the relations of the nerves to their corresponding neuromeres, at least in the Chick, deriving them from the constrictions between, and not from the crests of, the neuromeres; and holds that the internal ridge described by Orr is composed of cells which converge to the root of origin of the nerve from that region. Hence she connects the latter with both the neuromeres between which it arises, and upon this ground assumes the individuality of the seventh and eighth nerves.

I cannot agree with Miss Platt upon this point. I have never observed any such conditions even in very early stages of Chick embryos. From the fact that both McClure's observations and my own support the original statement of Orr concerning the point of nerve origin, I find her statements difficult to accept.

It will be seen that these investigations left the primitive condition of the fore-brain very doubtful and that of the mid-brain undetermined. I have attempted by the study of Fish and Amphibian embryos to confirm the points already made and to add some new ones, regarding especially the fore- and mid-brain.

The investigations, of which this paper is a résumé, were undertaken during the winter of 1889–90 in the Morphological Laboratory at Princeton under the direction of Dr. Henry F. Osborn, to whom I wish to express my deep obligation, not only for the kindly interest which enabled me to complete the work, but also for many valuable suggestions. It was intended, by the study of some low form of Ichthyopsida, to determine the total number of segments or neuromeres, and especially to clear up the doubt in which my predecessors have left the mid-brain. The form studied was Gadus morrhua, embryos from six to eleven days' incubation being used, for which I am greatly indebted both to Mr. H. V. Wilson, of the United States Fish Commission Station at Wood's Holl, and to Dr. William Libbey, of Princeton; embryos of Amblystoma punctatum were also used by way of comparison. I greatly regret that my efforts to obtain the embryos of Petromyzon were without success, as my observations are thus limited to Teleostean forms. However, the results obtained from the investigation of young stages of the lamprey will, I hope, form a second part of this paper.

In the early stages of the Cod the small amount of cranial flexure renders a horizontal longitudinal section of the entire neuron possible, and in such sections the walls of the brain are closely approximated, there being no proper lumen anterior to the fourth ventricle, its course and extent being indicated merely by the cell nuclei. The brain in section through the ventral portion, i. e. below the forming cerebral hemispheres and cerebellum, shows a perfectly straight and narrow tube, the walls of which are in apposition but not fused, as the line of their demarcation is perfectly apparent. In the earliest stages examined (about six days) the optic diverticula were well formed, as was also the auditory pit. The side walls of the fore- and mid-brain regions, however, were perfectly regular in extent, and showed no traces of neuromeric segmentation (see fig. 1). This I found to be true of all stages under ten days' incubation, at least as far as the fore- and mid-brain regions are concerned, certain of the sections showing some of the characteristic hind-brain neuromeres. This fact is difficult to explain if, as seems probable, these segmentations are the remains, in part atavistic, of a primitive condition, on any other ground than that of the gradual abortion and disappearance of these structures. McClure has referred to the degeneration of the neuromeres, and it seems to me not unreasonable to conjecture that these constrictions, being essentially primitive and in a state of degeneration, have gradually been more and more crowded out by the specialising brain development, and hence appear at a much later period in the ontogeny than would be expected. However that may be, their tardy appearance is a strong proof of their intimate relation to the brain itself, and affords a striking refutation of one hypothesis which has been suggested, viz. that they are the mechanical results of mesoblastic pressure. Moreover, as Miss Platt has pointed out in her recent paper, the neuromeres often appear before the corresponding proto-vertebræ, and consequently must be independent of any formative influence of the latter.

In sections of about ten days' incubation the eyes are most prominent, appearing abnormally large and apparently in advance of the other parts in development (see fig. 2). Cranial flexure is more marked, and renders section of the entire brain area impossible. However, a series taken at a slight angle from the horizontal shows the ventral portion of the brain to be a simple tube, the walls of which are of uniform thickness and separated by a considerable lumen. In embryos of this age the neuromeric constrictions seem first to become prominent, though I find them also in stages about twenty-four hours younger.

Fore-brain.

As it was my object to study the mid-brain, almost all my sections were made with reference to that region. At first I had some difficulty in satisfying myself of its extent and location, the eyes being so large relatively that they were of no service as guides to this region. Later the determination of the anterior extremity of the medulla and the posterior commissure perfectly defined its extent. The Cod brain is a long narrow area made up of closely placed small cells, round or spindle-shaped, with a clear undifferentiated border—the forming white brain substance. A short distance behind the axis of the eyes it is crossed by a broad band of white fibres, which, except for a few scattered cells, are continuous with the outer white border (see fig. 2, *p.c.*). This I consider the posterior commissure, and that it defines the backward limit of the primitive fore-brain. This area has a peculiar club-shaped or trefoil appearance, and nothing can be seen of the brain cavity or of the canalis centralis, which appears as a faint line, except where the drawing away of the brain walls, to accommodate the budding out of the optic vesicles, forms an irregular lozenge-shaped opening into the cavity of the third ventricle (fig. 2, *op. lu.*). Directly in front of the eyes, and in apposition with the anterior extremity of the thalamencephalon, lie the olfactory vesicles (figs. 2 and 3, *ol. v.*). These I find connected with the brain by a short thick mass of cells on either side, the olfactory nerves, which even in the late stages seem to have no connection with the prosencephalon, so that for the Cod I am able to confirm the observations of Marshall (17, *c*) in regard to this nerve in other forms. While I can affirm nothing as to the persistence of the neural ridge to the forward extremity of the fore-brain, all my sections, even the earliest stages, show the olfactory pits lying on either side, and slightly in front of the fore-brain, and there is in no section the slightest trace of an olfactory lobe. The nerves themselves in relation and histological structure agree closely with the other cranial nerves, except that so far as I am able to observe they are developed somewhat in advance of them. My sections being longitudinal I am not able to state with certainty their precise point of origin, but I can see no reason to doubt that it is at the anterior extremity of the fore-brain. They certainly pass downward and outward and at right angles to the longitudinal axis of the head—the characteristic course, according to Marshall, of a segmental nerve. They consist of rounded or oval cells with a very few nerve-fibres. Many earlier stages show a distinct proliferation of the cells into the white substance on either side, behind and above the position occupied by the developing nerve, which seems to support Marshall's idea that these nerves have been shifted downward and forward from their original point of origin. The region of brain-wall giving rise to them shows markedly the characteristics of a true neuromere as determined by Orr, and is, I think, the first or olfactory neuromere, as from its crest occurs the proliferation of cells already mentioned. I cannot be certain in regard to this point, as lack of early stages renders accurate determination of the boundaries of the medullary plate impossible, and differentiation between primary and secondary fore-brain extremely difficult. The point is an important one, and deserves further careful investigation.

Immediately back of what, for convenience, I have termed the first neuromere, and in a line with the forward portion of the orbit, the brain-wall on either side begins to bulge out into broad, somewhat bluntly rounded diverticula (fig. 3, *op. lu.*). These are the remnants of the optic vesicles, the distal portions having been constricted off to form the second nerves. Now, while none of my Cod sections give any reliable evidence of a neuromere at this point, I will show that in Amblystoma there is certainly a second neuromere, and that the optic diverticula hold a curiously significant and close relation to it. Behind the optic vesicles the brain assumes its narrow and uniform tract-like appearance (fig. 3). The closely compacted oval cells show little or no lumen, and are enclosed on either side by a narrow border of white cortical matter (figs. 2 and 3, *cm.*). At a point somewhat behind a line drawn through the axis of the eyes, these borders join across the brain by a narrow band of white fibres—the posterior commissure,—thus marking the junction of the fore- and mid-brain. The distance from the posterior commissure to the termination of the second neuromere is about one third the entire neural length from before backward to this point. It is not possible in this space to observe any nerve or any proliferation of cells, however slight, neither can the cells of the brain-walls be said to have any radial arrangement. However, the condition of my material is quite unsatisfactory, permitting no clear observation of cell boundaries; and from the fact that there is just sufficient room at this point for another neuromere, and that in Amblystoma I have been able more satisfactorily to prove its existence, I have called this the third neuromere, thus making the fore-brain contain three neuromeres (see figs. 6 and 7, *n*. 3). I think that this conclusion is strengthened by the fact that both Orr and McClure assigned to the fore- and mid-brain together five neuromeres, though they did not definitely determine the number composing each; and I feel sure that investigation will confirm my observations on this point.

Mid-brain.

Orr has stated that this region of the brain appears equal in length to two hind brain neuromeres. McClure has made it even longer; but I think he is mistaken in assigning to it, as he does, though on purely speculative grounds, a third neuromere. I think it most probable that accurate measurements would make it slightly longer than Orr has estimated it; for while I find it contains but two neuromeres, I have also found that the segments increase in length toward the fore-brain, those of the spinal cord, the myelomeres, being uniform in size, but smaller than the encephalomeres, the largest of which is the first, or olfactory. This fact may be accounted for perhaps on phyletic grounds by the rapid development of the forward portion of the brain. Sections of Cod of about eleven or twelve days, the plane of section having reached almost to the floor of the canalis centralis, exhibit a region extending from the posterior commissure to a point some little distance behind the eyes (see fig. 3). Within these limits there appear two well-marked convolutions of the brain-wall. Owing to the cranial flexure at this stage it is difficult to obtain true longitudinal sections, but by comparison with those of younger stages I have fairly well identified this region as the mid-brain. The constrictions are slightly smaller than those of the fore-brain, and rather more semicircular in shape. The characteristic radial arrangement of cells is present, but I have not been able to satisfy myself with regard to their relation to nerves. The first one, at a low level, seems to give origin to some fibres which may correspond to the third nerve; from the second I have observed no nerve originating. I am convinced, however, that an osmic acid, or some other more distinctive paeparation, would show each of these neuromeres to be connected with a nerve-root. In regard to the segmental value of the two nerves of this region Gaskell (9) has said, "Both these nerves possess within themselves structures which appear to me to have been originally the nerve-cells and nerve-fibres corresponding to the cells and nerve-fibres of the stationary ganglion on the posterior root of a spinal nerve; so that in the possession of afferent fibres with a stationary ganglion, as well as in the possession of efferent fibres, these two nerves conform each to the type of a segmental nerve." Kupffer, in a recent paper (16, *b*), speaks of a short fibrillar cord which springs from the ventral aspect of the mid-brain; also of a cord springing dorsally from the mid-brain, of the position of which as an eye muscle-nerve he is in doubt. Should it prove to be constant he would assign it to the branchial system, thus establishing its primitive character. The existence of such nerve-elements in connection with what must now be granted to be segmental structures seems at last to define the position of these nerves, in explanation of which so many different opinions have been held.

The results obtained from the preparations of Amblystoma are offered mainly in confirmation of those already stated. They are more satisfactory as regards the enumeration and location of neuromeres, less so as to the nerve origins, the stages being so young that the latter are indefinite, and their determination much obstructed by the abundance of yolk spherules. While it has been said that the neuromeric segmentation seems to be retarded, this must be understood as being only relatively true, and, as degeneration of the segments begins with the most anterior, early stages were necessary. The figures show a series taken as nearly as possible in a horizontal plane through the mid-brain shortly after the closing in of the medullary folds, the section at the lowest level showing, in slightly oblique section, the fore-brain, the obliquity being due to a slight amount of cranial flexure. Anteriorly is seen the first or olfactory neuromere with the characteristic radial arrangement of cells, which toward the crest become more numerous, more compacted, and larger; while beyond the brain itself the proliferated cells of the first nerve extend down on either side to the already well-formed olfactory pits. The first neuromere finally loses itself posteriorly in a large but gradual inward convexity of the brain wall, which in sections at a lower level may be seen to occlude the lumen, while toward the dorsal surface they fall rapidly away from the lateral walls (figs. 5, 6, 7, and 8, *c. s.*). These are the corpora striata. Immediately behind these the brain-walls sweep outward again to form the well-marked second or optic neuromere. Here there is no evidence of nerve origin; but tracing this region through successive sections from lower to higher levels, it may be seen that the optic diverticula are thrust out immediately dorsal to this segment on either side, and merge insensibly into it below (figs. 5, 6, 7, and 8). This position occupied by the optic diverticula relative to the second neuromere is strangely homologous to that held by nerves of acknowledged segmental character to their respective neuromeres, and seems to me to point to the conclusion that the second pair of nerves, before their great specialisation, may have been perfectly comparable to the other cranial nerves, and were probably in connection with the second neuromere, and are, therefore, deserving of a place in the list of segmental nerves. In speaking of the primitive nerve relations of Ammocetes, Kupffer (**16**, *b*) notes that of the lens of the eye to the ganglionic chain, and remarks that as the auditory organ is related to the principal ganglia, so the eye appears to belong to the epibranchial series. Behind the optic is seen the third neuromere of the fore-brain, in connection with which here, as in the cod, there seems to be no nerve. For this the early stage of the material may perhaps be held to account, at the same time that it affords proof of the fact that the first nerve is much in advance of the others in development. Behind the third neuromere there appears to be a small portion of brain wall, which is either unsegmented or a part of an additional segment; for as the series is traced dorsalwards the fore-brain runs out by very oblique sections separated by a slight interval from oblique sections of the medulla (figs. 5 and 6). The latter gradually lengthens, running into horizontal sections of the mid-brain, the extent of the latter being finally marked out anteriorly by the small round tubular process of the epiphysis, which in Amblystoma is well developed, and has considerable lumen (fig. 9, *ep.*). Within this area—bounded in front by the epiphysis, and behind by a well-marked neuromere, from which a considerable number of cells are proliferated, and which I consider the trigeminis—two fairly well outlined neuromeres may be seen, viz. the oculo-motor and trochlear. From the latter, at a high level, some cells are proliferated, which correspond in position at least to the roots of origin of the sixth nerve (see figs. 9 and 10).

Hind-brain.

McClure's investigations of the hind-brain are so satisfactory that little need be added here. I have been able to verify his results as follows:

(1) In the hind-brain of the Cod six neuromeres are to be seen, corresponding in number to those observed by him in the Lizard and the Chick.

(2) In Amblystoma only five neuromeres are to be found in the hind-brain, the sixth or abducens being absent.

(3) These neuromeres exhibit closely the characteristics already described.

I have not been able to verify McClure's statement that the vagus neuromere greatly exceeds the others in size, and I am inclined to think that the point will not prove constant, but that, as I have said, the neuromeres decrease gradually in size, i. e. in length, from the first to the eleventh inclusive. In this way only have I observed that the trigeminis exceeds the others of the mesencephalon. In Amblystoma, however, in which no abducens neuromere is apparent, the trigeminis is especially prominent, but I think owes its increased length to its fusion with the abducens neuromere, as it is about equal to two hind-brain neuromeres. This variation in the primitive structure of Amblystoma may be explained, as McClure has suggested, by the departure of recent Amphibia from the main Vertebrate line, and the potent retarding and formative influence of a large amount of food yolk; but, as I shall have occasion to note, it seems more rational to ascribe it, on purely phyletic grounds, to variation in position of the sixth nerve itself. In regard to the other segments and nerves of the hind-brain, I have seen nothing which would lead me to doubt the observations already made.

Béraneck has pointed out that certain of the hind-brain segments are in direct relation to certain corresponding nerves. Orr has derived the fifth, sixth (seventh, eighth), ninth, and tenth nerves by ganglionic cell masses from the dorsal surfaces and crests of the fifth, sixth, seventh, ninth, and tenth neuromeres respectively, and the sixth at a later period from the ventral surface of the sixth neuromere of the hind-brain, no nerve being given off from the eighth neuromere proper, the space adjoining it being occupied by the auditory vesicle. McClure has been able to confirm these points, with the exception of the point of origin of the abducens nerve. This he has been unable to locate exactly, but has placed it approximately between the fifth and seventh neuromeres. I have been able to observe in young Amblystoma embryos that the sixth nerve arises by a proliferation of cells from the base of the brain, ventral to and slightly in front of the root of origin of the seventh and eighth, though it has no connection with it (see figs. 11 and 12). In the Cod, which, as I have said, shows six hind-brain neuromeres, I have not been able to satisfy myself in regard to this nerve, but at least am positive that its origin is ventral to and much in front of the seventh and eighth. In other words, I am inclined to think that Orr is correct in placing its origin at the ventral surface of the sixth neuromere in the Lizard, and that it has such origin in all species in which six neuromeres are present in the hind brain, i. e. forms in which the nerve has retained more or less perfectly its primitive character; and that its deviation from this position and gradual shifting backward, together with the coalescence of the fifth and sixth neuromeres, has brought about the condition of affairs which may be observed in Amblystoma. That the absence of the sixth neuromere in Amblystoma is due to the degeneration of the sensory portion of the corresponding nerve I think improbable, even as a matter of conjecture as suggested by McClure, for except for the great deviation of recent Amphibia, which alone seems to be an insufficient one, there appears to be no other valid explanation of the variation. The fact remains that the nerve itself, or its representative, is present in low forms, and that in those much higher in the scale of development both neuromere and nerve have been shown to be present, and to occupy almost, if not exactly, their theoretical position.

McClure's observation in regard to the probable double origin of the seventh and eighth nerves seems to me to be well founded.

The auditory vesicle develops rapidly and comparatively early, invading all the space lateral to the auditory neuromere, and might thus easily have caused the eighth nerve to shift forward and rise secondarily with the root of the seventh, thus accounting for the absence of nerve origin from the eighth neuromere. This theoretical evidence seems to me to be further enforced by the fact that the seventh, in containing both motor and sensory elements, is clearly segmental; while the eighth, in being purely sensory, retains thus so much of its primitive character, and renders probable its posterior origin, its anterior root and its motor fibres having been lost or differentiated.

In regard to the myelomeres and spinal nerves, I have nothing to add to the observations of McClure.

In the preceding pages I have attempted to contribute a few points to the solution of the problem of Vertebrate brain segmentation. The evidence is far from being conclusive, but enough has been done to suggest the results that may finally be attained through this method of investigation. I have endeavoured to make the following points:

(1) That the fore-brain is composed of at least two well-marked neuromeres.

a. Of the existence of the first I am in doubt. The first nerve arises in the same manner, though at an earlier period than the other cranial nerves, thus indicating, however slightly, its segmental character.

b. From the second no nerve springs, but it is directly opposite to the eye, and the optic diverticula spring from its dorsal crest in a manner entirely comparable to the other cranial nerves; thus pointing to the conclusion that, though highly specialised in existing Vertebrates, it was originally not so closely identified with the brain itself, but was homologous with the other segmental nerves.

c. From the third no nerve arises, but I think it probable that still lower forms in earlier stages will show some nerve arising at this point.

(2) That the mid-brain consists of two neuromeres, from which I have every reason to think the third and fourth nerves take origin, and hence deserve to be recognised as segmental structures.

(3) That the hind brain consists of six neuromeres. In regard to this region I think the observations of McClure and Miss Platt are sufficiently satisfactory, except as regards the origin of the sixth nerve and the abducens neuromere. This nerve I have found to occupy its theoretical position when the neuromere exists; when fusion has taken place between the trigeminis and abducens neuromeres, the sixth nerve has been shifted backward toward the seventh and eighth nerves.

It seems reasonably certain that the central nervous system of the primitive Vertebrate form consisted of a series of symmetrical segments, of which those of the neuron held the same relation to the mesoblastic head segments as did those of the cord to the protovertebræ, i. e. were intersomitic; that those of the head, ten or eleven in number, gave origin to their respective nerves precisely as did those of the cord to the spinal nerves; that, in fact, the two regions were perfectly homologous in origin, character, and function. Hence from the primitive neuron, i. e. the first ten or eleven segments, by a direct differentiation and specialisation, the complex region known as the encephalon has been evolved. That striking fact of Vertebrate embryology, viz. the rapid increase of the anterior brain region and its great differentiation, seems to account for the relatively greater size of the fore- and mid-brain segments, and their early degeneration, and for the persistence of those in the hind-brain, which is more primitive in character.

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26. Von Baer.—'Entwickelungsgeschichte der Thiere,' Th. i, p. 64.

27. Waters.—"Additional Points on the Primitive Segmentation of the Vertebrate Brain," 'Zoologischer Anzeiger,' No. 362, 1891.

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EXPLANATION OF PLATE XXVIII,

Illustrating Mr. Bertram H. Waters's paper "On the Primitive Segmentation of the Vertebrate Brain."

Index Letters.

I. n., *II. n.*, *III. n.*, &c. First, second, third, &c., cranial nerves. *ap.* Apex and internal edge of neuromere. *t. c.* Thalamocœle. *m. c.* Mesocœle. *ol. v.* Olfactory vesicle. *op. lu.* Optic lumen. *c. s.* Corpora striata. *au. v.* Auditory vesicle. *c. m.* White cortical substance. *p. c.* Posterior commissure. *spt.* Neural septa. *N.* 1, *N* 2, *N* 3, &c. First, second, third, &c., neuromeres. *epi.* Epiblast. *Ep.* Epiphysis. *4th V.* Fourth ventricle. *F. B.* Fore-brain. *M. B.* Mid-brain. *H. B.* Hind brain.

All figures of sections have been drawn with the Abbey camera lucida and a Zeiss's microscope, a Zeiss's ocular No. 2 and objective A being used.

Fig. 1.—Longitudinal horizontal section of Gadus morrhua, six days' incubation, showing unsegmented fore- and mid-brain region, and hind brain neuromeres.

Fig. 2.—Same at ten days, showing olfactory region and nerve (*ol. v.*), the thalamocœli and region of optic lumen (*op. lu.*), posterior commissure (*p. c.*), the region of the third and fourth neuromeres, and probable place of origin of fourth nerve.

Fig. 3.—Same at ten days, showing olfactory region, and diagrammatically representing the third, fourth, and fifth neuromeres.

Fig. 4.—Same at eight days, showing thalamocœle (*t. c.*), and third, fourth, and fifth neuromeres with radial cell arrangement.

FIG. 5.—Longitudinal horizontal section of Amblystoma punctatum, showing the olfactory region, the supposed olfactory neuromere, and the optic neuromere, with the relation to them respectively of the first nerve and the optic lumen with the cavity of the thalamocœl (*t. c.*).

FIG. 6.—Same at a lower level.

FIG. 7.—Same at a lower level.

FIG. 8.—Same at a lower level.

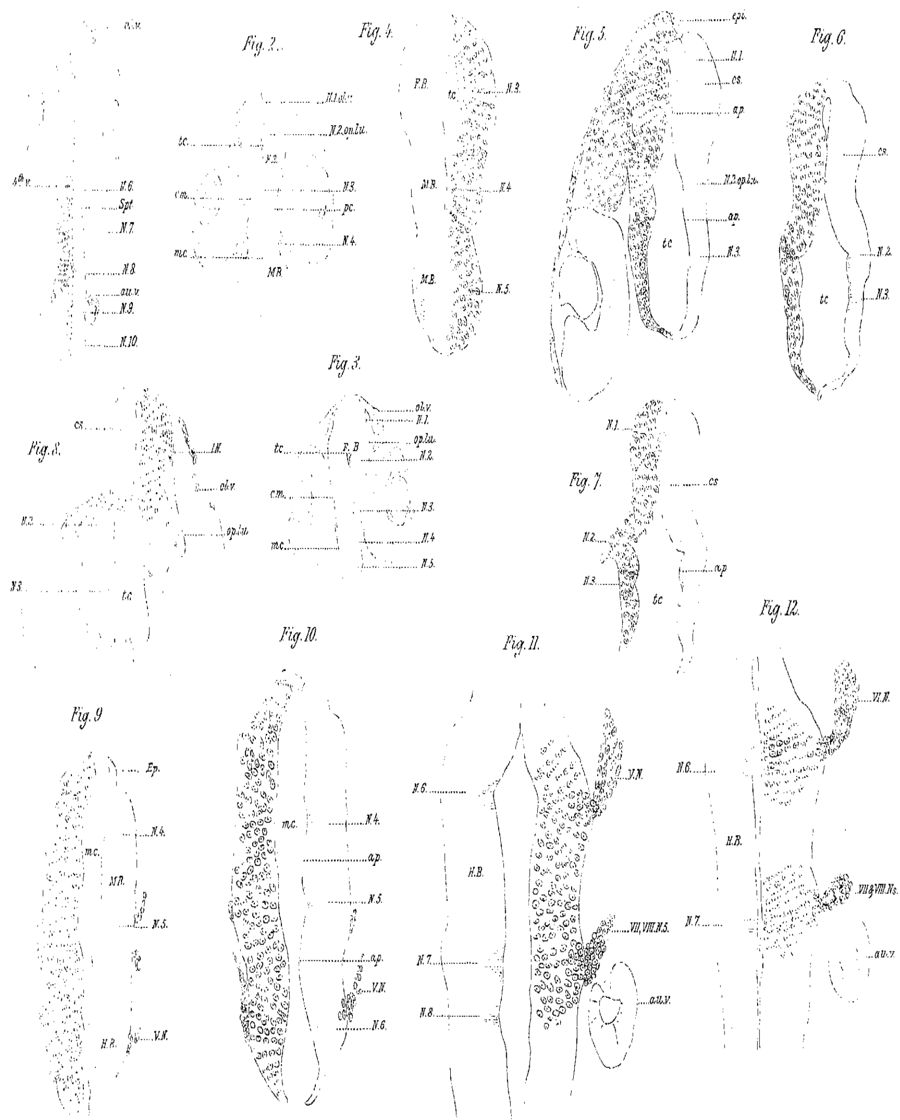
The above series of the same specimen shows the gradual merging of the second neuromere into the optic diverticula (*op. lu.*), and their immediate dorsal situation. The last also shows the first nerve in relation to the most anterior (neuromere?) segment.

FIG. 9.—Same, younger stage, shows the cavity of the epiphysis, the mesocœle (*m. c.*), the fourth and fifth neuromeres, and fifth nerve.

FIG. 10.—Same, shows same points as above, with part of sixth neuromere.

FIG. 11.—Same, older stage, shows the sixth, seventh, and eighth neuromeres; and the fifth, seventh, and eighth nerves and auditory vesicles (*au. v.*).

FIG. 12.—Same specimen at a low level, showing the sixth nerve ventral to the fifth.



Waters del.

F. Huth, Lith. Edin.