2. The Primitive Segmentation of the Vertebrate Brain.

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The investigations, of which the following is a brief review of Part I, were carried on in the Morphological Laboratory of Princeton under the direction of Dr. Henry F. Osborn.

The object of this paper is to show that the symmetrical constrictions or folds found in the lateral walls of the Embryonic brain are remains of the primitive segmentation of the neural tube, in part atavistic, extending into the primary fore brain.

The following types were studied: Amphibia, *Amblystoma punctatum*; Reptilia, *Anolis sagroei*; also chick embryos.

The folds in the side walls of the medulla or hind brain have been frequently noticed and commented upon, but only recently has their importance as segmental structures been recognized. Remak[1] in 1850 observed these folds in the medulla and rightly considered them as structures formed in connection with the »Anlagen« of the cranial nerves. They were observed by von Baer[2] in 1828 and Dursy[3] in 1869; the latter counted six folds in the hind brain. In 1875, Dohrn[4] pointed out the segmental significance of these folds with relation to the mesoblastic somites, and in the joint resemblance to the segmentation of an insect embryo. In 1876, Foster and Balfour[5], and in 1877, Mihalkovics[6] inclined to give a mechanical explanation to these medullary folds. Béraneck[7] quite recently observed 5 folds in the medulla of the Lizard and described and figured their connection with the origin of some of the cranial nerves. Kupffer[8] finds in the

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[1] Untersuchungen über die Entwicklung der Wirbelthiere. Berlin, 1850—1855. § 28.

[2] Entwicklungsgeschichte der Thiere. I. Th. p. 64.

[3] Entwicklungsgeschichte des Kopfes. Tübingen, 1869. Atlas, Taf. III Fig. 15.

[4] Der Ursprung der Wirbelthiere und das Princip des Functionswechsels. Leipzig, 1875. p. 1.

[5] Grundzüge der Entwicklungsgeschichte der Thiere. Aus dem Englischen übersetzt von N. Kleinenberg. Leipzig, 1876.

[6] Entwicklungsgeschichte des Gehirns. Nach Untersuchungen an höheren Wirbelthieren und dem Menschen.

[7] E. Béraneck, Recherches sur le développement des nerfs craniaux chez les Lézards. Recueil Zoologique suisse. T. I. p. 557.

[8] C. Kupffer, Primäre Metamerie des Neuralrohrs der Vertebraten. Sitzung der math.-phys. Classe (Akad. München) vom 5. December 1885.

mid and hind brains of the Trout and Salamander at least 8 segments and, if I understand him correctly, says, these segments not only correspond to the lateral somites (p. 476) but that there is something similar to these brain segments to be observed in the spinal cord. He concludes however by expressing the opinion (p. 477), that the fore brain is not to be reckoned in the segmental region. He does not, in this brief paper, give any of the histological characteristics of the segments. I am indebted to this paper for many bibliographical references.

Gegenbaur[9] has recently expressed the following opinion: »So interessant und so vielversprechend diese Thatsachen sind, so wenig scheinen sie mir gegenwärtig geeignet, zur Beurtheilung der Metamerie des Kopfes selbst als Factoren in Geltung gebracht zu werden. Das wird erst eintreten können, wenn ihre Beziehung zu anderen, den Kopf aufbauenden Organen erkannt ist.« In 1887, Orr[10] described 6 folds in the hind brain of the Lizard, 5 of which of equal size and the 6th, from which the 10th nerve originates, somewhat longer than the others. He described the mid brain as consisting of one fold and in addition to this described two folds in the primitive fore brain. He gave the name »neuromeres« to these folds, a name previously used with a somewhat different significance by Ahlborn[11]. Orr found that the V, VII, VIII, IX and X nerves each originated in connection with a neuromere which degenerated after the nerve was formed. He fully described the structure of a »neuromere«, which I quote, as it bears directly on my own work.

1) »Each neuromere is separated from its neighbors by an externo-dorso-ventral constriction, and opposite to this an interno-ventral ridge, — so that each neuromere (i. e., one lateral half of each), appears as a small arc of a circle.«

»The constrictions are exactly alike on each side of the brain.«

2) »The elongated cells are placed radially to the inner curved surface of the neuromere.«

3) »The nuclei are generally nearer the outer surface and approach the inner surface only towards the apex of the ridge.«

4) »On the line between the apex of the internal ridge and the pit of the external depression, the cells of adjoining neuromeres are

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9 Die Metamerie des Kopfes und die Wirbeltheorie des Kopfskelettes. Morph. Jahrb. 13. Bd. p. 37.

10 A Contribution to the Embryology of the Lizard. Journ. of Morphol. Vol. I. No. 2. Dec. 1887.

11 Über die Segmentation des Wirbelthierkörpers. Göttingen, 4. Januar 1884. p. 312.

crowded together, though the cells of one neuromere do not extend into another neuromere.«

I find that the above structure is characteristic of the embryonic folds in the medulla of the Newt, Chick and Lizard, in every detail.

I now give some of my own observations.

1) I find that the neuromeres of the primary fore brain conform in every respect to the structure described above as characteristic of the hind brain neuromeres. These fore brain neuromeres are prominent in *Amblystoma*, in *Anolis* and in the chick, persisting in the latter till 62 hours, or slightly later.

2) The lateral walls of the spinal cord are divided into neuromeres which while less conspicuous, have all the cellular characteristics seen in the typical neuromeres of the hind brain and in fact are a continuation of the latter. The transition from one into the other is gradual, the folds becoming larger anteriorly.

Now the point I wish to emphasize, is this:

That the structure of these folds in the lateral walls of the Myelon (which I have called »myelomeres«), conforms in every respect to the four characteristics which are found in the hind brain and primitive fore brain folds of all three forms studied, Conversely, that the structure of the neuromeres of the brain (Encephalomeres) conforms in every essential detail to that of the myelomeres, which goes to prove that the Encephalomeres are not only remnants of segments similar to the myelomeres, but that they were originally continuous, and held similar relations to the mesoblastic somites. I also find that the dorsal roots of the spinal nerves take their origin from the apex of their respective myelomeres in exactly the same manner as the nerves of the medulla do from their respective encephalomeres.

The most anterior encephalomere is connected with »or gives rise to« the olfactory nerve — this nerve arising from its neuromere apparently in exactly the same manner as the hind brain nerves do from their neuromeres, that is from the apex of the ridge. The second encephalomere does not give rise to any segmental nerve; immediately opposite this is the optic vesicle. I do not, with Orr, consider the mid brain as equivalent to a single encephalomere, but rather, relying upon the observations of Kupffer, as equivalent to two, which have degenerated in the forms above studied but persist in the Teleosts and probably in other fishes. The total number of encephalomeres was thus probably 10, these corresponding theoretically to the spaces between the 9 mesoblastic head somites observed by van Wijhe, divided as follows:

Fore-brain — 2, and possibly a portion of a third.
Mid-brain — 2 or 3.
Hind-brain — 6 or 5.

As regards the origin of the cranial nerves I can fully confirm the observations of Orr, except as to the origin of the VI from the most anterior neuromere of the hind brain. This point is somewhat obscure.

General conclusions.

I consider that the primitive vertebrate brain consisted of a series of segments, similar to those found in the Embryonic spinal cord, and that the encephalomeres probably held the same relation to the mesoblastic head segments as the myelomeres do to their respective mesomeres, that is they were intersomitic, the centre of each neuromere being opposite the space between two somites and giving off a mixed nerve from the apex.

The region known as the Encephalon is the result of a great differentiation and specialization of the anterior segments of this primitive structure. That differentiation first began and has been the greatest in the most anterior segments, which may account for the greater size of the folds in this region than in the hind brain, which, less differentiation and specialization having taken place, naturally conforms more to the primitive vertebrate type. I am aware that the forms examined are insufficient to enable us to reach any positive conclusion in regard to the number of segments, but I feel confident that the method which I have adopted is the one by which this vexed question of the primitive segmentation of the head region, both of the neural tube and surrounding mesoblast, will be eventually decided.

In conclusion I may say that I feel confident that the full number of primitive encephalomeres will be found in Elasmobranch, Ganoid or Teleost embryos, the investigation of which will form the second part of this paper.

Princeton, June 14th, 1889.

3. Hyalophyllum Hæckel = Copilia Dana ♂.

Von Dr. W. Giesbrecht, Neapel.

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Das Corycaeiden-Genus *Copilia* und mehr noch das Genus *Sapphirinella*, oder wie es später von Hæckel genannt wurde, *Hyalophyllum*, ist aus den anatomischen und histologischen Untersuchungen, welche Forscher wie Leuckart, Hæckel, Gegenbaur, Claus, Grenacher, an diesen ungemein durchsichtigen Thieren anstellten,