

## The Gastrulation Question.

By

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In consequence of the frequent discussions that took place in the course of the summer between Professor Hubrecht and myself concerning the gastrulation of the Vertebrates, he kindly sent me his paper on this subject for inspection before its publication. I would like to add a short explanation to his argumentation.

(1) Hubrecht is undoubtedly justified in demanding that the definition of gastrulation should be so formulated that it can apply to all the Metazoa. I have already acknowledged that this was admissible in my paper: "Ueber die Gastrulation und die Keimblattbildung der Wirbelthiere," p. 1112, with special reference to Lwoff,<sup>1</sup> but then, starting from Amphioxus, I gave a definition which could only apply to Vertebrates (p. 1113). I now hold that this compromise with the current views is no longer justified, and on this point I entirely agree with Hubrecht.

(2) I am, further, in perfect agreement with Hubrecht that in the definition of the phenomenon of gastrulation the pro-

<sup>1</sup> We read there: "Dagegen ist die Definition, dass die Gastrulation ein Vorgang ist, bei dem die dem Darm oder genauer das Darmepithel bildenden Zellen, in das Innere des Eies gelangen nicht so ohne Weiteres abzulehnen. Lwoff der diese Definition vertritt, ist durchaus consequent und da wir bei den Wirbellosen Organismen kennen welche dem Mesoderm und der Chorda der Wirbelthiere ohne weiteres zu vergleichende Bildungen nicht besitzen, ist seine Definition vom Standpunkt der die Gesamtheit der Metazoa betrachtenden Zoologen durchaus berechtigt."

cess of invagination should in no way be involved. My arguments have been ventilated before (l. c.,<sup>1</sup> p. 1109 and 1110), and I had come to the conclusion that in formulating the phenomenon of gastrulation the final result should be kept in view, and the special mode in which it is brought about should not be considered. I would then define as follows: Gastrulation is the process by which the cells of the Metazoan embryo are differentiated into ecto- and entoderm. By entoderm should only be meant those cells that will form the gut.<sup>2</sup>

(3) Hubrecht is, in my opinion, also justified—and it is a logical consequence of the definition—in emphasising that the primitive streak of the Amniota cannot be homologous with the primitive mouth (Urmund) or with the border of the blastopore. The primitive streak is a formation which has close and important connections with the blastopore, but which may not be without reservation homologised with it.

(4) The difference which Hubrecht establishes between cephalogenesis and notogenesis should decidedly be acknowledged. The publications of Kopsch<sup>3</sup> (1896) and Jablonowski<sup>4</sup> (1898), to which I have already referred in a similar sense in 1901 (l. c., p. 1055–1061) should here be kept in view, and it should be specially insisted upon that the formation of the primitive streak stands in intimate relation to the phenomenon of notogenesis, and should thus for this

<sup>1</sup> Keibel, F., "Die Gastrulation und die Keimblattbildung der Wirbelthiere," 'Ergebnisse der Anatomie und Entwicklungsgeschichte,' Bd. x, 1900. Wiesbaden, 1901.

<sup>2</sup> In his article "On Growth-centres in Vertebrate Embryos," 'Anat. Anz.,' T. xxvii, p. 167, Assheton has misunderstood the sense of my definition of gastrulation, as will be found out by what I have said here. I do not think it necessary to treat the question with more detail in this paper.

<sup>3</sup> F. Kopsch, "Experimentelle Untersuchungen über den Keimbaustrand der Salmoniden," 'Verhandl. Anat. Gesellsch.,' 1898.

<sup>4</sup> Jablonowski, J., "Ueber einige Vorgänge in der Entwicklung des Salmonidenembryos nebst Bemerkungen über ihre Bedeutung für die Beurtheilung der Bildung des Wirbelhierkörpers," 'Anat. Anzeiger,' Bd. 14 pp. 532–57.

additional reason not be homologised unreasonably with the blastopore.

(5) I agree with Hübner in this, that I look upon *Amphioxus* as a form which occupies a position far away from the direct line of descent of the Vertebrates. I would, however, for the present, reserve my opinion as to the advisability of any comparison with *Balanoglossus*, notwithstanding the observations which Hübner mentions concerning the formation of the pericardium in embryos of *Tarsius*, *Tupaja* and *Sciurus*.

(6) It is my opinion, as it is Hübner's, that the facts which have up to now come to light concerning the development of Vertebrates can, without difficulty, be brought into line with Hübner's interpretation of the gastrulation process. The way to effect this has already been indicated by the hypothesis of the gastrulation in two phases, simultaneously formulated by Hübner and by myself, which I have later worked out more fully, and which has since been fully accepted also by Oscar Hertwig. However, in future we will only be allowed to call gastrulation that which I have defined as the first phase of gastrulation. The so-called second phase of gastrulation may no longer be looked upon as such. It is the process of formation of notochord and mesoderm, and is peculiar to Vertebrates. It should be borne in mind that in many cases it may often prove difficult to draw a strict line between the two processes, because, as in so many other chapters of embryology, processes may overlap which have phylogenetically been originally separated.

In conclusion, I can say that in all the important points I agree with Hübner. In detail, several points of difference may be noted. Thus I believe that in the gastrulation of Vertebrates a more considerable part is played by invagination than Hübner would be willing to concede. I am also in doubt as yet concerning the comparability between the development of the pericardium in mammals with certain features in *Balanoglossus*. Still, these and other points about which we have not come to an entire agreement while inspect-

ing and discussing the preparations have no direct connection with the chief question concerning the definition of gastrulation and the interpretation of the primitive streak in Amniota. They will be solved in the course of time by special researches, some of them of a more complicated nature.

Here I only wanted to express, and to establish to a certain extent, that it would be well to follow Hubrecht in the definition of gastrulation and that we should introduce certain corresponding alterations in our nomenclature.