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LVIII.—*A Criticism of a Modern Hypothesis of the Transmission of Hereditary Characters.* By R. S. BERGH, of Copenhagen *.

IN the following pages it will be my endeavour to refute an hypothesis which has been disseminated exceedingly widely during the last six or seven years and is often designated as the "Theory of Heredity." I am unfortunately at present unable to advance the subject by new observations of my own, and still less can I introduce a fresh hypothesis by way of compensation. Nevertheless this essay will not be altogether useless, since the hypothesis in question is nowadays supported by the most distinguished investigators and is even represented in text-books as a proved reality, and because the arguments upon which it is based, in spite of the conspicuous importance of the matter, are nowhere discussed in detail from the opposition side. I have for a long time been an opponent of this hypothesis by reason of previous knowledge; thus in my lectures upon general embryology † I have already represented this matter from another point of view, and I took up a position still more decisively opposed to the theory in my addresses upon General Histology ‡. And now an investigator, whose knowledge of the processes of fertilization entitles him to the highest consideration, has this year published a paper § which shows in the clearest manner that the theory alluded to was built upon sand.

The hypothesis which we have to discuss may be summed up in a very few words: it really consists only in the supposition that the nucleus (or, as certain authors imagine, the chromatin itself) is the sole substance which has a part to play in the transmission of hereditary characters, and that consequently the cell-substance, or whatever lies outside the nucleus, is of no importance in the connexion named. Among the very numerous representatives of this doctrine let us here mention only a few of the most important:—O. Hertwig ||

* Translated from the 'Zoologischer Anzeiger,' xv. Jahrg., no. 333 (Feb. 1, 1892), pp. 43-52.

† These appeared in print in February 1887.

‡ In the autumn of 1889; not yet published.

§ H. Fol, "Die Centrenquadrille, eine neue Episode aus der Befruchtungsgeschichte," Anatomischer Anzeiger, 6 Jahrg., 1891, nos. 9, 10.

|| O. Hertwig, "Das Problem der Befruchtung und die Isotropie des Eies, eine Theorie der Vererbung," Jenaische Zeitschr. N. F., 11 Bd., 1884.

(1884), Strasburger* (1884), Weismann† (1885), Kölliker‡ (1885), van Beneden§ (1887), Weigert|| (1887), and Boveri¶ (1889). Kölliker, in his 'Handbuch der Gewebelehre' (6 Aufl., 1889), states the theory with great confidence; and in 1890 Bütschli** also, who formerly held similar views to my own on the question, was converted to it in consequence of an experiment by Boveri, which will be discussed more closely below. Only isolated sceptics declared from time to time in quite general terms that the positive foundations of this hypothesis were too weak; thus this view was already expressed by Hensen†† in the year 1885, and subsequently also by Whitman‡‡ and Waldeyer§§; these remarks, however, were passed over in silence by the representatives of the "Theory." So far as I am aware no one has as yet expressed himself in emphatic opposition to the theory; this is indeed intelligible when we consider how great is the weight of authority by which it is supported.

In the first place let us draw attention to the important difference between the original idea of Nägeli||| upon the subject of idioplasm and nutritive plasm in their relation to heredity and the ordinary theory which is here under discussion. From the fact that spermatozoon and ovum, in spite of their enormous difference in size, take an equal share in the transmission of parental characters, Nägeli concluded that the matters which are of importance for the phenomenon of

* Strasburger, 'Neue Untersuchungen über den Befruchtungsvorgang bei den Phanerogamen als Grundlage für eine Theorie der Zeugung' (Jena, 1884); 'Ueber Kern- und Zelltheilung im Pflanzenreiche, nebst einem Anhang über Befruchtung' (Jena, 1888).

† Weismann, 'Die Kontinuität des Keimplasmas als Grundlage einer Theorie der Vererbung' (Jena, 1885).

‡ Kölliker, "Die Bedeutung der Zellkerne für die Vorgänge der Vererbung," Zeitschr. f. wiss. Zool., 42 Bd. (1885).

§ E. van Beneden and A. Neyt, "Nouvelles recherches sur la fécondation et la division mitotique chez l'*Ascaride mégalocéphale*," Bull. de l'Acad. de Belgique, sér. 3, t. xiv. (1887).

|| Weigert, "Neue Vererbungstheorien," Schmidt's Jahrb. d. gesammten Medicin, 215 Bd. (1887).

¶ Boveri, "Ein geschlechtlich erzeugten Organismus ohne mütterlichen Antheil," Sitzungsber. d. Ges. f. Morphol. u. Physiol. in München, 5 Bd. (1889).

** Bütschli, 'Ueber den Bau der Bakterien u. verw. Organismen' (Heidelberg, 1890).

†† V. Hensen, "Die Grundlagen der Vererbung nach dem gegenwärtigen Wissenskreis," Landwirthsch. Jahrbücher, 14 Bd. (1885).

‡‡ Whitman, "The Seat of Formative and Regenerative Energy," Journal of Morphology, vol. ii. (1888).

§§ Waldeyer, "Ueber Karyokinese und ihre Beziehungen zu den Befruchtungsvorgängen," Arch. f. mikr. Anat., 32 Bd. (1888).

||| Nägeli, 'Mechanisch-physiologische Theorie der Abstammungslehre' (München, 1883).

theredity are present in relatively far greater abundance in the spermatozoon than in the ovum, and that by far the greatest mass of the ovum consists of nutritive plasm. Now the newer doctrine maintains that those matters which are active in heredity are situated in the nucleus alone, and the demonstration of such a transmitter of hereditary characters, the existence of which is not merely inferred, but which is actually visible, has usually been regarded as an important advance. In my opinion such a display of precision should rather be termed a retrocession or deviation; for Nägeli's idea was simply a delicate logical construction which was thoroughly consistent with the facts, and its justice has subsequently been proved most unmistakably by the experiment of Boveri, to which reference shall shortly be made. For the more modern view, on the contrary, not only were the actual starting-points too slight, but many facts made themselves felt against it even at the time; that it is untenable as a theory is moreover demonstrated by the above-mentioned communications from Fol.

I shall now adduce the chief arguments which are brought forward in favour of the doctrine of the seat of the processes of heredity in the nucleus and give an analysis of each.

In the first place it is alleged as the chief reason that the heads of the spermatozoa consist solely or almost solely of nuclear substance, and that this is the only portion of the spermatogenic elements which is active in the process of fertilization. Kölliker goes furthest in this respect, since he declares the spermatozoa of certain animals to be simply nuclei. The majority of investigators do not follow him in this, doubtless partly because we otherwise know nothing of an existence and activity of naked nuclei, and because the greater number of those who have watched the process of spermatogenesis have maintained the cellular nature of the spermatogenic filaments. Moreover, most of the adherents of the theory which is here to be criticized assume the presence of an extremely thin protoplasmic envelope round the nucleus of the spermatozoon, even when such an envelope is hardly to be detected or is absolutely invisible, thus allowing the tail of the spermatogenic filament to rank as protoplasm; and at any rate in the process of fertilization the layer surrounding the nucleus must penetrate with it into the ovum, as has indeed positively been proved to be the case in certain instances. But, in addition to this, the following also must be conceded: the spermatozoa arise from cells through repeated indirect nuclear division (and finally cell-division). Now recent investigations have shown that in indirect nuclear division the so-called polar bodies or "centrosomata" (*Centrosomen*) are of quite general

occurrence, and these have also been proved to appear, at any rate in certain cases, in spermatoblasts *. Let us now consider how long it has taken to increase our knowledge with regard to these bodies; let us further consider that it is now gradually becoming possible to demonstrate the existence of centrosomata in resting-cells also; let us, moreover, remember how greatly reduced in size the nucleus of the spermatozoon usually is, and how difficult it must be to prove the presence of a centrosoma in the spermatozoon should its bulk be proportionately diminished †; finally, let us reflect that a centrosoma and a star-shaped figure appear near the male pronucleus in the ovum. On considering all these points the idea soon suggests itself that this centrosoma originates from the spermatoblast and was present in the spermatozoon also, although it is not always possible to demonstrate its existence. As a matter of fact the origin of the centrosoma from the protoplasm of the spermatozoon was actually maintained by Boveri ‡ also—an hypothesis which Kölliker imagined he could “pass over in silence” (*Gewebelehre*, p. 67). That Boveri’s view nevertheless contained a grain of truth is shown by the investigations of Fol (*cf.* below). It is also possible to arrive at a similar conclusion with reference to the ovum. In the formation of the “directive bodies” very distinct star-shaped figures appear both proximally and distally in the majority of ova, from which we are entitled to infer the existence of centrosomata, the more so since these have been positively demonstrated in certain cases §. Consequently besides the female pronucleus a centrosoma must have remained behind in the ripe ovum.

As another argument in favour of the theory it is usually alleged that the nucleus exercises a leading or directing influence in cell-division; but it is altogether impossible to prove this with reference to the cases which have been most closely investigated. I will merely adduce the following instance:—In the first two segmentation spheres of *Ascaris megalocephala*, with regard to which the excellent investigations of van Beneden and Neyt, as also those of Boveri, are available, the centrosomata divide, even before the nuclear contents have differentiated into loops and the archoplasm (“sphère attrac-

* *E. g.* by O. Hertwig (“Vergleich der Ei- und Samenbildung bei Nematoden,” *Arch. f. mikr. Anat.*, 36 Bd., 1890).

† It has recently been proved by an important paper by Platner that centrosomata actually occur in the spermatozoa of certain mollusks (*Arch. f. mikr. Anat.*, 33 Bd., 1889).

‡ Boveri, ‘Zellen-Studien,’ 2 Heft (Jena, 1888).

§ *E. g.* in the case of *Limax* by E. L. Mark (*Bull. Mus. Comp. Zool. Harvard College*, vol. vi. no. 12, 1881).

tive") has divided, and before the longitudinal fission of the loops has taken place. The case is also precisely similar, according to Kölliker's own statement, in the segmentation spheres of the Axolotl; moreover, according to Rabl*, in the epithelial cells of *Salamandra* the achromatin spindle is distinctly visible, and consequently the centrosomata have in all probability divided, before the occurrence of the cleavage of the chromosomata.

This at once weakens everything else which is asserted by Kölliker and Weigert with respect to the importance of the nuclei for the growth and metabolism of cells. Probably no one will nowadays deny that the nucleus is of eminent importance for the processes of growth, assimilation, and secretion in cells. This, however, proves nothing whatever with regard to the question whether the nucleus is the sole agent in heredity. And with regard to the circumstances which have been rendered applicable by Strasburger from the botanical side, I think that I may here leave these out of consideration, because until recently hardly any attention has been paid to the centrosomata and their rôle in the cells of plants. It was not until the present year that the fact that they are of general occurrence here also was maintained by Guignard †.

We now come to the argument, which nowadays probably ranks as the most important of all, as the actual experimental basis of the theory, in consequence of which even so independent and far-sighted an investigator as Bütschli found himself compelled to alter his views. This is the attempt of Boveri, of which mention has already several times been made, to produce an organism devoid of maternal characters. Boveri found that, in Echinids, fragments of ova devoid of nuclei (obtained by shaking) are capable of being fertilized and developing into larvæ. He further makes use of the experience obtained by O. and R. Hertwig as to hybridization in these animals: on fertilizing the ova of one species (A) with the spermatic fluid of another (B), larvæ are formed which are intermediate in character between the typical larvæ of A and B. Boveri now fertilized an egg-fragment of A, from which the nucleus had been eliminated by the process of shaking, with sperm from B, and it was found that a larva developed which entirely possessed the characters of the

* C. Rabl. "Ueber Zelltheilung," Morphol. Jahrbücher, 10 Bd. (1884).

† Guignard, 'Comptes Rendus,' March 9, 1891. I became acquainted with this paper through a statement by van Tieghem in the 'Journal de Botanique,' 5 année, no. 7, p. 101; for the reference to this I am indebted to my friend Dr. Kolderup-Rosenvinge.

typical larvæ of B, and consequently was "devoid of maternal participation." This experiment of Boveri's is ingeniously carried out and very instructive; but it in no way proves what the author himself* and many other investigators maintain. It demonstrates that the yolk of the ovum (not merely the nutritive, but also the formative yolk—apart from the centrosoma) is of no importance for the transmission of parental characters, and consequently substantiates Nägeli's doctrine of the difference between idioplasmic substances and those consisting of nutritive plasma. But the experiment in no way proves that the nucleus is the sole vehicle of heredity; for in his memoir on this subject Boveri makes no mention of the centrosomata, which is the more astonishing since he belongs to the investigators to whom credit is due for the recognition of the importance of these bodies. But now it is clear, since the division of the cells took place in the normal course, and a typical larva was developed, that centrosomata were present in the fertilized egg-cell and in the segmentation cells. Whence did these arise? It is well known that the centrosomata, in cases where they have been shown to exist in the resting-cell, are always situated in the immediate neighbourhood of the nucleus; and it is therefore in the highest degree probable that the centrosoma of the ovum was eliminated with the nucleus by the process of shaking, and that the new centrosomata, which displayed their activity in the fission of the egg-cell, developed from the spermatozoon which penetrated the latter. Fol's observations in particular, which we shall discuss directly, render this explanation very probable, and indeed they show that it is really the only possible one. In order to prove the theory that the hereditary characters are situated in the nucleus, a corresponding experiment would have to be carried out in the following manner:—The ovum of a species (A) must be deprived of its nucleus, but must retain its centrosoma. Then if, after fertilization with the sperm of another species (B), a larva developed which agreed in all its characters with the typical

* At the commencement of his communication Boveri writes:—"Although the proposition, that the substances of the cell which determine and transmit character are exclusively contained in the nucleus, is expressed in many places no longer merely as a highly probable hypothesis, but already as a fact, it would nevertheless be easy to show that it can neither be proved by the phenomena of the fertilization of the ovum, with which we are acquainted, nor by the experiments which have hitherto been instituted upon the rôle of the nucleus in the Protozoa." And after communicating his experiment he then says:—"Thereby also the proposition, that the nucleus is the sole vehicle of heredity, is proved."

larva of B, I should know of no further objection to raise. This experiment, however, would be difficult to perform. Consequently Boveri's experiment, as it at present stands, proves, as I have already said, only the theory of Nägeli, and not that of Kölliker, Hertwig, and others.

Lastly, I have yet to speak of one or two other experimental investigations—"Attempts at artificial fission and regeneration of Protozoa,"—and to analyse the conclusions which have been deduced from them. It has been shown by very instructive experiments on the part of Nusbaum*, Gruber†, and Balbiani‡, that non-nucleated fragments produced by cutting-up Infusoria, even when they remain alive and capable of movement for some days, are nevertheless unable to feed, increase in size, and regenerate the lost parts, while those fragments which contain a portion of nucleus do this readily. The facts in question are interesting, since they prove that protoplasm is not capable of permanent existence when deprived of its nucleus, just as we are unacquainted with cases in which isolated nuclei are viable. But it is an unjustifiable and illogical conclusion to suppose, as, for instance, Weismann maintains ('Keimplasma,' p. 29), that these experiments show that the nucleus is the sole vehicle of heredity and the sole formative element of the cell—for to say that the nucleus is indispensable for the formative processes is very far from asserting that it alone is indispensable. In dwelling a moment longer upon the Protozoa, the following remark may be made: it is stated by Kölliker ('Gewebelehre,' p. 67) that in *Euglypha* the polar body is attached to the nucleus. I do not know whether Kölliker was led to make this assertion by his own observations; he at any rate makes no mention of this. But we find it stated by Schewiakoff§, who was the first to demonstrate the existence of these bodies in the case of the Protozoa in the Rhizopod in question, that the polar bodies lie not in the nucleus, but in the substance of the cell, pressed into a hollow of the nuclear membrane; and this author is also of opinion that they arise, at least in part, from "the differentiating cytoplasm." Beyond this these bodies are not yet known in the Protozoa, and before their existence has been

* M. Nusbaum, "Ueber die Theilbarkeit der lebendigen Materie," Arch. f. mikr. Anat. 26 Bd., 1886.

† A. Gruber, "Ueber künstliche Theilung bei Infusorien" (I., II.), Biol. Centralbl. 4 & 5 Bd. 1885.

‡ Balbiani, "Recherches expérimentales sur la mérotomie des Infusoires ciliés," Recueil Zool. Suisse, t. 5, 1889.

§ Schewiakoff, "Ueber die karyokinetische Kerntheilung der *Euglypha alveolata*," Morphol. Jahrb. 13 Bd., 1888.

proved it would be premature to enter into a discussion as to what is the *primum movens* in the fission of the Infusoria. I have, however, really no doubt that sooner or later corresponding structures will be found in these forms also.

Until quite recently great uncertainty prevailed as to the origin of the polar bodies or centrosomata in the fertilized ovum. Many authors made no precise statements at all on the point. Boveri's hypothesis, according to which they arise from the protoplasm of the spermatozoon, has already been alluded to. This year this deficiency in our knowledge was supplied by the new investigations of Fol upon the ova of Echinids, and thus the last vestige of foundation was withdrawn from the theory that the nuclei are the sole vehicles of heredity. Fol's memoir marks, so to speak, the last stage in the present purely morphological knowledge of the process of fertilization. The investigator alluded to examined the fertilized ova of Echinids (as also those of other types) by means of thin sections, with the following results:—On the penetration of the spermatozoon into the ovum, its tip separates from it, and forms the "spermocentrum" (the polar body which precedes the male pronucleus); this, as well as the "ovocentrum," which was pre-existent in the ovum beside the female pronucleus, having arisen from the directive amphias-ter, elongates into a dumb-bell shape, when the pronuclei have come together*, and undergoes division. A migration of the halves resulting from the fission now takes place, in such a way that each half of the spermocentrum finally comes into contact with a half of the ovocentrum and fuses with it. The bodies which are thus constituted, each of which consists of a male and female half, are the polar bodies or centrosomata ("astrocentres" of Fol) of the first segmentation amphias-ter. For the present these are the only conclusions which Fol deduces from his investigations:—"Fertilization consists, not merely in the aggregation of two pronuclei, which proceed from individuals of different sexes, but also at the same time in the union of two pairs of half-centres ('Halb-centren'), of which one unit is derived from the father and the other from the mother, to form two new bodies—the astrocentres. Since all the astrocentres in an individual presumably originate through fission from the two centres of the first amphias-ter, they all proceed in equal portions from the father and the mother."

Now if anyone, on the basis of these results, were to maintain, in an assemblage of zoologists, that the centrosomata

* Fol agrees with van Beneden in stating that in the normal course no fusion of the pronuclei takes place.

are the sole vehicles of heredity, he would probably be received, and justly, with general derision. I, however, maintain that if, for the present, anyone continues to assert that the nucleus is the sole vehicle of heredity, his hypothesis is of no greater value than that just mentioned.

The above conclusions and remarks will perhaps appear to unprejudiced investigators to be somewhat self-evident. That they were nevertheless not entirely superfluous is proved to me by a new paper by Weismann*, which actually appeared during the preparation of this little essay. For, in spite of cognizance of Fol's investigations, this author stands fast by his old opinions, and indeed is rather inclined to regard the former as a confirmation of his views. He would most of all prefer to consider the centrosomata as parts belonging to the nucleus; but here he will scarcely meet with the approval of specialists. And as for his other proposition, that the activity of the centrosomata is to be regarded as determined and guided by the nucleus, it is wholly artificial and arbitrary; indeed it has been demonstrated above that there is not the slightest foundation for such a supposition. We are fully entitled to ask, Why is not the position reversed? Why is not the activity of the nucleus equally well to be regarded as dependent upon that of the centrosoma?

In the present state of the case it would be much better to say, the theory that the nucleus alone is the seat of the processes of heredity was premature, and provisionally we know nothing about it. But if we wish to express conjectures, it is much more probable that the processes of heredity, as well as most of the other vital processes in the cell, depend upon intimate relations between nucleus and plasma (or, to be precise, the directing portion of the plasma—the centrosoma), and that in this respect we have no reason to favour one of these parts more than the other.

Copenhagen, November 1891.

LIX.—*Description of a remarkable new Semnopithecus from Sarawak.* By OLDFIELD THOMAS.

MR. CHARLES HOSE has kindly submitted for my examination the flat skin of a monkey obtained by him some years ago on the coast of North-eastern Sarawak, and this proves to represent a species not merely new, but entirely different in its coloration from anything previously described. Among the many

* A. Weismann, 'Amphimixis oder die Vermischung der Individuen, Jena, 1891.