Biologisches Centralblatt.

Unter Mitwirkung von

Dr. K. Goebel und **Dr. R. Hertwig**

Professor der Botanik — Professor der Zoologie

in München,

herausgegeben von

Dr. J. Rosenthal

Prof. der Physiologie in Erlangen.

Vierundzwanzig Nummern bilden einen Band. Preis des Bandes 20 Mark.
Zu beziehen durch alle Buchhandlungen und Postanstalten.

XXII. Band. **1. Juni 1902.** **Nr. 11.**

Heredity and the epicycle of the germ-cells

by **J. Beard**, D. Sc.,

University Lecturer in Comparative Embryology, Edinburgh.

Owing mainly to the writings of Brooks, de Vries, O. Hertwig, Nägeli, Herbert Spencer, and above all others, Galton and Weismann, the problems of heredity have occupied a prominent position in the scientific discussions of recent years.

The progress of research into the life-history of the cell, the structure and functions of the nucleus, the phenomena of cell-division, more especially those of the „ripening“ of the „sexual products“, have naturally played important parts in these. Indeed, so much has this been the case, that H. F. Osborn might well say „the study of heredity will ultimately centre around the structure and functions of the germ-cells“.

It is not my intention to attempt the task of writing a history of these discussions and theories: what is proposed is merely to indicate the broad and obvious bearings of certain of my results, relating to the history of the germ-cells, on the general problem of heredity.

In order to obtain a clear insight into the process or processes, by which in a wide sense germinal continuity, resulting in the phenomena of heredity, is brought to pass, it is a requisite postulate, that an uninterrupted and continuous panorama of the whole course of development from one generation to the next should be secured. Heredity must be dependent on some sort of germinal continuity; whether of a special germ-plasm in Weismann's sense, or a consequence of an uninterrupted sequence of germ-cells, or a result of an intracellular pangenesis, or something else.

In this way it comes to be a problem of embryology and development, and as such it falls within the province of the embryologist. This being so, is it not remarkable, that the chain of germinal continuity should hitherto not have been completely grasped in any single case? From my researches on the germ-cells[1]) it is clear, that hitherto no complete survey of the development from one generation to the next has really been made. One phenomenon in the Metazoan life-cycle has entirely eluded the observation of embryologists; or, if they have noted and recorded it, they have failed to realise its full significance. This is the formation of the primary germ-cells with the epoch, at which these appear upon the scene.

Their very early origin — before any trace of an embryo had been laid down — was long ago recorded in certain cases, among others by Weismann, Bütschli, Grobben, Ritter, Metschnikoff and O. Hertwig. But these very instances only serve to strengthen my contention; for in them the few primary germ-cells — from 2 to 8 in number — were apparently so insignificant, that their formation at a particular time seemed to be an incident of no moment; and its discovery, like many other important finds, was passed over; because no estimate could be set upon its value.

Long ago Nussbaum concluded, that the germ-cells must differentiate themselves at a very early period, before there was any trace of histological differentiation in the embryonic foundation. But Weismann[2]), carrying with him practically all other zoologists[3]), has decidedly rejected this view; „because, as a matter of fact, the sexual cells of all plants and those of most animals do not separate themselves from the beginning from the somatic cells".

And this is just the question at issue. To allow the statement to pass unchallenged might be taken as a tacit admission of its accuracy, although every page of the present writing asserts its incorrectness. The passage was written more than fifteen years ago, much has happened in the meantime, and it may no longer represent Weismann's views. But the objection is recorded in the literature of embryology, and it requires refutation.

The argument contains two fallacies, and these rob it of all force. Taking these in the order of their occurrence, the first is, that the sexual cells of all plants do not separate themselves from the beginning

1) J. Beard, The Morphological Continuity of the germ-cells in Raja batis. Anat. Anz. V. 18, p. 465—485, 1900.

2) A. Weismann, Die Kontinuität des Keimplasmas, Jena 1885, p. 44.

3) Thus, for example, Oskar Hertwig (Zeit- und Streitfragen der Biologie, Heft I, p. 76, 1894). Here it is written „Zweitens gehören die Geschlechtszellen ebensogut zum Körper eines Organismus, von welchem sie sogar oft den beträchtlichsten Teil, wie z. B. bei vielen Parasiten, ausmachen, wie jedes andere Gewebe etc."

from the somatic cells. Probably all the higher plants, the Metaphyta, are here referred to; for in many of the lower plants all the cells might be regarded as potentially reproductive, or „sexual". In the higher plants the „sexual cells" do appear at a very early period in the sexual generation. The higher one ascends the earlier is this epoch; for in the flowering plants, for instance, the life-span of the sexual generation, the gametophyte, is exceedingly short, and it is concerned solely with the differentiation of, and the provision for, the sexual cells. These latter certainly do not appear as such in the asexual generation or sporophyte, nor is it to be expected, that they should. Were they to do so, the sporophyte would lose this character, and become a gametophyte. Moreover, even in the asexual generation, the sporophyte, the morphological continuity is unbroken, for in this the future germ-cells are represented by their direct ancestors, the one or more cells forming the apex[1]).

What Nussbaum rightly insisted upon was, the early appearance of the germ-cells in the sexual generation of animals, i. e., in the em-

1) Compare Noll's eloquent testimony in the following: „The continuity of the embryonic substance. — The vital capacity of the cells of the functioning permanent tissue is always limited in time, mostly, indeed, very closely so. Without limit, on the contrary, and never finding a natural close the vital power of the embryonic substance is preserved. This it is, which forms the growing points of the perennial plants, and from this, as Sachs first demonstrated, the growing points of the sexual progeny are directly derived through the substance of the germ-cells. This embryonic substance does not age, it produces new passing individuals, but it is permanently preserved in their progeny: it is always productive, always growing young and increasing. Thousands upon thousands of generations, which have arisen in the course of millions of years, were its products, but it lives on in the youngest generations with the power of giving origin to coming millions. The individual organism is transient, but its embryonic substance, which produces the mortal tissues, preserves itself imperishable, everlasting, and constant. Regarded from this standpoint, the differences in the duration of life between short and long-lived plants, between annual herbs and the thousands of years old giants of the plant-race appear in another light. Out of the embryonic substance of that lime tree of Neustadt every year new leaves and buds form, but these remain in connection with the dying remains of structures of earlier years. In the annual plant, on the contrary, the embryonic substance separates itself every year in the embryo from the mortal remains, and forming new branches, leaves, and roots, becomes a completely new individual.

At the basis of the old and well-known dictum of Harvey, omne vivum ex ovo' there thus already lay the continuity of the embryonic substance. This is, at the same time, in eternal youth and organic immortality the substance of the unicellular organisms, which reproducing by fission, are used up in one another without residue."

F. Noll, in Strasburger's Lehrbuch der Botanik, zweite Auflage, 1895, p. 208—209.

bryo, before this had undergone histological differentiation. In urging this Nussbaum really took up a very moderate attitude. To refute his argument from the botanical side, it is necessary to compare the conditions in the corresponding generations in the two kingdoms, that is, to place the embryo and the prothallus together, not the embryo and the sporophyte. It should also be pointed out, that even now the early history of the germ-cells of „most animals“ has as yet been very inadequately investigated. Where it has been traced back to the farthest possible point, there a very early origin has been invariably made out. This is now so in Moina, Cyclops, Ascaris, Strongylus, Cecidomyia, Chironomus, Sagitta, Phalangium, Lernaea, Micrometrus, Scorpions (Brauer), several insects (Heymons), some sponges (Maas), and Cephalopoda (V. Faussek), and, lastly, in Pristiurus (Rabl), Scyllium, and Raja.

Hitherto the apparent phenomena in the Vertebrata stood in the way. Here even a segmental origin of the „sexual cells“ had been recorded in relatively late stages. This is, however, only one of the ever recurring instances of the earliest observed appearance of a thing being taken to represent its first origin. This is only permissible in embryological research, when an earlier origin is absolutely out of question.

From a fair acquaintance with the embryological literature treating of the germ-cells and their origin the writer must maintain, that there is really no reliable evidence, pointing to the very late appearance of the germ-cells in any single case. On the other hand, there is a steadily accumulating body of strong testimony in favour of their early separation off in many different divisions of the animal kingdom. Even the case of the Hydroid polypes cannot be cited in disproof, for Weismann's own great researches reveal not so much the origin of the germ-cells in these as their remarkable migrations.

In saying the foregoing in face of the known facts concerning Moina, the Dipterous insects, etc., Weismann defined not only his own standpoint towards the question, but also that of most other zoologists. The exception meets with no favour, until it ceases to be such, and adapts itself to the rule. But „die Natur geht ihren Gang, und was uns als Ausnahme erscheint, ist in der Regel“. And this is so, simply because what we regard as the rule is often false, the real law being that, with which the apparent exception conforms.

While only from 2 to 8 primary germ-cells were found very early in the development of this or the other form; while, as in the higher animals, one could study the early development without seeing any germ-cells — their „segmental origin“ even being witnessed at later periods — the good old rule, in plain language, the superstition, that the offspring was formed by the union of a small portion of each of its parents, seemed to be the only logical conclusion. Thus is hap-

pened, that so great an investigator and thinker as Darwin could set up his provisional hypothesis of pangenesis.

When in one of the higher animals, the skate, the formation of a whole battalion of germ-cells is found to take place prior to the appearance of any trace of the embryo, a change comes over the scene: the apparent law and its exceptions exchange positions, with the consequent disappearance of the former.

In the life-cycle of the skate (including in this all that happens from the union of egg and sperm, until new eggs and sperms are formed) the origin of the germ-cells fills in so large a space as to overshadow completely everything else. For this reason the formation of an embryo may be described as a mere incident in the life-cycle.

Two primary germ-cells and five hundred and twelve are very different numbers. If the full significance of this should not be apparent, a glance at the diagrammatic representation of the life-cycle of the skate may serve to make it so. The diagram is, however, incorrect! In the portion showing the origin of the primary germ-cells these have only been drawn to six divisions, giving 64. To exactly embrace the full significance of the discovery the drawing ought to include three further divisions, yielding 512 germ-cells at P. G. C.

That is to say, to accurately represent the conditions in embryo no. 454, for example, the diagram ought to be at P. G. C. eight times as wide as it is at present!

When I see in this diagram some of the results of twelve years of work, the reader will, perhaps, pardon me, if I linger to say something more concerning it and its origin. Some parts of it will be familiar to every embryologist, thanks to the work of Boveri, O. Hertwig, and others: the other and unfamiliar portions are my own.

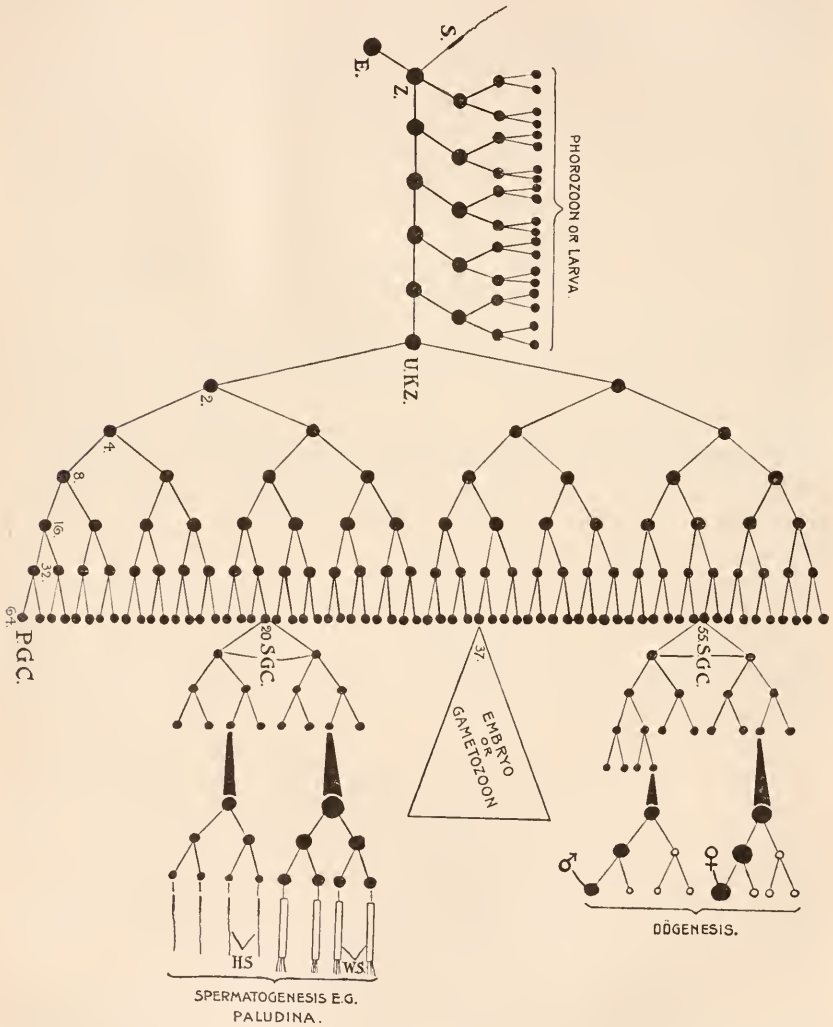
Following out the full history of the diagram I am carried back more than twelve years. As long ago as 1888 my researches on larval structures in fishes commenced. Their results in course of time carried the investigator in the direction of the recognition of an antithetic alternation of generations. Since that standpoint was attained, no facts adverse to it have been encountered. The doctrine has never been seriously attacked: it has been simply ignored. It has not as yet won many adherents: the truth never does at first. For myself I have been content to follow out the inquiry, and from time to time, as opportunity offered, to glean a few more facts, supporting this theory of development. During part of this period a watch has been kept for something equivalent to the formation of spore-mother-cells in the higher plants or Metaphyta, but in vain. Hitherto, as at length clearly recognised, the search had not been made in the right place.

The investigator is often the creature of circumstances. These in

the present case brought about an investigation of the early history of the germ-cells without associating with this inquiry any ideas concerning spore-mother-cell formation or alternation of generations.

Only when the work was practically ready for publication, and

Fig. 1.



when a proper survey of the results had been obtained, by drawing them up in diagrammatic form, as shown in the table, the full force of the discovery became apparent. The formation of the primary germ-cells in the skate — and in all probability in every other Metazoon — corresponds broadly to the genesis of spore-mother-cells on the asexual generation of a plant, the sporophyte.

With this recognition it becomes possible to compare together, so as to show their essential similarity, the phenomena of the life-cycles of the Metazoa and Metaphyta.

In the same way the discovery of the formation of the primary germ-cells and of the epoch of their coming-into-being throw new and unexpected light on the course and nature of heredity.

These are the chief results of my work on the germ-cells: and, though other and doubtless important finds have been made, the latter sink into insignificance, when placed beside the former.

Certain parts of the diagram have been adopted, as already stated, from the writings of other embryologists. This, however, has not been done without important modifications, for which the writer is alone responsible.

Originally towards the close of last year (1900) Boveri's diagrams of oögenesis and spermatogenesis formed and filled in portions of the life-cycle. Doubts however, arose as to their completeness, and the working out of the probable course of oögenesis in the skate finally resulted in the modifications here depicted. The first part of the figure, from the zygote Z, formed by the union of egg and sperm, to the primitive germ-cell U. K. Z. (the „Urkeimzelle" of German authors) is from Boveri's and Weismann's figures. In their diagrams, however, from Z to U. K. Z. marks what Weismann terms the „germinal track" (Keimbahn), and the products to the left of it are assumed to be cells of the embryo. As in the skate there is no possibility of the existence of any part of the embryo prior to the formation of U. K. Z., it is out of question, that the said cells can be part of this. It is an assumption, that they are parts of the embryo; for in Ascaris megalocephala, for instance, the form to which Boveri's identical diagram refers, it has never been established, that directly from the cleavage of the fertilised egg the sexual generation or embryo takes its origin. The later history is here unknown. Indeed, it may be safely predicted, that, when the facts become known, of the two primary germ-cells of Ascaris, formed by division of the cell U. K. Z., the one will be seen to form the embryo or sexual generation, while the other will furnish its sexual products[1]).

1) In Ascaris megalocephala it is at least possible, that the primitive germ-cell is separated off at the fourth cleavage instead of at the fifth. The latter cleavage would then divide the primitive germ-cell into two primary germ-cells, of which the one would go to form the embryo and the other would represent the „sexual products". If this be the correct interpretation of the conditions in Ascaris — a point upon which I do not venture to express an opinion — the subsequent division of the cell, regarded by Boveri and others as the primitive germ-cell, would correspond to the formation of secondary germ-cells in Raja, that is, the parent cell would be a primary germ-cell.

Regarding the life-history of such a Nematode as Ascaris megalocephala,

It will doubtless be urged, that on my part also it is an assumption, that the cells to the left of the line Z — U. K. Z. give origin to the larva. In a sense this is true, but the one assumption is prima facie as good as the other; and on the further evidences to be adduced it is a good deal better. (Schluss folgt.)

Das Energieprinzip und die energetische Betrachtungsweise in der Physiologie.

Von Dr. **F. Mareš**,

Professor der Physiologie an der böhmischen Universität zu Prag.

(Schluss.)

Fast alle im Tierkörper frei werdende Wärme entwickelt sich bei der Muskelthätigkeit. Man nimmt an, dass dabei Verbrennungen namentlich der Kohlenhydrate im Muskel stattfinden. Seitdem Hermann und namentlich Pflüger gezeigt haben, dass die Muskelthätigkeit vom gleichzeitigen Sauerstoffverbrauch unabhängig ist, stellt man sich auch vor, dass es sich dabei um exothermale Stoffumwandlungen mit Kohlensäureabspaltung handelt. So wird also die Kohlensäurebildung als direkter Ausdruck des Stoffumsatzes bei der Muskelthätigkeit angenommen. Nun zeigen aber die Untersuchungen von Fleteher (The Journal of Physiol. vol. 23, S. 79), dass die Thätigkeit eines ausgeschnittenen Froschmuskels von keiner Vermehrung der Kohlensäureausscheidung begleitet ist, wenn Muskelstarre sich nicht einmischt. Es zeigt sich zwar während der Muskelthätigkeit eine bedeutende Vermehrung der ausgeatmeten Kohlensäure, auch zeigt das aus dem thätigen Muskel kommende Blut vermehrten Kohlensäuregehalt, welche Vermehrung aber ausbleibt, wenn bloß Blutserum durch den Muskel geleitet wird. Schon Minot glaubte dieser Beobachtung entnehmen zu müssen, dass die Kohlensäure zu den im thätigen Muskel entstehenden Stoffwechselprodukten nicht gehört. Nun zeigt Fletcher, dass im ausgeschnittenen Muskel keine Kohlensäurevermehrung während der Thätigkeit stattfindet. Es ist also eine offene Frage, wo und wie die Kohlensäure entsteht, welche im Blute und den Atmungsausscheidungen während der Muskelthätigkeit konstant vermehrt erscheint.

Daraus ist nun so viel zu entnehmen, dass die Muskelthätigkeit an sich mit der Kohlensäurebildung nicht unmittelbar verbunden zu

---

what is written above concerning the part unknown needs no justification. But if it be imagined possible, that here directly from the fertilised egg the sexual form as it occurs in the horse can arise, a reference to the account of Maupas' results of investigations into the life-histories of a number of Nematoda will dissolve the illusion. (Vide: Arch. Zool. Exper. V. 8, p. 463—624, 11 pl., 1900.)