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. **15. Juni 1902.** **Nr. 12.**

Inhalt: **Beard**, Heredity and the epicycle of the germ-cells (Fortsetzung). — **Schultz**, Ueber das Verhältnis der Regeneration zur Embryonalentwicklung und Knospung. — **Lämmel**, Ueber periodische Variationen in Organismen. — **Marchand**, Ueber das Hirngewicht des Menschen. — **Wasmann**, P. Petrus Heude †. — **Zacharias**, Zur Fauna der Umgebung von Buitenzorg. — Bei der Redaktion eingegangene Werke.

Heredity and the epicycle of the germ-cells

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

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(Fortsetzung.)

From the existence of a transient nervous system, a blastoderm, and other evanescent structures the conclusion was long ago arrived at, that there was a larva or asexual generation in the life-cycle of the skate. From all the known facts of embryology such a larva cannot arise out of an embryo, it must precede an embryo. There is no embryo by the time the period P. G. C. is reached, the formation of such commencing here. Therefore, the first products of the cleavage, apart from the line leading to U. K. Z., must be the larva.

Evidence from another side will be found in, for instance, E. B. Wilson's published researches on the development of Nereis[1]). There was some hesitation in the writer's mind as to the possibility of using Wilson's results in support of the view here presented as to the nature and destiny of the first cleavage-products. A perusal of the lecture, cited below, served to remove this. His work of 1892 and his more recent results must be taken together, for Wilson himself has seen reason to alter his earlier interpretation in some slight but important respects. These amendments are exactly of the kind required for my reading of his table of the cell-lineage.

1) E. B. Wilson, The Cell-Lineage of Nereis, Jour. of Morph., V. 6, p. 361—480, 1892. Cell-Lineage and Ancestral Reminiscence. Wood's Holl Biol. Lectures, p. 21—42, 1898 (published 1899).

In fig. 2 Wilson's table, so far as it concerns us, is reproduced, and in fig. 3 the same results are shown after the manner of Boveri's figure, or the part of my diagram from Z to U. K. Z.

The main difficulty to the writer in his reading of Wilson's diagram has hitherto been the supposed destiny of the cell d2 = x. From p 30 of his recent lecture it may be gathered, that the author, following the finds of Lillie in Unio, now looks upon this cell x as representing a larval mesoderm-cell. This is exactly the fate it ought to have; for, as we have seen, everything to the left of the line Z — U. K. Z. must belong to the phorozoon or larva.

The primitive germ-cell has not yet been identified in Annelida. From my interpretation of Wilson's finds it would appear to arise in Nereis at the fifth cleavage as the cell in fig. 3 labelled D = U. K. Z.

Fig. 2.

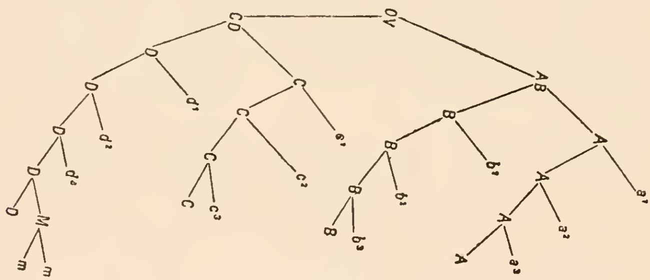
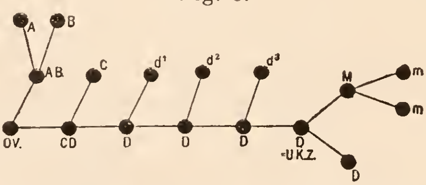


Fig. 3.



This then divides into (two primary germ-cells) D and M. M is the primary mesoderm-cell or somatoblast of various authors. Its division initiates the period of bilateral cleavage. Its two products form the two „mesoderm-bands". In contradistinction to other authors the writer must maintain the opinion, that M is a primary germ-cell, and that it gives rise to the whole of the sexual generation, in this case the worm. In this connection it may be of interest to recall the circumstance, that long ago Hatschek expressed the view, that the two products of M, the well-known „pole-cells" of Hatschek, were originally eggs[1]). This suggestion has been criticised by Kleinenberg.

1) Wilson approves of E. Meyer's amendment of Hatschek's view into correspondence of the mesodermal bands with paired gonads. In the sense indicated above there is much to be said in favour of Hatschek's interpretation: the other idea is wildly impossible.

If the pole-mesoderm-cells be not eggs, they at least arise by the division of the next thing to an egg, a primary germ-cell.

In Nereis the remaining primary germ-cell D comes to form part of the hypoblast. There is no difficulty about this. Even in the skate many of the primary germ-cells may for a time lie in the hypoblast, but they do not give rise to hypoblastic cells. As Wilson remarks, „the ultimate court of appeal — lies in the fate of the cells“ (loc. cit. 2 p. 41).

Another apparent difficulty, more especially to the view of the complete similarity and equivalence of the primary germ-cells, would be, that sometimes the embryonic cell may perhaps exceed (?) the primary germ-cells in size. As an instance, that D and M mentioned above may be of different sizes (?). But this very difference in size may serve to explain why some particular primary germ-cell is chosen to form an embryo instead of some other. Position alone cannot always be at the bottom of this. In the skate, for example, the embryo does not invariably begin to arise at one certain spot upon the blastoderm. It may be, that the stimulus afforded by an extra amount of food-yolk may have much to do with the initiation of development.

Very suggestive and significant in the light of my results in the skate are the following passages from E. B. Wilson's memoir on „The Cell-Lineage of Nereis“. Statements equally pregnant with meaning will be found in various parts of Eisig's work on the development of Capitella (Mitteil. a. d. Zool. Stat. zu Neapel, V. 13, p. 1—292, 1898).

On page 398 Wilson writes: „Transition to the Bilateral Period. As far as the development of the permanent organs is concerned, the transition from the spiral to the bilateral type of development is remarkably abrupt.“

It may be mentioned, that at the close of the spiral period there are, according to Wilson, 38 blastomeres present. That is to say, the majority of them are products of the fifth cleavage.

On page 444 he asks „what is the significance of the spiral and bilateral forms of cleavage, and where lie the causes that determine the transformation of the one into the other?“ Further on he writes: „The most striking feature in the cleavage, and the one on which the entire discussion may be made to turn, is the sudden appearance of bilateral symmetry in the cleavage. The meaning of the bilateral cleavages in themselves is perfectly obvious. They are the forerunners of the bilateral arrangement of parts in the adult; and, as such, their explanation belongs to the general problem of bilateral symmetry, which need not be considered here. The all-important point is that the bilaterality does not appear at the beginning of development[1]). It

1) Spaced in the original.

appears only at a comparatively late stage, and by a change so abrupt and striking as to possess an absolutely dramatic interest[1])." And so on. I refrain from further quotation, because Wilson's work contains no real solution of the problem.

To my mind the solution was lacking, because, on the one hand, it was not recognised, that the mode of development was by means of an alternation of generations; and, on the other, the history of the primary germ-cells in Nereis was, and is, unknown.

If the reader will compare Wilson's statements with the course of development depicted in my diagram — not forgetting, I trust, that the latter is a diagram, and nothing more — the meaning of the spiral cleavage and of the sudden and abrupt change, of which Wilson speaks, may become apparent.

The apical mode of growth, so characteristic of the early formation of the asexual generation in both plants and animals, and which is retained for the whole life-span of the sporophyte of plants, might also be described as spiral. Indeed, it is so regarded and described by botanists. Then with the cutting off of the connection between the primitive germ-cell and the asexual generation or phorozoon we witness the practical end[2]) of the spiral mode of cleavage, and the commencement of the bilateral period. With this the formation of the primary germ-cells is connected, following the genesis of these a start is made in the building up of the embryo.

In this way my diagram gives a general interpretation of Wilson's finds, not to mention those of other observers. And thus, the phenomena observed in the development of Nereis are seen to be due to an antithetic alternation of generations, where the asexual generation arises in a spiral or apical manner, where the sexual generation is characterised by a bilateral mode of formation, and, lastly, where one may predict the formation of a primitive germ-cell and of primary germ-cells from this between the two generations, that is to say, prior to the development of the sexual generation.

In the course of more than twelve years, spent in the attempt to elucidate the mode of Metazoan development, at various times many things have seemed inexplicable; but, wherever their history has been discovered, they have been found to fit into an antithetic alternation of generations, and into nothing else.

If Wilson's finds be not based in such an alternation, but be in connection with a „direct" mode of development, they seem to me to

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1) Spaced by me.

2) The practical end but not the actual termination; for, as Wilson points out (p. 393), „it is only in the peculiar changes involved in the formation a larval organ, the prototroch, that the spiral form of division overlaps the bilateral period".

include facts, which will never be explicable, for such a roundabout kind of development can hardly be termed „direct". Or shall we „explain" and describe them as the development of the Scyphozoa is explained and described in almost all the current text-books, by the omission of any reference to the main portion of the asexual generation, the stolon, discovered by Sars[1])?

Such a course may simplify matters, but it hardly makes for the discovery of the facts of Nature.

Reverting to the diagram of the life-cycle of the skate, I consider it to be possible at present only by comparison and induction to show the fate of the cells to the left of the „germinal track" as far as U. K. Z., the primitive germ-cell. The comparison with other cases only goes to show its correctness, and, I am convinced, the number of such will increase in the proportion as the study of cell-lineage, so ably established by Whitman, Mark, and E. B. Wilson, replaces the pursuit of the three sacred layers of embrylogists.

Up to the point U. K. Z. of my diagram the germinal track in Weismann's sense lies apparently in the larva. It may be objected, that in making this substitution the embryo has been displaced, in order to establish a more or less problematical larva, and that the germinal track is here somatic. The reply to this is, that the cell U. K. Z. and its immediate ancestors never form part of the larva, and that the period[2]) from Z. to U. K. Z. — no matter how long it be, whether four generations or four thousand — is marked by a mode of growth and cell-division, conspicuous by absence in other parts of the diagram[3]).

This statement requires both elucidation and emphasis.

The mode of growth of the sporophyte in plants is essentially apical, that is to say, wherever there is an apex there are always one or more apical cells, which by their division give off products towards the centre.

In the sexual generation of a Metazoon the mode of growth differs in toto from this; for here all the products ultimately undergo differentiation, and embryonic or germ-material, corresponding to apical cells, has no existence. The older embryologists, of the first half of

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1) M. Sars. Ueber die Entwicklung der Medusa aurita und Cyanea capillata. Arch. f. Naturgesch. Vol. 7, 1841.

2) In the skate this period includes more than five mitoses, probably ten.

3) Spemann has already compared the mode of origin of the first cleavage products in Nematodes, more especially in Strongylus, to the apical mode of growth in the sporophyte of a plant. He notes, that the cell along the line Z — U. K. Z. in my diagram acts as though it were an apical cell of a sporophyte (H. Spemann, Die Entwicklung von Strongylus paradoxus, Zool. Jahrb. Morph. Abteil. V. 8, p. 304, 1894—95.

the nineteenth century, thought differently, and some pathologists still cling to their views, but these have no shadow of foundation in fact.

The initial mode of growth and formation of the asexual generation or larva in animals — an organism never of a very high degree of organisation is entirely comparable to that of the sporophyte. As in simple cases of the latter, there is here one „apical cell", which never itself forms part of the larva, but instead thereof gives off into the latter a greater or less number of products, while retaining its own unicellular or Protozoan character. Nor would the conditions be altered, if there were several growing points, as generally met with among the Hydrozoa[1]).

It may be objected, that whereas the early cleavage of Nereis, Ascaris, etc., is spiral, in the Vertebrata, such as the skate, it is bilateral. The objection would not, I think, be a valid one. The meaning of such a bilateral cleavage in the early development — assuming it to exist — would simply be, that there were two spirals instead of one, and, possibly, two primitive germ-cells. For various reasons I regard the actual larva or phorozoon of the skate as at the basis very like the tadpole larva of Ascidians. Indeed, I would go further; and, following the example of Roule with his classification of certain Invertebrate groups as „Trochozoa" by their asexual generation or larva, so also in the tadpolelike larva of the Ascidians I would see — not the Vertebrate relation of many embryologists — but the like or even homologous asexual generation of Ascidians, Amphioxus, and the true Vertebrata.

Returning to the diagram. Sooner or later upon the larva the primitive germ-cell enters into activity. It may divide before the larva or phorozoon is properly differentiated, as nowadays is certainly the case in many instances, or, theoretically, its divisions may happen at a later period. These divisions, however, must precede the formation of the embryo or sexual generation.

In the skate the divisions of the primitive germ-cell, which give birth to the primary germ-cells, take place before the larva or phoro-

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3) It should be mentioned that de Vries and Weismann have already noted the resemblance in mode of growth between the sporophyte and the colonial Hydrozoa. Many of the latter also possess the indefinite unrestricted power of growth, so characteristic of the sporophyte of the higher plants. As a rule the asexual generations of the higher Metazoa do not exhibit this faculty. They rarely obtain a chance of showing it, for it is their usual fate to undergo early suppression by the sexual generation. When, as happens sometimes in cases of abortion in the human subject, the embryo is got rid of prior to the critical period, or at any rate before the asexual generation has here been suppressed, the latter may go on growing indefinitely, if left in the uterus. I refer, of course, to the unrestricted and pernicious growth of the chorion, when left in the womb after an abortion.

zoon is fully differentiated, and, of course, before there is any trace of the embryo.

For reasons to be fully given in my memoir on the germ-cells the division of U. K. Z. the primitive germ-cell, is considered to go back to about the tenth cleavage products, and in the skate there are either eight or nine divisions.

The publication of the present writing has been delayed for several months, in order that time might be gained for the tabulation and counting of the primary germ-cells in a series of embryos. This has now (March, 1901) been done in 18 embryos of Raja batis and in 8 of Scyllium canicula.

The number of primary germ-cells in the embryology of R. batis may be taken at 256 in the male and 512 in the female.

It may be added, that the number appears to be much smaller in Rana esculenta and in Petromyzon planeri. In the former 8 and in the latter 32 primary germ-cells would seem to arise.

These latter numbers have not yet been confirmed on a material large enough to afford any certainty of their correctness.

The division of the primitive germ-cell into primary germ-cells is a well-marked epoch in the life-cycle, and one of the greatest possible moment. Hitherto its import has been overlooked by every embryologist, and the record of it is now made for the first time as the result of my work.

From every point of view it is as important as the phenomena of maturation; and, probably, its essential necessity in development will not need to wait long for ample recognition.

The number of the products of the primitive germ-cell is very large in the skate, as many as 512. But it must be pointed out, that this number furnishes no criterion for other animals. There may be cases, in which it is larger; though, I imagine, the occurrence of many such is unlikely. Undoubtedly there are instances, in which it is much smaller: and, probably, these are well represented among the Invertebrata. In short, it may be as low as two; but, as the sexual generation or embryo must arise from one product, and as this must contain some sexual elements, it can never be lower than two. In other words, the primitive germ-cell must divide at least once, yielding two primary germ-cells, of which one will give rise to the embryo and the other will supply the „sexual products". Apparently it divides once in Cyclops and Ascaris megalocephala, twice in Cecidomyia, and thrice in Chironomus[1]).

In other chapters of my work the essential similarity, the equivalence of all the primary germ-cells, whether their number be 2, 16, 128, 512, or anything else, has been insisted upon. The point is one of the utmost importance, and, therefore, it may be well to once more briefly indicate the grounds for the conclusion.

All the primary germ-cells have the same ancestry from the primitive germ-cell. One of them forms the embryo, and there is nothing to show that this one differs in any respect from its sister-cells[1]). If two primary germ-cells undergo independent development on a blastoderm, the result is, and must be, the production of like twins. The dermoid cysts or embryomas of Wilms are, as this able investigator has established, rudimentary embryos. These abnormal embryos must have taken their origin from persistent primary germ-cells, and the development of an embryoma is embryologically the abnormal formation of a twin, identical with the embryo.

The likeness of all the primary germ-cells is certain, or almost so: absolutely nothing suggests unlikeness among them. This essential identity or equivalence of all the primary germ-cells is immensely important from the point of view of heredity. This will be quite obvious.

(Schluss folgt.)

Ueber das Verhältnis der Regeneration zur Embryonalentwicklung und Knospung.

Von **Eugen Schultz.**

(Vortrag gehalten auf dem XI. Kongresse russischer Naturforscher und Aerzte in St. Petersburg. Dezember 1901.)

Eine ganze Reihe Arbeiten, die dem Wesen der Regeneration näher treten wollten, stießen auf so große Geheimnisse, dass sie sich gezwungen sahen, besondere, fast transcendentale Kräfte anzunehmen, die ordnend und richtend, stets zweckmäßig und regulatorisch, immer wieder aus einer Unzahl von Einzelfällen der Verletzung ausgehend, das konstante Ziel des normal funktionierenden Organismus erzielten. Ein solches Ergebnis, wenn es auch vollkommen der Wirklichkeit entspricht, gewinnt erst dann Wert, wenn die Begriffe der Regulation und Regeneration näher analysiert werden und mit uns bekannteren und geläufigeren Begriffen verglichen und zusammengestellt sind. Deswegen glaube ich doch, das Gesunde und Zeitgemäße eines Standpunktes, wie ihn Driesch und Herbst phyletischer Betrachtungsweise gegenüber einnehmen, vollkommen anerkennend, dass die experimentale Methode mit der historischen sich wird vereinigen müssen, und dass deswegen ein Vergleich regenerativen und embryonalen Geschehens und die Einordnung der neu entdeckten regenerativen Erscheinungen in schon bekannte Kategorien immerhin eine Erkenntnis ist, die tieferen Verallgemeinerungen vorhergehen muss.

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1) In Strongylus Spemann has commented upon the equivalence of what he terms the primitive germ-cell and the primitive mesoderm-cell, indeed, he speaks of them as „Geschwisterkind“ or cousins (Zool. Jahrb. Morph. Abt. V. 8, p. 313). His primitive germ-cell is, however, a primary germ-cell, and the true primitive germ-cell is that from which the two cells compared together took their birth.

Zeitschrift/Journal: Biologisches Zentralblatt

Jahr/Year: 1902

Band/Volume: 22

Autor(en)/Author(s): Beard John

Artikel/Article: Heredity and the epicycle of the germ-cells 353-360