Heredity and the epicycle of the germ-cells

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

University Lecturer in Comparative Embryology, Edinburgh.

(Schluss.)

It is it, and it alone, which permits of the handing down of the characters of one generation to future generations. It is the very basis of heredity. The formation of like primary germ-cells and their essential similarity or equivalence show how in sexual reproduction the offspring resemble their „parents", while differing from them. The likeness in the primary germ-cells leads to likeness in the offspring, and along with this unlikeness is bound to come in. For the primary germ-cells themselves give rise to secondary germ-cells, which have lost their powers of independent development. It is these, and these only as a rule, which are present in the finished embryo. They and their progeny are never capable of normal independent development[1]); but it is their destiny to go through the process of reduction of chromosomes, with the ensuing formation of „sexual products", or gametes, eggs and spermatozoa. Here, as is of course now generally recognised, unlikeness enters. Although the egg or spermtraces its long ancestry to one of a certain set of primary germ-cells, of which one also gave rise to the „embryo" or form, whose „offspring", according to social and commonly accepted ideas, the egg or sperm itself was, this said egg or sperm unites with another sperm or egg, the „offspring" of a different individual, which in its turn with its reproductive elements traces a similar origin and ancestry from another set of primary germ-cells. With the union the new cycle begins.

It is thus that the formation of primary germ-cells underlies the fundamental facts of heredity and explains these. And it is thus without their knowing it, that the formation of primary germ-cells at a certain epoch of the development, prior to the production of the embryo, is the real basis of Weismann's finds in heredity, and, to a still greater degree, of those, associated with the name of Galton.

The application in detail of the results to the phenomena of heredity is beyond the scope of my researches. To indicate the way may suffice.

Galton has been led by his studies and researches on inheritance to what is known as Galton's law[2]). According to this law, „the two parents between them contribute on the average one-half of each inherited faculty, each of them contributing one quarter of it. The

1) In the Vertebrata!

2) Francis Galton, The average Contribution of each several Ancestor to the total Heritage of the Offspring. Proc. Roy. Soc. Lond. Vol. 61, p. 401—408, 1897.

four grandparents contribute between them one-quarter, or each of them one-sixteenth; and so on, the sum of the series, $1/2 + 1/4 + 1/8 + 1/16 +$ etc., being equal to 1, as it should be. It is a property of this infinite series that each term is equal to the sum of all those that follow: thus $1/2 = 1/4 + 1/8 + 1/16 +$ etc., $1/4 + 1/8 + 1/16 +$ etc., and so on. The prepotencies or subpotencies of particular ancestors, in any given pedigree, are eliminated by a law that deals only with average contributions, and the varying prepotencies of sex in respect to different qualities are also presumably eliminated".

Assuming for the moment the correctness of this, its embryological basis is furnished by the formation etc. of the primary germ-cells. The germ-cells in any embryo, possessing from their mode of formation like qualities and having these and the like ancestry with that, which formed the embryo, these qualities are necessarily halved at the following determination of sex and reduction. At the close of this halving the „parental" qualities can embryologically under Galton's law only be represented by at most $1/2$, or $1/4$ for each „parent", and so on for each preceding generation; for in these also primary germ-cells of like characters were formed, of which one gave rise to an embryo in every case.

The line of ancestry is, of course, from and through these germ-cells, and never from the embryo or sexual generation of a proceding generation.

But, as the germ-cells, associated withany given embryo, are all of like characters among themselves (including that from which the embryo arises), on the production of eggs and sperms, and the subsequent union of these with other sexual products, the result is the same, as if the line of ancestry had been through the embryo; so far at any rate as the ancestral characters are concerned. According to Galton the parental qualities are at most represented in their progeny by $1/2$ ($1/4 + 1/4$).

In the same way, and because between offspring and grandparent there are two sets of germ-cells (in addition to those still immature in the offspring) and two reductions, the grandparental portions taken together can only be half of the parental portions taken together, that is to say, $1/4$, and so on through any number of generations. It will be quite unnecessary to carry out the examination further; for study of the diagram will make evident the light it throws from the embryological side on Galton's law, and how it furnishes this law with its basis in the facts of development.

In his book on the „Germplasm" (English edition p. 257) Weismann has adversely criticised Galton's law. His objections would be valid in cases where in-breeding had taken place. For, Galton's law can only hold good, if no in-breeding occur, and if none have happened[1]). This law really demands, that there shall be no inbreeding.

But there is another aspect of Galton's law, and this arises from the following embryological facts. The reduction of chromosomes was probably in its origin merely an undoing of the previous union, and even now it is not the halving of a unit, but of two such. Therefore, it is not a reversion to half cells or half entities or individualities, but to whole ones (Strasburger). From this it follows, that at fertilisation we have to deal with the union of two individualities, of two complete lines of ancestry. The union of these is continued in the primary germ-cells, as evidenced by their duplicated nuclei, until the initiation at least of the ensuing determination of sex, and the united lines are broken up in two separate complete lines, not necessarily identical (like two strings of many coloured beads) with the original two, at the ensuing sex-determination and reduction.

All along the line from the fertilised egg to that primary germ-cell, which unfolds as an embryo, this duplication is evident and, of course, it must at first be in this cell too. As I have recognised in lectures, there must be a competition between the two components of the duplicated nucleus, when development begins[2]). This will be such, that of the total nuclear constituents, which together make up the inherited characters of the two lines, one half must be suppressed, or remain latent, in the development. If these characters be symbolised by the letters of the alphabet in such a way, that the first half of these represent the characters of the one line, the second half those of the other, in the development of the embryo only half of this total can be made use of. Where one letter drops out, its place is occupied

---

1) W. K. Brooks has already drawn attention to this matter. He points out that Galton's theory demands absence of relationship among all the ancestors. He then goes on to show, that in the case of three persons living on a small island their known ancestry goes back 7—8 generations. The maximum number of distinct ancestors for all three persons together should be 1146, according to Brooks. Of these 452 are recorded, but these are not 452 distinct persons, being in fact only 149 (The Foundations of Zoology, 1899, p. 143—145).

2) Haecker has quite recently referred to this in the following words: „Eine ähnliche Konkurrenz kommt vielleicht auch in den Bildern aus den Gonadanlagen von Diaptomus zum Ausdruck, und würde für das Verständnis mancher Vererbungserscheinungen (Dominieren des einen Elters) von Bedeutung sein". Anat. Anz., V. 20, p. 451.

I make no comment whatever upon the foregoing, but leave it to the reader to determine the extent of the agreement between Haecker's brief and vague statement and the ideas and conclusions developed in the text of the present writing.

by the corresponding letter of the other half of the alphabet[1]). In this way the phenomena of prepotency of a parent or ancestor become somewhat more comprehensible.

On p. 257 of the „Germplasm" Weismann writes: „it is evidently more than inaccurate to fix the limit of the hereditary power — as is done by animal-breeders — of a parent at $^1/_2$, of a grandparent at $^1/_4$, etc." To the writer there would appear to be more correctness in doing this than in limiting it to half this amount, as is done by Galton. Owing to the nuclear duplication, referred to above, and the evidences afforded by it and others factors as to the union of two individualities and two complete lines of ancestry, it seems to the writer, that Galton's formula should be represented by something different.

The total inheritance would be $^1/_2$ ($^1/_2 + {}^1/_4 + {}^1/_8$ etc. $+ {}^1/_2 + {}^1/_4 + {}^1/_8 +$ etc.). In the formula[2]), as thus written, the results obtained by breeders find their full recognition.

Before leaving the subject let me briefly indicate, how the diagram elucidates the phenomena of in-breeding. In ordinary sexual reproduction in nature a set of primary germ-cells, exactly like those of a given case, even those of a given ancestor, can never reappear. This is clear from the law of reduction, which in succeeding generations is always leading further away from the particular ancestor. But with in-breeding along two closely allied lines, and by their final union, it may ultimately be possible to approach the qualities of a given ancestor, though probably mathematically an exact result is unobtainable.

The theory of heredity, outlined in preceding pages, has little or nothing in common with previous ones. Underlying it is something more than a mere morphological continuity of germ-cells. From its nature it might be termed „the understudy-theory of heredity. „Given in a certain life-history the period of formation of the primary germ-cells. Of these let there be for simplicity but two ‚A and A‚. On one of these falls the lot of developing into an embryo. To which of the two this happens is not of consequence for the argument. In all its essential characters the remaining primary germ-cell (whose immediate destiny it is to become the founder of the „sexual products" of the said embryo), is the exact counterpart of the developing one.

1) A better simile would be two backs of cards, a red one and a blue one. In the formation of the „embryo" only one pack can be employed, but it may be made up of red or blue cards in any proportion. Prepotency is the preponderance of one or more suits of either red or blue colour.

2) Mathematically, dealing with abstract numbers only, this formula is at the basis identical with that of Galton; but, as the factors are characters, not abstract numbers, this is not the case.

So much so is this the case, that if both form embryos, these are like twins.

In the ancestry neither of the primary germ-cells ,A and A, had ever been a Metazoon: neither they nor their ancestors had ever formed parts of a Metazoan body. But their ancestry is continuous with a long line of germ-cells, and at regular intervals these were exactly like certain sister-cells, which did develop and form embryos. Although the cell A does not itself give rise to an embryo, it retains for itself and for all its immediate progeny the properties of A, those characters which, were it or its progeny to develop, would make it or them like-twins with A.

In the drama of heredity there are always understudies, which for a certain essential period are endowed with all the identical properties of that germ-cell, from which the player arises. These understudies, the primary germ-cells, are never employed upon the stage as such — except in instances of like-twins — but some of them, in new guises and after new conjugations, are the immediate ancestors of those, which become the acting characters in new scenes of the cyclical drama of life.

We now pass to the consideration of the primary germ-cells as the equivalents of the spore-mother-cells of plants. The theory of an antithetic alternation of generations as the basis of Metazoan development postulates something resembling the formation of spore-mother-cells in plants. It is clear, that the final reduction of chromosomes has been deferred to a later portion of the life-cycle in Metazoa as compared with plants, and this fact was insisted upon some years ago by J. A. Murray and myself[1]).

At that time we compared the two modes of development in tabular form, and we postulated the formation of the embryo upon the asexual generation or larva from a spore-mother-cell. Certain facts, supporting this view, were cited, including E. B. Wilson's teloblasts of the earthworn, which must be derivable from one cell. Finally, the spore-mother-cells have appeared in the primary germ-cells of the present research.

In the above table „n“ equals the number of chromosomes prior to the duplication („2 n“) at conjugation, that is, fertilisation.

N. B. Although the primary germ-cells and the spores are shown in the table in the same line, they are not equivalent. The former correspond to the spore-mother-cells.

In 1895 the writer was not sufficiently sanguine to believe it

1) J. Beard and J. A. Murray. On the phenomena of reproduction in animals and plants. Anat. Anz. V. 11, p. 234—255, and also in Ann. of Botany V. 9, p. 441—468, 1895.

possible, that at present the embryo would be found to arise in any case from such a spore-mother-cell. Only its formation at some time in the past from a spore-mother-cell was spoken of, because the facts of development at that time known seemed to point to its origin from at least a few cells.

And, moreover, everything then seemed to go to prove the production of the „sexual organs", i. e., the germ-cells, by the embryo itself. Such was the belief of almost every embryologist, and there appeared little or no reason for doubting its correctness.

Revised Comparison of Metazoan and Metaphytic Life-Cycles.

	Metazoon.	Metaphyte.
Asexual generation	zygote (2 n)	zygote (2 n)
	„larva" or phorozoon (2 n)	sporophyte (2 n)
	formation of primitive germ-cell (2 n)	formation of primitive spore-mother-cell (2 n)
	formation of primary germ-cells (2 n)	formation of spore-mother-cells (2 n), probable determination of sex and reduction
	„apospory" (reduction postponed)	spore-formation
Sexual generation	primary germ-cells (2 n)	spores (1 n)
	(Initiation of Determination of Sex) origin of embryo or gametozoon from one primary germ-cell, inclusion of rest in gametozoon (2 n)	origin of gametophyte from one spore (1 n)
	End of determination of sex, and reduction of chromosomes, ripening of germ-cells	ripening of germ-cells, reduction previously effected
	spermatozoon (1 n) — egg (1 n)	male gamete (1 n) — female gamete (1 n)
	zygote (2 n)	zygote (2 n)

The effect of these two factors was to bar further progress in that direction, at any rate for a time. In face of the apparent facts, I confess, that it was impossible to foresee how the formation of the spore-mother-cell was effected, with the natural result, that only its former existence, i. e., in past times, was suggested. Moreover, there was not the slightest suspicion in my mind or Murray's that the germ-cells had anything to do with the matter.

It is possibly a humiliating confession to make, but it is quite true, that I was never able to conceive how Nature could carry out this formation of a spore-mother-cell and of the embryo from the latter, until my researches had revealed how she actually accomplished it. No one could have been more astonished than the writer at the revelation. Never had it for a moment been imagined, that the germ-cells themselves would play the part they actually do in the life-drama of an antithetic alternation of generations. Only when the work was practically complete and ready for publication, was it seen, that the missing link in the alternation had been discovered in the primary germ-cells and in the epoch of their formation.

I hardly feel called upon to prove that the primary germ-cells do represent spore-mother-cells. If each of them were to undergo a reduction with the subsequent production of four „spores"; and, if then each animal spore were to develop into an organism, we should have the exact equivalent of the gametophyte of one of the higher plants.

Instead thereof they remain together, and only one becomes sterilised to form a sexual individual or gametozoon. Their remaining together and the continued and progressive amplification of the gametozoon in course of ages have naturally deferred their ripenings, sex-determinations, and reductions to later and later periods. It is obvious, that this could easily be effected by starving them, but this may not have been Nature's method of delaying their ripenings. A potent factor has probably been delay in the period of the determination of sex.

In the higher plants it is the spores, whose name is legion, while the „sexual cells", eggs and sperms, are few and far between. In animals the „sexual cells" exhibit the reverse condition, corresponding in their multitude to the spores of plants; while, as we at length know, the spore-mother-cells — there are no spores in the Metazoa — are not very numerous, being represented in some cases by but one cell, in addition to that which forms the sexual generation.

Why this difference[1])? In the embryo-sac of Pinus, which is the gametophyte, there are only four germ-cells. In the corresponding structure in flowering plants there are perhaps three, or at most six or eight; while, as is well known, the male gametophyte of a flowering plant is represented by one or two vegetative cells and one or two germ-cells.

No Metazoan sexual generation has so small and scant an endowment as these, while such an animal may contain and harbour a number of germ-cells thousands of times greater.

1) „Zu vielen Tausenden zählen die vegetativ erzeugten Sporen, welche ein einziges Farnblatt ausstreut. Bei der geschlechtlichen Fortpflanzung der folgenden Generation wird dagegen von einem Prothallium selten mehr als ein neues Einzelwesen gebildet etc." F. Noll in Strasburger's „Lehrbuch der Botanik", zweite Auflage, 1895, p. 255.

The difference is solely due to the different procedure adopted at the formation of the primary germ-cells or spore-mother-cells. The plan carried out in animals has been such as to favour and foster the ever greater and greater amplification of the sexual generation. In plants, as elsewhere already insisted, the reverse is the case. Here the asexual generation has undergone increased amplification without ever being able to attain any very high degree of histological differentiation. The sexual generation of plants is at the best a miserable failure from the morphological point of view, and this must be set down to the factors already indicated.

The higher one ascends the smaller it becomes, until in the highest flowering plants it has almost reached the vanishing point, without, however, being able to disappear entirely.

In animals it is the larva, the phorozoon, or asexual generation, which makes the bravest show in the lower Metazoa; but even here it is always overshadowed in degree of morphological differentiation by the „embryo" or sexual generation. In the higher forms it becomes reduced; but, like the rudimentary sexual generation of the higher plants, it cannot vanish, for it also has its assigned task in the reproductive round, and in the Metazoa „direct development" is as much an impossibility as epigenesis or the formation of germ-cells from somatic cells!

The sexual generation or gametozoon, thanks to the importance of the precious cargo of germ-cells, which it carries, has received the kindly attentions of Nature, with consequent higher and higher evolution. From a variety of causes the larva or phorozoon, on the other hand, tends to simplification the higher one ascends. At the best its organisation is simple, but even this simplicity leans to meagreness in the Vertebrata as they now exist.

With the formation of the primary germ-cells the next item in the life-cycle is the production of an embryo or sexual generation by the self-sacrifice of one for the good of the rest. This is indicated in the diagram as having fallen to the lot of the 37th germ-cell from the bottom.

In the skate the embryo at first contains no germ-cells, and the primary germ-cells enter it as such: but, and this is another of the facts established by my work, by the time the embryo is completely laid down, the primary germ-cells divide and form secondary ones. So that, as a rule, by the time the evolution[1]) of the embryo is over

1) The word „epigenesis" is here deliberately avoided. After very prolonged study of the mode of vertebrate development my conclusion is, that epigenesis has no existence. In the preface to his „Germ-plasm" Weismann writes „I finally became convinced that an epigenetic development is an impossibility. Moreover, I found an actual proof of the reality of evolution etc."

and the critical period is reached, the embryo contains only secondary germ-cells, incapable of independent development.

It may be of interest to record the further fact, that in the skate this formation of secondary germ-cells precedes the announcement of the sex of the embryo, and is possibly causally related to it. Aswe have already seen, the future sex is betrayed by the nature of the egg itself. It is announced by differentiation of ovary or testis.

So far as the germ-cells themselves are concerned the union of the paternal and maternal nuclear portions is one of no long duration; for a commencement of the undoing of it is made at the formation of the secondary germ-cells. That is to say, the union brought about by the conjugation only persists until the primary germ-cells cease to be such, and divide to form secondary ones. Moreover, the tendency of research goes to demonstrate a certain looseness in this union. As Rückert and Häcker independently showed a few years ago, the paternal and maternal chromosomes remain distinct during the cleavage of Cyclops, indeed, in such a manner as to suggest a duplex-nucleus in each of the cells along the germinal track (in Weismann's sense). The like observation was subsequently made by the former in the cleavage-cells of Torpedo, without, however, suggesting any connection with germ-cells. The same duplication was recently noted by the writer in cleavage-cells of Raja, as well as in the primary germ-cells here, and the two were brought into connection. The interesting point about the matter appears to the writer to be, that if the reduction of chromosomes at the determination of sex for the following generation be ever a mere undoing of the previous lax union, the resulting germ-cells may reproduce or mimic more or less exactly, if not indeed absolutely so, the corresponding germ-cells of a grandparent. After such a reduction and new conjugation the reduced halves of the nuclei have, of course, lost the previous loose union referred to above, in order to acquire a new one of the like nature. Therefore, they cannot so easily revert to a great-grandparent. It is, I take it, the looseness of this union of chromosomes and the ease with which it may be un-

---

Though there be no preformation, there is a predestination, and this is finally brought to pass by an evolution or unfolding. In my own work the facts of the development of the thymus, of the lateral sense organs, of the whole gut, etc. are only explicable and intelligible on this view. Evidence of the like kind is also afforded by the facts as to the developmental origin of identical twins. The very instance, chosen by Caspar Friedrich Wolff, that of the development of the alimentary canal, in reality demonstrates in the clearest fashion, that its history is one of an evolution. The detailed facts concerning this may be brought forward on an early occasion.

With Weismann I must emphatically maintain epigenesis to be an impossibility in Metazoan development.

done at the reduction and sex-determination, which explains why a child, for example, often bears more likeness to a grandparent than to a parent.

As to the rest of the diagram, this relates to the determination of sex and to the final phases of oogenesis and spermatogenesis. With the exception of the portions relating to the determination of sex the data concerning oogenesis are taken, as will be recognised, from Boveri's well known figures. Of course, the embryo is not supposed to be hermaphrodite; both sexes being included in one diagram merely for purposes of convenience.

For fuller details concerning the determination of sex the reader may be referred to my recent communication on this subject. In the upper part of the diagram, attached to the 55th primary germ-cell, the probable course of oogenesis in the skate is shown. With the final division of the oogonium into two oocytes o. c. the determination of sex is depicted as happening in the formation of male oocytes and a female ones. These enter the period of growth and then pass on to ripen. Lower down, for comparison, the spermatogenesis of Paludina, with its two kinds of spermatozoa, is represented after the statements of Meves.

The portions of the diagram, appended to the 55th and 20th primary germ-cells, can naturally be applied to any of the remaining primary germ-cells, other than that, which goes to form the embryo.

What Weismann has termed the „germinal track" nowhere here touches the cells of the embryo. Neither, as we have seen, does it really lie within the asexual generation or phorozoon. It is along a line of unicellular organisms, which pass a portion of their life-cycle between one conjugation and the succeeding one within a sterilised individual, formed by the self-sacrifice of one for the good of the rest.

As revealed by the diagram, throughout this line of unicellular organisms, which are ever such, until one or other of them gets into the cul-de-sac of embryo-formation, there is a direct morphological continuity of germ-cells.

This is all Nature demands: this she accomplishes by the aid of unicellular organisms. All the observed phenomena of development, all those of heredity are possible in this way[1]). Notwithstanding apparent

1) Were proof wanting of the application of the results of the present research even to the highest animals, it might be found in Hubrecht's remarkable researches into the early development of Tup. aja javanica. (A. A. W. Hubrecht, Die Phylogenese des Amnions und die Bedeutung des Trophoblastes, Amsterdam, 1895.) Here the first products of the egg-cleavage are a small number of cells, forming a sac, the trophoblast, and containing one central cell, out of which the entire embryo arises.

As is now well-known, Hubrecht homologises the trophoblast with the complexity, the process is simplicity itself, the simplest kind of continuity conceivable.

On the Circle of Life revolves the epicycle of the germ-cells. The circumference of the former is filled in by an uninterrupted succession of such epicycles. The constant sequence of these is the rhythm of reproduction, the gamut of Life.

Fig. 1. Diagram of the life-cycle of the skate, Raja batis, illustrating the union of egg and sperm, E and S, to form the zygote Z, the origin of the phorozoon, or larva, or asexual generation, the germinal track from Z to U. K. Z., which is the primitive germ-cell, The division of the primitive germ-cell is carried to six mitoses, giving 64 primary germ-cells, P. G. C., instead of the full number of nine divisions in a female skate, yielding 512 primary germ-cells. Diagrammatically the evolution of one primary germ-cell, the 37th, is depicted as forming the embryo or gametozoon. To complete the track of heredity from generation to generation through the morphological continuity of the germ-cells, to the 55th primary germ-cell a diagram of oogenesis with the formation of male-and female-eggs, and of spermatogenesis (as in Paludina after Meves' work) to the 20th germ-cell have been added. In the latter the formation of the ordinary spermatozoa H. S. and of the non-functional wormlike ones, W. S. are shown.

Fig. 2. A portion of E. B. Wilson's diagram of the egg-cleavage of Nereis.

Fig. 3. The egg-cleavage of Nereis, depicted in fig. 2, represented after the fashion of fig. 1.

Autolytische Vorgänge in gesalzenen Heringen.

Von **Sigval Schmidt-Nielsen** (Bergen).

Vortrag gehalten in der biol. Gesellschaft zu Christiania am 18. Februar 1902.

M. H. Bei einer früheren Gelegenheit habe ich ihnen mitteilen können, dass beim Reifen der gepökelten Heringe eine Reihe von Spaltungsprozessen enzymatischer Natur statthaben[1]).

---

larval skin of an Amphibian: it is by no means a new idea to the writer, that the trophoblast represents the whole or the greater part of the asexual generation in mammals. The single clear cell in the sac in Tupaja must be the primitive germ-cell, which must give rise not only to the embryo, but also to the sexual products, or it must become the primitive germ-cell after one or two additional mitoses. It may be regarded as eloquent testimony of the correctness of my conclusions, that in Tupaja Hubrecht should have found the very things, which might have been postulated.

1) S. Schmidt-Nielsen: Beitrag zur Biologie der marinen Bakterien. Diese Zeitschrift Bd. XXI, Nr. 3, 1901.