

## CHAPTER XII

### HEREDITY AND DEVELOPMENT

*“To think that heredity will build up organic beings without mechanical means is a piece of unscientific mysticism.”—WILHELM HIS. But would even an omniscience of mechanical means explain the facts?*

- § 1. *Theories of Development*
  - § 2. *Weismann's Theory of the Germ-Plasm*
  - § 3. *Note on Rival Theories*
  - § 4. *Weismann's Theory of Germinal Selection*
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#### § 1. *Theories of Development*

**The Secret of Development.**—In his forty-ninth exercitation on the “efficient cause of the chicken,” Harvey (1578–1657), quaintly expressed his bewilderment before the baffling problem of development. “Although it be a known thing subscribed by all, that the foetus assumes its original and birth from the male and female, and consequently that the egge is produced by the cock and henne, and the chicken out of the egge, yet neither the schools of physicians nor Aristotle's discerning brain have disclosed the manner how the cock and its seed doth mint and coine the chicken out of the egge.” How much nearer a disclosure are we to-day? The visible sequences in the process of development are in many cases familiar, the external conditions of development are in many cases well known, and we have a little insight in regard to what is called the mechanics of development; but, on the whole, we have to confess that we

do not know the secret of development, which is part of the larger secret of life itself.

No doubt the process of development is objectively an orderly sequence of chemical and physical events, just as the growth of a crystal is. The developing embryo is the arena of intricate processes of chemical construction and disruption, of physical attractions and repulsions; but the characteristic feature of the whole business is, that it is co-ordinated, regulated and adaptive in a manner for which it seems at present, to say the least, very difficult to suggest any analogue in inanimate nature. For this reason not a few embryologists, such as Driesch, believe themselves warranted in frankly postulating a vitalistic factor—an Aristotelian "Entelechy."

**An Outline of what is known.**—We know that the germ-cells, and their nuclei more particularly, form the physical basis of inheritance; that there is a genetic continuity between the fertilised egg-cells which gave rise to the parents and those which gave rise to their offspring and those of their offspring; that fertilisation implies an intimate and orderly union of two individualities, condensed and integrated for the time being in the ovum and spermatozoon; that the sperm acts as a liberating stimulus on the ovum, as well as being the bearer of the paternal half of the inheritance and of a peculiar little body, (the centrosome), that plays an important part in the subsequent division of the fertilised egg-cell; that the mode of all development is by division of nuclei and the integration of the living matter into unit areas or cells, each presided over by a nucleus; that differentiation comes about very gradually—the obviously complex slowly arising out of the apparently simple; that paternal and maternal characteristics are distributed in exact equality by the nuclear or cellular divisions, and that the paternal and maternal contributions usually form the warp and woof of the web which we call the organism, and persist in the germ-cells thereof, though the expression or realisa-

tion of the bi-parental heritage varies greatly in each individual case ; that the parental heritages include ancestral contributions which may be expressed in development or may lie latent ; that normal development implies an appropriate environment, and that, during the development, there are subtle interactions between the growing organism and this environment, and between the different constituents of the growing organism ; that the development is in certain aspects like the building-up of a mosaic out of many independently heritable and variable parts, and that it is in other aspects the expression of an integrated unity, with subtle correlations between the parts, and with remarkable regulative processes working towards an unconsciously predetermined end ; that in a general way the individual development of organs progresses from stage to stage in a manner which suggests a recapitulation of the steps in racial evolution ; that many items in the inheritance, presumed to be present because of their re-expression in subsequent generations, may lie latent and find no realisation in the individual development ; that minute peculiarities of an ancestor may be handed on from generation to generation, although other peculiarities of that ancestor find no expression ; that the offspring of two parents differing in regard to some well-defined character may all resemble one parent as regards that character ; that the inbred offspring of these hybrids may have offspring divisible into two groups, one group resembling the one ancestor and the other group resembling the other ancestor ; that in other cases the expressed inheritance seems as if it were a mosaic of ancestral contributions from parents, grandparents, great-grandparents in a diminishing geometrical ratio according to the remoteness of the ancestors : and we know much more than all this !

**A Glimpse of our Ignorance.**—On the other hand, we have still to confess our inability to solve the old problems : How are the characteristics of the organism potentially contained

within the germ-cells? how do they gradually find expression in development? what is the nature of the compelling necessity that mints and coins the chick out of a drop of living matter? what is the regulative principle that secures the order and progress which, by devious and often circuitous paths, results in the fully-formed organism?

The solution is still far off, and perhaps we shall never get beyond saying that a germ-cell has the power of developing, just as a crystal has the power of growing. But this need not hinder us from trying imaginatively to formulate what takes place, for it is largely through these provisional hypotheses that research is provoked and facts are won.

It may be said that there are two main ways of considering the fundamental problem of "individual becoming" which embryology raises, and as these are *analogous* to the theories of "Epigenesis" and "Evolutio" which were so much discussed in the seventeenth and eighteenth centuries, the same catch-words may be retained.

**The Old Evolutio and Epigenesis.**—Without going into the details of an often-repeated story, we may recall how men, like Bonnet (1720-93) and Haller (1708-77), maintained the preformation of the organism and all its parts within the germ. The egg, Bonnet said, contained *très en petit* the elements of all the organic parts. "*Es gibt kein Werden,*" Haller said ("There is no becoming"). Those of this preformationist school regarded the apparent new formation of organs during development as an illusion; what occurs is only an unfolding (*evolutio*) of a preformed miniature. How the germ came to have this preformed miniature, they could not tell.

On the other hand, Caspar Friedrich Wolff (1733-94) was the pioneer of another school, in maintaining the reality of what he saw—a gradual differentiation from apparent simplicity to obvious complexity. The various organs of the developing embryo make their appearance successively and gradually,

and are to be seen being formed. There is no "evolutio"; there is *new formation* or "epigenesis." But how a germ that seems to start anew every time "from the pit of material homogeneity" can develop as it does, the upholders of epigenesis could not tell.

In fact, the preformationists and the believers in epigenesis came to a dead-lock, and both schools usually fell back on the assumption of hyperphysical agencies. Until the genetic or germinal continuity which links generation to generation was realised, there could be no real progress in theories of development.

**The New Evolutio and Epigenesis.**—With the growth of embryology the whole venue has changed, and it would be misreading history to say that students of development are still facing the dilemma expressed in the opposition between the eighteenth-century schools of evolutio and epigenesis. Yet there is to-day an *analogous* antagonism, which we must briefly discuss.

**The Mosaic Evolutio Theory.**—On one view it is supposed that the germ-cell has an architectural organisation, predetermined before development begins, and that development is in part a "histogenetic sundering" of the pre-existing germinal mosaic. Some authorities have suggested that the predetermination is in the organisation of the egg-cytoplasm—the central idea of the theory of "organogenetic germinal areas" which His elaborated in 1874. This theory may find support in experiments such as those of Roux on the frog ovum, in which one of the first two cleavage-cells was punctured, and its intact neighbour developed into a *one-sided* embryo; though the edge is taken off this case by the observation of Hertwig that in *other* conditions the intact blastomere may develop into a complete embryo of half the normal size. T. H. Morgan has shown that if the ova experimented with are kept stationary the result observed by Roux is likely to be seen, while if they are allowed free movement in the water the result observed

by Hertwig is likely to be seen. The theory may find support in the experiments of Morgan and Driesch on Ctenophore ova, where a defect in the cytoplasm (not involving the nucleus) is often followed by a modified cleavage and a defective embryo, as if the architecture had been seriously injured; but it may be opposed by Delage's experiments on merogony, where a small (and non-nucleated) fragment of a sea-urchin's egg may be fertilised and give rise to a complete larva. In some cases like the last it seems impossible to maintain that different parts of the egg are predetermined in relation to particular structures, and the same conclusion is suggested by Wilson's experiments on the lancelet ovum, where an isolated blastomere of the four-cell stage develops into a complete larva. In other cases, however, it *seems* as if the egg had a fixed and set architecture, which cannot be damaged without affecting the embryo. The experimental evidence is inconclusive.

**The "Preformation" must be Nuclear.**—But the researches of Kölliker, Strasburger, Hertwig, and others led to a transference of attention from the cytoplasm of the germ-cell to the nucleus. From the importance of the nucleus in metabolism, in the regeneration of Protozoon fragments, in maturation, in fertilisation, and in cleavage, it was argued—most forcibly, perhaps, by Weismann—that the nucleus must be the bearer of the heritable qualities. Meanwhile, many were recognising the value of Nägeli's conception (1884) of a specific idioplasm—a complex substance which, in its molecular organisation and in the metabolism it induces, is different for each species. Weismann developed this in his theory of the germ-plasm, which he regarded as wholly resident in the chromosomes of the nucleus. Thus, the locality of the pre-established organisation was shifted from the cytoplasm to the nucleus, though it is not inconsistent with this to suppose that in certain cases at least a cytoplasmic predetermination may arise as a secondary result of idioplasmic influence from the nucleus. In plainer words, perhaps, the

essential mosaic or organisation within the chromosomes of the nucleus may induce a secondary mosaic or localisation in the building material which the general substance of the egg-cell affords. It need hardly be pointed out that the organisation or architecture which is thought of in such cases is something infinitely finer than the microscopically visible (reticular or alveolar) structure which all living matter exhibits.

**What is Distinctive in Development?**—Unicellular organisms divide and redivide rapidly; it is their normal mode of multiplication. The germ-cells of multicellular animals do the same in the early chapters of their history. The fertilised egg-cell does the same; but the daughter-cells or blastomeres cohere to form an embryo, just as the daughter-cells into which some Protozoa divide also cohere to form a "colony." For a time there is no growth among the cleavage-cells into which the fertilised ovum divides, so that an embryo of sixty-four cells or more is no larger than the undivided egg. This, again, is paralleled by cases of spore-formation in Protozoa, where many divisions occur in a short time and within the limited space of the mother-cell. In some cases the young embryo shows a large number of nuclei derived from the division of the fertilised nucleus of the egg-cell, while the cell-substance is slow in being segregated around the nuclei into unit-areas or cells. This, again, is paralleled by some multinucleate Protozoa.

Thus the really distinctive fact in development is the progressive differentiation. The daughter-cells do not remain homogeneous; some start a lineage of nerve-cells, others a lineage of digestive cells, and so on. In a gradual, orderly fashion the apparently simple gives rise to the obviously complex, and throughout the process there are striking phenomena of adjustment to temporary conditions, of "self-differentiation" on the one hand and mutual influence on the other, and of integrated "regulation" throughout. We are so familiar with the orderly succession of events that we hardly realise the

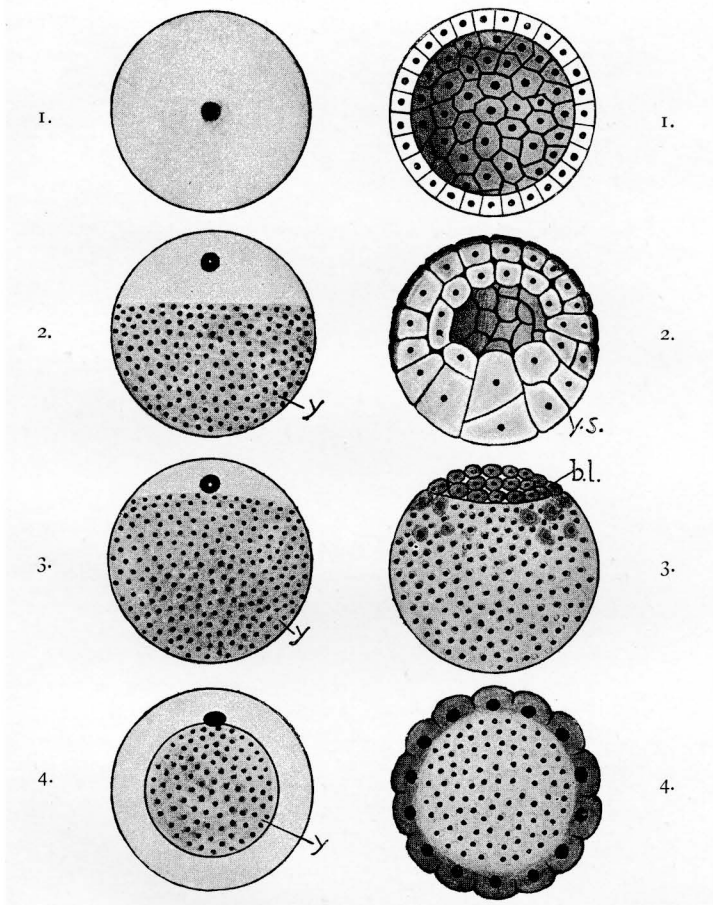


FIG. 42.—Modes of segmentation.

1, Ovum, with little yolk, segments wholly and equally into a ball of cells (blastula), *e.g.* sea-urchin; 2, ovum, with a considerable quantity of yolk (*y*), segments wholly but unequally, *e.g.* frog; *y.s.* larger yolk-laden cells; 3, ovum, with much yolk (*y*) towards lower pole, segments partially and discoidally, forming blastoderm (*bl.*), *e.g.* bird; 4, Ovum, with much central yolk (*y*), segments partially and peripherally, *e.g.* crayfish.

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marvel of it, until we play some trick with the developing egg, introducing disorder, and see how equilibrium and normality are restored. Thus the one-sided half-embryo of the frog proceeds at a certain stage to develop the missing half.

**Roux.**—Starting from the assumption that the nuclei of the germ-cells contain a specific idioplasm or architectural substance (the vehicle of the heritable qualities), and with the further assumption that this substance is a complex aggregate of different kinds of particles (the material expressions of different sets of qualities), Roux invented the hypothesis of two kinds of nuclear division, *quantitative and qualitative*. The former results in equivalent, the latter in dissimilar nuclei; the former is an integral, the latter a differential division. Roux supposed that the latter mode was characteristic of the early stage of development, during which the different components or qualities of the idioplasm are distributed among the blastomeres. Thus it comes about that each blastomere, though not independent of its neighbours, is endowed with a power of "self-differentiation" along particular lines defined by its specific share of the idioplasm.

**Weismann.**—Similarly, but even more elaborately, as we shall see, Weismann pictured development as a gradual process of differential division, distributing the representative particles or primary constituents of the germ-plasm. While this is going on there is also a process of quantitative division, which gives rise to the lineage of future germ-cells bearing the complete equipment of germ-plasm, and this quantitative division also occurs amid the qualitative divisions when many cells with identical characters are produced.

**Criticism of Mosaic Theories.**—These mosaic theories of development have been criticised from many sides. Thus it is pointed out that no visible phenomena of nuclear division suggest that the partition may be *qualitative*; on the contrary, that the whole elaborate process of nuclear division seems

adapted to secure the exact equivalence of the two daughter-nuclei. It may be, however, that while there is always a general equivalence, in the sense, for instance, that the large nuclear bodies or chromosomes are accurately split, and that each daughter-cell gets the same number, there may be at the same time a more intricate qualitiveness in the division. Again, the critics have brought forward some of the results of experimental embryology which seem at first sight to tell against the hypothesis of differential division, especially where one of the first two or first four blastomeres is seen to form a complete and normal embryo, or where under artificial conditions (of pressure, etc.) certain cells develop into tissues which in normal conditions are formed by quite different cells. To explain these and other difficulties—*e.g.* regenerative phenomena—various ingenious sub-hypotheses have been invented. It seems highly probable that the distribution of particular characters (if it be a reality at all) occurs sooner in some developing eggs than in others; in other words, that the cells of some embryos are “set” and defined at an earlier date than those of other embryos.

**Non-Mosaic Theories**—All embryologists agree that a germ-cell has a specific organisation, but many will not admit that it is necessary or useful to people the nucleus with a large body of representative particles, ready to distribute themselves and work upon the virgin soil which the protoplasm affords. All agree that there is gradual differentiation of cells as development proceeds, but many will not admit that it is necessary or useful to think of this in terms of a distribution of representative particles from the original depot in the nucleus of the fertilised egg-cell.

Oscar Hertwig may be named as a prominent representative of those who give the facts of development an interpretation somewhat different from that suggested by Roux and Weismann. We may suppose that, from the youngest ovarian ovum onwards, the nucleus exerts a “control” upon the surrounding cytoplasm, whether by the migration of “pangens” (De Vries), or of

specific formative substances (Sachs), or of enzymes, or by a propagation of molecular movements (Nägeli). In some such way—varying greatly in degree in different cases—the nucleus prepares in the cytoplasm of the egg a framework for its future operations. This may be so slightly pre-established that from a minute fragment of the egg a complete larva may be reared (as in sea-urchins), or so well established that if a part of the unsegmented egg be removed the remainder forms a defective larva (ctenophore). We may think of the controlling agency of a new colony laying down some preliminary lines of exploitation in the surrounding territory, making a railroad here, a canal there, a mere telegraph line somewhere else, but not sending out specialised settlers into the various areas, as the theory of differential divisions would suggest.

The nucleus of the fertilised egg-cell divides into equivalent halves, but these find themselves in more or less different territory, as the result of the preparatory framework which the nucleus, before division, had established in the cytoplasm. In technical language, the nuclei, though equivalent, find themselves in a not altogether isotropic medium. This incites further differentiation, both in the nuclear material and in the cytoplasmic sphere of influence. If the initial cytoplasmic differentiation was slight, the first steps in differentiation will be correspondingly slight, and in these cases an isolated cleavage-cell or blastomere may still form a complete embryo, as in the lancelet. If the initial cytoplasmic differentiation was more pronounced, an isolated blastomere may not be able to do more than form a partial embryo; the “setting” of the cytoplasm may be too strong to be overcome even by the completely equipped blastomere-nucleus.

Thus we reach the idea, expressed, for instance, by Driesch, that “the relative position of a blastomere in the whole determines in general what develops from it; if its position be changed, it gives rise to something different; in other words, *its prospective*

*value is a function of its position.*" But the "position" has a more than merely topographical connotation; it means, as Prof. E. B. Wilson says, "the physiological relation of the blastomere to the inherited organisation of which it forms a part."

But, here again, even when we recognise as fully as we can (a) the importance of the initial inherited organisation, (b) the influence of segment upon segment as development proceeds, and (c) the continually operative influence of the normal environmental stimuli, we have still to confess that the process of development remains very mysterious.

*The Antithesis of the Two Views.*—The student who is not yet clear as to the antithesis of the two views of development outlined above should read Dr. Chalmers Mitchell's admirably lucid introduction to his translation of Prof. Oscar Hertwig's *Biological Problem of To-day* (London, 1896). It concludes with the following contrast: "Hertwig says that all the cells of the epiblast, hypoblast, mesoblast, and of the later derivatives of these primary layers receive identical portions of germ-plasm by means of doubling [quantitative or integral (*erbgleich*)] divisions. The different positions, relations to each other and to the whole organism, and to the environment in the widest sense of the term, cause different sides of the capacities of the cells to be developed; but they retain in a latent form all the capacities of the species. Weismann says that the nuclear divisions are differentiating [qualitative (*erbungleich*)], and that the microcosms of the germ-plasm, in accordance with their inherited architecture, gradually liberate different kinds of determinants into the different cells, and that, therefore, the essential cause of the specialisation of the organism was contained from the beginning in the germ-plasm."

That differentiation may occur at very early stages is certain; that it has potentially occurred, although there is no visible evidence of it, is also certain; it seems to us difficult to interpret this without the hypothesis of differential division.

At the 2-cell or 4-cell stage of the development of the egg of the sea-urchin, the cells are equipotential, for an isolated blastomere (even at the 8-cell stage) may develop into a complete larva (Driesch).

But a little later, when invagination has occurred, when two germinal layers are established, the cells are no longer equipotential.

They can no longer regenerate complete larvæ. Even when several cells are separated off, they are not able to develop into complete larvæ. They grow into monstrous forms, which soon die. It is difficult to see why this should be so, unless differential division has occurred.

**An Analogy.**—A well-organised body of colonists reaches a new land, which they will develop. Soon after they land they distribute themselves in bands, according to their bent, as hunters, shepherds, fishers, farmers, miners, and so forth. As they possess the new land more and more fully, they segregate more and more, dividing into increasingly specialised bands; and as these find themselves in appropriate areas they settle down, and they stamp the areas with their particular character. Here a farm arises and there a factory, here a sheep-ranch and there a store, here a mine and there a fishing village. We can quite well understand that certain interpreters or historians would lay emphasis on the fact that, as the emigrant bands journeyed, they segregated persistently into smaller and more specialised groups, according to the old-established—indeed, hereditary—predispositions or qualities of the members composing the bands. This is a far-off image of the mosaic theory of development with its hypothesis of differential divisions.

On the other hand, we may imagine another well-organised body of colonists reaching another new land, which they will develop. They have a complex organisation with many potentialities, and they work best together. It cannot be said that some are preformed to be hunters, others to be shepherds, others to be fishers, others to be farmers, others to be miners, and so on. They begin by marking out the surrounding area into localities, and into each locality a representative band of emigrants proceeds to journey. They divide into homogeneous bands, each with a full representation of the capacities of the original body of colonists. But as they spread they are necessarily influenced by the area in which they find themselves,

and by their relations to neighbouring bands, and gradually they, too, differentiate into distinctive kinds of settlements. We can quite well understand that certain interpreters or historians would lay emphasis on the fact that, as the originally similar bands of colonists journeyed, they became differentiated in response to the varied environmental conditions and in relation to their neighbours. Their prospective value at any moment is "a function of their locality." This is a far-off image of the non-mosaic theory of development. *It is surely conceivable that both interpretations are correct.*

**Summary.**—According to the mosaic theory, the main mode of differentiation is *qualitative* nuclear division, which sifts out the various items of the mosaic (the representative particles or primary constituents) into different cells. Thus, if the fertilised ovum had the qualities or potential qualities *abcxyz*, its first four daughter-cells or blastomeres might have the qualities *abcxyz*, *abxyz*, *abcxy*, and *abcxz*. What each cell becomes is primarily determined by the particular contingent of representative particles which possesses it.

According to the non-mosaic theory, the division of the nucleus is always *quantitative*—*i.e.* without any sifting out of particular potentialities—and differentiation is due to the varied relations in which the nuclei find themselves. The prospective value of an embryonic cell, Driesch said, is "a function of its location." Each of the early cells is supposed to have a complete set of specific characteristics *in potentia*; but some of these remain latent, while others become active, this being determined by the relations of the cell to the whole system of which it forms a part.

Thus, while the two views agree in attributing to the essential germinal material a specific organisation corresponding to the hereditary qualities, they differ in their picture of what differentiation implies, the mosaic theory relying on the hypothesis of qualitative division which segregates representative particles,

the non-mosaic theory denying qualitative division and emphasising the importance of environmental interaction in the widest sense.

As far as experiment goes, evidence can be adduced in favour of both interpretations, and difficulties can be urged against both ; the question comes to be—since both views are unverifiable, which gives the most complete and consistent formulation of what we know to be facts? In their extreme forms the two theories are irreconcilable, but with some mutual concessions it seems possible to combine them.

### § 2. *Weismann's Theory of the Germ-plasm*

No one has done more to further the scientific study of heredity than Prof. August Weismann, of Freiburg, although his work has been on different lines from that of the statistical school which we particularly associate with the names of Mr. Francis Galton and Prof. Karl Pearson, or from that of the experimental school which we particularly associate with the names of Gregor Mendel and Mr. Bateson. In general we may say that Weismann has thought out a *theory of heredity*, coherent with a theory of development and a theory of evolution, which has inspired much research and has commanded the admiration of his most resolute opponents. He has done for the study of heredity what Dalton with his atomic theory did for chemistry, and though his theory will doubtless be developed, as Dalton's has been, it seems unlikely that the fundamental ideas of Weismannism will be discredited in the future evolution of biology.

As Weismann's interpretations have gone on growing as facts accumulated and as his insight increased, they present difficulty to those who have not followed their development, and it is therefore necessary to present a brief statement of Weismannism as developed, for instance, in *The Evolution Theory* (1904).

**The Material Basis of Inheritance.**—It seems that the botanist Nägeli was the first to point out that the material basis on which the hereditary tendencies depend must be a *minimal* quantity of substance. The inheritance from the father and from the mother is potentially equal; the vehicle of this inheritance is in the germ-cells; the mass of a spermatozoon may be only  $\frac{1}{100000}$ th part of the mass of the ovum which it fertilises; in one respect the two sex-cells are equivalent—they have the same number of stable readily stainable bodies or chromosomes in their respective nuclei; the number of these bodies is constant for each species, except that the number in the mature sex-cells is half that found in the ordinary cells of the body; the chromosomes play an obviously important part in the intermingling or amphimixis which occurs in fertilisation and in the subsequent divisions of the fertilised egg: for these and other reasons, Weismann concluded in 1885, as Strasburger and O. Hertwig did about the same time, that *the hereditary substance is in the chromosomes of the nucleus of the germ-cell.*

Microscopic vivisection experiments on Protozoa—*e.g.* the trumpet animalcule, *Stentor*—show that a fragment of a cell with a portion of nucleus will live on and reconstruct an entire organism, whereas a portion without nucleus, though it lives for a time, is unable to assimilate or recuperate its losses and soon dies. “It is in the nucleus, therefore, that we have to look for the substance which stamps the material of the cell-body with a particular form and organisation—namely, the form and organisation of its ancestors.” It goes without saying that the sex-cell is a unity, a minute organism, that its cell-protoplasm (in the case of the ovum at least) represents the building-material (trophoplasm), in which alone the hereditary substance (idiotoplasm) can unfold its wonderful powers; but it must be remembered that even a non-nucleated fragment of an ovum may develop (into a larva at least) if it be fertilised—*i.e.* supplied



with a sperm-nucleus. *Everything points to the conclusion that there is a definite hereditary material, and that it has its seat in the chromosomes of the nuclei of the paternal and maternal germ-cells.*

*Evidence that the Germ-plasm is Nuclear.*—No one can doubt that a germ-cell is a unity, that it represents a “cell-firm,” that its virtue is dependent on the interaction of nucleoplasm, cytoplasm, and centrosome, or that the substance of the egg is the actual building-material out of which the embryo is constructed. And yet, there are many facts which compel us to conclude that the essential basis of inheritance is in the *chromatin* of the nucleus. Repeating, in part, what we have said in Chapter II., we may note the following facts :

1. In some cases almost the whole cytoplasmic differentiation of the spermatozoon—namely, the locomotor apparatus—is left outside the ovum, and what enters is the head, which is almost purely chromatin-material, and the minute mid-body or centrosome, which functions as a dynamic centre in division.

2. The chromatin-bodies or chromosomes have a constant number for each species, except that in the mature sex-cells the number is half the normal, *i.e.* half the number found in the body-cells.

3. In nuclear division the chromosomes are longitudinally split, and are in various ways so distributed that each of the daughter-cells into which a mother-cell divides receives a precisely equivalent quota of chromosomes.

4. In many cases it is certain that the chromosomes of the spermatozoon entering the ovum are precisely equivalent in number to those which the mature ovum contains.

5. Throughout the whole world of life, the chromosomes—whether during the growth, or the maturation, or the amphimixis of germ-cells—behave in a generally similar manner, though there are many differences in detail.

6. Boveri succeeded in fertilising with a spermatozoon of one species of sea-urchin the cytoplasm of the ovum of another species of sea-urchin bereft of its nucleus, and the larva had *only paternal* characters. Delage succeeded in rearing normal larvæ of sea-urchins from non-nucleated fragments of ova fertilised by normal spermatozoa. Loeb succeeded in developing ova of sea-urchin, annelid (*Chaetopterus*), and mollusc (*Lottia*), without the introduction of spermatozoa at all. These facts, *taken together*, increase our con-

vidence in the conclusion that the nuclear material is the physical basis of the heritable qualities.

7. Microscopic vivisection has shown that the continued vitality of a cell-fragment depends on whether that fragment has any nucleoplasm or not.

**Ancestral Plasms.**—Assuming that the chromatin substance of the nucleus of the germ-cell is the vehicle of the inheritance, Weismann argued that it “contains not only the primary constituents of a single individual of the species, but also those of several, often even of many, individuals.” In fact, it is a mosaic of “ancestral plasms.” But what evidence is there of this?

A fertilised egg develops into an organism by cell-division. For a time it is demonstrable that the nucleus of each of the daughter-cells into which the fertilised egg-cell divides contains paternal and maternal chromosomes in equal number. Gradually differentiation sets in, and various kinds of body-cells with specialised structure and function appear; but often it is quite demonstrable that the maternal and paternal contributions are forming the warp and woof of the organism. While most of the ever-increasing crowd of embryonic cells undergo differentiation, some do not, but remain unspecialised, retaining the characters of the fertilised ovum. From this lineage of unspecialised cells, as we have explained in Chapter II., the germ-cells of the new organism arise. By-and-by when the organism becomes mature, these germ-cells are liberated, and each of them will have, by hypothesis, chromosomes derived from the original father and mother. But fertilisation will occur between these liberated germ-cells and others whose chromosomes are likewise derived from another father and mother, assuming that the usual cross-fertilisation occurs. Thus there comes to be an accumulation of contributions from different ancestors, though the actual number of visible stainable bodies or chromosomes is always kept the same. *It seems impossible to evade the conclusion that the material basis of inheritance is a mosaic of ancestral plasms.*

As a non-nucleated fragment of egg fertilised by a sperm will in some cases—*e.g.* sea-urchins—develop into a normal larva, as an unfertilised ovum—*e.g.* of sea-urchin—may under certain treatment develop into a normal larva, it is obvious that each of the germ-cells has in its nucleus a complete set of hereditary qualities.

As a single egg often produces two complete organisms (true twins), and in some cases—*e.g.* the parasitic Hymenopteron *Encyrtus*—produces a legion of embryos, it is obvious that, however the hereditary qualities are contained in their chromatin vehicle, they can be very readily and rapidly multiplied by division; and every one is aware how many germ-cells can be produced in a short time by a sexually mature animal.

It is now well known for a large number of animals and plants that during the maturation of ovum and spermatozoon the number of chromosomes is reduced to half the normal number characteristic of the body-cells of the species, so that the union of sperm-cell and egg-cell results, not in a doubling of the usual number of chromosomes (as would be the case were there no reduction), but in a restoration of the normal number. It therefore follows that a reduction of the number of chromosomes by a half does not in any way affect the completeness of the heritage. "The halved hereditary substance still contains the whole mass of primary constituents."

By following up this line of argument, Weismann was led to the theoretical conclusion that each of the chromosomes must contain a complete equipment of hereditary constituents, and that the germ-plasm represented by all the chromosomes in the germ-cell must include several "complexes of primary constituents," each complex sufficient in itself to form a complete individual. In other words, the fertilised egg-cell is a mosaic of "ancestral plasms."

'I call the idioplasm of the germ-cells *Germ-plasm*, or the

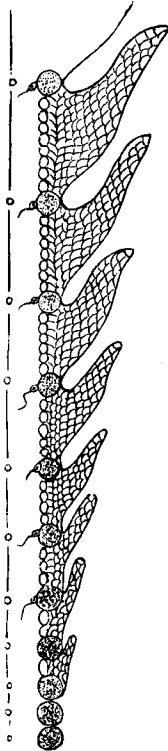


FIG. 43.—The relation between reproductive cells and the "body." The broken vertical line to the left represents a succession of ova from which "bodies" are produced. The other part of the figure indicates a chain of "bodies,"—successive generations. For convenience of the diagram, the "bodies" are represented as if larger at each generation. A sperm fertilising an ovum at the beginning of each generation is indicated.

primary-constituent-substance of the whole organism; and the complexes of primary-constituents necessary to the production of a complete individual I call *Ids.*" [In some cases these "ids" are probably the chromosomes, but many band-like chromosomes (or "idants") are visibly compound, consisting of several ids.] It is through the cooperation of these ids that the precise constitution of the individual which develops from the fertilised ovum is determined.

Every one admits that the germ-cell has a complex organisation, with the details of which every year makes us better acquainted. Every one admits that the whole substance of the fertilised ovum cannot be equally important as regards inheritance. Every one admits that small but still visible units—the ids or the chromosomes—behave as if they were of fundamental importance. If we admit that there is a hereditary substance at all, the theoretical interpretation begins when we regard these ids as containing a com-

plete set of hereditary qualities, as containing implicitly all the parts of a perfect animal, as the units in that multiply mosaic which makes up an inheritance.

There is more than a superficial resemblance between this doctrine and the Buddhistic theory of Karma. As Huxley said, "the tendency of a germ to develop according to a certain specific type is its Karma. It is the 'last inheritor and the last result' of all the conditions that have affected a *line of ancestry* which goes back for millions of years to the time when life first appeared on the earth. The germ-plasm is the last link in a once continuous chain extending from the primitive living substance; and the characters of the successive species to which it has given rise are the manifestations of its gradually modified Karma." (See *Evolution and Ethics*.)

**Determinants.**—"I assume," Weismann says, "that the germ-plasm consists of a large number of different living parts, each of which stands in a definite relation to particular cells or kinds of cells in the organism to be developed—that is, they are 'primary constituents' in the sense that their co-operation in the production of a particular part of the organism is indispensable, the part being *determined* both as to its existence and its nature by the predestined particles of the germ-plasm. I therefore call these last *Determinants*, and the parts of the complete organism which they determine *Determinates*" (1904, vol. i. p. 355).

But how many determinants are to be postulated in any given case? Weismann supposes that every independently variable and independently heritable character is represented in the germ-plasm by a determinant. A lock of white hair among the dark may reappear at the same place for several generations; it is difficult to interpret such facts of particulate inheritance except on the theory that the germ-plasm is built up of a large number of different determinants.

It may be pointed out that almost all biologists who have

tried to form a conception of the ultimate structure of living matter have been led to the assumption—expressed in very varied phraseology—of ultimate protoplasmic units which have the powers of growth and division. It is in no way peculiar to Weismann to imagine biophors and to credit them with the powers of growing and dividing. This cannot, indeed, be proved, but many facts point to it. The cell divides, but this is preceded by the division of the nucleus; the nucleus divides, but this involves splitting of the chromosomes; and the chromosomes are sometimes visibly composed of still smaller bodies, arranged like beads on a string. As Prof. E. B. Wilson says (1900, p. 84), "Our study of nuclear division reveals to us, not a homogeneous dividing mass, but a descending series of dividing elements, which, as if seen through an inverted telescope, recede from the eye almost to the limits of microscopical vision. There is no reason to place the limit of this series at the point where it vanishes from view, and we are thus almost irresistibly driven to the conclusion that the division of the nuclear substance as a whole must be the result of division on the part of invisible elements, by the aggregation of which the visible structures are formed." Moreover, in many cases the cytoplasm or extra-nuclear part of the cell contains minute bodies or "plastids"—*e.g.* chlorophyll corpuscles—which also multiply by division.

Those who find it difficult to believe in the theory that there are multiple sets of analogous determinants in the germ-plasm should consider, for instance, the facts of sex and sexual dimorphism. A queen bee lays an unfertilised egg which develops into a drone or male, which is in many detailed ways different from the queen, and is primarily different in producing spermatozoa, not ova. But since this drone has only a mother, no father, there must have been in the fertilised ovum which developed into the mother-bee the potentiality—*i.e.* the determinants—of male reproductive organs and masculine characters.

Yet there was no hint of these in the queen bee herself. They must have lain as latent elements in her inheritance. In the case of plant-lice (Aphides) and some water-fleas (Daphnids), where there is a succession of parthenogenetic females, the primary constituents of masculine characters must remain latent for several generations. In some cases—*e.g.* sea-urchins—the sexes are so closely alike, even as regards their reproductive organs, that we may almost say that they differ only in ‘physiological gearing,’ and that to postulate one army of determinants is sufficient without complicating matters by postulating at least two analogous armies. But in the great majority of cases there is marked dimorphism between the sexes, and, even in the cases above referred to, it has to be remembered that the spermatozoon itself is a very complex structure, with apical piece, head, middle piece, tail, and other minutiae, many of which have no analogue in the ova, and are, indeed, specially adaptive peculiarities which aid the spermatozoon in finding the ovum. Thus it is difficult to escape Weismann’s conclusion that both kinds of sexual characters must be present, some active, some latent, in every germ-cell and in every organism.

Another good example may be found in wheel-animalcules or Rotifers, where the primitive germ-cells divide into two kinds of eggs, externally identical, and yet so different that from the one kind only females develop, and from the other kind only males. Neither kind is fertilised. The ova which develop into females must carry with them determinants corresponding to masculine characters, though these remain quite latent, for these females give origin to males as well as females. It may be that nutritive and other environmental influences determine whether the determinants corresponding to the female sex or those corresponding to the male sex become active; but the point at present is, that it is difficult to think out what occurs except on the hypothesis that the germ-plasm

contains both male and female determinants, analogous but distinct.

**Summary of Weismann's View.**—"The germ-substance owes its marvellous power of development not only to its chemico-physical constitution, but to the fact that it consists of many and different kinds of primary constituents—that is, of groups of vital units equipped with the forces of life, and capable of interposing actively and in a specific manner, but also capable of remaining latent in a passive state until they are affected by a liberating stimulus, and on this account able to interpose successively in development. The germ-cell cannot be merely a simple organism; it must be a fabric made up of many different organisms or units—a microcosm" (1904, vol. i. p. 402).

A living creature usually takes its origin from a fertilised egg-cell, from a union of an ovum and a spermatozoon—two dimorphic germ-cells. These germ-cells are descended by continuous cell-division from the fertilised ova which gave rise to the two parents; they have retained the organisation of those fertilised ova, and this organisation has its vehicle in the stainable material of the nuclei—the germ-plasm. This germ-plasm consists of several chromosomes or idants, each of which is made up of several pieces or ids, each of which (here hypothesis begins), is supposed to contain all the potentialities—generic, specific, and individual—of a new organism. Each id is a microcosm with an architecture which has been elaborated for ages; it is supposed to consist of numerous determinants, one for each part of the organism that is capable of varying independently or of being independently expressed during development. Lastly, each determinant is pictured as consisting of a number of ultimate vital particles or biophors, which are eventually liberated in the cytoplasm of the various embryonic cells. All these units of various grades are capable of growth and of multiplication by division.



### Summary.

- The physical basis of inheritance—the germ-plasm—is in the chromatin of the nucleus of the germ-cell.
- The chromatin takes the form of a definite number of chromosomes (or idants).
- The chromosomes consist of ids, each of which contains a complete inheritance.
- Each id consists of numerous primary constituents or determinants.
- A determinant is usually a group of biophors, the minutest vital units.
- The biophor is an integrate of numerous chemical molecules.

**Maturation and Amphimixis.**—It is necessary here to inter-plate a reference (*a*) to the facts of maturation—the processes that occur in the immature egg-cells (oocytes) and in the immature sperm-cells (spermatocytes); and (*b*) to the facts of amphimixis or fertilisation—the intimate and orderly union of the (reduced) nuclei of the two kinds of sex-cells.

Since the spermatozoon is known to bring into the mature ovum the same number of chromosomes as the mature ovum contains in its nucleus, each act of fertilisation would double the *normal number* of chromosomes if there were not some process obviating this. The doubling of the normal number does not occur, because the mature spermatozoon and the mature ovum have already undergone a reduction of the number of their chromosomes to half the normal number.

In various ways, during the divisions of the sperm-cells antecedent to their complete differentiation, and during the process which is called the maturation of the ovum—the two divisions which result in the liberation of two polar bodies—the normal number of chromosomes is reduced by a half. Thus, when fertilisation occurs, the number of chromosomes is restored to the normal. This fact has been securely established by the researches of Van Beneden, Oscar Hertwig, Boveri, Henking, and others.

**Reducing Divisions.**—Since Van Beneden discovered that

each of the two nuclei which unite in fertilisation contains one-half of the number of chromosomes characteristic of the somatic cells, though the nuclei of the earlier stages of the germ-cells have the same number as the somatic cells, it has been plain that a reducing process must occur at some stage, and there is now general agreement that the reduction takes place in the last two cell-divisions by which the definitive germ-cells arise—namely, when the ovarian ovum gives rise to the mature ovum and two or three

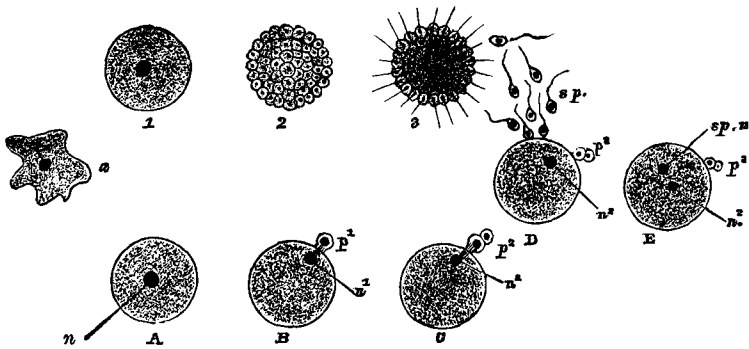


FIG. 44.—Diagram of maturation and fertilisation. (From *Evolution of Sex*.)

The upper line shows development of spermatozoa. The lower line shows maturation of the ovum. The middle line to the right shows fertilisation. *a*, an amoeboid primitive sex-cell; A, ovum, with nucleus or germinal vesicle (*n*); B, ovum, liberating first polar body (*p*<sup>1</sup>); C, extrusion of second polar body (*p*<sup>2</sup>); *r*, a mother-sperm-cell or spermatogonium; 2, 3, balls of immature spermatozoa, resulting from the division of (*r*); *sp.*, mature spermatozoa; D, the entrance of a spermatozoon into the ovum; E, the male and female nuclei *sp.n* and *n*<sup>2</sup>, approach one another.

polar bodies, and when a spermatocyte divides into four spermatozoa or young spermatozoa. The parallelism in the two cases is very striking, but as O. Hertwig says, "while in the latter case the products of the division are all used as functional spermatozoa, in the former case one of the products of the egg-mother-cell becomes the egg, appropriating to itself the entire mass of the yolk at the cost of the others, which persist in rudimentary form as polar bodies." The hypothesis of Minot, adopted also by

Van Beneden, that each germ-cell is originally hermaphrodite, and that the maturation processes imply the removal of male qualities from the ovum and of female qualities from the spermatozoon, has been abandoned; and the reducing divisions are recognised as securing a constancy in the number of chromosomes characteristic of each species, for without some such preliminary reduction the number would obviously be doubled at each fertilisation. That a reduction does really occur in both plants and animals seems now incontrovertible, but the precise manner of the reduction seems to differ considerably in different organisms. It should be noted, moreover, that in some parthenogenetic ova—*e.g.* of Aphides—only one polar body is formed and no reduction in number is effected; while in other parthenogenetic ova—*e.g.* those eggs of bees which develop into drones—two are formed: a strange fact, in part at least explained by Brauer, who showed that in the parthenogenetic ova of *Artemia* both types occur, but that when two polar bodies are formed the second remains in the egg and behaves practically like a sperm-nucleus.

Minute inquiries have gone so far that it is possible to assert that in some cases the young germ-cell has an equal number of paternal and maternal chromosomes. And similar minute inquiries—which almost baffle us with their intricacy—make it exceedingly probable that in the reduction divisions maternal chromosomes separate from paternal chromosomes, and yet not so thoroughly that all the paternal chromosomes pass into one cell and all the maternal into another. If this be true, we can better appreciate the importance of the reduction-divisions which occur in maturation, for they afford opportunity for new permutations and combinations of hereditary qualities. They do not originate anything new, but they shuffle the cards, so to speak. In some cases, at least, it seems quite certain that entire chromosomes are separated off into different cells, into polar bodies which come to nothing, or into other sperma-

toocytes which become spermatozoa. It may be said, we think, in perfect fairness that many of the quite impartial studies on maturation, and the associated reducing-divisions, confirm Weismann's view that there is a segregation of individual chromosomes (vehicles of several complete sets of hereditary equipments); and that there is, therefore, in this process, a *modus operandi* for new permutations and combinations of ancestral plasms. In other cases, however, this view is *not* corroborated as yet.

**Fertilisation.**—Recent work has forcibly suggested that there are in fertilisation two more or less distinct processes: on the one hand, the process by which the gametes, bearing the hereditary characters, unite to form the beginning of a new individuality; on the other hand, the process by which the spermatozoon supplies some stimulus, prompting the ovum to divide. The first aspect is that of amphimixis, believed by many to be of importance in initiating—and, it may be, also in checking—variations, but in any case effecting the union of hereditary qualities contained in the two gametes. The second aspect is that of mitotic stimulus, believed by some to be afforded by an enzyme—for which the name of “ovulase” has been suggested—and by others to be localised in the sperm-centrosome. It is seen in many cases that equivalent numbers of chromosomes are contributed by the two nuclei; it is evident that the ovum contributes by far the larger quantity of cytoplasm; it seems to have been securely demonstrated in some cases that “from the father comes the centrosome to organise the machinery of mitotic division by which the egg splits up into the elements of the tissues, and by which each of these elements receives its quota of the common heritage of chromatin.” “Huxley hit the mark two-score years ago when he compared the organism to a web, of which the warp is derived from the female and the woof from the male. What has since been gained is the knowledge that this web is to be sought in the chromatic substance of the nuclei, and that the centrosome is the weaver at the

loom" (Wilson, 1896, p. 171). While the ovum-centrosome of many animals seems to disappear, that introduced by the spermatozoon divides into two, and around each a system of rays develops. The sperm-centrosomes migrate to opposite sides of the segmentation nucleus, and between them appears the spindle of the first cleavage. It may be hasty to call them "kinetic centres," but they seem to have an important rôle in the division-process.

Let us suppose that a young egg-cell has sixteen chromosomes or idants, 16A ;  
 in the course of maturation the number is reduced by a half to 8A ;  
 the mature egg-cell is fertilised by a (reduced) spermatozoon with eight chromosomes, 8B ;  
 the fertilised egg-cell has then eight maternal and eight paternal chromosomes, 8A + 8B ;  
 the young germ-cell capable of initiating a new generation has the same ;  
 in the maturation of this young egg-cell reduction occurs to 4A + 4B ;  
 it is fertilised by a sperm of analogous history with 4C + 4D ;  
 the fertilised egg of the second generation has therefore 4A + 4B + 4C + 4D ;  
 similarly, the fertilised egg of the third generation may have 2A + 2B + 2C + 2D + 2E + 2F + 2G + 2H ;  
 similarly, in the fourth generation the chromosomes may be A + B + C + D + E + F + G + H + I + J + K + L + M + N + O + P (sixteen all different).

But the number of different chromosomes *need* not mount up so rapidly, for some of the paternal chromosomes may be the same as maternal. Moreover, the reducing division need not leave the maximum number of different chromosomes. The number sixteen, by hypothesis characteristic of the species, cannot be exceeded; but the heterogeneity may spread into the individual chromosomes, affecting the ids.

**Summary.**—Put as simply as possible, the case is as follows.  
 The independently heritable and variable qualities of an

organism are represented in the young germ-cell by a number of material elements (determinants).

As the young egg-cell ripens it divides in such a way that its determinants are reduced in number by one-half. Not that it need lose any particular kind of determinant, corresponding let us say to the colour of the eye or the colour of the hair, for each kind of determinant is represented in multiplicate. It loses one-half of its sets of determinants. The same happens with the ripening sperm-cell.

When the mature egg-cell is fertilised by the mature sperm-cell, the number of sets of determinants is once more raised to what it was in the young cells before maturation. But though the number of sets is the same as before, the collocation of the sets is not the same. At any rate, it need not be the same; for there is an *apparently* random reduction.

*The character of the offspring depends upon the adjustments arrived at among the different sets of determinants of maternal and paternal origin.*

**Hypothesis of Development.**—Postulating an equipment of primary constituents or determinants within the germ-plasm, Weismann proceeded to elaborate a hypothesis as to the manner in which these determinants determine the cells or cell-groups to which they correspond.

The fertilised egg-cell divides and redivides, and at first the resulting cells (blastomeres) of the embryo are often equivalent to one another. This is demonstrable experimentally, for if the first four cells of the lancelet's ovum, for instance, be shaken apart, each goes on developing on its own account and forms a complete larva. In other cases, the resulting cells are heterogeneous from the first division onwards; and, in any case, they soon become heterogeneous—that is to say, they form certain parts of the embryo, and these only. In other words, there must be a distribution of determinants in the course of segmentation.

But if the various kinds of determinants are to get into appropriate cell-groups, this cannot be a matter of chance. Therefore, we must further postulate that from the first each determinant has a definite position in relation to its neighbours, that the germ-plasm is not a mere loose aggregate of determinants, but that it possesses a structure, an architecture, in which the individual determinants have each their definite place. It must be borne in mind that the germ-cell is a unity, a potential organism, and not a heap of hereditary contributions. Weismann supposes that the determinants are kept in relation to one another by "vital affinities," by internal forces, some exhibition of which is, indeed, demonstrable, as when a chromosome or ribbon of ids splits into a double ribbon of ids.

But if the mechanism of the distribution of determinants is by cell-division—one of the features of which is that the chromosomes are halved with minutiose accuracy, so that each of the two daughter-cells obtains a longitudinal half of each chromosome—how does it come about that different determinants pass into different cells of the embryo? This difficulty led to the further hypothesis that, while ids may divide into two identical halves, they may also divide into two dissimilar halves. Weismann supposed that besides integral (*erbgleich*) division of the nucleus, there is also differential (*erbungleich*) division. The reality of this differential division—which many histologists vigorously dispute—cannot be directly demonstrated any more than the splitting up of a complex molecule into different molecules can be demonstrated. But in both cases we may infer the occurrence from the results. It is not a hypothesis, but a fact, that a cell may divide into two daughter-cells, one of which goes to form ectoderm, while the other goes to form endoderm, and this implies some sort of differential division. What internal forces or vital affinities are concerned we do not know.

If an egg-cell can divide differentially into a primordial ectoderm-cell and a primordial endoderm-cell, or into a formative

cell and a purely nutritive cell, and so on, it seems legitimate to suppose that corresponding differential divisions on a finer scale go on in the course of development. The embryonic cells go on dividing into daughter-cells having dissimilar developmental import or prospective value, and "such differential divisions will continue to occur until the determinant architecture of the *ids* is completely analysed or segregated out into its different kinds of determinants, so that each cell ultimately contains only one kind of determinant, the one by which its own particular character is determined. This character, of course, consists not merely in its morphological structure and chemical content, but also in its collective physiological capacity, including its power of division and duration of life" (1904, vol. i. p. 378).

It goes without saying that development also includes many integral divisions. Cells are continually producing their like, especially when there are numerous similar organs or parts in the organism. It must also be noted that the segregation-process cannot be pictured unless we suppose that the determinants—being alive—can multiply among themselves, so that a cell dominated by one kind of determinant may contain a whole army of determinants of that kind. We must also suppose that determinants may remain for a long period in an inactive state, and that it is only when they find themselves in an appropriate environment, largely determined by the cellular neighbourhood, that liberating stimuli awaken them to their controlling power.

**The Breaking-up of the Determinants.**—The segregation or distribution of the determinants goes on, and each unit-area or cell of the developing organism becomes the seat of a particular kind of determinant or of a contingent of these. What then happens? Weismann supposes that the determinant, having attained mature strength and its appropriate environment, breaks up into the biophors which compose it, and that these



migrate from the nucleus into the cell-substance. But there a struggle for food and space must ensue between the protoplasmic elements already present and the newcomers, and this gives rise to a more or less marked modification of the cell-structure. The biophors need not be supposed to correspond in advance to particular constituent parts of the cell, such as muscle elements or chlorophyll corpuscles; it is more plausible to suppose that they are the architects of these. Of course, they must have some definite character, but they need not be the infinitesimal rudiments of what they form. Many of them may be regulative, rather than formative. They may be organisers as well as architects. We need not stint their qualities, for they are *alive*.

Weismann does not conceive of the determinants as "seed-grains of the individual characters of the organism"; they are "codeterminants of the nature of the part which they influence." Like colonists entering upon a new territory, they owe their power to their co-operation. Again, the "character" of the cell—its size, intimate structure, length of life, and so forth, is not determined by a number of special determinants for each feature in the character. "There are only determinants of the whole physiological nature of the cell," and they work out the character of the cell in co-operation with one another and with the cell-body into which they have penetrated.

We cannot give a short account of the ingenious elaborations of the theory of determinants, by the aid of which Weismann has endeavoured to give a consistent all-round interpretation of special phenomena, such as budding, fission, regeneration of lost parts, alternation of generations, dimorphism, polymorphism, and so on. He supposes, for instance, that in those organisms which can multiply by liberating a bud or a fraction of the body there must be in many of the cells a residual contingent of determinants—amounting, it may be, to a representation of the entire germ-plasm—and that this contingent

remains latent until special circumstances arise which call it into activity.

**Note on Regeneration.**—When half of a highly differentiated Infusorian like *Stentor* regenerates the missing half, we suppose that it does so because in each half there are diffusely distributed “specific units” or “groups of determinants,” which can in appropriate environment grow into wholes. We are encouraged to hold this hypothesis since we know that slices of *Stentor* a millimetre or less in thickness can re-grow wholes.

We shift the experiment to a slightly higher level, and we find that fragments of relatively simple multicellular animals, such as Hydra and Planarians, can grow into entire organisms. We suppose that the excised groups of cells have among them a sufficient complement of “specific units” to ensure the development of a complete organism.

But as we ascend higher in the scale, we find that while the earthworm can re-grow a new head or a new tail, a few median segments cut out of the middle of an earthworm will soon die. A crab can re-grow a lost limb, but the limb cannot re-grow a crab. The inference is that as differentiation increases the diffuse distribution of “complete specific units” ceases, so that the excised part is no longer a viable fragment. All this points to the reality of differential cell-division.

If the eye-bearing horn of a snail be cut off, it is regenerated over and over again, with the complex eye complete. If the eye of a crab be excised, there is usually regenerated an antenna instead of an eye, but if the optic ganglion is not injured a normal eye is regenerated. If the front of the eye of a newt or of a salamander be cut off, a new lens is regenerated. All this points to the hypothesis that within limits, probably punctuated by natural selection, the maimed stump or foundation of an important organ retains in reserve a contingent of units capable of growing the whole of that organ. Thus, while the distribution of complete residual specific units or ids becomes more and more

restricted, there is a much more useful retention, at spots liable to injury, of local contingents of "organ-forming units" which can replace lost parts.

**Difficulties.**—1. If definite determinants are distributed in development as the number of unit-areas or cells increases, how is it that an isolated group of cells, cut off from a begonia-leaf, a potato-tuber, a hydra-polyp, a sea-anemone, a simple worm, may in appropriate conditions grow into an entire organism? It must be noted, in the first place, that this capacity is more or less restricted to relatively simple organisms. In the second place, the theoretical answer is that in such cases the cells retain a representation of the whole germ-plasm in an inactive state, though each one of them is differentiated under the control of a particular set of determinants.

2. A man has a peculiar "crooked nose" and his son has the like. Are we to suppose that the inheritance includes "crooked nose"-determinants? Weismann would say "emphatically not." A large number of different kinds of determinants are concerned in the up-building of the nose, and they work co-operatively towards a general result. There may be some *slight peculiarity in those that contribute*, let us say, to the cartilage of the nose, and this peculiarity may, in the course of the co-operative development, lead to a crooked nose as the result of some inequality of pressure during the early formative period. The results of experimental embryology show clearly that the behaviour of particular cells in development is not absolutely stereotyped; they will do their best, as it were, to work out a constant result, but if this is interfered with environmentally they will do something else. At the same time, it is very interesting that abnormal larvæ—*e.g.* the so-called Lithium-larvæ of sea-urchins—have a remarkable power of righting themselves when they are relieved from the disturbing influence of the abnormal environment.

**Objections to the Theory of Determinants.**—Some biologists

have objected to Weismann's theory of determinants, because, as they say, no one has ever seen or can ever hope to see one. Determinants are scientific fictions and all discussion of them is in the air. But the same sort of objection may be raised against the theory of, let us say, the ether. The point is whether the concept of determinants helps us to interpret visible phenomena. Science works from beginning to end with imaginative concepts which facilitate description and formulation, and which are so truly representative of the invisible that we can utilise them in prediction.

Other biologists, who are aware of the impossibility of a science without imaginative concepts, object to the theory of determinants on the ground that they can be done without. Thus Prof. Yves Delage rejects all determinants, primary constituents, or *particules représentatives*, and will only postulate a germ-plasm with "an extraordinarily delicate and precise physico-chemical composition." "There are not," he says, "in the germinative plasm any distinctive particles representing the parts of the body or the characters and properties of the organism" (1903, p. 749). What is there, then? According to Delage, the germ-cell contains a number of characteristic chemical substances—which every one admits—characteristic of the chief categories of cells; and its development is comparable to the flow of a river, now running deep and again shallow, here forming a waterfall and there an eddy, but always explicable in terms of action and reaction between the flowing water and its surroundings. Given the power of developing (which no one understands), given a characteristic chemical composition (which every one admits), and given an appropriate environment (which nobody can deny), and *voilà tout*. There is no more need to cumber biology with determinants and biophors than there was to cumber astronomy with Ptolemaic circles and epicycles.

But even in the apparently simplest cases it seems impossible

to dispense with the concept of "units," or "primary constituents" or "determinants" or groups of these including all the specific characters. Take the case of the common Infusorian *Stentor*. It seems to be certain that a thin slice, a millimetre thick, of this unicellular organism may, in appropriate conditions, grow into a complete individual, with vibratile oral cilia, smaller superficial cilia, a mouth, a long necklace-like nucleus, three smaller nuclei, a contractile vacuole, internal contractile fibrils, and so on. Is it possible to think of this marvellous regeneration of a highly differentiated unity from a thin slice, without postulating "units" of some sort, which, when removed from the system as a whole, have yet the power of reconstituting that system? (See Weldon, 1905, p. 42.) Similarly, a thin slice of the multicellular Hydra-polyp may, in appropriate conditions, grow into an entire and complete Hydra. Is it possible to conceive of this apart from the postulate of diffusely distributed "specific units"?

Prof. H. E. Ziegler has briefly and temperately stated the two most frequent objections to the theory of representative particles.

1. When we try to interpret any result or occurrence we must refer it to what is known. If we interpret it in terms of a something invented for the purpose we are simply making a fictitious hypothesis. When we refer facts of inheritance to observable processes—*e.g.* in the chromosomes of the nuclei—we are making scientific progress; but when we deduce the phenomena of inheritance from the behaviour of pangens or determinants which have been invented we are simply indulging in verbal speculation. As it appears to us, this is not a just statement of scientific procedure. The imaginary pangens or determinants are elements in a notation like the graphic symbols of chemical molecules: their utility does not depend on any visible reality; their validity is tested by the degree in which they enable us to formulate conceptually what does occur, and

to reach forward from this formulation to more precise observation and experiment. It goes without saying that the moment the symbolic notation is shown to be inconsistent with demonstrable facts, it must be thrown overboard and replaced by another.

2. It is difficult, Ziegler says, to think out clearly what we mean by a unit-character and by its being represented by a unit-germinal-constituent, whether pangen or determinant. Many a quite definite character of an organism depends upon a multitude of growth-conditions, and to conceive of the character being represented in the germ by one representative particle is as difficult as it is to conceive of an infinite number of representative particles, one for each item in the character.

But it should be noted that Weismann simply assumes as many determinants in the germ-plasm as there are parts in the organism capable of independent and transmissible variation. The fiddling string and bow on a grasshopper's thigh and wing will have at least one determinant each, but one determinant may suffice for all the millions of red blood corpuscles in man. Again, Weismann expressly emphasises his view that "determinants are not seed-grains of individual characters, but co-determinants of the nature of the parts which they influence. There are not special determinants of the size of a cell, others of its specific histological differentiation, and still others of its duration of life, power of multiplication, and so on; there are only determinants of the whole physiological nature of a cell, on which all these and many other 'characters' depend." Or again, "There are no determinants of 'characters,' but only of parts. The germ-plasm no more contains determinants of a 'crooked nose' than it does those of a butterfly's tailed wing; but it contains a number of determinants which so control the whole cell-group in all its successive stages, leading on to the development of the nose, that ultimately the crooked nose must result, just as the butterfly's wing, with all its veins, mem-

branes, tracheæ, glandular cells, scales, pigment deposits, and pointed tail, arises through the successive interposition of numerous determinants in the course of cell-multiplication."

In any case, whether the idea of representative primary constituents commends itself to us or not, we must remember that it is a *fact* that the organism—unified as it is—is built up of a very large number of independently variable, independently heritable items.

**The Persistence of the Germ-plasm.**—We have given an outline of the consistently-thought-out scheme which Weismann has suggested as an interpretation of development—the distribution of the determinants, their "maturation," their "liberation," their migration from the nucleus, their dissolution into biophors, and the manner in which the biophors may control the area or cell in which they find themselves. But it remains to inquire how the germ-cells which start the next generation are constituted. If the building-up of the body involves segregation of the determinant architecture into smaller and smaller groups, how does the organism produce germ-cells—that is, cells with intact germ-plasm—with a complete equipment of determinants? The answer, already given in Chapter II., is that it does not in the strict sense produce them; *they are there all the time.*

In more detail, Weismann's answer (1885)—*the theory of the continuity of the germ-plasm*—is that in the divisions of the ovum the whole of the germ-plasm is not broken up into determinant groups; part of it is kept intact and handed on from cell to cell along a lineage or "germ-track," which may be very short or very long, until, sooner or later, it stamps a cell as a primordial germ-cell. In other words, while most of the cells, derived by division from the fertilised ovum become differentiated as body-cells, some of the cells retain a quota of intact germ-plasm, and eventually give rise to recognisable germ-cells. Body-cells and reproductive cells alike owe their being to the

germ-plasm of the fertilised ovum, and are its lineal descendants ; but the somatic cells are dominated by particular segregated and liberated sets of determinants, whereas the germ-cells are those, or the descendants of those, that retain the complete equipment.

In studying the development of the threadworm of the horse (*Ascaris megalocephala*), Boveri found that the two first segmentation-cells both receive the four chromosomes characteristic of the species; one gives rise to all the body-cells, the other to all the germ-cells. In the lineage of the former there is a visible reduction of the chromatin ; in the lineage of the other there is no such reduction. This is perhaps the clearest of all cases, and the case of some of the Diptera is almost as clear. But theoretically it makes no difference how long the "germ-track" may be, or how long it may be before recognisable germ-cells are seen in the developing organism. In some familiar cases—the alternation of generations in Hydroids—the reproductive cells, as such, are not demonstrable till after the asexual generation forms a sexual bud ; and yet, even here, we know some very interesting facts regarding the germ-cell lineage.

### § 3. *Note on Rival Theories*

**Darwin's Theory of Gemmules.**—Darwin's provisional theory of pangenesis suggests, as we have already seen, that particular cells of the body give off representative gemmules, and that these are collected in the reproductive cells. When the fertilised egg-cell divides and redivides, the army of gemmules is contained in each cell ; but at every stage of development particular kinds of gemmules are stimulated to activity, and proceed to influence the area in which they find themselves—an area corresponding to that from which they were originally given off. As Weismann points out, this hypothesis requires us to postulate an enormous number of specific stimuli, distributed through the crowd of



embryonic cells, which almost amounts to assuming the differentiation which the theory was intended to interpret.

Weismann tries to avoid this difficulty by assuming an automatic dissolution of the determinant complexes, though he does not reject the view that the differently related vital areas or cells in which the determinants find themselves may serve as liberating stimuli. In a marching army the differently related localities serve as liberating stimuli to the diverse kinds of men composing the army; here the sappers and miners go to work, there the commissariat erects a depot, in a third place a heliograph is set up, and so on.

**Herbert Spencer's Theory of Physiological Units.**—Spencer postulated "physiological units," ultimate life-bearing elements, intermediate between the chemical molecules and the cell. Just as the same kinds and even the same number of atoms may compose, by different arrangements, numerous quite different chemical molecules—*e.g.* in the protein-group—so out of similar molecules diversely grouped an immense variety of "physiological units" may be evolved, like the variety of patterns in a kaleidoscope. But for each kind of living creature Spencer postulated "physiological units" or "constitutional units" of one kind.

Spencer credited his "constitutional units" with much.

1. They carry within them the traits of the species, and even some of the traits of the ancestors of the species; the traits of the parents, and even some of the traits of their immediate ancestors; and the inborn idiosyncrasies of the individual organism itself.

2. They "must be at once in some respects fixed and in other respects plastic; while their fundamental traits, expressing the structure of the type, must be unchangeable, their superficial traits must admit of modification without much difficulty; and the modified traits, expressing variations in the parents and immediate ancestors, though unstable, must be considered as capable of becoming stable in course of time."

3. Moreover, "We have to think of these physiological units

(or constitutional units, as I would now rename them) as having such natures that while a minute modification, representing some small change of local structure, is inoperative on the proclivities of the units throughout the rest of the system, it becomes operative in the units which fall into the locality where that change occurs."

4. Furthermore, Spencer supposed "an unceasing circulation of protoplasm throughout an organism," such that "in the course of days, weeks, months, years, each portion of protoplasm visits every part of the body"—a wild assumption. Therefore, "we must conceive that the complex forces of which each constitutional unit is the centre, and by which it acts on other units while it is acted on by them, tend continually to remould each unit into congruity with the structures around; superposing on it modifications answering to the modifications which have risen in these structures. Whence is to be drawn the corollary that in the course of time all the circulating units—physiological, or constitutional, if we prefer so to call them—visit all parts of the organism; are severally bearers of traits expressing local modifications; and that these units, which are eventually gathered into sperm-cells and germ-[egg]-cells, also bear those superposed traits."

5. According to Spencer, "sperm-cells and germ-[egg]-cells are essentially nothing more than vehicles in which are contained small groups of physiological units in a fit state for obeying their proclivity towards the structural arrangement of the species they belong to"; and "if the likeness of offspring to parents is thus determined, it becomes manifest, *a priori*, that, besides the transmission of generic and specific peculiarities, there will be a transmission of those individual peculiarities which, arising without assignable causes, are classed as spontaneous."

We have illustrated Spencer's position at some length because so many British biologists have recoiled from what they call the complexity of Weismann's theory. But a little consideration will show that the protagonist of British biology invented a system in comparison to which Weismann's is simplicity.

Nor can we close our exposition without recalling how Spencer confessed that "the actual organising process transcends conception. . . . It is not enough to say that we cannot know it;

we must say that we cannot even conceive it. . . . If even the ordinary manifestations of the dynamic element in life which a living body yields from moment to moment are at bottom incomprehensible, then still more incomprehensible must be that astonishing manifestation of it which we have in the initiation and unfolding of a new organism. . . . Thus, all we can do is to find some way of symbolising the process so as to enable us most conveniently to generalise its phenomena ; and the only reason for adopting the hypothesis is that it best serves this purpose."

But Spencer's hypothesis only serves the purpose because the constitutional units are gradually invested with the powers of effective response, co-ordination, and the like which remain the secret of the organism as a whole—the secret of life, which many think will never be read until we recognise that it is also the secret of mind.

**De Vries's Theory of Intracellular Pangenesis.**—A theory different from Darwin's and also from Weismann's has been suggested by Hugo De Vries under the title "Intracellular Pangenesis." The gist of it may be summed up as follows :

1. Organisms are built up of unit-characters, independently variable and independently heritable.

2. These unit-characters are represented *in potentia* in the hereditary substance of the nucleus of the germ-cell by definite bodies (pangens), far too minute to be visible, but together constituting the chromosomes of the nucleus.

3. The pangens multiply in the idioplasm of the nucleus, and some of them migrate into the surrounding cytoplasm, where they become active, dominating it, and giving it a particular character. But a representative contingent of pangens always remains in the nucleus and is handed on from cell to cell by nuclear division. Into each cell as it is formed a fresh migration of pangens occurs.

**Other Suggestions.**—It need hardly be said that many other

schemes have been suggested with the laudable end of throwing some light on one of the most familiar facts of life—the development of the germ. Thus the illustrious physiologist of Prague, Ewald Hering, and that acute English thinker, Samuel Butler, have suggested that development is, as it were, a materialised recollection of the past; Ernst Haeckel conceived of development as due to the persistence of characteristic and complicated wave-motions acquired in the past by the organic molecules; many others have looked at the matter chemically, “the same substances and mixtures of substances being reproduced in similar quantity and quality with regular periodicity.”

A scholarly account of these and other suggestions will be found in Delage’s great work on heredity, where every known view is presented with fairness and lucidity and criticised with unrivalled acuteness and justice. There also will be found the finest exposition of the view, which we find ourselves quite unable to entertain, that it is possible to dispense with any postulate of “representative particles.”

#### § 4. *Weismann’s Theory of Germinal Selection*

In 1895-6 Weismann expounded an ingenious hypothesis, the main idea of which is expressed in the phrase “Germinal Selection.” It is an extension of the biological concept of “struggle” to the individual items which compose the germ-plasm—*i.e.* the inheritance.

**Extension of the Struggle-and-Selection Formula.**—In human affairs there is often struggle between different societal forms—as in war and international commercial competition; and no one doubts that this involves a process of selection. This is often so complex that it must be termed superorganic. An adumbration of it is seen in the wars of the ants, and in the competition between a pack of carnivores and a herd of herbivores. Similarly, within one human societal form there may be

struggle between rival organisations and rival institutions, and no one doubts the reality of an intrasocietary selection. This, again, is more complex than the ordinary personal or individual selection.

**“Personal” Selection.**—Of personal or individual struggle there are many forms and phases, notably (*a*) the competition between fellows of the same kin for food and foothold, which is not self-regarding only, but for the sake of mates and family as well; (*b*) the opposition between foes of quite different kin—*e.g.* between birds of prey and small mammals; and (*c*) the struggle between organisms and the changeful inanimate environment. Besides these three main forms there are many special cases, such as the battles between males of the same species for the possession of females, as in the case of seals and stags, and the sometimes serious disagreements between mates, so quaintly illustrated in some spiders. Corresponding to these different forms of struggle there are different modes of selection and elimination.

**Intra-organismal Selection.**—In 1881 Roux introduced the idea of a *struggle of parts within the organism*. He pointed out that functional stimulus tends to strengthen an organ, that there is a “quantitative self-regulation of an organ according to the strength of the stimulus supplied to it.” It may be over-compensated for its expenses, and grow, just as the opposite conditions may lead to atrophy. It is well known that if all the work of renal excretion be thrown on *one* kidney, that organ increases greatly in size, and that if the nerve to a muscle or gland be cut, that muscle or gland begins to degenerate. If we pursue this line of thought we begin to realise what is meant by a struggle of parts within the organism, and by intra-organismal selection. Some change occurs in the conditions of nutritive and other stimuli; there are limitations affecting the nutritive supply, the amount of available space, and so on; and there has to be an internal give and take, a mutual re-

adjustment of parts—in fact, a struggle. This is often referred to as intra-selection or histonal—*i.e.* tissue—selection.

As Weismann says, “The tissues and the parts of the tissues have to distribute and arrange themselves so that each comes to fill the place in which it is most effectively and frequently affected by its specific stimulus—that is, the stimulus in regard to which it is superior to other parts; but these places are also those the occupation of which by the best reacting parts makes the whole tissue capable of more effective function, and therefore makes its structure the fittest. . . . The cells which assimilate more rapidly because of the more frequent functional stimulus increase more rapidly, draw away nourishment from the more slowly multiplying cells around them, and thus crowd these out to a greater or less extent” (1904, vol. i. p. 247).

As Weismann points out, it is impossible at present to give any precise limitation of the respective spheres of personal and histonal selection. The intra-organismal struggle may be, so to speak, the internal adjustment necessary towards a result which the external process of personal selection is bringing about. “The differentiation of the particular kinds of cells is an ancient inheritance, and depends upon personal selection; but their distribution and arrangement into specially adapted tissues, so far as there is any plasticity at all, depend upon histonal selection.” The architecture of every organ is implicit in the germ and must be referred to a long-drawn-out process of personal selection, but the particular *local* modifications of the architecture may be adjusted by the intra-organismal struggle. And, again, it must be borne in mind that personal selection may put a full stop at any moment to the achievements of histonal selection if they affect the viability of the creature as a whole. A hypertrophied organ may express the organism’s internal endeavour to make the best of a new situation, but it may be fatal.

In so far as a process of intra-organismal struggle is of *normal*

*occurrence* in development, where we often see one organ waxing and another waning, we must regard it as part of the plan of campaign which is hereditarily predetermined in the germ-plasm. But since the organism develops in intimate dependence on a changeful environment, we are prepared for local modifications of adjustment arising as the results of histonal selection. Many malformations represent attempts on the organism's part to solve an insoluble problem forced upon it by peculiar environmental conditions; many individual adaptations are wrought out by the *modus operandi* of histonal selection in the individual lifetime, and are of real value to the organism that acquires them. But there is no good reason for believing that either can be entailed on the offspring.

None the less, it is important that the student of inheritance should vividly realise the existence of this *modus operandi* which Roux called the "struggle of parts within the organism." For, although we cannot say that it has any direct evolutionary importance in securing new steps in evolution, and although we do not understand how it is that parts regulate themselves appropriately in reference to new conditions of stimulus—for that is obviously part of the secret of life itself—it is useful to bear in mind that there is in a real sense a competition among organs, a struggle of parts, and a warfare among cells. Vivid illustrations may be found in the histolysis or disruption of tissue associated with metamorphosis (*e.g.* in many insects), in the behaviour of teratogenic growths, in the involutions or degenerations associated with senility (*e.g.* in the invasion of the brain of the aged parrot by hungry "neurophagous" cells), and in the familiar fact that the hypertrophy of one organ may handicap or even suppress another organ.

In short, the concepts of struggle and selection may be extended to the parts of the organism.

**Struggle between Gametes.**—There may be struggle between groups of organisms, struggle between individual organ-

isms, struggle between organisms and their surroundings, and struggle between parts within the organism—between organs, tissues, and cells. Can the formula be extended further ?

Before we pass to Weismann's proposal to extend the concept "struggle" to the determinants within the germ, it may be of interest to call attention to a form of struggle and selection which may be interpolated between Roux's histonal selection and Weismann's germinal selection. Although Weismann does not seem to favour the idea, it seems to us that there is a real and important struggle between the germ-cells as such.

1. There is a well-known struggle between potential ova. In many cases the majority are sacrificed to a minority, which sometimes literally feed upon their fellows. In the common freshwater polyp, *Hydra*, and in a common marine polyp, *Tubularia*, only one egg-cell usually survives out of an originally numerous sisterhood, reminding one of the combat to the death which may occur among sister queens in a beehive.

2. There is a kind of struggle between the hundreds of spermatozoa in their race towards the ovum, which only one of them in normal conditions will fertilise. In the familiar fertilisation of frog's ova, several spermatozoa may be seen boring their way through the jelly surrounding the ovum; but after one has entered the ovum a rapid change in the peripheral protoplasm seems to shut the door on others. It may well be, allowing a margin for the purely fortuitous, that the most vigorous, most sensitive spermatozoa tend to fulfil their particular office of fertilising the ova, and *this will tend to be to the advantage of the species*. Again, we are quaintly reminded of the race between the drone-bees to overtake the queen in her nuptial flight. Usually, one drone effects sexual union, and all the rest are futile.

3. There is sometimes, according to Iwanzoff and others, a struggle between ova and spermatozoa, for young ova may literally *digest* intruding sperms. There is also a form of selection



involved in the fact that in some cases there are more ova than sperms, though the reverse is usually the case. Thus Maupas has shown that in *Rhabditis* and some other threadworms only about a third of the ova *can* be fertilised ; there are no sperms left for the other two-thirds produced later.

Many other illustrations might be given, but our point here is simply this, that a vivid realisation of the visible struggle among germ-cells or gametes, and the frequently discriminate nature of the ensuing elimination, may lead us naturally to an appreciation of germinal selection which deals with the wholly invisible.

**Statement of Weismann's Theory.**—As we have seen, Weismann pictures the germ-plasm as composed of *an army of living determinants*—that is to say, of an aggregate of primary constituents (or potentialities), of particular parts of the organism. These particular parts will not arise if their determinants are absent from the germ-plasm, and we *know* in some cases—*e.g.* in the development of some Ctenophores (usually globular free-swimming Cœlenterates)—that the abstraction of certain cells from the embryo means an absence of certain structures from the adult.

Let us suppose, then, that the physical basis of inheritance is composed of a multitude of representative vital particles, which have the capacity of feeding, growing, and multiplying. As the supply of nutriment necessarily fluctuates continually in the reproductive organs as a whole, “we may therefore assume that there are similar irregularities and differences in the minute and unobservable conditions of the germ-plasm likewise, and the result must be a slight shifting of the position of equilibrium as regards size and strength in the determinant system ; for the less well-nourished determinants will grow more slowly, will fail to attain to the size and strength of their neighbours, and will multiply more slowly” (1904, vol. ii. p. 117).

Every one must admit that there are fluctuations in the nutritive supply of the germ-cells, and to these, according to

Weismann, we must refer those individual germinal variations which form part of the raw material of evolution. But it can hardly be imagined that all the determinants or hereditary constituents are equally vigorous, or have equal assimilating power. Thus, a determinant may become weaker because there is less food for it, and also because it has less power of utilising the available food. If a determinant is thus weakened, its determinate—the structure to which it corresponds—will also be weakened ; and we call this a germinal variation on the down-grade. On the other hand, a vigorous determinant with strong assimilative power will tend to become stronger if it is well and appropriately fed. Its determinate will be correspondingly strengthened, and we call this a germinal variation on the up-grade.

“ To the ascending progression there are limits set, not only by the amount of food which can circulate through the whole id (a complete system of determinants), but also by the neighbour determinants, which will sooner or later resist the withdrawal of nourishment from them ; but for the descending progression there are no limits except total disappearance, and this is actually reached in cases in which the determinants are related to a part which has become useless ” (Weismann, 1904, vol. ii. p. 118).

“ If the germ-plasm be a system of determinants, then the same laws of struggle for existence in regard to food and multiplication must hold sway among its parts that obtain between all systems of vital units—among the biophors which form the protoplasm of the cell-body, among the cells of a tissue, among the tissues of an organ, among the organs themselves, as well as among the individuals of a species and between species which compete with one another.”

When a structure becomes useless in the life of a species, those individuals who have more of it are no better off than those who have less of it ; natural selection no longer operates

as far as that structure is concerned ; a state of panmixia, as it is called, sets in ; and the structure in question tends to dwindle. But this external selection is abetted by the germinal selection, for when a determinant corresponding to the useless structure becomes weaker through the intragerminal fluctuations of nutrition, " it finds itself upon an inclined plane, along which it glides very slowly but steadily downwards. The determinant whose assimilative power is weakened by ever so little is continually being robbed by its neighbours of a part of the nourishment which flows towards it, and must consequently become further weakened." By hypothesis, personal selection cannot help it to persist—*i.e.* cannot favour those individuals in whose inheritance it is relatively stronger ; therefore, by an internal struggle and selection, which may be quite real though quite unverifiable, the determinants of a disused part dwindle away in the course of many generations. On the other hand, when personal selection favours the increase of a part—*i.e.* favours individuals whose inheritance includes strong determinants of that part, again the internal struggle will back up the external sifting. In short, nothing succeeds like success.

The theory helps us to understand the slow dwindling of useless structures, but it is also applicable to the augmentation of useful parts. Suppose it be important for humming-birds to have a longer tongue, and that natural selection favours variants with longer tongues. Corresponding to the tongue there are, by hypothesis, in the germ-plasm, several sets of homologous determinants. (We need not complicate the argument by recognising that many different kinds of determinants will be required for a complex structure like the tongue.) There are fluctuations in the food-supply and some tongue-determinants get the advantage ; they become stronger, they exhibit a plus variation, and as they become stronger they increase in assimilative capacity. They therefore tend to predominate more and more over other tongue-determinants which

may exhibit a minus variation ; and personal selection favouring the birds with longer tongues—*i.e.* birds in whose inheritance there is a predominance of tongue-determinants varying in the plus direction—the direction of variation will remain positive. In the case of artificial selection the continuance in the plus direction may go much further and much more rapidly than in the case of natural selection, for rapid increase of any part is apt to prejudice the viability of the whole organism, which in the case of domesticated animals is artificially preserved. Thus we have the Japanese breed of cocks with feathers six feet long.

**Illustration.**—It is admitted by all that in the course of evolution the hind-limbs of whales have dwindled away and are now represented simply by vestigial structures. As the far-back ancestors of the whales of to-day became thoroughly aquatic and took to swimming with great strokes of the tail, the hind-limbs became functionless, futile, and actually in the way. Natural selection would favour those individuals whose hind-limbs varied in a retrogressive or minus direction ; that is to say, natural selection would favour those individuals in whose germ-plasm or inheritance determinants of the hind-limb varying in a minus direction came to be predominant over those varying in a plus direction. As the result of persistent personal selection the determinants varying in a minus direction would come to be more and more dominant. Weismann's point is, that when a bias in favour of minus determinants or short hind-limb determinants was thus established, it would go on increasing automatically because of germinal selection. Determinants varying in a plus direction, in the direction of longer hind-limbs, would be more and more thoroughly vanquished in the germinal struggle with the more numerous, more vigorous, perhaps larger determinants varying in the direction of utility. And after personal selection had ceased to operate—*e.g.* when the hind-limbs had quite sunk beneath the surface—

the germinal selection would still continue, and thus we can picture to ourselves a *modus operandi* whereby the useless organ would dwindle more and more.

Similarly, every one admits that the huge canines of various mammals have evolved from relatively small teeth in the same position. For many generations natural selection would favour variants with larger canines—*i.e.* those in whose germ-plasm or inheritance canine-determinants varying in the direction of greater size and strength of teeth were predominant. “The moment that these come to predominate in the germ-plasm of the species, at once the tendency must arise for them to vary *still more strongly* in the plus direction, not solely because the zero-point has been pushed further upwards, but because they themselves now oppose a relatively more powerful front to their neighbours—that is, actively absorb more nutriment, and upon the whole increase in vigour and produce more robust descendants. From the relative vigour or dynamic status of the particles of the germ-plasm an ascending line of variation will thus spontaneously arise, precisely as the facts of evolution require.” Furthermore, if we admit this consideration we can in some measure understand why the ascending line of variation often tends to go too far; and sometimes does go too far when the check of natural selection is removed by the artificial conditions of domestication.

**Value of the Theory.**—Weismann emphasises the following, among other advantages of the theory of germinal selection. It suggests an interior mechanism which interprets the occurrence of definitely directed variations, the occurrence of appropriately useful variations at the *right place and time*, the diminution of organs below the level touched by personal selection or its cessation (panmixia), the occasional exaggeration of organs beyond the limits of demonstrable utility, the simultaneous occurrence of many similar variations, and so on.

It must remain a question for personal judgment whether

these and other alleged advantages of the theory are real advantages. Does the theory clarify our conception of inheritance? and does it suggest experimental work, on which, after all, we must base our conclusions as to these abstruse questions? Do the advantages of the theory outweigh the difficulties?

**Objections.**—What we have stated above is not more than an outline of a theory which Weismann has developed with great subtlety and in great detail, and many objections may occur to our statement of the theory which are well met in the author's own presentation. But we may allude to a few of the current criticisms.

1. It has been objected that the whole concept of germinal selection is visionary and unverifiable. But the same may be said of modern speculations as to the constitution of matter; it may be said that the conception of an atom as a constellation of electrons is visionary and unverifiable. The point, however, is: does this hypothetical construction enable us to interpret the facts better? does it harmonise with visible facts? is it consistent with what we know of the behaviour of observable living units? It seems to us that an affirmative answer may be given. The concept of germinal selection deals with an invisible world, but it helps us to understand such facts as the dwindling of useless parts, the definiteness of variation, the excessive growth of more or less indifferent parts (*e.g.* some decorations), the persistence of indifferent malformations for a limited number of generations (*e.g.* six fingers in six successive generations), and so on.

2. It may be objected that we can hardly think of invisible bodies such as determinants struggling for food. But why not? Size seems an irrelevant consideration. Cells which are invisible to the naked eye are seen under the microscope struggling for food. The germ-cells in the ovary of *Hydra* devour one another just as really as the embryos of the dog-whelk in their egg-capsules on the sea-shore, just as really as the locusts

in a swarm. And if there is competition among cells for food, why not among the chromosomes within the cell, and why not among the determinants within the chromosome ?

Yet, is not the supply of food brought by the vascular fluids of the body always more than sufficient ? Who can tell ? When we consider, for instance, the enormous ovary of a cod—the familiar cod-roe of the breakfast-table—and its legions of eggs, can we be sure that the food-supply is always superabundant ? Moreover, it is very improbable that all the hungry units are equally well-placed ; how much more is there likely to be inequality within the labyrinth of the ovum-nucleus, which is a little world in itself ? And again, it by no means follows that all the food supplied is appropriate, or that all the homologous determinants are equally able to use it.

As Weismann says, to suppose that food is always superabundant “ seems to me much the same as if an inhabitant of the moon, looking at this earth through an excellent telescope and clearly descrying the city of Berlin, with its thronging crowds and its railways, bringing in the necessaries of life from every side, should conclude from this abundant provision that the greatest superfluity prevailed within the town, and that every one of its inhabitants had as much to live upon as he could possibly require ” (1904, vol. ii. p. 156).

As an instance of severe criticism by an expert who sees no utility in these imaginative interpretations, we may quote the following passage from Prof. T. H. Morgan's *Evolution and Adaptation* (1903, p. 165): “ Weismann has piled up one hypothesis on another as though he could save the integrity of the theory of natural selection by adding new speculative matter to it. The most unfortunate feature is that the new speculation is skilfully removed from the field of verification, and invisible germs, whose sole functions are those which Weismann's imagination bestows on them, are brought forward as though they could supply the deficiencies of Darwin's theory. This is,

indeed, the old method of the philosophisers of nature. . . . The worst feature of the situation is not so much that Weismann has advanced new hypotheses unsupported by experimental evidence, but that the speculation is of such a kind that it is, from its very nature, unverifiable, and therefore useless."

These are hard words, but it would have been more to the point to inquire whether Weismann's imaginative picture of what may go on within the microcosm of the germ-plasm is in any way contradictory of known biological results. Of course, the theory is "unsupported by experimental evidence," and "removed from the field of verification"; but why it is therefore "useless" we fail to see. It appears to us quite on the same plane as many symbolic interpretations in chemistry and physics, where we say that if we picture atoms and molecules, electrons and corpuscles, in such and such a way, then we can redescribe more clearly the observable sequences of conditions and results, and devise further experiments which will test the adequacy of our symbols and enable us to improve them. The struggle of determinants may not be quite as Weismann supposes, but the idea is a logical extension of the selective process which occurs at many different levels; it clarifies our picture of observable facts, and it stimulates further inquiry.

**Summary.**—Convinced that the theory of natural selection in the Darwinian sense required some rehabilitation, dissatisfied with the assumption of merely "accidental" variations, confronted with evidence of definitely directed variations, Weismann devised this theory of germinal selection. The personal selection of the possessors of a plus or minus variation in any part means, of course, that those organisms are favoured in which the corresponding determinants within the germ-plasm are varying in a plus or minus direction. But if there be inequality (in size and assimilating power) among the homologous determinants, and if there be fluctuations in the nutritive supply, there may come about a germinal struggle among the homologous deter-



minants. Those that are weaker will tend to become weaker still, those that are stronger will tend to become stronger still, and thus germinal selection fosters and strengthens personal selection. In other words, there is an internal reason for progressive variation (either plus or minus) in the direction of utility.

**A Suggestion.**—If we admit the concept of representative particles in the germ-plasm, which it seems to us is almost demanded by the facts of particulate inheritance, by the independent variability and heritability of often trivial peculiarities; and if we admit the probability of some sort of germinal struggle among these living units, which seems to us warranted by what we know of the behaviour of visible living units and by general biological considerations—then it seems at least interesting to ask whether we need limit the conception of germinal struggle to a competition between *homologous* determinants, as Weismann always does.

In personal selection, as we have seen, there are three distinct types of struggle—classified according to the parties involved—(a) between kindred or homologous organisms, (b) between organisms which are not akin, and (c) between organisms and the inanimate environment. Logically, we may look for the same three modes of struggle in the course of germinal selection. They might be illustrated (a) by struggle between, say, the maternal and the paternal, or the parental and the grand-parental, homologous determinants of a single determinate; (b) by struggle between determinants of quite different kinds—*e.g.* between determinants of the notochord and the determinants of its more effective substitute, the backbone; and (c) by struggle between all or any of the determinants and a disturbing external influence, such as some toxin in the parent's blood or lymph, or some change in the osmotic conditions of the sea-water. Is there any theoretical reason why we should restrict the concept of germinal struggle, as Weismann does,

to competition between homologous determinants in relation to the fluctuating food-supply ?

**Testing the Theory.**—The chief objections that have been brought against the theory of germinal selection are,—(1) that it is bound up with a particular notation and theory of development and evolution—in terms of representative particles or primary constituents, the determinants, which many regard as at once unverifiable and gratuitous ; (2) that it cannot be objectively verified or directly tested by experiment, being, like many other scientific theories, part of an intellectual game with invisible counters ; and (3) that it is gratuitous, since the results of evolution can be interpreted without this extension of the selection-process into the invisible microcosm of the germ-plasm. In answer to these objections, Weismann's original essays and later lectures on germinal selection seem to us quite sufficient, and we must ask the interested reader to consult the original documents and not to base his verdict upon a necessarily brief and incomplete presentation of the case. We offer this commonplace advice because some objectors raise difficulties which a perusal of the original documents would have shown to be inept.

The progressive course seems to be to take a set of facts from different fields, and to see whether the key which Weismann has given us does or does not fit. We propose, therefore, to assume the concept of a germinal struggle between primary constituents (not necessarily *homologous* determinants), and to inquire whether Weismann's suggestion has interpretative value.

1. No one is very willing to predict the hereditary result of pairing two organisms. Average predictions may be ventured in regard to the issue of a hundred or a thousand pairings. These predictions may be Galtonian or Mendelian, and they may be justified *on the average*. But individual results continually crop up which are unpredictable ; and even apart from these valuable

generalisations—Galtonian and Mendelian—we are accustomed, in predicting the issue of crossings, to say that the offspring will exhibit a blended, or exclusive, or particulate expression of the parental characters. How often, however, must we not frankly admit, the individual result seems anomalous! Now, is not this result just what we should expect if germinal struggle is a reality?

2. No phenomenon of inheritance is more familiar than that of preponderant and exclusive inheritance, where, in regard to the expression or development of a given character, the offspring follows one parent preponderantly or exclusively, instead of being merely a "blend." If we suppose that ovum and spermatozoon have each a complete organisation of hereditary qualities (as we seem bound to suppose), and that the fertilised ovum has determinants representing the character in question from both parents and from the ancestors of both parents, may we not consistently interpret the hereditary re-expression of only one set, by supposing that there is a struggle for expression between the various sets—a struggle in which the most vigorous have for the time the mastery?

3. A frequent phenomenon of inheritance is a change in the direction of preponderance in the successive children of a large family. Suppose a virile middle-aged father and a much younger mother: the older children may be markedly paternal in the expression of their inheritance, the younger children as markedly of the maternal type. Introduce the conception of germinal struggle; suppose it to occur not only in the germ-cell lineage within the gonads, but in the fertilisation and afterwards; recall the fact that the ova tend to be more stable than the spermatozoa, being formed and to some extent fixed in very early days, whereas the spermatozoa continue to appear in crop after crop. At first we picture a victory on the part of the determinants of the relatively prepotent father; but gradually, in his post-mature spermatogenesis, there is a weakening of paternal determinants such that, in fertilisation, those from the mother have now a better chance of asserting themselves. Naturally enough, the Benjamin is after the mother's image and after the father's own heart.

4. A very young pigeon of hooded or frilled breed is mated with an old one: the first young are smooth-headed and smooth-breasted, but those of later broods have the specialised characteristics of the parents. May this not mean that in the too-young egg-cells the more recent determinants as to head- and breast-feathers—though in the

ascending line through selection—yielded to the old-established combinations? After a period of nutrition, however, they were strong enough to assert themselves. Give them time, Prof. Ewart says, and they will become so prepotent that they may hand on all the peculiarities even when the pigeon is crossed with another breed.

Similarly, the first fertilised almost immature ova of a rabbit, liberated by an ovulation subsequent to the first serving, result in offspring which take after the male. In the fertilisational struggle the paternal determinants have the mastery. If, on the other hand, a doe is served, not at the right time, but a week or ten days after, when the next young come they are all exactly like the mother. The expression of inheritance is after the parent whose germ-cells were the riper.

These results, Prof. Ewart said, “were altogether different from Weismann”; from another point of view they are altogether illustrative of Weismann’s theory of germinal selection.

**Conclusion.**—If we accept the concept of ancestral plasms—that is to say, the idea that an inheritance is a mosaic of ancestral contributions, and that a complete hereditary equipment is present not merely in dual but in multiple form within the fertilised egg—then we pass naturally enough to the idea of a struggle among the hereditary tendencies, which Darwin indeed suggested—which Weismann, however, has elaborated into a fascinating hypothesis.

If there are multiple analogous but not identical determinants corresponding to any independently variable and heritable part of the organism, what is to decide the expression of these? It is plain that the organism is not usually a *mélange* or blend of the ancestral contributions which made up its inheritance. Must we, then, simply fall back on the general assumption of a regulative entelechy which determines the determinants? In other words, perhaps, is the mysterious unity of the organism, which applies to the fertilised egg-cell as well as to the full-grown creature, such that it determines, by the very fact that there is a unified organisation, which determinants

shall be in the foreground and find expression, and which shall remain in the background, and latent? Or is it enough to suppose that the cytoplasmic soil—the cell—in which the analogous determinants find themselves, and environmental influences in the widest sense, decide which determinants are to be liberated and to find expression? Weismann suggests that we may reach a clearer possible image of occurrences if we introduce the concept of struggle.

The analogous determinants need not all be of equal strength, and when they liberate their biophors in the appropriate area there may be a struggle amongst these; or long before it comes to the actual liberation and dissolution of determinants there may be a struggle between them. They are by hypothesis living units, feeding, growing, and multiplying, and if there are inequalities amongst them, as there may well be, since some are older and others younger and since they have had diverse histories, then there may be struggle amongst them, and here too—as in the wider world of nature—the weaker may go to the wall. Moreover, the analogous determinants need not be all different from one another; similars may, so to speak, support one another in development, while incompatibly different forms may be in a minority and have little chance of asserting themselves. All this is apt to become anthropomorphic speculation, but then the determinants are *alive*.