CHAPTER II

THE PHYSICAL BASIS OF INHERITANCE

> " Gebt mir Materie, und ich will daraus eine Welt schaffen."—KANT.

> " We may regard the nucleus of the cell as the principal organ of inheritance " (a prophecy proved *true*).—HAECKEL, *Generelle Morphologie, 1866*, vol. i. p. 288.

> " The cell is not only the seat of vital activity, but is also the vehicle of hereditary transmission ; and the life of successive generations of living beings shows no breach of continuity, but forms a continuous vital stream in which, as Virchow said, rules an ' eternal law of continuity.' "—WILSON, 1900, p. 76.

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§ 1. *What is true in the Great Majority of Cases*

The Inheritance is usually carried by the Germ-cells.—What was for so long quite hidden from inquiring minds, or but dimly discerned by a few, is now one of the most marvellous of biological commonplaces—that the individual life of the great majority of plants and animals begins in the union of two minute elements—the sperm-cell and the egg-cell. These microscopic individualities unite to form a new individuality, a potential offspring, which will by-and-by develop into a creature like to, and yet different from its parents. If we mean by inheritance to include all that the living creature is or has to start with in virtue of its genetic relation to its parents and ancestors, then it is plain that the physical basis of inheritance is in the fertilised ovum. The fertilised egg-cell *is* the inheritance, and at the same time the potential inheritor. What might be compared to an inheritance of property as apart from the organism itself is the store of food which may be inside the egg, or round about it.

To the general fact stated in the preceding paragraph, a few exceptions must be made—*e.g.* for bananas which have no longer any seeds, for potatoes which are multiplied by cutting, for the drone-bees and summer green-flies who have mothers but no fathers, and for simple unicellular organisms in which there is no sexual reproduction ; but the exceptions are trivial compared with the vast majority of living creatures, in regard to which it is certain that each life begins in a fertilised egg-cell.

An organic inheritance means so much, even when we use the comfortable word potentiality, that, although we are quite sure that the germ-cells constitute the physical basis of inheritance, we may consider for a moment the difficulty which rises in the minds of many when they are told that the egg-cell is often microscopic, and the sperm-cell often only $\frac{1}{100000}$th of the ovum's size. Can there be room, so to speak, in these minute elements for the complexity of organisation supposed to be requisite ? And the difficulty will be increased if the current opinion be accepted that only the nuclei within these minute germ-cells are the true bearers of the hereditary qualities. Darwin spoke of the pinhead-like brain of the ant as the most marvellous little piece of matter in the world, but must we not rank as a greater marvel the microscopic germ-cells which contained potentially all the inherited qualities of that ant ?

From one microscopic egg of a sea-urchin cut into three, Delage reared three larvæ. In another case he reared an embryo from $\frac{1}{37}$th of an egg. Twin animals are often developed from one egg. Wilson obtained quadruplets by shaking apart the four-cell stage in the development of the lancelet. Marchal describes a " legion of embryos " developing from a single ovum of a peculiar Hymenopterous insect *Encyrtus.* In development, indeed, a half may be as good as a whole.

In reference to the difficulty raised in some minds by the minuteness of the physical basis, it may be recalled that the students of physics, who make theories regarding the sizes of the atoms and molecules which they have invented, tell us that the image of an ocean liner filled with framework as intricate as that of the daintiest watches does not exaggerate the possibilities of molecular complexity in a spermatozoon, whose actual size is usually very much less than the smallest dot on the watch's face. Secondly, as we learn from embryology that one step conditions the next, and that one structure grows out of another, there is no need to think of the microscopic germ-cells as stocked with more than *initiatives.* Thirdly, we must remember that every development implies an interaction between the growing organism and a complex environment without which the inheritance would remain unexpressed, and that the full-grown organism includes much that was not inherited at all, but has been acquired as the result of nurture or external influence.

The fact is that size does not count for much in these matters, and the difficulty that some beginners feel in believing that the inheritance of the whale is packed into a pinhead-like egg is mainly due to ignorance of what may be called the fine complexity, or from another point of view the " coarse-grainedness," which must form part of our conception of every speck of matter. Nowhere more than in biology are we made to feel that " a little may go a long way."

It should be noted that the degree of *visible* complexity, even in the microscopic nucleus of a germ-cell, is often very considerable. Thus Eisen observed in the nucleus of a species of salamander twelve chromosomes, each of six parts, and in each part six granules—altogether 432 visible units.

§ 2. *Diverse Modes of Reproduction*

In the preceding paragraph we have given prominence to what is true of the great majority of living creatures,—that a new life begins as a fertilised egg-cell. It is necessary, however, to refer to the other ways in which a new organism may arise, for some of them help us to understand what the hereditary relation means. The following scheme will probably serve to recall the familiar facts :

Multiplication
- *In unicellular organisms.*
  - By division into two.
  - By budding, a modified form of division.
  - By sporulation, or division into many units.

  The reproduction may be wholly asexual : (1) in the sense that there is nothing corresponding to fertilisation or amphimixis ; and (2) in the sense that there are no special germ-cells. But in *many unicellular organisms there are elaborate processes of amphimixis*, and in colonial forms, like *Volvox*, there is a definite beginning of egg-cells and sperm-cells. Among the parasitic Sporozoa or Gregarines in the wide sense there is also a close approximation to the mode of sexual reproduction seen in most multicellular organisms. No hard-and-fast line can be drawn.
- *In multicellular organisms.*
  - I. Without special germ-cells—*e.g.* by division of the body, by giving off buds (and as the result of *artificial cutting)*.
  - II. With special germ-cells :
    - (*a*) Eggs from one parent are fertilised by sperms from another parent—heterogamy, the commonest mode ;
    - (*b*) Eggs from one parent are fertilised by sperms from the same (hermaphrodite) parent—autogamy, a very rare mode.
    - (*c*) Eggs may develop without fertilisation—parthenogenesis.

    [A multicellular organism may also multiply by spore-cells—specialised germ-cells, yet hardly equivalent to eggs—which do not require fertilisation.] *

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* If we lay emphasis on the presence or absence of special reproductive elements, the classification of the modes of multiplication would read as follows :

- I. Without special reproductive elements.
  - Division, budding, etc., in most unicellulars.
  - Division, budding, etc., in some multicellulars.
- II. With special reproductive elements.
  - More or less distinct specialisation of reproductive elements in some unicellulars.
  - Specialised ova and spermatozoa in most multicellulars.
  - Formation of spore-cells in some multicellulars.

If we lay emphasis on the occurrence or non-occurrence of amphimixis (= fertilisation) the classification of the modes of reproduction would read as follows :

- I. Without any form of amphimixis.
  - Without special reproductive-cells : (*a*) division, budding, etc., in many unicellulars ; and (*b*) division, budding, etc., in some multicellulars.
  - With special reproductive-cells : (*a*) formation of spores in some multicellulars ; (*b*) parthenogenetic ova.
- II. With some form of amphimixis.
  - Without specialised reproductive elements, amphimixis occurs in most unicellulars.
  - With specialised reproductive elements, amphimixis occurs in a few unicellulars and in most multicellulars.

The reasons for lingering over the modes of reproduction—which it is confessedly difficult to arrange in a perfectly clear scheme—are (1) that our general view of the hereditary relation must be one which is applicable to all cases and not merely to the most frequent, and (2) that some of the simplest cases shed light upon the more complex. It is also important that we should make clear that the common phrases, "asexual reproduction" and "sexual reproduction," are somewhat ambiguous, since attention has to be directed to two distinct points—(*a*) whether there are specialised reproductive elements, and (*b*) whether there is any form of amphimixis.

§ 3. *The Hereditary Relation in Unicellular Organisms*

At what is called "the limit of growth," when the cell has attained to as much volume as its surface can adequately supply with food and oxygen, and so on, a unicellular organism normally divides into two, obviating the difficulties which would ensue if volume increased out of proportion to surface. The halves separate and grow. Two more or less exact replicas of the original unit result. It has been demonstrated that the division is often preceded by that intricate and orderly process of nuclear division, known as karyokinesis, which results in an equal partition of the nuclear constituents between the two daughter-cells. As each of the halves is in the strictest sense half of the organisation of the parent unit, we are not surprised that each should in appropriate environment grow into an almost exact image of the original whole. In most cases we have no methods subtle enough to detect any difference. There is complete hereditary resemblance, and it would be puzzling if it were otherwise. Even when the unit divides into many units (as in spore-formation), there is no puzzle in the fact that each reproduces the likeness of the original whole, except the puzzle of growth—of life, which is at present insoluble. Analogies may be found in methods of treating chemical molecules so that one gets at the end of the operation twice as many molecules as one had to start with; or in the multiplication of crystals by breaking them into fragments and placing them in solutions of the same substance; but, at the present time, these analogies are of no particular service, since we do not understand the nature of living matter. That a fragment of a unicellular's organisation may, in an appropriate environment, reproduce an apparently perfect replica of the original unit, is not in any way explained by pointing out that there may be reproduction of like by like in the case of crystals or chemical molecules.

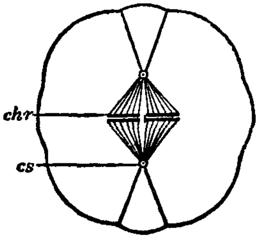

FIG. 2.—Diagram of cell division (after Boveri).
chr. chromosomes, forming an equatorial plate; *cs.* centrosome.

In slightly more complex cases there is a difference between the two units into which the unicellular organism divides. Thus, in the oblique division of the slipper animalcule (*Paramœcium*), the one half goes off with the "mouth," the other has none. In a short time, however, the mouthless half forms a "mouth," and each half grows into a replica of the original. But as the organisation of each half is essentially the same as, and directly continuous with the organisation of the original cell, the development of the halves into similar wholes presents no special difficulty. Similar organisation and similar surroundings yield similar results. That an injured infusorian should by re-growth repair its loss is an analogous phenomenon. Thus we are led to see the force of Haeckel's definition of reproduction as discontinuous growth.

But in many unicellular elements, what is liberated to begin a new life is not a half of the original nor anything like it, but a minute unit often called a "spore." It also grows into a complete reproduction of the original. In such cases, we again try to make the matter more intelligible, by saying that each spore is a representative fragment of the organisation of the original unit, and will therefore, in appropriate surroundings, grow and differentiate as the original did. Exactly the same often occurs when the unicellular organism is artificially divided into several parts; and the results of these microscopic vivisection experiments, to which no one can on any grounds object, show that, if the excised fragment is to survive and develop, it must have a portion of the nuclear substance as well as of the general cell-substance. Without the nuclear constituent it may live for a time, as in *Stentor*, moving and responding to stimuli, but it cannot assimilate. Therefore, if we are asked what we mean by "organisation," we may say, at this stage, a certain protoplasmic architecture which implies essential relations between nucleoplasm and cytoplasm. The protoplasmic unit is like a firm with many partners of different kinds, each kind having many representatives; and the retention of vitality, the possibility of regeneration on the part of the fragments, has this for its essential condition, that the integrity of the firm—in which lies its secret—is maintained by each fragment having at least one representative of the different kinds of partners.

The reader who is not familiar with the subject should linger over the fact that a fragment or a minute spore, separated from a unicellular organism, may grow into (literally, *reproduce*) a unit, which to our senses is exactly like the original. This is (within the limits of our senses) *complete hereditary resemblance*, and we interpret it as due to the fact that the fragment or spore has to start with the essential organisation of the original. This is, without complications, the fundamental fact in regard to inheritance.

It should also be borne in mind that many of the unicellular organisms (Protozoa, at the base of the animal series; Protophyta, at the base of the plant series) are highly differentiated—*i.e.* with great complexity of structure even within the narrow limits of size (where a diameter of $\frac{1}{100}$th of an inch is considered large)—and that many have very definite and interesting modes of behaviour, such as swimming in a spiral, seeking light or avoiding it, approaching certain substances and retreating from others, trying one kind of behaviour after another,—functional peculiarities—some of which cannot be described without using psychical terms—which are also included in the inheritance.

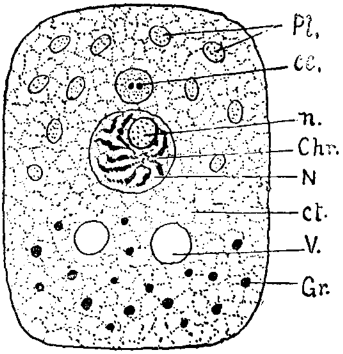

FIG. 3.—Diagram of cell structure. (After Wilson.)

Pl. Plastids in cytoplasm or cell-substance; *cc.* centrosome; *n.* nucleolus; *Chr.* chromosomes; *N.* nucleus; *ct.* general cytoplasm; *V.* vacuole; *Gr.* granules.

The case of a fragment of crystal growing into a complete crystal is interesting enough, but that a fragment or spore of apparent simplicity should reproduce the obvious complexity of the unit from which it was separated is relatively more marvellous.

A note is needed in regard to the misunderstanding which has led many to cite cases of inheritance in unicellulars as relevant to the discussion on the transmission of "acquired characters." Although we can no longer say that unicellular organisms are without sexual reproduction, since many exhibit *the liberation of special reproductive units and the occurrence* of amphimixis, we may still say that, apart from transitional forms (like *Volvox*, which form colonies or "bodies" of one thousand to ten thousand cells), there is among the unicellulars only the beginning of the important distinction between somatic or bodily and germinal or reproductive material which distinguishes multicellular organisms. This makes a notable difference.

§ 4. *The Hereditary Relation in the Asexual Multiplication of Multicellular Organisms*

In many of the simpler, but multicellular, plants and animals, a portion of the parent is separated off to form the beginning of a new life. The freshwater sponge multiplies in part by minute gemmules, which float away from the corpse of the parent and develop into new sponges; many polypes produce buds which may be set adrift, as in the freshwater Hydra, or may remain attached and help to form the great colonies that we see in zoophytes and Anthozoa; not a few worms also multiply by dividing or by budding, and the examples highest in the scale are found among the Tunicates, which are really vertebrate animals. Moreover, in some cases where asexual multiplication does not normally occur, it may still be a possibility, as is shown by the fact that cut-off portions may, in appropriate conditions, grow into entire individuals. Thus, two earthworms may occasionally be produced by cutting one; a sponge which does not normally liberate buds may be cut into pieces and bedded out successfully; the arms of the starfish, which the fisherman tears asunder, may give rise to several new individuals. From nine excised fragments of a single Planarian worm, Voigt reared nine individuals (*see* Weismann, 1904, vol. ii. p. 25).

Similarly, in regard to plants, many of the simpler multicellular forms produce detachable buds, familiar in the case of the liverworts ; and even in the flowering plants the same may occur, as in the bulbils of the tiger-lily. As in animals, great colonies may be formed, consisting of many individuals materially continuous, well seen in strawberries, whose creeping stems root here and there and give rise to independent plants. It is also a familiar fact that cut-off portions of a plant may readily give rise to entire individuals ; a little piece of moss, a Begonia leaf, a corner of a potato tuber—and hundreds of instances might be given—will suffice to start a new plant. In many ways the whole vegetable kingdom seems comparable to the sedentary sections of the class Cœlentera among animals (zoophytes, sea-anemones, corals, etc.), *e.g.* in the various forms of alternation of generations which occur, and in the readiness with which representative fragments will regrow the whole. This capacity of regenerating the whole from a small piece implies, on the one hand, that there is relatively little division of labour in the body, and on the other hand, that the differentiation of body-cells

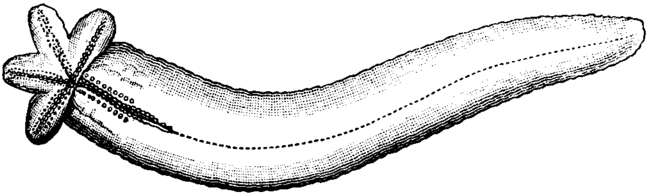

FIG. 4.—" Comet-form " of Starfish, showing how one arm regenerates the other four. (After Haeckel.)

and germ-cells has not gone far. For if the leaf of a plant, or a quarter of a zoophyte, or an eighth of a sea-anemone, may grow into an entire organism with reproductive cells, we must infer that the characteristic heritable material, usually segregated in the reproductive cells, is diffusely present in the cells of the body in these organisms. Or else we must infer, as some have done, that there is no characteristic heritable material.

The feature common to the ordinary forms of asexual multiplication is, that the reproduction is independent of eggs or sperms, or of any process comparable to fertilisation. What starts the new life, and forms in this case the material basis of inheritance, is a liberated portion of the parent. The heredity-relation is one of obvious material continuity.

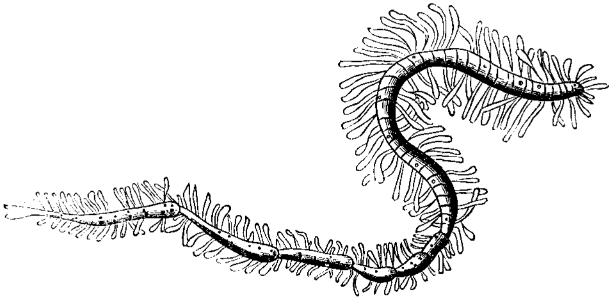

FIG. 5.—Asexual reproduction. A sea-worm (*Myrianida*) which buds off a chain of individuals. (After Milne-Edwards.)

As regards inheritance, the feature characteristic of asexual multiplication is that the resemblance between parent and offspring tends to be complete. As Sedgwick (1899) expresses it: "The offspring do not merely present resemblances to the parent—they are identical with it; and this fact does not appear to be astonishing when we consider the real nature of the process. Asexual reproduction consists in the separation of a portion of the parent, which, like the parent, is endowed with the power of growth. In virtue of this property it will assume, if it does not already possess it, and if the conditions are approximately similar, the exact form of the parent. It is a portion of the parent; it is endowed with the same property of growth; the wonder would be if it assumed any other form than that of the parent."

In asexual reproduction the resemblance of the offspring to the parent tends to be very complete, and the reason for like producing like is no puzzle, when the separated off-portion is a representative sample of the whole organism.

§ 5. *Nature and Origin of the Germ-cells*

Re-statement of the Central Problem of Heredity.—The central problem of *inheritance* is to measure the resemblances and differences in the hereditary characters of successive generations, and to arrive, if possible, at formulæ which will sum up the facts, such as Galton's Law of Ancestral Inheritance and Mendel's Law. The central problem of *heredity* is to form some conception of what is essential in the relation of genetic continuity, which binds generation to generation. Weismann's theory of the continuity of the germ-plasm is, in the first instance, a theory of *heredity*, and as important as Galton's law of *inheritance*.

We know that almost every multicellular plant or animal has the beginning of its individual life in the union of two germ-cells (ovum and spermatozoon), and what must be found if the problem of heredity is to be illumined at all is some reason why the germ-cells should have this power of developing, and of developing into organisms which are on the whole like the parents. In what respects are the germ-cells peculiar, and different from the ordinary cells of the body? Let us, then, concentrate our attention for a little on the nature and origin of the germ-cells.

It is inexpedient to lay on the shoulders of the student of heredity the burden of problems which are not in any special sense his business. It is no doubt interesting to ask how an organisation, supposed to be very complex, may be imagined to find physical basis in a microscopic germ-cell, but the same sort of question may be raised in regard to a ganglion-cell. It is not distinctively a problem of heredity. It is interesting to inquire into the orderly and correlated succession of processes by which the fertilised egg-cell gives rise to an embryo, but this is the unsolved problem of physiological embryology. It raises questions distinct from those of heredity and inheritance, and apparently much less soluble.

We shall return in the historical chapter to the various theories of heredity which have been suggested; in the meantime, we require to refer to them only in outline.

The Typical Ovum.—The germ-cell produced by the maternal parent is usually a relatively large sphere of living matter (cytoplasm), and various not-living included substances, such as nutritive yolk, pigment, oil-globules, and so forth. In the cytoplasm there lies a central kernel surrounded by a delicate membrane, the nucleus—a microcosm in itself. It contains a network or coil or some arrangement of delicate (linin) threads, carrying minute masses of a readily stainable material, the chromatin. Under high magnification the chromatin is seen to be built up of small corpuscles, sometimes like beads on a string, the microsomes. In certain phases of activity the chromatin forms a definite number of separate masses. They are then called chromosomes or idants, and the same number is always present in all the cells of the body of any particular species. In the nuclear sap which fills the nucleus there is often a rounded body or vesicle—the nucleolus; or there may be

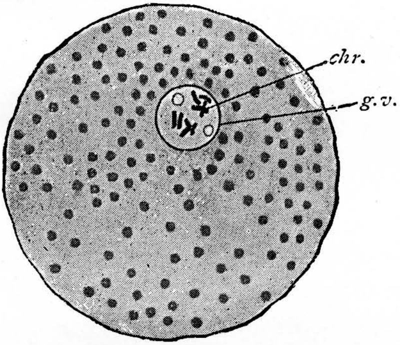

FIG. 6.—Diagram of ovum, showing diffuse yolk-granules. *g.v.* germinal vesicle or nucleus ; *chr.* chromosomes.

[*Facing p.* 38.

several nucleoli. As they are very variable and often transient, the nucleoli are not regarded as very important. Often they seem to be aggregations of reserve material or of waste-products.

The Typical Spermatozoon.—The germ-cell produced by the male parent, the spermatozoon, is very different from the ovum in appearance and structure, and is also very much smaller. When the egg is swollen with yolk, which does not count as living material, the spermatozoon may be less than a millionth of its volume. Most of the cytoplasm of the spermatozoon forms a locomotor flagellum or tail, often of intricate structure, which drives the "head" or nucleus before it, always working against

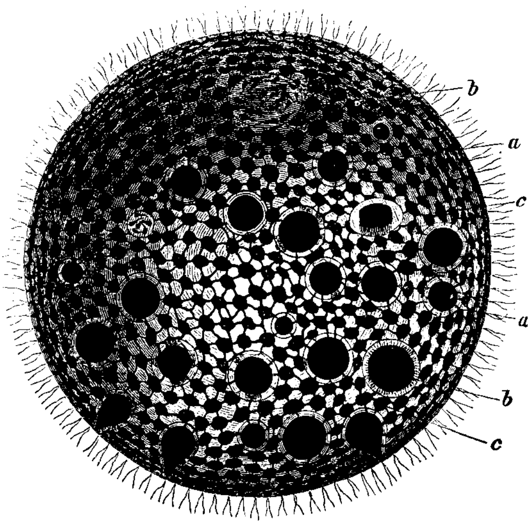

FIG. 7.—*Volvox globator*, an Infusorian forming a colony of cells, showing the ordinary cells (*c*) that make up the colony or incipient "body"; *a* and *b*, the special reproductive cells, both male and female—the beginning of the distinction between germ-cells and somatic cells.

a current if there is one. It is obviously a specialised adaptation which helps the spermatozoon to find the ovum, and it may be absent in cases where no journey or search is required. The so-called head of the spermatozoon contains the stainable material or chromatin, and in many cases it has been shown that the ripe spermatozoon has the same number of chromosomes as the ripe ovum. At the junction of the " head " and the " tail " there is a short " middle piece " or " neck," in which there is often seen a minute " centrosome."

There is in animals in most cases a great superficial contrast between the two kinds of germ-cells when fully mature. The typical ovum is relatively large, often laden with yolk, usually passive, and surrounded by some sort of membrane. The typical spermatozoon is relatively very minute, with no reserve material, and adapted to active locomotion. It is significant, however, that both contain the same number of chromosomes.

Old Attempts to interpret the Uniqueness of the Germ-cells.—In the preformationist theories, which held sway in the seventeenth and eighteenth centuries—theories which asserted the pre-existence of the organism and all its parts, in miniature, within the germ—there was a kernel of truth well concealed within a thick husk of error. For we may still say, as the preformationists did, that the future organism is implicit in the germ, and that the germ contains not only the rudiment of the adult organism, but the potentiality of successive generations as well. But what baffled the earlier investigators was the question, How the germ-cell comes to have this ready-made organisation, this marvellous potentiality. Discovering no natural way of accounting for this, the majority fell back upon a hypothesis of hyperphysical agencies—that is to say, they abandoned the scientific method, and drew cheques upon that bank where credit is unlimited as long as credulity endures.

An attempt to solve the difficulty which confronted the preformationists—the difficulty of accounting for the complex organisation presumed to exist in the germ-cell—is expressed in a theory which seems to have occurred at intervals in the long period between Democritus and Darwin, *the theory of pangenesis.* On this theory the cells of the body are supposed to give off characteristic and representative gemmules; these are supposed to find their way to the reproductive elements, which thus come to contain, as it were, concentrated samples of the different components of the body, and are therefore able to develop into an offspring like the parent. The theory is avowedly unverifiable in direct sense-experience—the same may be said of other conceptual formulæ—and is not in itself to be objected to. It is more to the point to notice that it involves many hypotheses, some of them difficult to accept even provisionally. Galton long ago tried, by experiments on the transfusion of blood, to test one of these hypotheses, and found no confirmation. But it is still more to the point to notice that there is another theory of

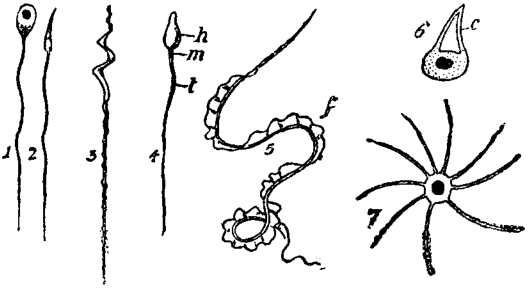

FIG. 8.—Forms of spermatozoa, enormously magnified, not drawn to scale.

1 and 2, Immature and mature spermatozoa of snail; 3, of bird; 4, of man—*h*. head, *m*, middle portion, *t*, tail; 5, of salamander, with vibratile fringe (*f*); 6. of Ascaris, slightly amœboid, with cap (*c*); 7, of crayfish.

heredity which is, on the whole, simpler—which seems, on the whole, to fit the facts better, for instance the fact that our experience does not warrant the conclusion that the modifications or acquired characters of the body of the parent affect in any specific and representative way the inheritance of the offspring.

The Idea of Germinal Continuity.—As is well known, the view which many, if not most, biologists now take of the uniqueness of the germ-cells is rather different from that of pangenesis. It is expressed in the phrase "germinal continuity," and has been independently suggested by several biologists, though Weismann has the credit of working it out into a theory. Let us state its purport. There is a sense, as Galton says, in which the child is as old as the parent, for when the parent's body is developing from the fertilised ovum, a residue of unaltered germinal material is kept apart to form the future reproductive cells, one of which may become the starting-point of a child. In many cases, scattered through the animal kingdom, from worms to fishes, the beginning of the lineage of germ-cells is *demonstrable* in very early stages before the differentiation of the body-cells has more than begun. In the development of the threadworm of the horse, according to Boveri, the very first cleavage divides the fertilised ovum into two cells, one of which is the ancestor of *all* the body-cells, and the other the ancestor of *all* the germ-cells. In other cases, particularly among plants, the segregation of germ-cells is not demonstrable until a relatively late stage. Weismann, generalising from cases where it seems to be visibly demonstrable, maintains that in all cases the germinal material which starts an offspring owes its virtue to being materially continuous with the germinal material from which the parent or parents arose. But it is not on a continuous lineage of recognisable germ-cells that Weismann insists, for this is often unrecognisable, but on the continuity of the germ-plasm—that is, of a specific substance of definite chemical and molecular structure which is the bearer of the hereditary qualities. In development a part of the germ-plasm, " contained in the parent egg-cell, is not used up in the construction of the body of the offspring, but is reserved unchanged for the formation of the germ-cells of the following generation." *Thus the parent is rather the trustee of the germ-plasm than the producer of the child.* In a new sense, the child is " a chip of the old block." As Sir Michael Foster put it, " The animal body is in reality a vehicle for ova ; and after the life of the parent has become potentially renewed in the offspring, the body remains as a cast-off envelope whose future is but to die." To use another metaphor, the germ-plasm is the lighted torch handed on from one runner to another. " Et quasi cursores vitaï lampada tradunt."

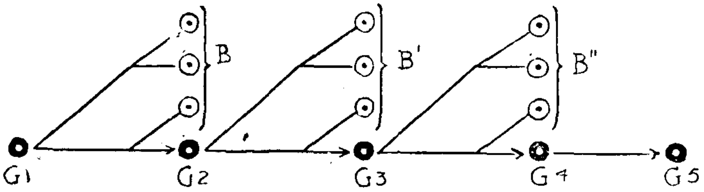

FIG. 9.—Diagram illustrating idea of germinal continuity. (After E. B. Wilson.)

G^1, fertilised ovum dividing into lineage of body-cells (B) and lineage of germ-cells—the base line; B', B'', the bodies of two successive generations; G^1, G^2, G^3, G^4, G^5, the chain of germ-cells.

Early segregation of the germ-cells is in many cases an *observable* fact—and doubtless the list of such cases will be added to ; but the conception of a germ-plasm is hypothetical, just as the conception of a specific living stuff or protoplasm is hypothetical. In the complex microcosm of the cell we cannot point to any one stuff and say, " This is protoplasm " ; it may well be that vital activity depends upon several complex stuffs which, like the members of a carefully constituted firm, are characteristically powerful only in their inter-relations. In the same way, it must be clearly understood that we cannot demonstrate the germ-plasm, even if we may assume that it has its physical basis in the stainable nuclear bodies or chromosomes. The theory has to be judged, like all conceptual formulæ, by its adequacy in fitting facts.

Let us suppose that the fertilised ovum has certain qualities, *a*, *b*, *c* . . . *x*, *y*, *z* ; it divides and re-divides, and a body is built up ; the cells of this body exhibit division of labour and differentiation, losing their likeness to the ovum and to the first results of its cleavage. In some of the body-cells the qualities *a*, *b*, find predominant expression, in others the qualities *y*, *z*, and so on. But if, meanwhile, there be certain germ-cells which do not differentiate, which retain the qualities *a*, *b*, *c* . . . *x*, *y*, *z*, unaltered, which keep up, as one may say figuratively, "the protoplasmic tradition," these will be in a position by-and-bye to develop into an organism like that which bears them. Similar material to start with, similar conditions in which to develop—*therefore*, like tends to beget like.

May we think for a moment of a baker who has a very precious kind of leaven ; he uses much of this in baking a large loaf ; but he so arranges matters by a clever contrivance that part of the original leaven is always carried on unaltered, carefully preserved for the next baking. Nature is the baker, the loaf is a body, the leaven is the germ-plasm, and each baking is a generation.

§ 6. *Maturation of the Germ-cells*

We have seen that the germ-cells owe their capacity of development to the fact that they are the unspecialised descendants of the parental fertilised ovum—the custodians of the characteristic germ-plasm. In some cases the lineage of germ-cells is from the first distinct and apart from the lineage of body-forming cells, and we argue from these clear cases of germinal continuity to the more numerous and less obvious cases where the germ-cells are not recognisable as such until later stages in development.

There is no need for our present purpose to follow the generations of the germ-cells within the body, or to trace the stages of growth and differentiation between primitive germ-cells and the fully formed ripe ova and spermatozoa. It is necessary, however, to allude to the process of maturation, which has a direct bearing on the problems of heredity and inheritance.

Maturation.—1. It is an elementary fact of histology that the nucleus of each cell in the body of an organism contains a number of readily stainable bodies or chromosomes. In many cases it has been possible to count these, and it has been found that (with a few explicable exceptions) the number is *constant for each species.*

As Prof. E. B. Wilson says (1900, p. 67): "The remarkable fact has now been established with high probability that *every species of plant or animal has a fixed and characteristic number of chromosomes, which regularly recurs in the division of all of its cells, and in all forms arising by sexual reproduction the number is even.** Thus, in some of the sharks the number is 36; in certain Gasteropods it is 32; in the mouse, the salamander, the trout, the lily, 24; in the worm *Sagitta*, 18; in the ox, guinea-

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* In a few insects the females have in their body-cells one chromosome in addition to the number possessed by the males.

pig, and in man * the number is said to be 16, and the same number is characteristic of the onion. In the grasshopper it is 12 ; in the hepatic *Pallavicinia* and some of the nematodes, 8 ; and in *Ascaris*, another thread-worm, 4 or 2. In the crustacean *Artemia* it is 168. Under certain circumstances, it is true, the number of chromosomes may be less than the normal in a given species ; but these variations are only apparent exceptions [p. 87, Wilson]. The even number of chromosomes is a most interesting fact, which, as will appear hereafter [p. 205, Wilson], is due to the derivation of one-half the number from each of the parents."

2. About 1883, Van Beneden made the important discovery that the nuclei of the ovum and of the spermatozoon which unite in fertilisation contain each one-half of the number of chromosomes characteristic of the body-cells. This has been confirmed in regard to so many plants and animals that it may now be regarded as a general fact. The student should refer to the partial list given by Wilson (1900, pp. 206-7), where it will be seen that if the somatic nuclei have 12, 16, 18, or 24 chromosomes, the germ-nuclei have 6, 8, 9, or 12 respectively. A striking case is found in the large thread-worm (*Ascaris megalocephala*) of the horse, which occurs in two varieties,—the one, var. *univalens*, with two chromosomes in its body-cells has one chromosome in its germ-nuclei ; the other, var. *bivalens*, with four chromosomes in its body-cells, has two chromosomes in its germ-nuclei.

3. If each of the nuclei which unite in fertilisation has only half as many chromosomes as are characteristic of the species, it follows that a reduction of the number must take place in the history of the germ-cells, and this is the outstanding fact in the process of maturation. Alike in the history of the egg (oogenesis) and in the history of the sperm (spermatogenesis),

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* "Flemming believed the number in man to be considerably greater than 16." It is now generally stated to be 24.

there is a parallel reduction in the number of chromosomes to one-half.

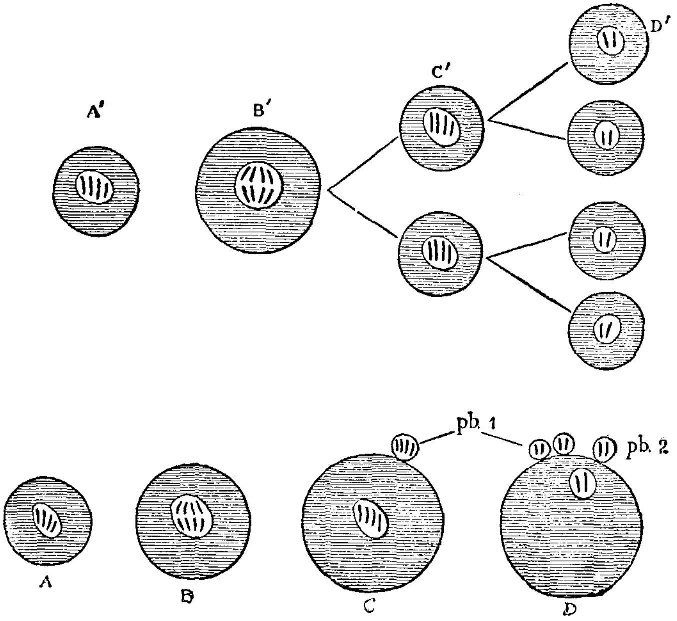

FIG. 10.—Spermatogenesis and polar bodies. (After Hertwig and Weismann.)

A', Primitive sperm-cell of *Ascaris megalocephala*, var. *bivalens*, with four chromosomes; B', sperm mother-cell (eight chromosomes); C', two spermatocytes formed, each with four chromosomes; D', four spermatozoa formed, each with two chromosomes; A, primitive egg-cell with four chromosomes; B, fully developed ovum, with eight chromosomes; C, formation of first polar body (pb. 1) which divides into two, each with two chromosomes; D, formation of second polar body (pb. 2). The nucleus of the now mature ovum has two chromosomes, like the ripe spermatozoon.

"The one fact of maturation that stands out with perfect clearness and certainty amid all the controversies surrounding it is *a reduction of the number of chromosomes in the ultimate germ-cells to one-half the number characteristic of the somatic cells.* It is equally clear that this reduction is a preparation of the germ-cells for their subsequent union and a means by which the number of chromosomes is held constant in the species. With a few exceptions the first indication of the numerical reduction appears through the segmentation of the spireme-thread, or the resolution of the nuclear reticulum, into a number of masses *one-half that of the somatic chromosomes.* In nearly all higher animals this process first takes place two cell-generations before the formation of the definitive germ-cells, and the process of reduction is completed by two rapidly succeeding 'maturation-divisions,' giving rise to four cells, all of which become functional in the male, while in the female only one becomes the egg, and the other three—the polar bodies or their analogues—are cast aside. During these two divisions each of the original chromatin masses gives rise to four chromosomes, of which each of the four daughter-cells receives one; hence, each of the latter receives one-half the somatic number of chromosomes.* In the higher plants, however, the two maturation-divisions are followed by a number of others, in which the reduced number of chromosomes persists, a process most strikingly shown in the pteridophytes, where a separate sexual generation (prothallium) thus arises, all the cells of which show the reduced number" (Wilson, 1900, p. 285).

As Boveri has said: "Thus at some stage or other in the generation-series of the germ-cell there occurs a reduction of the number of chromosomes originally present to one-half, and this *numerical* reduction is therefore to be regarded, not as a mere theoretical postulate, but as a fact" (*Zellen-Studien*, iii. 1890, p. 62).

* Suppose the characteristic number of chromosomes for the species to be 12, the primitive germ-cells share this; the number is reduced to 6; each is increased to 4, and thus each of the 4 daughter-cells receives 6; and in fertilisation the number 12 is restored. (12 is reduced to 6; $6 \times 4 = 24$; $\frac{24}{4} = 6$; $6 + 6 = 12$.) After the reduction from 12 to 6, each of the six is seen to consist of two longitudinally split chromosomes, that is of four parts, forming what is called a tetrad group.

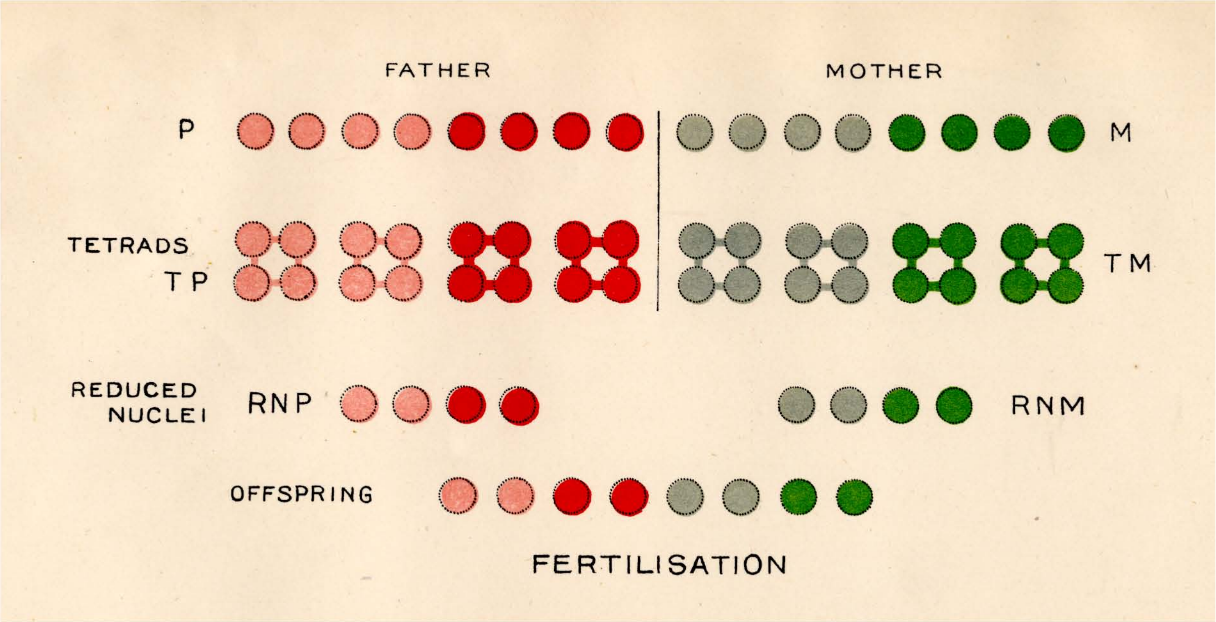

Fig. 11.—Diagram to illustrate reduction of chromosomes and amphimixis. (After H. E. Ziegler.)

P, paternal chromosomes, supposed to be eight in number and of two sets, the light-red from the paternal grandfather, the deep red from the paternal grandmother; M, Maternal chromosomes, supposed to be eight in number and of two sets, the blue from the maternal grandfather, the green from the maternal grandmother; TP and TM, Tetrads formed in maturation; RNP, the four chromosomes of the reduced nucleus of the ripe spermatozoon; RNM, the four chromosomes of the reduced nucleus of the ripe ovum. In the offspring there are eight chromosomes, four paternal, four maternal, and of four different sets—contributions from the four grandparents. In this case four *other* combinations are possible so that there might be five different kinds of offspring.

Facing p. 48.

§ 7. *Amphimixis and the Dual Nature of Inheritance in Sexual Reproduction*

Apart from exceptional cases, the inheritance of a multicellular animal or plant is dual—part of it comes from the mother and part of it from the father; in other words, the material basis of inheritance is a fertilised egg-cell. The new individuality has its origin in the fusion of two potential individuals, for as such the ovum and spermatozoon must be regarded. The exceptions referred to are cases of asexual multiplication by buds or otherwise, as in the freshwater Hydra; cases of parthenogenesis, as in the case of the unfertilised eggs which develop into green flies (Aphides) in the summer; and cases like liver-flukes, where an animal is both mother and father to its offspring. Apart from these exceptions the inheritance does at the start consist of maternal and paternal contributions in intimate and orderly union.

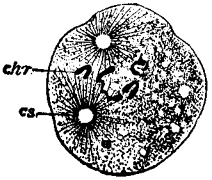

FIG. 12.—Fertilised ovum of *Ascaris*. (After Boveri.)

chr. chromosomes, two from ovum-nucleus and two from sperm-nucleus; *cs.* centrosome, from which "archoplasmic" threads radiate, partly to the chromosomes.

When a spermatozoon, outstripping its fellows (for there are usually very large numbers), reaches an ovum and bores its way into it, the cytoplasmic flagellum is left behind, having performed its function, and the sperm-nucleus and the ovum-nucleus move towards one another. By a rapid change in the periphery of the ovum, the enveloping membrane becomes firmer, and the ovum becomes non-receptive to other spermatozoa. When several effect entrance at once, abnormalities usually result. In the mature ovum there is no centrosome ; if it was originally present, it disappears. The spermatozoon, however, introduces, along with its nucleus, its centrosome, and this divides into two. The two centrosomes appear to take an active part in the approximation and intimate apposition of the maternal and paternal chromosomes, and in their subsequent partition between the first two daughter-cells.

Prof. E. B. Wilson states the general opinion of experts somewhat as follows. *As the ovum is much the larger, it is believed* to furnish the initial capital—including, it may be, a legacy of food-yolk—for the early development of the embryo. From both parents alike comes the inherited organisation which has its seat (according to most biologists) in the readily stainable (chromatin) rods of the nuclei. From the father comes a little body (the centrosome) which organises the machinery of division by which the egg splits up, and distributes the dual inheritance equally between the daughter-cells.

Let us now proceed to expound four important theorems.

1. **In Ordinary Sexual Reproduction the Inheritance is very precisely Dual or Biparental.**—Recent discoveries have shown that the paternal and maternal contributions which come together in fertilisation are, for several divisions at least, exactly divided among the daughter-cells, thus confirming a prophecy which Huxley made in 1878 : " It is conceivable, and indeed probable, that every part of the adult contains molecules derived both from the male and from the female parent ; and that, regarded as a mass of molecules, the entire organism may be compared to a web of which the warp is derived from the female and the woof from the male." " What has since been gained," Prof. Wilson says, " 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."

After the paternal and maternal chromosomes have united,

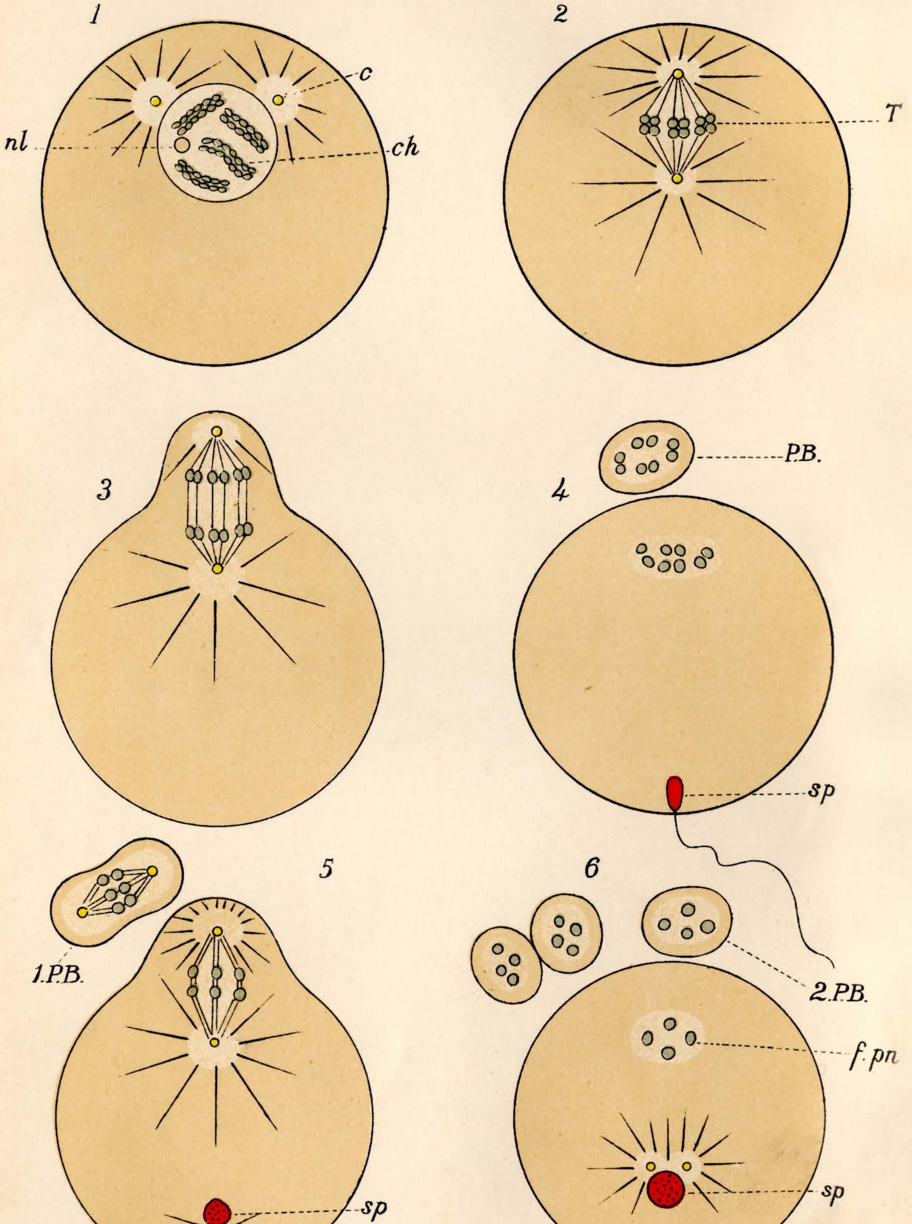

Fig. 13

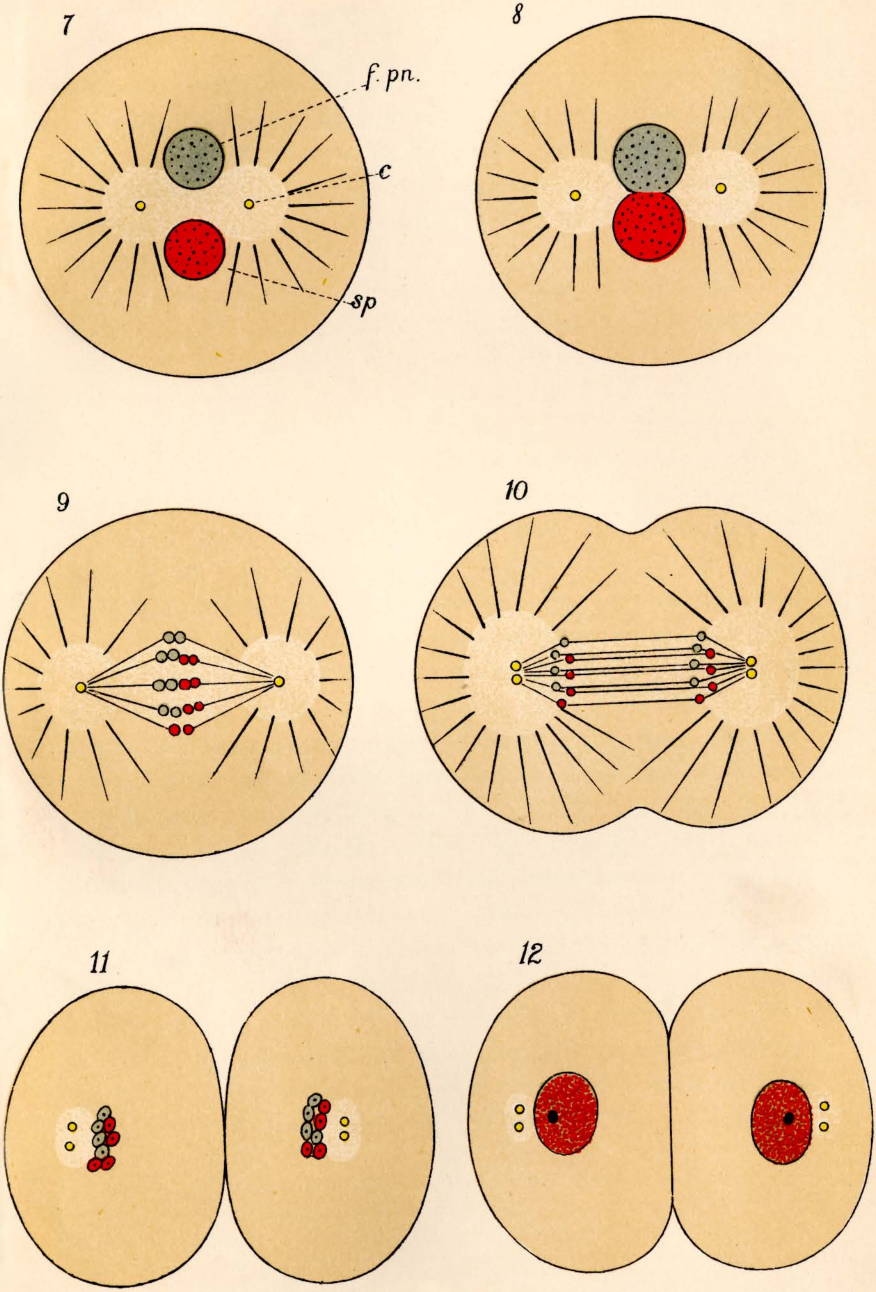

Fig. 13

[Facing p. 51

FIG. 13.—Diagram of maturation and fertilisation and first stages of cleavage. (From Prof. H. E. Ziegler, with his kind permission.) The colours have been added.

1.—The immature ovum, with four double chromosomes, longitudinally cleft; *c*, centrosome; *ch*, chromosomes; *nl*, nucleolus.

2.—First maturation division; the nuclear spindle has at its equator four groups of tetrads, three of which are visible.

3 and 4.—Formation of the first polar body (P.B.). In fig. 4 a spermatozoon (*sp*) is entering. The paternal chromatin is shown throughout in red, the maternal in blue, the centrosome which is brought in by the spermatozoon is shown in yellow. The ovum-centrosome disappears.

5.—The formation of the second polar body and the division of the first (1 *P.B.*). The head of the spermatozoon has formed the male pronucleus (*sp*). The centrosome introduced by the spermatozoon is surrounded by a clear area and rays.

6.—The second polar body (2 *P.B.*) has been set adrift. The first has divided into two. The three polar bodies and the now mature ovum have in their nuclei half the normal number of chromosomes. Thus four are seen in the female pronucleus (*f.pn*). The centrosome has divided into two.

7.—The male and female pronuclei (*sp* and *f.pn*) have become like one another, and are near together. The centrosomes (*c*) have become the centres of two large systems of rays.

8.—The two pronuclei are in contact and are coalescing.

9.—The nuclei have lost their membrane, and the first segmentation-spindle or cleavage-spindle has been formed, a centrosome lying at each pole. The spindle has the normal number of chromosomes, but each has divided, so that eight pairs are present.

10.—The egg-cell is dividing. The chromosomes are separated into two groups, each group with eight chromosomes. The centrosome at each pole has divided into two.

11.—The division or cleavage is complete. The rays have disappeared. The chromosomes are represented by minute vesicles or karyomeres.

12.—The new nuclei have been constituted by union of the vesicles. The centrosomes lie closely apposed, but will occupy the poles of the spindle at the next division.

but never fused, to form one nucleus—the segmentation-nucleus —the cleavage or segmentation of the fertilised ovum begins.

There is a centrosome, derived from the sperm-centrosome, at each pole of the nucleus, and a system of fine rays radiates from each, some of these rays entering into close association with the chromosomes.

Each chromosome is halved *longitudinally*, as a piece of stick might be split up the middle, and after a very complex routine the halves of each split chromosome migrate, either actively or passively, to opposite poles. Thus, near each centrosome there comes to be a group of chromosomes, half of each group being of paternal origin and half of maternal origin. Each group in an orderly fashion rounds itself off into a unified nucleus, the body of the cell (the cytoplasm) constricts across the equatorial plane, and two cells are formed.

The gist and import of the whole process is the precisely equal partition of the maternal and paternal contributions, so that each of the daughter-cells has a nucleus half maternal and half paternal. For many successive divisions (*e.g.* in *Cyclops*) the duality has been demonstrated,* so that we may fairly say that the maternal and paternal contributions form the warp and woof of the growing organism.

2. **Inheritance, though Dual, is strictly Multiple.**—Although the whole inheritance which constitutes an offspring usually comes from two parents, and may therefore be called dual, it is obvious that the heritable material of each parent was also dual, being derived from the grandparents, and so on backwards; so that inheritance is strictly not merely dual, but in an even deeper sense multiple. Amphimixis or fertilisation implies the subtle mingling of two minute organisations so that they become physiologically one, but each of them was already

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* According to Haecker's careful observations on the water-flea *Cyclops*, the paternal and maternal contributions, *i.e.* chromosomes, are traceable as distinct individualised items throughout the whole of development.

the complex product of ancestral lineage. We shall return to the subject when we come to consider Galton's Law of Ancestral Inheritance.

Though a comparison with the inheritance of property is apt to mislead, it may be of use to think for a moment of a youth inheriting an estate, of which one might accurately say that it had belonged in half to his father and in half to his mother. Yet a genealogist with a full knowledge of the family might be able to go further back, and might show, with even greater accuracy, how this corner was due to a grandmother and that to a great-grandfather.

This conception is so fundamentally important that I cannot refrain from quoting an illustration from Mr. Galton's *Natural Inheritance,* which puts the matter very clearly. "Many of the modern buildings in Italy are historically known to have been built out of the pillaged structures of older days. Here we may observe a column or a lintel serving the same purpose for a second time, and perhaps bearing an inscription that testifies to its origin; while as to the other stones, though the mason may have chipped them here and there and altered their shape a little, few if any came direct from the quarry. . . . . This simile gives a rude though true idea of the exact meaning of Particulate Inheritance—namely, that each piece of the new structure is derived from a corresponding piece of some older one, as a lintel was derived from a lintel, a column from a column, a piece of wall from a piece of wall. . . . We appear to be severally built up out of a host of minute particles of whose nature we know nothing, any one of which may be derived from any one progenitor, but which are usually transmitted in aggregates, considerable groups being derived from the same progenitor. It would seem that while the embryo is developing itself, the particles more or less qualified for each post wait, as it were, in competition to obtain it. Also that the particle that succeeds must owe its success partly to accident of position and partly to being better qualified than any equally well-placed competitor to gain a lodgment. Thus the step-by-step development of the embryo cannot fail to be influenced by an incalculable number of small and mostly unknown circumstances." (*Natural Inheritance*, p. 9.)

3. **Duality of Inheritance may be real, though it is not expressed.**—It must be carefully observed that the demonstration of the dual nature of inheritance afforded by the facts of amphimixis does not necessarily imply that the dual nature of the inheritance will be patent in the full-grown offspring. The offspring is often like both its parents, often particularly like one, often not very like either. The parent of children, the breeder of animals, or the cultivator of plants, has often occasion to remark in the offspring what looks like an entire absence of the characteristics of one of the parents. The foal may seem to take entirely after the sire, as if the maternal inheritance counted for nothing. It is likely that this so-called " exclusive " or "unilateral" inheritance is often more apparent than real, our observation being arrested and preoccupied by a few outstanding features. The certain fact that the resemblance, apparently absent, often reappears in the next generation, shows that the incompleteness was not in these cases in the inheritance, but simply in its expression. We shall return to this subject in connection with the different modes of inheritance.

4. **Each Germ-cell has a Complete Equipment of Hereditary Qualities.**—It is usually assumed that each of the two sex-cells which unite in fertilisation has in it the potentiality of an organism with a full equipment of the essential characters of the species ; but since the spermatozoon always dies unless it enters the ovum, it is difficult to give experimental proof of the assumption. Some recent daring experiments, which demand confirmation, are very suggestive in this connection.

Prof. Yves Delage (1898) divided the minute egg of the sea-urchin under the microscope into two parts, one containing the nucleus and its companion-body the centrosome, the other being necessarily simply half of the living matter of the egg without any nucleus. Beside them he placed an intact ovum, and then let the spermatozoa in. All the three objects showed equal "sexual attraction" in respect to the spermatozoa; all three were fertilised; all three segmented, the intact ovum most rapidly, the nucleated fragment more slowly, the non-nucleated fragment more slowly still. In one case the development proceeded for three days; the intact ovum had become a typical gastrula (two-layered embryo), the nucleated fragment a smaller gastrula, and the non-nucleated fragment also a gastrula but with a very much reduced cavity. All the cells of these embryos showed nuclei. Thus the experimenter was led to the conclusion that *fertilisation and some measure of development may occur in a fragment of ovum without nucleus or centrosome.* The nucleus of the spermatozoon must have been in this case sufficient in itself, though it will be noticed that in the experiment cited the fragment did not develop far. Delage makes the important suggestion that in fertilisation two things must be distinguished: (*a*) the stimulus given to the ovum by some specially energetic substance brought in by the spermatozoon, perhaps in its centrosome; and (*b*) the mingling of heritable characteristics, Weismann's "amphimixis."

In subsequent experiments Prof. Delage (1899) reached even more extraordinary results. Non-nucleated fragments of the ovum of *Echinus* (sea-urchin), *Dentalium* (elephant's-tooth shell), and *Lanice conchilega* (a seashore worm), were effectively fertilised and gave rise to the characteristic larval forms—pluteus, veliger, and trochophore respectively. Three larvæ were reared from one ovum of a sea-urchin; a normal blastula embryo (a hollow ball of cells) was reared from $\frac{1}{37}$th of a sea-urchin ovum; a non-nucleated fragment of a sea-urchin ovum, after fertilisation by a spermatozoon with nine chromosomes (nuclear rods), gave rise to a larva whose cells had the normal number of eighteen chromosomes: such are some of the extraordinary results reached by this clever experimenter. It seems, then, as if *fertilisation may, in many cases, be effective without there being any ovum-nucleus present,* as if the essential fact were the union of a sperm with a mass of egg-cytoplasm.

Delage's experiments cited above seem to prove that the nucleus and centrosome of the ovum are not essential to fertilisation. Professor Loeb (1899), of Chicago, has made experiments which seem to show that the spermatozoon may be dispensed with. In other words, he has been able to induce parthenogenetic development artificially in cases where it does not normally occur. He has been led to believe that the only reason why the eggs of many marine animals do not develop parthenogenetically is that something in the constitution of the sea-water prevents it. This something is the presence or absence of ions of sodium, calcium, potassium, and magnesium, the two former requiring to be reduced, the two latter to be increased. "The mixture of about 50 per cent. $\frac{10}{8}n$ $MgCl_2$ (magnesium chloride) with about 50 per cent. of sea-water was able to bring about the same effect as the entrance of a spermatozoon. The unfertilised eggs [of the sea-urchin *Arbacia*] were left in such a solution for about two hours. When brought back into normal sea-water they began to segment and form blastulæ, gastrulæ, and plutei, which were normal in every respect. The only difference was that fewer eggs developed, and that their development was slower than in the case of the normal development of fertilised eggs. With each experiment a series of control experiments was made to guard against the possible presence of spermatozoa in the sea-water. . . . From these experiments it follows that *the unfertilised egg of the sea-urchin contains all the essential elements for the production of a perfect pluteus.* The only reason that prevents the sea-urchin from developing parthenogenetically under normal conditions is the constitution of the sea-water. The latter either lacks the presence of a sufficient amount of the ions that are necessary for the mechanics of cell division (Mg, K, HO, or others), or it contains too large a quantity of ions that are unfavourable to this process (Ca, Na, or others), or both. All the spermatozoon *needs* to carry into the egg for the process of fertilisation are ions to supplement the lack of the one or counteract the effects of the other class of ions in the sea-water, or both. The spermatozoon *may*, however, carry in addition a number of enzymes or other material. The ions and not the nucleins in the spermatozoon are essential to the process of fertilisation."

These remarkable experiments are confirmatory of the general assumption that spermatozoon and ovum are completely equipped potential organisms. Further confirmation may be found in cases of partial parthenogenesis—*e.g.* the development of drone-bees from unfertilised eggs; from the close similarity in the history of ovum and spermatozoon respectively; from the exactly equal way in which the paternal and maternal nuclear contributions are distributed to each cell, during the early stages of cleavage at least.

When we consider the ovum and spermatozoon as two fully equipped potential individualities which unite to form the beginning of a new individuality, we see more clearly how, on the one hand, there is a double likelihood of the essential specific characters being sustained, and how, on the other hand, there is every likelihood that the intermingling will lead indirectly, if not directly, to something new.

§ 8. *Inheritance in Cases of Parthenogenesis*

It would be interesting to know with precision what the facts of inheritance are in cases where development proceeds from an unfertilised ovum, particularly in those cases where the parthenogenesis continues uninterruptedly for many generations.

On general grounds, from the absence of fertilisation, one would expect to find few new departures or progressive variations; but rather, on the other hand, hints of degeneracy. The observed facts are still very few.

Experiments which Prof. Weismann (*1893*, p. *344*) *made on* a small crustacean (*Cypris reptans*) showed a very high degree of uniformity between parent and offspring, with occasional exceptions, which he regarded as exhibiting reversions to an ancestral form many generations removed.

Dr. Warren's (1899) measurements of successive parthenogenetic generations of *Daphnia magna* also gave evidence of slight variability (*i.e.* of incompleteness of hereditary resemblance). They seemed to favour the view that "inheritance in parthenogenetic generations resembles that from mid-grandparent to grandchildren."

§ 9. *Wherein the Physical Basis precisely consists*

The fertilised egg-cell divides into many cells; these arrange themselves in various ways; they grow and multiply; they exhibit division of labour and the structural side of this—which we call differentiation; they form tissues and organs; they become integrated into a body; they reproduce the likeness of the parental type with variations. Meanwhile, some of the cells remain apart from body-making or differentiation, and form the beginnings of the reproductive organs, whence their descendants—the mature germ-cells—are by-and-bye liberated to start another generation. That this next generation is also after the parental type is due to the continuous lineage of cells containing unspecialised germinal material. In similar conditions similar material produces similar results.

But, if this has become clear, we have now to inquire into the precise nature of the physical basis which conserves the heritable qualities. Is it the germ-cell as a whole that is essential, or is the cytoplasm most important, or is it the nucleus only ?

A Cautious Acceptance of the Conclusion that the Germ-nuclei are the Bearers of the Hereditary Qualities.—Many observations go to show that the nucleus of a cell plays an important part in nutritive and constructive processes, and it is certain that a cell artificially bereft of its nucleus will soon die if left to itself. The nuclear material (karyoplasm or nucleoplasm) is an essential part of the vital organisation. The view has gained ground and general acceptance that the nucleus is the chief or exclusive bearer of the hereditary qualities, and as this is important in connection with some developments of the theory of heredity, we must give some attention to the basis on which the conclusion rests.

1. *Argument from cell-division.*—Roux, Hertwig, Kölliker, Strasburger, and many others, have emphasised the fact that, in the ordinary (mitotic) form of cell-division, the chromatin or readily stainable material of the nucleus is divided " with the most scrupulous equality " to form the basis of the nuclei of the daughter-cells, while the cytoplasm or general cell-substance " undergoes on the whole a mass-division—a most remarkable contrast." As Prof. Wilson says (1900, p. 351) : " This holds true with such wonderful constancy throughout the series of living forms, from the lowest to the highest, that it must have a deep significance. And while we are not yet in a position to grasp its full meaning, this contrast [between nuclear and cytoplasmic behaviour in division], points unmistakably to the conclusion that the most essential material handed on by the mother-cell to its progeny is the chromatin, and that this substance, therefore, has a special significance in inheritance."

2. *Argument from maturation.*—In the changes which lead up to the ripe egg and the fully-formed spermatozoon, there is, as we have seen, an elaborate preparation whereby the germ-nuclei which unite in fertilisation are rendered precisely equal

as regards the number of their chromosomes. On the other hand, the cytoplasm of the relatively large, passive, often food-laden and ensheathed ripe ovum is typically as different as possible from that of the very minute, actively mobile, usually short-lived spermatozoon. The constancy and frequent complexity of the reduction-processes which secure the equivalence of chromosomes suggest that these bodies are of paramount importance in inheritance.

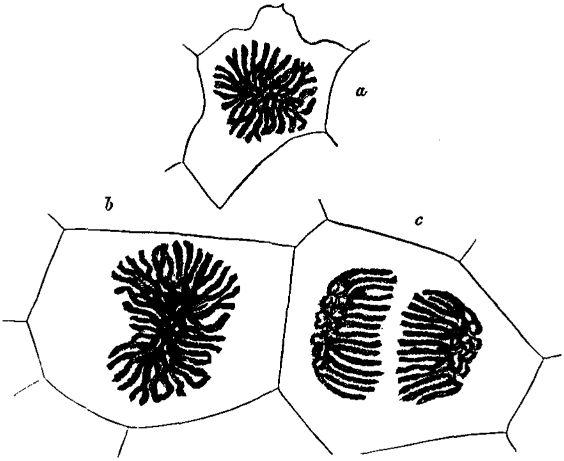
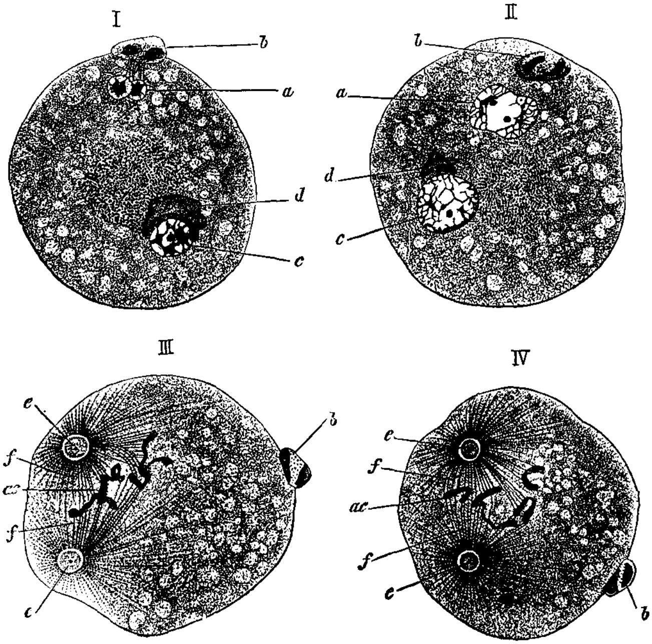


FIG. 14.—The chromatin elements of the nuclei in coil (*a*), double star (*b*), and almost divided stages (*c*). (After Pfitzner.)

3. *Argument from fertilisation.*—In typical cases of fertilisation in animals, and in many plants as well, a spermatozoon enters an ovum, sometimes a hundred thousand times larger than itself. As it enters it may leave behind it the locomotor "tail," which has discharged its function, thus further reducing its infinitely small stock of cytoplasmic material. The "head" of the spermatozoon, which is mostly nucleus, and the little "middle piece" which carries the centrosome, are apparently

the important parts, and it is the ovum which furnishes the cytoplasmic basis of further operations. The very gist of fertilisation, *so far as we can see it,* is the intimate and orderly combination of the paternal and maternal chromosomes to form one nucleus—the segmentation-nucleus. Moreover, the maternal and paternal contributions are, as we have noted, distributed with scrupulous equality, certainly to the first two cells of the embryo, and probably to all later-formed cells.

"The latter conclusion, which long remained a mere surmise, has been rendered nearly a certainty by the remarkable observations of Rückert, Zoja, and Haecker. We must, therefore, accept the high probability of the conclusion that the specific character of the cell is in the last analysis determined by that of the nucleus—that is, by the chromatin; and that in the



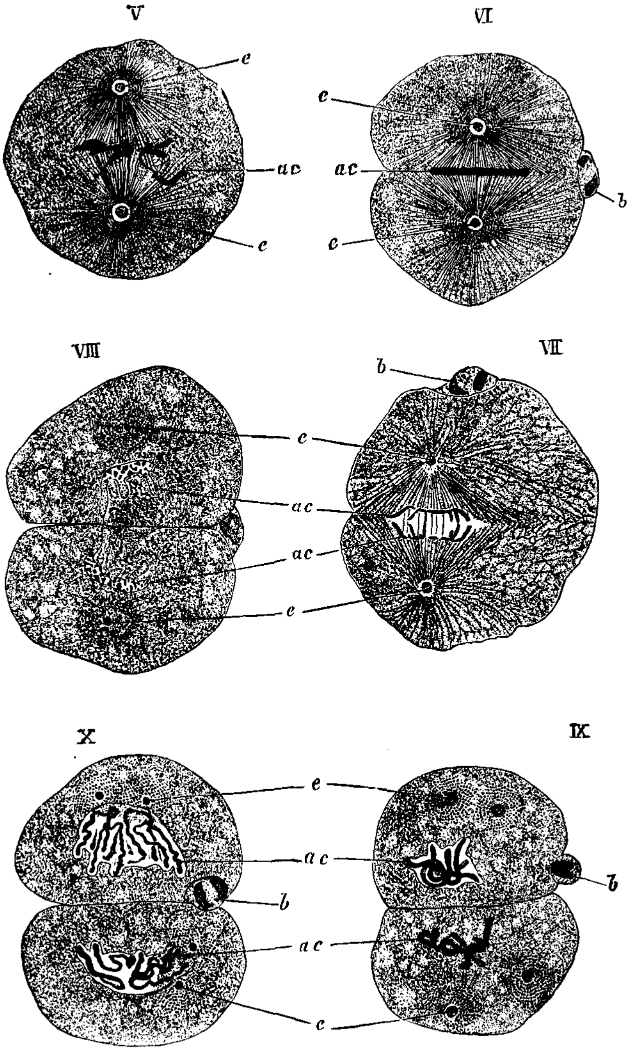


FIG. 15.—Diagram of the process of fertilisation in *Ascaris*. (After Boveri.)

a, female pronucleus ; *b*, polar bodies ; *c*, sperm pronucleus ; *d*, sperm-cap ; *ac*, chromosomes of united female and male pronuclei (*a* and *c*) ; *e*, centrosomes ; fine (archoplasmic) threads radiating from the centrosomes. I–V show union of paternal and maternal chromosomes ; VI shows equatorial plate of segmentation nucleus ; VII–X show the division into the two first cleavage-cells or blastomeres.

equal distribution of paternal and maternal chromatin to all the cells of the offspring, we find the physiological explanation of the fact that every part of the latter may show the characteristics of either or both parents" (Wilson, 1900, p. 352).

4. *Argument from Boveri's ingenious experiment.*—Taking a hint from the experiments of the brothers Hertwig, who showed that non-nucleated fragments of unfertilised sea-urchin ova (broken by shaking) might be successfully fertilised and might segment, Boveri (1889, 1895) showed that such fertilised fragments developed into dwarf, but normal, larvæ. In these, as T. H. Morgan (1895) afterwards showed, the nuclei contain *only half the normal number of chromosomes,* having had only a sperm-nucleus to start with.

Interesting as this was, Boveri's further experiment was yet more striking. He fertilised the enucleated egg-fragments of one species of sea-urchin (*Sphærechinus granularis*) with spermatozoa of another species (*Echinus microtuberculatus*), and obtained in a few cases dwarf larvæ (plutei), which showed, except as regards size, the paternal characters only. Therefore he concluded that the nucleus is the exclusive bearer of the hereditary qualities, for it seemed from the experiment that the enucleated maternal cytoplasm had remained without specific influence.

It is admitted by Boveri himself that further experiments are necessary, and it must be granted also, as has been pointed out by Seeliger, Morgan, and Driesch, that in cases of hybridism, as in Boveri's experiment, there may be a marked illustration of what is called unilateral or preponderant inheritance. While most hybrids are intermediate, some "take after" the father and others after the mother. But the experiment remains uncontroverted, if unsubstantiated, and it is as suggestive as it was ingenious.

Generally accepted Conclusion.—The general conclusion from the foregoing and other arguments may be illustrated by two or three quotations from recognised authorities. Prof. O. Hertwig says: "The female nuclear material transmits the characters of the mother, the male nucleus those of the father, to the offspring." Prof. Strasburger says for higher plants: "The process of fertilisation depends upon the union of the sperm-nucleus with the nucleus of the egg-cell; the cell-substance (cytoplasm) does not share in the process; the cell-substance of the pollen-grain is only the vehicle to conduct the generative nucleus to its destination." Prof. Weismann says: "We can hardly ascribe to the body of the ovum a higher import than that of being the common nutritive basis for the two conjugating nuclei."

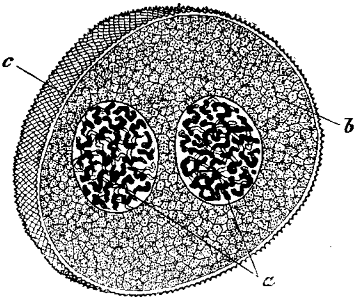


FIG. 16.—A pollen grain. *a*, the two nuclei, with their chromosomes; *b*, the general protoplasm; *c*, the outer wall. (From Carnoy.)

Criticism.—1. "The life of a complex multicellular organism certainly depends upon the inter-relations and interactions of many parts; the life of a cell apparently depends upon the inter-relations and interactions of different parts of the cellular organisation, especially on the give-and-take between nucleoplasm and cytoplasm; and it is not unlikely that life itself—*i.e.* vital activity or function—may depend upon the inter-relations and inter-actions of a number of complex substances, *none of which could by itself be called alive.* Just as the secret of a firm's success may depend upon a particularly fortunate association of partners, so it may be with vitality." * "We are compelled by the most stringent evidence to admit that the ultimate basis of living matter is not a single chemical substance, but a mixture of many substances that are self-propagating without loss of their specific character." † Holding firmly to this view, which we have elsewhere expressed, that life is a function of inter-relations, we confess to hesitation in accepting without saving clauses any attempt to call this or that part of the germinal matter the exclusive vehicle of the hereditary qualities.

2. The sperm-nucleus brings with it into the ovum a little cytoplasm, and it is also accompanied by the minute central-corpuscle or centrosome, which seems to play an important part in regulating the mechanism of cleavage. It may be that the minimal quantity of cytoplasm is also important, though we cannot trace its behaviour as we do that of the centrosome. Strasburger says that if it were important there would be more of it, but in these matters size and mass seem of small moment; the little cytoplasm there is may act like the little leaven which leavens the whole lump. It seems in this connection very desirable that the experiments which have been begun (Piéri and Winkler) of extracting a ferment ("ovulase") from seminal matter and using it as a fertilising agent, should be confirmed or confuted.

3. In Loeb's experiments unfertilised sea-urchin's eggs developed into complete and normal larvæ; the sperm-nucleus was dispensed with. In Delage's experiments non-nucleated fragments of the ova of sea-urchin, worm, and mollusc were fertilised and developed into normal larvæ; the ovum-nucleus was dispensed with. But it must be noted carefully that in both cases there was *a* nucleus present.

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* J. Arthur Thomson, *Science of Life*, p. 115 (London, 1899).

† E. B. Wilson, *The Cell in Development and Inheritance* (1st ed., 1896).

At the same time, the possibility of some ingenious combination of Loeb's method and Delage's seems to suggest that we should be chary in committing ourselves unreservedly to the conclusion that the heritable organisation is *exclusively* resident in the chromatin of the nuclei of the germ-cells.*

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* Dr. Hans Driesch has called my attention to some remarkable experiments by Dr. Curt Herbst, which seem to show that the nuclear sap as distinguished from the chromosomes may be of importance as a vehicle in inheritance.