THE PROGRESSIVE SCIENCE SERIES

PROBLEMS OF LIFE AND REPRODUCTION

MARCUS HARTOG

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WITH ILLUSTRATIONS

LONDON
JOHN MURRAY, ALBEMARLE STREET, W.
1913

PREFACE

The idea of this volume first presented itself to me many years ago as a general treatise on Reproduction, suited to the layman interested in biological questions and without any technical preparation for their study. There seemed to be a need for this, accentuated by the tendency of many authors catering for this public to put forward the views of their own school as the final conclusions of biologists at large: a need which has certainly not diminished since the inception of the task. But though much of the systematic survey was completed, it was interrupted by more urgent tasks which I could not refuse, and the typoscript lay by. On taking it up again I found that a work of this scope could hardly be made suitable for that public to which I desired to appeal; while, on the other hand, the views that were important lay already exposed in various essays, or rather, buried in the back numbers of periodicals. My publisher was good enough not only to forgive me my long delay, but to accede to my suggestion to collect these essays into a volume. Two of the essays have been much modified: the first, on "Fertilisation," has been rewritten in great part, and the other, which appeared in *Science Progress* as "The Dual Force of the Dividing Cell," has been completely remodelled, I may say, with its essential contents expanded and brought up to date, under the title of "The 'New Force,' Mitokinetism."

In the revision, indeed, I have endeavoured to bring everything up to date, and have not hesitated to do so without note or comment wherever no question of priority was involved: but where this was the case I have pointed it out by the inclusion of new matter in square brackets [], according to established custom.

A well-entrenched position needs strong weapons and unflinching attacks; and I have not hesitated to use all the legitimate arms of scientific controversy in assailing certain views; for they have been widely pressed on the general public with an assurance that must have convinced many that the position was protected by the universal consensus of biologists.

It is more grateful to express here my warm thanks to many friends. My wife has been a most useful critic, and my brother Philip has constantly given me stimulating and helpful suggestions, and has spared no pains in revealing that perspective which an author cannot alone obtain for his own work. To my son-in-law, William Cramp, I owe that co-operation on the physical side without which I should never have dared to attack what are, after all, essentially physical problems. With the drawings I have had the assistance of my demonstrator, Mr. J. L. Johnson, D.Sc., of Lady Windle, and the highly trained services of Miss Lynton, who, when this book was in preparation, attended to the making of the illustrations on behalf of Mr. Murray. To the courtesy of the Editors of *The Contemporary Review* and of *The Fortnightly Review* I owe the opportunity of republishing the essays that have appeared therein; to that of Mr. Fifield and Mr. Streatfield the republication of the essay on "The Biological Writings of Samuel Butler."

M. H.

August 15, 1912.

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PROBLEMS OF LIFE AND REPRODUCTION

CHAPTER I

SOME PROBLEMS OF REPRODUCTION

Conjugation, Fertilisation, and Rejuvenescence

I propose in the following pages to give a short account of some of the chief discoveries bearing on Life and Reproduction that late researches have brought forth, and to show how all the facts may be welded into a coherent and consistent theory. This survey cannot be absolutely complete, from the very technical nature of some of the points, which are better treated in the pages of a scientific journal.[1] Yet the subject is so fascinating, and possessed of such wide-reaching interest, that I make no attempt to apologise for bringing it to the notice of the wider circle of the "cultured laity"; who, without direct teaching, can but slowly learn what matters

[1] This I have done in the *Quarterly Journal of Microscopic Science*, December 1891; while the present essay represents fairly the spoken account of the same paper delivered at Cardiff before Section D of the British Association.

are being discussed in the restricted group of professional students of biology. The problem I have essayed to solve is the meaning of the process of fertilisation, its origin, essence, and objects; and, as a rider, I have examined the use and need of cross-fertilisation, and the validity of the aphorism, "Nature abhors perpetual self-fertilisation."

I

In the course of my inquiry I soon found that the favourite field of most recent theorists—the Animal Kingdom (limited to the Metazoa or animals of complex structure)—was as unfavourable a one as could be chosen. In the Vegetable Kingdom, however, I espied a path, not wholly free from awkward gaps, but still easy to pick up afresh after each break; and this we may follow down to that very primitive group, the Green Flagellates, of which the lower Algæ are, indeed, only highly developed examples, leading for the most part a stationary life, in permanent groups or "colonies." Each Flagellate is a single cell, formed of protoplasm or living matter; this again is divided into a peripheral layer, the *cytoplasm*, and a central body, the *nucleus*, differing from the cytoplasm in its chemical composition and in the complexity of its structure. The cytoplasm is prolonged into one or more whip-like lashes, the "flagella," organs of motion, which give their name to the group. Such a cell grows and enlarges to double the size, and then undergoes fission—that is, it splits or divides into two equal "daughter-cells," which, in their turn, repeat more or less closely the life and behaviour of their "parent." But, besides this alternation of growth and division—or *multiplication*, if you will—there is yet another mode of reproduction, that usually comes in at distant intervals only. In this mode, a cell, after enlarging, it may be, to many times its original bulk, undergoes not a single fission only, but a series of fissions; for the daughter-cells also divide immediately after their formation, and so on, without any interval for nutrition and growth. In this way a brood of many cells is formed, minute in proportion to their numbers. Such cells are frequently very active, and are hence called "swarmers," or "zoospores." I shall call them, irrespective of their activity, "brood-cells," and the original cell a "brood mother-cell."

With this explanation we may now examine the reproduction of the pretty filamentous Alga, *Ulothrix zonata*, which often forms a green down on stones in running water, and whose life-history was studied in great detail in 1876 by Prof. Arnold Dodel of Zurich. *Ulothrix* consists of cylindrical cells growing end to end, each invested by a protective layer of cellulose, so that the filament may be described as a tube, subdivided by transverse partitions into chambers, with a protoplasmic cell in each chamber (Fig. 1). Each cell may grow and divide by transverse fission, a new horizontal wall separating the daughter-cells. In this way the whole filament

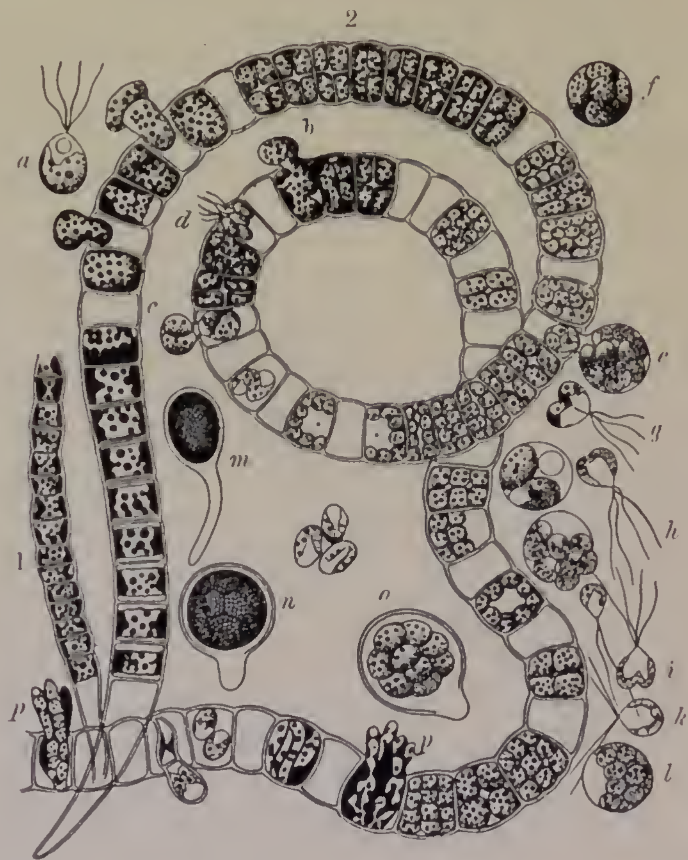

Fig. 1.—*Ulothrix zonata.*

1, Young filament, showing cells all dividing transversely. 2, Portion of adult filament showing cells escaping from cavity as single 1-flagellate zoospores at *a*, escaping after a single division at *b*, after two divisions at *c*, after numerous divisions as microzoospores or facultative pairing cells at *d*, *e*, *f*, *g*; *g*-*k*, stages of fusion (syngamy); *l*, fusion-cell enlarging; *m*, fusion-cell encysted at rest; *n*, fusion-cell dividing into a brood of, liberated at *o*; *p p*, cells of filament of which the protoplasm has divided into brood-cells, which grow out into filaments at once.

grows in length. Sometimes, however, there is no new partition formed, and the two daughter-cells shrink a little from the wall of the parent-cell and from one another, rounding off at the same time.

These "naked cells" may each produce four flagella, escape from the chambers in which they were formed, and swim off as zoospores (*b*), or else they each form a fresh cell wall *in situ*, and grow out into a new filament at right angles to the parent one (*p*). In the same way, a cell may by repeated fissions form broods of from four to one hundred and twenty-eight naked cells, small in proportion to their number, and with only two flagella; and the brood-cells may develop in either of the above ways.

All the swarmers, whatever their size and numbers, after swimming freely for a short time, may at last come to rest, attach themselves by one end, acquire a cell wall, and grow out into a new multicellular filament; nay, may even do so *in situ* (Fig. 1, *p*). But the smallest swarmers, under certain conditions, will first approach in pairs, and then fuse to form single cells of double the size before coming to rest (Fig. 1, *g*-*l*). This union involves their complete fusion, cytoplasm to cytoplasm and nucleus to nucleus, so that the resulting cell has the structure of a normal uni-nucleated cell when it finally comes to rest (*m*).

The process we have just studied is termed "conjugation," the cells that unite are termed "gametes," or "pairing cells," and the resulting cell called a "zygote," or "fusion-cell"[1]; and we have here the key to all processes of conjugation and of

[1] [Originally I used the term "coupled cell."]

fertilisation, since this is the most primitive type. In certain forms allied to *Ulothrix*, more than two gametes—as many as six—may unite to form a single zygote. In other cases, again, such as *Eudorina elegans* (Fig. 2), a small green organism floating in fresh-water pools, we find the gametes all similar in

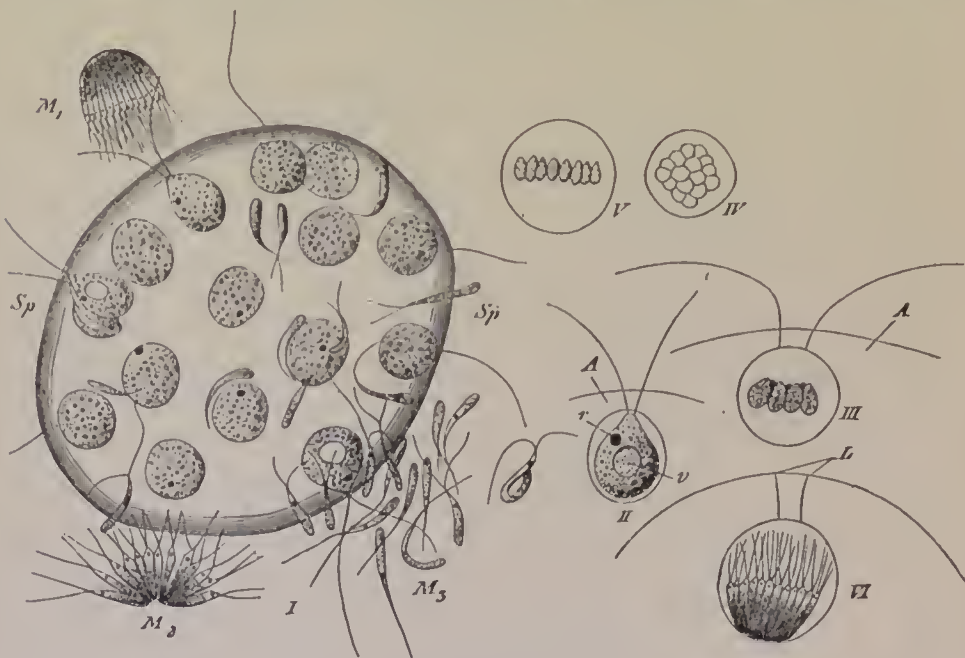

Fig. 2.—*Eudorina elegans.*

I, Female colony with sperms (*Sp*) entering to fertilise the oospheres. II, unit cell of indifferent or female colony; *v*, nucleus, *r*, red eye-spot; *A*, boundary of the gelatinous mass of the spherical colony; III, similar cell dividing *in situ* to form a new similar colony. IV–VI, brood-divisions to form a male colony; *L*, lash-like organs (flagella) of the mother-cell, M_1 M_2 M_3, male colony separating into single cells at the surface of the female colony *I*.

form, but evincing in size and behaviour a division into two types: the one smaller and more active, the other larger and more sluggish. This differentiation affects the cytoplasm far more than the nucleus. It may advance so far that the larger cell is enormous and motionless, or nearly so, while the smaller cell is reduced to a nucleus, with just enough cytoplasm to enclose it and carry it to its destination. This differentiation of size and activity is what we term *sex*. The larger gamete is the *female*, oosphere, or egg[1]; the smaller is the *male*, spermatozoon or sperm, whose flagellate type is retained in the highest animals, betraying still their lowly origin.

The term *conjugation* is seldom used in speaking of such highly differentiated types. We say that the ovum is *fertilised* by the spermatozoon. But, despite the advantages of familiarity, "fertilisation" is not a good word to employ, as it has an erroneous connotation; for the process is not a one-sided one, but its very essence is the fusion of two cells: their difference of size and behaviour is, as it were, a mere accident from our present standpoint. [I have suggested its replacement by "syngamy" (see p. 149).]

To pass on: we have found that gametes, whether equal or sexually differentiated, are in their origin brood-cells; and we may expect everywhere to find some trace of their origin in their development. I take a few instances which indicate alike the origin of the process and the character of the facts that may, by masking this origin, lead to false interpretations and erroneous theories. The lower members of the group of Olive Seaweeds, so common on our seashores, show at most but slight differentiation in

[1] The word "egg" lacks scientific precision.

the size and behaviour of their gametes; the limited order of the *Fucaceæ* or Wracks, however, have well-developed eggs and sperms. In the type genus *Fucus* the ova are formed in broods of eight (Fig. 3, 2-9), and indications of this number are found in all the other genera of this order. But in a second genus (*Ascophyllum*) only four of these ova have enough cytoplasm to be of any use, while the other four are reduced to nuclei with but a trace of cytoplasm around them, incapable of fertilisation, and mere abortive rudiments (Fig. 3, 13); in a third (*Pelvetia*) only two of the eggs are functional and six are abortive (Fig. 3, 10); and in *Himanthalia* one of the ova retains nearly all of the cytoplasm of the brood mother-cell, and the seven others are abortive (Fig. 3, 11, 12).

Such abortions of certain members of a brood or group to the favour of others are not exceptional in nature. Many flowers produce far more ovules than ever ripen into seed; the Acorn, for instance, is a unilocular and seeded fruit, proceeding from a three-chambered fruit-vessel in the flower, with two ovules in each chamber. Space will not allow me to cite more examples of what is a very common occurrence. With this clue we can explore some more intricate problems. Thus in Mosses, Ferns, etc., we find the oosphere is a large cell lying in the cavity of a flask-shaped structure, while the three other cells of the same brood of four occupy the neck of the flask, and are hence called "canal-cells" (Fig. 4). These canal-cells ultimately degenerate into a slimy substance, holding

FIG. 3.—Oogeny in the Wracks (Fucaceæ).

1, Female inflorescence of *Sarcophyces*. 2–9, Oogone of *Fucus* (common Bladder-Wrack), its liberation, division, and separation into eight oospheres. 10, Oogone of *Pelvetia* with two zoospheres functional and six dwarfed and functionless. 11, 12, Oogone of *Himanthalia* with one functional and seven rudimentary oospheres (not all seen). 13, Oogone of *Ascophyllum* with four functional and four functionless oospheres (only three of each in view).

matters in solution which attract the spermatozoa, and lead them down to the ovum. Here it is very clear that three of the four brood-cells are not merely aborted, but degraded into an accessory apparatus for ensuring the fertilisation of their more favoured sister. In the higher animals (Metazoa) the "ovarian egg," as it is called, is not a gamete, but a mother-cell, producing a brood of four cells by two successive divisions (Fig. 5). The first division is a very unequal one, forming a large cell and a small one called the "first polar body." The small cell may or may not

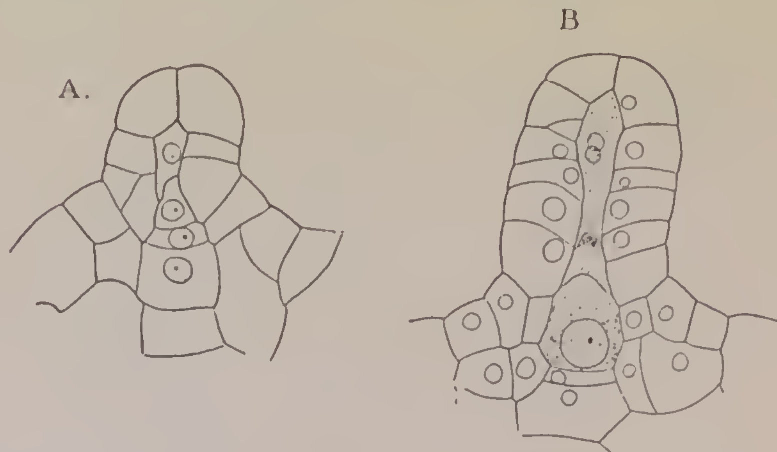

Fig. 4.—Flask-shaped structure (archegone) of a Fern.

A, young with the brood of four reproductive cells. B, the three upper ones degenerating as "canal-cells," the lowest enlarged as the oosphere.

undergo a second equal division; the large cell undergoes a second division, unequal like that of the "ovarian egg." The large cell thus finally formed is the true egg or oosphere, now susceptible of fertilisation; the small one is the "second polar body." We can only interpret "polar bodies" in the light of our previous study as aborted functionless ova. These brood divisions of the ovarian egg have been studied most elaborately by zoologists of the highest distinction, and some of them, like Giard, Mark, Bütschli, and the brothers Hertwig, have recognised the facts as stated above; but others have ignored or neglected the process of brood-formation

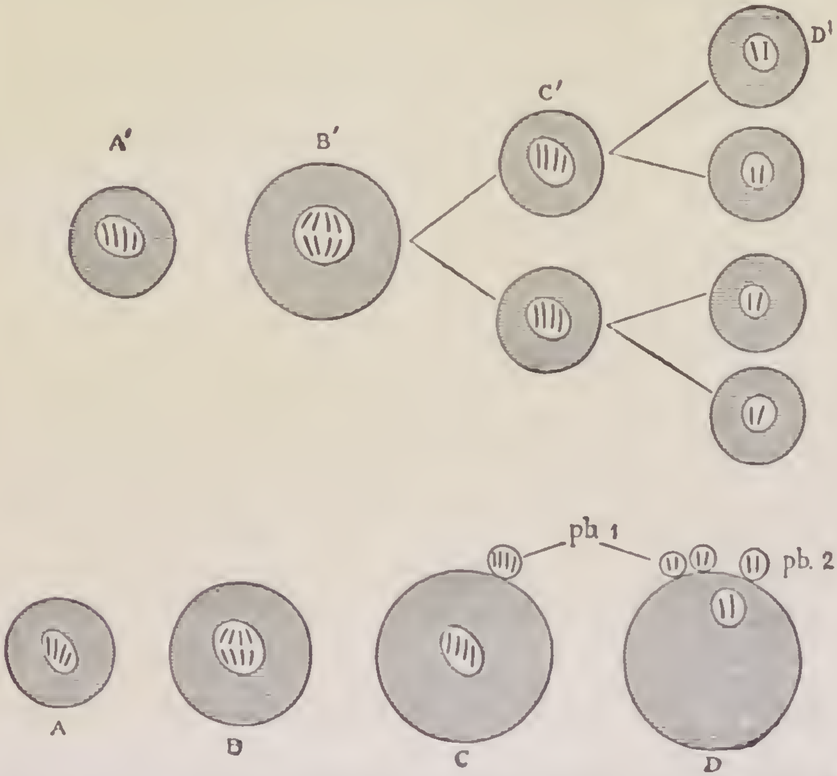

FIG. 5.—Comparison of formation of reproductive cells (in this case pairing cells) in male and female of higher animals.

The primitive cell, or oogone in either case produces four cells by two successive divisions; in the male, A'–D', they are all equal and functional; in the female the divisions are unequal, and only one functional pairing cell, or oosphere, is formed, the other three being functionless as "polar" bodies, *pb*. The lines in the nucleus are chromosomes. For more detailed illustration of the same facts see below, Plate I, after p. 148).

that forms gametes in more primitive types, and have essayed to interpret this as a process standing apart from all others of organic life.[1] Hence, dis-

[1] [This view of the polar bodies as rudimentary oospheres has since received absolute confirmation; for in certain marine Flatworms their size is relatively large, and they may be fertilised by sperms.]

regarding the obvious explanation that this, like so many other processes of individual development, reealls the past history of the race, they have sought for physiologieal explanations; and urged that in the formation of polar bodies, the egg eliminates what would, if retained, interfere with fertilisation and its object. But if this were so, similar processes should take place in all cases of the formation of the female gamete; which is not the case, as we have seen. To take a familiar explanation, we may easily conceive a breed of cats that had only enough milk for one of a litter; should we ascribe the eontinued production of three or four extra kittens, always doomed to starvation, to a physiological excretion, or rather to the inheritance from a raee of better milkers? This parallel was suggested to me by a friend, and clearly expresses the view we take of that much-vexed question—"The signifieance of the polar bodies."

Like the ovarian eggs, the mother-cells that form spermatozoa may sometimes (in Sponges) form other products than functional gametes among their brood-cells; but there is never more than one cell so modified in each brood, and this exeeptional cell is always degraded for the proteetion or nutrition of the rest of the brood, not merely aborted and wasted like the polar bodies. Again, while in some cases any two or more of the gametes of a species may unite together irrespective of their origin, we early find restrictions on these unions, other than those of sex. Thus, in *Ulothrix* itself no gamete will pair with another of the same brood, and fusion only takes place between those sprung from different mother-cells; in other cases we find that this reluctance to enter into kindred unions extends to all the gametes formed on a single individual. This incompatibility of close blood-relations may fairly enough receive the familiar name of "exogamy." Its occurrence seems to be antecedent to the appearance of binary sex; and may be superadded thereto in varying degrees of strictness. Thus, many flowers are so extremely exogamous that the pollen even of another flower of the same plant is not fitted for their fertilisation; and without cross-fertilisation from other plants of the same species no good seed can be produced. Yet, despite this fact, the appearance of exogamy has been regarded as a primitive foreshadowing of true sex; though to admit this proposition is to give the word "sex" a connotation very different from the usual one, and indeed incompatible therewith.[1]

The real origin of sex is, as implied above, the gradual differentiation of pairing cells into categories of distinct size and habit; and we have one remarkable instance that bridges the gap between the equality and identity of the gametes, on the one hand, and true binary sex on the other. In our group of the Green Flagellates is included a colonial

[1] See also Chapter VI, p. 147.

form, known as *Pandorina Morum* (Fig. 6). This organism, not uncommon in rain-fed pools, is a tiny sphere, composed of sixteen or thirty-two flagellate cells imbedded in the surface of a globular mass of jelly that binds them into a colony. For conjugation each cell divides into sixteen or thirty-two swarmers, which are strictly exogamous. But the brood mother-cells vary in size, and with them their offspring; so that we find three distinct sizes of gametes, small, medium, and large. The small ones can conjugate with one another, with the medium, and with the large ones; the medium also can conjugate with one another, as well as with the small and large gametes; but the large gametes are incapable of conjugation together. Thus, the large gametes are exclusively female in behaviour; the medium may play the part of males to the large ones and females to the small ones, as well as enter into equal conjugation with one another; the small ones behave as males to the two larger sizes, but are equal in conjugation with one another. We have, then, here a very rough attempt at sexual differentiation; if we omitted the power of equal union of the first two sizes, we might describe the small, medium, and large gametes as male, hermaphrodite, and female respectively. It is easy to conceive how by natural processes of evolution the middle form might be eliminated; the smaller forms, by an increase in their exogamy, lose their power of uniting together;

and the sexual union of small and large gametes set up as the only type of conjugation for the species.

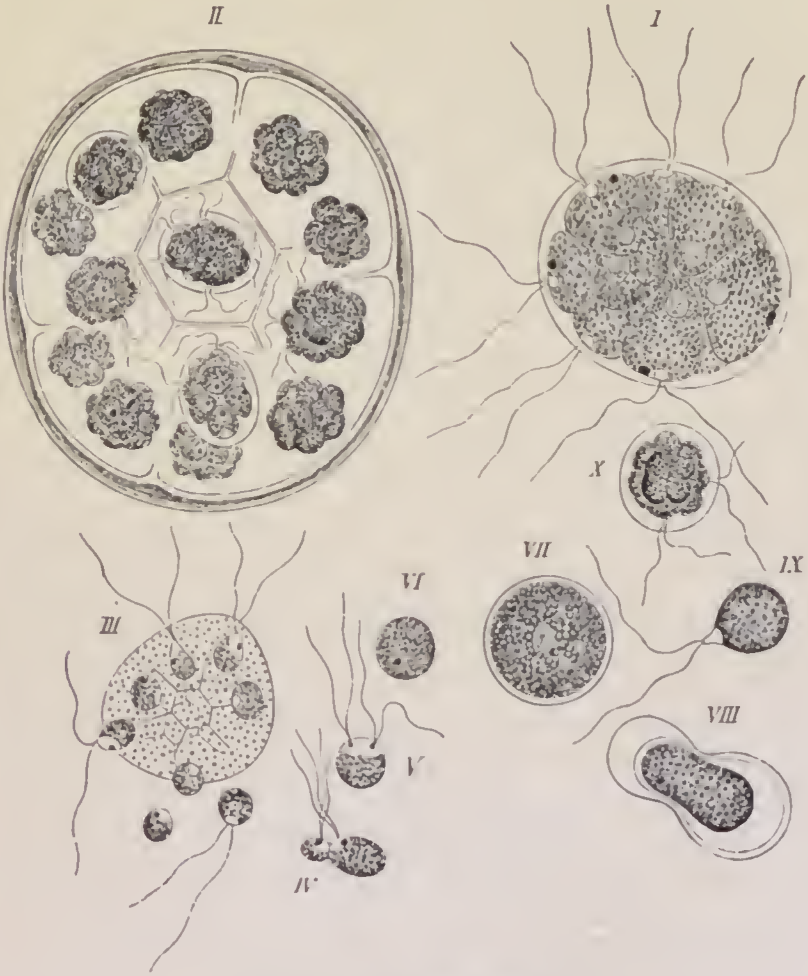

Fig. 6.—*Pandorina Morum.*

I, colony, showing motile lash-like organs (flagella); the dark spots are the red eye-spots. II, colony with all its members undergoing brood-division. III, Separation of individual cells as gametes. IV–VI, Pairing of two gametes differing only in size. VII, Fusion-cell at rest. VIII, Growth and solution of wall of fusion-cell. IX, Fusion-cell free, as a large-size swarmer (nega-zoospore. X, Its brood-division to form a fresh colony.

The *juste-milieu* is ever a slippery platform, in Nature as in politics. Such processes of sexual differentiation there is good reason to believe have arisen more than once in the life-history of primitive organisms.

II

Now that we have studied the main facts of conjugation, we pass on to inquire what was its original purpose or function. Certainly not mere reproduction, for binary unions suppress one-half the number of individuals ultimately formed from the brood-cells; and multiple unions still further lower the propagative output of the species. Yet no mode of reproduction dissociated from conjugation exists in the higher animals; and from every side we have evidence that the process must be endowed with singular virtues for the preservation and progress of the race. Three distinct answers have been given to the question as I have stated it.

Professor Weismann of Freiburg in Baden, who has enlisted in his following the majority of our English biologists, holds the following views:[1] The

[1] [I leave this discussion as it was written in 1892 describing the views expressed in "Amphimixis" (Eng. Trans. 1892). Weismann modified these views very decidedly in 1893 in his "Germ-Plasm" (see *infra*, p. 69). "The cause of hereditary variation must lie deeper than this; it must be due to the direct effect of external influences on the biophors and determinants [hypothetical components of the supposed personalities or 'ids' that constitute the germ-plasm]" (p. 416). In an unindexed footnote to p. 435, Weismann wrote in reference to a criticism of mine on the Amphimixis theory (*Nature*, Dec. 1891), which was treated by some English Weismannians as presenting a garbled and incorrect account of the Weismannism of that date: "The deductions made by this

original reproductive cells contain germs ("ids") representing a limited number of ancestors; by the formation of polar bodies the egg eliminates half its germs, more or less at random: and similarly the spermatazoon contains only half the full number of ancestral germs. Each fertilised egg formed by the union of the two would therefore contain the full number of the ancestral germs; but these would be a different selection in each case, even with the same parents, owing to the random method of elimination of half the germs on either side of the preceding process. Hence the offspring would vary because of their different ancestral composition; and from these variations natural selection would have every opportunity to pick out those most advantageous to the progress of the race. We can understand this by supposing all the primitive reproductive germs of the one parent to be represented by identical red packs of cards, those of the other by blue packs, and the mature ovum or spermatozoon to contain only half the cards of a pack (red or blue as the case may be) taken at

author from my former views are logically correct, but are no longer justifiable, since in the meantime I myself have gained further insight into the problems concerned." It is noteworthy that the Master's candour was never imitated by a similar withdrawal by his followers of the charges brought against my intelligence and good faith. The views of the "Germ-Plasm" have been further modified by the subsidiary hypothesis of germinal selection (see below, p. 194). But it is impossible to ascertain how much of the card-shuffling theory of variation is still retained by Weismann himself, or by the writers of his school. They still reject the admissibility of *rejuvenescence* by cell-fusion.]

random. If the number of cards in each pack were limited to twelve only, there would be $\frac{\lfloor 12}{\lfloor 6 \times \lfloor 6} = 924$ combinations of germs possible for ovum or spermatozoon, and $(924)^2 = 853{,}776$ combinations possible for the germs of a fertilised egg of a single pair of parents; and with packs of fifty-two cards the latter number would be replaced by one of thirty (30) digits beginning 245935, etc. But the facts, which at the time the hypothesis was broached seemed to allow of its being applied to the higher animals at least, can no longer be interpreted in Weismann's sense. Moreover such a shuffling process should rather tend to breed out variations than to produce them.

The second answer given is that of Professor Strasburger of Bonn. He thinks that any degradation existing in either one parent only, and not in the other, will tend to be eliminated from the offspring of conjugation, and that, as it is improbable that similar deterioration will be present in both the parents, conjugation is conservative of the integrity of the race.

The third explanation, which has probably the largest following abroad, and the smallest in England, is, that the conjugation and fertilisation bring about *rejuvenescence*; and this is the view that we shall now examine.

If we are asked, "What is rejuvenescence?" we can only answer, "The escape from senescence," and we must go on to examine what we mean by "senescence"; and if we find it hard to give at the outset a precise connotation to the term, we may at least see what kind of processes it denotes in the organic world. There has long been a general feeling among naturalists that plants suffer in the end from long-continued asexual propagation by buds, cuttings, and grafts alone, though seedlings produced by fertilisation regain their primitive vigour. Many much-prized varieties of our fruit trees seem to be on the wane from this cause. Here, in Ireland, the Champion Potato, from its resistance to the blight, was largely cultivated for many years; but we have seen it in turn lose its resisting powers after separated years of propagation by "sets."[1] Many instances, more or less striking, of similar deterioration are to be found in the literature of the subject. On the other hand, attention has recently been directed to a body of facts which would show that the asexual reproduction of certain plants and animals can be prolonged indefinitely without evil results. We have, therefore, not only to study the deterioration, but to find some explanation that will cover the

[1] [While the practical farmers in Ireland have for decades found it advantageous to import potato-sets from Scotland, the Royal Horticultural Society found that Irish sets gave the best results in their trials in England. This points to rejuvenescence by change of external conditions.]

exceptional cases I have just quoted; for without this no explanation can be satisfactory.

Till lately our evidence of this kind of deterioration was rather appreciable in the court of common sense than of the rigorous character demanded by the rules of the tribunal of science. But science already owes many a heavy debt to the honourable body of devoted amateurs, including such men as Buffon and Charles Darwin, Lyell and Murchison. One of these, M. Maupas, sub-librarian[1] to the city of Algiers, has recently given us an absolute proof that in one group, at least, degeneration must needs follow propagation by division only; has shown the exact character of this degeneration, and its goal in the death of the race; and has brought it into line with similar degradations elsewhere by terming it a "process of senescence." With exceptional skill and patience, and well-earned success, Maupas has studied for some years past the Ciliate Infusoria. These lowly organisms are so minute that the unit we use to measure them is the one twenty-five thousandth of an inch, and few exceed, or, indeed, attain, the hundredth of an inch in length. Yet Maupas devised such conditions to breed and grow them that he could feed and observe them, count their numbers, or transfer them at will. The tiny animals, as is well known, habitually multiply by binary fission, like

[1] [Now Librarian.]

the Flagellates. Under certain circumstances, now for the first time clearly defined, they conjugate in pairs, but separate shortly afterwards instead of fusing into a single cell. In this process either animal receives a nucleus from its fellow which fuses with its own nucleus; so that in this respect the animal, after conjugation, or "exconjugate," resembles the zygote of other groups. Maupas discovered that if he founded a colony with a single exconjugate, it grew and underwent fission regularly, increasing and multiplying in the most literal sense for a certain time. But, in due course, if conjugation was prevented, the offspring became more stunted at each fission, and their nuclear apparatus was more and more reduced; then conjugation became impossible, and the cycle closed by the degradation and ultimate death of its members.[1] If, however, conjugation had been induced early enough, two new and vigorous cycles made a fresh start from the exconjugates, to run a similar course, and end again either in conjugation or in degradation and extinction. The decline in the nature and vigour of the later members

[1] [Much work has been done in this field, notably by Gary N. Calkins and his pupils. They have found that changed conditions, the administration of small doses of beef-extract or of alcohol will tide over periods of depression which would otherwise end with extinction; and this confirms Maupas's view that cell-fusion determines rejuvenescence, and the present thesis that cell-fusion is one of several remedies for the senescence due to reproduction through a long cycle of monotony. By varying the food from time to time, a series extending over three years and a half, and numbering 2,000 cellular generations, has been grown by L. L. Woodruff.]

of a cycle Maupas terms "senescence," since it resembles the decline of old age in the multicellular individual of the higher animal or plant groups. Thus senescence in the Infusoria is the spontaneous failure of vigorous life and reproductive power—always determined by the prolonged sequence of reproduction by fission without conjugation, and is avoided by conjugation. Therefore *conjugation averts senescence*, or *conjugation determines rejuvenescence*; whichever way we phrase it the facts are the same, and the proof here is absolute. And it seems likely that in most other organisms that enjoy a process of fertilisation or conjugation, the exclusion of this process determines senescence—the diminution of all vigour in life, nutrition, growth, and, above all, reproductive power.

There are, however, certain organisms whose life-history is thoroughly well known, and which show no signs of ever having possessed such a process as conjugation; and others probably descended from ancestors that possessed a process of conjugation, but which appear to have lost it completely. The little group termed Monadineæ by Cienkowsky (Fig. 7) belongs to the former class; the great majority of Fungi to the latter.[1] In both

[1] [This statement requires modification, for a syngamic process has been since made out in many groups of Fungi; but the fusion is usually "endogamous"—that is, between nuclei enclosed in the same cytoplasm; and often "autogamous"—that is, between nuclei of the closest relationship. (For explanation of cellular relationship see Chapter II, p. 37.)]

groups we find that there are well-marked resting states, and for reasons stated below we may well believe that the *rest* is sufficient without conjugation to restore the jaded energies of the organism and repel senescence. Moreover, many species of Fungi exist in more than one state, and those that

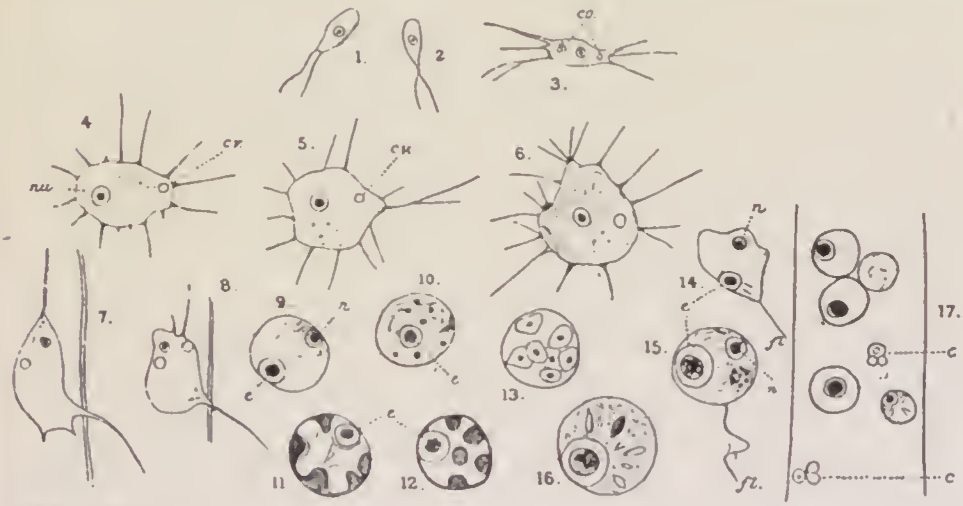

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FIG. 7.—Life history of a Monadine, *Pseudospora Lindstedtii*, parasitic in the aquatic Moulds called Saprolegnieæ.

1, 2, Flagellate zoospores. 3–8, Amœboid form in various stages. 7, 8. Perforation of cell wall of mould to effect entry. 9, Adult at rest; *n*, nucleus; *e*, deposit of excreta. 10, Nuclear brood-division is complete. 11–13, Resolution into zoospores. 16, Another mode of resolution. 14, 15, Adult forms which have developed a single lash (" flagellum "). 17, Tube of Mould empty of its original contents, except some granules of cellulin, and containing adult states of parasite.

are parasitic frequently change their host with the state in which they live. Prof. Marshall Ward, of Cooper's Hill, wrote on this point in 1884: "We may not inaptly compare the sojourn of the fungus in its second host to a trip to the sea-side, where the wearied and enfeebled organism enjoys fresh diet and association for a time, which in their turn pall, to prepare the recipient to renew the old modes of life."[1]

III

We have seen that the rejuvenescence may be effected by *rest*, by *change of mode of life*, by processes of *conjugation* or *fertilisation*: it is next necessary to seek for the probable causes of senescence, in order to discover the mechanism of rejuvenescence in each case. Every cell, whether a complete organism in itself, or one of the units that go to build up a complete animal or plant, consists, as we know, of two parts, the *cytoplasm* and the *nucleus* lying within the cytoplasm (Fig. 8). The cytoplasm is that part which comes directly in contact with the surrounding medium, which feeds, breathes, moves, and has the power of protecting the cell as a whole by secreting an investment of membrane or cell wall when needed. The nucleus, lying inside the cytoplasm, can have no direct action on the external world, and can receive no direct influence from it; it is nourished by the cytoplasm, and, for matter as for energy, there must be direct interchange with the cytoplasm, and with that only. On this ground, and on many others which we cannot go into here, a general belief has grown up among biologists that the nucleus has to the cytoplasm much the same relations as a nerve-

[1] "On the Sexuality of the Fungi," in *Quarterly Journal of Microscopical Science*, 1884. (Reprint, p. 60.)

centre has to the organism of a complex animal. During the active life of a cell the nucleus would then be constantly doing exhaustive work. Moreover, we know that nerve-centres lose in time their ready response to stimuli of the same kind and from the same quarter, when too frequently repeated; just as the weaver loses all sense of the din from

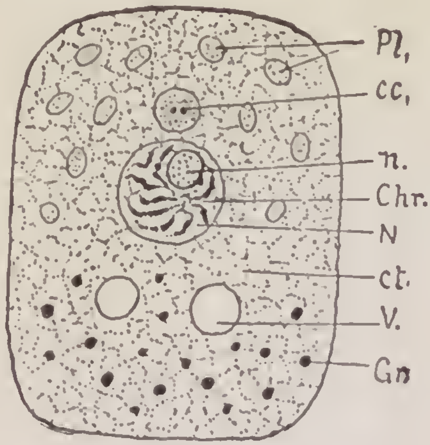

FIG. 8.—Diagram of cell.

Ct, Cytoplasm. *cc*, Centrosome. *N*, Nucleus; containing *n*, nucleole and *chr.*, chromatic network. *V*, Vacuoles, or spaces containing liquid. *Gr*, Granules. *Pl*, Plastids, individualised masses of cytoplasm which in plants are the containers of the green and yellow colouring matters, and have the power of forming starch.

the busy looms around him, deafening though it be to the unaccustomed ears of the visitor. We may well conceive that the nucleus also during the continuance of active cellular life gradually loses its readiness of response to the stimulation from the cytoplasm, and with its sensibility the power to guide and control aright the functions of the cytoplasm; so that the life of the cell is impaired. During fission the nucleus and cytoplasm are divided evenly among the daughter-cells, and the life of the parent-cell is continued in them, just as the life of a Fuchsia or Geranium plant is continued in the cuttings into which it is divided. Thus any disorder is handed down from cell to cell in the cycle of fission; and if the cause that originated the disorder persists, the disorder itself will increase, to the ultimate ruin of the race. If the lessened sensibility of the nucleus from prolonged association with the same cytoplasm be the cause of senescence, we can see how this disorder would steadily augment throughout a cycle of reproduction by fission alone. But a prolonged period of rest would restore the sensibility of the nucleus, and therewith revive the flagging energies of the cell; and we must remember that in the resting state the nucleus is probably well fed at the expense of food-material previously stored in the cytoplasm.[1] So the Lancashire operative, after passing his Whit-week at Southport or Blackpool, has a vivid sense of the whirr and clack on returning to the weaving-shed. Thus, *rest* alone may determine rejuvenescence.

In the case of a *change of habit* (or *of host* for parasitic organisms) we see that the protoplasm, being placed in new conditions, must transmit new stimuli to the nucleus, which was jaded only to the old stimuli of its former state. We can now feel the

[1] [The occurrence of dissonance of function between cytoplasm and nucleus, noted by Maupas, insisted on by me, has been confirmed and developed (from observations on Heliozoa mainly) by R. Hertwig.]

full force and beauty of Ward's comparison with the invigoration produced by a trip to the sea-side.

Let us now return to *conjugation*. By our hypothesis we have succeeded in explaining the virtues of rest, and those of changes in the conditions *external* to the organism. We may well believe that an alteration of the *internal* arrangements of the organism will produce a similar benefit. Such an internal reorganisation is most surely achieved by a change in the constitution of one or both of the structures of which the cell is formed, so that it is no longer the same nucleus associated with the same cytoplasm; and this change is effected in conjugation and fertilisation. We might, indeed, compare the association of the nucleus and cytoplasm in the cell to that of a great industrial house: the nucleus would represent the firm, the masters guiding the business of the house and maintaining its traditions; while the cytoplasm would represent the staff of employees, clerks and hands, whose work is conditioned by three factors—namely, their own powers, the direction of the firm, and the action of the external world and things at large; and when such a house begins to go downhill, new blood in firm or staff, or both, will often save it from bankruptcy. Nay, we may push the simile a step further, for the incoming member must be suitable in character and temperament: a man who revels in mechanical contrivance alone may be a pillar of strength to a firm of engineers, but is clearly out of place in a solicitor's office, or the counting-house of a wholesale linen-draper. So the renewal of the cell-life by the introduction of "fresh blood" is always subject to the condition that the new element be not too alien to the race; and thus hybridisation is of rare occurrence.[1] The reorganisation we speak of takes place in the simplest way in *equal conjugation*, by the fusion of two or more similar cells, cytoplasm with cytoplasm, nucleus with nucleus, to form a new cell whose cytoplasm and nucleus are alike fresh creations, never before associated by the very nature of the case. In the more specialised process of *fertilisation* the nucleus is still a fresh creation formed by the union of two old nuclei, the male and female respectively; but the cytoplasm is practically the old cytoplasm of the female only, the amount brought in by the spermatozoon being very small, and perhaps inappreciable in many cases.[2]

If the explanation put forward is valid, a further step in specialisation would be the union of the nucleus of one cell with the cytoplasm of another to form a new cell, whose constituents were both old, but whose association would be a new one. Such a union is unknown in Nature; indeed, we know of no means by which the cytoplasm could

[1] [Mr. Samuel Butler has given a similar explanation of hybridisation from a somewhat different standpoint in "Life and Habit" (London, 1877), pp. 173–185.]

[2] [But see the note on the Rôle of the Sperm in Metazoa, p. 166.]

spontaneously expel its nucleus and remain alive to receive another.[1] But the astounding fact remains that even this union, unknown to Nature, has been effected by art, and with the result demanded by our theory. Prof. Oscar Hertwig, of Berlin, observed that the egg of a Sea-urchin, when shaken violently in sea-water, breaks up into fragments, which all retain their vitality for some time, though of course only one of them has a nucleus; and he saw spermatozoa enter these non-nucleated fragments of cytoplasm, which then began developing like the normally fertilised eggs. Prof. Th. Boveri, of Munich, carried the observation a stage further, and found that these bodies—female cytoplasm and male nucleus—underwent normal development and became larvæ; in fact, they behaved exactly like the ordinary fertilised eggs, which possess female cytoplasm also, but a nucleus formed by the fusion of both male and female nuclei.[2] This goes very far to prove the truth of my proposition—that *the essential process of conjugation or fertilisation lies in the creation of a new cell, whose nucleus and protoplasm have not been previously associated in a common cell-life.* We have already seen that the object of these processes is rejuvenescence, and with this proof the solution of my problem is complete; we now turn to the rider.

[1] [Hickson has since found this process general in the Alcyonariæ.]

[2] [This variation from ordinary "fertilisation" has since been amply confirmed, and termed "merogony" (see below, p. 161 f.).]

IV

Since the renovation of the cell as an *association* is the very essence of conjugation and fertilisation, it is most effectually brought about when the cells that fuse are not too closely akin. This principle finds expression in various ways and degrees. We have seen the frequent reluctance of gametes of the same brood to pair together; and this antipathy exists sometimes between equal gametes of different broods but produced on the same individual. Hermaphrodite animals are usually cross-fertilised; the same is true of hermaphrodite flowers, which show an infinite variety in the arrangements ensuring the frequency and efficacy of those insect visits that transfer the pollen of one flower to the stigma of another. Many flowers are absolutely sterile with their own pollen; and the offspring of crosses between distinct families of the same species, animal or vegetable, usually contrast by their vigour with those that have been bred "in and in." It is on such facts as these that the aphorism, "Nature abhors self-fertilisation," was founded. Yet there are many facts that show that Nature's abhorrence of self-fertilisation is, to say the least of it, capricious in the extreme. We know of strictly endogamous Algæ, where of necessity the equal gametes of the same brood must always pair together[1]; certain

[1] [Most Fungi are endogamous.]

flowers and certain hermaphrodite animals are always self-fertilised, and these are among the hardiest of their kind[1]; some groups of men, like the inhabitants of certain fishing villages, are bred "in and in" to the closest extent compatible with the canon law, in bonds of the utmost complexity, and yet present some of the finest types of human health and beauty. These antinomies require reconciliation, and this will be the close of our task.

We have seen that rejuvenescence is necessary to all beings in some form or other; but the mode adopted varies with the species. Resting stages probably effected rejuvenescence in primitive organisms; and other modes came in and became habitual in consequence of the greater good they did to the individual and the race. Thus (1) simple conjugation, (2) exogamy, (3) binary sexual fusion, (4) cross-fertilisation,—each was in turn an improvement and a benefit; but in the course of time each by habit became a necessity. For in the nature of living beings every beneficial luxury tends to become an acquired need. We know too well how much easier it is for us to live up to our wonted luxuries, than to retrench and do without them; for this it is that gives the sting to adversity among the privileged classes of society. What is true of the individual is true of the

[1] Among Darwin's many experiments he found that one seedling from a self-fertilised Ipomaea ("Convolvulus") was so exceptional in its personal vigour, which it transmitted to its offspring, that he termed it "Hero."

race; here also the accustomed benefit is become no less a need because it began as a luxury.

One or two concrete instances will add plainness to what is really everywhere recognised in non-scientific regions. Wild beasts are invariably infested by parasites of all kinds; no doubt they would fare better without having the constant charge of these unbidden guests: but still their presence cannot be really very harmful to life or to health. Civilised man, who cooks his food, thus wards off the visits of internal parasites, and is in consequence remarkably free from them; but what does this habitual immunity entail? Why, the European, when by exception he does become the host of parasite worms, suffers terribly from their presence: yet the Abyssinian who feasts daily on raw beef (when he can get it) thinks it positively unlucky to be without a tapeworm; and so precludes us from aphorising, "Man differs from the beasts of the field in not tolerating Tænia." Again, the improved means of locomotion of the present day are a benefit gained within the last eighty years; but we have so lived up to this benefit that in three generations it has become an organic need of the community. Thanks to this benefit, it is true, we have enlarged trade, cheapened food, and increased human life in duration, comfort, and numbers; but every exceptional snowstorm tells us that easy communication has ceased to be the mere luxury it was at the outset, and has become an absolute condition of modern social life. We see then that every improved mode of rejuvenescence has a twofold effect on the race that enjoys it, strengthening it in one way by rendering it more infirm in another; for the preservation of the vigour of the race comes to depend entirely on a process that circumstances may render difficult or impossible of accomplishment. In such cases it may befall only the hardiest of the race to survive the stress of adversity, and, deprived of the wonted higher mode of rejuvenescence, to content themselves with a lower one. Thus we find the winter flowers of many plants self-pollinated, while those born in a more genial season are crossed by insect visits: thus we find some races able to breed in and in, or capable of merely asexual reproduction to an indefinite extent, without any deterioration; while their close allies, habitually more favoured and more pampered, would degenerate or die off under the same circumstances. This view alone can explain the perplexing antinomies, which have hitherto remained unreconciled by any theory.

The saying, "Nature abhors perpetual self-fertilisation," was based, as we have seen, on a one-sided view, extending over a limited field. But if we rise to a general survey of the whole facts of reproduction, in all forms from lowest to highest, we may say, "All organic races in their cycles, like man in his daily life, require Rest and Change"; and we shall not be far from the truth.

CHAPTER II

THE CELLULAR PEDIGREE AND THE PROBLEM OF HEREDITY

In the recent elaboration of the Theory of Descent, as first fully published by Charles Darwin, two schools of thought have arisen. The one, though professing discipleship pure and simple, has laid extreme stress on the principle of Natural Selection, which owes so much to Darwin, but has rejected his belief in the internal tendencies of races to vary in adaptation to changed surroundings; while the other has attributed the greater share in the transformation of species to the latter factor, and sent Natural Selection into the background. The two most illustrious leaders of scientific thought have been August Weismann on the one side and Herbert Spencer on the other. Their debates have long since obtained an audience among the cultured laity; but while the arguments are well known, some of the most important facts have been rather taken for granted than fully stated and clearly co-ordinated even in the scientific press. I allude especially to the coarser relations of the actual *mechanism* of reproduction and of the act of transmission from one generation to the next of the form which clothes on or assumes the parental characters. Such an exposition as we have to make cannot be limited to the higher organisms which are familiar to us in our daily life, for these are complex elaborations; while the primitive types, though still existing abundantly, are only to be studied with the microscope. It is in this field, hidden if not buried, that we must first labour, if we wish to understand aright the foundations of the wonderful superstructure of the higher Organic Kingdoms. We shall endeavour to use as few unfamiliar terms as possible, bearing in mind that the reader has no Handy Atlas to help him in following the exploration of this foreign country, with its outlandish names.

Only two centuries ago the microscope revealed to mankind an immense world of minute living creatures as well as the details of the structure of the familiar Animals and Plants. Naturally enough the early observers, or "philosophers," as they were then called, inferred that these strange small creatures must have as complex a structure as our own. They proceeded zealously to search for, and sometimes to proclaim, the existence therein of brain, heart, blood-vessels, etc., just like those of ordinary bird, beast, or fish.[1] Since then we have learned that the ultimate units of

[1] Thus Baker writes in the middle of the seventeenth century: "Search we further and examine the Animalcules—many Sorts whereof it would be impossible for an human Eye unassisted to discern; those breathing Atoms, so small they are almost all Workmanship! in them too we shall

structure of the familiar organisms are identical in character with the entire organism of one of such microscopic beings; and the search we have referred to would be now regarded as equivalent to seeking in a limestone pebble the pillars and buttresses, the vaults and domes of a great cathedral in miniature. Such units of structure are called "cells," an ill-chosen term indeed, whose signification, however, as a nucleated unit of protoplasm, is familiar to every one. The lower organisms consist of single cells or of aggregates of similar cells: the higher ones consist of complicated arrangements of those dissimilar aggregates of cells which we call tissues. The former we call Protists, distinguishing between Protozoa and Protophytes according as the mode of existence is animal or plant-like: the higher animals and plants we term Metazoa and Metaphytes respectively, the appropriate conjoint term, "Metists," not having been coined by any recognised authority.

Throughout the higher groups the act of reproduction[1] of the race consists in the separation from the complex organism of single reproductive cells, which may either independently grow up into the original

discover the same Organs of Body, Multiplicity of Parts, Variety of Motions, Diversity of Figures, and Particular Ways of Living as in the larger Animals.—How amazingly curious must the Internal Structure of these Creatures be! The Heart, the Stomach, the Entrails and the Brain. How minute and fine the Bones, Joints, Muscles and Tendons! How exquisitely delicate beyond all Conception the Arteries, Veins and Nerves!" ("The Microscope Made Easy," by Henry Baker, ed. v., 1767.)

[1] In the limited sense, distinguished from "propagation," as defined immediately.

form, or else one with another fuse to produce a new cell which grows up. Again, in most Plants and many Animals multicellular portions of the body may become detached, and finally develop into complete organisms; this we shall call "*propagation*," not "reproduction." In either case the parent body continues to exist, alive or dead, after the detachment of these cells or groups of cells. In Protists, matters are very different; for here, when the cell individual has attained its full size, it usually divides into two new cells, and is itself no more, alive or dead. We call the original cell a "*mother-cell*," the new ones "*daughter-cells*," by a convenient metaphor; but we must remember that the devoted mother here absolutely merges her very existence into that of her offspring, a self-denying type of maternity often imagined but never realised among ourselves. Thus, as Weismann first explicitly stated, the Protists may escape personal death by the sacrifice of their individual life; he therefore terms them "immortal." It is with *cellular pedigree*, according to the mode of parentage we have just explained, that we shall mostly have to deal in this chapter.

The modes of reproduction among Protists are many and various. The most familiar is the simple halving of the cell each time it has attained double its original bulk (Herbert Spencer's "limit of growth"),[1] a process termed in Hibernian phrase "*multiplication*

[1] See p. 79.

by simple division." Sometimes, however, the first division is followed immediately by another, and so on, so as to produce with little delay grandchildren or great-grandchildren, etc.; this process is called "*brood-division*," or, when the progeny do not immediately separate, "*segmentation*."[1] Again the progeny of brood-divisions may assemble in groups, usually in pairs, which fuse to form a new or "*fusion-cell*"; this process is called "*conjugation*," or, if the "pairing-cells" are dissimilar, "*fertilisation*." We must bear in mind that conjugation processes are not, strictly speaking, processes of multiplication; for the act of pairing halves the total number of cells for the time being, one replacing two: the two literally become one flesh.

We very often find these three reproductive processes recurring in cycles, *e.g.* a succession of simple divisions at the limit of growth is wound up by brood-formation, and the brood-cells conjugate; the fusion-cell then initiates a fresh cycle. But the order of the processes varies in different cases, and sometimes even different modes of brood-division may alternate. The Malaria parasite is found in the blood (Fig. 9, 1–5) as a little amœba-like being that enters the blood-corpuscles and grows till it fills it, then it undergoes brood-formation and is resolved into eight or sixteen cells that destroy the remains of the corpuscle in escaping, and each enters a fresh

[1] The terms "*schizogony*," "*sporogony*," "*sporulation*," have also been applied to this process in special groups.

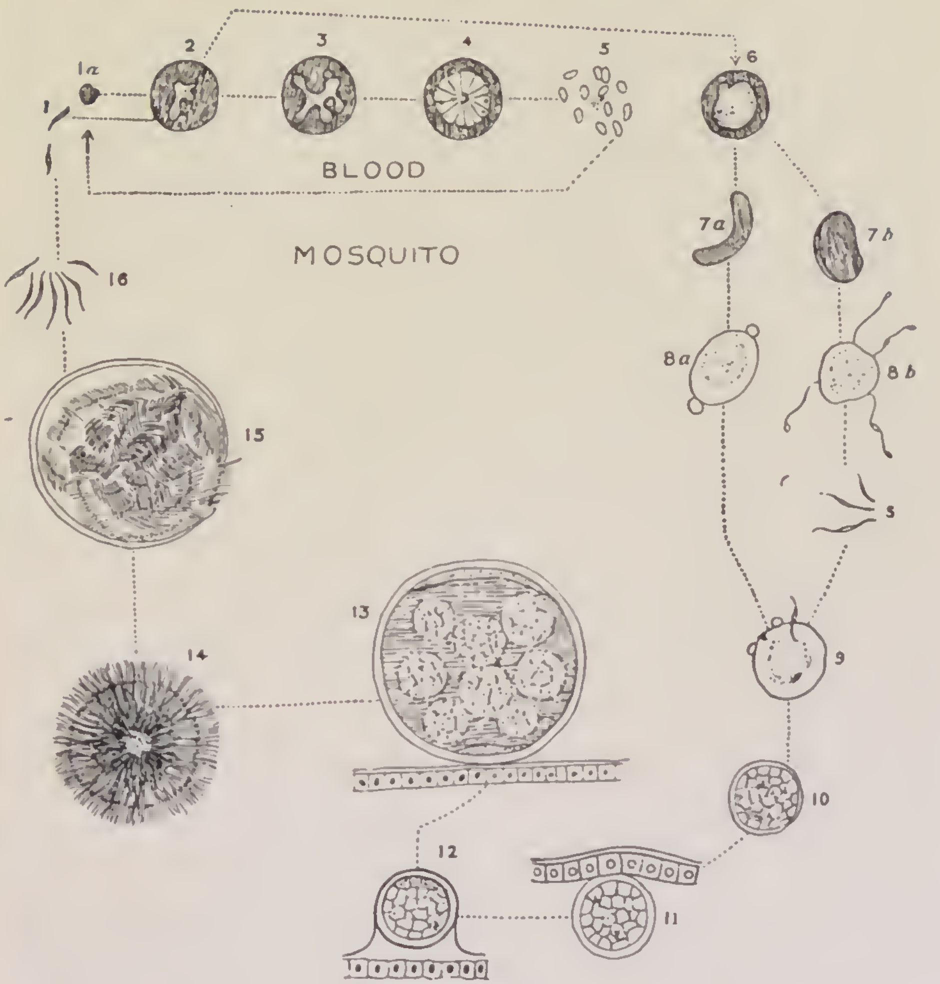

Fig. 9.—Diagram of the life-cycle of the parasite of Malarial Fever.

1, Young germ from saliva of Spotted Gnat or Mosquito. 1*a*, Young germ liberated from a red blood-corpuscle destroyed by the ripening of the brood of such germs (see 5). 2, 3, Growth of parasite within the corpuscle. 4, Brood-formation of parasite within the corpuscle. 5, Brood-cells liberated. 6, Full-grown parasite which has not undergone brood-formation, and destined to be the brood-parent of pairing cells. 7 *a*, *b*, Its growth when liberated in the Gnat's stomach. 8 *a*, Its differentiation into an oosphere and polar bodies (compare Fig. 10). 8 *b*, Differentiation as a male cell into four sperms and a cytophore destined to disintegrate (see p. 90). *s*, Isolated sperms. 9, "Syngamy" or fertilisation. 10, Enlarging oosperm within the Gnat's stomach. 11, 12, Its migration through the wall into the body cavity. 13, First brood-division of oosperm. 14, Second brood-division of one of the cells to form the minute zoospores (sickle-germs), more highly magnified. 15, Matured product of the oosperm filled with zoospores ready to migrate into the salivary glands, and seen free in 16.

corpuscle (Fig. 9, 6). After a time certain of them cease dividing, and stay at full size in the corpuscle till a Mosquito[1] takes it in with the blood which it sucks (Fig. 9, 7). Within the Mosquito it behaves as a gamete mother-cell: either it divides into four, each growing out as it separates into a long filament (the sperm, Fig. 9, 8*b*), or else it shows phenomena which are similar to the formation of the polar bodies (see p. 10), and so constitutes an oosphere or female pairing cell (Fig. 9, 8*a*). The fusion-cell (Fig. 9, 11–12) migrates through the gut wall into the body cavity of the Mosquito, and there enlarges greatly and divides to form several spheres (Fig. 9, 13). This first brood-division is followed by a second, carried to an enormous extent, so as to give rise to thousands of sickle-like cells (Fig. 9, 14–16), which migrate to the salivary glands of the Mosquito, and pass into man the next time the insect takes a feed. Thus we see that brood-formation of one type takes place in the multiplication of the organism within the blood of man; a second type (or rather two correlated types, male and female) occur in the gut of the insect, and give rise to the pairing cells. The fusion-cell within the body cavity of the Gnat shows yet a third type producing the spheres; while the formation of the minute sickle germs, destined to infect a new host, is the result of the last type of brood-fission displayed.

[1] Or Gnat: "Mosquito" is the Portuguese term for our good English word.

In many cases the separation of the daughter- or brood-cells is not complete, and they remain associated in more or less close union. Such an assemblage of cells of common origin is called a biological "*colony*" in the strict sense, the term "*social aggregate*" being used for an assemblage formed like a human colony by the flocking together of originally isolated organisms. Protist colonies may be formed in three ways, the third being only a combination of the first two:

(1) *Cell-division*, alternating with intervals of growth, gives rise to daughter-cells which remain united together.
(2) *Brood-division* (*segmentation*) produces a number of cells which remain united together.
(3) *Mixed formation:* a colony first formed by segmentation continues to enlarge by the division after growth of its several cells, the daughter-cells still remaining connected.

Colonies of the first and third type may be *propagated* by the separation of a part of the colony; if the separated part consist of a single cell, this merges into *true reproduction*.

In the most primitive colonial Protist, all the cells of a colony are practically alike; and the colony ultimately breaks up into its individual cells, which reproduce in one or other of the ways described above. But in some cases the colonial habit has induced differentiation among the cells. There is a striking example of this in *Proterospongia haeckelii* (a small organism found in pond-water by Savile Kent), which consists of a large mass of cells united by a gelatinous secretion (Fig. 10). Those at the outside of the mass are provided with a waving lash, the base of which is surrounded by a funnel or collar

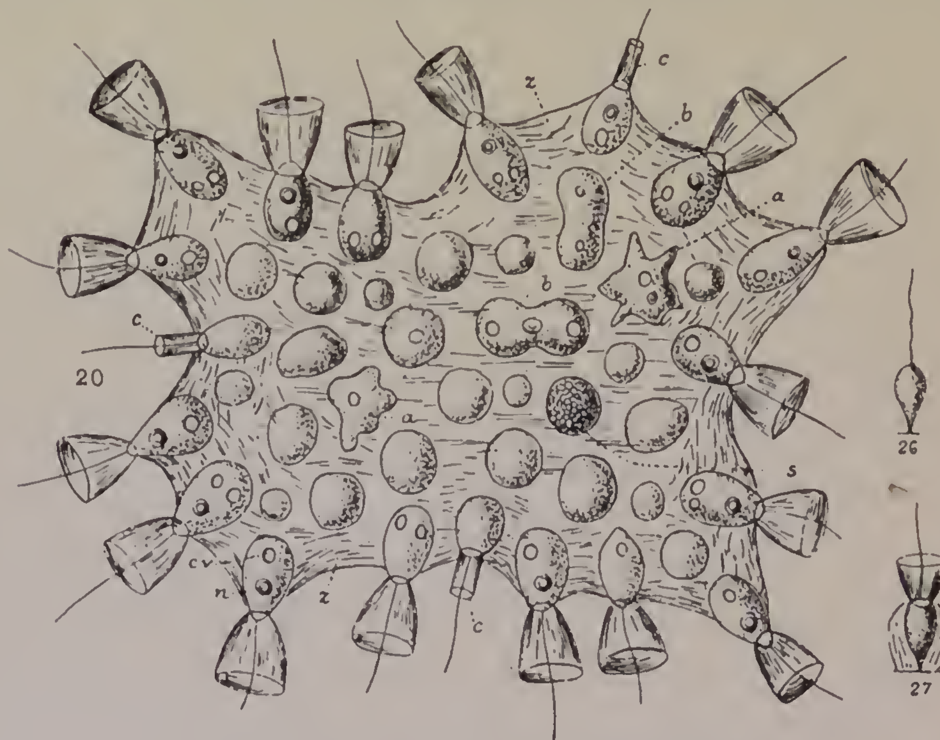

FIG. 10.—A colony of *Proterospongia haeckelii.*

20, Colony. *a a*, Central cells, "amœboid." *b b*, Similar cells dividing by simple constriction after nuclear division. *s*, Central cell undergoing brood-division or "sporulation." *c*, Collar of external cells. *n*, Nucleus, and *c.v.*, Contractile vacuole. 3, Colonial jelly. 26, Young solitary cell. 27, Solitary cell with collar and gelatinous investment.

of protoplasm. These cells take in the food particles brought into contact with them by the waving of the lashes in the surrounding water; while the cells at the centre of the colony (*a*, *b*) appear to be only indirectly nourished by the food, which is digested and transmitted to them from the collared-cells. Our knowledge of the life cycle of the organism is still very incomplete, but it appears certain that only the central cells can truly act as reproductive cells by segmentation (*s*), while outer cells may possibly separate to propagate the race also by the slower process of nutrition and growth, followed at intervals by simple division. We might almost regard this as a Metazoon with two tissues—the outer one nutritive, the inner reproductive, and ascribe the specialisation to the relative position of the two layers: the outer one is favourably situated for obtaining food from the ambient water; while the inner, debarred from all activity by its position, and fed and sheltered from the stress of contact with the unkind world by the outer layer, devotes its energies to the reproduction of the species.

Indeed, this organism, as its name implies, is, as it were, a forerunner of the Sponges, and probably represents a last survivor of their ancestral type. For a simple Sponge (Fig. 11) is a sack attached by the bottom and widely open above (*Os*), with the wall pierced by numerous pores (*po*). This wall consists of three layers—an outer *epidermic* layer (*Ec*), an *intermediate* layer, and an inner or *stomach* layer (*En*), the cells of the last possessing lash and collar. The lashes of the stomach-cells produce a constant current of sea-water through the sack, which passes in through the pores and out through the mouth, and brings with it the food particles which the stomach-cells alone can take up, the two other layers being nourished by them. In this case it seems that only

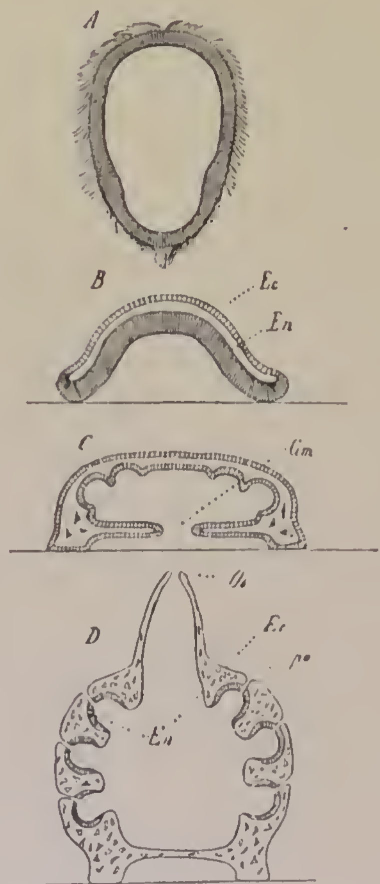

FIG. 11.—Development of a simple Sponge, *Oscarella* (after Haider).

A, Blastula stage, a hollow ball of cells in a single layer. *B*, Gastrula stage, doubling in or invaginating into a double-layered cup. *C*, Attachment and commencing closure of mouth of cup ("blastopore")—a few "middle" cells seen on either side between the two layers. *D*, Young Sponge approaching its definitive form. *Ec*, Epidermal, *En*, stomach, layer of cells. *Os*, Oscule. *po*, Pore.

such fragments of the Sponge as contain all three layers can propagate it; and in nature, indeed, hollow outgrowths of the sack are formed as branches, and may even be detached as buds. But only the intermediate layer, sheltered as it is on every side, differentiates certain cells as reproductive-cells. These by brood-divisions produce male and female pairing cells; and the fusion-cell after fertilisation grows up into a fresh Sponge. We have here a very marked advance on the primitive colonial Protists; for here the colonial organism can only be propagated by the co-operation of all three kinds of cells. The individual cell is no longer a Jack-of-all-trades, but it has been so specialised that it needs the association and co-operation of cells specialised in other directions to form a complete self-sufficing organism; and each kind of cell can by growth and division only reproduce its own type and tissue, but not the complete organism of which it formed a part. This has been aptly termed by Prof. Orpen Bower a process of *sterilisation.*

We have noted the richer endowment of certain of the intermediate cells. We must now follow up (Fig. 11) the fate of the fusion-cell (fertilised egg, oosperm). This divides afresh repeatedly, and by its segmentation gives rise to a hollow spherical colony (A), one hemisphere being composed of smooth cells, while the other is provided with lashes. The latter now sinks into the former so as to give the colony the form of a lined skull-cap (B).[1] The lining is composed of collared cells, which are the *stomach-cells*; the outer layer of cells again divides into two

[1] The "gastrula" stage of the embryologist.

layers, the *epidermic* and *middle* cells respectively. This is essentially the processes of reproduction and early embryonic growth found in all Higher Animals, save that the middle layer may be formed from the inturned cells instead of, or as well as, the outer ones, and that the reproductive cells may be formed in different layers in different classes. The annexed genealogical table (I), starting with the fusion-cell and ending with the pairing or sexual cells, represents the cellular pedigree in a Sponge.

From the above it is clear that the fusion-cells, though they are descended from middle cells only, yet produce by their divisions offspring that ultimately become cells of kinds which are different, and have never been in the line of their direct ancestry. We might compare this with a race of which the older and the younger members of a family were always sterile and different in character and endowments from the intermediate, fertile children; but where every fertile couple produced among its progeny some resembling the parents, others with the endowments and characters of the sterile uncles and aunts.[1] We must, however, bear in mind that any comparison of a strict cellular pedigree with the genealogical table of the members of a Metazoan race is only an analogy. While the main features of reproduction in the Higher Animals run on the same general lines as

[1] The case we have suggested for comparison is actually found in social Insects with their "sterile castes" in each generation.

the Sponges, certain of them may present differences; and especially, as above noted, the relation of the middle and the reproductive cells to those of the two original germ layers respectively, varies in different groups.

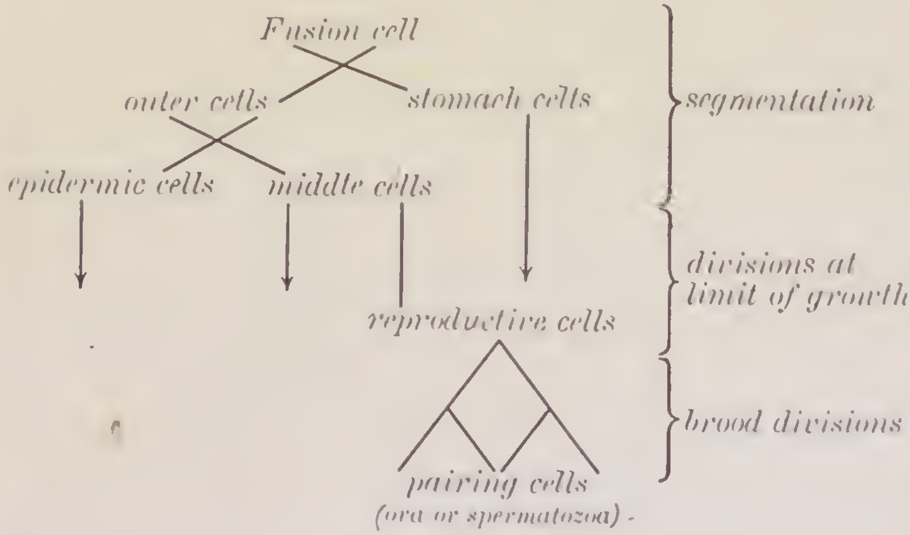

TABLE I.[1]

Propagation by budding in the Higher Animals, and *regeneration*, or the repair of injuries, are essentially two different aspects of the same phenomenon. In both cases the cells of one or more tissues multiply rapidly, and revert more or less closely to the state they possessed in the developing embryo. In some cases these "embryonic cells" can only give rise to tissues like those they respectively sprung from, or,

[1] In this and the tables to follow we use the signs X to indicate segmentation, ∧ ∧ to indicate brood-divisions, and | | to indicate divisions alternating with growth.

at least, to tissues belonging to the same layer; but in the lowest Worms the middle cells are capable of thus forming other layers. In the Vertebrata the regenerative functions are strictly limited; thus, if the surface of the skin is completely removed over an ulcer or burn, the new epiderm only grows over by gradual extension of the living epiderm at the edges, not by its direct growth upon the raw. This is the rationale of the modern practice of "skin grafts," which implanted at intervals over the surface of a healing wound give so many centres for the new overgrowth of epiderm to start from, thus accelerating the process of "skinning over."

Most tissues of the Higher Animals retain sufficient "vitality" to be able to enter at once on processes of regeneration of their own individual kind in cases of wounds; and in the Newts, for instance, even a complete structure like a limb can be renewed after amputation. The epiderm of Vertebrates (Fig. 12) retains in its deepest layer an almost indefinite power of growth and reproduction, the cells next the true skin forming a continuous stratum, each cell of which is constantly growing and dividing, the upper cell at each division becoming horny, to be ultimately cast off as other horny cells are formed beneath it, while the lower retains the original power of growth and division. This layer is absolutely comparable to the layer of cells that forms cork in most green plants (see Fig. 19, p. 66). The periosteum or layer of cells overlying the bone has similar but less active powers.

Reviewing the facts, we find that—

(i.) In Protista, each cell retains the power of reproducing in its offspring its own characters or those of a direct ancestral cell, which we may term the law of *direct cellular transmission, uninterrupted*

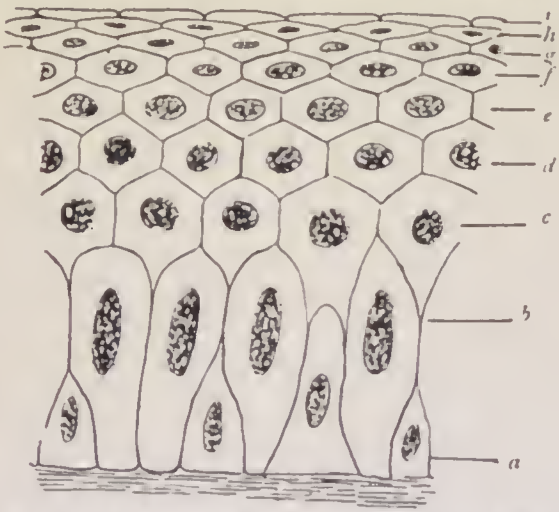

Fig. 12.—Vertical section of epiderm of a Vertebrate.

Showing the basal *embryonic* layer (*a*, *b*) and the progressive rounding off and flattening of the horny cells to which it gives origin.

or *alternating*, according as only one or several alternating modes of cellular reproduction constitute the genetic cycle.

(ii.) In Metazoa, the power of reproducing a complete organism is confined to certain reproductive cells, which must beget in their progeny cells like those which are only related to them collaterally; this we call the law of *collateral cellular transmission.*

(iii.) The remaining cells of the Metazoan can seldom or never revert closely enough to a primitive type to produce all those other tissues of which they are collaterals, though their propagative power may be very great. This limitation of reproductive power we may call the *law of specialised sterility.*

(iv.) In most cases of animal budding (as in repair) we find that the several tissues co-operate to produce a complete organism; this we call the *law of co-operative propagation.*[1]

The power of propagation of animals by small fragments is possessed very largely by Sponges, some Cœlenterates, Starfishes, and certain Flatworms; it is practically lost in the higher groups for several reasons, considerations of nutrition being most important. An Animal fragment can only obtain the nutritive matter for forming new cells by eating up, as it were, part of itself, until it has formed new organs for the prehension and digestion of food. To do this, the fragment must be always big enough to render this sacrifice possible; and, moreover, the tissue-cells must not be too specialised to adapt themselves to the altered conditions. Thus, the complex tissues of a human arm, accustomed to be served by a constant supply of blood current bearing in an abundance of food and oxygen and carrying off all waste materials, and to the guidance of a highly developed nervous system, can never

[1] A good account of these phenomena will be found in "Regeneration," by T. H. Morgan.

adapt themselves to a life of isolation. In this respect Animals contrast markedly with Plants. Budding is, indeed, unknown in Arthropods, Molluscs, and true Vertebrates, though it plays a large part in their lowly relations, the Tunicates or Sea Squirts.

To study in the way we have applied to Animals the laws of reproduction and propagation in Plants, we must revert to those Protists whose life is essentially vegetal. These possess a coloured portion of protoplasm (green, yellow, or red), in which, under the stimulus of light, inorganic materials are combined to form the organic food on which (like animals) they feed. As these inorganic materials exist in solution they can soak into the cell, which needs neither mouth nor stomach; and the cell can exist, grow, and multiply by division at the limit of growth, even while invested with a thin coating of the papery material, cellulose. If the cell start as a cylinder or ovoid, and the divisions are always in the same direction, at right angles to its length, the product (a colony of our first type) is an elongated filament, like those which form the green, slimy scum on our wayside ditches (see Fig. 1); if the divisions take place in two planes, the colony will form a plate or disk, which may curve as it grows to form a hollow sphere (Fig. 2); if in three, a solid mass, which is much more rare. When a period of increased vital activity ensues, brood-formation sets in; the brood-cells are at first naked, lacking the cellulose wall, and usually provided with swimming lashes. The brood-cells may in one and the same species[1] have very different fates. They may (1) settle down within the wall of the parent-cell, and grow out into filaments, which finally rupture the parent-cell wall by their elongation; or (2) they may escape, and only settle down to grow into filaments after swimming about for a short time; or (3) they may pair first of all, and then the fusion-cell, after a rest, makes a fresh start of life and growth and multiplication within the cell wall. The life cycle may be very complex. We may even find states of *Ulothrix* in which the cell walls of the filament gelatinise, and the cells themselves round off, the colony forming a very irregular mass.

In some forms that are in other respects very primitive we find a true differentiation that has advanced further than *Proterospongia*, the lowest animal type we have selected as an illustration. *Volvox globator* is a beautiful green sphere the size of a small pin's head, found actively rolling over and over, as its name implies, in still waters fully exposed to the light. On microscopic examination it is seen to consist of many hundreds or even thousands of green cells imbedded in the surface of a spherical mass of gelatinous cellulose, and sending their active lashes into the water. Scattered among

[1] The filamentous Alga *Ulothrix zonata* (see Fig. 1, p. 4).

these are a few larger cells, which may be seen in all stages of segmentation; and as these grow and segment they protrude into the cavity of the sphere, and finally rupture it and become free as new individuals. The ruptured sphere sinks to the bottom, and the colonial cells at its surface soon

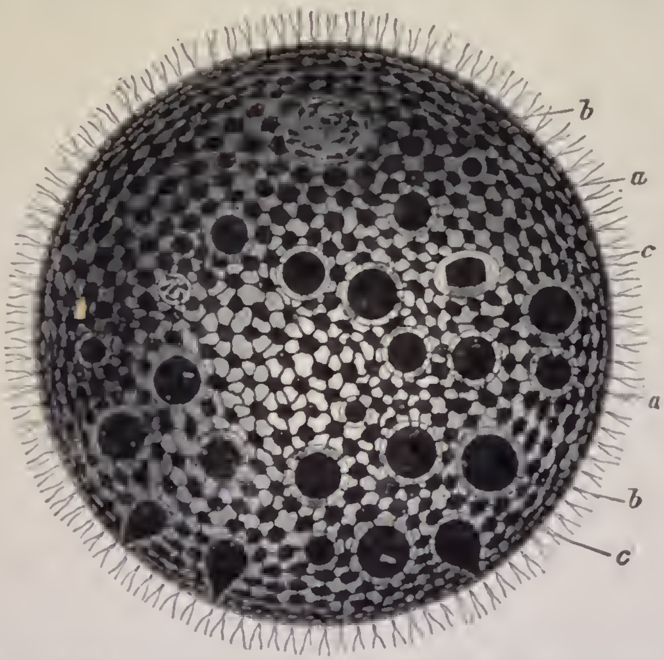

Fig. 13.—*Volvox globator*, a green colonial organism, showing the vegetative cells.

The reproductive cells, female (*a*) and male (*b*): in the upper male colony the resolution into sperms is visible; *c*, ordinary cells.

die, whether from the unfavourable conditions or no it is impossible to say. At the time for pairing it is only the few large cells that become or give birth to pairing cells; the resulting fusion-cell segments to form a new colony. Here again we have a well-marked sterilisation of tissue-cells, and their characters are transmitted only through the reproductive cells, their collaterals. From our standpoint *Volvox* must rank as a lowly Metaphyte (Fig. 13).

The majority of Metaphytes show a much higher differentiation and a power of colonial propagation far greater and more continuously exercised than in any Animals.

The first that we shall consider are the Scale- and Leaf-mosses. As is well known, the little capsule or "urn" is full of a fine dust consisting of reproductive brood-cells or "spores." These germinate and grow, as in Protophytes, into filaments consisting of elongated cells, some of which are green, and run on the surface of the ground, while others penetrate it and serve as roots (Fig. 14, *p p*, *r r*). But so little specialised are they that the reversal of a minute sod containing them will determine a change of their relative character and functions. On branches of these other cells are formed, which are short and thick. These divide, and by their colonial growth the proper leafy Moss-plant is formed; but only the lower part for the time being assumes the condition of the moss tissues, the uppermost cells being colourless, nourished by the green cells of the stem and leaves, and assuming and retaining the functions of an *embryonic* tissue. This constitutes the "growing point" characteristic of all the higher plants.

Ultimately, in the deeper parts of flask-shaped outgrowths, near the growing point, are formed reproductive cells, which give rise to pairing cells, male or female, as the case may be. Fertilisation is internal, the male cell swimming up to the immovable female, and fusing with it *in situ*. The fusion-cell

FIG. 14.—Vegetative system of a Leaf-moss.

A, Base of leafy shoot giving off filaments, colourless root-hairs (*rr*) and green "protonema" (*pp*); *b*, a bulbel or resting mass of cells; *k*, a young leafy plant. *B*, *C*, *D*, Development of a spore into protonema.

remains imbedded in the Moss-plant (Fig. 15), and is nourished thereby as a parasite, and, undergoing segmentation, is converted into a colonial mass. The outer layer of this colony in the most primitive Scale-mosses is converted into a capsular wall, while the inner cells are reproductive cells, each of which forms a brood of four spores. In the Leaf-mosses the colonial body formed by the segmentation of

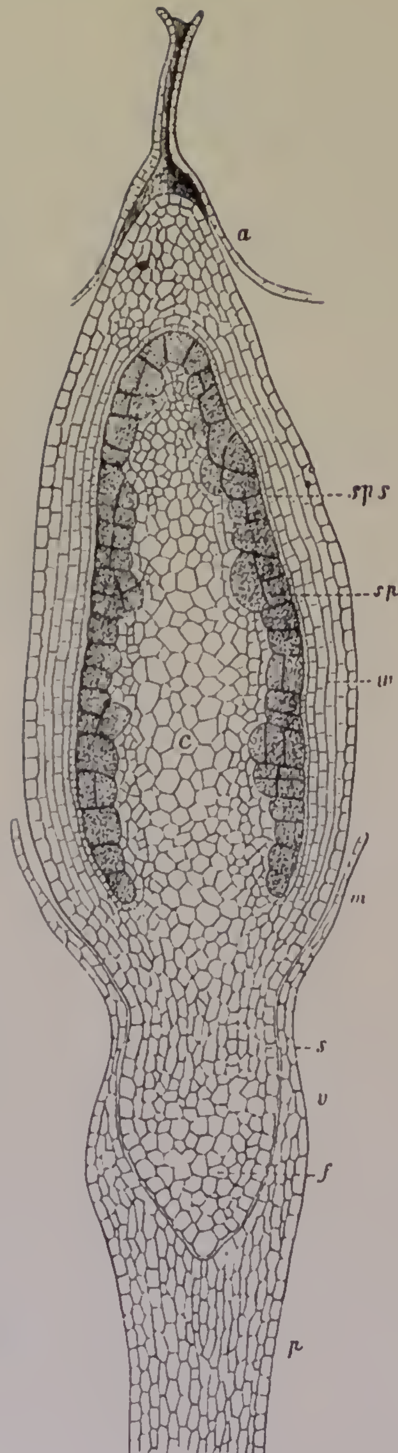

FIG. 15.—Young capsule or urn of a Leaf-moss formed from oosperm.

f, "Foot" for attachment and nutrition from *p* the leafy plant. *m*, Base; and *a*, Apex of the ruptured flask or archegone in which the capsule was formed. *sp*, Reproductive cells destined each to form a brood of four spores. *s*, Constricted part of urn destined to elongate into its bristle-like stalk.

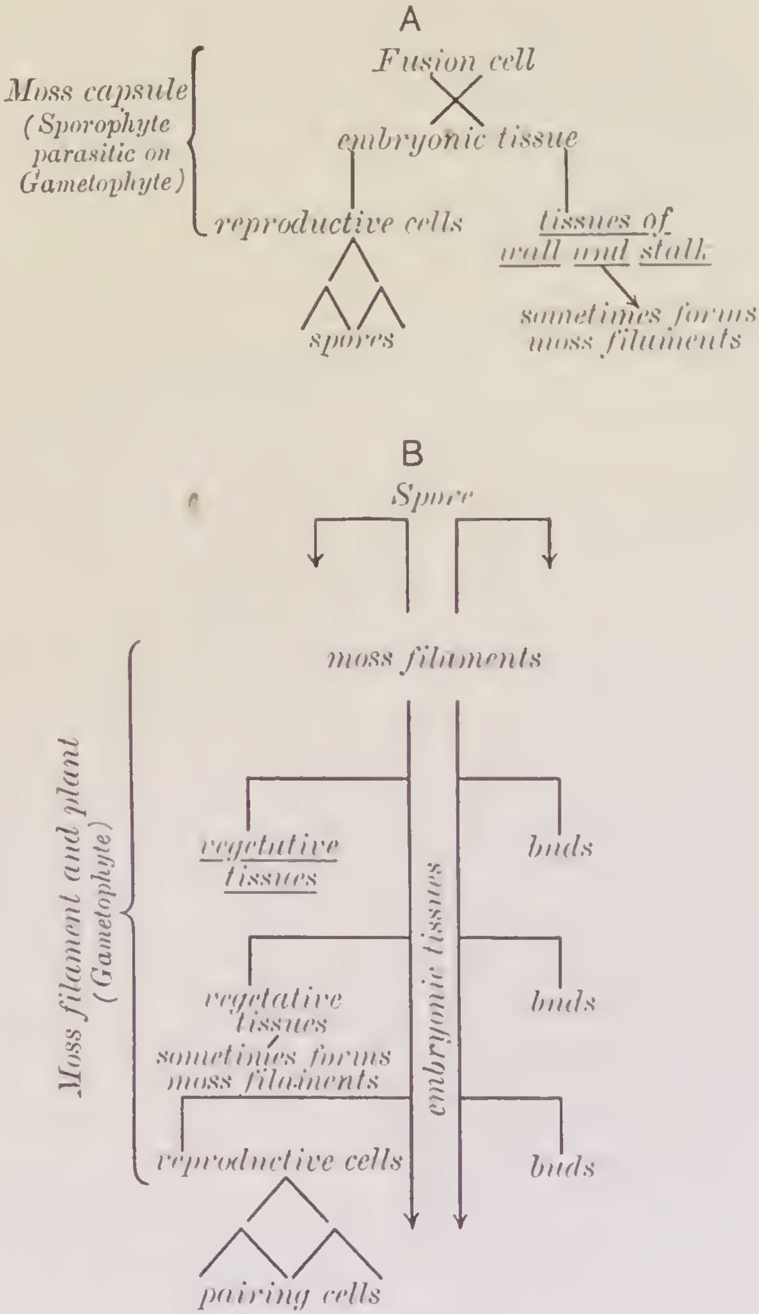
A
Fusion cell
Moss capsule
(Sporophyte
parasitic on
Gametophyte)
embryonic tissue
reproductive cells
tissues of
wall and stalk
spores
sometimes forms
moss filaments
B
Spore
moss filaments
Moss filament and plant
(Gametophyte)
vegetative
tissues
buds
embryonic tissues
vegetative
tissues
sometimes forms
moss filaments
buds
reproductive cells
buds
pairing cells

TABLE II.

the fusion-cell is much more modified, with increase of specialisation and corresponding sterilisation; for its lower part is converted into a bristle-like stalk (*s*), and the wall and centre of the urn-shaped capsule are both composed of green tissue adapted for the formation of organic food materials.

Before we group these facts into a table we must notice the extraordinary powers of *propagation* of the Moss-plant: if cut up into fragments, almost any green cell, whether of the Moss-plant or the young urn, is capable of growing out into a green filament that will produce new leafy plants; and this in addition to the propagative power by ordinary branching or budding of the embryonic tissues at the growing point. We will, according to custom, begin our table (II) with the fusion-cell.

It will be seen here that there is no necessary colonial death (as in *Volvox*) of the leafy Moss-plant, though the older tissues of the stem and the leaves *usually* die down after the maturation of the parasitic capsule; and that the power of propagation possessed under certain circumstances by the green cells of the Moss-plant and urn makes them possible direct ancestors of reproductive cells.

Still, in what we may regard as the normal cycle, the reproductive cells produce among their offspring collaterals as well as direct ancestral forms. The character of the cycle is noteworthy: two systems of colonial growth each beginning with a single cell are determined or closed by the production of brood mother-cells ; and these systems contrast both in the characters of the colony and in the nature of the brood cells. The colonial outcome of the spores is the filamentous growth and the leafy Moss-plant, and the brood-cells formed therefrom are the sexual pairing cells ; the colonial outcome of the fusion-cell is the capsule, and its brood-cells are the asexual spores. This is then an "alternation of generations" in the sense of colonial or habitual terminology (as distinguished from the alternation of cell-cycles in the Protists). Botanists have termed the contrasting colonial plants "Sexual" and "Asexual," "Gametophyte and Sporophyte," respectively, from the character of the brood-cells which each produces in turn.

In the ascending scale of the Vegetable Kingdom we first meet in the Moss-plant with those tissue-cells which we term "*embryonic*" ; these must be defined as *colonial cells nourished by the adult part of the colony, and having for their sole function growth with differentiation, or continued division at the limit of growth, to form new cells and organs.* Such cells are obviously not at all "primitive," as they are frequently called, but on the contrary are the essential outcome of high colonial differentiation. That the whole colony may exist in this condition in the early stages of development is only rendered possible in the case of the Moss-urn by its receiving nourishment as a parasite from the leafy plant.

The Fern is only comparable with the Moss by a complete detachment from preconceived ideas. Most readers know that the Fern sheds from the brown ridges or spots on the under side of its leaves a fine dust, whose particles are the spores. Each spore in germinating produces a cellular filament, which soon expands into a green plate (Fig. 16), the equivalent of the leafy Moss-plant, or, better, the "plant" of the Scale-moss or Liverwort, to which it bears a close resemblance. On this are borne sexual organs, flasks or archegones, and sperm-capsules or antherids, which produce sexual cells (Fig. 17). The fusion-cell, as in the Moss, is at first parasitic on the scale (Fig. 18), and develops into a Fern "plant," such as we know it with stem, roots, and leaves, and finally spores. The essential difference here is that in the Mosses the spore-forming plant is entirely parasitic and of limited growth, while in the Fern it becomes independent, and is of unlimited growth, being provided with organs of support and conduction as well as of nutrition. We may well say that the sterilisation (to use Bower's term) of part of the colony has led to so extended a power of colonial growth and branching, that the power of forming reproductive cells is in the end enormously increased. The propagative capacities of Ferns by buds from embryonic tissue are very great; those of fragments of the spore-bearing plant are slight; but the sex-bearing scale may be artificially propagated by being cut into small pieces, although its normal life is usually limited by the formation of the parasitic Fern-plant

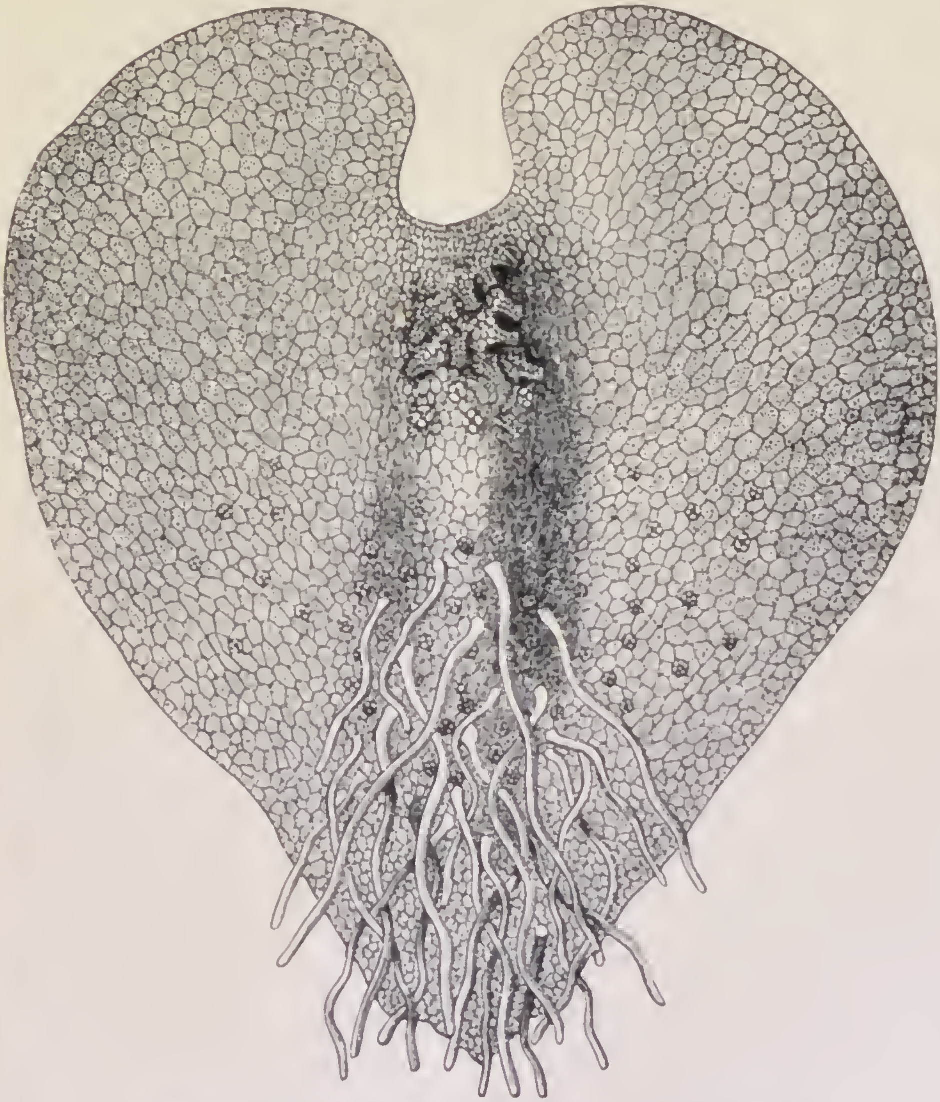

Fig. 16.—Fern-scale (Prothal), under surface, showing behind a group of flask organs, and further back sperm-capsules and root-hairs. The notch is the growing point of embryonic tissue.

from the fusion-cell (Fig. 18). Ferns then show the same alternation between spore-bearing and sex-

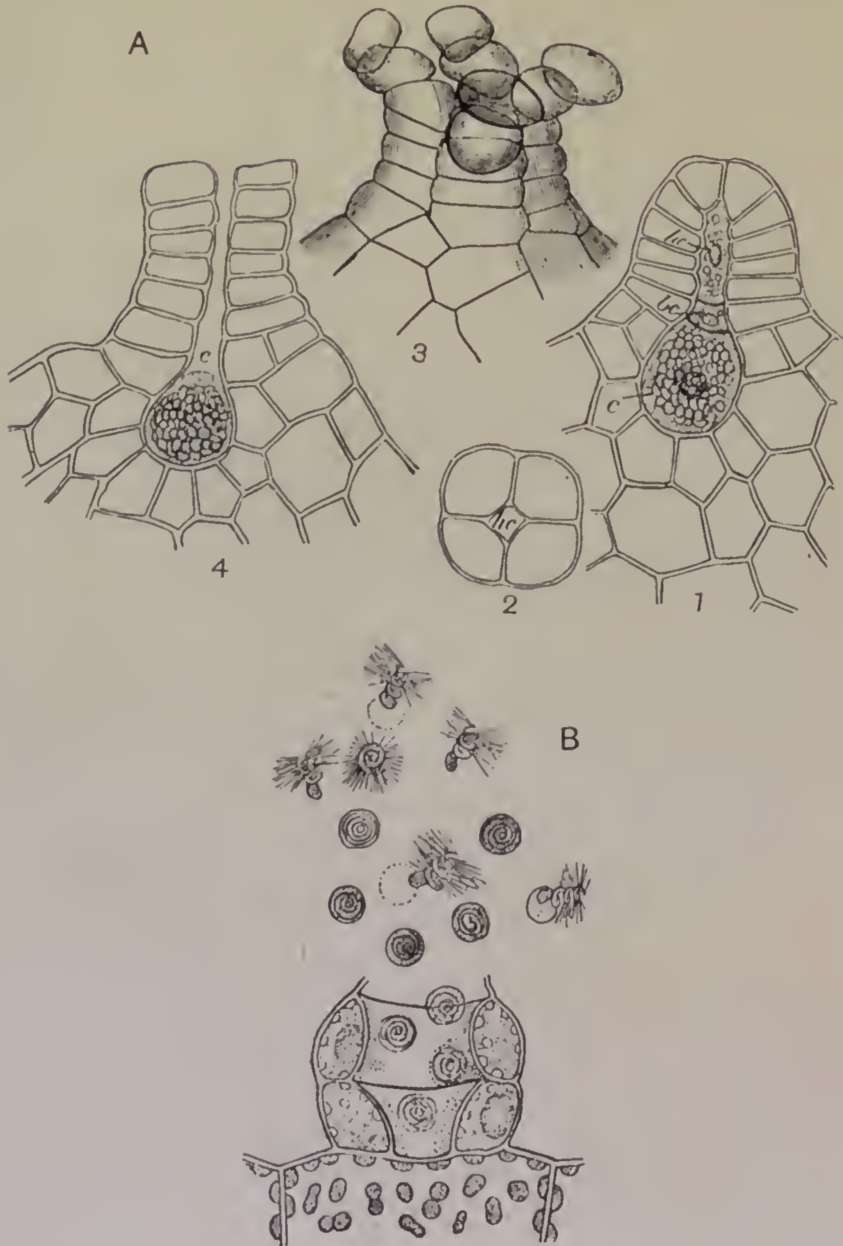

Fig. 17.—Sexual reproductive organs of Fern-scale.

A, Female (archegone); 1, flask nearly mature; 2, section of neck showing central canal; 3, neck opening for admission of sperm; 4, lower part containing oosperm or fertilised egg. B, sperm-capsule (antherid) discharging sperms.

bearing generations as Mosses; but the order of relative conspicuousness and abundance of colonial

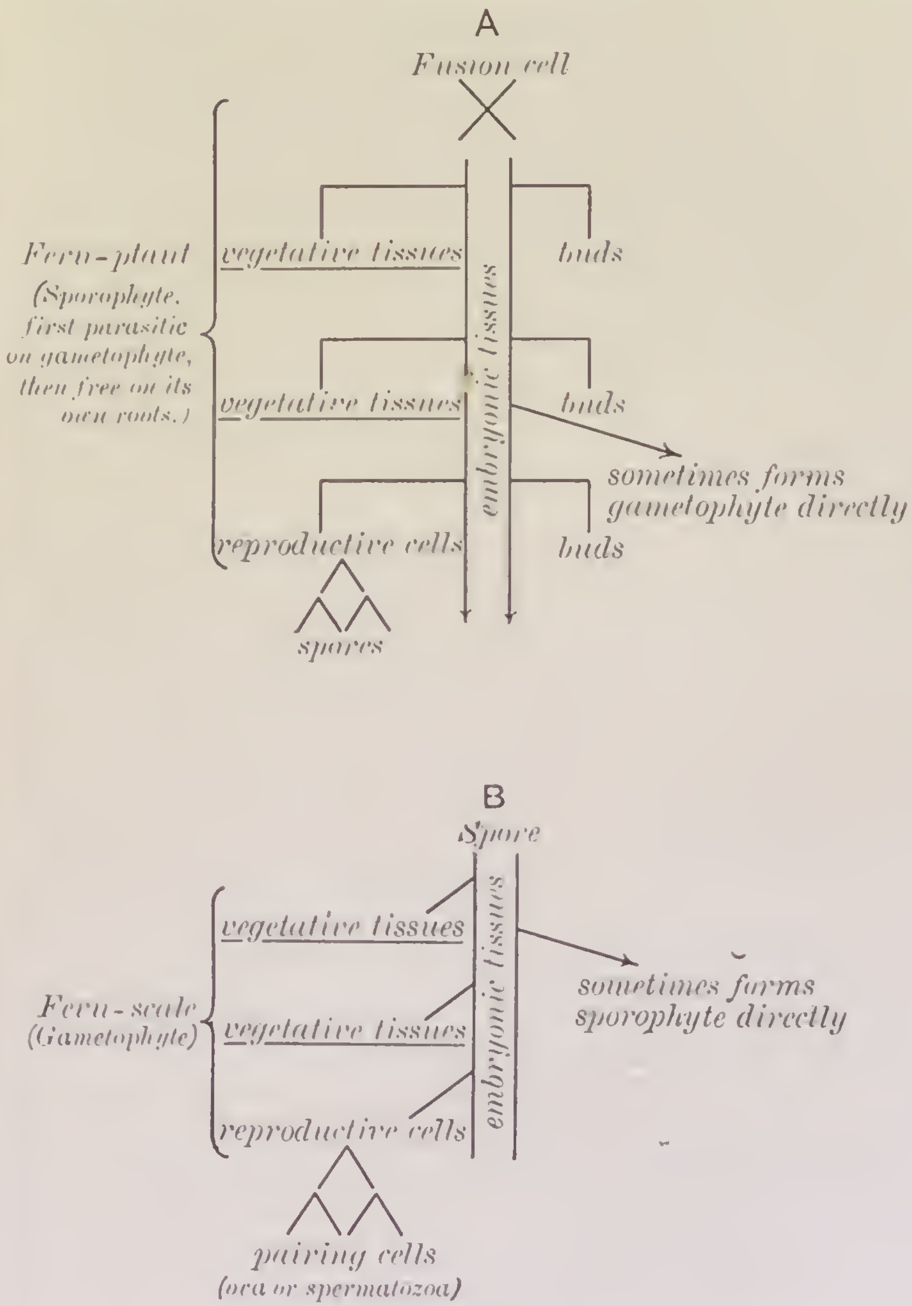

TABLE III.

growth is inverted (Table III). We have seen that in Mosses a vegetative transition by cell-growth might take place from the spore-bearing generation to the other. In Ferns similar transitions are possible both ways, so as to cut out the stage of brood-cell formation, which we regard as the critical reproductive stage.[1] Thus in many Film-ferns, instead of producing spores, the leaves grow out into scale-plates bearing sexual organs ("apospory"); while in the common Cretan

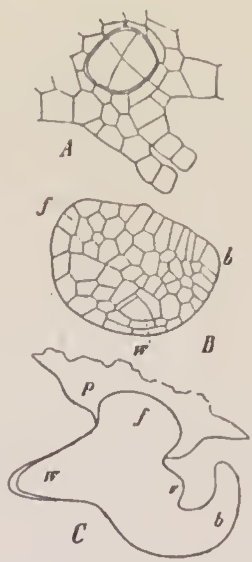

Fig. 18.—Embryonic Fern Plant parasitic in mother-scale.

A, Young Fern-plant in flask. *B*, More advanced stage; *b*, leaf-origin: *w*, root-origin; *f*, foot for parasitic ingrowth into Fern-scale. *C*, Outline section a little later; *p*, fern-scale; *r*, growing point of Fern-stem; *b*, first leaf; *w*, first root.

fern, the scale produced from the spore grows out directly into the spore-bearing leafy Fern-plant instead of giving rise to sexual cells ("apogamy"). In Flowering plants the relations of the sex-bearing plant are much obscured, and it would lead us too far to explain them here. Suffice it to say that the "plant"

[1] These transitions have been aptly termed "short-circuitings" by Sir Edward Fry.

as we know it corresponds to the Fern-plant or Moss-capsule: it is the Sporophyte, not the Gametophyte. The parasitism of the embryo formed from the fusion-cell is usually intense and prolonged.

A very remarkable character of Dicotyledons or Exogens shared by some other Flowering-plants is the continuation downwards from the growing point of a zone of embryonic tissue, the "*cambium*," which habitually by its growth and multiplication forms zones of wood on the inner side, and inner bark (or bast) on the outer (Fig. 19). This layer has, in cuttings, an especial tendency to form buds. But all the living cells retain a power of forming a similar tissue at or near an exposed surface; for instance, such a layer is formed a little within the surface of trees to produce the cork—this is known as the cork-cambium. We are all of us familiar with the little brown scars on plums, etc., that have been slightly injured when green: these are due to the local development of a layer of embryonic tissue below the injured surface, and the formation of a thin protective layer of cork therefrom.

Colonial propagation in Flowering-plants may take place by the separation of buds (which form normally at the growing point), or by development of so-called adventitious buds from the embryonic cambium zone of the stem or roots. Such propagation by minute fragments as occurs in Mosses is unknown here; but larger fragments of leaves can frequently produce

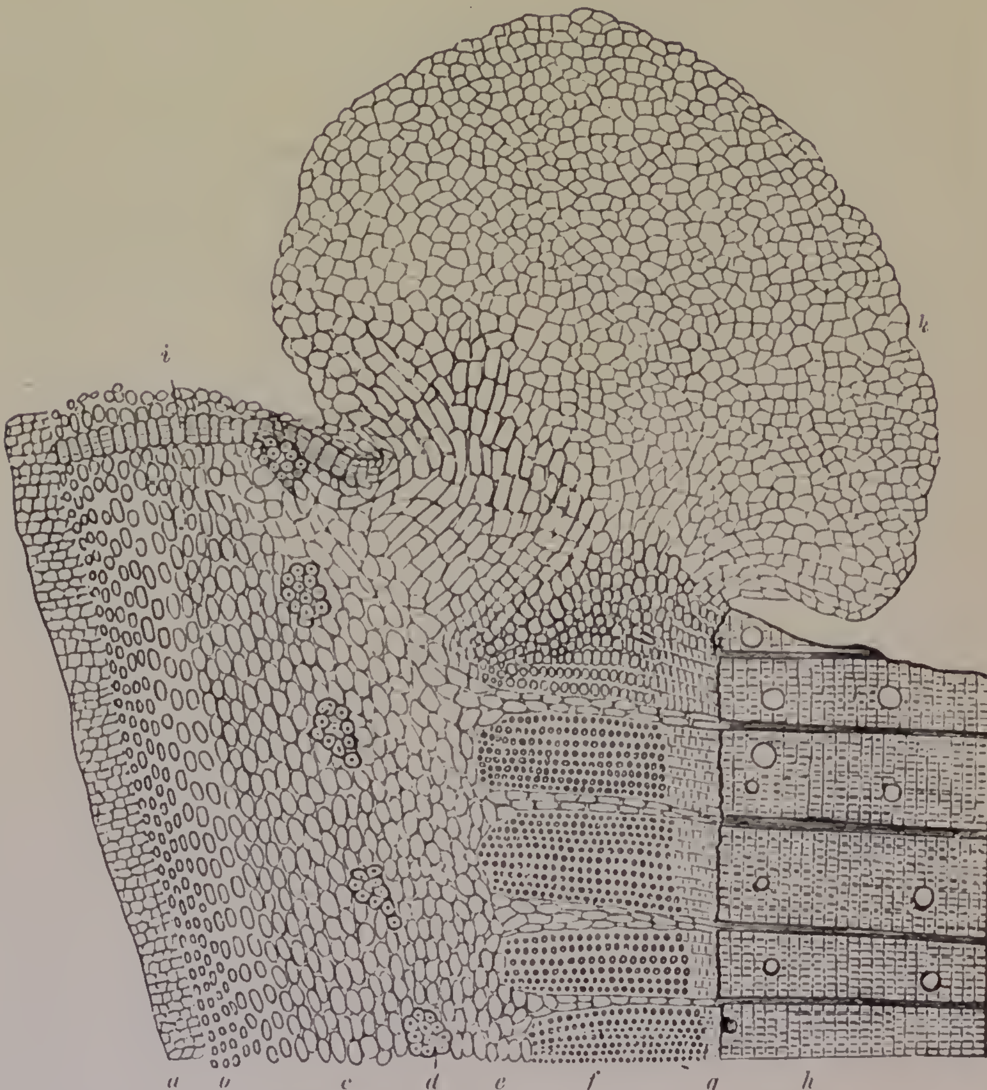

FIG. 19.—Part of transverse section of a stem which has been cut at the upper side and undergone repair and regeneration; the lower and right edges only mark the part selected, and in the plant would be continued, so that normal relations are shown (after Hartig).

a, Superficial cork. *b*, Embryonic cork-forming zone, "cork-cambium." *c*, Herbaceous layer, "cortex." *d*, Bundles of fibres. *e*, Inner herbaceous layer. *f*, "Phloem," "liber," or inner bark. *g*, Cambium proper. *h*, Wood. *i*, Showing outside disintegrated wounded layer and within "wound-cork" growing from a secondary cork-cambium. *k*, Callus formed partly from cambium, partly from cortex.

buds and ultimately plants. Just as with the stem, the cells within the cut surfaces produce an embryonic tissue callus (*k*), which gives rise both to a protective skin of cork (*i*) and to adventitious buds.

The readiness to form cork and adventitious buds in this way varies extremely, and with this the power of leaf-propagation. For the formation of cork is an indispensable protection against the opposite dangers of drying up on the one hand, and of the attacks of microbes and moulds on the other. Again, most Begonias are readily propagated by pieces of leaf; but in the bulbous varieties the leaf-fragments form a mass of embryonic tissue, well protected by cork, which remains for months or years before active buds are developed, so that they were long thought incapable of this mode of reproduction. Not only Begonias, but Gloxinias and other members of the showy order Gesneriaceæ, the Peperomias with their massive speckled or veined foliage, and Chrysanthemums, are habitually multiplied in this way; and the list of possibilities in this direction is daily increasing.

On reviewing these facts we see that the law of collateral transmission applies to Plants as well as to Animals, but that they have much greater powers of colonial propagation, by the formation of embryonic tissue from already specialised colonial cells, and by the persistence of a portion of the colony (the growing point, and in Exogens the cambium layers) in the embryonic state. The fact that green cells can manufacture plant food in the light explains the greater vitality and propagative power of small Vegetable fragments as compared with those of Animals; and it is needless to assume any more recondite intrinsic differences. Even in this mode of propagation, the law of collateral transmission holds; for many of the cell-forms of plants, such as hairs, wood-cells, etc., are absolutely sterile, and consequently can never take part in the formation of an embryonic tissue capable of giving rise to a new plant.

Thus, throughout the Higher Kingdoms we find the problem of heredity rests on different data to those supplied by the Protists. In these lowly forms, where the law of direct transmission prevails, it is easy to admit that when a cell resolves itself into two new ones which exactly reproduce its original state, they should each possess its original qualities; even where the transmission is alternate, we may admit that the different conditions at the different stages of a genetic cycle modify the organisms produced. In the simplest case of collateral transmission, as presented by *Volvox globator*, the sterilised colonial cells so closely resemble more primitive independent forms in their behaviour and character, that we may well believe that they have inherited such forms, directly and unaltered, from some Protist ancestor, while the reproductive cells have become modified. But it is impossible to suggest such an explanation for the higher Animals and Plants, since a nerve-cell with its outgrowths many feet long, or a woody fibre which has expended all its living protoplasm in the building up of a firm wall, can only have been evolved as portions of a highly specialised colonial organism.

The difficulty of explaining the mechanism of collateral transmission in Metazoa and Metaphytes by the direct transmission in Protista has been the origin of the recent lively discussions on heredity. To biologists saturated with the implicit conviction that direct cellular transmission was alone possible, some mysterious agency, that should be contained in the reproductive cells, and be handed down by them in their direct cellular descent, was an essential assumption; and this agency is supplied by Weismann in his Germ-Plasm theory, which replaced or supplemented that of Amphimixis (see p. 16). The reader will do well to bear in mind that it has been presented to the world in successive editions; each has been greeted as final by the disciples, who have made light of the objections raised thereto, though on every occasion such objections induced the Master to recast the theory in his next work. Our presentment of the theory upheld in the "Germ-Plasm; A Theory of Heredity," published in London in 1893, may therefore, for aught any one can tell, become obsolete very shortly, owing to the author's "having (to use his own phrase) in the meantime gained a deeper insight."[1]

[[1] This prophetic suggestion was fulfilled in the supplementary "Theory of Germinal Selection," published, like this Essay, in 1898 !]

Weismann conceives that in the nucleus of what we have termed "reproductive" (and also, in part, "embryonic") cells is a mixed plasm, the "germ-plasm," composed of certain entities, the "determinants" for the several organs of the colony; that when the cell divides at the limit of growth into two similar cells, the germ-plasm and the several determinants divide in the same way, so that the determinants are the same in each of the daughter-cells as they were in the parent. But in those divisions which give rise to specialised cells the germ-plasm divides as a whole, in such a way that the determinants are only *distributed* between the daughter-cells, some to one, some to another; we may say that there is *distribution* or *repartition*, not the true *division* of the several determinants. Similarly, the determinants each contain a group of minor entities the *biophors*, and in the ultimate divisions of the cells of an organ these biophors are shared between the cells; and the proper biophors in each cell constrain it to play its specific part in the organism.

Those cells which constitute the direct line of descent between the reproductive cells of one generation and those of another are formed by true divisions of the germ-plasm, with all its determinants. But we are met by the facts of propagation by fragments composed only of tissue-cells in Animals, and still more in Plants, where specialised tissue-cells revert to an embryonic condition, or rather beget embryonic cells with a *complete* germ-plasm (Fig. 19, p. 65 f.). To explain this difficulty, we must suppose that in these cases a portion of complete germ-plasm has passed at their formation into such tissue-cells, and that it has remained *dormant* until the stimulus of separation from the colonial organism has revived its vitality. Again in the four-celled stage of the segmented embryo of various widely distinct Animals (even in the sixteen-celled stage of some) it is possible to isolate a single cell,[1] which then develops into a complete embryo, though had it remained associated with its fellows it would have formed only a definite part of the embryo. Here again we find the assumption of the existence of "dormant determinants" that become active only in the separated cell, adduced by Weismann to save the theory. This assumption is also used to explain alternation of generations, where the Moss-plant and Moss-urn, or the Fern-scale and Fern-plant, alternate; their germ-plasm must contain two sets of determinants, one for the first, the other for the second generation, alternating in sleep and waking like the printer and the hatter in *Box and Cox*. We are reminded of the complex epicycles required to render the universe workable on Ptolemy's geocentric hypothesis, and the Spanish king's comment thereon: "Had I been consulted at the creation, I could have simplified matters."

[1] See Fig. 38, p. 237.

So far, indeed, this might be held as a *formal* or *fictive* hypothesis to explain the mechanism of heredity on the basis of Special Creation—each organism being created at the outset fully equipped with its own proper germ-plasm, determinants, biophors, and all. But no! Weismann is a firm believer in the theory of common descent, and, as we have seen, he and his school profess to be the only true Darwinians; and we come to his Theory of Variations.[1]

The germ-plasm with its contained determinants, as it lies in the reproductive cells of the body, is subject to nutritive changes, and consequently to constant slight variations which apparently are not correlated with anything else whatever. The haphazard variations of the determinants induce corresponding, and therefore haphazard, variations of the organism; and the Almighty Natural Selection now steps in, weeds out the unfittest, and so induces the endless variety of form and function in the Organic Realm. This has been irreverently termed the "toss-up" or "dice-box" theory of variation. It is hard to see how variations in feeding or starving hypothetical determinants can have ever ended in the development of a vertebrate eye, or in the exquisitely co-operating organs that render possible the parasitism of the offspring on the viviparous mother: it would be difficult if we had limitless æons of biological

[1] Weismann's supplementary hypothesis of germinal selection makes no difference to the present argument.

time at our disposal, instead of the paltry million of centuries conceded as an outside limit by Lord Kelvin, even when multiplied by 4,000, as Perry and Poulton suggest.[1] We have all heard of the German astronomer who was reading Lucretius, and said to himself as noontide approached, "So if the atoms had been flying about for all time, cold beetroot, oil, vinegar, garlic, and salt might have combined to form a salad." "Yes, dear," said his wife, who had come in unperceived to call him to dinner, "but not as good as you shall have with your cold beef."

It must be admitted that marvellous ingenuity is shown in giving explanations on this theory to cases where they are not needed; we may cite the limitations of propagation by small fragments of Animals or Plants, and the variations in the power of leaf-propagation in the latter, which are so readily explicable without the germ-plasm hypothesis. On this hypothesis, indeed, we are asked to overlook the plain and obvious questions of nutrition, cork-formation, and bud-formation, and to concentrate our ideas on the presence of more or less dormant germ-plasm in the tissue-cells. We may well note here that among "Inductive Fallacies" Bain cites the error of assigning more causes than a phenomenon needs. "It is involved in the very idea of cause that the effect is in exact accordance with the cause; hence

[1] Later estimates put the time at from 50,000,000 to 360,000,000 years.

the proof that more causes were operative than the effect needs defeats itself."[1]

But the cardinal defect in the theory is its objective baselessness. It professes to be founded on the microscopic study of the changes in the nucleus in cell-division; but there we find nothing to justify the assumption of two modes of nuclear division in the embryo, the one dividing the determinants, and the other only distributing them between the daughter-cells. To justify such a theory there should at least be some such basis in fact, as indeed there is for the author's "id" theory of the relations of "amphigonic" inheritance (from two parents),[2] which does not come within the purview of the present article. As it is, the theory falls under the ever-trenchant blade of Occam's "razor," "Entia non sunt multiplicanda præter necessitatem."[3]

The antagonistic school, of Herbert Spencer, regard Living Beings as characterised by their continuous

[1] "Logic," by Alexander Bain. Part II., Induction, ed. 2, 1873, p. 395.

[2] To avoid complication and the undue lengthening of this essay we have been obliged to omit the consideration of the effect of double parentage in the higher organisms that reproduce by syngamy. But it is obvious that of itself it must tend to efface and not to accentuate the variations from the average standard of the race [wherever Mendelian segregation does not occur: for this subject the reader is referred to "Heredity," by Prof. J. A. Thomson].

[3] This has been termed the "principle of parsimony." But "economy" is surely the better word, for *parsimony* is economy pushed to inadequacy. If we omit the words "praeter necessitatem" it becomes, indeed, a principle of parsimony.

adjustment of internal relations to external conditions, and cannot see *a priori* grounds for regarding the *reproductive cells* as especially lacking in this power of adaptation. They regard instinct as only explicable as *habit*, transmitted and relatively fixed by constant transmission from one generation to the next; and are disinclined to admit (even as a formal hypothesis) any scheme that leaves all such considerations on one side. They therefore are compelled to refer variations in the offspring to the adaptive reaction of the parent to the environment, and hold that there must be some mechanism of transmission *other than that of direct cellular inheritance*, by which the reproductive cells hand down to their differentiated cell-offspring the characters of the corresponding cells in the parent organism as a whole.

Charles Darwin felt this need so keenly (in a way largely ignored by those who style themselves his only true disciples) that he formulated his elaborate provisional hypothesis of Pangenesis to supply the mechanism that he postulated. He supposed that every cell in the body gave forth minute buds or "gemmules" which circulated in the blood, and were carried by its current to the reproductive cells where they were stored up, and that in the development of the embryo they induced the formation of cells like those from which they were given off. Galton tried the crucial experiment of transfusing blood from one breed of rabbits to another, and found that this had no effect on the purity of the offspring; and thus shattered for the time Darwin's theory of Pangenesis.

The second theory is that of Herbert Spencer, of "biological units," of definite form and relation, which by their polarity tend to complete the organism. I shall describe that development of it recently put forward with great skill and ingenuity by Wilhelm Haacke under the title of the "Gemmaria theory."[1] He holds that all living plasma is composed of minute units, the "gemmæ," grouped together in aggregates, the "gemmaria," both being of definite form and size, in virtue of which they tend to assume certain relations of equilibrium in the cells and in the whole organism. Owing to this being a labile equilibrium, any disturbance due to an altered condition of the environment will alter the "set" of the gemmaria and change the conditions of their equilibrium. It is as the result of their relation to the organism at large that the gemmaria of the reproductive cells R of an organism A are compelled to reproduce the likeness of A; consequently when the continuance of altered surroundings alters A to A′, the gemmaria of the reproductive cells will get a "set" changing them to R′, which will reproduce the altered organism A′. Now, as a *formal* hypothesis,

[1] See "Gestaltung und Vererbung," Leipzig, 1893, and "Schöpfung der Tierwelt." Both these works are written in a German style of exceptional charm, ease and vivacity.

this serves to give a very pretty provisional explanation of many phenomena of organic life; but we have no sufficient microscopic evidence in its favour, and, to me at least, much that speaks against it. We know too little of the physical relations of cell-life to be able to accept, even provisionally, a theory based mainly on geometrical and mechanical conceptions.

The most satisfactory explanation, perhaps, is that put forward by Hering and Samuel Butler,[1] the latter of whom has written with singular freshness and an ingenuity which compensates for the author's avowed lack of biological knowledge. This theory has indeed a tentative character, and lacks symmetrical completeness, but is the more welcome as not aiming at the impossible. A whole series of phenomena in organic beings are correlated under the term of *memory*, *conscious* and *unconscious*, *patent* and *latent*. Our memory is conscious, when we say a lesson or remember a birthday; unconscious, when we let our fingers play of themselves a piece of music of which we could not write down a note; patent, when we remember to call at a friend's house; latent, during the interval while the servant is waiting at the open door, until the sight of the familiar stick in the hall recalls the owner's name which had

[1] "On Memory as a Universal Function of Organised Matter" (Vienna, 1870, translated by S. Butler in "Unconscious Memory," p. 97 f.); S. Butler, "Life and Habit," 1878.

suddenly evaded our consciousness. Of the order of *unconscious memory*, *latent* till the arrival of the appropriate stimulus, is all the co-operative growth and work of the organism, including its development from the reproductive cells. Concerning the *modus operandi* we know nothing ; the phenomenon may be due, as Hering suggests, to molecular vibrations, which must be at least as distinct from ordinary physical disturbances as Röntgen's rays are from ordinary light, or it may be correlated, as we ourselves are inclined to think, with complex chemical changes in an intricate but orderly succession.[1] For the present at least the problem of heredity can only be elucidated by the light of mental, not material processes.

[1] This view is essentially the same as that developed by Delage in his "Théorie des Causes Actuelles" ("l'Hérédité," p. 7), and by J. T. Cunningham in his "Hormone Theory of Heredity" (see Chapter IX, p. 264).

CHAPTER III[1]

THE RELATION OF BROOD-FORMATION TO ORDINARY CELL-DIVISION

The general tendency of cells is to grow to a certain size, and then divide into two, either of which repeats the same story. The function of cell-division appears to be to maintain within sufficiently narrow limits the ratio of surface to bulk, for by its surface the cell comes into contact with its environment for supplies of matter and of energy, and for the discarding of waste. Now, this explanation put forward by Herbert Spencer and by Rudolf Leuckart needs a little examination. If a body of no matter what form increases in bulk while maintaining that form, as we have stated its relative surface is reduced. Take the most simple case, illustrated in Fig. 20. A cube a centimetre long has, we all know, the bulk of a cubic centimetre; and since its six sides are each a centimetre square, its surface must measure six

[1] Written anew from a paper read at the British Association (Dover), 1900, and printed as part of "Some Problems of Reproduction" II., in the *Quarterly Journal of Microscopical Science*, vol. 47, 1904.

square centimetres (Fig 20, A). Take now a cube two centimetres (Fig. 20, B) across: its bulk is eight cubic centimetres, and, since each face measures four square centimetres, its total surface is twenty-four square inches, or only three square centimetres of surface for each cubic centimetre of bulk, or only half the original ratio. We may say, that for every doubling of bulk the relation of surface to bulk is reduced in round numbers to four-fifths of what it

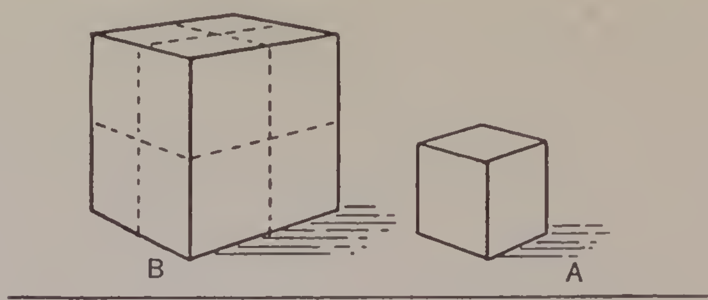

Fig. 20.—Showing necessary reduction of the ratio of surface to bulk by increase of dimensions.

was. Thus when there is a regular rhythm of cell-division, the daughter-cells, if after formation they revert to the form of the mother-cell, and divide at double their early bulk, have by then had their surface area diminished by about one-fifth, while fission restores it. This law applies absolutely to all bodies of constant form. Every architect has to face the problems of lighting and ventilation that come into view with the rising importance of the tasks confided to him. We have then here a *final cause* explanatory of the limiting of the size to which beings of determinate form and structure can attain.

But we have seen in our previous chapters that what we may call the Spencerian rhythm of alternating growth and binary fission is often departed from in favour of another. Here the cell grows to many times its original size, and then divides into two new cells; these divide again and again to form a brood of cells, in the processes known by the various names of "multiple cell-fission," "brood-division," "sporogony," "sporulation," "schizogony" and "segmentation," some of which we have already described; and the importance of this is the greater since we have recognised that pairing cells are in their origin brood-cells. We have to seek, then, the relation between the two modes of cellular reproduction: how is it that in these reproductive "cells" growth proceeds until they pass into rest (including the enormous "egg" of the bird); and that when once they start from rest and begin to divide, they go on doing so till a brood of small cells is produced, numerous in proportion to the bloated dimensions of the original brood-mother?

Recent researches on the utilisation of reserves in plants had shown that in every case examined a digestive ferment or "enzyme" was present, which, under fitting circumstances, could effect *in vitro*—as we term laboratory conditions—the same digestive process which the living organism performs. Thus, the green cell under the influence of light accumulates during the day reserves of starch, which is removed at night to where it is wanted ; well, from these parts a *diastatic* ferment can be extracted which will effect the same transformation in the test-tube. From germinating seeds can be extracted ferments which like those of the pancreas will transform proteids (white of egg, etc.), into peptones, and these further into amides, such as we find passing from the seed into the growing parts of seedlings. Again, Krukenberg, Le Dantec, Miss Greenwood, and A. Dixon and myself have isolated similar peptic ferments from Protists, where the food is taken into the cell-protoplasm and there digested. Moreover, we know that when tubers, bulbs, and other resting parts of plants start into growth, the process is accompanied by the presence of enzymes that enable their stores to be directly utilised for the growth of their cells and tissues.

It seemed, then, probable on the one hand that the enormous growth of reproductive cells might be due to the absence of any possibility of their utilisation of their own reserves, and on the other hand that this utilisation could only occur when the cell started to produce digestive ferments within its body. Investigations on the segmenting eggs of the Frog[1] and of the Hen amply

[1] First published in *British Association Report,* 1900.

confirmed this conjecture; and all the evidence goes to show that in the animal, as in the Plant, a cell can only utilise its internal reserves for the growth of its living substance secondarily and *mediately*, by the internal production of a ferment that dissolves them and makes them available.

The term "metabolism" is used by physiologists to designate the chemical changes that occur within the organism, and in the eighties Gaskell introduced the distinction between "*anabolism*" and "*catabolism*." "*Anabolism*" is what the chemist terms an *endothermic* process, in which energy is made latent, and usually complex substances are built up of simple ones; while "*catabolism*" is "*exothermic*": energy is liberated, usually in the form of heat, and complex substances are broken down into more simple ones, sometimes by mere splitting up of the molecule, sometimes by splitting accompanied by the taking up of water (hydrolysis) or by taking up oxygen (combustion). This distinction of Gaskell's is doubtless of capital importance, and has played a great part in biological theory. But admirable as it is from the point of view of energetics in the eyes of the physicist and the chemist, it overlooks one additional distinction of at least equal import to the biologist. A cell receiving available matter for anabolism may dispose of it in one of two ways, both falling under the rubric of "anabolism," yet sharply contrasting with one another.

1. The cell may *grow by increase of living substance* which we may term "*anatrophism*"; or,

2. The nutritive matters may be built up into reserves, *in* the protoplasm but not *of* it; this process we may term "*anasorism*" or heaping-up. Anatrophism, plasmic anabolism or *growth*—true *assimilation* as we may call it—increases the total amount of living matter with all its activities and needs: anasorism or *accumulation* means the mere *enlargement* of the cell by the heaping up of products which are inert until an internal ferment be formed to dissolve them again—which is of course a catabolic process.

A cell during a purely *anasoric* period—a period of accumulation—is gorged with this inert matter, but its need for increased surface need not, and as a matter of fact does not, increase with its bulk, like a cell whose living protoplasm has enlarged by assimilation; and so it does not divide, even though Spencer's limit be seemingly long past: the formation of internal ferments to utilise the stores and so arrest their accumulation does not occur. A time comes when the cell, from its own gluttony, is too obese for even this activity—"it has bitten off more than it can chew"—and it "goes to rest." If now, owing to changed circumstances,[1] germination sets in,

[1] The change in circumstances may vary in many ways; and this statement applies equally to groups of gorged cells that have gone to rest, such as tubers, seeds, and gemmules. Mere lapse of time, desiccation followed by wetting, a certain minimum of temperature, and, as we shall see, various other physical and chemical stimuli may be efficient (see p. 124 f.).

it forms the necessary ferment, the cytoplasm starts growing at the expense of the digested stores; the need for extended surface forthwith arises and determines cell-division, which continues to go on until the stores are exhausted, and the cells must live "on their own," either in co-operation, as in Higher Organisms, or individually, as in the Protists. On this view we can bring into correlation Spencerian fission and brood-division. If we wish to accumulate a store of Greek words we may term the correlated catabolism of the reserves and anabolism of the living tissue "*metatrophism.*" But we see that in its way the segmenting egg is as strongly anabolic as the growing ovarian egg. To deny its anabolic character because of the concurrent digestion of the reserve granules would be as rational as to term the infant mainly catabolic because of its obvious digestion of its mother's milk or the pap supplied by its nurse; although the breaking down here is greater than the building up and growth. The growing calf and the stalled ox are both anabolic, but to very different purpose. The thesis of the brilliant authors of "The Evolution of Sex"[1] requires new treatment in face of this distinction, which strangely escaped their notice.

[1] Professors Patrick Geddes and J. Arthur Thomson. They regard the female as essentially anabolic and the male as catabolic. The term *anasoric* aptly characterises the behaviour of the oogamete; and the sperm within the egg is *metatrophic*. How far these characters are reflected on the Protistic cell-cycles, or Metazoic individuals, varies in different cases.

Not the accumulation of reserves alone may condition the enlargement of the cell to more than double its original bulk. In our discussion of this limit, we considered that the reduction of the surface-area is associated with the retention of the original form and character. But this is not always the case: in *Ulothrix* (Fig. 1, p. 4), as in many Lower Plants, the zoospore is approximately spherical with but small and few vacuoles, or cavities containing liquid. When they develop a cell wall, their character is changed by that fact; the mere loss of motility probably renders a lessened surface-area admissible. But furthermore, a large central cavity or vacuole develops, around which the protoplasm is stretched in a thin layer, allowing of a still greater enlargement with the retention of sufficient surface. Thus the new structure in the cells of the *Ulothrix* filament demands a new limit of growth. But when the protoplasm rounds off again the demand for increased surface is greater, and brood-division sets in. The larger the units, the more sluggish they are. Again in Radiolarians and Foraminifers the cytoplasm is produced into enormous networks, or fine radiate expansions, which increase the surface-area indefinitely: binary fission is rare, brood-formation common in these groups.

We pass to yet another mode in which a cell is able to grow to enormous dimensions without suffering from disproportionate bulk. It would seem as if one condition for effective working is the sufficient proximity of the nucleus to the working cytoplasm; for we find that where the activities of the cell are confined to one end, the nucleus approaches that end.

In certain organisms, not only is the cytoplasm extended by a great vacuole so as to become thin and expanded, but, in response it would seem to the needs of life, the nucleus undergoes repeated division; the nuclei separate and become scattered at fairly even intervals, so that no part of the cytoplasm is unduly remote from a nucleus. This is the case in many Fungi (Fig. 22), and in one group of Green Algæ, the Siphoneæ or Phycophyceæ. In these cases the multi-nuclear mass is called a "cœnocyte," or, perhaps better, an "apocyte": ultimately it is resolved into individual cells, by the cytoplasm concentrating about the individual nuclei. Sometimes a portion of the cytoplasm escapes this rearrangement, and then is doomed to death: such a residue of cytoplasm is called "epiplasm,"[1] and when it is left over from the brood-cells formed by "resolution of an apocyte," it has received the special name of "cytophore" as with the Malaria sperm. An excentric cytophore occurs with the sperms of many Metazoa, and the segmenting zygote of *Noctiluca* (the little pinhead-like Flagellate that is the main source of the phosphorescence of our British seas). It corre-

[1] The epiplasm in Ascomycetes (Truffle, Morel etc.), is peripheral and surrounds the brood-cells (resting spores), on which it secretes an additional outer coat.

sponds in a measure with the mass of food-yolk at first left uninvaded by segmentation in large eggs, such as those of Birds, Reptiles, and Sharks, where

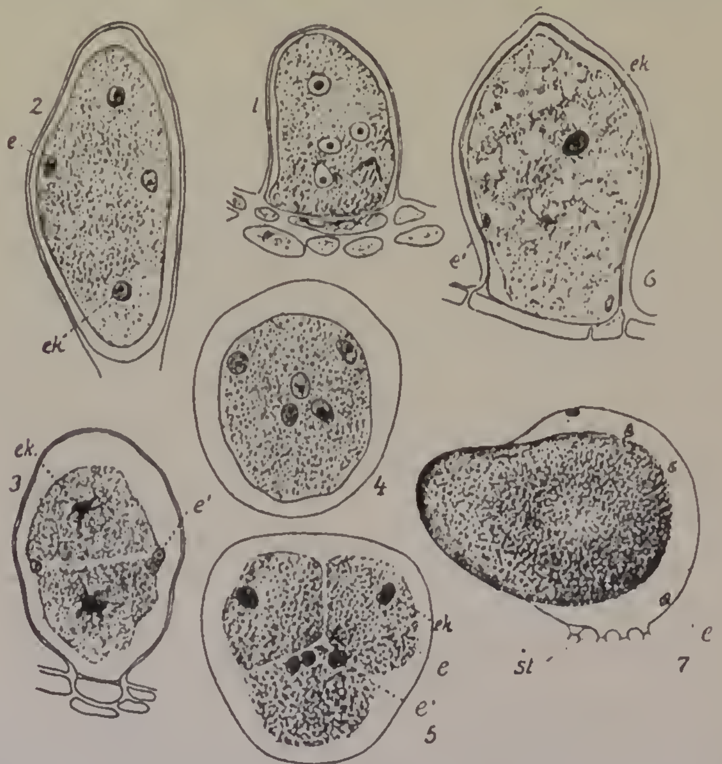

FIG. 21.—Delayed brood-formation (bradyschist division) in the Wracks (after Oltmanns).

1–3, *Pelvetia*: 1, the nucleus has divided twice to form four nuclei; 2, another division has produced eight nuclei, of which four are seen; 3, by simultaneous cleavage the apocyte is resolved into eight cells, of which only two are large enough to be functional. 4. *Ascophyllum*: eight-nucleate stage; 5, resolution into cells, four functional, four reduced. 6, 7, *Himanthalia*; 6, eight-nucleate stage; 7, resolution into one functional and seven reduced cells; *ek*, nucleus of functional cell; *e'*, reduced cell.

it is excentric, or of Arthropods (Insects and Crustacea, etc.), where it is central.

Thus we may classify the modes of brood-formation as follows:

1. The simplest and most *direct* is where cell-division alternates regularly with nuclear division, so

Fig. 22.—False brood-formation in the Water-moulds (Saprolegnieæ)

1, Structure of the young apocytial filament, with multinucleate protoplasm around a central space (vacuole). 2, Surface view. 3–4, Optical sections of aggregation of cytoplasm around individual nuclei. 5, Swelling up of cytoplasm by absorption of water. 6–7, Excretion of water into vacuoles, and separation first into irregular blocks and finally into single uni-nucleate cells, the zoospores; 9, The zoospores finally rounding off.

that no apocytial stage occurs, as we find in the segmenting egg of the Frog and many other animals. We term this "*euthyschist.*"

2. The second type is the *delayed* or "*bradyschist,*" where nuclear divisions progress consecutively for a time, uninterrupted by divisions of the cytoplasm (Fig. 21). Here the brood mother-cell passes for a time into the condition of an *apocyte*, and is finally *resolved* into single cells by the concentration of the cytoplasm around the several nuclei; this process may be immediate, each nucleus acquiring its cytoplasmic investment simultaneously, or indirect, by segregation into blocks, which ultimately divide up into single cells (Fig. 22). A noteworthy case of this is where the brood-cells have a particular configuration, so that they grow out from the surface of the brood mother-cell, as in spermatogenesis and in the zoospores of the Coccidiaceæ, etc.: this has been termed "*schizogony*" (Fig. 9, p. 39).

3. "False brood-formation" applies to the case where the organism is in its ordinary state multinuclear (apocytial), as in the case of the sporange of Phycomycetes, and without any special stage of nuclear divisions the cytoplasm divides into uninucleate cells (Fig 22).

These modes, I think, practically exhaust the processes by which single reproductive cells are formed, whether spores or gametes, and by which the early stages of colonial organisms arise from the reproductive cells. In cases where the reproductive cell contains an excess of nutriment, there may be a combination of the *direct* type, giving single cells, and the *delayed* type, giving rise to blocks of cells with an apocytial condition of the yolk below the blastoderm, as in the bird's egg, etc.

CHAPTER IV

THE "NEW FORCE" MITOKINETISM[1]

I

Every discovery of crucial importance made at the present day in the laboratories of the physicist and chemist is certain to be expounded without delay to the general public in accounts of varying value, whose accuracy is frequently in inverse relation to their picturesqueness; and its recognition soon passes into the mental assets of all well-informed people. But such rapid diffusion is rare with biological matters, save in so far as they may be of direct social or medical import. Thus it befalls that the most important find in the minute processes of the living organism made during the last forty years

[1] It is necessary to explain that by "force" I mean what the layman means when he speaks of electricity, magnetism, and steam power as "forces," or what is implied in the current phrase "the *forces* of nature." I am perfectly aware of the limitations now made by physicists in the use of the term, to designate "an acceleration multiplied by a mass"; when they can supply any other suitable term, understanded of the people, I will gladly adopt it. As Lodge writes: "Until a term is accurately defined, *and even afterwards for some purposes,* it is permissible to use a word of large significance in more than one sense" ("Life and Matter," note on the word "Life"). Of course, when such licence is taken, the wide sense in which the term is used should be set forth explicitly at the outset, as I set it forth here.

has hitherto escaped general notice. By this time our knowledge of the processes in the dividing cell has grown enormously through the co-operation of numerous workers at home and abroad; and we may confidently state that these processes display the working of a new type of force analogous to statical electricity, but distinct from it, as from all known forces outside the organism.

It seems, therefore, high time that some attempt were made to introduce this discovery to what the Germans call "the cultured laity."

II

In the seventies biologists were wont to speak of protoplasm—"the Physical Basis of Life," as Huxley termed it in his celebrated essay—as a "structureless jelly," though *dough* would have been the apter word—and even to speak of it as a unitary chemical substance; and this belief still survives among many who look on themselves as well-informed. Yet within the first half of that very decade improved microscopes and improved technic were to show how really complex is the structure of the cell, the living unit of protoplasm. Even in the forties the cell was known to consist of two parts: the outer layer, or "cell body," which obviously discharged most of the duties of ordinary life; and the "nucleus," or inner kernel, which appeared to have some direct connection with the processes of reproduction; and "protoplasm" was distinguishable into what we nowadays call the "cytoplasm" and the "nucleoplasm." When a cell divides into two, it was found that as an antecedent to the actual division there had been a replacement of the old nucleus by two new ones, the "daughter-nuclei," one for each daughter-cell. In some cases the nucleus does divide by constriction, narrowing like a dumb-bell, till severance takes place through the waist. But in other cases—we may say, the majority—the old nucleus becomes obscure in the living cell before the two new ones appear; and thus the intermediate processes escaped recognition until improved methods of microscopic study were devised. In the use of high magnification it is necessary to examine very thin transparent layers; and to obtain these "sections" the tissues or cells must be infiltrated with some coherent substance like paraffin-wax or collodion. Again, structure is revealed in the living object by slight differences of refractivity; whereas death renders the substance so opaque that it is necessary to "clear" the sections by saturation with a highly refractive medium like Canada-balsam, in which, however, the original differences of refractivity are more or less effaced. But, since different structural elements fortunately take up dye-stuffs in different ways, we replace the original differences of refractivity by differential "staining." Lastly, we find that in spontaneous or slow death the tissue undergoes post-mortem changes that vary, and alter the structure in diverse ways; but by appropriate coagulants we "fix" the tissues as we kill them, so that only *known* and limited changes occur. Suitable planing machines (microtomes) have been devised that enable us to obtain from a specimen a complete series of sections of equal thinness, and

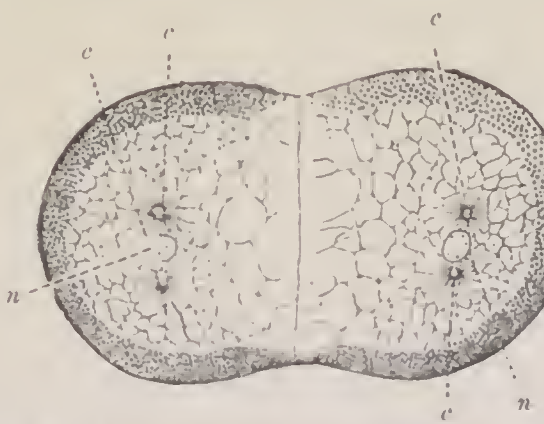

FIG. 23.—Early figure of mitokinetic field, the initial stages of next division of the two-celled stage of the segmenting egg of Geryonia.

c c c c, Centrosomes; n, Remains of nucleus.

that, if we wish, of not much over $\frac{1}{25000}$ of an inch, the thousandth of a millimetre.[1] By all these means combined we are enabled to examine organic structure with a precision far above that which is applicable to the living cell. Since advances in the optical powers of the microscope accompanied progress in technic, a new horizon was opened to the biologist in the seventies and the following decade.

[1] The "mikron" of the microscopist, designated by the Greek letter μ.

Passing over what the mathematicians call "first approximations," Hermann Fol, of Geneva, was the first to see clearly and describe clearly the intermediate stages between the disappearance of the old nucleus and the appearance of the two new ones which had hitherto eluded the search of the histologist. In 1873, in the course of his work on the development of the Geryonidæ (a group of Jelly-fish), he wrote :

"On either side of these remains of the nucleus are seen aggregates of plasma, closely associated granules which form two starlike figures. The rays of these stars are formed of the granules, serried into straight files. Several of these files stretch in bows from the one star or attraction-centre to the other. The whole picture is extremely clear, and has a vivid resemblance to the way in which iron-dust strewn between the two poles of a magnet arranges itself."

We might almost say that the whole history of cytology has been founded on this discovery. Before Fol's publication, all that was known of the changes of nucleus and cytoplasm was that the nueleus beeame obseured ; that a peculiar dumbbell-like strueture extended along the axis of the cell ; that two new nuclei appeared ; and that the cell divided aeross the axis, joining them. Within a dozen years most of the faets that we are about to examine had been made out in their essentials, and combined into an intelligible scheme, notably by Strasburger, Flemming, and Guignard.

III

During the life of the cell and its accomplishment of the task thereof, the nucleus in its functional condition—too often miscalled the "resting-state"—has the structure shown in Figs. 24, 25; within the

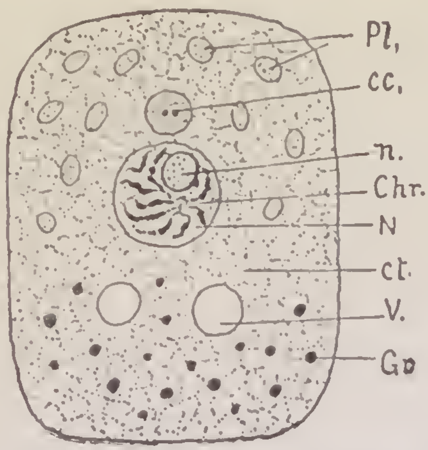

FIG. 24.—Diagram of "resting-cell."

ct, Cytoplasm. *cc*, Centrosome with centrioles. *N*, Nucleus; containing *n*, nucleole and *Chr.*, chromatic network. *Gr*, Granules. *Pl*, Plastids. *V*, vacuoles.

nuclear wall is a thin coating of protoplasm, "nucleoplasm" or "linin," continuous with an internal network of the same substance; it appears to be in constant motion. This plasm or linin stains poorly, if at all, with basic stains, and is hence also termed "achromatin"; but embedded in it are deeply stained granules of various sizes, termed "chromatin-granules." Besides these we see one or more larger droplets of stainable material, lying free in the nuclear sap, or attached to a thread of linin: these are the "nucleoles," which appear to be mere stores of unorganised chromatic matter to be dissolved and redistributed where needed. On the approach of cell-division, which we may regard as the *maturity* or even the *old age* of the cell, the chromatin increases enormously in amount (Fig. 25, *A*). The chromatin-granules grow in size and in number; they become approximately uniform and evenly distributed along the threads of linin, which they may distend at the points where they are seated. The linin now forsakes its irregular distribution, and forms often a single thread, sometimes re-entrant on itself, and soon breaks up into short lengths, the "*chromosomes*": or the network may resolve itself into chromosomes directly, without passing into the single-thread stage[1] (Fig. 25, *C*, *D*).

The physical conditions that determine this change escape us completely, and we can only compare it to the transverse segmentation of other elongated living structures. The next change is the duplication of the chromatin granules into pairs, separated by the width of the chromosome (Fig. 25, *F*).[2] This is possibly due to elongation at right angles to the filament, followed by transverse division, under conditions like

[1] The chromosome arrangement of the nuclear network is sometimes apparent in the "resting" nucleus.

[2] A different explanation of the early stages of the splitting has lately been given by Farmer, Digby, and Fraser.

the similar fission of bacteria—or, more strictly speaking, "micrococci." The achromatin of the filaments seems to concentrate around the granules, so that

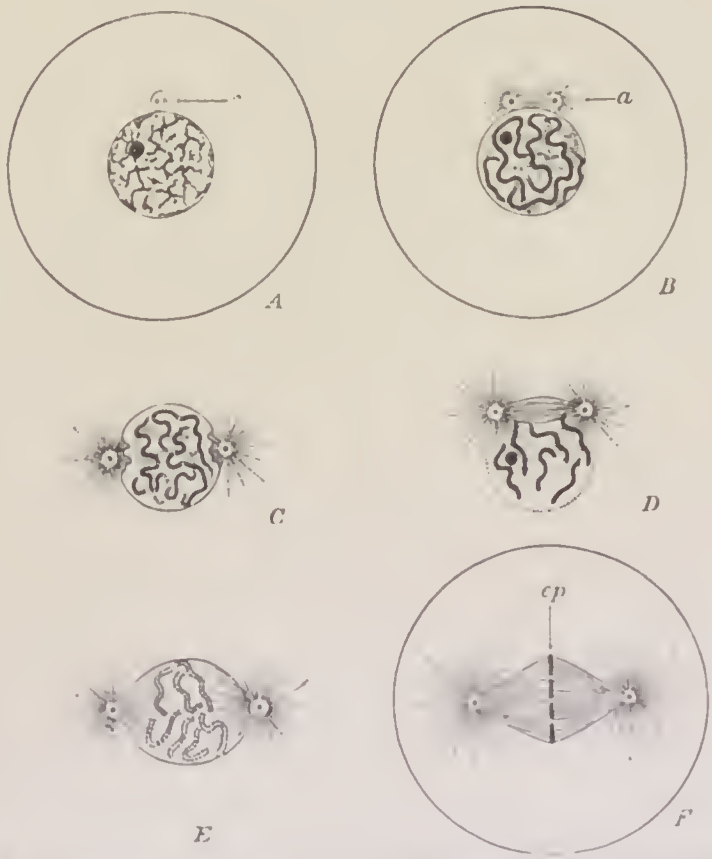

FIG. 25.—Diagrammatic history of first stages of mitotic cell-division in Echinoderm embryo (after Wilson).

A, Resting-cell; *c*, centrosome with two nuclei. *B*, Early prophase, the chromosomes apparently forming a single skein; the centrosome has divided, and a small spindle has formed in connection with the two daughter-centrosomes. *C*, Divergence of centrosomes. *D*, *E*, Late prophases; the nuclear wall giving way on one side in *D*, on both in *E*; the chromosomes are split. *F*, Early "metaphase" or equatorial-plate (*ep*) stage. For completion of process see Fig. 26.

the thread becomes moniliform, or necklace-shaped, except for the representation of each bead by a pair, and for the fact that the beads are embedded in the substance of the thread instead of being strung upon it. Owing to this concentration, the section of the thread through a pair of granules has the form of a horizontal figure of ∞. We may fairly ascribe this partial splitting of the chromosome to the "like"[1] attractions exerted by each chromatin-granule on the surrounding linin, and the persistence of the continuous longitudinal strip to the viscidity of the linin just balancing the splitting force. The granules have now apparently fulfilled their purpose; they cease to be visible, and the whole chromosome is stainable, as if the staining substance of the granules had dissolved in and saturated the linin substance of the chromosome. The alternation of growth and resolution of the chromatin-granules is surely a strong argument against attributing to them such living personalities as Herbert Spencer's "physiological units" or Weismann's "ids"[2] if we are to attach any importance to the evidence of our eyes, aided by the best available methods; and this is the only evidence we have on the matter. And if the chromosomes as a whole are to be considered as aggregates of "units," it is the linin stretches between successive granules that would represent such units, and the chromatin-granules the boundaries between them.

Each thread is now, as we have seen, partially split lengthwise into two "*daughter-chromosomes.*" We

[1] Comparable to "like" electric or magnetic poles, as will be explained immediately (p. 113).

[2] As postulated in Weismann's theories of heredity (see p. 17).

may well admit the probability that the sister-threads are in their successive zones counterparts one of the other; and possibly that each successive zone has its own peculiar character to be transmitted to the daughter-nucleus. If this be the case, and it be of primary importance that every portion of the nucleoplasm should be transmitted in absolutely equivalent parts to both the daughter-cells, we have the function of the chromatin-granules set forth in broad daylight: in the terms of the Schoolmen, their "final cause" is to effect this "*partitive*" division. It is hard to see what other means could effect so difficult a physical problem as the longitudinal splitting of a viscid thread. For us, then, the *linin*, not the *chromatin*, is the essential constituent of the chromosomes; and this view, put forward by us in 1898 (see Chapter V, p. 138), has since been advocated independently by one of the greatest of our living cytologists, Theodor Boveri.[1]

The completion of the splitting, and the repartition of the sister-halves of each chromosome between the two daughter-cells, is accomplished under the dynamic agency of the "cell field," and is comparable to the effects of electrostatic or magnetic induction.

The structural changes in the cytoplasm that determine the cell field are more or less indepen-

[1] "Ergebnisse über der Konstitution der chromatischen Substanz des Zellkerns," 1904.

dent of those that take place in the nucleus, and vary in different cases. The following is the case in Animals, with but slight differences in detail. In contact with the nuclear wall is a sphere of cytoplasm, the centrosome, with a central granule, the centriole (Fig 25, *A*). The centriole divides by constriction, and the two new centrioles separate. Then, while the outer part of the old centrosome undergoes changes that merge it into the surrounding cytoplasm, around each of the two new centrioles there forms a new centrosome that enlarges by growth, and is soon seen to be formed of regularly honeycombed plasm—"alveolate" is the technical word for it (see Figs. 29, 31, 36, pp. 115, 117, 158). The two new centrosomes appear to be united from the very first by fine plasmic threads forming a spindle (Fig 25, *B*); while from each radiate the "astral" threads that branch into the cytoplasm on all sides but that of the nucleus, tangential to which the young spindle lies (*C*, *D*). The spindle and asters grow both by the elongation of the existing threads and the intercalation of new ones: notably the spindle grows by the incurving of the more internal astral threads, which meet those from the other aster, and fuse with them along the middle line or equator of the spindle. As this growth of the spindle goes on, the nucleus passes, as it were, into the spindle at its equator, and some of the spindle threads abut on the nuclear wall, and appear to start its liquefaction (Fig. 25, *C*, *D*)—a process that, once begun, continues until the wall has disappeared, when the chromosomes come to lie free in the cytoplasm, as modified by the formation of the

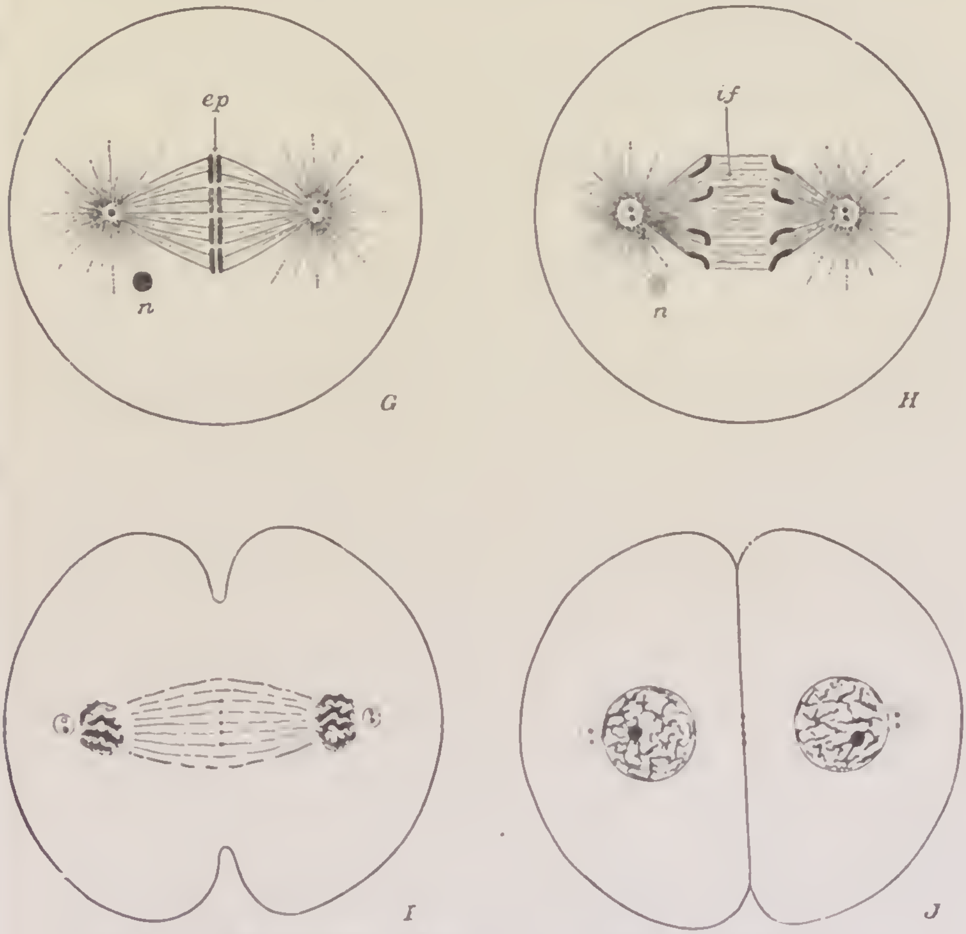

FIG. 26.—Diagrammatic history of final phases of cell-division (after Wilson).

G, Late metaphase or equatorial plate (*ep*); *n*, nucleole; the daughter-chromosomes are separating. *H*, Anaphase, the daughter-chromosomes moving up to the centrosomes, and the centrioles divided. *I*, Telophase, the chromosomes coalescing to form the daughter-nuclei, and the cytoplasm constricted. *J*, Completion of the process.

spindle and asters (Fig. 25, *E*). Thus the structure of the whole central region of the cell is now one of threads: the spindle and asters delicate and but slightly stainable (achromatin), and the chromosomes more massive, even passing into rods or large granules at times, but always flexible and plastic. This resolution into threads is aptly designated by the Greek word MITOSIS. The chromosomes now lie on, or rather across, the equator of the spindle, where under low powers they appear to form a dark plate, whence both the aggregation itself, as well as the particular stage, has been termed the "equatorial plate" (Fig. 25, *F*, 26, *G*). The present usage, however, is to reserve this term for the material aggregation of chromosomes, and to term the stage itself the "metaphase," or "metakinesis."

The separation (repulsion?) between the chromosomes and between their split halves now increases, and they start apart from one another. After lingering for some time at the equator, the half-chromosomes finally part company altogether, and glide away from one another to opposite poles of the spindle, where they lie huddled in a group just on the inner side of either centrosome. This stage of the "*discession* of the half-chromosomes" is called the "anaphase." Judging from the relative abundance of the different stages seen in a preparation where cell-divisions are frequent, we justly infer that the metaphase lasts a long time, and that the earlier stages of the anaphase are not so rapid as the later ones. Now, this is precisely what would happen if their motion expressed the action of a polarised centred force analogous to statical electricity—a "*Newtonian*" force whose intensity is inversely proportional to the square of the distance. The chromosomes of either group now round up against the centrosomes, swell up and become vacuolated, and finally coalesce to form a daughter-nucleus. This last stage is called the "telophase." If a prolonged period of individual cell-life is to follow, the nucleus becomes poor in chromatic substance; but if a new division is to follow close on the heels of the past one, the chromatin of either daughter-nucleus increases in amount, as we might expect. The outer part of the centrosome swells up and becomes confounded with the cytoplasm at large; but a central part remains with a centriole, which may early divide into two, as if for the preparation for a new division (Fig. 26, *H*). Cell-division, whether by constriction or by the appearance of a dividing-plane across the equator of the spindle, may follow immediately on the construction of the daughter-nuclei, or it may remain in abeyance so as to give rise to a multinuclear structure which is strictly speaking not a cell, and has received the name of "cœnocyte," or, more aptly, "apocyte," such as we find in Saprolegnieæ (Fig. 22, p. 89). Thus, though cell-division usually follows close upon nuclear division, the two processes are absolutely distinct. Such is the process in Metazoa, and in some Cryptogamic Plants. In Flowering Plants there are no obvious centrosomes, and the spindle is formed in a different way. The cytoplasm immediately around the nucleus becomes fibrillate, and the fibres group themselves into bundles, which ultimately lay themselves side by side, their free ends converging to two opposite points. In other respects the process of mitosis shows no marked differences.

We have seen that the chromosomes hang together in a group at the equator, diverging, it is true, as far as their stickiness or viscidity will allow them to, and the split halves, or daughter-chromosomes, also show an increased separation here. We may call this the "Mahomet's coffin position," for the chromosomes and their halves behave much like bars of magnetic iron would do if they lay in a very viscid medium midway between the opposite poles of an electromagnet. We may compare their action to those of such bars (Fig. 27, *a*), lettering the poles as + and – instead of N and S. For simplicity we have represented the split halves of a single chromosome parallel to one another on a single thread of the spindle. The least disturbance that tends to separate them will put them in a position (*b*) where the one is nearer the one pole, and the other to the opposite one, and they will glide apart, very slowly at first, but quickening up afterwards as they near opposite poles (*c*). This accounts for the relative frequency with which we observe the stage of metaphase as compared with anaphases. More rarely

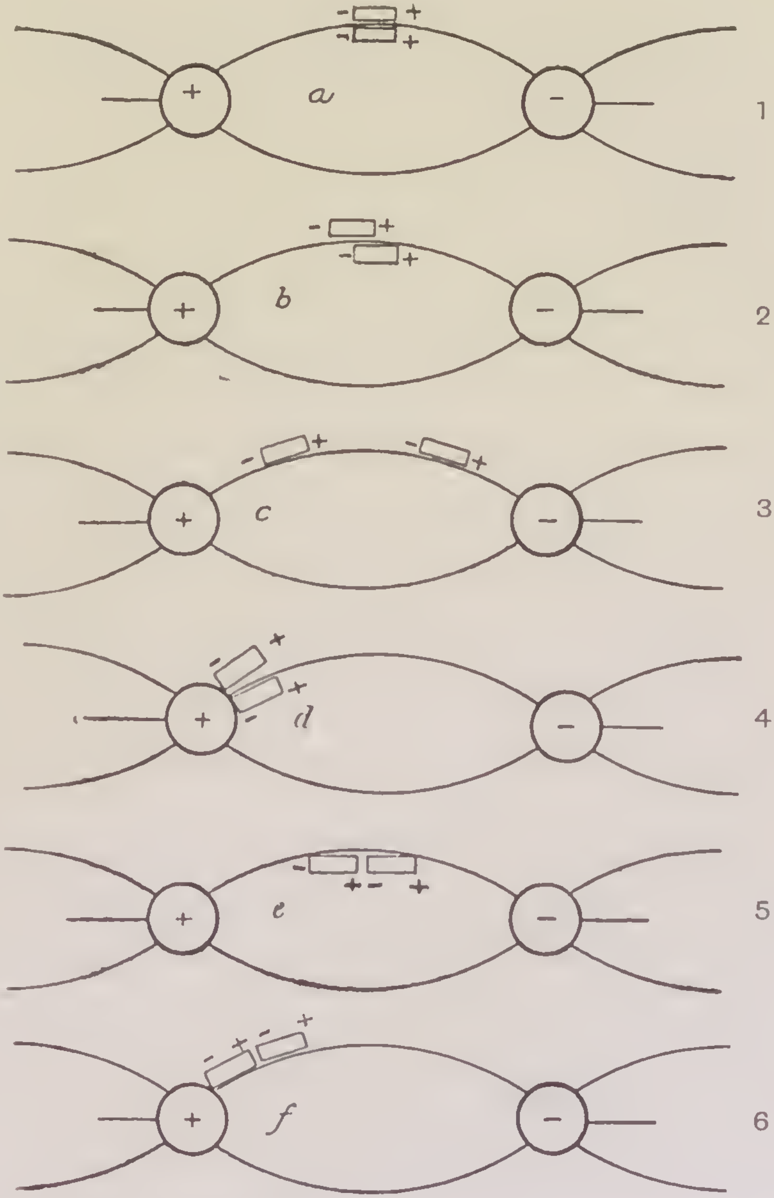

FIG. 27.—Diagrams to show passage of a pair of inductors (corresponding to chromosomes) in a bipolar field to the poles.

a. The "Mahomet's coffin position" (equatorial-plate metaphase. *b*, *c*, Transitions to anaphase. *d*, Abnormal anaphase of both to the same pole. *e*, *f*. Passage of both inductors to one pole—a rare occurrence in cell-division. The signs + — indicate the polarity or "charge" of the centres of the ends of the inductors. The fine lines represent the achromatin fibres of spindle and asters in a field with a "permeable" envelope, as in many cells.

the displacement eventuates in the two coming end to end, in file, so that they proceed to the one pole in that order (*e*, *f*), or both may shift towards the same pole, diverging as they do so (*d*).[1]

If, however, we imitate long thin chromosomes by flexible strings of soft iron beads, they would bend in their passage. If a string lay in a .∧. pointing outwards on the equatorial plate, either leg would curve as it moved away into a ·¬, with the straight leg pointing to the pole; and then the straight leg would bend back, and the curved loop straighten out so as to approach the pole as a ·<, or a ·⊂. (The full stop indicates the polar end of the disceding chromosome.) This change actually takes place where the chromosomes are long and slender, as in the vegetative tissues and endosperm of Liliaceæ.

We have now seen that the cytoplasm and the nucleoplasm divide in different ways: the former divides "directly," the latter "indirectly." We may compare the cell with a melon, the cytoplasm with its skin and flesh, and the nucleus with its stringy pulp and seeds in the central cavity. Cut the melon across the middle, or, better still, imagine it to be so constricted across the middle as to develop a waist, and divide into two, the one the stalk-half,

[1] I should say that I have found it so hard to regulate the physical conditions that my model rarely behaves satisfactorily, though all right in theory.

the other the eye-half; and we have a fair model of cell-division as far as it affects the cytoplasm. If, however, before this process is completed we imagine every string and every seed of the inner pulp to split, we shall have a model of the mode in which the nucleus is resolved into two: this type of division with its complete halving of every element we have termed a "partitive" division.

IV

We may now proceed to analyse the force expressed in the cell-figure, which Fol at the outset compared to the "magnetic spectrum," or figure formed by sprinkling magnetic dust over a surface above two opposite magnetic poles; but this is not the only physical analogy to the cell-figure. As shown by Faraday and Gallardo, we may obtain an electrostatic "spectrum" by immersing two opposite poles of an electric machine into a non-conducting liquid such as paraffin oil or turpentine, containing in suspension short fibres of silk, crystals of sulphate of quinine, or (as I have found) magnesium powder: the essential being that the suspended matter shall be of higher "permeability"[1] to electrostatic force than the liquid. Again, if we attach two skeins

[1] "Permeability" was a term introduced by Lord Kelvin; and, though now almost exclusively confined to magnetism, he used it to include the kindred phenomena of the specific inductive capacity of dielectrics, conductivity to heat, and even refractivity to light or radiant energy.

of light silk to the opposite terminals of an electric machine we shall find them diverging from one another, and arched so as to be concave to the "axis of figure," or line uniting the terminals: if they are long enough the inner threads from opposite poles will meet across the centre, so as to form a spindle. In these cases the threads or files of powder are constrained to arrange themselves along what Faraday termed the "lines of force": that is, the lines along which a particle more susceptible to the force than the medium would travel under the stress of the force.

It must be remembered that Faraday's lines of force are ideal, *geometrical lines*; and what is to be found in the text-books refers to their distribution in a *uniform medium.* The material particles used to demonstrate the distribution of these lines are selected on account of their superior "permeability" or "susceptibility" to the force over that of the medium; and it is obvious that their presence must in a measure alter the distribution of the lines by disturbing the homogeneity of the medium in which the field is formed. We find the same thing with rays of light, whose path we may render visible by introducing floating dust into the air they traverse, although by scattering some of the light the motes slightly alter its distribution. We call particles of the more susceptible material "inductive particles"; and bodies of larger size that are more susceptible than the medium "inductors." The files of particles that arrange themselves along the lines of force we may distinguish as material "chains of force." If, instead of being held in place by the friction of the surface of glass or paper, as in the common magnetic figures of the lecture-room, these chains are formed by segregation from suspension in a liquid, they are found to possess a certain coherence or toughness, and behave as flexible inductors. Fol's "files" constituting the spindle and astral rays, and the nuclear "remains" or "chromosomes," both fall, then, into the category of flexible inductors. We must remember, however, that, unlike the chains of filings formed by segregation, the spindle fibres are formed by growth from and between the centrosomes. So far as I know, the conditions of "chains of force" have received no attention from the physicist; and it is only *lines of force* that are discussed in the text-books available to the biologist. Hence, owing to a confusion of two distinct categories, much false reasoning has been promulgated on this subject—such as might arise in financial discussion, for instance, where it was implicitly assumed that the "pound sterling" of account and the gold sovereign were terms of identical meaning, and universally interchangeable.

Owing to this omission of the physicist the behaviour of "chains of force" can only be studied by actual observation. We cannot do this in the cell, where they are only accessible to our view in fixed and stained specimens, and their history is a matter of the combination of images of successive stages: our only resource is the use of physical models, and in these we may observe *their formation by segregation, but not by such growth as takes place in the living organism.* Undoubtedly, as we shall see, an electrostatic model would be the closest we could find; but for this it is necessary to use high voltages, which are difficult to regulate, and involve the constant risk of severe shocks to the observer, while the apparatus will not work in a saturated atmosphere, such as we frequently have in Cork. I have therefore utilised what may be termed a principal plane in the magnetic field, across the poles of two vertical electromagnets; and found that in almost every respect the cell-field in its axial section resembles this, the chief difference being that *every* axial section of the cell-field is of the same character, whereas in the magnetic field it is only the horizontal plane containing the poles and at right angles to the magnets that shows the arrangement in question. The cell-field is clearly the seat of a stress-force, whose action with a single pole, were the medium uniform, would decrease inversely as the square of the distance from the centre, just like gravity. But the cell-field reveals two centres of opposite character: what is *attraction to* the one is *repulsion from* the other—in other words, it is "heteropolar." Thus the cell-force is a "DUAL" force, like magnetism or statical electricity. We may compare the distribution of lines of force in a uniform medium under two centres of opposite character to that of the flow of heat through a conductor containing a source of heat and a refrigerator, or, using Clerk-Maxwell's simile which has gained universal acceptance, to the stream-lines in a liquid between an upwelling "source" and a swallow-hole or "sink." In all cases of the kind the lines of force or of flow between "opposite" or "unlike" centres have the spindle distribution (Fig. 28A); but if there be two "like" centres the lines constitute what has been termed the "crossed figure" or "antispindle" (Fig. 28B). This is a geometrical truth which there is no eluding, though many biologists have failed to appreciate it.

We may best realise the significance of figures by imagining a float or boat to be cast up through the source and carried passively away from it along a stream-line. If the source be single and isolated, the boat will travel out in a radial straight line. If there be a "sink" near, say towards its left hand, it will experience a suck towards that side, and its course will be deflected, and concave to the axis between source and sink. If, on the other hand, there be a second source within reach, the flow from that will push the boat away, and its course will become convex to the axis uniting source and source. It is an easy matter to see that the flow lines between two sinks will have the same distribution as between two sources.

Of the dual forces that are known, every one has,

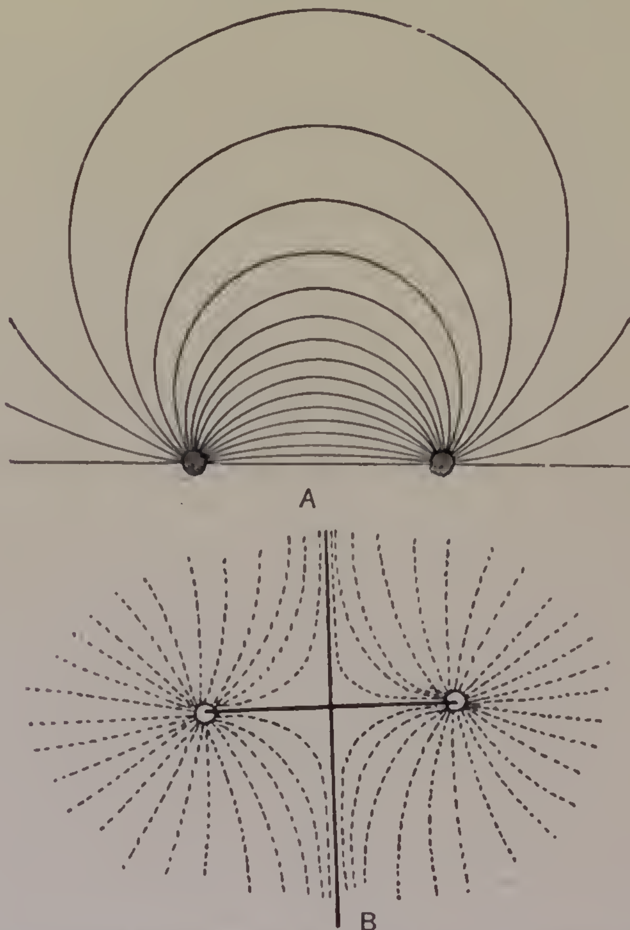

Fig. 28, A.—Spindle-field between two centres of opposite sign, upper half of axial section. The lines represent "unit lines."

Fig. 28, B.—Diagram of the crossed field, or antispindle, showing the directions of lines of force between two like poles. The lines shown are not "unit lines."

I think, been invoked in turn. *Magnetism* is out of the question, for the centrosomes behave like *isolated* poles, and every particle of magnetic substance, however small or large, has at least *two* opposite poles.

Were the elongated centrosome which sometimes occurs (Fig. 29)[1] the seat of magnetism, there would be a small spindle extending from *a* to *b*, and enveloping each of them, the chains incurving to either end.

Osmotic currents or stream-lines have also been suggested. If into a solution of a crystalline substance we introduce a tiny crystal at one point and

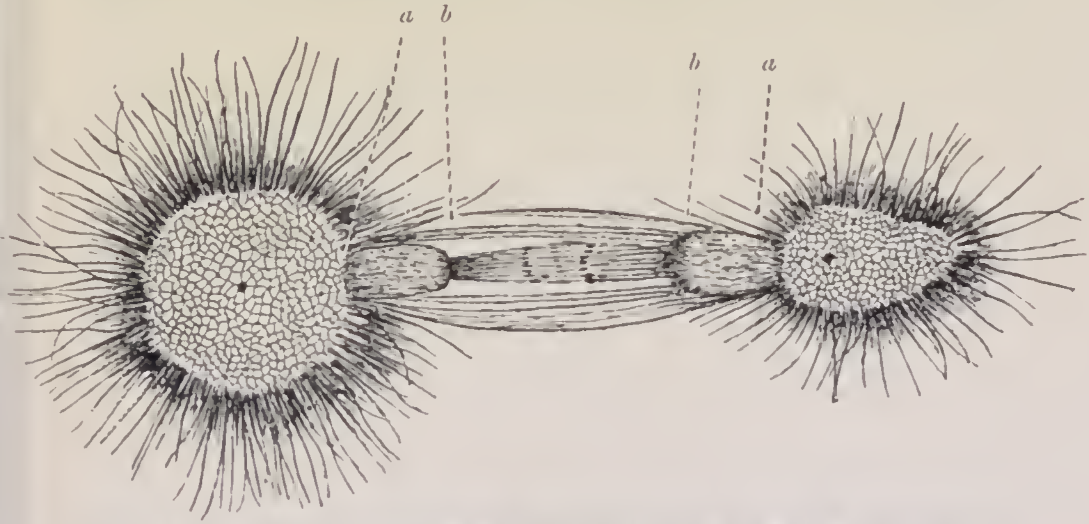

FIG. 29.—Spindle in anaphase with "blobbed" centrosomes of the Pond-worm *Rhynchelmis* (after Véjdowský and Márzek).

a drop of the pure solvent at another, stream-lines pass from the pure drop towards the crystal forming a spindle figure, which suspended particles of any light insoluble powder will serve to delineate. If we take two drops of the pure solvent, or two particles of the crystalline substance dissolved, the stream-lines will have the distribution of the crossed figure (Fig. 28B). Now, it is admitted on all

[1] The centrosomes have yielded and been drawn out into blobs under the pull of the spindle against some force pulling them apart (see p. 118).

hands that the centrosomes are "like" in respect of osmosis, and therefore the cell figure is not due to this force, which demands "unlike poles" to form the spindle.

So far we have dealt with an osmotic field of *flow*, but another kind of field—a field of *tension*—may be produced by osmosis. If there be osmotic attraction in a system of spaces full of liquid, and

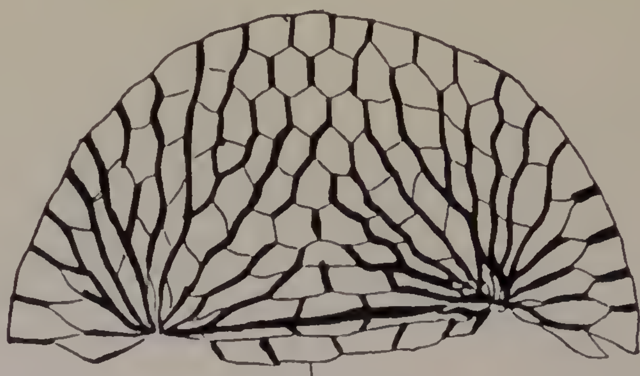

FIG. 30.—Half of Rhumbler's net, pulled in at two centres; the direction of the lines of force (tension) indicated by thickenings. This illustrates the meshes of an osmotic field of tension with two like centres of concentration in an alveolate structure; it will be noted that in the regions of greatest tension the short sides of the meshes are nearly obliterated (modified from Rhumbler).

bounded by extensible walls—what is called a foam structure, from its resemblance to the grouping of air-spaces in foam or froth—we find that, left to itself, the spaces are of hexagonal section, and very regular, as seen, indeed, in the centrosomes (Figs. 29, 31). But if the equilibrium of the field be disturbed by internal centres of greater or of lesser concentration, the lines of tension are indicated by the general trend of the longer sides of the hexagons.

This has been very prettily modelled by Ludvig Rhumbler: he stretches a hexagonal network of elastic threads over a hoop, and pulls down the network at two points through a circular disc lying below the hoop. The result is shown in Fig. 31, where the lines of force have been indicated by thickening the longer walls of the meshes. This

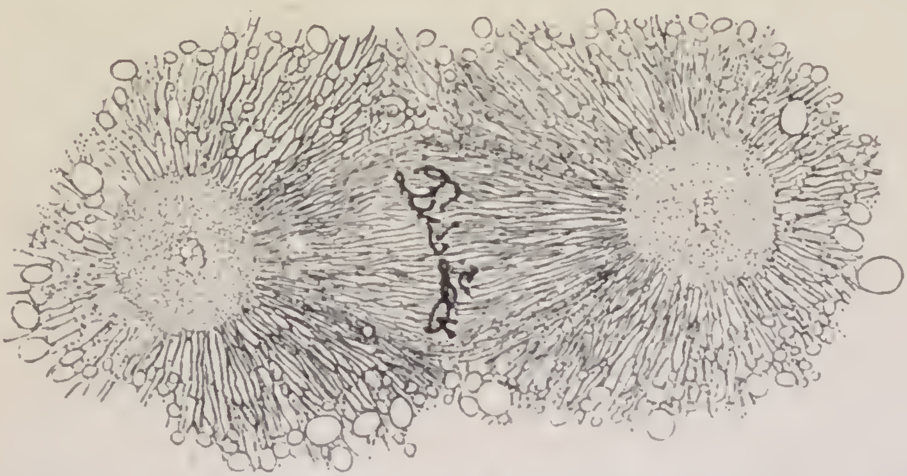

FIG. 31.—Oosperm of Axolotl showing spindle arrangement of plasmic threads along axis, and anti-spindle arrangement of the longer walls of the alveolar plasm further out, darkened on the left side to bring out the arrangement. The circular or oval areas represent yolk-granules (modified from Jenkinson).

represents a field of osmotic tension with two like centres of concentration. It is at once seen that the lines of tension are those of the crossed figure, not those of the spindle. From various facts we may infer that the cell field has in the centrosomes two like centres of osmosis. But these can only find visible expression where there is an alveolar structure of the cytoplasm to display them. This is sometimes the case with the cytoplasm, as, for instance, in the outer part of the oosperm of the Axolotl (Fig. 31, where we have followed the same course as in our modification of Rhumbler's figure of the elastic network, and represented the trend of the longer walls of the meshes by thickening the lines on the left-hand side of the figure). It is obvious that where the cytoplasmic structure is a foam it is the seat of a field of "like" forces, but where it is resolved into threads mitokinetism is lord and master; for the spindle figure between the unlike mitokinetic centres is typically shown. This contest between two distinct forces is visible elsewhere. In Fig. 29, where the centrosomes are blobbed, the spherical portion of the centrosomes, within which is osmotic equilibrium, and lying screened by the wall from mitokinetism, the meshes are hexagonal; whereas in the blobs the mechanical tension of the pull of the spindle, itself due to mitokinetism, has drawn out the meshes into oblongs. Here we have an obvious refutation of those theorists who, for simplicity's sake, would refer all the processes of the dividing cell to one force alone, solitary and supreme. To the effects of osmotic flow and tension we may attribute, at least in part, the **separation of the centrosomes,** another factor being the like electric charge.

A third force that has been invoked is *statical electricity*, and the discovery of Ralph R. Lillie that the chromosomes bear an electric charge was held to support this explanation. But it is clear that here again the centrosomes must have like charges, both opposite to the chromosomes; and that the electrostatic field would be the "crossed figure" (Fig. 28B), not the "cell-spindle," which latter must therefore be due to some other cause. Pentimalli, working out Lillie's line of thought, and confirming in the most striking way his discovery of the electric charge on the chromosomes, has contributed the final disproof of the alleged electric character of the spindle field of the cell. Yet, strangely enough, in his paper he showed that he had not realised the true import of this most important contribution to our knowledge. Pentimalli passed a continuous current through the young roots of a hyacinth, fixed them immediately, and examined them in thin sections. He found that the chromosomes manifested their negative charge by migrating towards the anode. But his figures showed that the spindle assumes no definite orientation with respect to the current, and that its electric condition does not appear different from that of the other parts of the cell (save, of course, the chromosomes) (Fig. 32). This experiment also negatives current-electricity as the spindle force. None the less do many respected cytologists cling to the belief that somehow electricity is at the bottom of the phenomenon, recalling the attitude of the credulous buyers of a certain appliance warranted to cure all diseases, with a touching faith in the saying "ELECTRICITY IS LIFE" that heads advertisements of the "Inventor and Sole Manufacturer."

Hydrodynamic fields of force may be produced in fluids in various ways, by centres of *vortices* or *whirls*, by *centres of oscillation* to and fro, or by *centres of pulsation* (the alternate swelling and contraction of

FIG. 32.—Cells which have been fixed after the passage of an electric current through the living plant. The + and — indicate the anode and cathode respectively.

the centres). But none of these would appear capable of giving rise to such a field in the cell-contents, heterogeneous and viscid, on account of the damping action. However, for completeness' sake, we may examine each of the three cases. The centres of vortex action will give rise to the spindle-field if they both rotate in the same sense. If now the two vortices have their axes *in line*, the field they give rise to will resemble the magnetic field, which, as we have seen, is inconsistent with the relations shown in the "blobbed" figure (Fig. 29). If, however, the two vortices have their axes *parallel*, at right angles to the axis of the cell, they could not give rise to the symmetrically ovoid cell-figure. But the extension of the rays into the protoplasm is a sure proof that no such mad waltzing of the centrosomes as is demanded can occur. This last criticism applies to *centres of oscillation*, as well as the fact that the field which oscillators produce is of the magnet type, which, indeed, we may call an "axially centred" type; whereas the mitokinetic field, like the electrostatic, centres on points (or spheres), not lines. The last field, that of *pulsators*, is free from this geometrical objection. The field between two pulsators whose phases are synchronous one with another is the crossed figure; but if the two pulsate in opposite phases, or alternate, as we say, the spindle-figure is the result. In the first place, such pulsations must be exceedingly rapid to elude notice, for nothing can be seen of them even when the achromatic cytoplasm is coloured in the living cell by Congo or neutral red; and, as noted before, it is pretty certain that minute rapid pulsations would be so damped in the cell-field as to lose their regularity.

But it has been suggested to me by Mr. William Cramp, M.Sc., M.I.E.E., that disturbances in the *ether* of a similar character to the pulsations of a liquid body might be invoked to explain mitokinetism, as, indeed, to explain statical electricity. This hypothesis would give a *formal* explanation of the force without carrying us further. The pulsation hypothesis was put forward by Arthur B. Lamb in 1908, but he failed to note the difficulty of applying it in its primitive hydrodynamic form.[1]

V

After this survey of the spindle fields known to physicists the only conclusion that we can come to is, that **the cell-field shows the greatest analogy in its formation and behaviour to the electrostatic field between oppositely charged conductors; but that the force is no more electrostatic force than it is any of the other known dual forces.** Some years ago we termed it provisionally "mitokinetic force" or "mitokinetism,"[2] not to prejudge the question of its nature; the name must now stand as denoting a "new force," so far unknown in the physical world of non-living material. The whole of the phenomena of the mitosis of the cell may be explained by assuming that the threads of spindle and of rays are highly "permeable" to this force,

[1] For a discussion of the fluid fields between pulsators and oscillators see V. F. K. Bjaerknes, "Die Kraftfelder," 1909. Vortex fields were especially studied by the elder Bjaerknes and by Sir W. F. Barrett. Lamb's paper, "A New Explanation of the Mechanic of Mitosis," appears in *Journ. Exp. Zoo.*, v., 1908.

[2] "Comptes Rendus de l'Académie des Sciences," June 10, 1904.

and that the chromosomes are still more "permeable" to it. The chief difference between the working of our physical models and the living cell is that (as noted above, p. 111), the "chains of force" of the model arise by *segregation* from the turbid medium, while the cell chains arise by *growth*. How the dual field arises is not absolutely clear anywhere, especially in Plants. In Animals we get some light: for a single centrosome divides into two between which a few threads are seen to stretch in spindle form, while others diverge as stars. The two centrosomes diverge and enlarge, and at the same time the spindle and rays grow both by the elongation of the existing threads and by the formation of fresh ones. The additions to the spindle are largely due to the formation, elongation, and incurving of astral rays which meet and unite on the equator. We may perhaps find an analogy in the formation of an electrostatic field: when two insulated brass conductors are made to touch, and then pulled apart, it will usually be found that they are "oppositely charged"—in other words, they are the opposite centres of a "spindle" electrostatic field. So the divergence of the centrosomes in Animals may initiate the field between them. Once formed, it is easy to suppose that the increasing energy of the field is due to the active chemical processes of the cell.

VI

We may summarise the forces at play in the dividing cell as follows:

I. **Well-known physical forces**, such as the mechanical tensions of the spindle-fibres, and of the astral rays on the peripheral cytoplasm: viscosity, altering the curve of long chromosomes on their way to the poles (p. 108): osmotic actions and electrostatic charge, which contribute to the divergence of the centrosomes: surface tension, which certainly also plays a part in the actual division of the cell. We must note that the actual division of the cell is due to concentration round two *like* centres, and though frequently following nuclear division may be quite independent of it, as in Saprolegnieæ and other habitually apocytial organisms.

II. Forces which occur elsewhere in living beings, but whose physical interpretation is uncertain: such as protoplasmic streaming; the separation of the chromosomes; growth of the rays through the viscid cytoplasm; and fission of the centriole, the chromatin-granules, and the cell-body.

III. **Mitokinetism,** the new dual heteropolar force.

IV. Forces without any clear analogies in the physical or the cell-world: the formation of the mitokinetic field when needed, the resolution of the nuclear network into chromosomes, the new organisations of the daughter-nuclei, etc.

VII

The discovery of a new force in the organism will doubtless raise once more the question of Vitalism versus Mechanicism: I may say at once that, to my mind, it leaves it where it was. Assuredly much of the persistent advocacy of the view that mitokinetism is identical with electrostatic force has been due to the latent fear that a "new force" within the organism, not known in the inorganic world, might strengthen the side of the vitalists. As a vitalist I may say that I should never dream of weakly attempting to strengthen my position by the shelter of so frail an argument: the past has taught me better. Time was when it was thought that complex carbon compounds, such as are produced within the organism, and are hence known as "organic" substances, could not be produced in the laboratory. To cite the words of Prof. H. E. Armstrong:

"Organic chemistry originally dealt only with substances more or less directly derived from the animal or vegetable kingdom, and it was long believed that the chemist was powerless to produce organic substances from their elements as they were formed in the animal or plant under the influence of life, it being supposed that therefore the interposition of a special force, termed the vital force, was requisite. The first step towards the disproval of this hypothesis was made by Wöhler, who in 1828 succeeded in artificially producing urea, the characteristic crystalline constituent of urine." (Prof. H. E. Armstrong in the "Encyclopædia Britannica," ed. ix., 1876, p. 520.)

To claim now the manifestation of a new force as the exclusive attribute of the living organism is to run the risk that, if the force were found at some future time outside the organism, there would be a big set-back in the position of vitalism, such as arose, we have seen, on the artificial production of urea. The prestige of a certain view of Nature may be destroyed for two or three generations by the occupation and fortification of a position liable to be stormed at any moment. Even if we do not come upon this force among things at large, there is still the possibility that human ingenuity, which has devised so complex a play of matter and energy as the Niagara Falls power-installations, may ultimately succeed with its intricate machines in producing mitokinetic force outside the organism. True, such machines are themselves the work of the living organism, and not the play of Nature. The cell originates for itself the mitokinetic field when, in Michael Foster's phrase,[1] "it wants" to divide, and to distribute the elements of the nucleus fairly between the daughter-cells; just as Man sets up an electromagnetic or a density plant when he

[1] See p. 220.

wants to sort out the minerals from the miner's heap. That such a mechanical plant could be produced save as the result of the intelligence and forethought of Man is unthinkable: the appearance of the mitokinetic field in the cell at the appropriate time is but one of the million cases where the occurrences of the organism are conditioned no less by final than by proximate causes. Thus the organism demands a "Why?" as well as a "How?" to explain its existence and its workings.[1] The future is an ever-present factor of life.

It has been urged—quite untruly—against the vitalist that only by the methods inspired by the mechanistic idea of life has physiology progressed. In the present instance the application of the methods of the physicist has indeed enabled us to realise the true character of the force at play in the dividing cell; but it has proved that this special force is, so far, peculiar to the living organism, and left us in the dark as to its relation to other physical forces, and to its proximate cause. Herbert Spencer and Leuckart showed, it is true, many years ago, that the cell and the nucleus would lose in their functional powers if they continued to grow in size indefinitely,[2] because the area increases only as the square of any linear dimension, whereas the bulk increases as the cube. To take a concrete

[1] See below, "Mechanism and Life," p. 225.
[2] See pp. 79 80.

instance: a cubical organism (could such exist) one inch in height) would have a surface of six square inches for one cubic inch of volume; if it increased to the dimensions of two inches cube, its bulk would have grown to eight cubic inches, while its enlarged surface would only be twenty-four square inches, or three square inches of surface to the cubic inch of bulk—just half the original ratio. Yet this explanation is merely that of the utility, the "why," of the final cause of organic multiplication, not of its proximate cause; and it is strange that this point has been so largely overlooked by Spencer and his disciples.

If the discovery of the new force, Mitokinetism, has done nothing to advance vitalism, it has certainly done nothing to retard its progress in this twentieth century.

CHAPTER V

"NUCLEAR REDUCTION" AND THE FUNCTION OF CHROMATIN[1]

I

THE following remarks should have found their correct place in "The Cellular Pedigree and Heredity" (Chapter II), published under the title of "The Fundamental Principles of Heredity" in *Natural Science* for October and November 1898, but were omitted not to overweight it with details of a somewhat abstruse character, and as lying apart from the main object of the study—the tracing out of the cellular pedigree of the organism, with insistence on the point that "collateral cellular transmission" was operative in all higher organisms. And I would ask the reader to refer to my previous paper in connection with the present one.

"Nuclear reduction" ["Meiosis" of Farmer and Moore] is an easy process to define after we understand normal nuclear division. When a nucleus is

[1] I have freely cut out from this chapter passages which I thought unnecessary or out of date in the light of subsequent knowledge.

about to divide, its formed matter resolves itself into a definite number of segments; these split each into two, one of which is destined to either of the daughter-nuclei resulting from the division. Such segments have received the name of "chromosomes." Usually, a nucleus on the approach of division reveals the formation of as many segments as entered into it at its formation; and thus the number of segments remains constant from (cell-) generation to generation in the same species: but at a certain point in the life-cycle the number of segments appearing on division is usually half that at the previous divisions of the cells of the parent-cycle; and this is, in its finally limited senses, called "nuclear reduction."

[The process involves two successive cell-divisions termed by Farmer "meiotic divisions"; both differ somewhat from normal karyokinetic cell-divisions, and were termed by Flemming "heterotype" and "homœotype" respectively. The assiduous labours of many cytologists for over two decades have failed to completely solve some essential problems in the process.]

Where does nuclear reduction occur? In Metazoa, usually during the peculiar two cell-divisions that give rise to a brood of four spermatozoa, or to the oosphere and the three polar bodies (abortive oospheres) respectively: that is to say, at the inception of the formation of the sexual pairing-cells.[1] The extension of this by zoologists to all cases was

[1] See above, pp. 10–11, Fig. 5.

tempting; and the demands of the Weismannism of the eighties made this extension appear imperative: reduction or excretion processes in gametogeny were diligently sought for, and of course found, everywhere; and in 1891[1] I enumerated and discussed as many as fifteen which had been accumulated in defiance of morphological homology or physiological equivalence. In the same paper I studied the question of nuclear reduction from the then state of our knowledge; and pointed out that in Flowering Plants reduction occurs in the pollen-mother-cell, and that this is the equivalent of the *asexual* spore-mother-cell of Archegoniate Cryptogams (Ferns, Mosses, etc.). "We must remember that the reduction takes place in the pollen-mother-cells of Flowering Plants, which are themselves homologous with the mother-cells that form tetrads of asexual spores in Archegoniate Cryptogams; hence we may be allowed to conjecture that reduction also takes place in the latter group; and by parity that it is not confined to gametogonia[2] [= the mother-cells of a brood of gametes]. . . ."

At the time there was only one case, that of a Liverwort, that had been at all fully worked out,

[1] "Some Problems of Reproduction" in *Quart. Jour. Micr. Soc.*, vol. xxxii, pp. 62–3.

[2] *Op. cit.*, 1891, pp. 57–8. The sentence closes thus: "but will be found in all mother-cells destined by multiple fission to give birth to a brood of reproductive cells." Of course the latter part of the conjecture has not held good, but the former part has maintained itself—namely, that reduction

but since then we have learned that in the ovule of Flowering Plants reduction takes place at the first division of the primitive nucleus of the embryo-sac; and that in the Archegoniatæ without exception [and in Florideæ and Ectocarpeæ among Seaweeds] reduction takes place at the inception of the formation of the tetrads of the spores, not at that of spermatozoa and oospheres, the equivalents of the sexual cells of Metazoa. Now, the spore of Mosses gives rise to the Moss-plant, capable of indefinite vegetative growth and propagation; that of the Fern to the Fern-scale, which in *Gymnogramme* (the Gold- and Silver-Ferns), for instance, is perennial also. Thus nuclear reduction is not a process that finds its direct function in gametogenesis, the formation of cells specially adapted for "sexual" (sit venia verbo[1]) fusion.

takes place in Cryptogams at *spore-*, not *gamete-*formation. The anticipation thus formulated by me in 1891 was repeated by Overton in 1893, and its enunciation has been ascribed to him by Strasburger (1894*a*, p. 291; 1894*b*, p. 825), while later the error has been continued by Wilson (1896, p. 196). I did not think such a question of priority worth noting for itself, but take this opportunity of correcting the mistake.

[1] The word "sexual" has two distinct meanings; the one relating to the fusion of two cells, etc., into one, the other the differentiation of such pairing-cells into two unlike categories such that cells of the one will only pair with cells of the other. "Sex," "sexual differentiation," "sexual processes," are terms as often used in the one sense as in the other; and we may easily avoid the confusion by describing the former as "pairing processes," or "fusion processes," and the like, and using the additional adjective "binary" with "sex," "sexual," to distinguish the latter meanings of the terms [I have since proposed the general terms "syngamy," "syngamic," "syngamous," to designate fusion processes of all kinds; see Chapter VI, on "Fertilisation," p. 149].

In the existence of the Higher Animals, or Metazoa, there is a long cycle of colonial cell-divisions, alternating with a short one of protistoid brood-divisions producing the sexual cells. In Higher Plants there are two such alternating cycles of colonial and protistoid growth, the Moss-plant or Fern-scale producing the sexual cells, and the Moss-urn or Fern-plant producing the asexual spores. In 1891 I wrote of nuclear reduction: "We may perhaps regard it as an adaptation to prevent the undue multiplication of chromatomeres [= chromosomes] in the zygote, and the cells produced therefrom." This view has been elaborated by Strasburger; but it will be better, as we shall see, to explain it in another form than his. Since, normally, each nucleus exhibits on its division the same number of segments that it had on its formation; the fertilised egg, oosperm, zygote, or whatever we please to call a cell formed by the fusion of two, on its division will present twice the number that were present in either of its two original constituents. If, then, at each sexual fusion this doubling continued, the number of nuclear segments in each cell would increase indefinitely in geometric progression, which is, of course, out of the question: a reduction *must* take place somewhere. This necessary reduction takes place at the *first resumption of protistoid multiplication, i.e.* cellular reproduction, as contrasted with multicellular propagation (see p. 37). In Higher Plants, where there are two such resumptions, this is obvious; in Metazoa there is only one such resumption,

FIG. 33.—Oogeny in the Wracks (Fucaceæ).

1, Female inflorescence of *Sarcophyces*. 2–9, Oogone (brood-mother-cell of oospheres) of *Fucus*, the common Bladder Wrack, its liberation and division into a brood of eight oospores. 10, Oogone of *Pelvetia*, with two oospheres functional and six (three only seen) abortive. 11, 12, Oogone of *Himanthalia*, with four oospheres functional and seven abortive (three only seen). 13, Oogone of *Ascophyllum* with four oospheres functional and four (three only seen) abortive.

which coincides with the formation of the (protistoid) sex-cells, and it is this mere *coincidence* that gave rise to the idea that reduction was a *preparation for* *cell-fusion*, instead of being the *necessary consequence of cell-fusion.* [Dr. Charles Walker aptly regards this as the passing out from the "somatic co-ordination"; and reduction occurs in the *emancipated* mother-cells of cancer.]

A very curious case is that of Fucaceæ, the Wracks (Fig. 33), which, like Animals, have only *one colonial form*—the familiar plant, and *one protistoid reproduction*—that producing the sexual cells; here, as we should anticipate, reduction occurs as in Metazoa at the inception of the latter process. Had this case been worked out before that of the Archegoniate Cryptogams, it would have afforded great support to the physiological hypothesis.

Again, the little fresh-water Algæ, the Conjugatæ, have their cells isolated, or at most in simple colonies of filaments, where the cells, placed end to end in a single row, divide each on its own account, so that they are really rather protistoid than comparable with the differentiated colonial cells of Higher Plants. In these plants nuclear reduction occurs at yet another point of the cycle—namely, at the very first cell-divisions of the zygospore, which is, as we see, the resumption of protistoid cell-division after conjugation.[1]

[1] [To summarise very briefly: Nuclear reduction takes place in all Higher Animals at the gametogenic fissions. In Archegoniate Plants it takes place at the formation of tetraspores, giving rise to an alternating type of plant (see "The Cellular Pedigree"). In Flowering Plants it takes place at the formation of the pollen-grains, which correspond to the

Strasburger's statement of this explanation is somewhat different. He writes:

"The morphological cause of the reduction in number of the chromosomes . . . is in my opinion phylogenetic. I look upon these facts as indicating a *return to the original generation* from which, after it had attained sexual differentiation, offspring was developed having a double number of chromosomes . . . it is the reappearance of the *primitive number of chromosomes* as it existed in the nuclei of *the generation in which sexual differentiation* [rather cell-fusion, for whether it be sexual or isogamous makes no difference to the point] *first took place.*"

If we are to take literally the phrases that I have

tetraspores of the Archegoniates, and at the first two divisions (out of three) in the embryo-sac, which are at the same morphological stage. In Fucaceæ (Wracks), where the oosperm, as in Higher Animals, grows into the sexual plant, the reduction and gametogenic divisions are coincident; but in the Phæocarpeæ, a closely allied group of Olive Seaweeds, reduction takes place at the formation of tetraspores as in Ferns and Mosses, and the tetraspore grows into an alternating vegetative type of plant which forms pairing-cells by brood-formation. In the Red Seaweeds (Florideæ) we find the same alternation of generations, and reduction at the same stage. In the unicellular (or filamentous) Conjugates, reduction takes place on the germination of the zygote, and is accompanied by a process which may be described as abortive brood-formation. In Infusoria the complication of the cell-body and nuclear apparatus is quite exceptional among Protista; reduction takes place on the return to simplicity of the nuclear apparatus, and is associated with what I have just noted as an abortive brood-division to form the pairing-nuclei: the process may well be compared with that of Higher Animals.

In many Ascomycetous Fungi two nuclear fusions are noted, the offspring of the fission of the first fusion-nucleus pairing with one another. Here reduction of the usual type follows at once, and is associated with the first two divisions, and a second reduction (brachymeiosis) takes place in the third of the three divisions that give rise to the eight spores.]

italicised, we shall have to assume that two such plants as the Onion and the Turban-lily have independently developed a pairing process; for the number of the nuclear segments is 8 and 16 in the former, 12 and 24 in the latter; the same would apply to the two forms of the Roundworm of the horse, with 2 (4) and 1 (2) segments respectively—which is absurd. Yet so much of the essay is taken up in proving that asexual reproduction is the older mode, not only in primitive organisms, but in individual groups of Higher Organisms, that one wonders if Strasburger has not really missed the inconceivability of his statement as it stands; and hence I cannot accord to the explanation above given the full weight of his distinguished authority, as I should wish to do.[1]

Again, we have seen that the process of "nuclear reduction," despite its name, involves no necessary reduction in the *quantity* of nuclear matter, but only in the *number* of the segments into which it is distributed. Hence the process cannot have the physiological function ascribed to it as a "*preparation* for gametogenesis"; and since we have noted the occurrence at the inception of a long series of cell-multiplications, this physiological function would be absolutely useless.

[1] The "reduced" number of segments is now termed "*haploid*," and the "doubled" number "*diploid*."

II

A word about the functions of the chromatin or nuclein in nuclear division. The amount of chromatin in a nucleus is constantly changing; very often after a cell is formed the nuclein is much reduced in amount, and with this reduced amount the cell does all its individual life-work. At the approach, however, of cell-division, the nuclein grows, and reaches a maximum at the commencement of the nuclear division that precedes that of the cell as a whole; the nucleus of the daughter-cell repeats the conduct of its parent. Whatever be the function of the chromatin in the "*working*" cell, as we may term it, it is evidently less important than its function in the *dividing* cell. The achromatic substance of the nucleus (linin) forms the basis, as it were, of the nuclear segments, the strands on which the chromatin is imbedded in the form of granules, like the string of a necklace, or better, the braid in beaded passementerie; these granules first split, and then the threads on which they are strung (Fig. 25, p. 99). An explanation far removed from current theories has forced itself on me—perhaps after all it is the *achromatic plasm* (linin) of the nucleus whose fair and equal division is the important matter, the final cause of karyokinesis. But the splitting of a viscid thread is one of the most difficult mechanical feats to accomplish. Suppose, then, that there is a certain polarity about the granules of chromatin, through which, after their division, they tend to recede from their fellows as far as possible; through this they will determine a splitting of the filament on which they are strung. The close of nuclear division sees their task accomplished; and, as we should expect, the chromatic granules, having fulfilled this appointed task, now atrophy, and remain in this state till the approach of a new cell-division determines a fresh growth of their substance. According to this view the *linin* is the transmitter of inherited properties, and the *chromatin* has a purely mechanical function in karyokinesis; it avoids the many difficulties due to the ascription by Weismann's school of hereditary constancy to a substance so subject to periodic atrophy and growth as the chromatin of the nucleus.

[This view was later put forward by Boveri; and we have developed it above more fully in Chapter IV. on "The New Force Mitokinetism."]

CHAPTER VI

FERTILISATION

At the Southport meeting of the British Association, Prof. Hickson, President of the Section of Zoology, asked me at very short notice to open a discussion on "Fertilisation" in the Section, to which I was about to contribute a Note on "Progamic Fissions." The following pages represent far more closely what I would have wished to say than what I actually said.

I

The word "fertilisation," like so many others in science, has come down to us from the days of ignorance, undergoing many changes of meaning, and acquiring new meanings by accretion on its way. Undoubtedly it was originally used in the sense in which we speak of a farmer "fertilising" his land—it conveyed the idea that a female became fertile, or was enabled to bear offspring, by a co-operative process on the part of the male; and to this the name was applied. This process is now distinguished as "insemination," or "fecundation," though in French the term "fécondation" has acquired all the meanings of "fertilisation."

When, later on, the germ of the young animal was always found to develop from the egg, actually produced by the female before and independently of insemination, the term was transferred from the mother to the egg; and was then habitually used to denote the process, or rather *one* among several processes, by which the egg, hitherto an inert "resting-cell," is induced (in the instances most familiar) to become active, and by its divisions to give rise to the young living embryo. At first, we know, this change was attributed to a mere emanation, an *aura seminalis* given off from the seed of the male; but Spallanzani demonstrated 150 years ago that the semen must actually come in contact with the egg. By the middle of the last century the change was recognised in all well-studied instances as due to the entrance of a sperm, one of the formed constituents of the semen, and its complete fusion with the egg; the term "fertilisation" was then applied to this fusion.

During the last three decades of the nineteenth century it was shown that the sperm is itself a cell, and that the fusion is a complete one, cytoplasm to cytoplasm and nucleus to nucleus, so that the germ begins life as a simple uni-nucleate cell, which we term the "oosperm," the equivalent of the "fertilised egg" of common speech. The latter term is falling into disuse from its undue exaggeration of the share of the egg; and is the more to be deprecated as the process is known to be in essence identical with other fusions, known as "isogamous" or "equal conjugations," where the two pairing-cells are similar to the point of identity, as in *Ulothrix* (Fig. 1, p. 4).

Meanwhile, dating from the last years of the nineteenth century, through the revival, principally by Jacques Loeb, of lines of research initiated a decade earlier by the brothers Hertwig, it has been found that by treatments of the most varied kinds (mechanical, osmotic, chemical) the eggs of certain Metazoa could be induced to develop without the intervention of the sperm. This result was too rashly called "artificial fertilisation," and was still more rashly invoked as the clue to the meaning of the fusion-process which constitutes "fertilisation" in its actual derived sense. Indeed, the lay press was full of marvellous accounts of "chemical fertilisation," for which, perhaps, the enthusiastic professors of the Chicago school were hardly to be held responsible.[1] Yet, as we have seen, this was no misuse of the term in its older senses—the egg, hitherto infertile, became fertile under the

[1] [The following pronouncement in *Nature* of June 22, 1911, over the initials "D. W. T.," though undoubtedly ironical, might well be taken as a genuine expression of certain antivitalists and writers on this subject: "In short, we have no doubt at all that what they assert they have actually demonstrated . . . that, so to speak, *they have raised a hybrid between a needle and a frog!*" The italics are mine, but not the note of admiration.]

treatment, and started as a germ into a new life. But that sense had become so entirely obsolete that now, by common consent, we apply to all these cases the uneontroversial term "artificial" or "induced parthenogenesis."

We must remember that in many groups of animals the eggs (or eertain types of them) can develop without any eo-operation of the sperm; and, indeed, this often occurs in the Eehinodermata, the very group on which the above experiments were chiefly tried. Again, in many lower organisms whose pairing-cells are not differentiated into sperm and oosphere, but are similar, should fusion fail to occur at the right moment, it is not only impossible, but needless; for the single cell will develop individually, its product taking the same course as would have done the product of a fusion (*e.g. Ulothrix, Spyrogyra*). Such development, known since the eighteenth century, had reeeived the name of "parthenogenesis." The proeess is clearly identical in nature with the development of *non-pairing* resting-cells, such as the resting-spores of Fungi, Algæ, and many Protista, and the spores of Mosses, Club-mosses, and Ferns, to which the term "*germination*" is applied. This same term is also given to the starting into development of such *multicellular* bodies as the seeds of Flowering Plants, and their bulbs and tubers, and similar bodies in Higher Animals, like the statoblasts of Polyzoa. For germination to take place favourable external conditions are sometimes needed ; whereas in other cases, as with the seeds of the Mangroves, there is no pause, and the seed develops as soon as formed. The renewed growth after rest, whether of spores or of seeds, single cells or cell-masses, appears to be due (1) to the *formation of ferments* that can dissolve the intra-cellular reserves ; and (2) to the conditions that *favour the action of such ferments*, and the consequent growth of protoplasm at the expense of the reserves rendered available by digestion. We may henceforward regard all such starting into growth as "*germination*," reserving the term "*parthenogenesis*" for the special germination of cells that normally (or rather, habitually) are capable of a fusion process with another pairing-cell ; in other words, "parthenogenesis" is the direct "germination" of a potential gamete.[1]

On the other hand, the germination of the resting-cell (of which to us the Metazoan egg is the most familiar type) and the process of cell-fusion are by no means invariably associated together in time. True, they are so connected in the cases most familiar to us, but in the bird's egg itself the development of the germ is arrested on laying, and the

[1] [That this is possible in the Highest Animals—even in man—is shown by the so-called "teratomata" which occur in the ovary, even of virgins, and sometimes in the testis. These are irregular masses containing all the tissues of the body and sometimes complete organs such as teeth. They can only be due to the parthenogenetic evolution of a primitive reproductive cell, whether ovarian ovum or sperm mother-cell. See J. Bland Sutton, *Lancet*, May 25, 1912.]

"fertilised egg"[1] of the Rotifer, the Greenfly, and the Entomostraean (in marked contrast to the parthenogenetic egg, which develops at once!), after at most a few segmentations, passes into a state of rest, to germinate only after a prolonged rest.[2] The same holds good with the seed of most Flowering Plants, as I know to my cost, being a raiser of Abutilons; the germ forms an embryo of many similar cells, whose development is arrested after a time. Then, only after a lapse of months, it may be, when exposed to suitable conditions—heat, moisture, and aeration—it starts to grow. The same applies to tubers and the statoblasts of Polyzoa, the gemmules[3] of Sponges, the resting-bodies of one Scyphistoma (larva of a Jelly-fish), etc.

If now instead of counting *species* of living beings we count *types* of reproduction, which are so varied in the Protista, the Algæ, and the Fungi, we shall find that in the majority of cases the pairing-cells are naked, but that the fusion-cell immediately invests

[1] The term egg denotes four cells morphologically distinct: (1) the ovarian egg; (2) its daughter, the sister-cell to the first polar body; (3) the "matured egg," sister to the second polar body and daughter of (2); (4) the "fertilised egg," or oosperm (see Plate I, pp. 149, 150). But, as all four are nearly identical in size and cytoplasm, it is convenient to retain the word "egg" to denote them indifferently.

[2] In Rotifers two kinds of eggs are formed: (1) large eggs, which always develop at once into females; (2) small eggs, which if unfertilised also develop at once—into males; but if "fertilised" go to rest and on germination grow into females.

[3] Gemmules and statoblasts are aggregates of embryonic cells surrounded by a firm envelope to protect them against drought or cold during the resting-period.

itself with a complete wall, and either goes to rest itself, or, as in most Sporozoa, divides into a limited number of cells, which themselves pass into the resting-state. Indeed, the almost universal formation of a cell-wall around the fusion-cell or oosperm, in Higher Plants and Animals, as soon as the process of fusion takes place, may be regarded as a survival of this tendency of the cell formed by the fusion of two to pass at once into rest. [The justification for this contention will be found in the Tabular View at the end of this chapter, p. 171 f.] Had our knowledge of reproductive processes been derived from these lower beings, we should never have associated the physiological process of the germination of the resting-cell with the morphological process of cell-fusion, nor included the former process under the term "fertilisation."

The word "fertilisation" labours under two disadvantages in its later restricted sense, which, historical considerations notwithstanding, must to-day be regarded as its *correct* sense: (1) in the minds of most naturalists it is still tainted with the idea of what we have differentiated as "germination"—the scent of the rose still clings to the emptied vase; (2) it will not conveniently yield an adjective to apply to its modes, etc. This latter objection has been tacitly felt by most writers, who have had to fall back upon the term "sex," "sexual," etc.—extending this term, which originally implied a *binary differentiation*, to all cognate phenomena, whether there exist such differentiation or no. Thus my friend Mr. Wager has written a most important and valuable paper on the "*Sexuality* of the Fungi," though no differentiation of male or female exists in some of the most important and, indeed, primitive types. The word is the more unfortunate, for the user of this terminology is unconsciously swayed by the implicit idea of such binary differentiation into finding everywhere two contrasting categories of beings or cells as exist among ourselves. Yet we have seen (Chapter I) that in the most primitive cases the fusing-cells are to all intents and purposes identical—nay, more than two may fuse into a single cell. Indeed, in isogamy with exogamy, so common in Protista, *any one* gamete will pair with *any other*, provided only that it belong to a different brood to its own. It has been suggested that here we have a sort of foreshadowing of sexual differentiation, but the suggestion will not hold water for a moment, as we have seen (p. 13). Let us consider twenty-six broods of pairing-cells matured at the same time, and letter them with the letters of the alphabet, and suppose that their exogamy be a glimmering of sex. Then we may suppose that A is of the male sex, and that with respect to it B, C, D, . . . Z are all more or less females; the same applies to B with respect of C, etc.; and in the same way we could show that any one brood is male and female at once—that is, that they are sexually undifferentiated. "Therefore, etc., Q.E.D."

Again, in the Heliozoan *Actinosphærium*, the pairing-cells are second cousins by the laws of cellular kinship (p. 37), and have had precisely the same history from the grandparent-cell; and the pairing-nuclei of *Amœba coli* are sister-nuclei.[1] The suggestion that there can be any binary differentiation in such cases has arisen simply from the associations inseparable from the word "sex"; and the only ground for the assumption of latent differentiations is the subjective effect of the word on the minds of the writers who have used it in default of a better word. For these reasons I have for some years past never used the word or its derivatives, save where there actually existed the binary differentiation, and then I have prefixed the word "binary" to avoid all ambiguity even to myself. As a substitute I have used the terms "pairing-cells," "pairing-" or "fusion-processes," etc., for all cases where no binary differentiation was necessarily involved or implied. But besides

[1] [Schaudinn and others, who have demonstrated the fusion of closely related nuclei, sisters or cousins, in several groups of Rhizopoda, have introduced the term "autogamy" to designate it. Prof. Helen Fraser (now Mrs. Gwynne-Vaughan) has further, in the Ascomycete Fungi, attempted to distinguish between "vegetative" and "sexual" pairing-nuclei, and introduced the terms "*homoiogamy*" for the pairing of two nuclei of the same kind, "*hylogamy*" for the pairing of different kinds, "*pseudogamy*" for that of two "vegetative nuclei."]

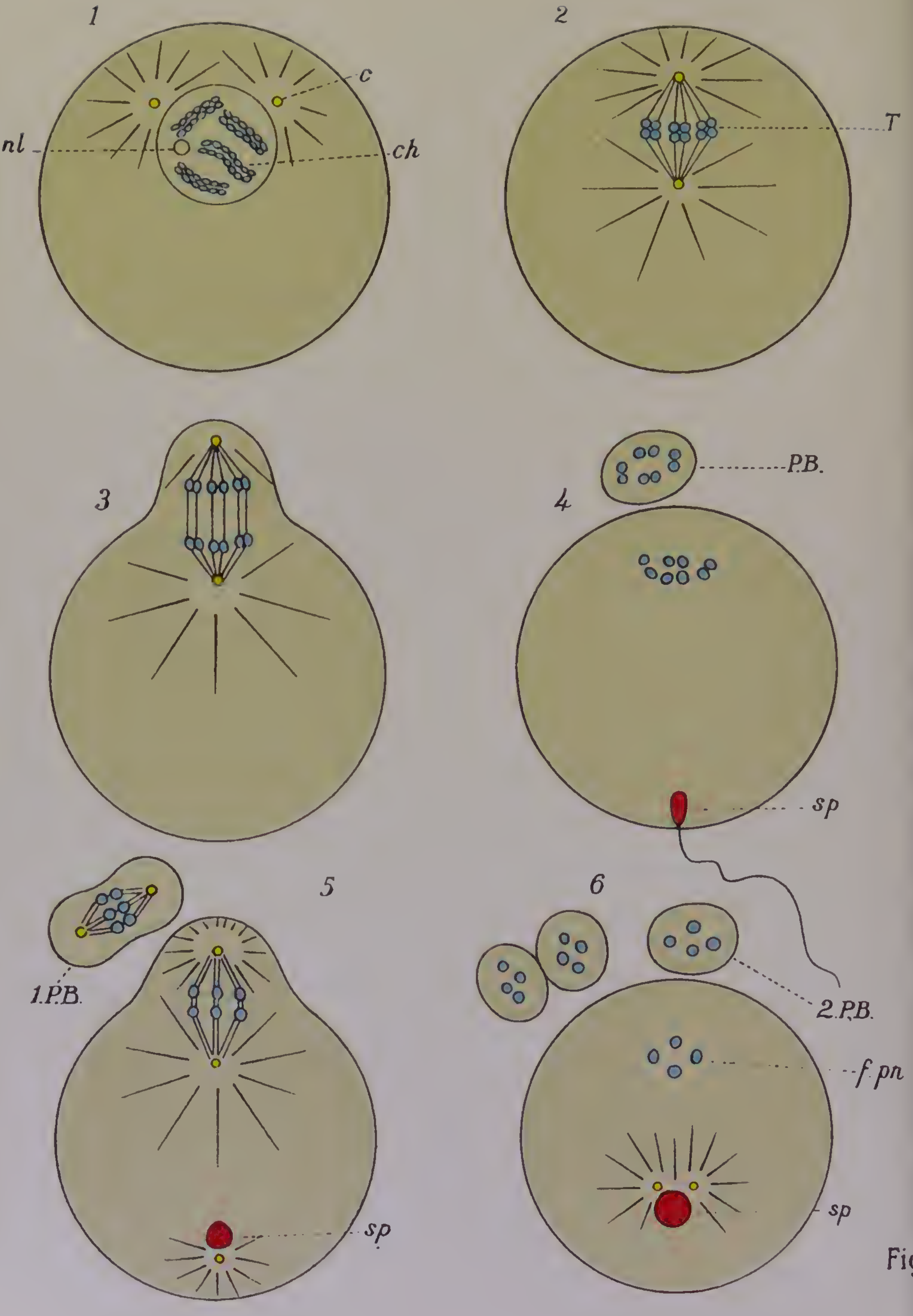

Fig. 13

PLATE I.—Diagram of nuclear reduction and syngamy in a Metazoon with eight chromosomes (after Ziegler).

1–4, First brood-division eventuating in formation of first polar body; in 4 the sperm is seen entering before the "reduction" processes are complete. 5–6, Completion of the reduction process and gametogenic divisions of the egg by the second division to form three polar bodies and the oosphere; in 5 the cytoplasm of the sperm has grown and developed a centrosome which has divided in 6 into two. 7–12, Approximation and association of nuclei, and division into first two cells with blended nuclei; *c.* = centrosome; *ch.* = chromosomes; *p.n.* = female pairing-nucleus; *nl.* = nucleole; *P.B.* = polar body; *sp.* = sperm or sperm nucleus; *T.* = equatorial plate of first division.

Between pp. 148–9]

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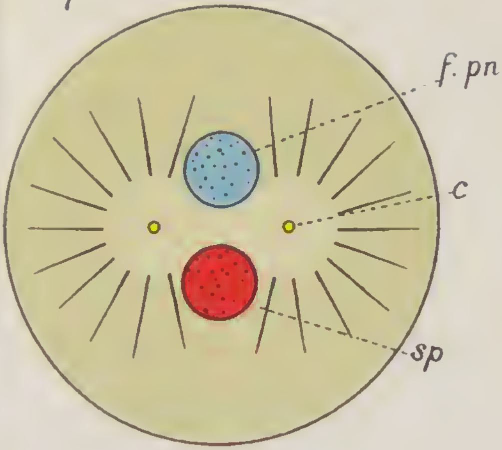

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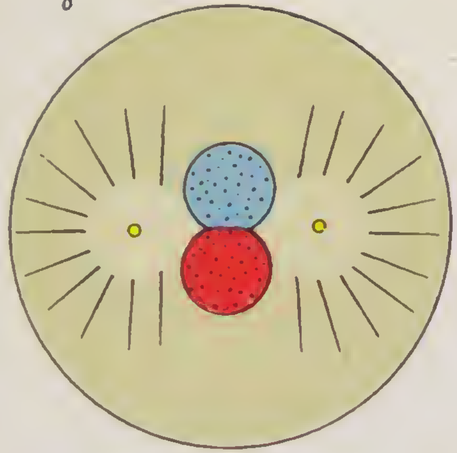

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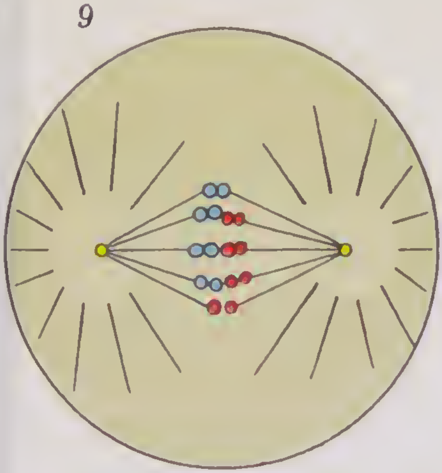

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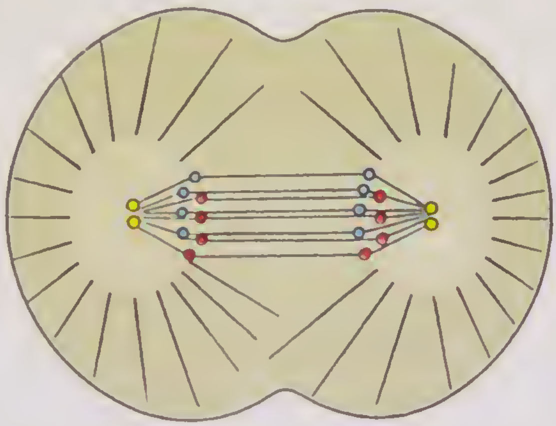

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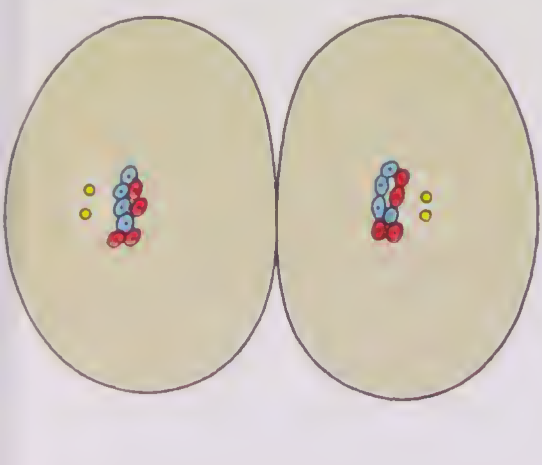

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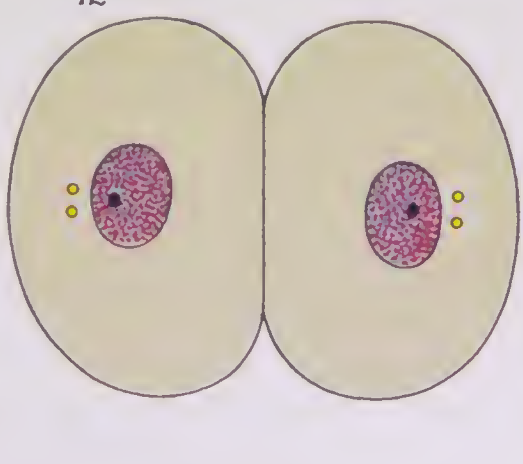

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being cumbersome, this terminology yields no good derivatives. Therefore I venture to propose the term "SYNGAMY" to replace "fertilisation" in its modern restricted sense, which will be followed, I anticipate, in to-day's discussions; and the derivative adjectives "syngamic" and "syngamous" follow naturally. The foregoing discussion is not a mere matter of words, but of the clarification of our thought, which is ever dulled and confused by the use of ambiguous or question-begging words, especially when such are the terms used to designate the main objects of our discussions and of our theories.

It has been suggested that one subject fitly touched upon here would be the function of the centrosome in syngamy.[1] As this organ is as completely absent from Flowering Plants, it can have no import of universal bearing in our general theory; though it has doubtless a partial bearing in Metazoa, where its presence is common. Since, however, even here the centrosome is of varied origin (intra-nuclear or extra-nuclear), and is seen to be formed anew in the parthenogenetic embryos of Echinoderms, its importance must have been much overrated; and we cannot to-day accept the views of those naturalists

[1] In Metazoa the centrosomes of the egg, that are seen in divisions to differentiate the oosphere and the polar bodies, undergo degeneration; and the centrosomes of the first division of the oosperm are formed by the division of one accompanying the sperm, and forming part of it (Plate I).

who have held that the chief function of the sperm is to introduce a centrosome into the egg (see below, p. 167 f.).

The most common type of syngamy is "cytogamy," the complete fusion of two cells, the "gametes," cytoplast with cytoplast, nucleus with nucleus, into a uni-nucleate cell, which we call the "zygote," the "oosperm," in cases of binary sexual differentiation. In the most primitive cases this union takes place completely and directly; but in some the union is delayed and incomplete up till the first cell-division, and, indeed, the two constituent halves of the successive nuclei along the new nuclear line may for a long series of divisions show their distinctness more or less defined.[1] This delay is clearly a derived and not a primitive phenomenon, and may be perhaps explained by the acceleration or precocity of the germination of the oosperm in Higher Animals and Plants.

II

One at least of the two pairing-cells is often the product of a cell-division or a series of one or more

[1] In Uredineæ (the Rusts) syngamy takes place in two successive stages. The union of cells takes place in the formation of the Cluster-cup (Æcidium fructification); but it is *plastogamic*; the cytoplasts fuse, while the nuclei remain separate. The æcidiospores are binucleate; and at each successive fission in the Rust (Uredo) state the nuclei divide simultaneously. But *karyogamy*, nuclear fusion, only takes place at the end of the Rust state; and its issue are the *resting*-teleutospores, which on germination grow again to form the type that again eventuates in the Cluster-cup.

preceded by a series of cell-divisions *immediately* preceding the fusion: these are the "PROGAMIC FISSIONS," which we have now to consider. When the syngamy is bisexual, either the male cells or the female cells, or both. may be the produce of such progamic divisions. The special type most familiar to zoologists as universal in Metazoa (with the possible exception of the Alcyonarians, p. 163) is the so-called "maturation of the egg." The large cell gorged with reserves, produced in the ovary, divides into two, the one with the greater part of the cytoplasm and retaining the "egg" character, the other with a minute cytoplast, though its nucleus is the counterpart of the other. The former cell then undergoes a similar unequal fission, and the larger cell is now the actual female pairing-cell, or "oosphere," often termed "mature egg"; and the two small cells are called the "first" and "second polar bodies" respectively (the first polar body may also divide into two). This process may even be delayed until the entrance of the sperm into the egg. At the very commencement of the modern cytological study of fertilisation, in the late seventies, Bütschli, Giard, and especially Mark independently interpreted these divisions as the reversion to a protistic type of reproduction, to form a brood of four reproductive cells, the one functional, the other three abortive. This view sank into neglect before suggestions made a little later by Balfour and by Minot, who regarded the process as one of *elimination* into the small cells of something interfering with reproduction by syngamy. A modification of their views by Weismann led to the identification with this of over half a score of non-homologous "reduction processes," and a succession of theories. of which it may suffice to say now that they have had their day. One ground for these theories is the fact that in Metazoa, where progamic divisions were first studied, they are marked by their coincidence with the meiotic or reduction divisions, and eventuate in the reduction of the number of chromosomes in the pairing-cells to half of that obtaining in the tissue-cells (to be doubled anew by the fusion of two cells to form the oosperm and the new being). Soon, however, it was seen that reducing divisions occur to produce the tetraspores of the Archegoniate Cryptogams [and of the Florideæ and Phæocarpeæ], which do not pair, but germinate into distinct plants, from the tissues of which the pairing-cells are only produced after long tissue-generations; when it became obvious that "progamic fissions" and "reducing divisions" are phenomena *distinct though sometimes coincident*, and that a separate explanation was needed for the former.

Oscar Hertwig, in 1890, showed that in *Ascaris* the "maturation divisions" of the eggs are absolutely homologous with those that form a brood of four equal sperms in the male. In a paper completed a year later I showed by comparison with numerous data that the view of the three oldest observers was alone tenable.

In 1889 Oltmanns described a process in the Wracks (Fucaceæ) comparable with the formation of the polar bodies, but of crystalline transparency of interpretation when the different species were collated. As we have noted above (pp. 8, 88, Figs. 3, 21), the oogonial cell always divides into a brood of eight; in some species these are all equal and functional oospheres; in others four (4) are functional and four (4) abortive; in others two (2) are functional and six (6) abortive; in others, again, only one (1) is functional and the other seven (7) are abortive. If additional proof were wanted that the polar bodies have this signification, it was furnished recently by Francotte, who found that certain marine Planarians have exceptionally large "polar bodies," which may be "fertilised" by sperms like the "matured egg" itself. Thus the morphology of the progamic divisions of the eggs of Metazoa is established; and generally such divisions may receive the same morphological explanation, which I will definitely state thus, as I did in 1891: the most primitive pairing-cells are zoospores, produced by brood-formation (multiple cell-division), and their descendants have to be formed in the same way: tissue-cells can never act directly as gametes.[1]

[1] *Quart. Journ. of Micr. Sci.*, Decr. 1891.

The objection has been justly raised that this gives no adequate reason for the retention of an atavistic

FIG. 34.—Oogeny in the Wracks (Fucaceæ).

1, Female inflorescence of *Sarcophyces*. 2–9, Oogone of *Fucus* (common Bladder-Wrack), its liberation, division, and separation into eight oospheres. 10, Oogone of *Pelvetia* with two zoospheres functional and six dwarfed and functionless. 11, 12, Oogone of *Himanthalia* with one functional and seven rudimentary oospheres (not all seen). 13, Oogone of *Ascophyllum*, with four functional and four functionless (only three of each in view).

process, which could not have survived had there not been some definite physiological good to the race. But a survey of the facts seems to show that *nuclei* *can rarely if ever fuse unless at least one or other of them is fresh from fission.*

In most isogamous organisms, if the zoogametes fail to pair within a short time of their liberation, from the absence of members of other broods than their own, they become incapable of pairing, and either develop directly, as in *Ulothrix*, go to rest, or die.

In the isogamous Confervas the zoogametes are usually formed by a cell-division superimposed on those that produce the ordinary non-pairing zoospores: this is indicated by their smaller size and their frequent possession of only half the number of flagella of the others (Fig. 1, p. 4).

The Rhizopod *Trichosphærium* is apocytial: that is, nuclear divisions are not followed by the cleavage of the cytoplasm, so that the organism becomes multinucleate. It exists in two not wholly similar alternating forms, each of which is determined by the *resolution* of the apocyte into uni-nucleate cells, which escape as zoospores. In the First Form, produced from the zygote, these are formed directly by resolution, are incapable of pairing, and grow into the Second Form. In the Second Form the resolution into zoospores is immediately preceded by the simultaneous mitotic fission of all its nuclei, and the zoospores are exogamous gametes. In the Heliozoan *Actinophrys* two adults approach: before fusion the nuclei divide, and either mate is divided unequally into a large functional gamete and a small abortive one, "polar body." In the Fungus *Basidiobolus*, whose filaments are composed of a single row of cells, multiplying by transverse fission, at a certain moment the cells conjugate two and two; the cells that unite are apparently sister-cells. But this statement needs to be modified: in either cell the nucleus divides by mitosis, and two *cousin-nuclei* fuse, while the other two are cut off with a trace of cytoplasm as "polar bodies." In most Desmids two adult cells approach to pair, but either divides into two, which fuse respectively with those formed from the other original mate (progamete); so that the actual pairing-cells are not those that approached one another in actual cellular life, but their daughter-cells. In the Conjugate *Spyrogyra* the adult cells fuse by the outgrowth of tubes that meet and anastomose; but the nuclei long remain merely approximated without fusion in the zygospore during its long rest. It would seem from the results of Chmielewsky that either nucleus at the approach of germination undergoes fission to form a pairing-nucleus and one that aborts, and that it is these daughters of the distinct nuclei of the original pairing-cells that actually fuse at last as gameto-nuclei.

In Diatoms the cells that approach may either divide so as to form two pairs of gametes, as in Desmids, or they may themselves apparently pair; but the process of pairing is only completed after the nuclei have divided once or twice, only one of the daughter-nuclei in either mate being functional, and the rest abortive. Similar divisions produce the pairing-nuclei of the Infusoria, in which the mates (progametes) are also adult.

In the Ustilagineæ (the Smuts) the gameto-nuclei are probably sister-nuclei of the same undivided cell; but the Basidiomycetes afford so far no support for my present thesis, for the origin of the several (2–7) nuclei that fuse to form the nucleus of the basidium is not *known* to be from recent mitosis.

In cases of unequal fusion the sperms usually need to be produced long in advance and strongly differentiated, so that they are indeed incapable of fission, and consequently the progamic fissions are usually on the part of the female. On the other hand, not to deprive the female of its essential character of size, these progamic fissions are usually of the unequal type which we have already noted in the Metazoan egg and in some Wracks, as well as in many isogamous forms in Protista. [But in Florideæ (Red Seaweeds) the nucleus of the motionless spermatium divides into two on the trichogyne, and only one of these two enters the oosphere to fuse with its nucleus.]

In the Conferva *Œdogonium* the oosphere is differentiated by transverse fissions producing a vertical row, of which the upper cell is the oosphere, the rest sterile cells. The same is the case with the Characeæ or Brittleworts. Again, in the Archegoniate Cryptogams the sperms have to be formed well in advance to be ready for the conditions for their discharge and travel to the archegone, or flask-shaped body in which lies the central cell (Fig. 35). This cell undergoes two divisions, both unequal. The first division early forms a small cell, which lies in the neck (and may again divide), "neck-canal-cell," and a central cell which fills the belly of the flask; this

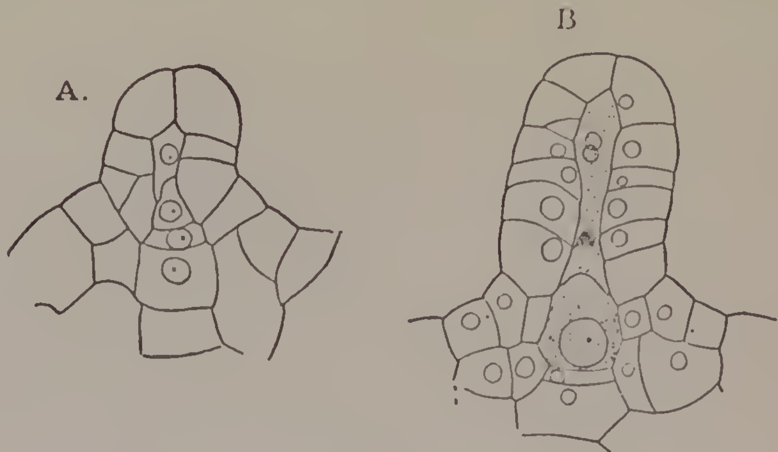

Fig. 35.—Contents of archegone of Fern.

A, The central cell has formed a brood of four by two consecutive divisions. B, The three upper cells are degenerating as canal-cells, the fourth has rounded off as the oosphere.

last cell only undergoes its unequal division very late under those very conditions that determine the travel of the sperms. The lower cell is here the oosphere, and the upper is an abortive cell known as the belly-canal-cell from its position at the apex of the belly of the flask.

In Flowering Plants the males and females are really homologous with the corresponding organs of the Cryptogams just mentioned, though certain difficulties of interpretation still exist. The pollen-grain and the embryo-sac are both formed a good while in advance, as each has to be ready on its side for the complicated process of pollination (including the growth of the pollen-tube, and the formation of the complex of cells in the embryo-sac, all naked, and including the oosphere), and therefore have arisen by early divisions. The pollen contains two nuclei—a "vegetative" and a "generative" nucleus: during the downgrowth of the pollen-tube the vegetative nucleus is in advance, and is connected with the growth of the tube and travel of the protoplasm; the generative nucleus divides in the tube itself into two, clearly homologous with the sperm-nuclei of the Fern,[1] and are carried down to the embryo-sac without performing any organic function to disturb their condition of "youth" before fusing with the oosphere. It was the consideration of the different relations of the progamic divisions in these two cases that first led me to lay down as an embracing formula the statement that *for fusion one at least of the two nuclei must be fresh from division.*[2] This is not yet, I admit, a full physiological explanation, but it is as near to one as we can at present go. It corresponds to what the physicist

[1] In the Cycadaceæ and in the Maiden Hair Pine (Gingko) the generative cell divides to form two well-developed spermatozoa; but the female cell here (oosphere) is fresh from division as in the Archegoniate Cryptogams.

[2] In many Coccidiaceæ a partial disruption of the nucleus of the "egg," and the expulsion of its fragments, replaces the unequal fission with the formation of functional oosphere and rudimentary polar bodies.

calls an "interpolation formula." He finds a series of results which, plotted out, give a curve, and that this curve can be expressed by an algebraical formula which embodies all the results obtained, and probably others to be ascertained by fresh experiment, though it would have been impossible to arrive at such by *a priori* reasoning. And with such formulæ we have often to be content as representing a distinct advance for the time in that systematisation of knowledge which we call Science.

An opinion broached in my 1891 paper which met with the greatest opposition, not to say discredit, was that nuclei contained in the same cytoplasmic investment, as, for instance, those of the Saprolegnieæ, might fuse, and so effect a truly syngamous process (endokaryogamy). Nowadays the cases where this occurs—namely, the Basidiomycetes, most Ascomycetes, the Ustilagineæ, as well as *Actinosphærium*, are very widely regarded as syngamous. And the conjecture of Boveri that certain cases of apparent parthenogenesis when only one polar body was formed might be truly syngamous, the nucleus of the imperfectly detached second polar body moving back and fusing with that of the oosphere, and so taking the place and the rôle of a sperm, has been brilliantly confirmed by Brauer, who has followed up the details in the Brine-shrimp *Artemia*. As we have seen, the second polar body is undoubtedly the morphological equivalent of an oosphere, and can in some cases be "fertilised" (*sit venia verbo*) by a sperm. This favours Maupas's view that in the actual process of syngamy there is neither "male" nor "female"; but that sex is in its origin a mere adaptation of the cytoplasm to ensure on the one hand a sufficiently large amount of cytoplasm and reserves to the young, and on the other enough mobility on the part of one gamete to ensure its finding the other and to favour crossing. This differentiation may be reflected back on the whole cellular cycle of the Protist or on the individual in Higher Organisms.

Lankester regards the independent germination of small zoospores as a case of male parthenogenesis, in cases where they never show any signs of pairing, and occur in a distinct stage of the life-cycle, as in the parasites of malaria, etc. (Hæmosporidia); but this seems to be an inversion of the facts. For pairing-cells assuredly originated from indifferent zoospores, which germinate independently; and where there are no symptoms of such zoospores being sperms gone wrong, we are not justified in presuming it.

III

Now, a very remarkable type of syngamy was first discovered by Boveri, as long ago as 1889. He found that the egg of Echinids, when shaken up, divides into fragments, only one of whieh can be nucleated ; that sperms enter whether these eontain the nucleus or no ; and that development follows in either ease. These experiments have been recently taken up and extended, notably by Delage, who has given the name of "merogony" to the process. Merogonic fertilisation has been obtained also by eutting the egg in pieees, and by piercing the vitelline membrane so that a portion of the egg cytoplasm protrudes and is separated off as an "extra-ovate." Giard has regarded it as really a parthenogenesis of the male which, when reduced to a differentiated sperm, has not sufficient cytoplasm for independent life. However, this assumes that the cytoplasm plays no part of its own in cell-life, but lies absolutely under the despotism of the nueleus—a view for which evidenee is absent. The differentiated sperm has but a minute investment of eytoplasm ; but, sueh as it is, it in Metazoa eontains the eentrosome, and may, in other respeets as in this, have the power of growing within the egg at the expense of the reserves during the very proeess of fusion with the female cytoplasm. Male parthenogenesis, strictly speaking, ean only exist where the sperm is slightly smaller than the oosphere, while the binary sexual differentiation is not too eomplete to afford it enough cytoplasm to start on a eareer of its own ; and the term should be reserved for cases of what may be ealled "anisogamy," whieh are notably to be found in certain Algæ, such as *Pandorina* (p. 14, Fig. 6) and the Ectocarpeæ.

The remarkable condition of the egg in Alcyonaria, where Hickson tells us that the female nucleus disappears completely as the egg matures, suggests that in this group the *germ-nucleus is entirely of spermatic origin* as in artificial merogony. Clearly we cannot speak of "*merogony*" where the *entire* egg is present to receive the sperm, if we pay any attention to the etymology of this word; and it is hardly old enough for us to forget it. But the essence of the process is that the cytoplasm of the germ is in this case almost wholly of maternal origin (with the above reservation), and the nucleus is wholly male. Therefore an Alcyonarian germ before segmentation, from which the unimportant ablation of a portion of the cytoplasm had been made, would be exactly equivalent to the merogonic germ of an Echinoderm. We will refrain from the creation of a new term to cover this process.

IV

With regard to the *function* of syngamy, taking the widest sense of the word, the only general formula that will cover the facts is that it *effects a cellular reorganisation that can be effected in no other way.* In many cases it takes place between cells or nuclei related by the closest bonds of cellular kinship, which is so much closer than Metazoan kinship. Where, however, the gametes are of different parentage, it undoubtedly, on the one hand, tends to breed out individual deviations from the norm, as Strasburger holds; and, on the other, it produces new combinations of individual variations which offer wider fields for natural selection, as Weismann postulates.

Finally, I would urge that no real advanee can be made in any branch of seienee so long as we use words without a preeise meaning attached to them, unless we perpetually bear in mind their ambiguity. We only hinder advance when we base theories of the most wide-reaching significance on facts obtained in a very limited field (such as, for instance, the study of reproductive processes in the Metazoa), and when we use such theories as Proerustean beds on to which we seek to make all other faets fit, whether by lopping them where they prove too much, or by stretehing them where they prove too little. For these reasons, as a student of Plant and Protistie life, as well as of that of Animals, I am grateful for the opportunity that my friend, the President, has given me of addressing Seetion D on the subjeet of fertilisation.

Summary

1. The term "fertilisation" as aetually used is too ambiguous for scientifie precision.

2. In its first and older physiological sense it denotes the starting into active cell-life and multiplication of a resting-cell, and should properly be regarded as one case of germination. The parthenogenetic development of eggs under chemical and mechanical treatment falls under this category.

3. In its second, morphological, sense, regarded nowadays as the "strict" sense, it denotes a process of cellular (or nuclear) fusion, and is better designated as "syngamy."

4. The terms "sexuality, sexual," etc., have been used also ambiguously, and would be advantageously (*a*) replaced by "syngamy" and its derivatives where no binary differentiation is necessarily implied, or (*b*) only used with the prefix "binary" where such differentiation is intended.

5. Syngamy is not necessarily associated with germination; on the contrary, in the most primitive types the cell freshly produced by syngamy (the zygote) passes into a condition of rest, or gives rise only to a limited brood of resting-cells, which will not germinate except after the lapse of time and under favourable conditions. The formation of a membrane round the oosphere at the onset of syngamy in Metazoa and Metaphytes is probably the last trace of this, the original consequence of syngamy.

6. Syngamy includes internal karyogamy, autogamy, "pseudogamy," and merogony, as well as the

pairing of separate individual cells. It seems possible that in the Alcyonarians the oosphere is non-nucleate, and that the nucleus of the oosperm is exclusively male, as in that produced by merogony.

7. Progamic cell-divisions come under three formulæ :

(*a*) Gametes are morphologically equal to zoospores, and are therefore produced by multiple cell-divisions.

(*b*) No tissue-cell ever becomes directly transformed into a gamete.

(*c*) Karyogamy (with the possible exception of the Basidiomycetes) is rarely possible where *both* the pairing-cells (or nuclei) have had a share in active cell-life or growth; therefore one or both must be fresh from division.

8. Progamic divisions and reducing divisions, though sometimes coincident (as in Metazoa), are not necessarily associated, but may be widely divided in the life-cycle where there is "antithetic alternation of generations."

The Rôle of the Sperm in Metazoa

This has been a matter of much debate. One school sees in it merely the bearing-in of the ferment that starts the oosperm into development, or of a new centrosome to the oosphere which has lost its own during the formation of the polar bodies.

Another school refuses to consider anything but the male nucleus, which indeed constitutes the bulk of the sperm at its entrance. Others, again, insist that however small be the cytoplasm of the sperm in quantity, it is by no means negligible in quality. A consideration of the facts as presented in Nature, and described and figured concordantly by numerous trustworthy observers, will convince us that the third view is a decided under-statement of the case.

The minute size of the sperm, with its bare envelope of cytoplasm, is correlated with the presence of large stores of unorganised reserves in the egg. When it enters, its nucleus is so concentrated and condensed that it cannot fuse with the female nucleus until it has attained a more normal condition; and for this purpose it must be nourished.

The first function, therefore, of the sperm on entering the egg is to procure this nourishment for itself, which it does by digesting some of the reserve of the egg; whereupon the cytoplasm of the sperm, with its centrosome, grows even more rapidly than its nucleus, till the organised living matter of the oosperm is seen to be largely constituted by this growth of the male element. This is clearly shown in the exquisite figures of Wilson (Echinoderms) and of Véjdovský and Mrázek (Oligochætes). We reproduce some of the latter (Fig. 36). Moreover, this secretion of a digestive ferment, and the consequent cytoplasmic growth, seems to explain fully the physiological function of the sperm here as an "activator" of segmentation.[1]

Now, we must insist that the yolk-granules are

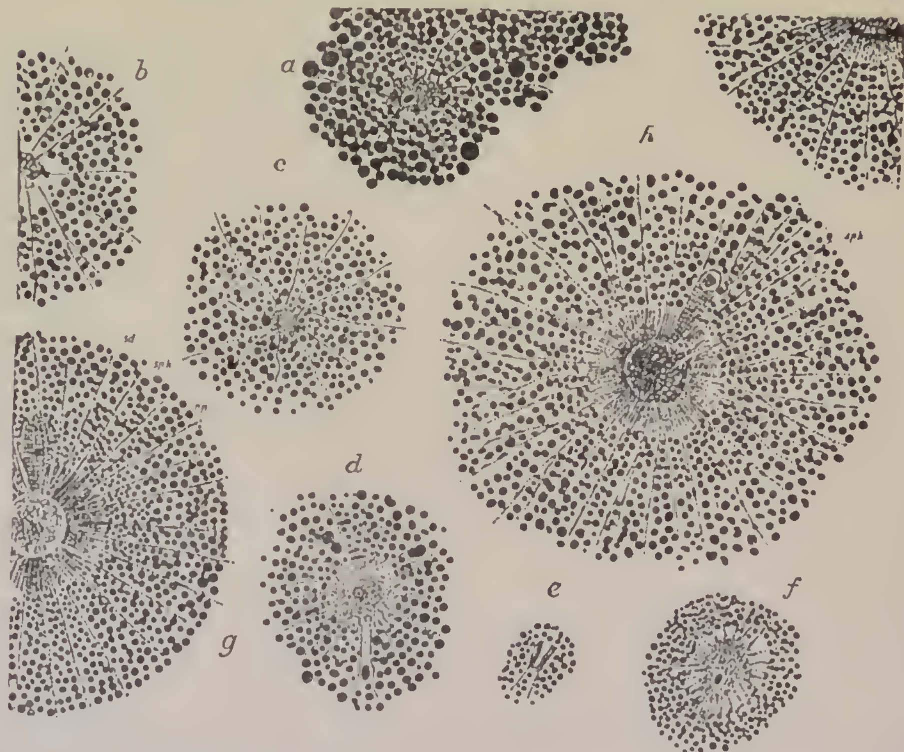

FIG. 36.—Growth of the sperm at the expense of the reserve yolk granules (black round spots) in the Pondworm (*Rhynchelmis*).

a, Young sperm nucleus and centrosphere with radiating processes. *b*, *c*, Successive sections through sperm centrosphere and nucleus; in *c* the tail is still seen persisting. *d*, A later stage with centriole (dot in central circle). *e*, *f*, Two consecutive sections at a similar stage. *g*, *h*, Sperm nucleus in cytoplasmic sheath projecting from the radial, alveolar cytoplasm outside the centrosome; the long rays seem here to serve as feeders, like the pseudopods of Heliozoa or Radiolaria.

not living matter at all, but mere inclusions within the living cell, absolutely comparable to starch-granules. The nature of protoplasm is determined

[1] [Loeb in his recent work has suggested the formation of oxidases (ferments determining that low-temperature combustion which liberates the energy for segmentation) as the physiological function of the sperm, which may be replaced artificially. To us it appears that the digestive function is of primary importance.]

by its origin rather than by its food, so that the fact that the male cytoplasm grows in this way within the egg does not lessen its essential maleness.

Complete conjugation in many Animals only takes place, we may say, with the formation of the segmentation spindle, when the male cytoplasm is probably equal in bulk to the female cytoplasm.

We have noted above that the oosperm in primitive types of syngamy has usually the character of a resting-cell, whereas the fertilised egg of binary sex in many cases among Higher Organisms immediately undergoes brood-division (segmentation). The key to this difference probably lies in the fact just recapitulated. Since the sperm must grow for the conjugation to take place and therefore secrete an enzyme to digest the food-granules, the female cytoplasm itself will also grow in presence of this digested food, as is clearly shown in the figures we have referred to. We have seen that such metatrophic growth at the expense of intra-cellular reserves is the starting-point for brood-division in general. Thus the impulse for division given by the sperm is no essential phenomenon of syngamous union: it is conditioned by the differentiation of binary sex, for it is the indirect consequence of that reduction of the sperm which makes its growth within the egg the necessary prelude of complete fusion therewith.

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P.S.—For the relations of Nuclear Reduction to Mendelian Inheritance see "Heredity" in this series, by Prof. J. Arthur Thomson.

TABULAR VIEW OF THE BEHAVIOUR OF THE ZYGOTE

1. The zygote is free or set free early, or is formed within a free cyst.

A. It is active in the medium.

It displays the ordinary behaviour of the species.

i. *Trichosphærium*, Marine Foraminifera, *Trypanosoma* (?), *Mastigella*, *Opalina*, Infusoria.

It segments into a number of zoospores.

ii. *Noctiluca*.

It is amœboid, but soon comes to rest, invests itself with a membrane and grows into a filament.

iii. Bangiaceæ.

It is amœboid, enlarges, encysts, and undergoes two successive modes of brood-formation to form a host of sickle-shaped zoospores that migrate to the salivary glands.

iv. Hæmosporidia.

It is flagellate, swims to a host-plant, encysts, and sends a tube into the plant.

v. *Chlorochytrium*.

It is flagellate, but soon comes to a standstill and germinates into a multicellular plant.

vi. Several Siphoneæ, *Cladophora*, Phæocarpeæ.[1]

It is flagellate, but soon comes to a standstill, encysts, and passes into a resting-state, during which it may at first enlarge.

vii. Most Chlorophyceæ (Green Seaweeds), including Phytoflagellates.

[1] In the Wracks (*Fucaceæ*) it is not flagellate, but moves by attached sperms that have failed to penetrate.

B. The zygote is not active, but, unless formed within a cyst, surrounds itself at once with a cyst-wall, or, if already provided with a perforated wall, closes the apertures, so as to form a "zygocyst."

It goes at once to rest as a "hypnozygote," in which nuclear division sometimes takes place.

viii. Many Rhizopods (*Entamœba*, *Chlamydophrys*, *Centropyxis*), *Actinosphærium*, *Actinophrys*, some **Diatomaceæ, Conjugatæ, Ustilagineæ, Uredineæ.**

It may undergo partial segmentation, but then goes to rest and will not germinate till a certain period has elapsed, or under special conditions.

ix. **Winter eggs of Turbellaria, Rotifers,** and certain **Crustacea** and **Insects,** whose summer eggs, which germinate directly, are parthenogenetic.

The zygotes are formed in numbers within a common cyst,[1] and each again encysts and immediately forms a brood of sickle-shaped zoospores, which are not liberated except as in ix.

x. **Gregarinaceæ.**

The plasmatic contents of the zygocyst at once divide into a brood of spores, which themselves encyst, and behave like the zygotes of x.

xi. **Coccidiaceæ.**

The plasmatic contents of the zygocyst undergo brood-division into simple spores, which may encyst and rest or be active zoospores on liberation.

xii. Several **Flagellates,** according to Dallinger.

[1] Two "*associated*" cells form a common cyst within which either breaks up into a brood of gametes, equal or sexually differentiated.

C. The zygocyst germinates at once to produce the typical animal or plant. This is the case that has been taken as the type by those who write of "Chemical Fertilisation."

xiii. **Fucaceæ (Wracks), Cladophoraceæ,** most **Metazoa.**

2. The zygote is produced within the parent, and remains there for some time, and is often parasitic upon it.

It segments within into a number of spores enclosed in a multicellular investment of parental origin.

xiv. **Florideæ (Red Seaweeds).**

It goes to rest within a preformed investment of parental origin.

xv. **Characeæ (Brittleworts).**

It develops at once as a parasite on its mother, but may soon go to rest in an investment derived from her or formed by her.

xvi. **Archegoniate Cryptogams, Gymnosperms, Flowering Plants, Ovoviviparous Amphibians** and **Fishes, Mammals.**

It may undergo partial segmentation within the parent, but is invested with a firm investment by the mother and is extruded.

a. It develops immediately.

xvii. Most **Fishes, Amphibians,** and **Reptiles.**

b. It goes to rest, and further development is only completed under certain conditions.

xviii. **Birds.**

3. The zygote is formed within the parental cytoplasm inside the cell-wall.

It goes at once to rest as a hypnozygote.

xix. **Phycomycetes, Ustilagineæ (Smuts), Uredineæ.**[1]

The zygote-nucleus undergoes brood-divisions, and the brood-nuclei attract a portion of the parental cytoplasm to form resting-spores, which often only germinate after rest and under special conditions.

a. The resting-spores are differentiated within the maternal cell-cavity.

xx. **Ascomycetes.**[2]

b. The maternal cell gives off processes into which the brood-nuclei pass, and which are cut off as hypnospores.

xxi. **Basidiomycetes.**

N.B.—I have endeavoured to make the above list fully repre-

[1] In **Uredineæ** (Rusts) the process of syngamy is divided into two stages separated by a long interval. *Plastogamy* first takes place—leading to the formation of cluster-cups (*Æcidium*)—by the union of two cells whose nuclei remain distinct. In all subsequent divisions during the Rust state the two nuclei divide simultaneously as "conjugate nuclei"; finally, immediately after division, each pair of nuclei undergoes fusion, and around each of the fusion-nuclei the protoplasm aggregates to form a resting-spore. Here *plastogamy* is followed by growth, *karyogamy* by rest.

[2] In some of the Ascomycetes, such as the **Blue Moulds** (*Eurotium*), the zygote germinates at once into a specialised part of the surrounding fungus on which it is parasitic, and within which it finally forms (by brood-formation) resting-spores.

sentative; but we still lack certain uncontroverted evidence of the syngamic processes of many of the lower organisms. In drawing up this table, besides consulting many original papers, I have freely utilised Oltmann's "Morphologie und Biologie der Algen" (1904) and Doflein's "Lehrbuch der Protozoenkunde" (1909).

CHAPTER VII

THE TRANSMISSION OF ACQUIRED CHARACTERS[1]

The merit of Charles Darwin was to present a theory of descent in a form which gave at least two *veræ causæ*: (1) The existence of variations, and (2) the survival of the fittest in the struggle for existence—or, to use that expression, really negative, which has found widest circulation, "natural selection." The causal factors of variation were but lightly touched by him, but in many places he laid great stress on the transmission to the offspring of characters acquired by the parent in response to the prolonged influence of external conditions—the inheritance of acquired characters which was recognised by his predecessors, and is usually termed "the Lamarckian factor." Since his death his co-discoverer, Alfred Russel Wallace, together with many who claim the right to wear Darwin's mantle,

[1] [A great body of additional experimental evidence on this question has grown up during the last three or four years: it is ably summarised and discussed by R. Semon in his essay, "Die Stand der Frage über die Vererbung erworbener Eigenschaften," in *Fortschritte des Naturwissenschäftlicher Forschung*, vol. ii., 1911.]

and who boast the title of his direct heirs, have rejected this factor as non-existent: to them variation is always blind, with one exception to be referred to later on; it takes place in no efficient correlation with external conditions, however strongly these may affect the parent organism. That this assumption adds immensely to the difficulties in the way of the evolution of new species well adapted to their surroundings, they admit without the smallest embarrassment. That, while the *organism* has a power of adapting itself to widely diverging conditions, the *race* could, on their showing, only do so by the slow process of eliminating the less fitted to survive, appears to them to be a matter for rejoicing on the whole—*credunt quia impossibile.* For while, like the majority of biologists, they appear to trouble very little about theology and its dogmas, they have elevated the non-transmission of acquired characters to the rank of a biological dogma, held more fervently in proportion to its difficulties; and they have gone very far on the way to the formal excommunication of those who cannot swallow it. In their exoteric utterances in lectures, essays, and letters to the newspapers, intended to reach the general public and to initiate them into the arcana of Science, they have denied all scientific value to contrary opinions or even to cautious suspension of judgment, and have implicitly or explicitly treated opponents and hesitators alike as a set of benighted nincompoops.

Thus it has been possible for writers of great individuality and original merit, taking their biology at second-hand from these self-proclaimed experts, to found wide-echoing social theories, such as Mr. Benjamin Kidd's "Social Evolution," on this doctrine as on a bed-rock; which, however, many competent surveyors, whom they know not, would describe as an inadequate footing or "raft" of concrete floated on a very quicksand of shifting views. It, therefore, behoves us to present in an accessible place and a readable form some arguments against this dogma that carry with them many, possibly the majority, of working biologists. And since the authority of scientific unanimity is claimed for the so-called "Neo-Darwinian" dogma, we shall recall the names of a few eminent leaders who repudiate it.

I

What is an "acquired character," such as might be transmitted? We should define it as a change in the characters, anatomical, physiological or psychologieal, determined by its environment, and usually one that will make it more efficient under changed conditions of life. This needs some discrimination. If the skin of a fair person be exposed to the more refrangible (the so-called "actinic") rays of light, as to sunlight on a snowfield or to the electric arc, it will become inflamed and blistered; this is mere damage, such as will probably be repaired by the healthy reaction of the organism; the "burn" will heal or suppurate, and we do not anticipate its transmission. But if a more lasting and less severe exposure induces tanning of the skin, which decreases the susceptibility to severe sunburn, we might look for a more pigmented skin in the offspring. We have no statistical account of the complexions of children of returned Anglo-Indians that would enable us to pronounce as to whether this does actually occur or not. But the fact that even in black races the permanently protected parts of the skin, such as the palms of the hands, are lighter in colour, suggests that the deposit of pigment in the skin was originally an adaptation that has by repeated transmission gained a high degree of permanency.

Much has been made of mutilations; it is well known that these repeated for thousands of years on the young of the human race are not transmitted, and have to be repeated in each successive generation. The same reasoning applies here as to the sunburn. Now, if a Newt's foot is cut off, the stump will grow into another foot; the same holds for a Lizard's tail: and for the limbs of Insects and other Invertebrates, *regeneration*, not *deficiency*, is the adaptive response to mutilation. Moreover, any tendency to transmit such deficiencies would in course of time result in a generation of formless imperfections, that must needs be eliminated by Natural Selection. The non-transmission of mutilations has been one of the arguments in favour of Weismannism, and we therefore dispose of it at once to clear the ground for more important points.

But before we come to these we must consider what is the *a priori* ground that has led naturalists themselves, not wholly devoid of that merit and reasoning power which they deny to their opponents, to assert the impossibility of such transfer. The reproductive bodies are not formed of a secretion in which the whole organism takes a part: in complex animals they are cells set apart at a very early stage in the development of the individual, and take no direct share in the life of the parent, which may almost be held to play the nurse to them in the way of feeding them ;—to push the view to an extreme, the reproductive or germ-cells are *in* the body, not *of* it (Fig 37). This was recognised in theory first by Francis Galton, who distinguished between the body, or "soma," and the aggregate of germs, the "stirp." Now, these reproductive cells may be fed, and grow and multiply at the expense of the nourishment brought to them by the organism in which they lie; but, so far as we know, there is no nervous apparatus connecting them with the body, to influence them; and without nerves we know of no transmission of impulse in animals. Therefore, for the majority of adaptations, there is no *ascertained mechanism* of transfer from the soma to the stirp, and as a consequence there *can be no transmission.*[1] This assumes the canon: "No mechanism can exist that escapes the modicum of knowledge that we have gained during the century and a half or so that we have had to learn physiology." We ourselves are provided with so magnificent and complex a nervous system for recording and correlating for the individual his relations with the external world, that we are tempted here to be over-anthropomorphic, and to assume that the germ-cells need somewhat of the same kind to receive and transmit impressions to them. The reasoning seems premature; and, to use an old comparison, it recalls the poor little girl from the barrack workhouse school, who, when first boarded out, said she could not wash a single handkerchief in a basin, for lack

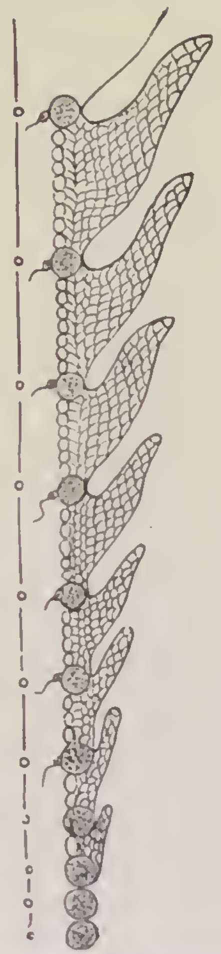


Fig. 37.—Diagram of relations between the reproductive cells ("stirp") and body ("soma") through several generations

The larger circles are the productive cells, interrupted by syngamy at the successive generations, shown by the fusion of the sperm with the large, well-nourished reproductive cell—the egg or oosphere. The triangular masses of cells to the right represent the successive "bodies." The lowermost cells represent reproduction by direct division in Protists, and as we rise we find an increase in the proportion of body to germ.

[1] See p. 68 f.

of the appliances of the steam laundry to which she had been accustomed.[1]

II

The stirp of Francis Galton, the germ-plasm of August Weismann, is, however, even in the estimation of the Neo-Darwinians, under the dependence of the soma or body at large in one important matter—the commissariat: it grows within the body, and must be nourished by it. If, then, the nature of the food-supply be altered in respect of the adaptation of the body to external conditions, the germ-plasm will undergo corresponding changes. This is well shown in the case of "immunity" to microbic diseases. When such a disease invades the body, if the invasion be not too strong, and provoke untimely death, the organism forms certain substances which act as antidotes: they are called "antitoxins," or "antibodies" (a barbarous name, indeed); but we may here use the vulgar name of "antidotes." Well, such antidotes must be formed in, or pass into, the germ-plasm, when the offspring will be born with the same immunity as the parent body has acquired,

[1] In Plants, which show purposive and co-ordinated reactions of the whole to stimulation of the parts, all research has failed to show any central controlling apparatus whatever comparable with the central nervous system of Animals; or, indeed, to adequately demonstrate a mechanism corresponding with their nerve-trunks and branches.

and retain this immunity for a time, which is, indeed, often limited, just as the immunity of the parent is often limited. Instances of such transmitted immunity are well known, and need not be cited here.

Again, the progressive weakening of the body, due to inadequate nutrition, may also be transmitted to the germ, and constitutional weakness may thus be inherited even when it was not congenital in the parent, but only acquired. It seems not unlikely that the effect of abuse in alcohol, weakening the will of the parent, may in the same way be transmitted to the offspring, though Dr. Archdall Reid will not have this at any price. Moreover, there are a number of phenomena of nervous reactions to the medium, which may be transmitted. I cite one (of which I have personal knowledge), which was recorded in *Nature* for March 14, 1891.

"A.B. is moderately myopic and very astigmatic in the left eye; extremely myopic in the right. As the left eye gave such bad images for near objects, he was compelled in childhood to mask it, and acquired the habit of leaning his head on his left arm for writing, so as to blind that eye; or (when this was checked) of resting the left temple and eye on the hand, with the elbow on the table. At the age of fifteen the eyes were equalised by the use of suitable spectacles, and he soon lost the habit completely and permanently. He is now the father of two children—a boy and a girl—whose vision (tested repeatedly and fully) is emmetropic,[1] so that they have not inherited the *congenital* defect of their father. All the same, they both have inherited his early *acquired* habit, and need constant watchfulness to prevent their hiding the left eye, when writing, by resting the head on the left forearm or hand. Imitation is here quite out of the question."

It was objected at the time by Sir Ray Lankester that the habit of leaning the head on the left arm or hand is so common among children beginning to write that no stress can be laid on this. To this the reply is that in no other children have I seen the attitude assumed so as to mask the left eye: most children who lean squint obliquely along the pen with both eyes; and the resting on the left hand supported by the elbow on the table is equally exceptional.

In the embryonic development of most Animals, the external layer that forms the general epiderm grows in along the middle line to form the central nervous system, which is ultimately buried deep within the body, like the brain and spinal cord in Man; and the nerve-branches to connect it with the surface then grow out between the other tissues and organs to reach the surface again. The only formula that has ever been put forward to explain

[1] I should qualify this by noting that the girl a few years later developed slight astigmatism, asymmetrical in both eyes.

this extraordinary migration and roundabout way of growth is that of F. M. Balfour: he suggested that the superficial layer of cells, that had first acquired nerve-characters from its direct relations with the outer world, had in successive generations become buried for protection, and that this adaptation required by the individual had become displaced in time in its heirs until it appeared in the very early stages of development. But in all Weismann's elaborate tapestry of interwoven hypotheses, not one thread is found as a clue to explain the extraordinary displacements, migrations, and outgrowths of the nervous system from its surface origin in the skin-layer of the embryo.

A whole series of unpleasant nervous changes produced in Guinea-pigs as the indirect results of certain wounds to the central nervous system are reproduced in their offspring, though the actual injuries were not of course reproduced in their young. These were observed by Brown-Séquard, and confirmed in many respects by G. J. Romanes.[1]

It is interesting in this connection to note that the overwhelming majority of psychologists who

[1] [I have always felt some hesitation about these cases as involving the transmission of *hurtful*, not *adaptive* characters, to which, of course, the reasoning about mutilations should apply. T. Graham Brown, on repeating Brown-Séquard's experiments, has found it possible to put a different interpretation on the results; however, his paper is not, I think, final or conclusive (see *Proceedings of the Royal Society*, Series B, vol. lxxxiv. (1912), p. 555 f.).]

accept the descent theory invoke the transmission of acquired characters to explain many phenomena of innate instincts, such as those of the Pointer and the Setter. The Neo-Darwinian ascribes all these to casual impulses, arisen by variation without rhyme or reason, and once present, growing stronger in each generation by the selection for breeding of those that evince them in the strongest manner.

The transmission of acquired characters in Plants from the highest to the lowest is admitted by all to a certain extent; but the Neo-Darwinian explanation is in every case that whatever acts on the plant acts directly on the germ-plasm. We may cite a few cases. In unicellular plants, such as bacteria, there is no distinction of soma and germ. The transmission of the characters of these under new modes of cultivation creates no difficulties either way. In low multicellular Plants, such as Moulds, changes in the medium in which the vegetative organs grow result in the formation of reproductive cells from the aerial parts, which have never dipped in the liquid; and these are better adapted to the special culture liquid than the original Mould. Here, too, the Weismannite holds that the conditions have also been such as to influence the germ by the nutritive substances passed up to it.

We come to the higher group. Cereals from seeds raised in Central Europe, when cultivated in higher latitudes nearer the Arctic Circle, ripen their seeds earlier and earlier. Such seeds produced after a year or two, when sown again in Central Europe, ripen their seeds as much as twenty-five days earlier than seeds that have been raised in continuous succession in their original home. Here, again, it is said that the effects of the long Northern days have affected the germ-plasm simultaneously with the plant at large. But why should the effect on the germ-cells of the seed be the same that has been so beneficial to the plant itself? Why is there *correlation* in this respect? The Neo-Darwinians appear to look at the individual elements of the organism as existing "on their own," *an und für sich*, and omit to notice that the connection of cells and organs everywhere determines peculiarities for the common good, which are replaced by other characters when they are separated.[1]

Within the last few months Kammerer has published a most striking instance of Lamarckian transmission in the two Salamanders of Central Europe.

[1] This co-operation is nowhere better shown than in certain facts of experimental embryology; when cells are separated at an early stage they develop to form complete organisms, instead of parts of organisms (see p. 236, Fig 28). In some Flowering Plants again, the cells of the leaf, mere nutritive cells whose duty it is to form organic substances from the inorganic food materials, if severed more or less completely will at once beget propagative cells and form embryonic tissue which may regenerate the complete plant (see pp. 65-6). If the end shoot of a conifer be removed, one of the first circle of horizontal branches below will gradually rise up and replace the "lost leader."

The Spotted Salamander (*S. maculosa*) is a lover of damp places: it produces numerous young, provided with gills—tadpoles, in fact—which it expels into the water, where they stay until they have exchanged these gills for lungs, when they come upon land. The Black Salamander (*S. atra*) is essentially a land animal; of its numerous fertilised eggs two only, the first in either oviduct, develop, living at the expense of their more sluggish sisters: they pass through their metamorphosis within the mother, and are born as lunged animals to live from the outset on dry land. By appropriate surroundings from birth the two species can be brought to exchange breeding habits, the Black Salamander producing a number of tadpoles for the adjacent water, and the Spotted only two lunged young fit to live on the land where they are born. Now, if the broods of exchanged characters be brought up under their proper original conditions, their brood is born not in the normal way of its respective species, but in the *changed* method that had been forced upon their mothers. It is most noteworthy that this change is a nutritive change indeed; but one secondary to what we may call a psychical change. It will be interesting to await the explanation of this acquired character on the germ-plasm theory, and to see what new subsidiary hypothesis will be spun to include this apparently glaring anomaly within the all-embracing net of Weismann.

[Since the above was written Kammerer has extended his experiments to the Obstetric Toad (*Alytes*)[1]. In the Toad, the male winds round his legs the eggs as they pass in a continuous string from the female, and retires to a dark hole during the day, coming forth at night to moisten his living burden in the water. The tadpoles finally hatch out into the water on one of these excursions, in a much more advanced state than that of the tadpoles of most Amphibians. On raising the temperature in which these Toads are kept to 77–86° F., the animals seek the water more freely, and pair in it: the eggs no longer cohere into a string, but fall separately into the water. After a time the males cease to try to wrap the eggs round their legs; and, moreover, the eggs laid by the female are much smaller, and the tadpoles hatched from these leave the egg at an earlier stage of development. Now, the young bred from the parents whose habits had been thus changed displayed the *new* habits, although kept under the normal conditions; they sought the water for pairing, the eggs were small, and the tadpoles hatched out in the early stage. So far this is a most interesting parallel to the results already obtained with the Salamanders. Kammerer carried the experiments a stage further here, and started breeding between individuals of

[1] "Mendel'sche Regeln und Vererbung erworbener Eigenschaften" in "Festschrift zu Mendel," 1911.

the same species, with the one parent a normal animal, the other the offspring of those that had inherited changed behaviour. He found the characters thus acquired behaved as unit (" *allelomorph* ") hereditary characters to the normal ones, and *Mendelised*[1] just as do the unit characters which have arisen spontaneously, or have been transmitted for generations. Of course, for the meaning of this statement I must refer the reader to Prof. Thomson's " Heredity " in this Series.]

Strange as it may appear, the bones and joints are exceedingly plastic, and adapt themselves to new situations and postures with wonderful facility. Thus, after fractures and dislocations, the bony framework is altered to supply new strength, and new joints replace the original more or less efficiently. Still more noteworthy is it that indications of postures and arrangements that are only effective in after-life appear even before birth ; the widening of the female pelvis, that only finds its explanation in the roominess that will be needed during pregnancy, makes itself apparent in advanced childhood, before puberty. Havelock Charles finds that the races that habitually squat and sit tailor-fashion on the ground have adaptive peculiarities in the hip, lower limbs, and

[1] Male normal and female modified gives *modified* character *dominant* ; male modified and female normal gives *modified* character *recessive* : in other words, the character of the male, whichever it be, is *recessive*.

foot-joints before birth. Now, these are absent from the modern Europeans, while they were probably present in their Neolithic ancestors, who were buried in *their* proper resting position, as, indeed, their descendants are buried nowadays in our resting position; only, that position was for the Neolithic man squatting on the heels (or, rather, the sole of the foot), not sitting on seats nor lying down.

Now, if such changes have come about so as to be visible before the habit has been acquired, how can they be accounted for? Surely by the assumption that the response of the bones and joints to the demands made by habits of life has been transmitted, so that it appears in the individual at an early stage. This case has long been known, and has been accounted for on Weismannic grounds; but the explanation put forward is too subtle for these pages; it is absolutely inadequate, and makes greater demands on faith than the admission of an unknown mechanism for transmission of an acquired character.

We may here indicate one possible method of transmission of even these by what we may term "special substances." It is found that when the thyroid body (which, when swelled up, is the well-known goitre of certain mountain valleys) is disordered, so that it does not provide the body with its special secretion, a disease of the mind—sluggish thought and quick temper—comes on, accompanied by certain changes of character: thus the secretion of the thyroid determines certain psychical results. If now to the sufferer be fed rations of the thyroid (usually dried, powdered, and compressed into tabloids), the nervous changes do not occur. Thus the presence or absence of certain substances will affect the nervous system, and conversely it is possible that every nervous change of adaptation to the surroundings may thus induce the formation of substances in the body, which, fed up to the germ-plasm, give the impulse to corresponding changes in the offspring.[1]

Thus there is no lack of *a-priori* presumption for the transmission of acquired properties, the "Lamarckian Factor" being characteristic of organisms generally; and this will even fit into the form of a symmetrical logical syllogism. (1) The Factor is one of extreme utility to the race, and useful characters tend to be retained. (2) If, then, it existed in the primeval ancestors of Higher Organisms, it would probably be retained unless its retention were a physical impossibility. (3) Now, *it undoubtedly does exist* in many Protista, which biologists agree are equivalent to the ancestors of

[1] We gave a hint of this possible explanation in "Fundamental Principles of Heredity" in 1897 (see above, p. 78). It has since been developed by J. T. Cunningham ("Arch. f. Entwicklungsmechanik," 1909): see below, p. 264.

Higher Organisms. (4) Again, its persistence in Higher Organisms *is not physically inconsistent* with the cellular differentiation characteristic of these; for it has been demonstrated in at least five different cases—the precocity induced in cereals by cultivation at high latitudes, the transmission of certain human adaptive habits, the facets of squatting races (or possibly their loss in the sitting and lying ones), the widening of the female pelvis, the breeding characters of the two European species of Salamander. Hence, we conclude, *it is extremely probable that the power to do this is generally present.*

III

We have pointed out a few cases readily explicable by the transmission of acquired characters—the so-called "Lamarckian Factor." The inference in Plants is admitted by most; those in Animals find their readiest explanation on this assumption. On the other hand, Weismann and his school, finding the absence of recognisable mechanism for such transmission an insuperable difficulty, have taken refuge in a theory that professes to explain all. The theory is extremely complex, but we may give a selection of its principal features. Each germ-cell contains in its nucleus a special "germ-plasm," or "idioplasm," made up of entities called determinants. These grow with the cell, and when the cell divides, each determinant divides into two identical determinants, one for either cell. During and by means of the cell-divisions which give rise to the organs of the body, these determinants (or, rather, their offspring and their like) are sorted out and distributed to the various organs, whose character they *determine* by their respective numbers, qualities, and dynamic energy (whence their name). Any given case can be explained by assigning the requisite qualities to its determinants. Moreover, any new case, as it arises, can also be explained by the inexpensive method of spinning out a little ingenuity, to invest the determinants with fresh qualities, active or dormant. Further, since a complete set of determinants lies in the nucleus of each germ-cell, where it is nurtured by the food soaking in from the body, we are told that these determinants must compete among themselves for their share of their food ; thus there is a "struggle for existence" among these determinants, and the fittest survive—the process hypothetised is called "Germinal Selection."[1] As the determinants correspond with the organs, and the organs show a magnified picture of the determinants of the germ, the apparent acquisition by the organism of new characters better suited to the environment is really due to the antecedent growth in vigour of the special determinants needed to produce

[1] This is the latest form of Weismannism ; but we may still look forward to future modifications of theory and "development of dogma."

this effect; and Lamarckian transmission is simulated so as to deceive the unwary and unenlightened.[1]

But we need not weary the reader by further elaboration. Suffice it to say that in all the nuclear divisions in the multiplication of the cells for the tissues and organs of the body, the visible nuclear elements divide in a most complete *partitive* manner, so as to ensure as far as possible equal distribution of these elements to the two sister-cells, however diverse be their ultimate goal; and that thus the theory lacks objective foundation just where it should be forthcoming. Did we follow the procedure of many Weismannists—or "Neo-Darwinians," as they call themselves—we should go on to say, "accordingly the theory must be rejected by all writers capable of forming a valid judgment." We do not go so far, for we greatly admire the theory as a brilliant piece

[1] [The hypothesis has been made more complex by its retention of that of "ids" (see p. 16 f.). Each id is conceived as a complete set of determinants; and Weismann, lucid as he usually is, nowhere defines what share is taken by the id as a whole, or by the several determinants in each id, in the struggle for nutrition on which germinal selection depends. Prof. Arthur Dendy in his valuable "Principles of Evolutionary Biology" (1912), puts very clearly what many have found a difficulty in the hypothesis of germinal selection, even as a mere formal explanation: "There would seem, however, to be a serious objection . . . in the fact that the nucleus of any germ-cell contains many ids, and that similar determinants must as a rule recur in each id. We can hardly suppose that the recurring determinants in each id are always subject to precisely the same advantages or disadvantages of position. It seems much more likely that variations in this respect in different ids would tend to neutralise one another, the kind of determinant which is unfavourably situated in one id being favourably situated in another, so that each kind would, on an average, have the same chance of nutrition" (p. 173, note).

of constructive ingenuity; but our admiration is purely æsthetic.

IV

Such arguments as we have given in brief have not been without weight among biologists of the highest eminence. As we have seen, Charles Darwin laid much stress on the Lamarckian Factor, and G. J. Romanes shared his views; Herbert Spencer advocated it in these pages [*The Contemporary Review*] some fifteen years ago,[1] and broke many a lance here with August Weismann; Ernst Haeckel, the Nestor of living zoologists, who rose into eminence in the early sixties as the most brilliant advocate and developer of "Darwinism," has never wavered. And even the flood-tide of Weismannism failed to carry conviction to many in the forefront of biological research and thought, who have clung to the doctrine of transmission of acquired characters, and rejected the complex theory of Weismann. Thus Oscar Hertwig, one of the founders of our present knowledge of cell and nucleus, one of the discoverers of the true nature and meaning of fertilisation, regards the transmission of acquired characters as proven. He declares that the determinant theory cannot explain the essence of organic development, and that the fundamental assumptions on which it is based are philosophically erroneous ("Schon in philosophischer

[1] [Written in 1908.]

Hinsicht beruht sie auf falschen Grundannahmen," "Allgemeine Biologie," Ed. 2, 1906, p. 460). On Germinal Selection he remarks:

"To escape the difficulties of explaining hereditary transmission, Weismann has put immeasurably (unendlich viel) greater difficulties in the way of a causal explanation of organic development. Anything like an adequate disproof of transmission he has given in none of his writings" (*op. cit.*, 621).

Let us turn to Yves Delage, one of the most skilled zoologists of France, distinguished especially by his brilliant researches on induced parthenogenesis,[1] no less learned in modern theories than able in his criticism of them; and what do we find? He says of Weismann's biophores (supposed units that are grouped into determinants):

"If they are possible they are useless; if they are useful they are impossible. . . . Thus the biophores are useless or incomprehensible, the number of determinants is inadequate. . . . The whole base of the theory is undermined and destroyed. . . . If we admit the possibility and existence of the whole constitution ascribed to the germ-plasm, we can show that the crown of the edifice is as flimsy as its foundations."

Felix Le Dantec, the glory of the French school of Mechanicists, writes, curtly enough:

[1] Better known perhaps under the absurd but catchy title of "Chemical (or Physical) Fertilisation" (see p. 142).

"Strictly speaking, there is never any hereditary transmission except of acquired characters. Yet a whole school of naturalists have for some years tried to deny the possibility of such transmission. To deny it is the logical consequence of the fanciful system of Weismann" ("The Nature and Origin of Life," Eng. ed., 1907, p. 200).

E. B. Wilson, of Columbia University, New York, whose book on "The Cell in Development and Inheritance" (ed. 2, 1900), is in the hands of every student of biology, writes on the biophore-determinant theory that "it demands for the orderly distribution of the elements of the germ-plasm a prearranged system of forces of absolutely inconceivable complexity" (p. 432). On the transmission of acquired characters, he writes (with complete reserve):

"Whether these variations first arise in the idioplasm of the germ-cells, as Weismann maintains, or whether they may arise in the body-cells and then be reflected back upon the idioplasm, is a question to which the study of the cell has thus far given no certain answer" (p. 433).

[Wilhelm Roux, editor of the *Archiv für Entwicklungsmechanik*, and one of the most distinguished of experimental embryologists, who accepts in many respects Weismann's views on preformation, writes:

"The hereditary transmission of variations arising in the body [what we term 'acquired characters'] is thus a most complex process dependent on the exact fulfilment of numerous conditions; so that we are not astonished to find it of regular occurrence in only limited categories of cases."[1]]

The majority of English botanists, like Prof. Reinke of Kiel, have ranged themselves on this side or at least have imitated Wilson's reserve. Prof. S. H. Vines, of Oxford, has written strongly against Weismann; and Prof. Bower, of Glasgow, in his *magnum opus* "The Origin of a Land Flora (1908)," cites with approval, if not acceptance, Goebel's strongly Lamarckian views.[2] Sir William Dyer, however, defends the Weismannic position.

V

The majority of English zoologists are, however, enthusiastic Weismannists and go so far as to deny the possibility of transmission where their master

[1] Die Vererbung somatogener Variationen ist also ein überaus kompliziertes, von den genauer Erfüllung vieler Bedingungen abhängiges Geschehen, so dass wir uns nicht wundern werden, wenn es nur in bestimmten Kategorien von Fällen regelmässig geschieht ("Festschrift zu Mendel," 1911, p. 314).

[2] [Bower writes (p. 207): "The question of symmetry of the flower has been treated so lately and so well by Goebel that it is unnecessary here to discuss it in detail." Then follows an account of Goebel's views in which we find: "According to the sensitiveness of the former [lateral flowers] to external factors the configuration of the flower will be changed more or less early. Such changes may be inherited . . ." To the reader of the whole passage it is obvious that Bower fully adopts Goebel's view of the acquisition of bilateral symmetry from primitive radial symmetry through the transmission of acquired characters. I have been challenged as to the accuracy of the statement, and therefore deem this reference necessary.]

would admit it. Thus in *The Times* of January 27, 1908, Sir Ray Lankester, whose headship no English zoologist would dream of questioning, writes:

"By degeneration is indicated a definite deterioration of the stock, or 'stirps' (as Mr. Francis Galton has termed it). There is no evidence that privation and injurious conditions cause deterioration of the stock in animals and plants. They may kill out a stock or race; but they do not alter its congenital qualities."

No wonder that a correspondent asked for chapter and verse, especially if we reflect that even Weismann allows that differences of nutrition of the body may affect the germ-cells, and consequently the stock. Again, in the January number of *The Fortnightly Review* (1908), Dr. Alfred Russel Wallace ascribes similar views to "almost all the chief biological thinkers and investigators." This attitude is shared by many smaller men; and the unproven doctrine is pressed by all of them into the service of whatever social and economic views they may advocate.

The fact is that at an earlier date undue stress was laid on inadequate observation, and the inferences of untrained observers, such as midwives and the like. This has led to an excessive reaction. Eager to combine into a harmonious whole the little we have learned of organic processes and connections during the last century or so, many modern naturalists have rejected the obvious and been attracted by the completeness and the apparent logical symmetry of Weismannism. The Master has indeed deftly woven his web of hypothesis, with its warp of forced interpretations of structures that are known, and its weft of assumptions of substructures that are unknown, into the gorgeous brocaded robe of his theory: but it is as airy and unreal as that which left Hans Christian Andersen's emperor stark naked in the birthday procession. We, with many others, are well content to moderate our ambition, and to wear clothes, old and old-fashioned, it is true, ragged and riddled with holes, it well may be: but made of real objective stuff, and giving us at least, a partial covering.

Postscript[1]

We may here note a criticism by Sir E. Ray Lankester, which he first put forth in 1894, in *Nature*, and to which he evidently attaches great importance. Its most recent restatement is found in the article "Zoology" in the new edition of the "Encyclopædia Britannica," 1911:

"Lamarck's first law asserts that a past history of indefinite duration is powerless to create a bias by which the present can be controlled. [For an accurate presentment of Lamarck's meaning the word

[1] Written June 1911.

absolutely should be inserted before "controlled."] He declares that in spite of long-established conditions and correspondingly evoked characters, new conditions will [substitute rather *may*] evoke new responsive characters. Yet in the second law he asserts that these new characters will [rather *may*] resist the action of newer conditions, or a reversion to the older conditions, and be maintained by heredity. If the earlier conditions were not maintained by heredity, why should the later be?"

As stated by Lankester the argument appears a thorough disproof by the *reductio ad absurdum*; and yet Lamarck was a philosopher, not a fool! But the slight alterations suggested in our brackets make all the difference. We may easily test the argument by repeating it with a small change of instances, which in no way affect its essence.

"It may be asserted of the *individual* that his whole past history is powerless to create in him a bias by which the present can be controlled: in spite of long-established conditions and correspondingly evoked *habits*, new conditions will evoke new responsive *habits*. Yet it is at the same time maintained that these new *habits* will resist the action of newer conditions or a reversion to older conditions, and be maintained by *custom*. If the earlier *habits* were not maintained by *custom*, why should the later be?"

Clearly the paralogism lies in the presentment: Lankester puts forth as universal what is regarded by the Lamarckian as occasional only. We cannot say under what conditions any man can acquire new habits: this much is clear, that such acquisition varies from man to man, and in the same man at different periods of his life; and similarly Lamarckians hold that capacity for the acquisition of new hereditable characters has varied from race to race, and at different periods during the history of the race.

CHAPTER VII *(Cont.)*

A REJOINDER

"Comment faites vous, monsieur, pour être si sûr de ces choses-là ?"

Dr. G. Archdall Reid's attack on modern Lamarckianism as a factor in evolution affords an interesting study in the methods of his school. It contains three admirable "episodes," as a musician would term them, two of which are but distantly related to the subject. The first, on what I have elsewhere called "collateral cellular transmission,"[1] is but short, and is utilised to show, what all Lamarckians admit, that there is no obvious mechanism for the transmission of acquired characters. The second, on the value of facts in science, differs from the others in being skilfully woven in with passages of the main theme, and will be dealt with below. The third is in itself an extended essay on the relations of memory and intelligence, habit and instinct, some 1,300 words long, very eloquent and convincing, but quite as compatible with the Lamarckian as

[1] Chapter II, p. 49.

with the Wallacian[1] view of evolution. Our only criticism is that this prodigal display of the uncontroverted, imported into a controversial article, is calculated to lure the unsuspecting reader to believe that all the wares offered by the author have the same indisputable virtues. Indeed, at the very outset he claims boldly that—

"in the latter part of the nineteenth century, Weismann and others pointed out that there are great difficulties in conceiving a probable means of [Lamarckian] transmission. . . . Thereupon scientific opinion, *as a whole*,[2] underwent a change."

This assertion as to the general consensus of scientific opinion, "quod ubique, quod ab omnibus," quite on the lines of theological controversy, recurs constantly in the writings of Dr. Wallace and those who share his views in England. Three times this year [1908] have I already pointed out the brilliant array of biologists whose opinions on this matter have not been materially altered by the arguments of "Weismann and others,"—the last time being in the September number of this Review [*C. R.*, 1908]. But the claim is ever repeated with unfailing assurance, like "Recommended by the Faculty" on the

[1] Dr. Alfred Russel Wallace was the first to urge Natural Selection without Lamarckiam transmission. He is antecedent to Weismann, and has no responsibility for Weismann's ingenious constructive hypotheses of heredity and variation.

[2] All passages between double quotation marks (" ") are Dr. Reid's, but I am responsible for the italics.

label of a quack nostrum. This incidentally disposes of the statement: "Mr. Francis Darwin . . . and Professor Marcus Hartog have *attempted to revive* the Lamarckian hypothesis." The hypothesis has never been even in a state of suspended animation: if thrust in undeserved disgrace from the schoolroom of certain English biologists, it has ever remained lively and lusty in the big world outside their door.

A critic may lighten his labours by misrepresenting the object of his criticism: Dr. Reid's presentment of modern Lamarckians is a gross caricature. Thus he supposes them to believe that "since parental characters are acquired all ill-conditions [,] that enfeeble the parent[,] enfeeble the child." He argues as if the sentence contained the commas I have inserted in square brackets, and as if we held that all ill-conditions necessarily enfeebled the parent. But the response of the parent to *prima-facie* "ill-conditions" may be, as in several cases cited by me in September, not enfeeblement or deterioriation, but an adaptive change, so that to the offspring the same conditions are no longer "ill-conditions," or at least not *so* "ill." Indeed, one danger from this transmissible adaptive response is suggested in the consideration of the slum problem. A high and complex civilisation tends to promote not only the continuance of the majority who are part of it and live in and for it, but also of that adaptable part of the minority who are thrust outside it and live *on* it. True, of the submerged one portion may be enfeebled and produce a yet weaker lineage, destined to die out and clear the ground. But another portion, who react by cunning, predacity, loss of shame and of social spirit, will turn their submergence to profit: their lineage might well be described in Horace's words:

> "Aetas parentum, peior avis tulit
> *Nos* nequiores mox daturos
> Progeniem vitiosiorem."

The best tillage favours the lushest growth of weeds; and if the farmer neglects them they will do their best to strangle his crops. It is the problem of to-day to devise means for dealing with those who turn the "ill-conditions" into which they are sunk by society to anti-social account.

Again, Dr. Reid insists that Lamarckians believe that scars and mutilations should be transmitted; yet elsewhere he refers to my essay of last September as if he had read it! Surely he must have missed the passage (pp. 179–80) in which I point out that regeneration or repair is the adaptive response that should be transmitted, and not the injury itself. This was brought out by Sollas and myself some seventeen years ago. Really the matter is obvious. Would any gardener expect the acorns from an ill-trimmed or overshaded tree to grow into lop-sided oaks? Yet most botanists admit the Lamarckian factor. In all the lower animals the response to any injury or mutilation of not excessive extent is at least *repair*—not so imperfect as, with us, to leave a scar—or very often *regeneration* of the part removed. Apparently this power has been reduced in the Highest Animals, owing to its incompatibility with their specialised complexity (see p. 50). Dr. Reid asks his readers to try to "conceive whether the persistence of life is compatible with the Lamarckian hypothesis,"—*as he presents it*; but we have shown that his picture omits the very features that give it life and reason. On a true presentment the reader may well answer that the persistenee of life *is* compatible with this hypothesis; and so achieve an intellectual feat of whieh our author deelares himself "ineapable."

"Episode 2" is the essayette on facts, from which we give some extracts:

"There are no scientific facts. All faets are equal before science. It is the elassifieation and interpretation of facts that constitute science. The greater the number of faets ineluded in our survey, the more complete our elassification, the more correct are our interpretations."

All this may be very good and true, provided we put a proper construction on the language. But the passage before this shows a very peeuliar standpoint:

"Most of the facts of nature lie patent under our eyes, open to interpretation if we tear aside the veils of familiarity and preconception. Some facts, however, are so obscured by the surroundings in which they are found that we must use experiment or some such method to make them plain. Experiment is valuable as a means of filling gaps in our knowledge, but it can do no more than render facts previously obscured as patent as the mass of those on which our knowledge is founded. In some sciences, for example physics, all facts are obscured [! !]. In others, for example *anatomy*, all are patent [! ! !]. In *biology*, especially in the case of the higher plants and animals, most facts are patent, but some are obscured [! ! ! !]"[1]

It is hard to take this paragraph as the serious expression of Dr. Archdall Reid's philosophy of the sciences.

But we may urge that all "facts" (which I suppose to mean correct observations of phenomena) are *not* "equal before science," in the sense that scientific questions are to be determined, like general elections, by a simple numerical poll. One single fact newly noted may suffice to overthrow a theory founded on countless other facts, if it cannot be brought into line with them on the basis of that theory. Dr. Reid's treatment of "experimental and laboratory facts" savours of inconsistency. Elsewhere he lays

[1] [Despite the expansion Dr. Reid has given to these aphorisms in his great book "The Principle of Heredity," I see no reason for withdrawing the above opinion.]

stress on some in disproof of the alleged transmission of acquired epilepsy. Here he disparages them; and he ignores them elsewhere, when they appear to afford crucial tests against his own views. Possibly he has skipped these last in his reading.

Great originality is shown in his "Second Subject," the Origin of Variations. It is not Wallace's, for Wallace has put forward no general theory of variation for the organic realm at large, only a limited theory for those variations that led up to Man from his nearest zoological kin. Assuredly, too, it has nothing to do with the special teaching of Weismann, who refers variation to the influences of nutriment and environment on the germ-plasm, as well as to the complex shuffling involved in the mixture of parents in the offspring. Dr. Reid's theory is, then, "quite his own idea"[1]: variations are conditioned, if at all, by the haphazard of the future; the non-existent and the unforeseen.

"We know that a germ-cell on becoming fertilised spontaneously produces many different kind of cells, such as muscle and skin cells. In the same way, apparently, it produces germ-cells which vary among themselves as regards their germ-plasm. These germinal variations are necessary if the species is to

[1] [I was mistaken in this: as Sir Bertram Windle reminds me, it had been put forward and rejected by Charles Darwin himself as early as 1869.—"Some have even imagined that natural selection induces variability, whereas it implies only the preservation of such variations as occur and are beneficial to the being under its condition of life" ("Origin of Species," ed. v. pp. 92–3).]

adapt itself to changing conditions. Evidently, then, not only are many variations spontaneous, but they are sufficiently numerous, diverse, and considerable to afford materials for selection, natural or artificial. A vast mystery is often made of the origin of variations. But, *if we admit that the regular variations of somatic cells are due to Natural Selection*, there seems no valid reason for refusing to admit that *the maintenance of the no less regular variability of germ-cells is due to the same cause*."

We can only take this to mean that the variation of germ-cells is due to the *future* chances of abundance or deficiency of food, of competition or co-operation with those of its own kind, of the presence or absence of foes or parasites, of the incidence of diseases new and old, of weather, and of the movements of earth and water: for these are the factors of Natural Selection. All selection is negative: a stern reality to the eliminated at the moment of their elimination, it is non-existent to the survivors. Dr. Reid personifies this recurrent negation as a sempiternal Deity; he transfers its action from the future to the past. This is the "All-Sufficiency" or "Omnipotence" (*All-mächtigkeit*, Weismann) "of Natural Selection" with a vengeance!

Charles Darwin showed (in "The Expression of the Emotions," 1872) as his son has just recalled, that the only forthcoming explanation of certain modes of expression lies in the transmission of acquired characters. Thus Sneering or Snarling is the clearing for action, as a menace, of the offensive canine teeth which are so well developed in Man's nearest zoological allies. This is not referred to by Dr. Reid. Yet it is no mere "islet of truth," "obtained by experiment or some such laboratory method"; but one of a category of what Dr. Reid calls—

"a huge volume of equally undisputed facts gathered by simple observation, and duly correlated with them, so as to make the hypothesis 'furnish a basis for the rigorous deductive inference of consequences,' and so ascertain 'whether it is in harmony with all other laws included in the conceived system of reality'" [I don't know from whom come cited quotations in single quotation marks]. "That which, rightly used, might bridge a gap between neighbouring continents is treated as the sole truth known to us."

How aptly and eloquently do these words characterise Dr. Reid's treatment of the experimental disproof of the non-transmission of mutilations and scars, his aversion to "use rightly" the facts on which Lamarckianism rests and is logically founded!

The discussion on immunity is largely one of words. I have not contended for more than is universally admitted: that the young acquires antitoxins through the processes going on in its mother, and, like her, retains immunity for a certain time (p. 183).

I have actually utilised this very point to suggest in my essay that the transmission of definite chemical substances may form part of the general mechanism of transmission which so eludes us (p. 192).

"In any case, the vast mass of experimental as of other evidence is against the Lamarckian hypothesis."

But evidence has to be judged; and this is a case where judges differ. From Alfred Russel Wallace, Ray Lankester, Thiselton Dyer, and Archdall Reid we turn to Charles Darwin, George Romanes, Sydney Vines, Francis Darwin, K. Goebel, Wilhelm Roux, Oscar Hertwig, Yves Delage. The court is divided on the facts at present before it: if a verdict has to be pronounced at this moment, it must go with the majority of eminent judges in science: that is, in favour of Lamarckian transmission as a factor in variation and evolution.

But Dr. Reid holds otherwise: he denies the competence of this court, and proposes another:

"The public will not accept *unaccustomed* views till they have been *long-formulated*,[1] or till they have received official sanction. Such sanction may be found in the recently published Report of the Royal Commission on the Care and Control of the Feeble-minded."

I am at present unable to procure this Blue Book;

[1] So a distinguished artist, of the Royal *Hibernian* Academy, once told me: "You know I never get on with strangers till I've seen a lot of them."

but I am sure there must have been great diversity in the evidence adduced. Thus, while Dr. Reid maintains in his article as strenuously as ever his old thesis, "However much drinkers suffer, there is neither physical nor mental deterioration of the race," Dr. W. A. Potts, who was Medical Investigator to this Commission, is strongly opposed to Dr. Reid. Speaking of the effect that alcoholism of the parents exerts on the offspring, he writes (Abstract of a Paper introductory to a discussion held by the Society for the Study of Inebriation, October 13, 1908; in *Medical Press*, October 14, 1908):

"The importance of this must be brought home more strongly by explaining the fallacy, in civilised life,[1] that alcohol acts more as an eliminator of the unfit than a producer of them. . . . Reference to Morel's work substantiates the conclusions, which derive much greater importance from MacNichol's demonstration of a much larger number of dullards [53 per cent.] among the children of drinkers than among the children of abstainers [10 per cent.]."

Evidently such views, diametrically opposed to Dr. Reid's, must have been laid before the Royal Commission; and it is hard to explain why he writes as if they were unknown or non-existent.

Thus Dr. Archdall Reid proclaims Peace during

[1] The two commas in this and previous line, inserted by me, are necessary to the sense, which without them is not obvious.

an active campaign, and sings the pæan of triumph in front of an unbroken foe. If the artillery of fact and reason in the hands of the anti-Lamarckians be as smashing as they represent, why does the effective damage to their foes fall so far short of the bulletins they publish?

CHAPTER VIII

MECHANISM AND LIFE

A STRANGE phenomenon in the growth of science is the alternation in the vogue of rival theories; and it has nowhere been more marked than in the domain of biology. During the latter half of the last century the "mechanical" or "physico-chemical" view of life laid claim to dogmatic orthodoxy; but in the last ten years the tide has changed. There are still many, indeed, who reluctantly admit the difficulties in the way of the proof of their mechanical theory, but express the fervent trust that our growing knowledge of physics and chemistry will overcome these difficulties, and give a full explanation of Life in terms of the laws of non-living things. But the majority of the biologists of the present generation are inclined rather to chaff these persons as the possessors of a "cheerful and optimistic temperament" than to share their pious aspirations.

I propose in this paper to survey the causes which gave rise to the two latest phases of thought on the subject.

The collapse of the older vitalistic school towards the end of the first half of the nineteenth century—the school which maintained, as modern vitalists do, but in a different way, that no complete explanation of the phenomena of living beings can be given in terms of the laws of non-living things—was, it would seem, largely due to the sudden increase in precision of our physical ideas, and to the general acceptance of the conception of the conservation of energy, as well as of matter. The peculiar behaviour of living beings had, down to that period, been referred to an abstract entity, called "Vital Force." When the physicists had limited the meaning of "force" by defining it as an "acceleration × mass," when the persistence of energy through all its transformations was recognised, and the intake and output of energy of the living organism were found to balance as well as those of any machine or apparatus whatever, the term "Vital Force" lost its propriety, and had to be dropped. Indeed, it became obvious that the peculiarities of living beings could not be classed as forms of energy, force, or matter; and it was easy to disregard as mere lumber that quality which found no place in the symmetry of physics and chemistry; to ignore, as an intruder into the orderly laboratory, that presence which had no name to give to the custodian. A further encouragement to the anti-vitalist lay in the glorious achievements of the chemist who—despite all predictions to the contrary—was now producing by combination and separation so many of those "organic" substances which had hitherto been only found in or produced by living beings; while he failed to see that the chemist himself was also a living being. Indeed, in the seventies the current belief among students of Physiology was that within a decade albumen and other proteids would be synthetised, and that by the end of the century protoplasm would also be manufactured, probably in a living state.

Again, the rise of the Descent Theory, mainly due to Charles Darwin's presentation of it, had put forth a scientific explanation of many biological problems that had received none theretofore. And religious prepossessions also had their influence: many freethinkers assumed, quite absurdly, that the mechanical view was antagonistic to all theistie hypotheses, instead of imperatively requiring them as we shall see; and so it was welcomed by such men as Carl Vogt and Ernst Haeckel, the most brilliant and dogmatic of the number.

In England, at least, the vitalists of the period had a bad time and a poor show. Their opponents had the advantage of recognised position and the command of the publie ear: they were incomparably the better writers; the taunt of theological prepossession was raised, not without reason, against the vitalists; and the protests of that inarticulately verbose genius, Lionel Beale, were overborne and swept out of sight by the brilliantly lucid dialectic of Thomas Henry Huxley. Thus the attitude of the accredited physiologists of the day appeared to their own students, and to the public at large, to be hostile to vitalism in any form or shape. I remember that at the Manchester meeting of the British Association in 1887, one speaker hinted at a vitalistic explanation. When he sat down a distinguished Professor of Physiology jumped up, and carried the meeting with him by quoting without preface Bret Harte's well-known lines:—

> "Do I wake? Do I dream?
> Do I wander in doubt?
> Are things what they seem?
> Or is visions about?"

We must remember that the official physiologists of the time found their main work, as we shall see, in ascertaining with great precision the changes, physical or chemical, at the surfaces or at the extremities of organs. To increase the delicacy and accuracy of their observations, they worked as far as possible with isolated organs, which, as Samuel Butler pointed out in "Erewhon," have, indeed, the character of internal machines in relation to the organism as a whole. Unconsciously they were impelled to magnify their office, and to exaggerate the theoretical value of their results: they assumed that if more were known of the internal workings of living beings, they would all prove to be of the same character as those that lay in the territory they were so brilliantly exploring with the apparatus of the physicist and the chemist. Yet a little consideration might have made them hesitate. The processes of growth and repair are most essentially physiological; and into these their manipulations and records gave no insight. The narrowness of this official school is manifest to the world in the practical exclusion from its text-books of the work done during the last two decades of the century on the physiological processes of reproduction and heredity, and in the astounding fact that nearly all progress within this field has been achieved by biologists to whom the title of "physiologists" is not habitually given. The reign of mechanistic views is coincident with the rise of this official school of physiologists: its decay is due to the enormous amount of broad physiological work done outside the bounds of their almost crystallised tradition. Yet we must remember that the most distinguished British teachers of the school were far from the extreme views of their disciples, just as Wilkes protested that he was not a Wilkesite. My own revered teacher, Michael Foster, said one day, when I was pointing out certain osmotic relations in connection with renal secretion: "My dear fellow, that isn't enough; you may be sure that the kidney cell gets rid of what it wants to." And Burdon-

Sanderson said, when talking to me and Prof. Ch. Richet in 1900: "The real meaning of life is adaptation," using the word evidently in the same sense as "self-regulation."[1] If all the processes in a factory were kept strictly secret, we can imagine a checker at the gate insisting that all that went on inside was some modification of carting; and possibly he might convince an outsider of that strange doctrine, on the ground that "Bill is employed at the factory, and he ought to know." We can now see, therefore, that the apparent consensus of physiologists until recently against vitalism need not have an undue weight with the man in the street.

It is always well to have clear definitions before us, or at least clear indications of what we mean by the words we use. Many a controversy has had a verbal confusion at its base, on one side or on both: and this question is no exception. "Machine," "Mechanism," meant originally a *contrivance*, an *arrangement* by a living being. Both these words have come metaphorically to mean an arrangement, an assemblage of things standing in a causal relation to one another (in their widest sense including purely psychical relations, such as the "mechanism of memory"). It is obvious that the most outrageous

[1] [To these we must add Ed. Pflüger, so long Professor of Physiology at Bonn, and the founder of the classical physiological periodical *Pflüger's Archiv* (see p. 270)].

vitalist, accepting the law of causality, would not reject this extension of "mechanical" explanation in the living world; but in this sense the term ceases to have any controversial value. I think that a fair definition of a machine[1] is *a portion or aggregate of matter chosen, fashioned, or arranged by a living being to effect some transformation in the relations of matter, or of energy, or of both.* This change is the *object* or the *purpose* of the machine, that is, of the mechanician who makes it; and in the making of the machine the purpose lies in the *future*. Thus are machines differentiated from "Things at Large."[2]

"Mechanism," the more abstract term, is that arrangement in a machine which is concerned with its purpose or effect. Thus, while we should call a selected flint chip, no less than a steel knife, a "machine," any ornamentation on the latter would form no part of its "mechanism" as a knife. "Mechanics" is the science of machines, and has been restricted to include that dealing with the equilibrium and the movements of solids,—readily extended to those of liquids, so long as they do not change their state of aggregation. The wider science—dealing with

[1] Though we distinguish the simplest forms of machines as "tools," it is impossible to except the latter from our definition.

[2] Prof. A. E. Taylor, of Montreal, has insisted on the character of machines in his "Elements of Metaphysics" (London, 1903), p. 236 f. [While this essay was in the press, an extract from the "Notebooks of Samuel Butler" appeared (April 1908) containing the same distinction; it dates from 1884.]

the equilibrium, strains, vibrations, and movements, molecular and molar, of substances, so long as they change no more than their state of aggregation, solid, liquid, or gaseous—has received the name of "Physics." The science dealing with interchanges of composition is "Chemistry"; and the older name of "Mechanical School," applied to the antivitalists, has given way to that of "Physico-chemical."

Before passing on, we must examine another term which has been much used with little precision of meaning and much vagueness of implication. "Automaton," "automatic," which mean self-moving, were first applied to human or animal motions performed without conscious will or reason, or even against these. Later they were applied to machines requiring a minimum of manipulation during their work, and also to working models of animals, with internal machinery designed to execute motions like those of the original. These meanings survive to the present; we may cite two illustrations. We measure time at the present day by counting the oscillations of a suspended weight or of a coiled spring, and we know that such oscillations are gradually damped by friction, and soon cease: we make the *automatic* watch or clock by introducing a coiled spring or a wound-up weight with a train of wheels; thus the oscillations are at the same time maintained for a long period, and recorded by the hands instead of being separately counted. In these respects we have made our time-counters "automatic." Again, in the first steam-engines of Newcomen the alterations in the steam-cocks by which the motion of the piston was periodically reversed were made by the hand of a boy in attendance. One boy, more playful or more ingenious than his mates, tied strings to various parts, and so made the reversals "automatic." The automatism of the machine is in every case the result of planning, and has to be explained by future purpose, as well as by past manipulation. Thus we can differentiate machines from other non-living aggregates of matter by their purpose in the future, as well as by their history in the past. Compare (1) a mountain talus, a river, a lake, with (2) an embankment, a canal, a reservoir: science finds no account of the past action of a living organism, no hint of a future purpose, in the production of the three former; but both these have to be forthcoming for a full explanation of the three latter.

A machine is distinguished, then, from other non-living aggregates by its definite purpose: in other words, the purpose defines the machine. A sharp-edged flint becomes a machine when a man takes it up to cut or to strike fire, whatever may have been the antecedent cause of its sharp edge: it was, however, a machine from the outset when it was produced by a "knapper" who split the original nodule to obtain it. If there has been a recent tendency to overlook this keynote of the machine idea, it is easy to explain it by reflection on our mental growth. The young child has not enough experience of the history and behaviour of non-living beings to understand the "How?"—the reference to their antecedents which is the sole scientific explanation of those that are not machines: his only anxiety is the "Why?" By and by, as the child gains experience, he learns that for all occurrences that are not the actions, direct or indirect, of living beings, the "How" is a great deal easier to learn than the "Why"; and that for many of these things the "Why" is unattainable. Moreover, in many cases of machines the "Why" is so obvious and so familiar that it ceases to be an object of consideration. Thus every one is interested in the kinematic arrangement of the typewriter, the linkage of keys, bars and types by which the pressure of the fingers is converted into a definite character on the paper[1]; but the "Why" explains itself, and is taken for granted. Yet what physico-chemical explanation, what geometric description would adequately explain the typewriter to the most intelligent of human beings who, let us suppose, is a master of physics and chemistry, but has no conception of written speech? It is just this recoil from childish anthropomorphism, carried to an extreme, which explains, though it does not justify, the mechanistic attitude of men of science during the latter half of the nineteenth century.

[1] This example is borrowed from Prof. J. Reinke.

Accident may invent a machine: reflection will duplicate it. The late Prof. Morrison Watson told me that his parrot, while playing with a bit of stick which it had gnawed to a point, casually scratched his back with it, and evidently liked the sensation. Thereafter, whenever he was given a bit of stick, he deliberately sharpened it first, and then used it as a scratch-back. The "Why" now determined the "How." If such a simple machine, a mere tool or implement, can receive its full explanation only by the admission of what the schoolmen termed the "final cause," how much more does purpose enter into the explanation of the complex physico-chemical relations of such a machine as a great electrical installation? Over and above the relations of forces, masses, chemical composition, etc., we must invoke the deliberate actions of intelligent beings foreseeing the future.

Seeing, then, that to explain machines we have to invoke the foresight of intelligent beings, the mechanical explanation of living beings demands for its completion the acceptance in full of Paley's "watch and design" argument, and the trespass across the boundaries of natural science into the domains of natural religion. And we saw at the outset that any wider definition of a "machine" will deprive the word of all controversial value.

It is easy to collect a few distinctions between machines and organisms. A machine requires to be set in place to perform its purpose: even if its purpose be locomotion it cannot direct itself without the intervention of an organism: it cannot, after completing one task, travel to a new site of operations. It may be so far automatic as to adapt itself to certain varying conditions of work, but the limits of this self-adjustment are always narrow in range and limited in character. It cannot compensate for the effects of wear and tear by taking up fresh material and depositing it in the worn parts, so as to restore their efficiency; nor can it form afresh parts lost or destroyed. It cannot accumulate material of its own kind so as to produce machines of its own type; nor can it divide into two or more machines like itself. A machine may, like an organism, have for its task the raising of energy to a higher type, and storing it up; but though both can only do this at the expense of the dissipation of other energy, the machine does not store up the energy within itself, but elsewhere. Thus the electric plant raises a portion of the energy derived from the combustion of coal to the form of the energy in the accumulators, while the rest of the energy of the coal is dissipated as heat at a low temperature; but the energy is transformed in the turbo-generator, and stored in the cells of the accumulator.

"Automatic machines" are no less essentially machines: they have the same disabilities that we have already considered. If we try now to get round the difficulty by calling animals "conscious automata," we are using contradictory terms; indeed, the use of "automatism" in biology is so conducive to question-begging, or at best providing decent fig-leaves for the naked ignorance which it is the duty of science to remove, that it should be wholly abandoned. It is curious to note here again that automatism found its first great exponent in the orthodox Descartes, and its last in the agnostic Huxley.

In the negative characters of machines mentioned above, we have foreshadowed the characters that distinguish living organisms. Only the highest organisms can make complex machines, it is true; but the beaver's dam, the parrot's scratch-back, the nest of the bird or the insect, and even the cemented shell of the lowly Foraminifer are all included under our definition. Yet we cannot adduce the production of machines as an essential or universal character of the living. But all do at some period of their existence take into themselves substances altering their composition and combination, with the ultimate result that they increase their substance in every part thereby —a long periphrase for the simple statement that *they grow*. This process is termed "assimilation." This must be qualified for certain reproductive cells that owe their chief increase to the direct reception from the parent organism of chemical substances, which for the time they only store; ultimately they digest these internal food-supplies, and grow and multiply at the expense of these stores.

Indeed, while part of the food taken up by the organism is utilised for present needs of work, repair and growth, a certain proportion is redeposited in reserve stores for the future needs of the organism itself, or for the nourishment of the reproductive cells (or of the offspring), which are, as it were, parasites for some time after their formation. Owing to these reserved stores that exist in the organism, the provocation of a minute external change may enable it to effect an absolutely disproportionate amount of work by the liberation of some of the stored energy: the external change is called the "stimulus," the discharge of energy, whether thus disproportionate or not, the "response," and the capacity for response to stimulus "irritability." So comparable with this is the discharge of a projectile by the minute work of a trigger, or it may be the still minuter work of an electric spark liberating foot-tons of energy in a cannon, that organic response is termed *action à détente* (trigger-action) by the French, and *Auslösung* (letting-off) by the Germans: we might term it "*release*."

On the whole, the organism shows a greed of energy and of matter, eventuating in the multiplication of its kind, quite unparalleled in the non-living world; as was shown in 1891 by Prof. John Joly in his brilliant essay, "The Abundance of Life." Reproduction is due to the geometrical difficulties in the way of unlimited growth through this efficient greed. For, as Herbert Spencer showed, if in a growing body the form be retained, the ratio of surface to mass decreases, until at length the organism can no longer fulfil its functions for want of adequate surface. To remedy this disparity—and here we see another indication of purpose—the organism reproduces or multiplies. It may divide into two, each half developing to the form of the original, in the lowest types; it may branch indefinitely; it may divide unequally; it may shed small parts of itself, such as buds, or simple reproductive cells which, alone or after pairing, reproduce the behaviour of the parent (or it may be the grandparent). The proportionate size of such reproductive cells to the organism which they reproduce, and which has formed them, may be extremely minute—in man of the order of 1·5 : 1 million.

The utilisation of part of the food in replacement of waste and in repair is familiar to us all: this the organism effects by itself, and for itself—I had almost used the forbidden term "automatically." It not infrequently happens that restoration goes beyond damage—repair is greater than wear; so that the organism is all the better off in the end for the strain on its working. Thus, what we may call *easy* fatigue of a muscle or group of muscles is followed by simple restoration; but if the fatigue be pushed to moderate distress, the restoration brings about increased growth, strength and efficiency. Contrariwise, no machine is the better for such straining, and the more frequently it occurs, the more serious is the resulting damage.

Muscles are not alone endowed with this privilege: it is general in the organism. Bones contain systems of struts and stays to withstand the stresses to which they are exposed normally: if a broken bone sets askew, new systems are formed to replace those old ones that have lost their strength of position. Trees strengthen themselves by sending out their roots further on the side that affords the firmest anchorage against the uprooting tendency of the prevailing winds; and an unsupported sapling develops stronger roots than one that is stayed. Side by side with the power of repair is that of compensation for permanent impairment of a portion of the body, often due to a corresponding increase of efficiency or of growth elsewhere. For instance, when the respiratory capacity of one lung is destroyed by disease, the other lung gains the power of carrying on double work; and if the one kidney is removed the other kidney enlarges to meet the twofold task thrown on it.

Motile organisms travel actively to obtain their supplies; plants anchored by their roots in the soil send them out most freely in the directions where they will find rich soil and water. H. M. Jennings, the most successful observer of the lower motile organisms,[1] finds that even the simplest of these, the amœba, failing direct indications to guide it to food, seeks it by a method of trial and error, which may well be compared to the behaviour of a pointer "quartering" the fields in search of game. Herbert Spencer tried to show that these "conservative" actions were the necessary result of physico-chemical laws, but in most cases his analysis stops short at the lucid statement of the problem to be solved. Thus in the matter of reproduction by division, he gives the very valid reason we have cited for the limits of possible growth of organisms; but his account of the proximate causes of the actual division are inadequate or absent. In many cases, it is true, a cell usually divides across its longest diameter, a method which has a modicum of physical justification; but in the cambium (formative layer) of trees (see p. 65, Fig. 19) the division is parallel to the length, and rather in accordance with the future needs of the plant than with what we know of the existing physical conditions. To use Foster's words, the cell divides "as it wants to," or rather, as the tree wants it to.

While all this must be well known to the physiologists, they have rather busied themselves in the domain where the peculiarities of the living organism were less marked. They have worked at the surfaces

[1] I may note that Jennings started his experiments and observations with the expectation that the movements of Amœba could be explained on purely mechanical lines.

or at the ends to investigate *resultant* physical and chemical effects: they have analysed the chemical substances discarded by the organism as waste, or obtained from its no longer living substance. But, as mentioned above, the *physiology of the organism as a whole*, the physiology of the cell, the physiology of the Protista (organisms which have the character of isolated cells), no less than embryology and heredity, have long lain outside the door of the physiological laboratory, and been fostered by outsiders. I may be excused, then, if I refer to an analysis that I have made of the normal reproduction by division of the cell—a study which, from the minuteness of the object, excludes the use of the apparatus of physical and chemical measurement. The processes may be distinguished into the following: (1) those known in the non-living world; (2) those which are known to occur elsewhere in the living organism, but which have as yet received no adequate physico-chemical explanation; (3) Mitokinetism, a strain-force similar to, but certainly distinct from, electrostatic force; (4) processes that find no clear equivalent elsewhere.[1] Moreover, the general *behaviour*, the orderly way in which the same end is in different cases reached from different starting points, and by different routes, is very characteristic of the living organism.

The chemical processes of the organism require

[1] See p. 124.

special attention. They may be distinguished into two classes: (1) the grosser actions that go on in cavities like the alimentary canal and the blood-vessels; and (2) the local changes that go on within the living tissues and the cells themselves. The former are, I believe, all, without exception, *destructive*, or retrograde changes, breaking down complex into simple chemical compounds, with liberation of energy, mostly in the form of heat, *dissipative* changes: and these it is usually easy to repeat in our apparatus of glass, metal, and caoutchouc, in our laboratory machines. But in class (2) we find, in addition, many constructive, *accumulative* changes, which have not yet been artificially repeated; and even among the destructive ones no chemist has produced those chemical organic ferments, such as pepsine, trypsine, etc., which play so important a part in the destructive changes of the cell and of the large cavities themselves. Again, the chemist resorts constantly to isolation and to separation: his vessels are of material that acts as an insulator or barrier to soakage ("osmosis"), to electricity, and, if needed, to heat; he resorts to crystallisation, precipitation, filtration, evaporation, and congelation; he utilises temperatures ranging far above the 30–40° C. of living beings, and solvents such as pure alcohol, petrol, benzol, and ether, which are deadly to the organism.

Now, the cell is composed of colloid substance saturated with solutions of electrolytes, more or less pervious to electricity, moderately conducting to heat, and often remaining at a uniform temperature; or in any case within the limited range of little over 70° F., or say 40° C.; such as outside the body will not suffice for the chemical transformations of the chemist, by which he synthetises organic substances. Hence it is admitted that our knowledge of the chemical transformations of the organism is inadequate. But the optimistic mechanicist consoles himself by proclaiming that our knowledge of the properties of colloids is incomplete. It is far less incomplete now than when this very explanation was put forward by Haeckel, over thirty years ago; but the growth of our physico-chemical knowledge, immense as it has been in the interval, has not removed the difficulties I have mentioned: it has not advanced the growth of the physico-chemical school; but, on the contrary, has coincided with its ever-increasing unpopularity among biologists. Much has been written of the "molecular structure" of living protoplasm; but it seems certain that *living protoplasm is not a chemical substance*, and therefore can have no molecular structure in the chemical sense of the word.

In embryology, the study of the evolution of the complex organism from a single cell, the morphological unit or equivalent of a single unit of the adult body offers remarkable examples of the peculiar characters of living organisms. This original cell has for its function to grow at the expense of its enclosed reserves, until it divides into two; and this process is repeated for some time without any marked differentiation, until there is an aggregate of cells which form in succession a rounded, mulberry-like heap (morula), a hollow spherical aggregate (blastula), and a double-sac (gastrula), like a lined skull-cap, the hollow being the primitive alimentary cavity. Only after these changes have taken place is there usually the beginning of differentiation of the cells among one another for the different tissues into which they are to be transformed. At the first division into two these are normally destined to give rise to the right and left halves of the body respectively. The second division specialises the front from the rear. But if at these early stages the embryo be violently shaken, the cells separate, and may develop, each "on its own," to form a complete animal, and not an incomplete one (Fig. 38). So if one cell at an early stage be killed and the other or others be left together, the result will be a complete animal, save in so far as deformity may be introduced by the mechanical hindrance due to the presence of the dead cell. Again, if a complete embryo at the stage of the hollow sphere or of the lined cap be cut into two, either half will develop into a complete animal, and that by direct differentiation—not by processes of

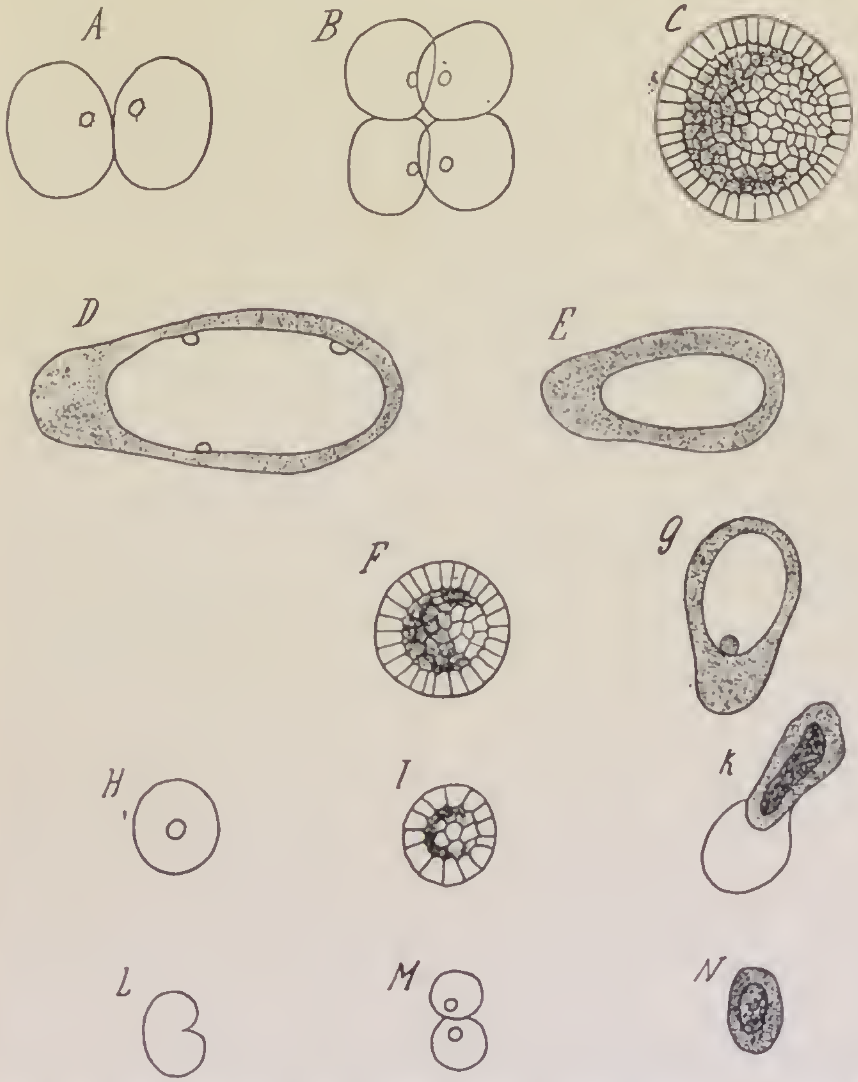


FIG. 38.—Segmentation and development of single separated segmentation cells of the Medusa *Laodice*.

A, One of the first two cells isolated and dividing into two; *B*, its second division; *C*, first larval stage produced from it. *D*, Normal larva of second stage (planula) from an entire egg; *E*, the same produced from one isolated of the first two cells, as in *A*. *F*, *G*, Blastula and planula produced from *one* of the four cells of the second fission of the egg. *H*, Single cell of eight of the third fission of the egg developing into: *I*, blastula; *k*, planula (which is leaving the eggshell; *l*, Isolated cell of sixteen of the fourth fission; *M*, its division into two; *N*, its planula.

repair and regeneration. The occurrence of such a division by some accident or by causes that completely escape us occurs—very rarely—in man, and gives rise to "identical twins."[1]

It is interesting to note that Galton has found in a number of cases that identical human twins, brought up under different conditions, have had grave diseases at the same age, and died at nearly the same time. I ascribe this to no mysterious telepathic agency, but to the power of the organism to go its own way and to reach its own end under widely different external conditions.

An instance of this persistent obstinacy of the organism is to be seen when for a short time, during the early stages of embryonic development, the "egg" is compressed, so as to lie in a Flatland, where all the divisions must be vertical, and all the cells lie in a single plane (Fig. 39). If the pressure be now removed, the cells group themselves so as to constitute a normal embryo, though the filiation of the cells of its different parts is wholly different from the normal arrangement. Thus, while we admit that development is according to causal laws, every step being conditioned by the antecedent ones, we cannot reach the threshold of complete understanding on

[1] Twins, generally, are due to simultaneous development in the uterus of distinct eggs, and they may be of opposite sexes; they are comparable to the brood of two or more that most animals throw in a single litter. "True" or "identical" twins appear to be formed as described above; they are always of the same sex, are singularly alike in form, feature, and constitution, and are surrounded by a single caul. In French, they are distinguished from *jumeaux* as *bessons* (from the conjectural Latin, *bissones*—"doublets"), a term familiar to the readers of George Sand.

purely necessitarian lines. Let us take a parallel case on our opponent's own mechanical ground. An engine breaks down on a railway, and blocks one line completely and seriously. The Superintendent of the Line during the time of blocking will despatch

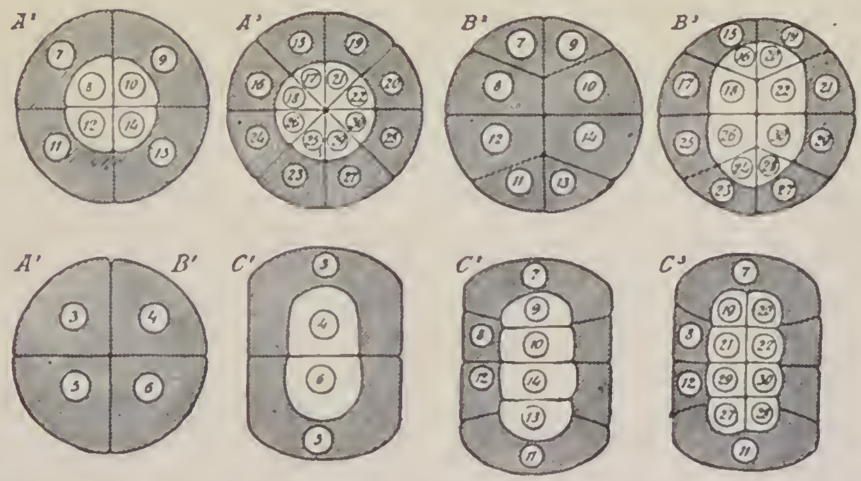
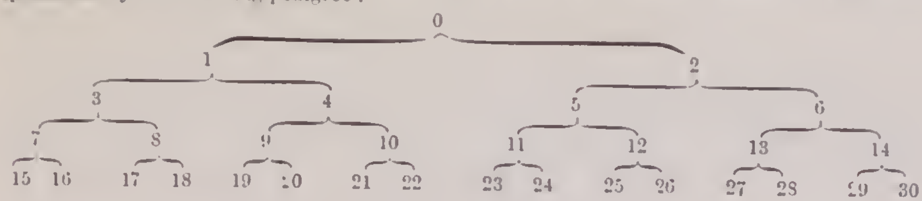


FIG. 39.—Diagram to show effects of compression on the Frog's embryo in early segmentation in varying cellular filiation.

A^1, A^2, A^3, Successive stages without pressure; B^1, B^2, B^3, compressed between two horizontal plates; C^1, C^2, C^3, between two vertical plates. The cellular filiation in every case is represented by the following pedigree :



all traffic both ways past the block over the free line, making temporary junctions and switches where such are needed; or he may even send the trains by another route. It is, I admit, possible to give an account of the course pursued in terms of necessitarianism only, each fact taking its place in a chain of *past* proximate causes. But the future problem—that of getting as many of the *future* trains to their destination as possible with a minimum of delay—is never absent from the despatcher's mind; and were he in such a condition as to be incapable of realising the future, these arrangements would be left undone. We know nothing of the mind of the embryo, or of the individual cell, nor even can we say that it has a mind; but we may safely say that the future is one of the determining factors of its behaviour under changed circumstances, and probably even under normal conditions. To declare it inadmissible is to clap the telescope to one's blind eye.

This power of what we call metaphorically "side-tracking" is in the organism known as "self-regulation": most apparent in the domain of embryology, but everywhere present, and including compensation, repair, and strengthening. Despite the antagonistic theories and practices of different nations, races rarely die out. The *a-priori* objections to compressing the skull or tight lacing are obvious to all; and yet the Flat-head Indians and the fine ladies of civilised nations continue their respective practices with a surprisingly small amount of harm—most disconcerting in the latter case to the dress-reformer—thanks to their *vital* powers of readjustment and compensation under widely different conditions. It is, indeed, consoling to think that the best-meant efforts of the faddist, who carries theories based on inadequate premises to practical conclusions that must needs be erroneous, cannot do one tithe of the harm that would be done were our bodies, indeed, machines.

Thus the organism differs from a machine in its *spontaneity* and in its *egotism*, which may, however, be a racial and not a personal egotism, as in the case of the Protistic parent that loses its individuality in its offspring when it divides, or the Insect-mother that dies in generation. The organism grows itself: it adapts itself for its own or its racial needs, unlike the machine that works for those of the mechanician, of the material organism which has selfishly made it for its own ends. This was well pointed out in "Life and Habit" by the late Samuel Butler,[1] to whose stimulating writings I owe a profound debt of gratitude.

To conclude: We may distinguish all aggregates of matter into three classes:

(1) ORGANISMS, which grow and store energy and matter for their needs and for those of their lineage, and which reproduce, and are self-regulated;

(2) MACHINES, which are aggregates of matter not in continuity with organisms, and which are selected, constructed, or formed by an organism for the purposes of the organism itself or of its race;

(3) THINGS AT LARGE, which do not come into

[1] It is true that in his later works, under the influence of the craving for unification, he adopted a monistic view near akin to Haeckel's (see p. 252).

either category, and which are conditioned by their antecedents only.

We may no longer speak of "vital force." Prof. Benjamin Moore has suggested the term "biotic" or "biological energy," which seems to me to be equally unavailable. If the transformations of energy were proved to be wholly due to material aggregation, we might speak of "vital arrangement." I think it better, however, not to go beyond the facts or to use terms connoting an unknown and assumed entity, such as Occam would have disallowed,[1] but to content ourselves with speaking of "vital behaviour."

For the preceding views I cannot claim more than their presentment in writing; they are those acted on implicitly in practice, and more or less consciously accepted in theory by the majority of working biologists (including psychologists) outside the physiological laboratory, and by a daily increasing proportion of those who work within its dignified portals, despite belated proclamations to the contrary.[2]

[1] "*Entia non sunt multiplicanda præter necessitatem.*"

[2] In justification of this assertion I may cite quotations from two unsigned reviews in large type in *Nature*, vol. 86, May 11, 1911:

"Since no complete physico-chemical redescription of any vital activity has as yet been given, it seems to us a great pity to give young students a prejudice in favour of mechanistic views" (p. 340).

"Although some would hold that the response of protoplasm to external stimuli is simply one of reaction, we think that the author's view of purposive action . . . is borne out by the facts cited, and that this is inherent in protoplasm just as the tendency to variation appears to be" (p. 342).

CHAPTER IX

THE BIOLOGICAL WRITINGS OF SAMUEL BUTLER

Foreword

In the reissue of Samuel Butler's works there has long been a gap; both stock and plates of "Unconscious Memory" had been destroyed in an accidental fire. As it was necessary to reprint the book, Mr. Streatfeild, Butler's literary executor, thought that it would afford a good opportunity for an introductory essay by a professed biologist, dealing with Butler's biological writings and his relation to biological thought during the last thirty years; and he requested me to undertake this work. I could not refuse so honourable a task; but no one can be more humbly aware how trying it is to find one's prose in the same covers as Butler's, and that too in front of it. Still, the macebearer who walks before the Chancellor, to do him honour, is yet not therefore regarded as immodest.[1]

[1] Owing to a misunderstanding this Foreword was omitted in the new issue of "Unconscious Memory," but appeared in the essay as published in *Science Progress.*

In reviewing Samuel Butler's works, "Unconscious Memory" gives us an invaluable lead; for it tells us (chaps. II, III) how the author came to write the Book of the Machines in "Erewhon" (1872), with its foreshadowing of the later theory, "Life and Habit" (1878), "Evolution, Old and New" (1879), as well as "Unconscious Memory" (1880) itself. His fourth book on biological theory was "Luck, or Cunning?" (1887).[1]

Besides these books, his contributions to biology comprise several essays: "Remarks on Romanes' 'Mental Evolution in Animals,'" contained in "Selections from Previous Works" (1884), incorporated into "Luck, or Cunning?"; "The Deadlock in Darwinism" (*Universal Review*, April–June 1890), republished in the posthumous volume of "Essays on Life, Art, and Science" (1904); and, finally, some of the "Extracts from the Notebooks of the late Samuel Butler," edited by Mr. H. Festing Jones, now in course of publication in *The New Quarterly Review*.

Of all these, "Life and Habit" (1878) is the most important, the main building to which the other writings are buttresses or, at most, annexes. Its teaching has been summarised in "Unconscious

[1] This is the date on the title-page. The preface is dated October 15, 1886, and the first copy was issued in November of the same year. All the dates are taken from the Bibliography by Mr. H. Festing Jones prefixed to the "Extracts" in *The New Quarterly Review* (1909).

Memory" in four main principles: "(1) The oneness of personality between parent and offspring; (2) memory on the part of the offspring of certain actions which it did when in the persons of its forefathers; (3) the latency of that memory until it is rekindled by a recurrence of the associated ideas; (4) the unconsciousness with which habitual actions come to be performed." To these we must add a fifth: the purposiveness of the actions of living beings, as of the machines which they make or select.

Butler tells ("Life and Habit," p. 33) that he sometimes hoped "that this book would be regarded as a valuable adjunct to Darwinism." He was bitterly disappointed in the event, for the book, as a whole, was received by professional biologists as a gigantic joke—a joke, moreover, not in the best possible taste. True, its central ideas, largely those of Lamarck, had been presented by Hering in 1870 (as Butler found shortly after his publication); they had been received with general favour, developed by Haeckel, expounded and praised by Ray Lankester. Coming from Butler, they met with contumely, even from such men as Romanes, who, as Butler had no difficulty in proving, were unconsciously inspired by the same ideas—"*Nur mit Bein ischen ander'n Wörter.*"

It is easy, looking back, to see why "Life and Habit" so missed its mark. Charles Darwin's presentation of the evolution theory had for the first time rendered it possible for a "sound naturalist" to accept the doctrine of common descent with divergence; and so given a real meaning to the term "natural relationship," which had forced itself upon the older naturalists, despite their belief in special and independent creations. The immediate aim of the naturalists of the day was now to fill up the gaps in their knowledge, so as to strengthen the fabric of a unified biology. For this purpose they found their actual scientific equipment so inadequate that they were fully occupied in inventing fresh technique, and working therewith at facts—save a few critics, such as St. George Mivart, who was regarded as negligible, since he evidently held a brief for a party standing outside the scientific world.

Butler introduced himself as what we now call "The Man in the Street," far too bare of scientific clothing to satisfy the Mrs. Grundy of the domain: lacking all recognised tools of science and all sense of the difficulties in his way, he proceeded to tackle the problems of science with little save the deft pen of the literary expert in his hand. His very failure to appreciate the difficulties gave greater power to his work—much as Tartarin of Tarascon ascended the Jungfrau and faced successfully all dangers of Alpine travel, so long as he believed them to be the mere *blagues de réclame* of the wily Swiss host. His brilliant qualities of style and irony themselves told heavily against him. Was he not already known for having written the most trenchant satire that had appeared since "Gulliver's Travels"? Had he not sneered therein at the very foundations of society, and followed up his success by a pseudo-biography that had taken in *The Record* and *The Rock*? In "Life and Habit," at the very start, he goes out of his way to heap scorn on the respected names of Marcus Aurelius, Lord Bacon, Goethe, Arnold of Rugby, and Dr. W. B. Carpenter. He expressed the lowest opinion of the Fellows of the Royal Society. To him the professional man of science, with self-conscious knowledge for his ideal and aim, was a medicine-man, priest, augur—useful, perhaps, in his way, but to be carefully watched by all who value freedom of thought and person, lest with opportunity he develop into a persecutor of the worst type. Not content with politely blackguarding the audience to whom his work should most appeal, he went on to depreciate that work itself and its author in his finest vein of irony. Having argued that our best and highest knowledge is that of whose possession we are most ignorant, he proceeds: "Above all, let no unwary reader do me the injustice of believing in me. In that I write at all I am among the damned."

His writing of "Evolution, Old and New" (1879) was due to his conviction that scant justice had been done by Charles Darwin and Alfred Russel Wallace and their admirers to the pioneering work of Buffon, Erasmus Darwin, and Lamarck. To repair this he gives a brilliant exposition of what seemed to him the most valuable portion of their teachings on evolution. His analysis of Buffon's true meaning, veiled by the reticences due to the conditions under which he wrote, is as masterly as the English in which he develops it. His sense of wounded justice explains the vigorous polemic which here, as in all his later writings, he carries to the extreme.

As a matter of fact, he never realised Charles Darwin's utter lack of sympathetic understanding of the work of his French precursors, let alone his own grandfather, Erasmus. Yet this practical ignorance, which to Butler was so strange as to transcend belief, was altogether genuine, and easy to realise when we recall the position of Natural Science in Darwin's student days at Cambridge, in the early thirties and for a decade or two later. Catastropharianism was the tenet of the day: to the last it commended itself to his Professor of Botany (Henslow), and of Geology (Sedgwick), towards whom Darwin held the fervent allegiance of the Indian scholar, or *chela*, to his *guru*.[1] As Geikie has recently pointed out, it

[1] Thus, "When I was starting on the voyage of the *Beagle*, the sagacious Henslow, who, like all other geologists, believed at that time in successive cataclysms, advised me to get and study the first volume of the 'Principles' [Lyell's "Principles of Geology"], which had then just

was only later, when Lyell had shown that the breaks in the succession of the rocks were only partial and local, without involving the universal catastrophes that destroyed all life and rendered fresh creations thereof neeessary, that any general acceptance of a descent theory could be expected. We may be very sure that Darwin must have received many solemn warnings against the dangerous speculations of the "Freneh Revolutionary School." He himself was far too busy at the time with the reception and assimilation of new facts to be awake to the deeper interest of far-reaching theories.

It is the more unfortunate that Butler's lack of appreciation on these points should have led to the enormous proportion of bitter personal eontroversy that we find in the remainder of his biological writings. Possibly, as suggested by George Bernard Shaw, his acquaintance and admirer, he was also swayed by philosophical resentment at that banishment of mind from the organic universe which was generally thought to have been achieved by Charles Darwin's theory. Still, we must remember that this mindless view is not implicit in Charles Darwin's presentment of his own theory, nor was it accepted by him as it has been by so many of his professed disciples.

been published, but on no account to accept the views therein advocated" (Charles Darwin's Autobiography, in the "Life and Letters of Charles Darwin," ed. 1887, p. 72).

"Unconscious Memory" (1880).—We have already alluded to an anticipation of Butler's main theses. In 1870 Dr. Ewald Hering, one of the most eminent physiologists of the day, Professor at Vienna, gave an Inaugural Address to the Imperial Royal Academy of Sciences: "Das Gedächtniss als allgemeine Funktion der organisirter Substanz" ("Memory as a Universal Function of Organised Matter"). When "Life and Habit" was well advanced, Francis Darwin, at the time a frequent visitor, called Butler's attention to this essay, which he himself only knew from an article in *Nature*. Herein Professor E. Ray Lankester had referred to it with admiring sympathy in connection with its further development by Haeckel in a pamphlet entitled "Die Perigenese der Plastidule." We may note, however, that in his eolleeted essays, "The Advaneement of Science" (1890), Sir Ray Lankester, while ineluding this essay, inserts on the blank page[1]—we had almost written "the white sheet"—at the back of it an apology for having ever advocated the possibility of the transmission of aequired charaeters!

"Unconseious Memory" was largely written to show the relation of Butler's views to Hering's, and contains an exquisitely written translation of the Address. Hering does, indeed, anticipate Butler, and that in language far more suitable to the persuasion of the seientifie public. It contains a sub-

[1] That behind p. 285: it bears no number of its own!

sidiary hypothesis that memory has for its mechanism special vibrations of the protoplasm, and the acquired capacity to respond to such vibrations once felt upon their repetition. I do not think that the theory gains anything by the introduction of this even as a mere formal hypothesis; and there is no evidence for its being anything more. Butler, however, gives it a warm, nay, enthusiastic, reception in Chapter V (Introduction to Prof. Hering's Lecture), and in his notes to the translation of the Address, which bulks so large in this book, but points out that he was "not committed to this hypothesis, though inclined to accept it on a *prima-facie* view." Later on, as we shall see, he attached more importance to it.

The Hering Address is followed in "Unconscious Memory" by translations of selected passages from Von Hartmann's "Philosophy of the Unconscious," and annotations to explain the difference from this personification of "The Unconscious" as a mighty all-ruling, all-creating Personality, and his own scientific recognition of the great part played by *unconscious processes* in the region of mind and memory.

These are the essentials of the book as a contribution to biological philosophy. The closing chapters contain a lucid statement of objections to his theory as they might be put by a rigid necessitarian, and a refutation of that interpretation as applied to human action.

But in the second chapter Butler states his recession from the strong logical position he had hitherto developed in his writings from "Erewhon" onwards; so far he had not only distinguished the living from the non-living, but distinguished among the latter *machines* or *tools* from *things at large*.[1] Machines or tools are the external organs of living beings, as organs are their internal machines: they are fashioned, assembled, or selected by the beings for a purpose, so they have a *future purpose* as well as a *past history*. "Things at large" have a past history, but no purpose (so long as some being does not convert them into tools and give them a purpose): Machines have a "Why?" as well as a "How?": "things at large" have a "How?" only.

In "Unconscious Memory" the allurements of unitary or monistic views have gained the upper hand, and Butler writes (p. 23):

"The only thing of which I am sure is that the distinction between the organic and inorganic is arbitrary; that it is more coherent with our other ideas, and therefore more acceptable, to start with every molecule as a living thing, and then deduce death as the breaking up of an association or cor-

[1] The distinction was merely implicit in his published writings, but has been printed since his death from his "Notebooks," *New Quarterly Review*, April 1908. I had developed this thesis, without knowing of Butler's explicit anticipation in the essay on "Mechanism and Life," *Contemporary Review*, May 1908, which was in the press at the time when Butler's posthumous work appeared; it forms Chapter VIII in this volume.

poration, than to start with inanimate molecules and smuggle life into them; and that, therefore, what we call the inorganic world must be regarded as up to a certain point living, and instinct, within certain limits, with consciousness, volition, and power of concerted action. *It is only of late, however, that I have come to this opinion.*"

I have italicised the last sentence, to show that Butler was more or less conscious of its irreconcilability with much of his most characteristic doctrine. Again, in the closing chapter, Butler writes (p. 275):

"We should endeavour to see the so-called inorganic as living in respect of the qualities it has in common with the organic, rather than the organic as non-living in respect of the qualities it has in common with the inorganic."

We conclude our survey of this book by mentioning the literary controversial part chiefly to be found in Chapter IV, but cropping up elsewhere. It refers to interpolations made in the authorised English translation from the German of Krause's "Life of Erasmus Darwin." Only one side is presented; and we are not called upon, here or elsewhere, to discuss the merits of the question.[1]

"Luck, or Cunning, as the Main Means of Organic Modification? an Attempt to throw Additional

[1] It has, since this essay was written, been fully discussed by Mr. H. Festing Jones in a pamphlet entitled "Charles Darwin and Samuel Butler; a Step towards Reconciliation" (A. C. Fifield, London, 1911).

Light upon the late Mr. Charles Darwin's Theory of Natural Selection" (1887), completes the series of biological books. This is mainly a book of strenuous polemic. It brings out still more forcibly the Hering-Butler doctrine of continued personality from generation to generation, and of the working of unconscious memory throughout; and points out that, while this is implicit in much of the teaching of Herbert Spencer, Romanes, and others, it was nowhere—even after the appearance of "Life and Habit"—explicitly recognised by them, but, on the contrary, masked by inconsistent statements and teaching. Not Luck, but Cunning, not the uninspired weeding out by Natural Selection, but the intelligent striving of the organism, is at the bottom of the useful variety of organic life. And the parallel is drawn that not the happy accident of time and place, but the Machiavellian cunning of Charles Darwin, succeeded in imposing, as entirely his own, on the civilised world an uninspired and inadequate theory of evolution wherein luck played the leading part; while the more inspired and inspiring views of the older evolutionists had failed by the inferiority of their luck. On this controversy I am bound to say that I do not in the very least share Butler's opinions; and I must ascribe them to his lack of personal familiarity with the biologists of the day and their modes of thought and of work. Butler everywhere undervalues the important work of elimination played by Natural Selection in its widest sense.

The "Conclusion" of "Luck, or Cunning?" shows a strong advance in monistic views, and a yet more marked development of the vibration hypothesis of memory given by Hering and only adopted with the greatest reserve in "Unconscious Memory."

"Our conception, then, concerning the nature of any matter depends solely upon its kind and degree of unrest, that is to say, on the characteristics of the vibrations that are going on within it. The exterior object vibrating in a certain way imparts some of its vibrations to our brain; but if the state of the thing itself depends upon its vibrations, it [the thing] must be considered as to all intents and purposes the vibrations themselves—plus, of course, the underlying substance that is vibrating. . . . The same vibrations, therefore, form the substance remembered, introduce an infinitesimal dose of it within the brain, modify the substance remembering, and, in the course of time, create and further modify the mechanism of both the sensory and the motor nerves. Thought and thing are one.

"I commend these two last speculations to the reader's charitable consideration, as feeling that I am here travelling beyond the ground on which I can safely venture. . . . I believe they are both substantially true."

In 1885 he had written an abstract of these ideas in his notebooks (see *New Quarterly Review*, 1910,

p. 116), and as in "Luck, or Cunning?" associated them vaguely with the unitary conceptions introduced into chemistry by Newlands and Mendelejeff. Judging himself as an outsider, the author of "Life and Habit" would certainly have considered the mild expression of faith, "I believe they are both substantially true," equivalent to one of extreme doubt. Thus: "the fact of the Archbishop's recognising this as among the number of his beliefs is conclusive evidence, with those who have devoted attention to the laws of thought, that his mind is not yet clear" on the matter of the belief avowed (see "Life and Habit," pp. 24, 25).

To sum up: Butler's fundamental attitude to the vibration hypothesis was all through that taken in "Unconscious Memory"; he played with it as a pretty pet, and fancied it more and more as time went on; but instead of backing it for all he was worth, like the main thesis of "Life and Habit," he put a big stake on it—and then hedged.

The last of Butler's biological writings is the essay, "The Deadlock in Darwinism," containing much valuable criticism on Wallace and Weismann. It is in allusion to the misnomer of Wallace's book, "Darwinism," that he introduces the term "Wallaceism"[1] for a theory of descent that excludes the

[1] The term has recently been revived by Prof. Hubrecht and by myself (*Contemporary Review*, November 1908).

transmission of acquired characters. This was, indeed, the chief factor that led Charles Darwin to invent his hypothesis of pangenesis, which, unacceptable as it has proved, had far more to recommend it as a formal hypothesis than the equally formal germ-plasm hypothesis of Weismann.

The chief difficulty in accepting the main theses of Butler and Hering is one familiar to every biologist, and not at all difficult to understand by the layman: [it is that of *collateral* cellular transmission, dealt with in Chapter II]. Every one knows that the complicated beings that we term "Animals" and "Plants" consist of a number of more or less individualised units, the cells, each analogous to a simpler being, a Protist—save in so far as the character of the cell unit of the Higher being is modified in accordance with the part it plays in that complex being as a whole. Most people, too, are familiar with the fact that the complex being starts as a single cell, separated from its parent; or, where bisexual reproduction occurs, from a cell due to the fusion of two cells, each detached from its parent. Such cells are called "germ-cells." The germ-cell, whether of single or of dual origin, starts by dividing repeatedly, so as to form the *primary embryonic cells*, a complex mass of cells, at first essentially similar, which, however, as they go on multiplying, undergo differentiations and migrations, losing their simplicity as they do

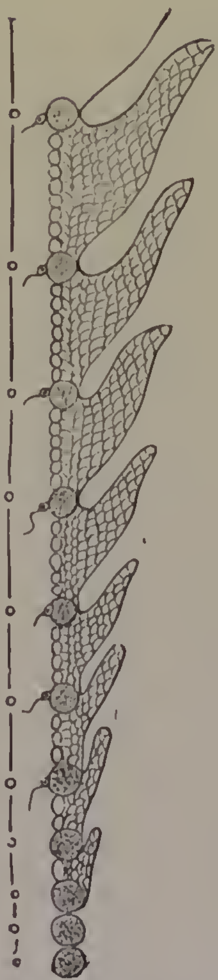


FIG. 40.—Diagram of relation between the reproductive cells ("stirp") and body ("soma") through several generations from below upwards.

The larger circles are the line of reproductive cells, interrupted by syngamy between the successive generations shown by the fusion of the sperm with the large, well-nourished reproductive cell—the egg or oosphere. The triangular masses of cells to the right represent the successive bodies. The lowermost cells represent reproduction by direct division in Protists; and as we rise we find an increase in the proportion of body to germ.

so. Those cells that are modified to take part in the proper work of the whole are called tissue-cells. In virtue of their activities, their growth and reproductive power are limited—much more in Animals than in Plants, in Higher than in Lower beings (Fig. 40). It is these tissues, or some of them, that receive the impressions from the outside which leave the imprint of memory. Other cells, which may be closely associated into a continuous organ, or more or less surrounded by tissue-cells whose part it is to nourish them, are called "secondary embryonic cells," or "germ-cells." The germ-cells may be differentiated in the young organism at a very early stage, but in Plants they are separated at a much later date from the less isolated embryonic regions that provide for the Plant's branching: in all cases we find embryonic and germ-cells screened from the life-processes of the complex organism, or taking no very obvious part in it, save to form new tissues or new organs, notably in Plants.[1]

Again, in ourselves, and to a greater or less extent in all Animals, we find a system of special tissues set apart for the reception and storage of impressions from the outer world, and for guiding the other organs in their appropriate responses—the "Nervous System"; and when this system is ill-developed or out of gear the remaining organs work badly from lack of proper skilled guidance and co-ordination. How can we, then, speak of "memory" in a germ-cell which has been screened from the experiences of the organism, which is too simple in structure to realise them if it were exposed to them? My own answer is that we cannot form any theory on the subject, that the only question is whether we have any right to *infer* this "memory" from the *behaviour* of living beings; and Butler, like Hering, Haeckel, and some more modern authors, has shown that the inference is a very strong presumption. Again, it is easy to over-value such complex instruments as we possess. The possessor of an up-to-date camera, well instructed in the function and manipulation of every part, but ignorant of all optics save a hand-to-mouth knowledge of the properties of his own lens, might say that *a priori* no picture could be taken with a cigar-box perforated by a pin-hole; and our ignorance of the mechanism of the psychology of any

[1] See also Chap. II.

organism is greater by many times than that of my supposed photographer. We know that Plants are able to do many things that can only be accounted for by ascribing to them a "psyche," and in co-ordination enough to satisfy their needs; and yet they possess no central organ comparable to the brain, no highly specialised system for intercommunication like our nerve trunks and fibres. As Oscar Hertwig says, we are as ignorant of the mechanism of the development of the individual as we are of that of hereditary transmission of acquired characters, and the absence of such mechanism in either case is no reason for rejecting the proven fact.

However, the relations of germ and body just described led Jäger, Nussbaum, Galton, Lankester, and, above all, Weismann, to the view that the germ-cells or "stirp" (Galton) were *in* the body, but not *of* it. Indeed, in the body and out of it, whether as reproductive cells set free, or in the developing embryo, they are regarded as forming one continuous homogeneity, in contrast to the differentiation of the body; and it is to these cells, regarded as a continuum, that the terms "stirp," "germ-plasm," are especially applied. Yet on this view, so eagerly advocated by its supporters, we have to substitute for the hypothesis of memory, which they declare to have no real meaning here, the far more fantastic hypotheses of Weismann[1]: by these they explain the

[1] See p. 193 f.

process of differentiation in the young embryo into new germ and body; and in the young body the differentiation of its cells, each in due time and place, into the varied tissue cells and organs. Such views might perhaps be acceptable if it could be shown that over each cell-division there presided a wise all-guiding genie of transcending intellect, to which Clerk-Maxwell's sorting demons were mere infants. Yet these views have so enchanted many distinguished biologists, that in dealing with the subject they have actually ignored the existence of equally able workers who hesitate to share the extremest of their views. The phenomenon is one well known in hypnotic practice. So long as the non-Weismannians deal with matters outside this discussion, their existence and their work are rated at their just value; but any work of theirs on this point so affects the orthodox Weismannite (whether he accept this label or reject it does not matter), that for the time being their existence and the good work they have done are alike non-existent.[1]

Butler founded no school, and wished to found none. He desired that what was true in his work should prevail, and he looked forward calmly to the time when the recognition of that truth and of his share in advancing it should give him in the lives of others that immortality for which alone he craved.

[1] See *Fortnightly Review*, February 1908, and *Contemporary Review*, September and November 1908 [the latter reprinted in this book, Chaps. V, VI]. Since these publications the hypnosis seems to have somewhat weakened.

Lamarckian views have never lacked defenders here and in Ameriea. Of the English, Herbert Speneer, who, however, was averse to the vitalistic attitude, Vines and Henslow among botanists, Cunningham among zoologists, have always resisted Weismannism ; but, I think, none of these was distinctly influenced by Hering and Butler. In Ameriea the majority of the great sehool of palæontologists have been strong Lamarekians, notably Cope, who has pointed out, moreover, that the transformations of energy in living beings are peeuliar to them.

We have already adverted to Haeckel's aeceptance and development of Hering's ideas in his " Perigenese der Plastidule." Oscar Hertwig has been a consistent Lamarckian, like Yves Delage of the Sorbonne, and these occupy pre-eminent positions not only as observers, but as discriminating theorists and as historians of the reeent progress of biology. We may also cite as a Lamarekian—of a sort—Felix Le Dantee, the leader of the French chemico-physical school of the present day.

But we must seek elsewhere for speeial attention to the points which Butler regarded as the essentials of " Life and Habit." In 1893 Henry P. Orr, Professor of Biology in the University of Louisiana, published a little book entitled " A Theory of Heredity." Herein he insists on the nervous eontrol of the whole body, and on the transmission to the reproductive cells of such stimuli, received by the body, as will guide them on their path until they shall have acquired adequate experience of their own in the new body they have formed. I have found the name of neither Butler nor Hering, but the treatment is essentially on their lines, and is both clear and interesting.

In 1896 I wrote an essay on "The Fundamental Principles of Heredity," primarily directed to the man in the street. This, after being held over for more than a year by one leading review, was "declined with regret," and again after some weeks met the same fate from another editor. It appeared in the pages of *Natural Science* for October 1898, and in the *Biologisches Centralblatt* for the same year [it constitutes Chapter II of this volume]. I reproduce its closing paragraph:

"This theory [Hering-Butler's] has, indeed, a tentative character, and lacks symmetrical completeness, but is the more welcome as not aiming at the impossible. A whole series of phenomena in organic beings are correlated under the term of *memory, conscious and unconscious, patent and latent*. . . . Of the order of unconscious memory, latent till the arrival of the appropriate stimulus, is all the co-operative growth and work of the organism, including its development from the reproductive cells. Concerning the *modus operandi* we know nothing: the phenomena may be due, as Hering suggests, to molecular vibrations, which must be at least as distinct from ordinary physical disturbances as Röntgen's rays are from ordinary light; or it may be correlated, as we ourselves are inclined to think, with complex chemical changes in an intricate but orderly succession. For the present, at least, the problem of heredity can only be elucidated by the light of mental, and not material processes."

It will be seen that I express doubts as to the validity of Hering's invocation of molecular vibrations as the mechanism of memory, and suggest as an alternative rhythmic chemical changes. Similar views have recently been put forth by Yves Delage ("Hérédité," 1903, p. 749), and in more detail by J. T. Cunningham in his essay on "The Hormone[1] Theory of Heredity," in the *Archiv für Entwicklungsmechanik* (1909), but I have failed to note any direct effect of my own essay on the trend of biological thought.

Among post-Darwinian controversies the one that has latterly assumed the greatest prominence is that of the relative importance of small variations in the way of more or less—*fluctuations*; and of "discontinuous variations," or *mutations*, as De Vries has called them. Darwin, in the first four editions of the "Origin of Species," attached more importance to the latter than in subsequent editions; he was swayed in his attitude, as is well known, by an article of the physicist, Fleeming Jenkin, which appeared in

[1] A "hormone," the name given by E. H. Starling to an "internal secretion," is a chemical substance which, formed in one part of the body, alters the reactions of another part, normally for the good of the organism.

The North British Review. The mathematics of this article were unimpeachable, but they were founded on the assumption that exceptional variations would only occur in single individuals, which is, indeed, often the case among those domesticated races on which Darwin especially studied the phenomena of variation. Darwin was no mathematician or physicist, and we are told by his biographer that he regarded every tool-shop rule or apothecary's measuring glass as an instrument of precision[1]: so he appears to have regarded Fleeming Jenkin's demonstration as a mathematical deduction which he was bound to accept without criticism.

Dr. William Bateson, late Professor of Biology in the University of Cambridge, as early as 1894 laid great stress on the importance of discontinuous variations, collecting and collating the known facts in his "Materials for the Study of Variations"; but this important work, now become rare and valuable, at the time excited so little interest as to be "remaindered" within a very few years after publication.

In 1901 Hugo de Vries, Professor of Botany in the University of Amsterdam, published "Die Mutations-theorie," wherein he showed that mutations or discontinuous variations in various directions may appear simultaneously in many individuals, and in various directions. In the gardener's phrase, the

[1] "Life and Letters," vol. i. pp. 147-8.

species may take to sporting in various directions at the same time, and each sport may be represented by numerous specimens.

De Vries shows the probability that species go on for long periods showing only fluctuations, and then suddenly take to sporting in the way described, short periods of mutation alternating with long intervals of relative constancy. It is to mutations that De Vries and his school, as well as Luther Burbank, the great former of new fruit- and flower-plants, look for those variations which form the material of Natural Selection. In "God the Known and God the Unknown," which appeared in *The Examiner* (May, June, and July), 1879, but though then revised was only published posthumously in 1909,[1] Butler anticipates this distinction :

"Under these circumstances organism must act in one or other of these two ways: it must either change slowly and continuously with the surroundings, paying cash for everything, meeting the smallest change with a corresponding modification, so far as is found convenient, or it must put off change as long as possible, and then make larger and more sweeping changes.

"Both these courses are the same in principle, the difference being one of scale, and the one being a miniature of the other, as a ripple is an Atlantic

[1] Possibly this book, the blossom of his earlier thought, was withheld as being in conflict with the monistic views which Butler had developed in or about 1880 ; see p. 252.

wave in little; both have their advantages and disadvantages, so that most organisms will take the one course for one set of things and the other for another. They will deal promptly with things which they can get at easily, and which lie more upon the surface; *those, however, which are most troublesome to reach, and lie deeper, will be handled upon more cataclysmic principles, being allowed longer periods of repose followed by short periods of greater activity* . . . it may be questioned whether what is called a sport [= mutation] is not the organic expression of discontent which has been long felt, but which has not been attended to, nor been met step by step by as much small remedial modification as was found practicable: so that when a change does come it comes by way of revolution. Or, again (only that it comes to much the same thing), it may be compared to one of those happy thoughts which sometimes come to us unbidden after we have been thinking for a long time what to do, or how to arrange our ideas, and have yet been unable to come to any conclusion" (pp. 14, 15).[1]

We come to another order of mind in Hans Driesch. At the time he began his work biologists were largely busy in a region indicated by Darwin, and roughly mapped out by Haeckel—that of phylogeny. From the facts of development of the individual, from the comparison of fossils in successive strata, they set to work at the construction of

[1] Mr. H. Festing Jones first directed my attention to these passages and their bearing on the Mutation Theory.

pedigrees, and strove to bring into line the principles of classification with the more or less hypothetical "stem-trees." Driesch considered this futile, since we never could reconstruct from such evidence anything certain in the history of the past. He therefore asserted that a more complete knowledge of the physics and chemistry of the organic world might give a scientific explanation of the phenomena, and maintained that the proper work of the biologist was to deepen our knowledge in these respects. He embodied his views, seeking the explanation on this track, filling up gaps and tracing projected roads along lines of probable truth in his "Analytische Theorie der organischen Entwicklung." But his own work convinced him of the hopelessness of the task he had undertaken, and he has become as strenuous a vitalist as Butler. The most complete statement of his present views is to be found in "The Philosophy of Life" (1908–9), being the Gifford Lectures for 1907–8. Herein he postulates a quality ("psychoid") in all living beings, directing energy and matter for the purpose of the organism, and to this he applies the Aristotelian designation "Entelechy." The question of the transmission of acquired characters is regarded as doubtful, and he does not emphasise—if he accepts—the doctrine of continuous personality. His early youthful impatience with descent theories and hypotheses has, however, disappeared.

In the next work the influence of Hering and Butler is definitely present and recognised. In 1906 Signor Eugenio Rignano, an engineer keenly interested in all branches of science, and a little later the founder of the international review, *Rivistà di Scienza* (now simply called *Scientia*), published in French a volume entitled "Sur la transmissibilité des Caractères acquis—Hypothèse d'une Centro-épigenèse."[1] Into the details of the author's work we will not enter fully. Suffice it to know that he accepts the Hering-Butler theory, and makes a distinct advance on Hering's rather crude hypothesis of persistent vibrations by suggesting that the remembering centres store slightly different forms of energy, to give out energy of the same kind as they have received, like electrical accumulators. The last chapter, "Le Phénomène mnémonique et le Phénomène vital," is frankly based on Hering.

In "The Lesson of Evolution" (1907, posthumous, and only published for private circulation) Frederick Wollaston Hutton, F.R.S., late Professor of Biology and Geology, first at Dunedin and after at Christchurch, New Zealand, puts forward a strongly vitalistic view, and adopts Hering's teaching. After stating this he adds, "The same idea of heredity being due to unconscious memory was advocated by Mr. Samuel Butler in his "Life and Habit."

[1] [Now translated into English.]

Dr. James Mark Baldwin, Stuart Professor of Psychology in Princeton University, U.S.A., called attention early in the nineties to a reaction characteristic of all living beings, which he terms the "Circular Reaction." We take his most recent account of this from his "Development and Evolution (1902):[1]

"The general fact is that the organism reacts by concentration upon the locality stimulated for the *continuance* of the conditions, movements, stimulations, *which are vitally beneficial*, and for the *cessation* of the conditions, movements, stimulations *which are vitally depressing*."

This amounts to saying in the terminology of Jennings (see below) that the living organism alters its "physiological states" whether for its direct benefit by the maintenance of beneficial conditions, or for its indirect benefit in the reduction of harmful conditions.

Again:

"This form of concentration of energy on stimulated localities, with the resulting renewal through movement of conditions that are pleasure-giving and beneficial, and the consequent repetition of the movements, is called 'circular reaction.'"

[1] He says in a note, "This general type of reaction was described and illustrated in a different connection by Pflüger in *Pflüger's Archiv f.d. ges. Physiologie*, Bd. XV." The essay bears the significant title "Die teleologische Mechanik der lebendigen Natur," and is a very remarkable one, as coming from an official physiologist in 1877, when the chemico-physical school was nearly at its zenith.

Of course, the inhibition of such movements as would be painful on repetition is merely the negative case of the circular reaction. We must not read too much of our own ideas into the author's mind; he nowhere says explicitly that the animal or plant shows its sense and does this because it likes the one thing and wants it repeated, or dislikes the other and stops its repetition, as Butler would have said. Baldwin is very strong in insisting that no full explanation can be given of living processes, any more than of history, on purely chemico-physical grounds.

The same view is put differently and independently by H. S. Jennings,[1] who started his investigations of living Protista, the simplest of living beings, with the idea that only accurate and ample observation was needed to enable us to explain all their activities on a mechanical basis, and devised ingenious models of protoplastic movements. He was led, like Driesch, to renounce such efforts as illusory, and has come to the conviction that in the behaviour of these lowly beings there is a purposive and a tentative character —a method of "trial and error"—that can only be interpreted by the invocation of psychology. He points out that after stimulation the "state" of the organism may be altered, so that the response to the

[1] "Contributions to the Study of the Lower Animals" (1904), "Modifiability in Behaviour" and "Method of Regulability in Behaviour and in other Fields," in *Journ. Experimental Zoology*, vol. ii. (1905).

same stimulus on repetition is other. Or, as he puts it, the first stimulus has caused the organism to pass into a new "physiological state." As the change of state from what we may call the "primary indifferent state" is advantageous to the organism, we may regard this as equivalent to the doctrine of the "circular reaction," and also as containing the essence of Semon's doctrine of "engrams" or imprints which we are about to consider. We cite one passage which for audacity of thought (underlying, it is true, most guarded expression) may well compare with many of the daring flights in "Life and Habit":

"It may be noted that regulation in the manner we have set forth is what, in the behaviour of higher organisms, at least, is called intelligence [the examples have been taken from Protista, Corals, and the Lowest Worms]. If the same method of regulation is found in other fields, there is no reason for refusing to compare the action to intelligence. Comparison of the regulatory processes that are shown in internal physiological changes and in regeneration to intelligence seems to be looked upon sometimes as heretical and unscientific. Yet intelligence is a name applied to processes that actually exist in the regulation of movements, and there is, *a priori*, no reason why similar processes should not occur in regulation in other fields. When we analyse regulation objectively there seems indeed reason to think that the processes are of the same character in behaviour as elsewhere. If the term 'intelligence' be reserved for the subjective accompaniments of such regulation, then of course we have no direct knowledge of its existence in any of the fields of regulation outside of the self, and in the self perhaps only in behaviour. But in a purely objective consideration there seems no reason to suppose that regulation in behaviour (intelligence) is of a fundamentally different character from regulation elsewhere" ("Method of Regulation," p. 492).

Jennings makes no mention of questions of the theory of heredity. He has made some experiments on the transmission of an acquired character in Protozoa; but it was a mutilation-character, which is, as has been often shown,[1] not to the point.

One of the most obvious criticisms of Hering's exposition is based upon the extended use he makes of the word "memory": this he had foreseen and deprecated.

"We have a perfect right," he says, "to extend our conception of memory so as to make it embrace involuntary [and also unconscious] reproductions of sensations, ideas, perceptions, and efforts; but we find, on having done so, that we have so far enlarged her boundaries that she proves to be an ultimate and original power, the source and, at the same

[1] See above, Chap. VII, pp. 178–80, 207–8, "The Hereditary Transmission of Acquired Characters."

time, the unifying bond, of our whole conscious life" ("Unconscious Memory," p. 68).

This sentence, coupled with Hering's omission to give to the concept of memory so enlarged a new name, clear alike of the limitations and of the stains of habitual use, may well have been the inspiration of the next work on our list. Richard Semon is a professional zoologist and anthropologist of such high status for his original observations and researches in the mere technical sense, that in these countries he would assuredly have been acclaimed as one of the Fellows of the Royal Society who were Samuel Butler's special aversion. The full title of his book is "DIE MNEME als erhaltende Prinzip im Wechsel des organischen Geschehens" (Munich, ed. 1, 1904; ed. 2, 1908). We may translate it "MNEME, a Principle of Conservation in the Transformations of Organic Existence."

From this I quote in free translation the opening passage of Chapter II:

"We have shown that in very many cases, whether in Protist, Plant, or Animal, when an organism has passed into an indifferent state after the reaction to a stimulus has ceased, its irritable substance has suffered a lasting change: I call this after-action of the stimulus its 'imprint' or 'engraphic' action, since it penetrates and imprints itself in the organic substance; and I term the change so effected an 'imprint' or 'engram' of the stimulus;

and the sum of all the imprints possessed by the organism may be called its 'store of imprints,' wherein we must distinguish between those which it has inherited from its forebears and those which it has acquired itself. Any phenomenon displayed by an organism as the result either of a single imprint, or of a sum of them, I term a 'mnemic phenomenon'; and the mnemic possibilities of an organism may be termed, collectively, its 'Mneme.'

"I have selected my own terms for the concepts that I have just defined. On many grounds I refrain from making any use of the good German terms 'Gedächtniss,' 'Erinnerungsbild.' The first and chiefest ground is that for my purpose I should have to employ the German words in a much wider sense than what they usually convey, and thus leave the door open to countless misunderstandings and idle controversies. It would, indeed, even amount to an error of fact to give to the wider concept the name already current in the narrower sense—nay, actually limited, like 'Erinnerungsbild,' to phenomena of consciousness. . . . In Animals, during the course of history, one set of organs has, so to speak, specialised itself for the reception and transmission of stimuli—the Nervous System. But from this specialisation we are not justified in ascribing to the nervous system any monopoly of the function, even when it is as highly developed as in Man. . . . Just as the direct excitability of the nervous system has progressed in the history of the race, so has its capacity for receiving imprints; but neither susceptibility nor retentiveness is its monopoly; and, indeed, rctentiveness seems inseparable from susceptibility in living matter."[1]

Semon here takes the instance of stimulus and imprint actions affeeting the nervous system of a dog—

"who has up till now never experieneed aught but kindness from the Lord of Creation, and then one day that he is out alone is pelted with stones by a boy. . . . Here he is affeeted at onee by two sets of stimuli: (1) the optic stimulus of seeing the boy stoop for stones and throw them, and (2) the skin stimulus of the pain felt when they hit him. Here both stimuli leave their imprints; and the organism is permanently changed in relation to the recurrenee of the stimuli. Hitherto the sight of a human figure quickly stooping had produeed no constant speeial reaction. Now the reaetion is constant, and may remain so till death. . . . The dog tucks in its tail between its legs and takes flight, often with a howl [as of] pain.

"Here we gain on one side a deeper insight into the imprint aetion of stimuli. It reposes on the lasting change in the eonditions of the living matter, so that the repetition of the immediate or synchronous reaction to its first stimulus (in this ease the stooping of the boy, the flying stones, and the pain on the ribs), no longer demands, as in the original state

[1] Semon's technical terms are exclusively taken from the Greek, but as experience tells that plain men in England have a special dread of suchlike, I have substituted "imprint" for "engram," "outcome" for "ecphoria"; for the latter term I had thought of "efference," "manifestation," etc., but decided on what looked more homely, and at the same time was quite distinctive enough to avoid that confusion which Semon has dodged with his Græcisms.

of indifference, the full stimulus *a*, but may be called forth by a partial or different stimulus *b* (in this case the mere stooping to the ground). I term the influences by which such changed reaction are rendered possible, 'outcome-reactions,' and when such influences assume the form of stimuli, 'outcome-stimuli.'"

They are termed "outcome" reactions or stimuli ("ecphoria") because the author regards them and would have us regard them as the outcome, manifestation, or efference of an imprint of a previous stimulus We have noted that the imprint is equivalent to the changed "physiological state" of Jennings. Again, the capacity for gaining imprints and revealing them by outcomes favourable to the individual is the "circular reaction" of Baldwin, but Semon gives no reference to either author.

In the preface to his first edition (reprinted in the second) Semon writes, after discussing the work of Hering and Haeckel:

"The problem received a more detailed treatment in Samuel Butler's book, 'Life and Habit,' published in 1878. Though he only made acquaintance with Hering's essay after this publication, Butler gave what was in many respects a more detailed view of the coincidences of these different phenomena of organic reproduction than did Hering. With much that is untenable, Butler's writings present many a brilliant idea; yet, on the whole, they are rather a retrogression than an advance upon Hering. Evidently they failed to exercise any marked influence upon the literature of the day."

This judgment needs a little examination. Butler claimed, justly, that his "Life and Habit" was an advance on Hering in its dealing with questions of hybridity, and of longevity, puberty, and sterility. Since Semon's extended treatment of the phenomena of crosses might almost be regarded as the rewriting of the corresponding section of "Life and Habit" in the "Mneme" terminology, we may infer that this view of the question was one of Butler's "brilliant ideas." That Butler at first shrank from accepting such a formal explanation of memory as Hering did with his vibration hypothesis should certainly be counted as a distinct "advance upon Hering," for Semon also avoids any attempt at an explanation of "Mneme." I think, however, we may gather the real meaning of Semon's strictures from the following passage:

"I refrain here from a discussion of the development of this theory of Lamarck's by those Neo-Lamarckians who would ascribe to the individual elementary organism an equipment of complex psychical powers—so to say, anthropomorphic perception and volitions. This treatment is no longer directed by the scientific principle of referring complex phenomena to simpler laws, of deducing even human intellect and will from similar elements. On the contrary, they follow that most abhorrent method of taking the most complex and unresolved as a datum, and employing it as an explanation. The adoption of such a method, as formerly by Samuel Butler, and recently by Pauly, I regard as a big and dangerous step backward" (ed. 2, pp. 380–1, note).

Thus Butler's alleged retrogressions belong to the same order of thinking that we have seen shared by Driesch, Baldwin, and Jennings, and most explicitly avowed, as we shall see, by Francis Darwin. Semon makes one rather candid admission, "The impossibility of interpreting the phenomena of physiological stimulation by those of direct reaction, and the undeception of those who had put faith in this being possible, have led many on the *backward path of vitalism*."[1] Semon assuredly will never be able to complete his theory of "Mneme" until, guided by the experience of Jennings and Driesch, he forsakes the blind alley of mechanisticism and retraces his steps to reasonable vitalism.

But the most notable publications bearing on our matter are incidental to the Darwin Celebrations of 1908–9. Dr. Francis Darwin, son, collaborator, and biographer of Charles Darwin, was selected to preside over the Meeting of the British Association held in Dublin in 1908, the jubilee of the first publications on Natural Selection by his father and Alfred Russel

[1] The italics are mine, not Semon's.

Wallace. In this address we find the theory of Hering, Butler, Rignano, and Semon taking its proper place as a *vera causa* of that variation which Natural Selection must find before it can act, and recognised as the basis of a rational theory of the development of the individual and of the race.[1] The organism is essentially purposive: the impossibility of devising any adequate accounts of organic form and function without taking account of the psychical side is most strenuously asserted. And with our regret that past misunderstandings should be so prominent in Butler's works, it was very pleasant to hear Francis Darwin's quotation from Butler's translation of Hering[2] followed by a personal tribute to Butler himself.

In commemoration of the centenary of the birth of Charles Darwin and of the fiftieth anniversary of the publication of the "Origin of Species," at the suggestion of the Cambridge Philosophical Society, the University Press published during the current year a volume entitled "Darwin and Modern Science," edited by Mr. A. C. Seward, Professor of Botany in the University. Of the twenty-nine essays by men of science of the highest distinction, one is

[1] [As Mr. Festing Jones recalls (*op. cit.*, pp. 24, 25), Dr. Darwin had in previous scientific publications referred with sympathy to Butler's published views.]

[2] "Between the 'me' of to-day and the 'me' of yesterday lie night and sleep, abysses of unconsciousness; nor is there any bridge but memory with which to span them" ("Unconscious Memory," p. 71).

of peculiar interest to the readers of Samuel Butler: "Heredity and Variation in Modern Lights," by Prof. W. Bateson, F.R.S., to whose work on "Discontinuous Variations" we have already referred. Here once more Butler receives from an official biologist of the first rank full recognition for his wonderful insight and keen critical power. This is the more noteworthy because Bateson has apparently no faith in the transmission of acquired characters; but such a passage as this would have commended itself to Butler's admiration:

"All this indicates a definiteness and specific order in heredity, and therefore in variation. This order cannot by the nature of the case be dependent on Natural Selection for its existence, but must be a consequence of the fundamental chemical and physical nature of living things. The study of Variation had from the first shown that an orderliness of this kind was present. The bodies and properties of living things are cosmic, not chaotic. No matter how low in the scale we go, never do we find the slightest hint of a diminution in that all-pervading orderliness, nor can we conceive an organism existing for one moment in any other state."

We have now before us the materials to determine the problem of Butler's relation to biology and to biologists. He was, we have seen, anticipated by Hering; but his attitude was his own, fresh and original. He did not, like Hering, hamper his original exposition by a subsidiary hypothesis of vibrations which may or may not be true, which burdens the theory without giving it greater carrying power or persuasiveness, which is based on no objective facts, and which, as Semon has practically demonstrated, is needless for the detailed working out of the theory. Butler failed to impress the biologists of his day, even those on whom, like Romanes, he might reasonably have counted for understanding and for support. But he kept alive Hering's work when it bade fair to sink into the limbo of obsolete hypotheses. To use Oliver Wendell Holmes's phrase, he "depolarised" evolutionary thought. We quote the words of a young biologist, who, when an ardent and dogmatic Weismannist of the most pronounced type, was induced to read "Life and Habit": "The book was to me a transformation and an inspiration." The learned writings of Semon or Hering could never produce such an effect: they do not penetrate to the heart of man; they cannot carry conviction to the intellect already filled full with rival theories, and with the unreasoned faith that to-morrow or next day a new discovery will obliterate all distinction between Man and his makings. The mind must needs be open for the reception of truth, for the rejection of prejudice; and the violence of a Samuel Butler may in the future as in the past be needed to shatter the coat of mail forged by too exclusively professional a training.

CHAPTER X

INTERPOLATION IN MEMORY[1]

Some years ago the education of my children led me to consider certain questions as to the methods of elementary teaching, very distinct from any involved in my own collegiate courses. The Art Syllabus of South Kensington, with its carefully graded steps towards the perfection of technique in form, tone, colour, and composition; the practice of a conscientious teacher, who objected to any pupil passing to a higher grade in the "three R's" so long as any part of the back-work was not accurately and irrevocably fixed; the various "Complete and Progressive" methods for piano, violin, and voice: all seemed to me on empirical and traditional grounds to err by their very correctness and completeness. It occurred to me to plan out a syllabus of instruction in the art of stone-throwing on a complete logical and progressive basis, and to see how it would work in the case of three imaginary pupils. The syllabus was as follows:

[1] Read at the British Association at Bradford, 1900.

Grade I. (Preliminary).—Measure distance along the ground; then estimate the distance of certain points and correct by fresh measurements. This exercise is to be practised constantly as an accompaniment to the succeeding ones.

Grade II.—Drop a stone on a point on the ground immediately in front of you: standing, sitting, and stooping at different degrees of inclination.

Grade III.—Practise throwing the same stone at known, increasing distances.

Grade IV.—The same as III., but with the substitution of stones of different *known* weights.

Grades V. and VI.—Different combinations of the unknown in weight and distance, at a fixed mark.

Grades VII., VIII., etc.—Throwing, first known, then unknown, weights at moving objects while still yourself; to be practised in all three positions. Etc., etc.

The reader will have had enough of this syllabus: so had two, at least, of my three imaginary pupils. The first of them stuck hopelessly fast at the third stage, and loathes the very sight of a stone; the other has constantly played the truant from that very stage. But I have ascertained that, engaging in illogical and illicit practice on his own account, he has long since killed off all the sparrows of the neighbourhood. And the third? He is a good, conscientious lad, and has worked through the course with assiduity; and if he fails, as he mostly does, to hit the mark, there is always a good reason in his mouth to account for the failure of his arm.

Now, it is perfectly easy to see what is the course of teaching that is followed by the ordinary boy, left to his own devices, and stimulated by the desire to imitate and the desire to destroy. He starts with certain more or less latent ideas of distance. He sets up an old bottle in the back garden, not too far off. After a certain number of shots he commences to improve, and progresses rapidly. Then he puts the bottle farther off; after a preliminary shot or two at the new distance he "gets the range," and now hits almost every time. The next thing he does is, like Tom Brown and Harry East, to fill his pocket with stones every time he goes out, and aim more or less casually as he walks along at any object fixed or moving that takes his fancy. Here the weights and distances are all unknown; they vary in each case; while his pace and attitude at the moment of throwing introduce new, unknown factors, in new, unknown combinations. He "allows" duly for all these, and very soon is expert enough to bring down a bird on a tree, or to hit a driver on the nose, with rarely failing precision. In any of these feats he has had apparently to estimate the rate of his own movements and the distance, and to remember and combine attitude and co-ordination of movements in strength and direction. He is impelled by a combination of movements and experiences—none of which probably are identical with previous movements and experiences—to execute without delay a new combination of movements which are perhaps, even singly, equally new.

If we analyse our memories, and the way they are pigeonholed in our consciousness, we find that they are in the first place arranged in order of time, and associated, as in a commercial "waste-book," with the transactions that go before and after. Our conscious mind, moreover, effects a sort of ledger-like rearrangement, and groups them in categories of *kind*; but mere arrangement can only manipulate what it has received—namely, the *individual, discontinuous* memories. But the facts that I have just dwelt on lead us to conceive that in the unconscious region of our memory there are not only the facts of memory, both impressions and expressions, classed in category, but that within each category there is a classification by magnitude; and that there is further a something intervening between the impressions of different magnitudes which unites them into a continuous whole, while it separates them by a distance proportional to their difference of magnitude. In other words, while the different members of a given category of facts are the only ones accessible to our consciousness, they form in our unconscious memory, in geometrical metaphor, a figure bounded by an "interpolation curve" uniting the separate actual past sense-impressions, be they few or many.

We are all familiar with the sort of curve I refer to. We have seen Mr. Galton's statistical curves, where magnitude of one kind is represented by a horizontal base-line, while magnitudes of another kind are represented by perpendiculars set off at the proper distances along that line. There may be only a limited number of the perpendicular lines; but we get a connected idea of the whole by joining up their tops into a broken line. Then, if we smooth out the angles, we get an "interpolation curve," and are able therefrom to obtain valuable, often valid, conclusions as to the relations of magnitudes of which we have no record, and which should lie between those we have got down on our chart. Nay, more: we may gain a probable insight into the future or the past by continuing the curve either way beyond the part drawn by mere interpolation: this is termed "extrapolation."[1] A common and unfortunately too familiar instance of the "interpolation curve" is the "temperature chart" of a fever-patient; where the base-line represents intervals of time, and the perpendiculars the corresponding observed temperatures of the invalid. If these temperatures are taken sufficiently often, the broken line joining the ends of successive perpendiculars approaches a continuous curve; and we can use this curve to extend our knowledge with the more precision, the more frequent the observations have been. Thus if we have taken the temperature every even hour during the day, we can infer what has been the temperature at an odd

[1] "Extrapolation" may rank as a special case of interpolation.

hour or half-hour by drawing a perpendicular from the proper point on the base-line to meet the curve, as shown in the diagram; where the cross indicates the presumable temperature at 1 p.m., and the dagger that at 6 a.m., two hours before the doctor arrived. Again, if the doctor have been only called in when the fever was in progress, and the conditions were fairly uniform, he can by extrapolation, continuing the curve on either side, divine what has been the past course for a day or two before, and predict what

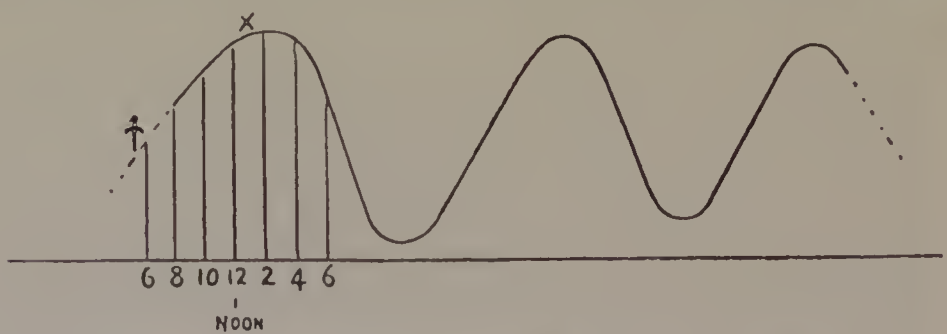


FIG. 41.—A temperature curve; see explanation in text.

will be its course for a day or two after. Of course, after the crisis, conditions change; nor can we utilise the continuation of the curve backwards to a time before our friend "took ill."

Thus do the facts of our memory seem to be arranged, in order of magnitude in each category, and to be separated by a space corresponding by a definite law to the differences between the magnitudes of the observed memories of the same category. In drawing on our memories for guidance we utilise not only the distinct memories of experience, but we are able to draw on a continuous curve, as it were, by interpolation and extrapolation, so that our categories of unconscious memory acquire a continuity, which is absent from the impressions we receive, and from our conscious memory. This continuous interpolated memory is as much a construct of the mind as the interpolation curve is a construct of the pen of the physician or statistician.

Now, I have been told by a friend, far better instructed than I in matters of psychology, that all this may be alleged to be implicit in the "principle of Association." To many, no doubt, the word "Association" has as comforting a sound as "Mesopotamia"; but all this comfort will not endow it with those ideas of continuity and proportionality we find in the metaphor of "interpolation."[1] However, this fact and factor, although unrecorded and unnamed by the professed psychologist, are well known to my friend the Man in the Street, and are equally familiar to his wife or sister, the Woman at Home. But the curious point is, that the faculty of interpolation in different categories is most differently developed in different individuals, and consequently has received most various names. Mrs. Beecher Stowe has given us the American name of *faculty* for it in the housekeeper, who, without watch

[1] I find that Mr. G. F. Stout has approached these views in his doctrine of "Relative Suggestion" ("Analytic Psychology," 1898). He has failed to note the essentially *unconscious* character of the process.

or clock, and with fires and "helps" of constantly varying capacity, is able to keep the complex household arrangements going "like clock-work." The artist calls it "feeling": feeling for colour, for form, for stability or balance (in sculpture), for expression, etc. When a painter endowed with feeling for colour mixes a new combination of pigments on his brown palette, and then lays it on his white canvas, he feels all the time that when it is surrounded by the other blobs that will form his picture it will "take its place," and give just the effect of that particular spot of the picture he sees before his eyes: in water-colour the matter is further complicated by the changes undergone in drying. Teaching will multiply the number of observed facts, multiply the number of perpendiculars from the base-line, as it were; experience will improve the power of combination: but a Leighton could never have been taught to paint with the glorious precision of colour and expression revealed to us by a Sargent. I know a little girl who has never been taught the elements of Statics, but whose feeling for stability is such that her earliest clay birds and rabbits "stood up of themselves," as a sculptor would say. A draughtsman may get every feature out of drawing, but the expression is there, the incorrect details have combined to yield a living likeness; and the caricaturist must needs possess this faculty

Again, the expert violinist who has a feeling for correct intonation, who has a "good ear," in common parlance,[1] has to adapt his fingering to each strange instrument, aye, and to each fresh string; for the intervals are never mathematically true, and vary with each fiddle and with each string. The pianist has to graduate differently the minute variations of touch to the varying resistance and resonance of each instrument. A billiard player may have learned something of the laws of reflection of moving bodies, and possibly have a hazy glimmer of the subjects of friction and spin and imperfect elasticity, though these involve such high mathematical powers for conscious solution that it is doubtful whether any champion has mastered them. But even had he done so, he would require for their application to each table, each ball, each cue, a preliminary investigation into their several "constants"; and given all these, such problems are not to be worked out in the limited time an expert spends between two successive strokes of a break. Nor could he thereby, after trying a few strokes on a new table, allow, *at once*, as he does, for its "fastness," resiliency, and truth, different from any he has known.

We now come to a far more subtle order of facts: those of language. Every one who had an early taste for reading will remember how each new word he

[1] A "good ear" for delicate intervals is not necessarily combined with the power of producing them accurately. I know more than one person whose incorrect singing shocks his own good ear, the very possession of which would be denied to him by the average listener.

came upon took its rightful place in his vocabulary, while he was yet ignorant of its pronunciation, and probably ashamed to use it openly, or even to prove the accuracy of his divination by an appeal to grown-ups, lest his mispronunciation should expose him to their ridicule. I remember (not without a blush) having *felt* the meaning of the word "misled" as a synonym for "deceived" or "cheated," with such shades of difference as synonyms always have, while I still pronounced it to rhyme with "drizzled"; and I well recall my relief when, without having betrayed myself to the adult scoffer, I discovered its connection with "mislead." [An exceptional instance of "feeling" for language has occurred to me recently. A bright baby-girl of twenty months, whose speech had not yet risen to the use of the verb in other than gerundive forms, employed three particles of assent: "Mmm," "Awy" (= "All right"), and "Yes." "Mmm" is general and undifferentiated; but she discriminated absolutely between the other two. "Yes" is the acceptance of the statement implied in a question: "Is your dolly a good girl?" "Did you put her to bed?"—"Yes." "Awy" is reserved for the acceptance of a proposed act: "Will you fetch me my shoes?" "Shall I carry you?" etc. During three weeks spent in her company I could detect no confusion whatever in this use.] A man with a gift that way will see from a single instance the difference of use of synonyms in his own language, and of dictionary equivalents in another. He will sympathise with Sentimental Tommy, who would rather lose a prize on which his whole future was to depend than use any other word when "hantle" was the only right one for his meaning; he will refrain from translating the French "*amusant*" by "amusing," when applied to technical workmanship.[1]

A card-player will profit by lessons drawn from the laws of chance, mathematically worked out and applied to his game; but the best players are hardly to be found among those who have memorised the deductions of these laws most successfully, and who carry out the precepts based on them with the greatest accuracy on all occasions.

The facts of the case demand that the interpolation conception should be extended, and that we should admit that the mind can, unconsciously and directly, combine two or more categories for the determination of correspondingly combined movements. Here, again, a geometrical construction comes to our aid. We are all familiar with the little automatic draughtsman, the toy made in Germany, which combines two curves (disposed here for convenience round the edges of two concentric discs) so as to produce a sketch in a single plane. There must be a capacity in our minds for a similar unconscious orderly combination between the curves of the various categories of our experience, so as to determine the

[1] "Fascinating" is our nearest equivalent.

co-ordinated response in our movements. In the same way a tide-predicting machine utilises the combination of many different records, real and hypothetical, to work on the pen; this pen traces, on the stretched roll of paper passing steadily before it, a curve, which represents time on its base-line, and the height of the successive tides, the combined produce of many factors, on its perpendiculars.

It may be objected that possibly at any given time there is a higher, *reasoning*, mental working-out of the problems which are set by impression, and to be resolved in action. But true reasoning requires adequate time, and we now know that thought is a good deal slower than we had been wont to assume. Prof. Charles Richet, in his lecture on the "Nerve Wave,"[1] given to the British Association in August 1899, adduced much converging evidence to show that the time required for any single mental operation is as long as the tenth of a second for a warm-blooded animal. Thus, if we are counting ourselves to sleep, we may easily note that the disyllabic numbers take longer than the monosyllabic ones; and every link in a chain of true reasoning proportionately delays its completion. *Conscious* evaluation, allowance, and judgment are among the slowest of our mental operations, for they require the comparison of successive mental images, successive "mentations," if I may be allowed to introduce a

[1] Translated in *Nature* for September 1899.

most useful word, made in America. On the other hand, unconscious evaluations, allowances, and judgments, and the actions based on them, are practically instantaneous. When, on a greasy day, the pedestrian crosses a crowded street, or the cyclist escapes from the bus swerving athwart his track on the near side to shave the galloping hansom on his off side, he does so by processes literally quicker than thought; or the accident insurance premiums would have to be considerably raised. Such unconscious processes have been termed "instinctive"; and indeed they are precisely of the kind that are to be met with in the lower animals. That they are not innate is, however, as certain in the one case as in the other. To justify the application of the term "instinctive," we should have to give that term an extension to all such actions as we cannot explain by our conscious reasoning powers. The result of this speculation has been to strengthen my disbelief in a good deal of *a-priori* pedagogics. and my belief in those empirical methods of teaching that have stood the wear and tear of centuries. The worst point of a logical syllabus is that the error or omission of a premiss makes the conclusion all wrong. Since these two principles of interpolation and of automatic combination have never been presented to the mind of the psychological designer of logical programmes of tuition, it is certain that his teachings have been, so far, altogether askew. And, on the other hand, it is equally certain, from these very considerations, that those with a "faculty" for teaching will have, at least, not swerved very far from the right track. Again, it is even likely that our learning may have been far more efficacious than our teaching: that we have taught ourselves better than our tutors have taught us. Thus, in cycling, we are instructed to maintain our balance, and to check the tendency of the machine to fall on one side by pulling the steering handle and turning its head to the falling side: and so we are *taught* to wobble along. But we soon *learn*, all unconscious, to balance ourselves without this wobbling; and instead of balancing by the steering handle, we even go one better, and, conversely, effect the steering, "hands off," by the mere balance of the body. Yet no one has given an explanation of the latter feat in terms intelligible to the mathematical tyro, much less to the professional teacher of cycling.[1]

The moral of all this is, that the teacher of a pupil with a distinct "faculty" for any subject is losing his own time and wasting the pupil's if he insists on making sure of every step before going on to the next one; he is performing ill what would be done spontaneously and well by the mind of the pupil. A teacher of the piano once said to me:

"I should very much like to teach Miss A. from Blank's 'Progressive Method'; but I daren't, as it's

[1] A mathematical explanation has since been given.

too complete. I find that a good pupil does not do well with steady progress straight through the book; but she ought to skip some of the work from time to time, and go ahead. On the other hand, if I gave Miss A. the 'Method,' her parents would never consent to her buying another piece till she had learned every piece in it, and got them all note-perfect."

With this true story I may close this essay.

CHAPTER XI

THE TEACHING OF "NATURE-STUDY"

An Address to Teachers[1]

I NEED not warn you that within the space of one hour I cannot attempt to cover the whole ground of my subject. The limits of time are far too narrow, and my personal experience in the teaching of young children has been far too restricted to warrant my presenting you with more than a bird's-eye view of the subject. I propose therefore to discuss general principles and generalities of practice; you, for the most part already engaged in teaching, will judge of their value in the arrangement of your courses, and in deciding on the character of your daily lessons.

At the present day there may be a tendency to glorify ourselves in the conceit that we are pioneers in a new subject; and this we certainly are not. I may recall Aikin and Barbauld's "Evenings at Home," written over a century ago, with its chapter,

[1] Delivered in Queen's College, Cork.

"Eyes and no Eyes," conceived in the very spirit of such men as Lloyd Praeger. About the same period, Miss Edgeworth, that most distinguished Irishwoman, wrote "Harry and Lucy," for which I feel grateful, since it first told me of the new worlds available to us through the microscope, as well as instructing me in the principles of the architecture of the home. I may as well at once urge that to teach our subject in the right spirit you will regard a house as no less interesting than a honeycomb, and erect no barrier to screen off from the inquisitive eyes of childhood that portion of the external world occupied by the works of man. These early attempts failed because they did not yet impress the official directors of education. Think of the discouragement of Charles Darwin at Shrewsbury, or, a generation earlier, that of Shelley at Eton! Darwin found his vocation in his later student years under the sympathetic guidance of Prof. Henslow, of whom I shall have to speak again later. But Shelley fell in with no such guide; and who can doubt that he would have been a more stable man—and no less great a poet—had he fallen under the influence of a science master of the best type? Pass on to a later generation, and turn over the pages of "Tom Brown's Schooldays," with its truthful, living presentment of the great Rugby head master, Thomas Arnold, and see for yourselves what short shrift poor Martin with his vocation as a naturalist received at his hands. Times have changed, and it was time they should change. If the Duke of Wellington could truly say that the Battle of Waterloo had been won on the playgrounds of Eton, we may to-day say with equal truth that the shortcomings of our Army, the loss of ground by the industry and commerce of these islands in the peaceful conflicts of nations, have been prepared in the class-rooms of our public schools. In private schools, especially girls' schools, and by the much-decried family governesses, a modicum of nature-study, too often, alas! divorced from the actual study of nature itself, continued to be administered through such books as Mrs. Marcet's "Conversations," Dr. Brewer's "Guide to Science," and the like. But the first organised introduction of nature-study into the primary school appears to have been due to George Henslow, Professor of Botany at Cambridge and Rector of Hitcham, in the middle of the last century. In the national school of his Suffolk parish he taught botany from actual plants to the village boys and girls. The district is one notorious for the ultra-Saxon stolidity of its folk; yet the children took kindly to the teaching, technical terms and all: we learn that Henslow's pupils developed when adult into good and profitable servants, who were eagerly sought for in the county. Botany, mainly descriptive and systematic, was, as we have seen, the chief subject, taught practically on the flowers of the field: but Prof. Daniel Oliver, who worked up Henslow's notes into the well-known "Lessons in Elementary Botany," tells that the instruction was broad as well as thorough. Thus the Elder, with its hollow cylindrical twigs filled with an abundance of pith, and used to make pop-guns, gave an insight into the materiality of the atmosphere and the elasticity of gases. From the utilisation of elder-pith by the physicist, a glimpse into statical electricity might well have been added; but I don't remember whether this was done. Again, in some of the great Quaker schools, the botanical side of nature-study has long been pursued: they have furnished the country with many professional botanists, such as Daniel Oliver, J. G. Baker, the well-known authority on Lilies and on Ferns, Potter of Newcastle. But apart from this, Henslow's experiment was followed by decades of neglect[1]; and it has only been within the last ten years or so that our theme has become the subject of general interest—I had almost said of universal interest, but I remember that in agricultural Ireland botany was for many years excluded from the Intermediate course for boys!

Thus what is new in nature-study is the recognition

[1] The British Association meets this year (1912) in Dundee for the first time for forty-five years. On looking up the Report of the 1867 meeting I found that Botany was taught on Henslow's lines to every boy in Rugby as a first year's course in science from the autumn of 1864; and that it was generally liked and very successful. When and why it was dropped I do not know.

of its value by authorities and by parents in every grade and class: the view that even elementary education should bring, or rather retain, children in observant relations with the world about them: the downfall of the barriers set up by boards of studies and head masters against the curiosity of the young child, whose whole previous education outside the school-house had been essentially on the lines of "nature-study."

In early and mid-Victorian education, a great part was no doubt played by the object-lesson, which you will find a most valuable introduction for young children to the methods of nature-study. It has been, I know, much decried for its sterility, as the mere giving of names to qualities, and the explaining by what needs explanation—as, for instance, replacing "heat" by "caloric," if not "water" by "aquosity." Yet in it we find more than the germ of most valuable teaching. Terminology is the indexed ledger of the arts and sciences, without which no big transactions are possible. Even the bare giving of names to the qualities of things seen and felt (and such alone can be the objects of true object-lessons) enriches the child's vocabulary, and enables it to bring together, to correlate facts otherwise widely separated. Take, say, a lump of sugar—"soluble," "sapid," "sweet," bring sugar into direct relation with hosts of other substances: "powdery," "crystalline," and "saccharine" applied to its structure afford you comparisons with such apparently different objects as whitening, Iceland spar, and statuary-marble. Thus we see that, science being essentially the study of relation, the much-abused object-lesson given on a *present* object, well selected, affords a very good opportunity to initiate the scholar into one essential of scientific method. We shall revert to this question of terminology later, since it is one on which I hold strong views, although hardly fashionable ones. An object-lesson on the orientation and topography of the schoolhouse, followed up by the drawing of rough plans to scale (on squared paper, of course), is the best possible introduction to map-drawing and reading and to the study of geography: the interpretation of mountain-shading and contour-lines may be illustrated by plans of dishes, bowls, or cups. Another development of the object-lesson is the "jewel game" that plays so important a part in the training of Rudyard Kipling's "Kim." You give your pupils a timed opportunity of seeing and noting a mixed collection of things—they may be an odd assortment of objects on a tray as in the book; or the figure, features, and attire of a lady passing the school—and you request a good account thereof. This account may be presented to you all of a muddle, or given in good orderly fashion. By insisting on order, as well as completeness and rapidity, you lead up to method in work, to orderly logical composition. Here you will come upon one difficulty inherent in all class teaching—the differences of individual aptitude. With the forward—those who possess "faculty," as the Americans call it[1]—your difficulty is an indirect one: you will have to damp their desire to shine on every occasion (inherent in the artistic and the literary temperament) by your tact, convincing them that your demands for self-effacement imply the highest compliment. This will give the opportunity of constant practice to the mediocre; but here, as everywhere, you will need all your tact and patience in coaxing on the backward, the dull, the inarticulate, quietly nursing in them the weakly germs of intellect until they grow into healthy vigour. And all the time you have to maintain the interest of the quickest. Your occupation has indeed been aptly compared to that of the gardener: yet his task is the easier, inasmuch as he is free to weed out the weakly seedlings, and so give more space and air and light to the vigorous. But you will not lose heart if you recall how many school dullards have become world geniuses; the stone that was rejected of the builders has often become the headstone of the corner. And have no fear of giving some uncongenial work to your pupils; a little of it is good for them, as for us: a certain amount of uncongenial work—grind—has to be done in every complete work. It is not fair that *all* the school grind should fall to the teacher's lot.

[1] See "Interpolation in Memory," p. 289.

To return to our object-lessons on the schoolhouse; from the building materials we pass to geology on the one hand, to trees and their growth on the other. The object-lessons on food lead us again to geography, and through the seeds of cereals to plant-life, which at the present day affords the favourite and most developed section of nature-study. You will not omit notions of transport and manufacture, bearing in mind the wide view we have taken of our subject, the extension of the definition of "nature-study." Now, in this special nature-study on plants, the Irish Intermediate Board have provided you, Irish teachers, with a most valuable botanical syllabus, drawn up by Dr. Turnbull, of the Department of Agriculture and Technical Education—a syllabus which, in essentials, I do not think can be much improved upon. But in following it you must beware of the snare of self-sacrifice. It is so easy for the enthusiastic, conscientious teacher to impose too much work on himself, and so to deprive the pupil of his rightful opportunities of independent effort. The children are, indeed, expected to make their own "spontaneous" observations: but you will be tempted to lead up to, to carefully prepare, these "spontaneous" observations, lest the observer go astray and be led into wrong inferences: and here it is that, as I say, you deprive the scholar of an opportunity for that independent effort on which we lay much stress. Again, I would warn you against one fallacy that may induce conceit in pupil and teacher alike. It is impossible to train young children to perform *original research*, even though you *make* them repeat for themselves those experiments of the Priestleys and the Darwins which led up to their discoveries in plant physiology, and you *induce* them to make correct deductions from their results. It is the invention, the method, the foresight, the preparation of the *experiment that has to be made* that make the researcher, not the mere manipulation and record of experiments and observations devised by others. This is the fallacy of much pedagogic "theory" put forward by the heuristic school. Yet it is much to train your children to observe patiently and to record systematically with system and accuracy under your direction.

Touching the matter of self-sacrifice, I would caution you against the prevalent idea that the good teacher's work can be, or should be, continuously strenuous. If you act on this supposition during the school-hours, what energy will you have left in your leisure to maintain and to extend your knowledge, so as not to become stale and groovy? During each school period the children have intervals of complete rest, when they banish all care, stamping and shouting in the playground; but such relaxation during the short intervals is impossible for you. And since this supposition is impossible and absurd, you may salve your unselfishness by reflecting also that excessive strenuousness on the part of the teacher imposes too great a strain on the attention of the child, which cannot be kept perpetually screwed up to the high pitch that your "strenuous teaching" would demand for its reception. Therefore, without compunction, see that your programme of nature-study provides for its pupils—*within school-hours*—work both individual and silent, like the routine of the dreary but essential long addition and multiplication sums, and comparable with the technical exercises of the musician.

For such work you will find ample opportunity in that branch of botany least insisted upon in your syllabus—the accurate technical description of plants based on neat and careful dissection and drawings. In the earlier stages the filling in of schedules may be used as a preparation for descriptions, as advocated and practised by Henslow; but dissections for inspection must always accompany the schedules. Nowadays we may carry the work of description further by appending interesting details of bionomics, such as the relative time of ripening of anther and stigma, adaptation to cross or self-pollination, etc. Finally the advanced pupil should be trained to find for himself in the flora the true systematic position of his plant—order, genus, species, and even variety. This should be done from the completed description, not from the plant in the first instance; for in this way the inadequacy of a description in details will at once reveal itself. I insist on this the more, as I have seen descriptions marked high by grinders, though hardly more than the Natural Order was ascertainable from them. Curiously enough, it is the characters of the pistil that are most shirked in this way: in examination papers, with descriptions from memory or from the plant, the description of the flower stops short at the stamens and leaps to the mature fruit, which is neither present nor asked for. This work must, of course, be led up to by class demonstrations: the teacher will distribute specimens and read aloud the alternatives, asking the pupils in turn "which alternative—A or B?" This work gives a familiarity with plants which is indispensable to all botanists, and an admirable preparation for other branches of science. I remember the great Professor De Bary, of Strasburg, when we were out for an excursion, insisting to me on the value of this sort of work, and inveighing against the idea of men expecting to become good botanists (even as physiologists) who had no personal acquaintance with plants generally.

We now come to my unfashionable views. I lay the greatest stress on the habitual use of the correct technical terms in current professional use among botanists and that *from the very outset.* No science, no art can be learned without its proper terms. The music-pupils find no difficulty in such words as *smorzando, arpeggio*; why should the nature-study classes boggle over "decussate" and "epigynous"? Technical terms remote from popular speech are often necessary to avoid ambiguity and confusion. What do you mean by speaking of the "top" and "bottom" of a *hanging* shoot? When you speak of the "front" of a cat, do you mean towards the head or towards the abdomen? To introduce the terms "base," "apex," "dorsal," "ventral," "anterior," "posterior," is to replace shipshod ambiguity by scientific precision. "But," I hear some one plead, "why not make all these terms out of English material, and not overburden the poor children's brains with long words of classical origin?" This objection is based on a profound lack of sympathetic insight into the psychology of the child—to speak plainly, it is tommy-rot, if you look into it. A new word to a child means a new idea, and an intelligent child welcomes the new word for the new idea that it brings.[1] Moreover, the new word is to the child a *new word*, and that is all: until its literary taste is developed—narrowed, if you will—the child cares naught whether the word

[1] Compare the following: "Now a person is limited by the number of things he is able to call by their names, qualify by appropriate epithets. This is no mere pedantic ruling; it belongs to that unfathomable mystery we call human nature. And the modern fashion of education, with its shibboleth of 'things not words,' is infinitely demoralising" ("The Basis of National Strength: Education and the Fullness of Life," by Charlotte Mason, *Times Educational Supplement*, June 4, 1912).

be Latin, Greek, Semitic, or Hybrid; though he will, of course, take a bigger pride the bigger the word he can handle correctly. Did any boy bitten with nautical enthusiasm ever find a difficulty in mastering the complex and absurd terminology of the good old three-master ship? It is only at a later age that technical terms become the burden and the indignity that parents and pedagogists feel them. Therefore, to remove technical words from the young defers no difficulty in the present: it actually creates one for the future if they are to pursue nature-study. Again, to substitute unrecognised vernacular terms is to make needless confusion. I have seen an old English botany in which the stamens were called "chives," which to any child familiar with a vegetable garden would suggest that they must always smell of onions! John Ruskin, in horror at the connotations of the word "flesh," proposed to replace it for fruits in botany by "ambrosia," a term singularly unsuited to the flesh of the crab-apple or the rowan berry. In other sciences we have seen the same countersense, the introduction of new, complex, ill-sounding words made in Germany, or inspired by an evil German spirit abroad in England. To replace the "impenetrability of matter" by the "unthoroughfaresomeness of stuff" was Horne Tooke's answer to a bet or a challenge, and not meant seriously; but why should we botanists be expected to model our terms on such harsh and unreasonable[1] barbarisms as "chalk-stuff gas?"

General neatness and deftness find their place in nature-study intelligently pursued—notably in botany, where, besides neat dissection, you will encourage the representation thereof by pencil or brush. Here comes a caution or two. The pencil sketch is essentially a translation, a selection; but the brush aims at a relatively complete presentation. You must therefore take care not to falsify at the outset your pupils' sense of colour and of tone by allowing them to paint each flower, each leaf for itself, with a background of white paper to give the lie to the whole. Consider: white paper affords our representation of the highest possible light, a cloud or a white wall in full sunshine. Hold up your flower before such a background, and see what has become of the glowing colours you put into the picture you have just completed as it lay on the dull drawing-board beside you. I do not ask you always to insist on a background of correct value being washed in; but you will do much by using a relatively dark brown paper for the pictures, and recognising the use of Chinese white. It is only when we recall the origin of water-colour, which began by tinting up conventional architectural

[1] Unreasonable, because the child who sees chalk resolved by heat into quicklime and a gas will consider the quicklime the "chalk-stuff," if he is told that such a word exists; and *logically* the carbon dioxide should be to him "*not*-chalkstuff gas."

drawings to make them look pretty, and the painting of flowers purely for decoration, that we can explain the absurd practice of using white paper for children to paint on.

It is due to the untrained feelings of parents, aided perhaps by an unwillingness to kill, that the study of animals is so much less accessible than that of plants. We all remember the indignant mother's letter of protest: "Please do not teach our Sarah Jane any more about her inside: it makes her feel uncomfortable, and it is not nice. Besides, it's rude." But the rearing of Caterpillars and Tadpoles, observations on the breathing and feeding of Fish, and so forth, are always open to you: you will not miss the opportunities you have of showing the trunk of Butterflies and Bees, and the pollen-brushes and baskets on the legs of the latter, etc. You may even go so far as to demonstrate the structure of the chief groups of Vertebrates on a Fish, a Frog, a Fowl, and a Rabbit, with rough dissections. In this way you will lay a foundation for the later teaching of enough physiology to explain the principles of hygiene. I would suggest that microscopic demonstrations be introduced sparingly in the lower classes—nay, reserved for an occasional treat. However, every pupil must be provided with a pocket-lens, and taught the use of it.

Whenever your lesson approaches lecture form, you will do well to follow it up by a question paper to be answered *against time*, in school. For the youngest the questions should be such as to require answers as direct and simple as you please. But you will insist that every answer be put in the form of a complete statement, definite and complete in itself, and not a mere substantive, with qualifications floating, as it were, in the air, and unintelligible in the absence of the question. For the older pupils, on the contrary, your questions should exact a certain amount of reflection: and the answers should be presented in good logical form and order, illustrated with apt sketches where useful. They must, of course, never be allowed to stray from the scope of the question—a favourite practice with examinees, whether from lack of understanding, from a wish to replace the unknown or forgotten which is asked for by what is known, or from a general desire to shine by the abundance of their knowledge. Put your foot down on "volunteering" in every shape, if from no other motive than fear of the external examiner, to whom it is an utter abomination. Your teaching in nature-study will by this course give invaluable practice in the art of composition.[1] I attribute much of whatever success I have obtained in life to my training on these lines, when a boy under eleven, by weekly lectures

[1] My experience since I wrote this lecture, as Examiner in Botany under the Intermediate Education Board in several successful years, has amply justified this claim for nature-study—that its practice teaches composition admirably. The "form" of the answers reached a very high standard, not only in exceptional papers, but throughout.

and question-papers from the late William Pinches, one of the founders of the College of Preceptors.

Outside the hours of class-teaching come the school calendar, the school museum, the school garden, and the school walks. The calendar will contain daily records of various phenomena, the name of the pupil recorder being always appended. "Phenological" observations come first: the earliest appearance of spring plants, the opening of the leaf-buds of the various trees and shrubs, the dates of their flowering, of the fall of the flowers, of the ripening of the fruit, the autumnal changes of tint, and the leaf-fall. With birds we record the birds that sing right through winter, the first spring and the last autumn song of the less persistent songsters, the arrival and the departure of the migratory, the times of nest-building, of hatching, and of fledging, etc. Since these facts are all associated with the weather, you will record that also, teaching meteorology as you go along, without necessarily naming the word. In practice I would recommend you to enter all records in a day-book as they come in, and keep a carefully arranged journal from it. You will do well to map out the daily meteorological observations on squared paper, so as to draw the weekly curves of maximum and of minimum thermometer and of barometer and paste these into your journal. Of course, you will need the two thermometers and the barometer, to which apparatus you should add a raingauge. You will find no difficulty in persuading your class that the care and record of these is a most honourable office—just as Tom Sawyer, when he was ordered to paint the fence, succeeded in persuading his mates who had assembled to jeer at him that it was so high a function that participation in it could only be obtained by payment in the good-conduct tickets of the Sunday school. The weather charts of *The Times* or of the Meteorological Office should prove no mysteries to your more advanced pupils.

But the lines of some of you may fall in big towns; and the town dweller should not miss his own opportunities of observation. Trees, birds, and wild flowers may be rather out of the way; but the town has its seasons, and its phenology should be recorded, for it is full of interest. Take the item of games. Trace the appearance of the hoop in winter, its vernal replacement by the whipping-top, and later by the peg-top, the prevalence of street hurley[1], the coming and going of marbles, and the irregular invasions of the squeaking balloon. The seasonal changes of toilette by men and women will add to the value of your record. More directly on the lines of nature study are the contents of the provision shops and costers' barrows—the fish, fruit, vegetables and flowers, from their earliest introduction in the high-class shops to their ultimate profusion at low prices in the streets, and their final disappearance.

[1] The equivalent of hockey.

The lessons on plants and the school walks should provide the nucleus for a herbarium for reference. Specimens that require preservation in liquid should be stored in formalin properly diluted, which is much cheaper than spirit, and not inflammable. Bottles are costly if they have to be purchased, but clear glass jam-pots and pickle-jars may often be provided by your pupils; for large corks or bungs, stoppers or crumpled paper soaked in paraffin wax (the cheapest candles melted down will do) are an admirable substitute. The curatorship, or rather the assistant curatorship, of the museum should always be entrusted to one or two selected pupils; and now that cheap editions are abundant, a library can easily be added to contain books for identifying the specimens, with such classics as White's "Natural History of Selborne," Waterton's "Wanderings," Darwin's "Naturalist's Journal," Moseley's "Notes of a Naturalist," the Travels of Bates, Belt, Wallace, etc.

The school garden is still more a question of possible accommodation than the school museum. You may have to content yourself with a window-shelf to carry flower-pots, jam-crocks, tins, and pickle-bottles, with a few boxes to hold the wet sawdust for germinating seeds; or you may be lucky enough to realise the teacher's dream of a bed for every plant and every plant in its bed, as in some of the wealthier schools for girls.[1] But you must at any cost of effort

[1] Thanks to Prof. Armstrong's enlightened counsels, botany has been recently introduced into some of the great English public schools for boys.

have the means of germinating seeds and of growing the seedlings from them.

There is much to be said on school walks; but I have no time for it. In some parts of Germany these form a regular part of the school routine; and you will see the long string of children, each with his tin collecting-box, escorted by the primary teachers, going afield for the plants that will be identified and studied in the school. The pupils are encouraged to preserve specimens for themselves and to form private herbariums. Haeckel, in his affectionate dedication of one of his books to his old comrade and friend, the great zoologist, Carl Gegenbaur, refers to the collections they made when he was a boy of twelve, and to their audacious criticisms on the text-book views of "good species," to which these collections gave the lie. Whatever be thought of Haeckel's claims to eminence as a philosopher on mind and matter, body and soul, none can refuse him a high seat among the greatest of living biologists. And it is to the foundations that he laid by nature-study when at school that he attributes the most important part in his school training. With this example of the value of our subject I must conclude.

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* The asterisk implies that the Latin word is not actually found in any writing, but inferred

Printed by Hazell, Watson & Viney, Ld., London and Aylesbury.