Mr Darwin has further endeavoured to give a physical explanation of hereditary transmission by his hypothesis of Pangenesis; while he seeks for the principal, if not the only, cause of variation in the influence of changing conditions.

It is on this point that the chief divergence exists among those who accept the doctrine of Evolution in its general outlines. Three views may be taken of the causes of variation:—

a. In virtue of its molecular structure, the organism may tend to vary. This variability may either be indefinite, or may be limited to certain directions by intrinsic conditions. In the former case, the result of the struggle for existence would be the survival of the fittest among an indefinite number of varieties; in the latter case, it would be the survival of the fittest among a certain set of varieties, the nature and number of which would be predetermined by the molecular structure of the organism.

b. The organism may have no intrinsic tendency to vary, but variation may be brought about by the influence of conditions external to it. And in this case also, the variability induced may be either indefinite or defined by intrinsic limitation.

c. The two former cases may be combined, and variation may to some extent depend upon intrinsic. and to some extent upon extrinsic, conditions.

At present it can hardly be said that such evidence as would justify the positive adoption of any one of these views exists.

Development a recapitulation of ancestral history.

If all living beings have come into existence by the gradual modification, through a long series of generations, of a primordial living matter, the phenomena of embryonic development ought to be explicable as particular cases of the general law of hereditary transmission. On this view, a tadpole is first a fish, and then a tailed amphibian, provided with both gills and lungs, before it becomes a frog, because the frog was the last term in a series of modifications whereby some ancient fish became an urodele amphibian; and the urodele amphibian became an anurous amphibian. In fact, the development of the embryo is a recapitulation of the ancestral history of the species.

If this be so, it follows that the development of any organism should furnish the key to its ancestral history; and the attempt to decipher the full pedigree of organisms from so much of the family history as is recorded in their development has given rise to a special branch of biological speculation, termed *phylogeny*.

Phylogeny

In practice, however, the reconstruction of the pedigree of a group from the developmental history of its existing members is fraught with difficulties. It is highly probable that the series of developmental stages of the individual organism never presents more than an abbreviated and condensed summary of ancestral conditions; while this summary is often strangely modified by variation and adaptation to conditions; and it must be confessed that, in most cases, we can do little better than guess what is genuine recapitulation of ancestral forms, and what is the effect of comparatively late adaptation.

The only perfectly safe foundation for the doctrine of Evolution lies in the historical, or rather archæological, evidence that particular organisms have arisen by the gradual modification of their predecessors, which is furnished by fossil remains. That evidence is daily increasing in amount and in weight; and it is to be hoped that the comparison of the actual pedigree of these organisms with the phenomena of their development may furnish some criterion by which the validity of phylogenetic conclusions, deduced from the facts of embryology alone, may be satisfactorily tested.

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LIMITS AND CLASSIFICATION OF THE VEGETABLE KINGDOM.

The fundamental difference which separates the *vegetable kingdom* from the *animal kingdom* is to be found in the modes of nutrition which obtain in each. If we compare a plant and animal reduced to their simplest terms, and consisting, therefore, in each case of a single *cell*, *i.e.*, of a minute mass of protoplasm invested with a cell-wall, while the unicellular plant draws its nutriment by simple imbibition through the cell-wall from the surrounding medium—a process which implies that all its nutriment passes into it in a liquid form—the unicellular animal is able to take in solid nutriment by means of interruptions in the continuity of the cell-wall, and is also able afterwards to reduce this solid food, if of a suitable composition, to the liquid state. And not merely is there a difference of this kind in the mode, there is also one no less important, although less general, in the materials of nutrition. While under present terrestrial conditions those substances, or chemical combinations, which are required for the nutrition of animal organisms, are, as far as we know, nowhere spontaneously produced—that is to say, nowhere apart from the influence of living organisms—materials derived wholly from the inorganic world are sufficient to sustain directly nearly the whole of vegetable life, and therefore, indirectly, of all other life as well. Roughly speaking, while plants are able to use for the purposes of nutrition binary compounds, such as carbon dioxide (CO_2), water (H_2O), and ammonia (NH_3), animals are essentially dependent on the same elements as enter into these compounds, but mostly in a higher state of chemical aggregation than the binary. Plants, therefore, are the "hewers of wood and drawers of water" for other living things. And this property which they so largely possess of constructing, from materials not directly available for animal nutrition, substances which are so, is found to be uniformly attended with the presence of a peculiar green colouring matter, known as chlorophyll, with which a portion of the protoplasm of their cells is tinged. Many plants, however, such as the whole group of *Fungi*, as well as some flowering plants, draw their nutriment from compounds derived from other organisms, and therefore in a higher state of chemical aggregation than those the green plants make use of. So far they approach animals in the mode of their nutrition.

At first sight it might seem a probable hypothesis that the part played by green plants is one which has always been filled by them from the earliest appearance of life upon the earth. It must, however, be noticed that the presence of chlorophyll in the organism depends upon a specialization of some only of its constituent cells, and of part only of the protoplasmic contents of those cells. The inference, which appears to be justified by general biological principles, is that such a specialization is not a thing of primary origin, but has been gradually attained. We are thus, therefore, led to the supposition that the very earliest plants—probably belonging to the same stock as the very oldest animals—were destitute of chlorophyll, and were nourished, as Fungi are now, by the imbibition of substances fitted for their nutrition, but which, in the conditions that accompanied the first appearance of life upon the earth's surface, were produced independently of any organisms. The development of chlorophyll would, therefore, on this view, have to be regarded as a later acquirement.

It is necessary to bear some considerations of this kind in mind in order to clearly apprehend the relation to one another of the different phases of nutrition which the vegetable kingdom includes. The plants, for example, which

we collectively term *Fungi* may, and probably do, include descendants of the original stock which existed before plants possessed chlorophyll at all. No doubt also Fungi comprise plants which are destitute of the chlorophyll possessed by their near allies, in consequence of the degeneration due to a parasitic mode of life. Amongst Flowering Plants we cannot doubt that this has been the case with *Cuscuta*, *Orobanche*, *Lathræa*, and many others. But besides plants which are actually parasitic, there are other degraded allies of green plants, which are content to work up again the imperfectly broken down products of decay. Such plants are termed *Saprophytes*; many examples of them exist amongst the *Orchidaceæ*, such as *Neottia*, *Epipogium*, and *Corallorrhiza*. They live upon the products of the decomposition of vegetable matter, and have more or less completely lost the characteristic green tint of chlorophyll, which would be useless to them if they possessed it. But perhaps the most curious case of the occasional disposition of even green plants to seize upon nutritive matter in an available state of chemical aggregation, is that which is met with in the numerous examples now known of insectivorous plants

In these latter cases we certainly find morphological adaptation of considerable complexity for purposes of nutrition. But in the vegetable kingdom generally this is certainly the exception rather than the rule. In the animal kingdom it is very different. Amongst plants, however, adaptations of structure which have reference to reproduction assume far greater importance, and these have to a large extent to be relied upon for taxonomic purposes.

Even in the highest plants the physiological division of labour is very small compared with the extent to which it exists amongst animals. From plants of the simplest structure up to the most complicated, the plan of nutrition retains the same broad features. There are few physiological facts of real importance to be observed in the highest terms of the series which may not be equally well studied in the lower.

Amongst such of the lower plants as are aquatic in their mode of life the protoplasm of individual cells is often broken up into fragments, very minute in size, which are set free in the surrounding fluid, and being furnished with *cilia* or motile filamentous prolongations of their protoplasm, rapidly disperse themselves over a considerable area. Such locomotive organisms are usually called *zoospores*. After a time each is invested with a cell-wall composed of *cellulose*; this differs entirely in composition from protoplasm, especially in containing no nitrogen. The production of the cell-wall is not therefore to be regarded as a modification of any part of the protoplasm, but as a segregation of particles of cellulose which were intermixed with it; such a segregation goes on repeatedly, wherever life exists in plant tissues. *Starch*, which is identical in ultimate composition with cellulose, we know to be fabricated from inorganic materials in the chlorophyll-granules (which are specialized portions of protoplasm) under the influence of light. Cellulose is derived from the starch so manufactured, and is dispersed in a state probably of molecular subdivision throughout the protoplasm.

The cellulose wall is not apparently essential to the conception of a vegetable cell, but it is, perhaps, not going too far to say that its existence has conditioned almost all the histological and morphological peculiarities of plant construction. The cell, as already pointed out, although bounded with what is relatively a tough and even rigid cell-wall, is by no means debarred from further nutrition and growth. If destitute of chlorophyll, it may take in nutrient matter, which only requires some moderate elaboration to suit it for incorporation with the protoplasm. If, on the other hand, chlorophyll be present, it will do a good deal of preliminary work in preparing the substances which then, as before, the protoplasm will further appropriate and work upon. In either case the protoplasm of the cell will grow, and as the processes which have been described are generally accompanied by the imbibition of fluid, the cell-wall is subjected in consequence to a considerable tension. The cell-wall, under these circumstances, grows also, and the experiments of Traube seem to show that, given the conditions under which it is known to take place, this growth is almost entirely a physical process. Carried beyond a certain point, tension must result in rupture; but just short of this there appears to be a limit at which the intercalation of new molecules of cellulose is permitted, and so the surface of the cell-wall is enlarged. In *Œdogonium* there is a peculiar arrangement in which fracture actually does take place repeatedly. A circular cleft is formed, which is repaired within by the apposition of an annular splice.

To the growth of a cell so conceived there would seem to be no limit, and in the *Siphophyceæ*, of which *Vaucheria* is a well-known type, there is apparently none. The vegetative portion of these organisms, however complicated, is always formed by the extension of a single cell; the protoplasm is continuous throughout every part, and except when zoospores are formed is never segmented.

This, however, is a rare arrangement. Generally speaking, there comes a time when the protoplasm, by a phase of contractility, divides itself into two masses, and between these a partition of cellulose is formed in the same way as the coat of the naked zoospores already alluded to. Each cell so formed possesses all the capacity for nutrition and growth which the whole possessed. It divides therefore in its turn, and in this way we get the first indication of an aggregate of cells. In the lower plants the cell is complete in itself; in the higher, its independence is more or less merged in that of the others with which it is associated.

This aggregation seems to begin in a purely mechanical way. In *Pleurococcus*, for example, cell division repeated a few times may produce aggregation of, at any rate, four cells. If it were not that the adhesion of these cells seems afterwards to fail, there would be no reason why the mere process of cell division should not produce larger aggregates. But the cell-wall common to two adjacent cells splits through its middle lamina, and the two neighbouring cells part company. In *Hydrodictyon* we have a remarkable example of the formation of an aggregate synthetically, owing to the action of some cause which is quite imperfectly understood, but which is probably purely physical. An enormous number of zoospores are formed from the contents of a parent cell, and these, after tumultuously moving within its cavity, come to rest, and at the same time arrange themselves in the well-known net-like fashion which is characteristic of the full-grown plant. The mechanical persistence of aggregates of cells formed by normal cell division is obviously the step which led to the evolution of such organisms as *Volvox* and *Ulva*, since these are merely aggregates of simple types, such as *Chlamydococcus* and *Pleurococcus*.

At first the independence of the individual aggregated cells would be little impaired. In a *Spirogyra* or *Oscillatoria*, for example, the number of cells present in a filament is probably a matter which does not affect the cells themselves individually, and which conversely they have no power of influencing. The constituent cells might go on dividing, and so form filaments of unlimited length, but which occasionally would be liable to be broken up by arbitrary accident. In *Cladophora*, however, the cells of a filament cease after a time to divide transversely, and branch by the production of lateral swellings, which are elongated and then divided off by cellulose partitions. It seems reasonable to suppose that branching in this case simply means that one part of the cell-wall is weaker, less fitted to withstand internal tension, than the rest. If the cell-wall were uniform it would stretch uniformly, and the want of uniformity in the cell-wall may probably be traced to its being part of an aggregate. The string of cells is moored by one end, and any motion of the water will cause it to assume an oblique position. It is then unequally influenced by gravity and by light, and these two forces are known to be competent to modify growth in an unsymmetrical manner under such circumstances.

Reasoning of this kind will at any rate suggest the way in which the specialization of individual cells would be a result of their aggregation. With this specialization they would lose an increasing amount of their capacity for independent existence. Specialization of function will, of course, be reflected in corresponding morphological modifications, and thus a mechanical aggregate of independent cell elements gradually passes into a physiological aggregate of interdependent ones.

One obvious penalty of specialization is the loss of the power of reproduction by individual cells when detached. Amongst plants, however, even the highest types preserve some measure of it. It is sufficient to adduce the common horticultural method of propagating Begonias from fragments of the leaves. Such a mode of reproduction in one of the highest plants is essentially the same as that which exists in *Pleurococcus*, and although reproduction from fragments of structures so specialized as a leaf is comparatively rare, there are in almost all plants provisions for agamogenesis, which depend upon the retention by fragments of the organism of this capacity for independent existence. And it may even happen that the perpetuation of the race for considerable periods may come to depend upon such a property. One of the most striking instances of this is the distribution over the British Isles of the American water-weed (*Anacharis*), of which, nevertheless, only the female plant exists in this country. If we had the male, we should have a good instance (and others might be given) of gamogenesis and agamogenesis proceeding side by side in individuals of the same generation, although probably not without the two processes reacting upon one another. Throughout the vegetable kingdom, however, we find gamogenesis and agamogenesis occurring in separate generations, which are often extremely different. The two modes of reproduction are then subject to a cyclical arrangement, and the comparison of the forms under which this *alternation of generations* occurs in different groups throws a good deal of light upon their taxonomic relations. It will be convenient to use the word "*Sporophore*" for the agamogenetic generation, in which special cells (*spores*) are detached from the parent to serve as a means of propagation; while for the gamogenetic generation, in which conjugation takes place, or in which special cells (*oospheres*) are fertilized by antherozoids, and become *oospores*, "*Oophore*" may be employed.

Our present knowledge has rather added to than diminished the difficulty of devising even a plausible phylogenetic classification of the vegetable kingdom. Greater success has, however, been attained in establishing the primary and larger secondary groups, so as to allow us to feel some confidence that they are really natural assemblages. The relation of these groups to one another is a problem, the more than approximate solution of which will probably have to be some time postponed. Many of them appear to represent the later developments of simpler types or aggregates than anything that these groups at present contain. The *Equisetaceæ*, for example, are extremely ancient, yet we know of no form, living or extinct, which enables us to trace the connection of their very remarkable organization with that of other groups. In the animal kingdom the "recapitulation theory" steps in, and obtains from the study of the development of the organism that kind of information which is wanting amongst plants as to the simpler ancestral forms of the different vegetable types. This information, however, is drawn in the animal kingdom to a large extent from the phenomena presented by the differentiation of the sustentative organs of the embryo. For reasons already pointed out, there is nothing analogous to this amongst plants, where the rapid extension of surface is usually the primary object to be attained. The earliest stages in the development of any plant are subject to conditions so simple that there is little room for specialization, and the economy of nutrition has probably generally led to the suppression of recapitulative structural details.

On the other hand, if we derive little help from recapitulation in studying the process of development in plants, from the unicellular stage of spore or oospore, it proves extremely suggestive, if we take in the whole cycle comprised between two processes of gamogenesis, and compare the relations to one another of the gamogenetic and agamogenetic generations, or using the nomenclature introduced above, of the Oophore and Sporophore.

THALLOPHYTA.

Endlicher, in 1836, divided the vegetable kingdom into *Thallophyta* and *Cormophyta*; and these divisions still hold good, though it is by no means easy to frame characters which will strictly limit them. With the exception of the absence in the one, and presence in the other, of the "opposition of stem and root," none of the distinctions which Endlicher pointed out are available now. Throughout the greater part of the *Thallophyta* anything like a distinct segmentation of an axis furnished with lateral appendages is altogether wanting. As thus limited by the absence of a clear differentiation of root, stem, and lateral appendages, this sub-kingdom comprises an assemblage of plants, which were divided by Bishop Agardh, in 1821, into the three well-known groups of *Algæ*, *Fungi*, and *Lichens*. And to these, for reasons which will be presently pointed out, must be added the hitherto problematical group of *Characeæ*.

It has long been seen that, with respect to the three former groups, it was impossible to assign morphological characters which would separate them strictly one from the other. Accordingly, Berkeley and Lindley were compelled to fall back on distinctions of a physiological kind. *Algæ* were defined to be generally *aquatic* in their mode of life; *Fungi* and *Lichens*, on the other hand, were *aerial*,—but the former drew their nutriment from the "substratum," while the latter obtained it from the air.

There are several grounds on which this arrangement appears to need reconsideration.

Contrasting, in the first place, *Algæ* and *Fungi*, we now know that the plants belonging to the former group invariably contain chlorophyll, while those belonging to the latter are equally devoid of it. In their morphological aspects, however, the two groups present a remarkable parallelism.

Now, the importance of the presence or absence of chlorophyll, and the difference in the mode of life which results, would have greater weight for classificatory purposes, were we not familiar with instances in other parts of the vegetable kingdom in which it proves to have no value at all. Amongst flowering plants we are acquainted with many cases where plants closely allied in structure to

others in which chlorophyll is normally developed, are entirely destitute of it. These considerations have recently led Cohn and Sachs to treat *Fungi* and *Algæ* as an assemblage of organisms the classification of which is to be attempted on purely morphological grounds. But the assemblage of plants formed by *Algæ* and *Fungi* which thus appear to require classification anew, has been further increased by the addition of two other groups, both regarded quite recently as entirely distinct. In 1868 Schwendener proposed his now well-known theory as to the true nature of Lichens; and although his views have been vigorously attacked, chiefly by writers who seemed to feel that they had a vested interest in their autonomy, the weight of testimony, in the case of those who have examined the matter in a wider spirit, has been to strongly confirm Schwendener's hypothesis. Lichens must now be regarded as composite structures partly consisting of an alga, partly of a fungus. Quite lately Sachs has pointed out (in the 4th edition of his *Lehrbuch der Botanik*) that *Characeæ* may be compared with the structure and mode of reproduction of some of the *Florideæ*.

Sachs has proposed a classification of the *Thallophyta*, which appears to be the best that our present knowledge admits of. He divides them into four classes—*Protophyta*, *Zygosporeæ*, *Oosporeæ*, and *Carposporeæ*.

1. The *Protophyta* include the simplest plants, and those in which at present gamogenesis is not known to occur. In the *Cyanophyceæ* the protoplasm of the cells is destitute of a nucleus, and, besides containing chlorophyll, is tinged with a peculiar bluish colouring matter, known by the name of phycocyan. In *Palmellaceæ* this peculiar pigment is absent. *Eugleneæ* is a group of well-known but little understood organisms, which must also be placed here provisionally. To these must be added *Schizomycetes* (Bacteria), which are the agents of putrefactive changes in nitrogenous organic matters, and *Saccharomyces* (yeast), which bring about the phenomena known as "fermentation." The *Schizomycetes* appear to be allied in some respects to *Chroococcaceæ* and *Oscillatoriaceæ* amongst the *Cyanophyceæ*. The true position of *Saccharomyces* must for the present be held as problematical; we are still without evidence to conclusively decide in favour either of its autonomy or of its being a peculiar condition of a member of some group of Fungi of more complex development.

2. The *Zygosporeæ* are an assemblage of organisms, none of the members of which attain any high degree of morphological complexity, and in all the subordinate divisions of which the simplest form of gamogenesis, known as *conjugation*, has been observed to take place. Conjugation only differs from the normal process of fertilization in the two protoplasmic bodies which take part in it being precisely similar in bulk and form. Till Thwaites pointed out the contrary in 1848, it was not supposed to be entitled to recognition as a sexual process. But fertilization, as ordinarily understood, only differs in the two conjugating bodies being unlike—that is, in their having undergone differentiation into *antherozoid* and *Oosphere*, the male and female bodies respectively.

The *Zygosporeæ* may be divided, perhaps artificially, into two groups, according as the conjugating cells are motile or non-motile.

In many of the simpler green *Algæ* it has long been known that two kinds of zoospores, differing in size, are produced. To these the terms macrozoospore and microzoospore may be applied. The function of the macrozoospores is purely agamogenetic. The microzoospores, on the other hand, meet in pairs, and fuse into a single protoplasmic body, which Areschoug has termed a *zygozoospore*.

The process was first observed by Pringsheim in *Pandorina*. It has also been observed in *Chlamydomonas*. On these grounds Sachs has placed the whole group of the *Volvocinaceæ* amongst the *Zygosporeæ*. This has, however, been reasonably objected to by Cohn, inasmuch as in *Eudorina* as described by Carter, and in *Volvox* as observed by himself, there is a true process of fertilization by means of antherozoids, and not a simple conjugation. It may be allowed, therefore, provisionally to break up the *Volvocinaceæ*, or rather to restrict the name to the two last-named genera, which may then be removed to the next class, using that of *Pandorineæ* for Volvocinaceous forms, which only exhibit conjugation. *Hydrodictyeæ* should probably be placed here, and also *Confervaceæ* and *Ulvaceæ* in which the conjugation of zoospores has been observed by Areschoug.

Sachs has proposed to associate with the *Zygosporeæ* the *Myxomycetes*, in which the formation of the plasmodium is a kind of complex conjugation. Closely allied in some respects to the *Myxomycetes* are *Chytridineæ* and, more doubtfully, *Protomyces*.

In the second division, in which the conjugating cells are non-motile, must be placed all the more familiar instances of the process—the *Desmidieæ*, the *Diatomaceæ*, the *Zygnemaceæ*, and the *Zygomycetes* as a fungoid type.

3. The *Oosporeæ* must include the *Volvocinaceæ*, in the limited sense already explained, and also *Sphæroplea*—a form divorced on much the same grounds from *Confervaceæ*. *Fucus* affords the best known type of reproduction belonging to this group. The antherozoids are ciliate bodies discharged from *antheridia*; the *oospheres* are naked protoplasmic masses originally contained in *oogonia*. The antherozoids gather round them in such numbers as to impart to them a movement of rotation. They eventually completely blend with the oosphere, which becomes surrounded with a coat, and sinks to the bottom of the fluid in which it has hitherto been suspended. It is now an oospore, and speedily undergoes a process of cell division, which gives rise to an individual of the new generation. Near the *Fucaceæ* a place must probably be assigned to the *Phæosporeæ*. The remaining groups which fall into *Oosporeæ* are *Cœloblastæ* and *Œdogonieæ*. *Cœloblastæ* have their protoplasm unsegmented throughout the vegetative portions of the organism. They include forms which are partly algoid, such as *Vaucheria* and the *Siphophyceæ* generally, partly fungoid, as *Peronosporeæ* and *Saprolegnieæ*. In all other respects, except the presence or absence of chlorophyll, they closely agree with one another, and the consideration of this fact has led, perhaps more than any other fact, to the breaking down of the barrier between Algæ and Fungi.

4. The *Carposporeæ*[1] agree with the *Oosporeæ* in so far that the two sexual organs contribute in very different proportions to the formation of the sexual product. While the male only stimulates its development, the female supplies the material for the whole subsequent growth.

The female organ, or *carpogonium*, may consist of one or more cells. The male organ varies very considerably in the different subordinate groups. Fertilization may, as in the *Oosporeæ*, be effected by antherozoids (which may be actively motile or passively locomotive), or by a kind of conjugation, or even by a mere apposition of the male organ and subsequent diffusion of the fertilizing medium. The product of the act of fertilization is sometimes a single cell developing directly into a new individual (*Chara*). In other cases the fertilized female organ produces zoospores, and still more commonly a multicellular mass in which spores are finally developed. This involves an alternation of the generations of the type of that met with in the sporocarp of *Muscineæ*.

[1] See Sachs's *Lehrbuch*, 4th ed. pp. 240–243.