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Parasitism as a Way of Life

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Of all the various factors which influence the phenomenon of life as it evidences itself in the multitudinous variety of living organisms, those involved in the acquiring of a proper and sufficient amount of food material are unquestionably most significant. If we eliminate from consideration certain accessory substances such as minerals, those things which serve as foods, in the commonly accepted sense, are organic in nature. They supply organisms with materials for construction and repair and at the same time release energy under the destructive action of the respiratory function. Every living organism, from the most minute unicellular individual to the complex higher forms, is dependent upon a more or less continuous supply of such organic compounds which can serve these functions.

It would naturally be expected that living organisms which occur in such amazing variety of size, form, and degree of complexity would also exhibit wide differences in the manner in which they acquire their foods. When the processes and conditions involved are carefully analyzed, however, it is discovered that there are few, if any, fundamental differences in the nutritional habits of most living organisms. The foods are commonly similar in nature; they enter into the cells under essentially similar conditions and perform comparable functions for the organisms. There may be, of course, differences in the physical or mechanical features of organisms, which depend for the most part upon the presence or absence of the pigment chlorophyll, the complexity of the organism, and the type of habitat in which it lives. Green plants are rightfully recognized as the source of organic foods for most other non-green organisms, both plants and animals. It is sometimes assumed that such green plants are capable of maintaining life independent of assistance from other organisms. This, however, is found to be only partially true when a study is made of their dependence upon various materials which are obtained from the environment and in the preparation of which other organisms have played important rôles. The food required by non-green organisms is obtained either saprophytically from the decomposition of the remains of dead plants and animals, which have fed upon plants, or parasitically from intimate contact with a living organism. It is often considered that the parasitic or saprophytic manner of securing food is a degraded type of nutrition and that the only self-respecting method is by means of the photosynthetic process practiced by chlorophyll-bearing plants. Such heterotrophic plants are believed to be "coasting down an inclined plane of degeneracy which will ultimately result in their extinction." Certain atrophies and morphological changes associated with the parasitic habit are commonly indicated as supporting this assumption. With this point of view exception may be taken. The atrophies found in plants associated with a dependent mode of life are, in large part, merely reductions of features which were originally developed in association with and for the purpose of aiding in the photosynthetic function. Mankind, which we in our egotism believe represents the ultimate in organic evolution, presents an excellent example of successful nutritional dependence. Furthermore, the numerous atrophies and morphological changes found in man, as compared with the lower animals, are usually not considered to represent degradation but rather to have resulted from more or less normal evolutionary changes brought about in consequence of changing environmental conditions and uses.

The term parasite is often used in a broad sense in referring to certain types of dependence among humans usually with a derogatory connotation implying an unpraiseworthy degree of laziness. This concept of parasites as representing undesirable members of human society has also, by popular usage, been applied to dependent individuals among the lower groups of organisms. This is illustrated, for example, by the following statement by one author:

> Parasitic plants indicate the length to which plant life will go in its determination to exist, but they also "point a moral" in which the examples elicit a degree of contempt. A parasite lives at the expense of another, doing no worthy labor, but always managing to propagate its degenerate kind.

When used in reference to humans the word parasite implies certain psychological, sociological, and ethical relationships quite foreign to any that are possible among organisms below the evolutionary level of mankind. The term parasite when applied to lower forms of life should always be used in a more technical sense. It should denote definite physiological, morphological, and ecological features and associations and thus possess a more exact and restricted signification. That dependence of one individual upon another is *per se* always bad and consequently undesirable would appear to be an assumption quite out of line with facts. Dependence of individuals upon each other, directly or indirectly, is a relationship which is common throughout all groups of living organisms. Whether the benefits of this relationship come from a direct physical contact or through some intermediate agency and whether the association results in injury to either of the organisms or not would seem to be insignificant distinctions when the basic nutritional aspects of the question are considered.

The world and all the things thereof may be divided into the two categories of the inorganic or non-living and the organic or carbon-containing substances characteristic of the composition of all living organisms. It appears probable that the nature of the primitive or early phases in the earth's development was wholly inorganic and that organic substances came into existence at some subsequent but as yet unknown period. It is in the realm of the organic that life primarily centers and upon which our interest is chiefly focused.

The locale of all life processes—the vehicle for the bearing of that which we recognize as life, as all students of science know—is the nearly transparent, somewhat viscid, and altogether quite unimpressive-appearing substance now known as protoplasm, which is the indispensable material of the living cells of all organisms. Protoplasm has long been, and still remains, the object of intensive investigations concerning the nature of its chemical, physical, and biological being. Much has been discovered about it. The phenomenon of heredity, the reactions to environmental forces, and many other biological characteristics of cells are becoming common knowledge. The principal classes of chemical constituents are generally recognized at the present time. Much has been learned about the physical make-up of cell structure, although some details still remain puzzling and are the bases of various theories which lend interest to further research.

Unquestionably, the most interesting feature of protoplasm is its capacity for carrying on those reactions and adjustments which we consider to be criteria of life. It is able to grow and increase itself and to reproduce in a variety of ways. It is sensitive to the innumerable environmental stimuli which impinge upon it and is able to adjust itself favorably in response to them. That life depends for its being upon a very delicately balanced system of biological, chemical, and physical factors is obvious to any careful observer. It is a simple matter to destroy life by various suitable means. Lethal forces unquestionably bring about physical and chemical changes and upset the balance so essential for its continuance. Precisely what has occurred is problematical to a large extent. It is sometimes difficult to detect any conspicuous structural difference between a living cell and one that has been carefully killed. If one could accurately identify and correctly interpret the changes which occur during senescence and death, the nature of life itself might be revealed, and man could perhaps develop a method of duplicating protoplasm and of endowing it with vitality.

How and when life first appeared are questions seemingly not amenable to satisfactory scientific solution. Students of organic evolution are agreed, in the main, that it probably originated in a very simple, non-organized mass of protoplasmic-like material. That this original living matter did not possess the form and specialization evident even in the most primitive and simple organisms now extant would seem to be a logical inference. It could be assumed that primal protoplasm was entirely similar to that which now exists. But can such an assumption be justified? There are many requirements essential to the maintenance and continuance of life. One of the most fundamental is that there be a supply of sufficient energy. Did primitive protoplasm utilize the same specific energy sources as does its modern descendant? Processes of evolution are inherent in protoplasm itself. It is not inconceivable, therefore, that primitive protoplasm may have been able to function without the same complexity of energy requirements that we now find.

It is reasonable to conclude that primal protoplasm was necessarily endowed with the ability to grow and to reproduce itself, to nourish itself through some synthetic process, and to adjust itself in response to environmental stimuli. Whether chlorophyll originated contemporaneously with the first protoplasm or came into being at some later date is a question of considerable significance when we consider the phylogenetic relationship of the lower plants. Protoplasm, as we now understand it, requires organic, carbon-containing compounds for food and a source of energy. Since the origin of chlorophyll, the chief source of such organic matter has been from green autotrophic plants. They are able, by the so-called photosynthetic process, to unite the carbon-dioxide of the air with water and to incorporate a part of the solar energy in the resulting carbohydrate molecules. The more complex foods such as proteins and fats are further elaborated presumably by non-photosynthetic processes through additions to and changes in these basic carbohydrates. While it is now true that practically all organic food is the product of green plants, it is, at the same time, known that a small number of fungi are able to synthesize food by utilizing energy obtained from the oxidation of inorganic compounds. Also, a few species of fungi are able to utilize solar energy and photosynthesize with pigments other than chlorophyll. These synthetic processes on the part of chlorophyll-less autophytes are now quantitatively unimportant. They are, nevertheless, of great significance when one canvasses the possible sources of foodstuffs in a hypothetical pre-chlorophyll period of organic life.

To many students of the question it appears that organic life probably existed for an indefinite period of time previous to the genesis of chlorophyll pigments. The sources from which these primitive organisms received their requisite food are not easily identified from a study of conditions now prevailing. The possibility of their dependence upon chemosynthesis or photosynthesis with non-chlorophyll pigments appears to be an inviting and plausible theory, inasmuch as these processes are both operative in some of our most primitive non-green plants of today. Unfortunately, it is impossible to obtain any definite knowledge of the physiology of primitive protoplasm. It seems reasonable, however, to assume that even in the pre-chlorophyll age at least some individuals must of necessity have possessed a synthetic process and that others at the same time undoubtedly acquired the ability of utilizing the products of such autotrophic species in a parasitic or saprophytic manner.

The origin of chlorophyll and its introduction into the cell structure and its utilization in the production of elementary, energy-carrying foods had an extremely great and far-reaching influence upon the evolutionary process. Organisms which until this time, according to the opinion of some, had been progressing along a more or less common highway of evolution became differentiated into the great plant and animal kingdoms. Evolutionary advance now proceeded along two progressively diverging lines of development, with green plants destined to become the manufacturers of foods for virtually all organisms lacking such pigmentation. The distinction is sometimes made between plants and animals to the effect that plants make food and animals do not. This differentiation is, of course, superficial and misleading when one considers the great numbers of plants which are as dependent upon outside sources for their foods as are animals.

Division of labor in unicellular organisms is obviously impossible, and, consequently, the single cell is required to carry on all of the physiological processes essential to the maintenance of its life and reproduction. One of the early stages in the evolutionary development of living organisms was the grouping of a number of cells into a colonial association. In many such colonial arrangements each cell apparently carries on its functions as completely as though it were wholly separate. Eventually, however, some cells became specialized for the purpose of doing work for the common good of the cell group, and we have then not a colony but a simple multicellular organism.

Chlorophyll is generally present in all or nearly all of the cells of primitive plants. As evolution progressed, however, plants became increasingly more complex with the photosynthetic function more and more restricted to special chlorophyll-bearing cells. One of the results of the specialization of the photosynthetic process is apparent in its effect upon the morphology of the plant. Leaf or leaf-like structures definitely designed to facilitate photosynthesis are a prominent feature of nearly all of our higher plants and are lacking only in the more primitive groups or in plants over which certain environmental forces have become dominant.

In the physiology of nutrition, if we except the synthetic processes, each cell of an organism acts essentially as though it were a separate unit. Materials entering any cell must first be rendered soluble before they are able to pass through the protoplasmic membranes, regardless of the phylogenetic position of the organism. The entrance of materials into the cell of any simple organism is believed to obey basic physical and chemical requirements similar to those necessary for their passage into any of the living cells of our most complex multicellular organisms. This appears to be true whether the movement be from outside the plant, as from the soil into the roots, or between adjacent cells within a tissue. The distinction commonly made between saprophytism and parasitism lies not in differences of food substances nor in the manner of acquiring them but solely on the basis of whether the food is obtained directly from an organism that is alive or from a non-living source. No organism is capable of utilizing and incorporating living substance into its own body. It would appear, therefore, that all foods are necessarily inanimate when they enter a cell. When organic material is taken from a living source there results in most cases a harmful or at least a detrimental effect on the host, inasmuch as it loses substances which were destined for use in the physiology of its own cells. The relationship which exists between the chlorophyll-containing cells of multicellular organisms and those which are colorless is similar in many respects to that prevailing between the host and its parasite. The colorless cells are as dependent upon their photosynthetic neighbors for basic carbohydrates as is a parasite upon its host. In this relationship, however, the nutritional balance between the various units is maintained in such a manner that the green host-cells apparently are not injuriously affected to any extent.

It is not uncommon to find two or more species of algae living in close association. It appears possible that under suitable conditions one of the species might obtain some food from its associates in a manner somewhat comparable to that in which the non-green cells of higher plants obtain theirs. Such food transfer might involve slightly different physical factors, but it would not, seemingly, need to differ materially from an exchange between the closely associated cells of an algal colony or between the green and non-green cells of a multicellular plant. The development of the simple haustoria exhibited by species of fungi would not appear to present any difficult evolutionary problem.

Fungi have developed along evolutionary lines quite distinct from those of their algal relatives. They are able to thrive in environments and under conditions impossible for green plants. This variation of habitat, as well as other factors, has probably played an important rôle in influencing the development of the reproductive habits and other characteristics peculiar to the various fungal groups. It is probable that parasitism appeared very early in the evolutionary development of living organisms. When once established as a specific characteristic, it has persisted and become amplified in succeeding groups. The study of evidences of pathology in fossilized plant and animal remains is interesting in itself but would not appear to throw much light on the origin of parasitism. There can be no sharp lines of difference drawn between parasitism and saprophytism, and the question as to which is more primitive does not seem to be significant. A number of dependent organisms are known which are able to adjust themselves either to a parasitic or to a saprophytic mode of existence as conditions demand, and it seems reasonable to assume that the earliest forms of dependence may have been as readily facultative.

Interesting examples of parasitical relationship are those existing between the gametophytic and the sporophytic generations of plants exhibiting alternation of generations. In general, the gametophyte of the lower plants bears chlorophyll and supplies a more or less dependent sporophyte with its necessary food. This nutritional dependence on the part of the sporophyte is illustrated by many bryophytes. In this group the sporophyte usually lacks chlorophyll and is commonly attached to a more prominent and photosynthesizing gametophyte by a haustorium-like structure called the "foot." The sporophytes develop chlorophyll and assume a degree of nutritional independence among some of the higher bryophytes, but all remain dependent to some extent for at least their water and mineral requirements. In the pteridophytes a complete reversal of sporophytic and gametophytic relationship occurs with the sporophyte becoming the dominant phase. While it apparently never becomes completely independent of the gametophyte for at least some of its food, especially in its early stages of development, it does assume at maturity the dominant rôle in food production for those plants evolutionarily superior to the bryophytes. The gametophytes of ferns appear to be nutritionally independent of the sporophytes. Among other members of the pteridophytes, however, there is a definite tendency towards the loss of the photosynthesizing function and the necessity of obtaining food from some external source. Some of the gametophytes of Lycopodium, for example, have no chlorophyll and must depend for their foods largely upon the activity of the mycorrhizal fungi with which they are invested. Among the seed plants the gametophyte remains wholly dependent upon the sporophyte. There appears to be little or no fundamental distinction, so far as nutritional factors are concerned, between the sporophyte-gametophyte relationship of many plants and that existing between a typical parasite and its host. It may not prove unprofitable to seek answers for some of the questions involving parasitism in this field of inter-generation relationship.

It might naturally be expected that an innovation as significant as the introduction of chlorophyll into the structural and physiological make-up of cells and the advantageous photosynthetic activity resulting would become permanent features. It would appear, also, that the food problems of chlorophyll-containing organisms would be largely solved, or at least greatly minimized, by the development of the photosynthetic process and that such organisms would be reluctant to discard this apparently easy way to nutritional independence. Since its inception, chlorophyll, however, has not remained a constant characteristic of all plants possessing it, and there are many species in which it has been partially or wholly eliminated. As previously stated, the photosynthetic function is common to all or nearly all of the cells of the more simple and primitive autophytic species. However, as plants developed greater complexity and division of labor became more emphasized, the chlorophyll-bearing cells became more and more segregated. Many tissues completely lost their ability to photosynthesize and consequently were dependent upon their chlorophyll-bearing associates. Furthermore, there are numerous species distributed throughout the plant kingdom which have developed the ability of securing some or all of their food requirements from a source external to themselves. Why plants which presumably possessed chlorophyll and, hence, nutritional independence should develop some other seemingly more precarious means of securing their food is one of the interesting problems of biology. On the other hand, whenever the parasitic mode of life has been adopted, it has commonly persisted and become a permanent feature in the life of the species. There is no evidence of the abandonment of the parasitic habit after it has been once initiated. The introduction of the parasitic habit ordinarily provokes a number of morphological changes, particularly in those structures associated with photosynthesis. The chlorophyll gradually disappears, the leaves are reduced, and normal roots are sometimes replaced by haustoria.

The largest and most notable group of dependent plants is the cosmopolitan aggregation known as fungi, which is one of the most important groups of plants when considered from an economic point of view. They are comparatively simple morphologically and are believed by many to represent chlorophyll-less descendants of autophytic algal ancestors. In no other group of organisms, aside from animals, has the dependent mode of life become so prominent and well established. That their loss of independence is not seriously disadvantageous is evidenced by the large number of species and their very obvious success in competition with autophytic plants. An interesting fact, which may have some significance when considering the phylogenetic relationship of fungi, is that several species of algae have been reported as able to supplement their photosynthate by absorbing organic substances from their environment. This might be interpreted as indicating a preliminary step in the establishment of a dependent mode of nutrition. As one would expect in a large and diverse group such as the fungi, there is to be found practically every conceivable variation in nutritional relationship, ranging from obligate parasitism on the one hand through various degrees of facultatism to obligate saprophytism on the other.

Parasites are commonly looked upon as being injurious to the hosts upon which they grow. There are, however, many parasite-host relationships in which the host is obviously not seriously affected and not infrequently is actually benefited by the association. The legume-nitrogen-fixing bacteria combination, the numerous mycorrhizal relationships, and many other examples illustrate such beneficial alliances. The large number of autophytic species now known to harbor mycorrhizal fungi is indicative of the advantage of this combination in which often both the fungus and the host are believed to be beneficiaries. Some higher plants have developed a dependency upon their mycorrhizal confederates to such a degree that it is difficult or impossible for them to thrive in the absence of the fungus. The fungus in such cases acts as an intermediate agent by assisting in the preparation and absorption of food substances from the soil for later utilization by the host. In Calluna, the Scotch heather, the mycorrhizal fungus grows abundantly in and upon the roots and may even penetrate to other parts of the plant. The heather does not thrive in the absence of the fungus, which is reported as having the ability to fix nitrogen. In the presence of an abundance of soil nitrogen, however, the fungus may become too aggressive and destroy its host. Study of the interrelation of fungus and host in cases such as the heather illustrates the complexity of the relationship and the delicacy of the balance which often exists between two such organisms. Monotropa, or Indian Pipe, long considered to be a rare example of a flowering plant living saprophytically upon decomposing organic matter, is now known to have its roots invested by a mycorrhiza. It is, therefore, to be considered more as a parasite upon these root fungi than as an example of a saprophyte. Thus, we have an illustration of a curious and anomalous situation where a higher plant becomes parasitic upon a fungus.

With the exception of mycorrhizal fungi and the inter-generation dependence, we find parasitism almost entirely limited to fungi and to certain flowering plants. It is exceedingly rare or lacking in the groups including the mosses and the ferns. Among the numerous parasitic species of flowering plants the variations exhibit every conceivable combination of interrelationship and dependence. The mistletoes of the family Loranthaceae contain chlorophyll and are dependent upon their hosts only for water and minerals. Such so-called "water parasites" represent, in the opinion of some, an early phase in the evolutionary development of the parasite which will eventually acquire the ability to absorb elaborated foods, lose its chlorophyll, and thus become completely parasitic. In the Scrophulariaceae or figwort family there are a number of species parasitic or partially parasitic upon the roots of other plants. Many of the genera are independent, but, on the other hand, species of Lathraea, for example, are completely parasitic. Species of Pedicularis are parasitic to a slight degree; those of the genus Tozzia live for part of their lives as complete parasites but eventually produce a chlorophyll-bearing aerial shoot and hence become partially independent. Selection of proper examples in this family gives a series of species illustrating a gradual transition from complete independence to complete parasitism.

In the genus Cassytha of the Lauraceae and Cuscuta of the Convolvulaceae we have examples of comparable evolutionary development in which the parasites become attached by haustoria to the aerial stems of their hosts. It is interesting to note the similarity in habit of growth and development of the species of these two quite unrelated genera. It is not unusual for specimens of Cassytha to be mistaken for the more common Cuscuta or dodder. Cuscuta is an example of complete parasitism and extreme morphological modification because of its nutritional dependence. Chlorophyll is present to some extent in the stems and flowers of certain species but for the most part it is lacking; the leaves are reduced to small, inconspicuous scales, and normal roots never develop. The embryo is slender and coiled about within the seed. Upon emergence one end becomes erect and assumes the attitude of a snake in a striking position. This erect portion describes circumnutation movements which upon contacting a suitable host enable it to coil about the plant. Haustoria soon develop in the region of the coils and the parasite thus becomes firmly attached. There may be traces of chlorophyll in the seedlings of some species, but, nevertheless, if they do not soon reach a host, they perish. An interesting form of self-parasitism in the dodder has been described as occurring during the seedling stage. It has been shown that the seedling, in a few species at least, is able to elongate at the erect or anterior end and thus increase to some extent its range of search for a host by transferring and utilizing food material obtained by digestion of the posterior portion. There are many additional species of flowering plants which, likewise, show parasitical habits to a greater or lesser degree. Many of these are of considerable interest.

Many interesting problems are found in the relationships existing between parasites and their hosts. There are varying degrees of host specialization shown by different parasites and also defensive reactions on the part of some host plants which might in some cases be interpreted as a form of immunity. It is difficult to imagine an immunity in plants involving antibody formation comparable to that developed in animals. An explanation of many of the selective or antagonistic relationships is, for the most part, however, to be sought in differences in structural and chemical features and also in the osmotic dissimiliarity of the host and parasite cells. It has been demonstrated in certain cases that the osmotic concentration of the cell sap of the parasite is necessarily higher than that of its host, and, unless this condition can be satisfied, it is impossible for the parasite to obtain material from the plant upon which it is growing.

Thus, as we survey the plant kingdom, we observe innumerable examples of nutritional dependence. In fact, dependence to at least some degree would appear to be much more common than is generally supposed. The use of the term independent in connection wtih chlorophyll-containing plants is purely relative. No organism can be said to be wholly independent and live in a state of "splendid isolation" from other organisms. It is true that green plants are able to synthesize carbon-containing compounds. It is equally true, however, that they are dependent for a number of their requirements upon the activities of organisms which inhabit the soil and which help prepare the various elements needed for the physiology of the green plant. These soil organisms, of course, are in turn largely dependent upon the compounds produced by the green plant which are made available when it dies and returns to the soil and is acted upon by the "wrecking crew" of soil microorganisms.

The various forms of parasitism, saprophytism, symbiosis, and mycorrhizal relationships are but variations of processes between which there is no obvious or definite line of demarcation. The gradations between mycorrhizal and various symbiotic relationships are slight, as are, also, those differentiating between typical parasitism and saprophytism. It is, likewise, difficult to distinguish between a true symbiosis and the various shades of relationship known as commensalism, helotism, etc. It appears obvious that these are but variations of the same theme with slight advantages in favor of one or the other of the organisms involved. The interrelationship of organisms often depends upon a finely balanced system of factors, and, when one or more of them are altered, the relationship may be definitely changed.

The circumstances which prompt a self-nourishing plant to assume a dependent mode of life are not conspicuous. That they have been frequently operative, however, is evidenced by the numerous examples of dependent species believed to be descendants from chlorophyll-containing ancestors. It is commonly assumed that an organism which obtains its food by parasitism rather than in an autophytic manner is degenerate. The successful manner in which parasites are able to maintain themselves in a highly competitive relationship, however, casts some doubt upon this assumption. Whether parasitism represents an occasional example of retrogressive evolution, as is popularly thought, or is, perhaps, a more general condition throughout all groups of living organisms, or even representative of progressive evolution, is a question which might well be raised. Why is any successful method of securing food by plants to be considered contemptible and degenerate? The evolutionary substitution of one process or structure for another would not necessarily indicate degeneracy if such changes do not impair the ability of the organism to maintain life successfully and to reproduce. Does the evolutionary change increase the organism's capacity to live successfully and survive? This is a question which might be asked when deciding whether the direction of evolution is progressive or retrogressive. The almost limitless number of examples of nutritional interdependence of every degree would lead one to the conclusion that such dependence, which we may term parasitism in a broad sense, is to be considered in plants at least a more or less normal way of life.