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Symbiosis and Mutualism

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SYMBIOSIS AND MUTUALISM.[1]

By Roscoe Pound.

Symbiosis and mutualism, in the vegetable kingdom at least, are phenomena accompanying parasitism. Parasites have various effects upon their hosts, according to the nature of the parasite, its mode of life and method of attack. In some cases the host is quickly killed and the parasite becomes a sort of saprophyte upon the remains. In others the host lives longer or is only partially affected. In still others the host lives on side by side with the parasite indefinitely. A further development is attained in cases where the parasite and host not only live together, but are mutually beneficial, and, perhaps, even, in extreme cases, inter-dependent. To the first phenomenon —namely, the living together of parasite and host—DeBary, in 1869, in a work entitled *Die Erscheinung der Symbiose*, gave the name of Symbiosis. The latter phenomenon—i. e., mutual assistance or inter-dependence of parasite and host—was named mutualism in 1873 by Van Beneden in his "Animal Parasites and Messmates." Symbiosis in the strict sense and mutualism are often confounded, that is, the term symbiosis is often used to mean mutualism as such; but, in strictness, while mutualism, in the case of plants, can only exist with symbiosis, in the larger proportion of cases of symbiosis there is no mutualism.

At the outset it should be noted that the mutualism of which we are here speaking is mutualism of parasite and host—not mutualism of independent organisms. Of the latter, we have many examples in the animal kingdom, and, indeed, the human race furnishes examples of it. There is a sort of mutualism between man and wheat, for example. Wheat is cultivated by man and enabled to grow in quantities, and in localities which, under ordinary conditions, would be impossible. It gains this partial exemption from the struggle for existence only at the expense of an immense number of indi-

[1]Read before the Botanical Seminar of the University of Nebraska, December 17, 1892.

viduals sacrificed, but it is, nevertheless, a great advantage which it gains. This may be called mutualism. But there is a case of mutualism of plant and animal much more closely resembling the mutualism of parasite and host in the vegetable world. The mutual inter-dependence of *Yucca* and a moth of the genus *Pronuba*, is probably the most unique and interesting case of mutualism to be found anywhere. This is well described by Mr. Webber in the AMERICAN NATURALIST for September, 1892. In this case the plant and the moth, if not strictly sustaining the relation of parasite and host, live together for a long period, and it approaches much closer to mutualism as found between vegetable organisms than phenomena like entomophily where animals and plants are mutually beneficial, without any approach to symbiosis. In the vegetable kingdom, mutualism is a relation of mutual benefit between organisms living together as parasite and host.[2]

The most conspicuous and earliest observed instance of mutualism in the vegetable kingdom is the relation of the Lichen fungi to their gonidia or algal hosts. The relation of the lichen thallus to its contained gonidia was, at one time, the subject of no little ridicule, not only because its discovery overturned many established ideas, but because it really did seem at variance with common sense. A parasite of far larger size than its host, controlling the growth of its host—not growing within or upon the host, and following its growth at a distance, but growing outside of the host, spreading in all directions of its own motion, and being followed by the slower growth of the host—such a parasite was indeed a novel phenomenon. We cannot blame the lichenologists of the old school for their facetious remarks about the horse parasitic upon the bot and the symbiotic relations of Jonah and the whale.

If all lichens were the large, robust parasites that the commoner lichens are, we should have reason to hesitate long before accepting so remarkable a phenomenon as established.

[2]The case of the bacteria in the "pitchers" of *Nepenthes* and other carnivorous plants seems, according to the investigations of Tischutkin, to been exception. See AMERICAN NATURALIST, May 1893.

Fortunately, the lichens exhibit several intermediate forms, and enable us to see the relation between the phenomenon found in the commoner lichens and ordinary parasitism.

Lichenologists have, for a long time, distinguished, under one name or another, two classes of lichens. In the one group the thallus is entirely or substantially homogeneous—there is no differentiation into rind, medulla, etc. In the other there there is a well-defined rind, and gonidial and other zones are differentiated. The former have been called homœomerous lichens, the latter heteromerous lichens. In the first group the alga is the principal part of the lichen. The hyphæ grow within the mass of algal cells and follow them in their growth. To this class belong *Collema* and like genera, which are fungi parasitic upon *Nostoc*, *Scytonema*, etc., and growing within the gelatinous membranes and sheaths enveloping those algæ. Here there is symbiosis—a living together of parasite and host—but no one will contend that there is mutualism.

In the second group the fungus is the principal part of the lichen. It contains in its thallus a zone of algæ, but they follow the growth of the thallus, and their bulk is a small proportion of the whole lichen. In these lichens the algæ are *Protococcoideæ* or *Palmellaceæ*, etc., and to the different mode of growth of these algæ the difference is largely to be attributed.

Between these groups there are a number of forms, usually classed as heteromerous lichens, which, nevertheless, show no differentiation of medulla and rind, and in which the thallus consists of a weft of slender hyphæ growing around filaments of *Chroolepus* and like forms. Still another fact is important in this connection. Some of the genera of this intermediate group have species which contain no gonidia and are saprophytes upon bark, and indeed the parasitic species are often saprophytes during a part of their existence. Many genera of fungi exhibit the same phenomenon.

It is seen, then, that mutualism does not exist in all lichens, and that the steps from an ordinary case of parasitism, such as that exhibited by the homœomerous lichens, which consist of a mass of algal cells permeated by the hyphæ of a fungus and often distorted by it, to the peculiar case of the heteromerous

lichens, where the fungus forms an extensive thallus in a zone of which are contained the algæ upon which it subsists, may be traced in existing species. Not only this, but there are genera, as has been said, in which there are species that do not attack algæ, but live independently as saprophytes, and the point to be noticed here is that these genera belong to the intermediate group of what I may call pseudo-heteromerous lichens.

These considerations, of course, do not prove the existence of mutualism in lichens, but they deprive it of much of its seeming unreasonableness. Other facts, now well established, make it certain that this relation really does exist in the heteromerous lichens.

Arthonia is one of the pseudo-heteromerous lichens. Moreover, it is one of those genera in which certain species, during their entire existence, live independently as saprophytes. Of its development, De Bary says: " . . . . the hyphæ of the thallus make their way into the outer layers of the periderm in the smooth stems of oaks and ashes and there grow as saprophytes independently, that is, without algæ, into a thallus formed of an abundance of slender hyphæ which spread through the cells of the periderm. Then its proper alga, *Chroolepus umbrinum*, finds its way from without through the cell walls of the peridermis into the previously formed hyphal thallus and is seized by it. The cells of the *Chroolepus* are in rows forming filaments with apical growth, and it is by means of this growth that they penetrate into the thallus in the same way as mycelial hyphæ pierce through membranes. The alga is a frequent inhabitant of the bark of trees, and makes its way into the periderm for its own purposes. Its penetration into the thallus of the fungus can scarcely be supposed to be caused by the fungus, but is merely an adaptation which favors the formation of a lichen." This is plainly an ordinary case of parasitism on the part of the lichen, but it not only throws light on the origin of the true heteromerous lichens, but it shows in what manner the fungus may be of benefit to the algæ. In the heteromerous lichen the thallus takes the place of the bark of the tree in these pseudo-heteromerous lichens.

The gonidia of the heteromerous lichens are usually *Palmellaceæ*, which, from their different structure and mode of growth, have not the power of getting beneath the bark as does *Chroolepus*. The thallus of the lichen serves the same purpose with them—protecting the colony of algæ and absorbing and retaining unusual quantities of moisture, and enabling them to live and multiply in places where, under ordinary conditions, life would be impossible.

That the thallus does do this is shown by the fact that lichens grow in places where algæ could not maintain themselves unaided, and by the fact that the gonidia multiply with great rapidity in the thallus, often more so we are told than without, and the individual cells attain a larger growth within the thallus than without, as has been shown by taking algae from the thallus and cultivating them independently. That the fungus does not do all this for nothing, the numerous exhausted cells to be found in the gonidial zone of any ordinary lichen abundantly testify.

There is another curious phenomenon exhibited in some lichens. In these species the algæ are not confined to the gonidial zone, but grow up into the tissues of the sporocarps between the paraphyses and among the asci, so that when the ascospores are ejected, cells of the algæ are ejected with them and are promptly seized upon by the germinating spores. This can hardly be accidental, and it should be observed that it is the alga which is the moving party, not the fungus. Surely some benefit must result to the alga or it would not be done.

It is possible, also, that there are other adaptations resulting from the symbiosis of fungus and alga in the lichen. Frank claims to have discovered several, one of which deserves mention. It is well known that algæ can be separated from the lichen, and that they will then vegetate in the ordinary way independently. Frank asserts that certain species of algæ have become so adapted to life in the lichen and so accustomed to it, that they have partially or wholly lost the power of independent growth. No examples of this, however, are certainly known.

Frank also claims that the fungus exhausts the protoplasm of algal cells without entirely destroying them. If by this is meant that it does not always entirely destroy the cells it attacks, it is probably so, but if anything more is meant, it seems, like some other theories of Frank, which I shall have occasion to mention presently, if I may say so, decidedly "fishy." Such a thing is not necessary to mutualism. The alga can purchase the protection of the thallus only by the sacrifice of a large number of individual cells. If it gets *quid pro quo*, why should it not prefer to sacrifice them to the fungus in return for the shelter of the thallus rather than to leave them victims to natural conditions without compensating advantage. To put the matter in another way, if the energy spent by the alga in producing cells to be destroyed by the fungus were put to making a shelter of its own, could it effect as much as it does by taking advantage of the thallus?

Two other cases in the vegetable kingdom where mutualism is thought to exist remain to be examined. These are the cases of "*Pilzsymbiosis*" or "*Wurzelsymbiosis*" of the roots of anthophytes and certain fungi. The first noticed was what is termed "*Mycorhiza*," and of this first.

T. Hartig, in 1840, and others since, had noticed mycelia apparently parasitic on the roots of trees. In 1885, Frank published the results of investigations of mycelia growing upon the roots of various *Cupuliferæ* in which he claimed that the sustenance of these trees depends upon fungi symbiotic with their roots. The title of his paper indicates his claim: "*Ueber die auf Wurzelsymbiose beruhende Ernaehrung gewisser Baeume durch unterirdische Pilze.*" To begin with, Frank found that certain *Cupuliferæ* have almost the whole of their root system covered with mycelium associated symbiotically with the root, and he claimed that these fungi took the place of root hairs, and were the only means of absorbing water, etc., possessed by the roots, though, of course, like the gonidia of lichens, the roots could be grown independently in water cultures for years.

The mycelia, of the existence of which there is no doubt, are probably connected with some of the *Gasteromycetes* or *Tuberaceæ*. But Frank observes that the presence of a mycel-

ium does not necessarily imply the presence of the perfect fungus fructification, as mycelia may, and often do, go on growing in a sterile condition for years.

Frank did not stop here. He found symbiotic fungi on the roots of many other trees, and others after him found mycelia on the roots of various plants to which he attributes the same relations of mutualism. His final statement is that this phenomenon belongs "to all trees under certain conditions;" that "the Mycorhiza is formed only in a soil which contains humous constituents or undecomposed vegetable remains;" that "the development of Mycorhiza increases or diminishes with the poverty or richness in these constituents;" and that "the fungus of the Mycorhiza conveys to the tree, not only the necessary water and the mineral nutritive substances of the soil, but also organic matters taken direct from the humous and decomposing vegetable remains." Finally, he claims that only through the fungus can the tree employ such organic matter directly.

If the fungus develops only in soil containing undecomposed vegetable remains, we might ask why it takes the trouble to attach itself symbiotically to the root and give the tree the benefit of its saprophytism; especially, as Frank says that the protoplasm of the cells and the fungus live together "without the former being parasitically affected or its vital phenomena disturbed." This reminds one of the exhausted gonidial cells which are still uninjured, and is not the only one of Frank's statements calculated to try our patience and credulity.

In 1886, Warlich (*Botanische Zeitung*, 1886, p. 481, et seq.) investigated certain fungi on the roots of orchids. He examined several hundred species, all of which he found affected on both aerial and subterranean roots with the mycelia of what he showed to be a species of *Nectria*. The hyphæ of this fungus affect spots here and there, forming knots or coils in certain cells and causing them to enlarge, but, as a rule, only partly filling the cell and not destroying the protoplasm. Frank, of course, took this up, and he claims that the protoplasm of the cell is not affected or disturbed by

the fungus; that the fungus is strictly connected with that part of the plant which absorbs the food materials; and that those orchids which are chlorophyll-less, and therefore depend on the humus of the soil for carbonaceous matter, always exhibit this fungus highly developed. Accordingly, he includes this too in Mycorhiza, calling it "endotropic Mycorhiza" (i. e. the hyphæ live *in* the cells) as opposed to "ectotropic Mycorhiza" in which the fungus is entirely *outside* of the cells.

As to Frank's statement that the protoplasm of the cell is not affected by endotropic Mycorhiza, Marshall Ward, in the *Annals of Botany* for February, 1888, says: "This can only be an assumption, and the impression I gather from the study of what is known of this orchid fungus is in favor of the view that the fungus *does* disturb or 'parasitically affect' the protoplasm of the cell, and that an outward and visible sign of some such action exists in the hypertrophy of the cells affected and in the turning yellow of the chlorophyll-grains."

R. Hartig, a more sober and trustworthy writer than Frank, said the last word so far on Mycorhiza in 1891. He admits that the mycelia of some of the *Tuberaceæ* or *Gasteromycetes* are found symbiotic with the roots of certain trees. But his conclusion is that they are of no use to the tree, and are probably injurious by taking nourishment properly belonging to the tree. It would seem that they must do this, even were there mutualism between them and the roots—else why are they there? Organisms are not given to gratuitously assisting one another. Mycorhiza undoubtedly exists—i. e., mycelial stages of many fungi of different groups are parasitic upon and in the roots of anthophytes. But that there is, in any of these cases, more than the ordinary symbiosis of parasite and host, has not been shown, and is improbable. That every tree has its root system covered with mycelia, proves nothing. Every tree has its bark covered with lichens, its twigs with black fungi, and its leaves with parasitic fungi of every description.

The second case of "*Wurzelsymbiosis*" is the root tubercles of the *Leguminosæ*. These tubercles have long been known upon clover, and of late years—since 1885, in fact—have been found upon nearly all of the *Leguminosæ*. Naegeli found a

Chytridium-like parasite in the cells of *Iris* which has never been seen since, and named it *Schinzia*. So when, in 1879, Frank first worked upon clover tubercle, he considered it similar to Naegeli's *Schinzia*, and named it *Schinzia leguminosarum*. Subsequently, a tubercle was found on the roots of *Alnus* by Woronin, called by him *Schinzia alni*. Tubercles have been found in this country on the roots of *Ceanothus*, and are known on a few other plants besides the *Leguminosæ*.

There has been considerable uncertainty as to the cause of clover tubercle and the nature of the parasite to which it is due. Schroeter took the parasite for a Myxomycete similar to *Plasmodiophora* and named it *Phytomyxa*. Marshall Ward, in the article cited, compares it to the yeast fungi. De Bary, in 1884, dismissed the matter with a sneer. Frank now puts the parasite among the *Schizomycetes*, and, indeed, the best view seems to be that the parasites are bacteria pure and simple. There are, in some tubercles, hyphæ, or something very like hyphæ, which Frank now calls "*Infektionsfaden*." Marshall Ward considered these the hyphæ of which what some call the "*baktroiden*"—i. e., the bacteria—were spores. Schroeter saw in them a plasmodium. Frank, always unique and startling, has finally (1891) decided that the "*Infektionsfaden*" have nothing to do with the fungus, but are products of the host for the purpose of self infection! These hyphæ are usually filled with the "*baktroiden*," and Thaxter's recent discovery of *Myxobacteria* may throw some light upon their true nature. In an article in the *Torrey Bulletin* for July, 1892, Mr. Schneider concludes that these tubes have nothing to do with the bacteria, or *Rhizobia*, as Frank now calls them, and considers them hyphal fungi related to the parasite of *Alnus* tubercle. As these tubes often contain the bacteria, this seems improbable. From all that I have read and seen, I am satisfied that the parasites are bacteria, and I see no reason for separating them from the rest of the *Schizomycetes* as Schneider does. I even doubt the necessity of creating a separate genus for them, as Frank did in 1890, under the name of "*Rhizobium*" (*Pilzsymbiose der Leguminosen*).

These tubercles are fine examples of symbiosis, and it has recently appeared probable that they exhibit mutualism of an unexpected kind, analogous to that claimed by Frank for his Mycorhiza. I can only go into this briefly. It is known that the plant cannot directly assimilate free nitrogen. Yet, as Marshall Ward puts it, "For a long time it has been generally known that the *Leguminosæ*, especially, have what we may term a special aptitude for seizing large quantities of nitrogenous substances from the soil, and this problem has become a classical puzzle in vegetable physiology." In 1886, Hellriegel and Wilfarth published some investigations of this matter. Subsequent experiments founded on theirs have been very numerous, and are yet in progress, but their researches remain our principal authority on the subject. Without detailing them, I may say that these researches seem to demonstrate that this power of taking up large quantities of nitrogen depends entirely upon the presence or absence of the tubercles —that without them it does not exist, and that it exists in greater or less degree according to their abundance. Conceding this, two theories are possible as to the cause.

In 1888, Marshall Ward appeared to think that the parasite stimulated the cells to extraordinary metabolic activity, and that was probably all it did. This view has had no followers so far as I can find.

The other possible theory is that the parasite does this work and the host takes advantage of it. Frank, as might be expected, takes this view. The most recent observations seem to have settled pretty thoroughly that the tubercles do assist the plant in some way in assimilating free nitrogen, and that here is a case of mutualism analogous to that of the lichens. The bacteria (as I assume that they are) are parasites. They are there for their own purposes, and are incidentally beneficial to the plant. The plant, it is generally admitted, can exist and thrive without them. In some cases it appears, and the analogy of the lichens makes this probable, that the bacteria are purely parasitic, and that there is symbiosis without mutualism. But, in most cases of the *Leguminosæ*, it seems to be shown that the plants affected do better than those unaf-

fected. Much research is needed in this matter. The manner in which the parasite acts and the host takes advantage of its work are not known with any certainty.

To these probabilities, Frank adds certain characteristic improbabilities. One has already been spoken of, namely, that the plant develops tubes or hyphæ for the purpose of self-infection which it sends through its tissues. This is somewhat like the algæ in some lichens which grow up among the asci in the sporocarp and are ejected with the spores. Only the latter is an established fact, the former a feat of the imagination. Another of his ideas, pronounced a "settled fact" by Schneider in the article cited, is that "at the close of vegetation and on other special occasions, the plant reabsorbs the protoplasm of the fungi." After all the trouble of self-infection to which the host has been, this seems rather like killing the hen that laid the golden egg. There is no sufficient evidence to establish so remarkable a phenomenon. Finally, Frank thinks that the roots of the *Leguminosæ* possess the power of attracting *Rhizobia*, due, as he considers, to some secretion. This is too much for his followers, and I think all will agree that it is the last straw of an unsupportable load with which he has already burdened our credulity. The exuberance of Frank's enthusiasm, however, should not blind us to the fact that some relation of mutualism between the *Leguminosæ* and the tubercle parasites probably—almost certainly—does exist.

It is not necessary, as Frank seems to think, in order to establish mutualism to show that the organisms do no injury to each other. Mutualism of the kind we meet with in the vegetable kingdom involves sacrifices on the part of the host. The parasite is not there gratuitously. It is there to steal from its host the living it is hereditarily and constitutionally indisposed to make for itself. If the host gains any advantage from the relation, it can only do so by sacrificing—by giving the parasite the benefit of its labor that it may subsist. If the plant or the plant colony benefits as a whole, it purchases the benefit by the sacrifice of certain parts or individuals. Mr. Webber, in a note on the Yucca moth in the AMERICAN NATURALIST for Sep-

tember, 1892, makes a significant remark to the same effect: "The larva of *Pronuba* uses up only from 10 to 12 seeds, so that even in those capsules where the most abundant larvæ develop, hundreds of good seeds are nevertheless developed. The few seeds destroyed may well be sacrificed to insure the pollination and development of the others."

Ethically, there is nothing in the phenomena of symbiosis to justify the sentimentalism they have excited in certain writers. Practically, in some instances, symbiosis seems to result in mutual advantage. In all cases it results advantageously to one of the parties, and we can never be sure that the other would not have been nearly as well off, if left to itself.