Symbiotic Algae: Definitions, Quantification and Evolution

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Abstract

Symbiosis is distinct from parasitism quantitatively as well as qualitatively, in ways which can and should be measured. Symbiotic systems exhibit different evolutionary tendencies from those of parasites.

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1. Definitions

I define **algae** broadly (without considerations of cytology or phylogeny) as photosynthetic plants that are neither bryophytes or tracheophytes. **Symbiosis** (in contrast to **parasitism**) implies mutualism in a close association between two dissimilar kinds of organisms, interacting spatially and metabolically so that, under certain natural conditions, each benefits from the association (Lewin, 1982). (In his memoirs – 5,81 – General Polybius used the Greek work "symbiosis" to indicate that Theodotus had lived in the royal household with Ptolemy, whom he later attempted to assassinate. That was about 200 B.C. Those who would exhume a later, 19th Century German usage, "Symbiose", seem not to appreciate that meanings evolve – even faster than biological associations! At the time when De Bary employed the term, words like "philosophy", "ether" and "virus" had popular meanings very different from those current today).

Here I respectfully take issue with Reisser (1992), who argues that the terms "mutual harm and benefit should be of only minor importance since they ... in most cases cannot be defined properly". Benefit or promotion on the one hand, and cost, burden or detriment on the other, can and should be at least roughly quantified, although in practice this may present considerable technical difficulties. (Cushman and Beattie, in 1991, discussed this subject in the context of interrelations between higher plants and insects: here I consider mainly algal symbioses). Such a **benefit** could be measured in terms of faster growth, reduced susceptibility to predation, an extended ecological range, or anything that would ultimately result in an enhanced production of viable progeny capable of maturing under natural conditions to complete the life cycle. Different ways of assessment will of course give different numerical values (the same could be said for measurements of growth), but this consideration should not detract from the recognition that benefits should be assessed objectively by some kinds of parameters.

Although Smith (1992) regards a symbiotic condition "primarily as a situation in which a host is exploiting a symbiont", I feel this definition is inadequate. Symbiosis entails give and take by both partners. For instance, in a lichen the contribution of the fungus partner to its algal symbiont should not be regarded as "of minor or secondary significance": it must be regarded as essential. The fungus absorbs and transmits inorganic nutrients, and protects its algal associates from desiccation and perhaps also insolation. On tree trunks and tombstones, as over vast areas of tundra, lichen algae exist only where their fungal associates permit them to do so. Neither partner is dispensable if such niches are to be successfully occupied. Most lichen fungi probably evolved in symbiosis long ago, since they are now highly specialized, not only physiologically, making it hard for us to grow them in axenic culture, but also anatomically, in the production of a specialized light-absorbing thallus with reproductive soredia. For hermatypic corals and many other kinds of algal symbioses, where the destruction of either symbiont would effectively eliminate the association, the same kind of argument applies.

Furthermore, unlike some authorities (Starr, 1975; Goff, 1983), I consider associations of two dissimilar organisms in symbiosis or parasitism to differ qualitatively, involving physiological and evolutionary tendencies in opposite directions. Let me explain in teleological terms (for which I hope to be excused!). In **parasitism**, the host prefers to avoid, reject or dispel the parasite; if the latter invades, the host tries to minimize its effects and to suppress it as much as it can, to neutralize it by walling it off, or to eject it or kill it. The parasite, on the other hand, does its best to encounter and invade or infest a host; when it does so, to take full advantage of its new environment at the expense of the latter (though generally avoiding a lethal effect, which would

harm both); and to avoid being eliminated. In contrast, in **symbiosis** both the host and its guest are in nature favored by the association, and the guest in its own interest tries to be as little trouble as possible and to benefit the host for mutual advantage; and it is in the interest of neither to dissociate except when this is necessary for reproduction and dispersal.

2. Quantification

Algal symbionts, or photobionts, occur in animals of many phyla; 80% of the animal genera reported to have symbiotic algae are marine (Reisser, 1992; Smith and Douglas, 1987; Goff, 1983). Most kinds of symbiotic algae are relatively small and undifferentiated, and presumably make only slight demands on the morphogenesis of their animal hosts. A few filamentous green and red algae, such as *Cladophoropsis* and *Ceratodictyon*, are associated with morphologically undifferentiated sponges (Sarà, 1966). There are also associations between two kinds of filamentous algae – for instance, nitrogen-fixing *Calothrix* filaments often occur among the utricles of *Codium* and perhaps thereby promote early growth in springtime (Jacob, 1961) – but these seem relatively unspecialized. However, harboring even unicellular symbiotic algae must entail some metabolic costs, which are obviously greater in darkness when the algae cannot photosynthesize and thereby constitute a net liability in the carbon balance of the symbiotic association. Ultimately, we must assume that symbiotic associations survive, and evolve by natural selection, only when the net ecological or metabolic benefits exceed the costs.

Put more quantitatively, if f(H) is the growth or reproductive efficiency, or ecological range, of the lone host, and f(H+S) is the corresponding expression for the host+symbiont association, then any increase of f(H+S)/f(H) will serve to promote the symbiosis. For an obligate symbiont (major or minor), which by definition cannot survive in the absence of its partner, f(H) or f(S) is zero, and the ratio becomes infinity. This is the case, for instance, for the endozoic prokaryotic green alga *Prochloron*, which has never been successfully cultured (Lewin and Cheng, 1989), and the several species of didemnid ascidians with which it is normally associated and which have never been found to lack it. Likewise, although the red alga *Ceratodictyon* can be grown in laboratory culture in the absence of its usual sponge symbiont, when such "cleaned" plants are set out in their natural oceanic environment, they are soon grazed away (Price et al., 1984).

For any kind of facultative symbiosis the value of this cost-benefit ratio will depend on conditions. For a host in daylight, a photosynthesizing algal symbiont may increase this benefit ratio to a value above unity, but as the light

intensity wanes and photosynthesis declines, the value will fall until, at night, it becomes less than one. A symbiotic association in the plankton may have a large cost-benefit ratio when days are long, and a smaller one in winter; if the cells sink below the euphotic zone, the ratio eventually falls below unity. Although in such latter conditions the algal cells act, in effect, like parasites, in a symbiotic system the net effect, averaged over days or seasons, is beneficial. Such a balance sheet has rarely been worked out experimentally, though a valiant attempt has been made for an alga+sponge symbiosis (Frost and Williamson, 1980).

3. Evolution

Symbiotic or parasitic relationships should not just be regarded as evolutionarily static, for there must be in each partner a constant natural selection of genes promoting, in one way or another, its own interests. A parasite exploits and debilitates its host, which may pine or die prematurely; cases of parasitism therefore tend to be shorter-lived than the more persistent symbioses. Hosts must do their physiological best to avoid infestation or ameliorate the results of infection, and so in the course of evolution they tend to develop resistance by the positive selection of special genes. Parasites do their best to fight back, and in parasites selective pressure favors genes conferring enhanced infectivity by somehow evading or overcoming barriers set up by the embattled host. Mycologists have provided us with a few genetic studies of the evolutionary war between host and guest/pest. A nice example is the infestation of the flax plant, *Linum,* by a rust fungus, *Melampsora,* in which one mutation after another helps the flax to ward off rust, and by one mutation after another in the rust genotype the fungus overcomes these defences (Flor, 1956). On the other hand, a symbiotic system tends towards the evolution of closer and closer accommodations between the partners, and ultimately from facultative to obligate associations. I know of no comparable genetic studies of any algal system. Perhaps one could find conditional mutants appropriate for such investigations.

One may guess that, in the first place, symbiotic algae have evolved, and are probably still evolving, from free-living types that may happen to be ingested. Ingested algae do not die instantly, of course: they may survive for a few minutes, hours or even days before they finally succumb to the digestive processes of their consumer. During this period there is no reason to suppose that all photosynthetic processes cease. Even disembodied chloroplasts can continue for a while to fix CO_2 and evolve oxygen when suitably illuminated, as they do in some sacoglossan molluscs, though these should not be regarded as

symbioses since whole algal cells are not involved. So it is perhaps not surprising to find that the transparent bodies of certain marine protozoa, after ingesting phytoplankton cells, carry out photosynthesis almost as if they were themselves members of the phytoplankton community (Stoecker et al., 1987). Presumably carbohydrates of some sort are formed, like those known to be produced and excreted by many photobionts, and made available to the animals with algae inside. One may also presume that, insofar as this process benefits the animals, they will evolve in such a way as to enhance and prolong it, and to become more and more closely co-adapted to symbiotic associations with algae.

Unicellular symbiotic algae can be expected to make relatively small spatial demands on their adult animal hosts, so that they can generally be tolerated, or even encouraged. In their free-swimming larval existence, foreign elements – the algae – may constitute a relative inconvenience in or among the animals' own cells. Perhaps for this reason many symbiotic animals produce aposymbiotic young which need to be re-infected with new algal symbionts at each generation. Such a "re-entrant" system has several biological corollaries. Firstly, there have to be special means for establishing reinfection by the right species, generally following ingestion. Such algae have to be able to live autonomously, to swim at least briefly, as can species of *Symbiodinium* and *Tetraselmis*, and to recognize their specific hosts, respectively corals and giant clams, and the flatworm *Convoluta*. We can expect that evolution, by selective pressures, would favor genes for chemotaxis in one (the algal) associate, genes for the production of specific attractants in the other (the animal host), and genes for interspecific recognition and incorporation in both. Such algae may also need mechanisms for turning the permeability of their outer cell-membrane off and on, as it were: "off" when living as free autotrophs which can ill afford to lose hard-won photosynthetic metabolites, and "on" when involved in the biochemical give-and-take of animal symbiosis (Taylor, 1973). The need for such biological plasticity may preclude a high degree of metabolic specialization, and it may also preclude, or retard, co-evolution by parallel speciation with the host.

In other cases, however, the symbioses persist by vegetative propagation, or through dispersive larval stages in what might be called "systematically inherited" or "systemic" associations. (For this kind of inheritance the term "vertical" has been used, but I think it could be misconstrued especially in marine ecological contexts). Here the symbiotic alga is adapted to only one kind of habitat, namely the interior of its animal host. Then the genetic speciations can run *pari passu*, as has been demonstrated in some parasites, e.g., on lousy gophers (Hafner and Nadler, 1988); as the host species differentiate and diversify in evolution, their symbionts can be expected to follow suit. Such

systemic algal symbionts do not have to be motile, being permanent residents in the hosts, and it is among these that we find non-flagellate algal genera such *Chlorella* (in green freshwater sponges, ciliates and hydra) and *Prochloron* (in several symbiotic didemnids). Here considerations of recognition and incorporation may not be relevant, and with time the metabolisms of the two associated organisms can become more and more closely integrated until eventually by evolution the symbioses may become obligate for both partners. Comparative genetic studies of such systems (re-entrant or systemic) might be worth pursuing.

Ultimately, distinctions between intracellular symbiont and organelle may become blurred, as they seem to have done in the *Glaucophyta* (Kies, 1984). Perhaps that is how chloroplasts arose, as intracellular prokaryotes became integrated by symbiogenesis. The case for the red alga plastid, as an evolved cyanophyte, seems now convincing, while that for green chloroplasts is already very persuasive (Lewin, 1993).

Acknowledgements

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