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Edited by Lynda J. Goff

Excerpt

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Introduction

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Nature abhors a pure culture; symbioses, whether ecto- or endo-cellular, are the rule rather than the exception.

Lynn Margulis, 1980

If it is the nature of living things to pool resources, to fuse when possible, we would have a new way of accounting for the progressive enrichment and complexity of form in living things.

Lewis Thomas, 1974

Biologists' perceptions of the interactions of organisms have changed profoundly during the past century. No longer is nature viewed as "red in tooth and claw," where only the strongest and most aggressive survive and dominate. Rather, studies of the complexity of organismal interactions within communities have clearly revealed that success is often linked to the ability of an individual, or a population of individuals, to interact intimately with other organisms within the community.

Selective advantage is attained through exploiting other members of the community. However, the exploitation is generally far more subtle than merely eating one's competitor. The fungi of lichen associations attain a selective advantage by capturing and enslaving the photosynthetic capabilities of their algal partners. In these highly refined interactions, the association is one of "controlled parasitism" (Smith 1980), in which the fungus exploits the alga but has little deleterious effect on the alga. Mutual exploitation between two members of a community may also evolve, to the advantage of both individuals. This is the case in some associations of invertebrates and algae, and in mycorrhizal associations of fungi and higher plants.

DeBary (1879) employed the term *symbiosis* (*sym*, together; *biosis*, living) to describe the intimate interactions of dissimilarly named organisms ("Zusammenleben ungleichnamigen Organismen") and, contrary to subsequent usage (Lewin 1982), indicated that symbiosis includes all degrees of parasitism as well as mutualistic and commensalistic associations (Goff

1982). A more current definition of symbiosis is an “association, for significant portions of the life cycles, of individuals that are members of different species” (Margulis 1981).

Since deBary introduced the term *symbiosis*, literally thousands of symbiotic associations involving plants, animals, fungi, protists, and prokaryotes have been described. Probably few groups of organisms have been more successful in forming intimate symbioses with other organisms than the evolutionarily diverse group of organisms known as the algae. Within every division of these organisms, and in every community they inhabit, symbiotic interactions have evolved, and in some cases these have had profound effects on the ecosystem. E. J. Ferguson-Wood (1967) states,

In the tropics, many, probably most of the recurring animals have algal symbionts and these extend through most of the invertebrate phyla . . . Quantitatively it is probably true that the symbiotic algae are more important than the phytoplankton and the free benthic algae in coral reefs and other shallow waters with calcareous sediments, and the productivity of such waters is essentially due to such symbionts, which are more usually known as zooxanthellae.

Algae occur as symbiotic extracellular (intercellular, exhabitational) or intracellular (inhabitational) associates of vertebrate, invertebrate, protistan, fungal, angiosperm, and algal hosts. In the extreme case, only the photosynthetic organelle of the alga, the plastid, is incorporated into the host's cytoplasm, where it remains active photosynthetically, providing fixed carbon to the heterotrophic host.

In many symbiotic associations, the algal symbiont's morphology is altered, as is its biochemical and physiological activity. As the symbiosis becomes progressively more obligate, a loss of capabilities for an independent life becomes evident. This may involve the loss of genetic information necessary for autonomy. In the case of the symbiosis between the cryptomonad-like flagellate *Cyanophora paradoxa* and its cyanobacterial endosymbiont *Cyanocyta korschikoffiana*, pigment synthesis (c-phycocyanin) in the cyanelle inclusion is under partial control of the host's ribosomes (Siebens and Trench 1978, Trench and Siebens 1978). This situation may be analogous to the synthesis of ribulose biphosphate carboxylase in plant cells, where both the nuclear and plastic genomes are necessary for enzyme synthesis.

During the past 25 years, nearly 1,500 papers have been published dealing with algal symbiosis. However, many of these papers are primarily descriptive and, as stated by Margulis (1981), “are often treated in the biological literature as exotic.” Until recently, experimental studies of algal symbioses have been few and for the most part have been undertaken to classify the interaction – that is, to determine if the association is parasitic, mutualistic, commensalistic, biotrophic, necrotrophic,

exhabitational, inhabitation, obligate, facultative, specific, permissive, transient, or persistent (Henry 1966, Lewis 1973, Starr 1975, Lewin 1982). However, biological phenomena involving organismic interactions are rarely abruptly discontinuous (Scott 1969, Smith 1980, Starr 1975, Goff 1982). More often they exist in a more-or-less smooth and continuous gradation or continuum.

As will be evident in the following chapters, algal symbioses are often difficult or impossible to classify. They form a continuum, each interaction being a function of the evolutionary history of the separate “players” as well as the partnership. This then is the basic theme of this volume. Each algal symbiosis is unique; although symbioses may be described, they cannot necessarily be categorized. In fact, it may be argued that attempts to do so may actually obscure the true physiological and genetic nature of the interaction, and quite possibly bias the scientific objectivity necessary for the required experimental quantitative and qualitative studies of the association.

The second theme of this book is that symbiotic systems provide biologists with extremely useful experimental tools to study important biological phenomena. For example, research on the lichen symbiosis (Ahmadjian and Jacobs, Chapter 8) is providing insight into intercellular transport mechanisms (apoplastic and symplastic), whereas intracellular (interorganelle) transport mechanisms are being examined in endosymbiotic associations of zooxanthellae and zoochlorellae and their invertebrate hosts (Pardy, Chapter 1; Taylor, Chapter 2; Lee and McEnery, Chapter 3; Anderson, Chapter 4), and in the association of the mollusc *Elysia* and its endosymbiotic algal chloroplasts (Hinde, Chapter 6).

In addition, algal symbiotic associations provide the means to examine (1) how different genomes may function in conjunction and how such an interaction is integrated, (2) the basis of cell – cell recognition mechanisms (Chapman and Good, Chapter 9; Ahmadjian and Jacobs, Chapter 8; Peters and Calvert, Chapter 7; Hinde, Chapter 6; Lee and McEnery, Chapter 3; Taylor, Chapter 2; Anderson, Chapter 4), (3) mechanisms by which new species, and through them higher taxa, originate, and (4) how the eukaryotic cell may have evolved. No longer should research in this area be considered “exotic”; rather, as stated by Margulis (1980), it is central to the understanding of cell biology and the origins of innovation in evolution.

References

- deBary, A. (1879). *Die Erscheinung der Symbiose*. Verlag von Karl J. Trubner, Strassburg.
- Ferguson-Wood, E. J. 1967. *Microbiology of Oceans and Estuaries*. Elsevier Oceanography Series, vol. 3. Elsevier, Amsterdam.

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- Goff, L. J. (1982). Symbiosis and parasitism: Another viewpoint. *BioScience*, **32**, 255–6.
- Henry, S. M. (1966). Association of microorganisms, plants and marine organisms. In: *Symbiosis*, vol. 1, ed. S. M. Henry. Academic Press, New York.
- Lewin, R. A. (1982). Symbiosis and parasitism – definitions and evaluations. *BioScience*, **32**, 254–9.
- Lewis, D. H. (1973). Concepts of fungal nutrition and the origin of biotrophy. *Biological Reviews* **48**, 261–78.
- Margulis, L. (1980). *Symbiosis as parasexuality*. In: *Cellular Interactions in Symbiosis and Parasitism*, ed. C. B. Cook, P. W. Pappas, and E. D. Rudolph, pp. 263–73. Ohio State University Press, Columbus.
- (1981). *Symbiosis in Cell Evolution*. W. H. Freeman & Co., San Francisco.
- Scott, G. D. (1969). *Plant Symbiosis*. Edward Arnold, London.
- Siebens, H. B., and R. K. Trench (1978). Aspects of the relation between *Cyanophora paradoxa* (Korschikoff) and its endosymbiotic cyanelles *Cyanocyta korschikoffiana* (Hall and Claus). III. Characterization of ribosomal ribonucleic acids. *Proc. R. Soc. Lond. (B)* **202**, 463–72.
- Smith, D. C. (1980). Mechanisms of nutrient movement between the lichen symbionts. In: *Cellular Interactions in Symbiosis and Parasitism*, ed. C. B. Cook, P. W. Pappas, and E. D. Rudolph, pp. 197–227. Ohio State University Press, Columbus.
- Starr, M. P. (1975). A generalized scheme for classifying organismic associations. *Symp. Soc. Exp. Biol.* **29**, 1–20.
- Trench, R. K., & Siebens, H. B. (1978). Aspects of the relation between *Cyanophora paradoxa* (Korschikoff) and its endosymbiotic cyanelles *Cyanocyta korschikoffiana* (Hall and Claus). IV. The effects of rifampicin, chloramphenicol and cycloheximide on the synthesis of ribosomal ribonucleic acids and chlorophyll. *Proc. R. Soc. Lond. (B)* **202**, 473–83.

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Phycozoans, phycozoology, phycozoologists?

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Experimental and quantitative studies on several algal-invertebrate symbioses have suggested or shown directly that these associations possess a variety of interacting systems that stabilize and perpetuate them. It is becoming evident that host-algal symbiont interactions occur at many levels of biological organization. Among some contemporary workers in algal-invertebrate symbioses there has been a shift away from the “reciprocal benefit,” the “who does what for whom,” and the catalog-categorization approaches (Starr 1975) to symbiosis research. There is a growing emphasis on studies probing the underlying mechanisms allowing or causing animals and algae to form stable entities that thrive and persist through time. We are becoming aware that algal-animal symbioses have unique biological identities. The association is an organism that makes its living in a particular way, in a particular ecological context.

Various aspects of algal-invertebrate symbiosis have been reviewed repeatedly in the last 10 years (Cook 1980, Muscatine 1974, Muscatine et al. 1975, Smith 1974, Smith et al. 1969, Trench 1979). My goal is not to present still another review but rather to offer a point of view and to suggest a paradigm that might help unify and enhance our understanding of algae-invertebrate symbioses. In the following discussion I use the words *symbiosis*, *host*, *symbiont*, and *aposymbiont*. These terms are used operationally, with symbiosis taken to mean the intimate physical association of unicellular algae and animals; with host and symbiont referring to the animal and algal components, respectively; and with aposymbiont referring to an invertebrate host disassociated from its algal symbionts. I also avoid the terms *mutualism*, *benefit*, *partners*, and other symbiosis jargon (except as previously noted).

The word *parasite* conjures up an image of an organism having a particular lifestyle. The word does not imply any particular systematic or phylogenetic grouping, but rather a functional category of organisms.

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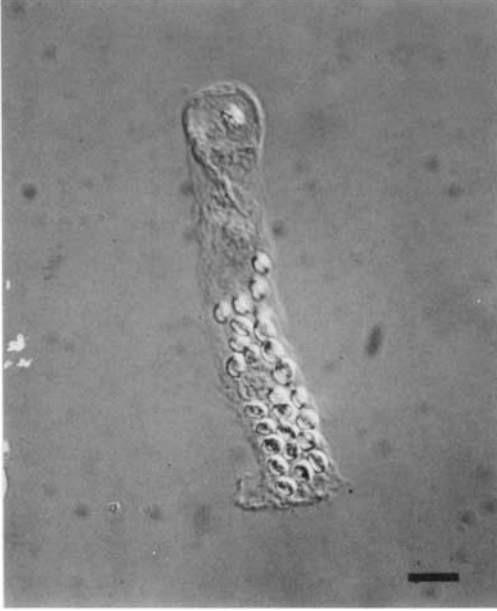


Fig. 1. Isolated digestive cell from *Hydra viridis* showing symbiotic algae (green spheres). Bar equals 10 μm , Nomarski optics.

Herbivore, *xerophyte*, *annual*, and *ectotherm* are other useful terms describing or grouping organisms of similar habits. I wish to introduce the term *phycozoan* (*phyco*, seaweed, *zoa*, animal) to denote the compound organism resulting from the intimate association of algae and animals. Phycozoans are symbioses where algal unicells (phycobionts = algal symbionts) live inside an animal (zoobiont = animal host), within its cells (Fig. 1), and/or among its tissues (Fig. 2). Because I intend phycozoa to be a functional category, I would consider the algal-bearing protists to be phycozoans. Occasionally algal plastids are symbionts as in the case of certain marine slugs that acquire and harbor chloroplasts from siphonaceous algae (see Trench 1975, for review and Chapter 6 in this volume). These are also phycozoan associations.

The phycozoan is an integrated amalgamation of (1) characteristics specific to and maintained by the associating bionts, (2) preadaptations that are modified, amplified, and recruited by the phycozoan, and (3) new features found only in the phycozoan or resulting from association. In these respects phycozoans are analogous to lichens (see Chapter 8 in this volume). The lichen thallus emerges as the biological unit having specialized characteristics and adaptations not found in free-living (not lichenized) fungi and algae. Fungi and algae making up a lichen thallus do not lose their identity even though the morphology and physiology of the thallus may be very complex. In phycozoans, the phycobionts invariably retain the ability to photosynthesize. Moreover, although free-

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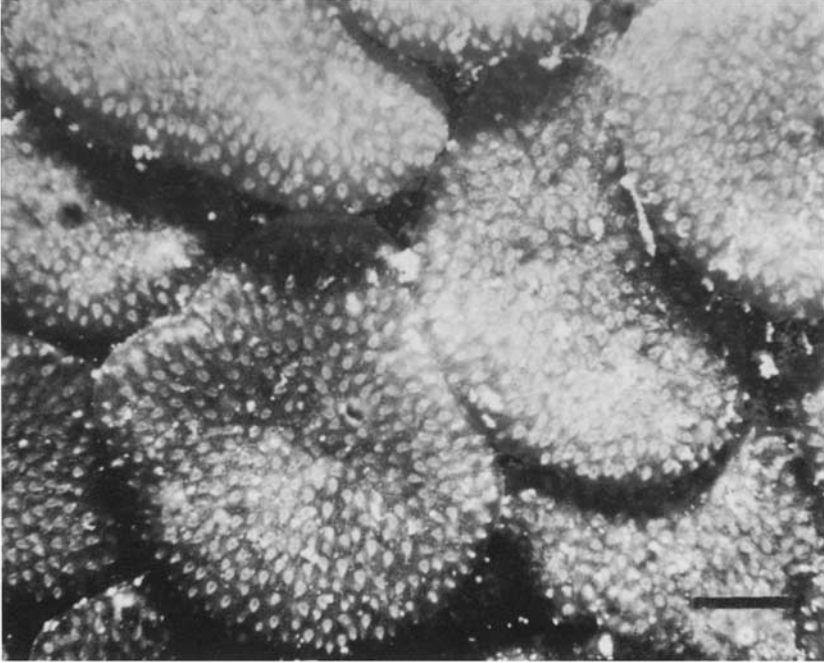
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Fig. 2. Colonies of *Trididemnum*, a colonial ascidian containing *Prochloron* cells. Bar equals 1 cm. Photograph courtesy of Dr. Charles Berkland, University of Guam.

living algae are known to leak or excrete organic substances (Fogg 1962), in symbiotic algae leakiness (a preadaptation?) is amplified such that large amounts of specific organic molecules are released. Finally, after becoming part of a phycozoan, symbiotic algae may undergo a variety of modifications such as the loss of flagella, modification of cell walls (Oschman 1966), and development of a new ensemble of surface antigens (Pool 1979).

Phycozoans have emergent properties distinguishing them from simply animals with algae in them. These properties enable the phycozoan to exist and thrive in niches from which its component bionts, as individuals, are excluded. Hence phycozoans may define an ecological niche (Hutchinson 1959) though presently little information exists on this aspect of phycozoan biology.

It seems reasonable to recognize phycozoans as stable biological units, real organisms, analogous to lichens, upon which the forces of evolution act. Mutations in either phycobiont or zoobiont have the potential for increasing or decreasing the fitness of the phycozoan. A novel possibility, arising either from mutation or immediate environmental factors, is that the phycozoan becomes extinct, even while one or both of its component bionts persist, though unassociated.

Table 1. *Diversity of phycozoans*

Phylum	Examples	
	Phycobiont	Zoobiont
Protozoa	<i>Chlorella</i>	<i>Paramecium bursaria</i>
	<i>Chlorella</i>	<i>Stentor polymorphous</i> , <i>Ophrydium</i> , <i>Vorticella</i>
	<i>Symbiodinium</i>	Radiolarians Foraminiferans
Porifera	<i>Chlorella</i>	<i>Spongilla</i> sp.
Coelenterata	<i>Chlorella</i>	<i>Hydra viridis</i> (green hydra)
	<i>Symbiodinium</i>	<i>Anthopleura</i> sp. (sea anemone)
	<i>Symbiodinium</i>	<i>Pocillopora</i> sp. (coral)
	<i>Symbiodinium</i>	<i>Cassiopeia</i> sp. (jellyfish)
Platyhelminthes	<i>Chlorella</i>	<i>Dalyellia viridis</i> (freshwater flatworm)
	<i>Platymonas</i>	<i>Convoluta roscoffensis</i> (marine flatworm)
Mollusca	<i>Symbiodinium</i>	<i>Tridacna crocea</i> (giant clam)
	<i>Vaucheria</i> chloroplasts	<i>Elysia viridis</i> (slug)
	<i>Chlorella</i>	<i>Anodonta</i> (freshwater clam)
Chordata	<i>Prochloron</i>	<i>Diplosoma virens</i> (compound tunicate)

Although a fairly wide assortment of invertebrates form phycozoans, comparatively few species of algae become involved. Table 1 is not an exhaustive catalog, but it illustrates the diversity of animals and kinds of algae that form phycozoans. Despite the apparent variety and various combinations of algae and invertebrates, all phycozoans seem to display the following characteristics:

1. The transfer of photosynthetically produced organic substances from the phycobionts is essential for the stability and persistence of the phycozoan.

2. Because of (1), photosynthesis is a central and critical aspect of the phycozoan's biology.

3. Phycozoans have mechanisms that assure continuity of the association through successive generations of the zoobiont.

Phycobionts from all phycozoans so far analyzed translocate substantial quantities of soluble organic molecules to the zoobiont cells and also release products to the medium when analyzed in vitro (Table 2 gives some examples). Experiments with ^{14}C have shown that photosynthetically reduced carbon produced by phycobionts enters the zoobiont's metabolic network, eventually appearing in all major biochemical fractions (Muscatine & Cernichiaro 1969, Pardy 1980, Trench 1971). Using

Table 2. Translation by phycobionts from various symbionts

Phycobiont	Zoobiont	% of photosynthesis translocated	Major product(s)	Reference
<i>Platymonas</i>	<i>Convolvata</i>	8	Ala, Gly, Pyr	Muscatine 1974
<i>Chlorella</i>	<i>Hydra</i>	40	Maltose	Cernichiaro et al. 1969
<i>Chlorella</i>	<i>Paramecium</i>	15–86	Maltose	Muscatine et al. 1967
<i>Chlorella</i>	<i>Spongilla</i>	4	Glucose	Muscatine et al. 1967
<i>Chlorella</i>	Mutant <i>Hydra</i>		Glucose	Muscatine et al. 1967
<i>Symbiodinium</i>	<i>Rhizostoma</i>	20	Glycerol	Trench 1971
<i>Symbiodinium</i>	<i>Cassiopeia</i>	23	Glycerol	Trench 1971
<i>Symbiodinium</i>	<i>Anthopleura</i>	49	Glycerol	Trench 1971
<i>Symbiodinium</i>	<i>Aiptasia</i>	35	Glycerol	Trench 1971
<i>Symbiodinium</i>	Fungia	25	Glycerol	Trench 1971
<i>Symbiodinium</i>	<i>Zoanthus</i>	42	Glycerol	Trench 1971
<i>Symbiodinium</i>	<i>Tridacna</i>	40	Glycerol	Muscatine 1967
<i>Symbiodinium</i>	<i>Pocillopora</i>	40	Glycerol	Muscatine 1967

green hydra and indirect calorimetry, Pardy and White (1977) showed that the flow of carbohydrate from the phycobiont was sufficient to induce a pronounced carbohydrate metabolism in the phycozoan. By comparison, aposymbiotic hydra exhibit a fat metabolism almost exclusively. Similar findings are reported for phycozoan sea anemones. Apparently this algal-to-animal flux of nutrients is the fundamental basis for the existence of phycozoans. It allows the zoobiont to inhabit environments that experience continuous or periodic shortages of exogenous food or to invade habitats usually foreclosed to them for lack of normal food items. In reef-forming corals mounting evidence points to the translocation of nutrients from phycobiont to zoobiont as being the major factor in promoting rates of calcification sufficiently high for reef building and maintenance (Muscatine & Cernichiari 1969, Muscatine & Porter 1977). If photosynthesis is inhibited, the zoobiont often experiences reduced growth rates and/or degenerates. Although aposymbiotic zoobionts of some phycozoans can be artificially produced and maintained in the laboratory (*Hydra*: Whitney 1907, Muscatine & Lenhoff 1965, Pardy 1976; *Paramecium bursaria*: Karakashian 1963; *Convoluta roscoffensis*: Provasoli et al. 1968, Boyle & Smith, 1975), such forms are rarely found in nature, probably because they cannot survive. The point is that the existence and well-being of the phycozoan depends upon a continuous or intermittent supply of nutrients provided by the phycobionts. Because the organic nutrients released by the phycobionts originate from photosynthesis, photosynthesis is a critical process upon which the stability of the phycozoan depends.

To photosynthesize at a useful rate, phycobionts require optimum supplies of carbon dioxide and photons. This means the phycobionts must be strategically located within the phycozoan so that carbon dioxide flow and light penetration are maximized. Hence, design limitations and requirements are placed on phycozoan structure. In most phycozoans the phycobionts are located in or among tissues near the host's surface. In coelenterate phycozoans the phycobionts occupy the gastrodermis, a tissue seldom more than a few millimeters from the animal's external surface. In worm and slug phycozoans, the phycobionts are often associated with the gut, which has many diverticulae or tubules ramifying throughout the animal and lying close to the surface (Dorey 1965, Oschman 1966). A remarkable adaptation occurs in the mantle of the giant clam, *Tridacna*. The phycobionts occupy cavities in the mantle tissue, which is extruded between the valves and comes partially to overlay the external surface of the clam. Imbedded in the mantle are lenslike structures that facilitate the penetration of light to the phycobionts. Finally, in a fascinating analysis, Porter (1976) has shown a relationship between the morphology of phycozoan reef corals and the degree of autotrophy