



Newsletter of the FRIENDS OF THE FARLOW

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R. K. Edgar, editor

Symbiosis

My first acquaintance with the idea of *symbiosis* was in grade school when I was introduced to lichens. Neural notes of that meeting endure: two different kinds of organisms -- a fungus and an alga -- physical intimacy (my adult translation) and that "it was good." Since then, examples of symbioses -- lichens, corals, and eukaryotic organelles (chloroplasts and mitochondria) -- have been the mainstay of my interactions with the concept. Occasionally my attention was caught by studies of the molecular resource traffic (often quite one-sided) between symbionts. So, when a colleague suggested an article for this newsletter on symbiosis, my initial thoughts were a parade of examples and biologists' accounting of molecular trading balances. However, my curiosity about what contemporary "symbiosis biologists" were thinking got the better of me, so I at least had to skim the literature before I farmed out the assignment. Within minutes I found myself immersed in discussions of genomic conflict and cooperation and how replicative autonomy can be transferred from entities to wholes. Ideas such as "recombination being favored as a means of enforcing reproductive fairness" seemed a long way from "Mr. Fungus and the friendly alga."

Symbiosis as a biological term entered the English language in 1877 in Bennett's translation of Otto Thomé's *Lehrbuch der Botanik* and not suprisingly with lichens as an example. Symbiosis conceptually, if not nominally, had been part of the analytical discourse of Anton de Bary, Farlow's mentor in Strasbourg, and Albert Frank in the late

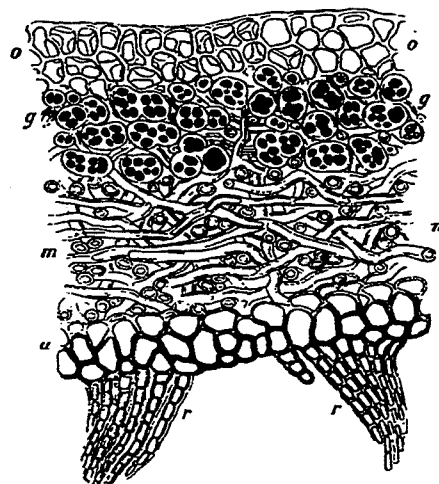


Fig. 173. *Sticta fuliginosa*. Transverse section through the foliaceous thallus; ...m, medullary layer, r, rhizoid strands, g, algal zone. The algal zone here consists of a species of *Chroococcus* with thick colourless gelatinous membrane and bluish green protoplasm which is black in the figure. After Sachs. From A. de Bary. *Comparative morphology and biology of the fungi, mycetoza and bacteria*. Translation by Garnsey & Balfour, 1887. (Farlow Library).

1860's and 1870's. However, for the two and a half centuries before biologists adopted the word, symbiosis was already a part of the English language indicating a "living together, socially...": "To study and intend things profitable for the publique Symbiosis" (Misselden's *Free Trade*, 1622). From the outset symbiosis has had the connotation of a mutually positive interaction.

But linguistically before there was *symbiosis*, there was *commensal*. In the 15th century, long before biologists coopted the word, we can find "O where hast thou bee so long commensal?" Commensals feed with their hosts -- literally, are "together at the same table" -- as sort of unobtrusive, odd-couple dinner companions. In contrast, to *parasites* the host is more dinner itself than simply a companion. Commensal entered biology in the writings of James Dwight Dana of Yale University on corals in 1872 and a little later in Wyville Thompson's *Challenger* Expedition reports in describing the eating habits of decapod crustaceans. One can imagine that the profitable interaction of a commensal with its host is contingent on the availability of food, and that if food were limiting, commensalism could turn into competition with neither benefiting, a situation Mother Nature would abhor as much as she does a vacuum. As I surveyed these interactions and despite an early mentor's warning about being anthropomorphic, I kidded myself that I had seen all these interactions before at 50 years of dinner tables at which I had fed, and I reminded myself how easily, even with the same diners, the social interactions of the day can change.

Symbiosis as a conceptual umbrella accommodates mutualism, commensalism and parasitism -- all associated with different kinds of organisms intimately living together. This is the sense in which de Bary promulgated it in the 1870s. But the connotation that holds sway publically and in biology texts generally is that symbiosis is



The opening of a marine sponge at the apex of a conical projection, which is surrounded by a dense growth (dark regions in the photograph) of the diatom *Tryblionella hungarica* which occurs within the tissues of a sponge. The sponge is from Jeffreys Ledge about 45 m deep in the Gulf of Maine. In well-lit surface waters such an association would be viewed as a commensalistic symbiosis with photosynthetically produced organic matter probably moving from diatom to sponge. However, at these depths in the Gulf of Maine light intensities are about 0.01% of those at the surface, well below what could adequately power photosynthesis in the diatom, so the movement of organic matter to support the population density observed in the diatom is more likely from the sponge to the diatom, which functions more heterotrophically than autotrophically. The diatom and sponge reproduce independently. From the perspective of these diatoms the Ledge landscape, which is mostly rocky, is a series of sponge islands, which are colonizable and exploitable. At these depths, the diatom only occurs in association with the sponges. (Photographed by J. Sears)

mutual and it is beneficial; -- and therefore that "it is good." For those who would set their moral compass based on the structure and operation of Nature, symbiosis viewed positively, is a God-send. It supports Paleyan rather than Malthusian views of Nature's face as one "bright with gladness." Symbiosis is an New Zealand company specializing in the harmonious integration of technology and music. Symbiosis is an American company specializing in conflict

management. Symbiosis is a rock group (Simon Phillips, lead guitar), and although I've never heard it, I can imagine how it supposed to make me feel.

Years ago, I began to subconsciously associate symbiosis and bees. I think, the link was simply that humans tended to view both as morally instructive, and that they conveyed a common message. There was a strong pre-Darwinian fascination with the moral lessons derivable from bee societies: industry, productivity, cooperation. That human society should be modeled on bee society was attractive to many *philosophes*. But, alas, whatever aspirations we might have to behave like bees is constrained enormously in that we've simply got non-facilitating genetics. We just can't get as close to one another genetically as bees can, unless of course, we too could routinely initiate virgin births. Even though lichens and bees might convey similar moral messages -- "cooperation is good" -- they would otherwise seem to share little with each other. My linkage was playful and historical for its philosophical foundations were admittedly shaky.

The experimental investigations of lichen synthesis by Vernon Ahmadjian (FOF member at Clark University) and others over the past few decades have taken the popular view of lichen mutualism and recast it as more realistically a "controlled parasitism" of the alga by the fungus. The face of Nature at a distance might be "bright with gladness", but on closer inspection, it is often pock-marked, as Darwin portrayed in his reverent inspection of the fate of Scotch fir seedlings below the cover of the heaths in Surrey. Ahmadjian's view of the lichen symbiosis certainly jolted my linkage of bees and symbiosis a decade ago, but I had not followed up on it.

Upon reading ideas about symbiosis by evolutionary geneticists, I confronted an interesting question: If two symbionts are

mutualists, how does one keep the other from hijacking the relationship? (My thoughts were returning to the familial dinner table.) The mutualism of the evolutionary geneticist is often a hard-won peace, a calm that is enforced after a storm, an arms race that has stalemated, temporarily. Mutualisms do not spring full-blown simply from the collisions of the bodies of two different species any more than Darwin (sarcastically) thought special creation might arise from the sudden collision of atoms. The conceptual tools of the evolutionary genetic analysis of symbiosis involve "policing strategies" and causal correlates of levels of kinship within symbionts. High levels of relatedness generally facilitate selection for cooperative interactions, and low levels more likely yield reproductive strategies that generate conflict. Levels of symbiont relatedness can be host-controlled by constraints on symbiont mixing and dispersal or by bottlenecking symbiont reproductive output, as might occur if a thallus had specialized locations from which it formed reproductive propagules and to which only a small subpopulation of the symbionts had access.

This brief excursion into the literature put asunder my innocent moralistic linkage of symbiosis and bees. But another sort of linkage emerged. Although I'd seen it in Darwin's interpretation of the evolution of hive-bee comb-making behavior, as rooted in natural selection operating on swarms (read *families*) of bees and more recently in revelations about genomic conflict between mother and child (*in utero*), I never imagined I'd look at lichens and other cryptogamic symbioses and begin to analyze the intimacies of structure and interactions with theoretical models of conflict and cooperation and especially kin selection. I am much struck - as was Darwin - that ideas so simple can be so consilient - lichens, bees and dinner table interactions included.

R. K. Edgar

News of the Farlow



Site of the 1997 Clara Cummings Walk at Myles Standish State Forest, Plymouth, MA. (Photographed by E. Kneiper)

The Spring 1998 **Clara E. Cummings Walk** sponsored by the Friends of the Farlow will be held on Sunday, April 26th in southeastern Massachusetts. Using the Biology Department at the University of Massachusetts Dartmouth as an initial base for forays and later examination of collected cryptograms, the walk will focus on special habitats in the region, including coastal dunes and white cedar swamps. Details will be mailed to FOF members in late winter.



Sam Hammer (left) and Joann Hoy scrutinizing lichens during the Spring 1997 Clara Cummings Walk. (Photographed by E. Kneiper)

In Aristotle's sense of a friend being one who when wishing you well means it for your sake, not their own, The Friends of the Farlow has valued the friendship and dedication that each of the four people described below - Gerry, Carolyn, Ben and Kristen - brought to the Farlow, and we wish them very well.

Geraldine Kaye, a founding member of the Friends of the Farlow, its newsletter editor in the early years and the librarian at the Farlow Reference Library for nearly a decade, retired from her position in the Environment and Public Policy Program in the Department of Earth and Planetary Sciences at Harvard University in June of this year. Her publication on *Wild and Exotic Mushrooms*, available through the Farlow, continues to be in demand.

Amanuensis extarodinaire, Farlow *gardien*, of its staff, its visitors and the Friends of the Farlow, and exceptional *chef de cuisine des champignons*, **Carolyn Hesterberg** has moved from the Farlow after more than a decade to the mountains of northern Vermont, to which she has more-or-less commuted from Cambridge for years.

Benito Tan, who for the past decade has been the resident bryologist at the Farlow and served as a strong and dynamic interface with botanists in the Far East, has taken a faculty position near the geographical epicenter of his scholarly interests. This fall Ben assumed responsibilities as a Senior Lecturer in the School of Biological Sciences, Faculty of Science at the National University of Singapore. From this position he continues to pursue his studies in Malesian and East Asian moss systematics and biogeography and Malesian rainforest conversation.

For the past year **Karen Hansen** has been a graduate student in Don Pfister's laboratory

probing the molecular aspects of the pan-tropical genus *Phillipsia* (Pezizales). She has now returned to her native Denmark to enter a doctoral program focused still in the Pezizales with Professor Thomas Laessoe at the Botanical Institute of the University of Copenhagen.

Dr. **Zhi Hong Zhong** has joined the Farlow from Beijing to work with Don Pfister on discomycetes.

Orson K. Miller, Jr., Professor of Botany and Curator of Fungi at Virginia Polytechnic Institute and State University, lectured on "Mycorrhizal Higher Fungi" at the 1997 Annual Meeting of the Friends of the Farlow Saturday afternoon, November 1st. Dr. Miller and his wife Hope are well known participants in European and North American fungal forays and the authors of several books on mushrooms and other fungi of North America.

David Hibbett, Farlow Research Associate, spent late summer in southwestern China collecting vascular plants and fungi with **Michael Donoghue**, Director of the Harvard University Herbaria. Also this fall, David with colleagues (**Elizabeth Pine & M. Donoghue** at Harvard, **Ewald & Gitta Langer** at Eberhard-Karls-Universität, Tübingen) published a comprehensive phylogenetic analysis of homobasidiomycete fungi covering 10 families of Agaricales, 18 families of Aphyllphorales, and 7 families of Gasteromycetes. As a result of sequencing the nuclear and ribosomal DNA in 81 species from these families and generating a phylogenetic tree of the species' historic relationships, they showed that although most gilled mushrooms are contained in a single clade, containing such genera as *Agaricus*, *Amanita*, *Coprinus* and *Schizophyllum*, the gilled mushroom morphology has also arisen independently at least six times within the fungi. Their work also indicated that species in groups (Hymenomycetes) with ballistatory

spore dispersal mechanisms have repeatedly lost the ability to forcibly discharge spores and given rise to a diversity of spore discharge mechanisms manifest among the Gasteromycetes, but the reverse has not occurred. Puffballs have apparently evolutionarily arisen independently at least three times: twice within a clade including *Coprinus* and *Amanita* and in a much more distant group including the Phallales, *Geastrum* and stinkhorn fungi, which despite their very different spore dispersal mechanisms are very closely related. The article appears in the *Proceedings of the National Academy of Sciences*, vol, 94, pp. 12002-12006 (1997).

Elizabeth Kneiper, FOF President, has produced an exhibit in the Cabot Science Library at Harvard on "Lichens and Monuments." The exhibit examines the role lichens play in the disfiguration and destruction of the surfaces of monuments and artwork and addresses the inherent conflict between lichen conservation and monument preservation. This two-month exhibit, which runs through the first of the new year, is the sixth consecutive annual exhibit produced and supported by the Friends of the Farlow focusing on cryptograms for the Harvard University community.

FARLOW RENOVATIONS

As result of funding from the National Science Foundation the moss herbarium in the Farlow basement has a new look and a new structure. The old storage cabinets have been removed, a new floor has been laid and a new compactor storage system has been installed. The Farlow office has also gained a new look during the year.

FOF BOOKSALE

The 1997 FOF Booksale netted \$1,430 as a result of the efforts of Phil May, Judy Warnement and Don Pfister and many contributors. Contributions for the 1998 sale are being welcomed now at the Farlow.

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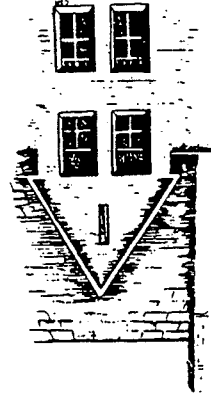
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FIRST CLASS

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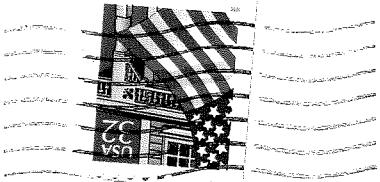
FRIENDS of the FARLOW

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FARLOW REFERENCE LIBRARY

OF CRYPTOGRAMIC



Friends of the Farlow is an international group of amateur and professional botanists concerned with supporting the programs and resources of the Farlow Reference Library and Herbarium of Cryptogamic Botany of Harvard University. Membership categories are: Associate member, \$5-25; Full member, \$25; Sponsor, \$50-100; Benefactor, \$1000 or more. To join please make your check payable to the **Friends of the Farlow** and send to the address below. The membership year runs from January 1st to December 31st. Members receive a discount on Farlow publications and services, participate in book sales, annual meetings and other events, and receive a special welcome at the Farlow. This newsletter is published twice a year, in April and October. For more information, contact the Farlow Reference Library, 20 Divinity Avenue, Cambridge, MA 02138 USA (Tel. 617-495-2369; FAX 617-495-9484).