Introduction: Seven Wonders of the Insect–Fungus World

Meredith Blackwell
Fernando E. Vega

This book first arose out of a passage in Borges, out of the laughter that shattered, as I read the passage, all the familiar landmarks of my thought—*our* thought, the thought that bears the stamp of our age and our geography—breaking up all the ordered surfaces and all the planes with which we are accustomed to tame the wild profusion of existing things, and continuing long afterwards to disturb and threaten with collapse our age-old distinction between the Same and the Other. This passage quotes a "certain Chinese encyclopaedia" in which it is written that "animals are divided into: (a) belonging to the Emperor, (b) embalmed, (c) tame, (d) sucking pigs, (e) sirens, (f) fabulous, (g) stray dogs, (h) included in the present classification, (i) frenzied, (j) innumerable, (k) drawn with a very fine camelhair brush, (l) etcetera, (m) having just broken the water pitcher, (n) that from a long way off look like flies." In the wonderment of this taxonomy, the thing we apprehend in one great leap, the thing that, by means of the fable is demonstrated as the exotic charm of another system of thought, is the limitation of our own, the stark impossibility of thinking *that*.

Michel Foucault
The Order of Things

Insects and fungi share a long history of association in the common habitats where they endure similar environmental conditions. Only relatively recently did mycologists stop killing the fungus-destroying insects they collected with their specimens and entomologists realize the fungal influence on insects. Prompted by an interest in understanding the associations between the two groups of unrelated organisms, an opportunity for people with interests in the interactions between the insects and fungi arose. Quentin Wheeler, a proponent of cladistic analysis, hoped to find new disciples for Hennig among mycologists and hoped to encourage entomologists and mycologists to work together to understand the interactions among the speciose groups of organisms. A symposium organized by Wheeler and one of us (M.B.) was held at the Entomological Society of America, Eastern Branch, meeting at Syracuse and then at Ithaca, New York, in 1981. An edited book was an outcome of the gathering (Wheeler and Blackwell 1984). Some people only noticed the book when it hit the remainder tables, and oddly enough a single—although five star—Amazon.com review, from "a reader from Ithaca, NY USA" suggests, "This is an excellent book about the relationships between fungus and insects. It shows how cladistics is the ultimate method to codify biological information into a framework common to all Biology." It is encouraging that some of the chapters have been cited in this volume. In fact, a cluster of edited volumes on a similar topic published over a 10-year period more than 20 years ago indicates that there was intense interest in the interactions of these organisms (Batra 1979; Pirozynski and Hawksworth 1988; Schwemmler and Gassner 1989; Wilding et al. 1989). This is, by complete coincidence, the 20th anniversary of the Wheeler and Blackwell volume that was slightly before its time, and the many advances in the study of the insect—fungal associations call for another look at these associations.

Foucault Made a Distinction between "the Same and the Other.". . . Twenty Years Later, It Is Not the "Same."

Over the intervening 20 years cladistics has become a way of life to systematists and other biologists. Entomologists and, especially, mycologists, who previously had had few characters to analyze, are now collecting and analyzing molecular data. Over the last 20 years the encounters between entomologists and mycologists have increased, and to some extent teams of these scientists work together. Several new scientists have been trained as symbiologists.

In late 2002, one of us (F.E.V.) suggested that the time had come for a new book on insect–fungus associations. The present volume is different in content from the range of topics covered two decades ago, but that is not the major difference. The revolution has come with our ability to collect genetically based characters, DNA sequences, and other molecular markers, for use in phylogenetic analysis, for identification, and for population markers. No longer do we need classifications as that of Borges' "encyclopaedia" with animals divided into artificial categories such as belonging to the Emperor, embalmed, or that from a long way off look like flies. We can distinguish a fly from a wasp or other fly-mimic with a convergent morphology. Other difficult tasks are possible, such as distinguishing among species of *Ceratocystis* and those of *Ophiostoma*, both of which have convergent perithecial morphologies selected for success in insect-associated spore dispersal. Not only can these fungi be distinguished, but a measure of their vast genetic difference that reflects their present taxonomy is also possible. As you read many of the chapters in this volume, consider what it was like not so long ago when the organisms could not be identified or their taxonomic position established. Insect–fungus research of only a few years ago often was done in ignorance of the identity of the fungus, let alone with population-level information. Even estimated dates of associations between insects and fungi and rates of evolution during establishment of symbiotic associations can be attempted, albeit sometimes with controversy, using molecular information and grounded by the fossil record (Berbee and Taylor 1993, 2001; Lutzoni and Pagel 1997; Blackwell 2000; Heckman et al. 2001). Another recently published book (Bourtzis and Miller 2003) emphasizes insect symbioses, including some involving fungi, and perhaps we are at the front end of another cycle of volumes on insect–microbial interactions.

In this volume, the types of associations among insects and fungi are divided into two groups: interactions in which fungi act against insects and those in which fungi form mutualistic associations with insects. The division is artificial and emphasizes the fact that we know more about the effect of the fungus on the insect, but with the molecular markers at hand, we are beginning to make progress toward understanding the direct benefits to the fungus. We like to think of the interactions discussed here as the wonders of the insect–fungal association world, contrived to number seven, as described below.

First we present a section on fungi acting against insects, including discussions of parasitism. Two of the most important necrotrophic parasites (1) are important for their insect control potential in a world that becomes increasingly polluted, especially in agricultural systems. Stephen A. Rehner, Michael J. Bidochka, and Cherrie L. Small discuss *Beauveria* and *Metarhizium*, asexual ascomycetes that kill a variety of insect hosts. The use of molecular markers has advanced the field, so a better understanding of host–parasite interactions is possible. Several necrotrophic interactions that are exciting topics for research include the complexity of multipartite interactions. Michael J. Furlong and Judith K. Pell report on interactions among three groups of organisms, insect parasitoids, predators, and entomopathogenic fungi, and the insects they attack. Other complex interactions involve fungi that are hidden away within the leaves of plants. A possible beneficial role for endophytes (2) in the broad-leafed plants they inhabit without symptoms has been suggested for many years. Elizabeth Arnold and Leslie C. Lewis outline the distribution of such fungi within plants and propose a role for at least one of them, *Beauveria bassiana*.

Analysis of molecular characters helps us discover what a fungus is. Slime molds and water molds are excluded from the kingdom Fungi, but several groups previously considered as protists (e.g., *Pneumocystis* and members of the "DRIPS" phylum, including protistan fish parasites, *Dermocystidium* and *Ichthyophonus*) are now considered to be fungi. Several chapters discussed in this volume help to place parasites with reduced morphology (3), for which morphological characters did not allow them to be recognized for what they are. Naomi Fast and Patrick J. Keeling discuss the evidence that leans toward recognition of fungal roots of Microsporidia, a group of parasites of a variety of organisms including arthropods. Some evidence suggests a relationship not just to fungi, but possibly to a group of necrotrophic parasites of insects. Another group that has benefited greatly from analysis of DNA sequence characters has been the Laboulbeniales. Fungal biotrophic parasites of insects are rare, except the very successful exception of the Laboulbeniomycetes. This group was once suggested as a connection between floridean red algae and ascomycetes, and also was considered as a member of three different fungal phyla. Alex Weir and Meredith Blackwell discuss the associations of these ascomycetes with certain arthropods and assess what phylogenetic analysis tells us about these uncultivable organisms. Certain Laboulbeniomycetes provide examples of complex methods of spore dispersal by arthropods (4).

An area of insect–fungus interactions that has prospered from the use of molecular techniques is that of farming mutualisms (5). These highly developed associations occur among different groups of insects, including one in the New World and another in the Old World. Ted R. Schultz, Ulrich G. Mueller, Cameron R. Currie, and Stephen A. Rehner make use of molecular techniques to develop a new body of symbiotic theory relating to attine ants, the two unrelated basidiomycetes that they cultivate, and a parasitic fungus controlled by the antibiotics of an associated bacterium. In this volume, they compare agriculture in humans and ants and arrive at new ideas concerning the benefit accrued to the organisms involved in the interaction. Phylogenetic analyses have enlightened us about the associations between the Old World fungus-growing termites and their fungal crop. Duur K. Aanen and Jacobus J. Boomsma provide evidence that the termite–basidiomycete association, unlike that of the ants and fungi, arose once. Their work traces the migrations that the termites and fungi made together.

Certain bark and ambrosia beetles also rely on fungi as a sole source of food; although they disperse fungi, they do not actively farm them in the manner of attine ants and termites. Mycophagy (6) occurs among some bark beetles and both ascomycetes and a few basidiomycetes, and Thomas C. Harrington provides insight into the ecology and evolution of fungus-feeding bark beetles and their fungal partners. His emphasis is on closely related fungal species pairs, detected by molecular markers. The fungi have different degrees of specialization with the beetles, and the pathway of evolution of mycangial associations is clarified.

Some fungi also interact with insects by providing nutritional supplements (7). Fernando E. Vega and Patrick F. Dowd emphasize the role of yeast–insect endosymbionts in aiding the digestion and detoxification of plant material ingested by insects and provide information on the basis of such interactions. Biodiversity studies have led to the discovery of an enormous variety of true yeasts (Saccharomycetes). Sung-Oui Suh and Meredith Blackwell describe the gut of beetles as a habitat for new yeasts that will increase the known number from about 800 species to almost 1000. It is suspected that these yeasts also might provide nutritional supplements for insects.

Insects involved in fungal associations include members of the Coleoptera, Diptera, Homoptera, Hymenoptera, and Isoptera, among others. The fungi involved in interactions with insects may be clustered taxonomically, as is the case for Ascomycetes in the Hypocreales (e.g., *Beauveria*, *Metarhizium*, *Fusarium*), ambrosia fungi in the genera *Ophiostoma* and *Ceratocystis* and their asexual relatives, Laboulbeniomycetes, Saccharomycetes, and the more basal Microsporidia. Other groups, however, have only occasional members (e.g., mushrooms cultivated by attine ants and termites) in such associations. The 11 chapters included in this volume, however, are only a beginning, and there are certain to be many more than seven wonders to observe in the study of insect—fungus associations.

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Edited by
Fernando E. Vega
Meredith Blackwell

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