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Why Are There So Many Different Kinds of Mushrooms?

David S. Hibbett

Mushrooms come in an almost unimaginably diverse array of morphologies, from robust polypores to ephemeral coral fungi. In my research, I have sought to understand how the various forms of basidiomycetes have come to exist — that is, how they have evolved. In this essay, I briefly recount the development of basidiomycete systematics and what we have learned about the pattern and tempo of morphological evolution in mushrooms.

My work uses techniques of molecular biology but addresses classical questions of evolution: What are the groups, and how are they related to each other? Are some groups more successful (in evolutionary terms) than others — and if so, why? Do new forms evolve rapidly or gradually? Are there constraints on the evolution of new forms?

These questions are not new, nor have they been ignored by mycologists. As early as the turn of the 20th century, mycologists studying microscopic anatomical features began to challenge the traditional groupings that had been based solely on outward form. For example, in the 19th century the gilled mushroom, *Lentinellus*, was grouped with all other gilled mushrooms in the family Agaricaceae, but it was later observed that the spores of *Lentinellus* bear a strong resemblance to those of the toothed fungus, *Auriscalpium*, and the coral fungus, *Clavicorona*. (In all three, the spores are elliptical, white in deposit, and have minute ornamentations that turn blue in iodine solution.) *Lentinellus*, *Auriscalpium*, and *Clavicorona* were once placed in three different families, but today it is generally accepted that they are closely related.

Anatomical characters have revealed relationships among many outwardly dissimilar groups of fungi, but there have been some taxa whose taxonomic placements could not be solved even using anatomy. Chief among these are the gasteromycetes, which include fungi such as puffballs, bird's nest fungi, and stinkhorns that produce their spores internally, rather than on exposed structures like gills, teeth, or pores. In both anatomical and macroscopic form, gasteromycetes have been highly modified through evolution, and they bear scant resemblance to any other basidiomycetes.

Thankfully for students of fungal phylogeny, a vast new source of taxonomic characters became accessible in the late

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1980s. The use of sequences of DNA, RNA, and proteins in systematics had been established in the 1960s, but it was not until 1988 that polymerase chain reaction (PCR) "amplification" made obtaining the new molecular data routine. The power of PCR is that it enables molecular biologists to selectively isolate a single gene from among the millions of base pairs of DNA in a fungal genome. (For example, the genome of baker's yeast, *Saccharromyces cerevisiae*, is about 12,052,000 base pairs.) Prior to PCR, laborious cloning methods were used to sift through the genome in search of target genes.

The methodological advances in DNA technology were coupled with (and in part drove) theoretical advances in the construction and evaluation of phylogenetic trees, which depict hypotheses regarding the pattern of ancestor-descendant relations that ultimately link all species. Simultaneously, improvements in the performance of desktop computers enabled researchers to apply the newly developed algorithms to the rapidly accumulating data. The stage was set for an explosion of knowledge regarding fungal phylogeny, which continues unabated today.

Not surprisingly, gasteromycetes were among the first targets of molecular phylogenetic studies. One classic early study in basidiomycete molecular phylogenetics was that of Thomas Bruns and colleagues, who examined relationships of the false truffle *Rhizopogon*, which produces underground, tuber-like fruiting bodies, and the mushroom genus *Suillus*. The work of Bruns et al. confirmed what had been suspected for some time based on spore morphology and pigment characters: *Rhizopogon* was derived from *Suillus*.

Later studies continued to explore the connections between morphologically disparate groups of basidiomycetes. Many hunches based on anatomy were confirmed or, more often, refined. A case in point is provided by the genus *Lentinus*, which is a group of wood-decaying gilled mushrooms. The British mycologists E. J. H. Corner and David Pegler noticed that *Lentinus* has anatomical similarities to certain polypores. Corner and Pegler agreed that *Lentinus* is closely related to polypores, but they disagreed about the polarity of evolution; that is, is *Lentinus* descended from polypores, or is it the other way around? In my Ph.D. research, with Rytas Vilgalys, I generated DNA sequence data which showed that some species of *Lentinus* are indeed derived from polypores, but also that *Lentinus* is composed of at least three distantly-related lineages.

Molecular studies have also provided a few genuine surprises. One surprise came out of work done by myself with Harvard undergraduate Elizabeth Pine (and confirmed in independent analyses by Joseph Spatafora and colleagues), which suggested that the coral fungus *Ramaria* is closely related to the gasteromycetous stinkhorns and earthstars (a kind of puffball). Along with results of other studies, this work contributed to a general picture of fungal morphological evolution that featured rampant convergence and parallelism.

Molecular phylogenetic trees not only show patterns of relationships, they can also provide estimates of the timing of historical divergences. This process, called molecular clock analysis, involves estimating the length of the branches in a phylogenetic tree, which is measured in terms of the number of mutations in DNA that are inferred to have accumulated along the branch. Because mutations are thought to occur at a roughly constant rate, the length of the branches is proportional to their duration in time.

Using this method, Bruns et al. made crude estimates of the rate of morphological evolution associated with the derivation of *Rhizopogon* from *Suillus*. Surprisingly, they found that the length of the branch leading from *Suillus* to *Rhizopogon* was very short compared to other branches in the tree. They therefore concluded that the evolution of *Rhizopogon* was associated with a sudden acceleration in the rate of morphological evolution.

Several other pieces of evidence suggested that morphologies of basidiomycetes could evolve rapidly. Work initiated by Rosinski and Robinson on a gasteromycete-like form of the gilled mushroom *Lentinus tigrinus* suggested that dramatic shifts in mushroom morphology could result from one or a few mutations of large effect.

In addition, numerous developmental studies showed that radically different morphologies could be produced by the same species under different environmental conditions. Most notably, Orson Miller showed that the gilled mushroom *Lentinellus* could produce coralloid fruiting bodies, resembling those of its relative *Clavicorona*, when grown at low temperature.

To recap, by the mid 1990s numerous molecular phylogenetic studies had shown close relationships among dissimilar taxa, developmental studies had demonstrated plasticity of form, and the work by Rosinski and Robinson on *Lentinus tigrinus* had suggested that large shifts in form could have simple genetic bases.

Like many mycologists, I was convinced that the form of basidiomycete fruiting bodies is evolutionarily labile. Consequently, I had little faith that groupings based on morphology alone could reflect evolutionary relationships. I still believe that fungal morphology has undergone extensive convergence and parallelism, but a brief foray into paleomycology convinced me that fungal form is not entirely unconstrained.

In 1995, David Grimaldi, a paleoentomologist at the American Museum of Natural History, contacted Michael Donoghue and me to ask if we were interested in examining a recently discovered fossil mushroom in Atlantic Coastal Plain amber from New Jersey. Atlantic Coastal Plain amber dates from the mid-Cretaceous period, about 90 million years ago. When Grimaldi called us, the oldest confirmed fossil mushroom was about 30 million years old. Needless to say, we were soon in Grimaldi's lab examining the "new" fossil. Looking upon that tiny mushroom for the first time was a breathtaking experience. Not only was it clearly a basidiomycete, it was strikingly similar to the extant genera *Marasmiellus* or *Marasmius*, which are common decayers of leaf litter in forests. We named the fossil *Archaeomarasmius*.

The discovery of *Archaeomarasmius* called for a revision of my views on fungal morphological evolution. At first glance, the fossil evidence and the molecular and developmental data seemed to be irreconcilable; one suggested that forms have changed slowly if at all over tens of millions of years, whereas the other suggested that rapid shifts in form have occurred repeatedly and easily. The resolution of this apparent paradox, I believe, involves the role of natural selection in the maintenance of form. Clearly, the morphologies of basidiomycete fruiting bodies can and have undergone repeated, rapid evolution (only a few cases have been cited here).

But *Archaeomarasmius* indicates that in some lineages there has been little change over great periods of time. Presumably, novel forms arise constantly in all lineages, but it may be that so-called stabilizing natural selection usually eliminates deviant morphologies. I say "usually" because it is obvious that not all the deviants have been purged (or else our world would not be graced by stinkhorns).

The challenge, therefore, for those of us who are interested in the causes of morphological diversity is to understand the circumstances that promote the survival of novel forms, as well as the genetic and developmental mechanisms by which they arise. The most productive question may not be "why are there so many kinds of mushrooms?" but "why aren't there more?"

For the truly interested, a list of references to this essay is available from DSH.

Tuckerman Award to LaGreca

The American Bryological and Lichenological Society has recognized Scott LaGreca with the Edward Tuckerman Award for the best paper in lichenology published in the 1999 volume of their journal, The Bryologist. Scott's paper, "A phylogenetic evaluation of the *Ramalina americana* chemotype complex based on rDNA ITS sequence data," appeared in volume 102, pages 602-618.

Congratulations, Scott!

Contributions Come in Many Forms...

Judy Warnement

Members of the Friends of the Farlow have always generously supported the Farlow Library. The library has benefited from funds made available to process archival collections, to aid in library renovations, and to purchase materials.

Another major contribution Friends can make is to let us know when new books or journals should be added to shelves of the Farlow.

In recent years some very active FOF lichenologists have alerted us to several serials of interest that are now available in the Library. Titles from central Europe include *Aktuelle Lichenologische Mitteilungen der Bryologisch-Lichenologischen Arbeitsgemeinschaft fur Mitteleuropa* published at the University of Essen, Germany; *Fritschiana* from the University of Graz (Austria) Institute for Botany; and *Bryonora: Zpravodaj Bryologicko-Lichenologické Sekce ÇBS* covering bryophytes and lichens in the Czech Republic and Slovakia.

Another new European title is *Bulletin d'Informations de l'Association Française de Lichénologie* published in Paris by the Society. Lichens from "down under" are covered in the Australasian Lichen Society's semi-annual journal, *Australasian Lichenology*. Another fairly new title from Sweden's Umea University is *Myconet*. Some of the published article also appear on their web site: www.umu.se/myconet/gamla/Myconet.html.

Web access to journals is increasing at a frenzied pace. The terms and costs to access these resources are as diverse as the publishers who provide them. Free resources are available from the Farlow's "Cryptogamic Links" page: www.herbaria.harvard.edu/Libraries/cryptogamic.html. Titles where fees and university site licenses have been negotiated will appear in the HOLLIS list of electronic journals. Full text access to *The Lichenologist* and *Fungal Genetics and Biology* is now available via HOLLIS to Harvard I.D. holders.

We hope you will visit the Farlow Library to try all of these new resources, to share your favorite sites with us, and to help us continue to make the Farlow Reference Library of Cryptogamic Botany the best collection of its kind in the world. Please send your comments and suggestions to: warnemen@oeb.harvard.edu.

FOF Book Sale in Progress

Don't forget the October 30 deadline for returning your book order. Where else will you find these cryptogamic gems?

FOF Annual Meeting

The Annual Meeting will be held on **Saturday, November 4** with the Business Meeting at 3:30 PM and a Reception to follow at 5:00 PM in the Farlow Reading Room. Dr. Peter Siver of Connecticut College will speak on "Elucidating Lake Histories Using Algal Microfossil Remains."

News from the Farlow

Scott LaGreca

The Farlow was well represented at the summer meeting of the Mycological Society of America in Burlington, VT. **Doug Greene** presented work done with **H. Thorsten Lumbsch** of Essen, Germany, and **Scott LaGreca** on the systematics of the *Lecanora symmicta* complex in New England. **Kris Peterson** and **Zhihong Zhong** presented posters on the discomycete genera *Cyttaria* and *Leotia*, respectively, and **Rick Weinstein** gave a talk on the tropical discomycete *Cookeina*.

The Bartram moss integration/renovation project continues. Through the summer **Eileen Adler**, Curatorial Assistant, was assisted by two part-time undergraduate Curatorial Aides, **Nina Mukhopadhyay** and **Micaela Chatman**, as well as part-time Curatorial Assistant **Jude Mulle**. This fall Eileen took time out from her busy schedule for her Chicago wedding to Jack Wozek.

As part of the ongoing lichen herbarium reorganization, a *Cladonia* Determination Workshop was held in the Farlow in late July. Eight FOF lichenologists, including **Jim Hinds** from Maine, identified a third of the Farlow's undetermined *Cladonia* holdings. We hope to hold another similar Workshop in the fall. If you would like to participate, please contact: **slagreca@oeb.harvard.edu**.

During the Cummings Foray this year, the lichenologists present discovered a large population of the rare European introduction, *Lecanora conizaeoides*, on cedars in the bog. This lichen has been reported only a handful of times in North America and just once before in the Boston area, this by **Elizabeth Kneiper** and **Martha Sherwood** over 20 years ago. A short paper is in progress.

Lichenologist **Dobri Ivanov**, Director of the Botanic Garden, Varna, Bulgaria, continued his visits to the Farlow through the summer. He provided much help in updating names in the lichen herbarium.

Sam Hammer, Elisabeth Lay and **Scott LaGreca** attended the fourth meeting of the International Association of Lichenologists in Barcelona, Spain in September. Scott gave a talk on the *Lecanora symmicta* complex, and Sam spoke about morphology in *Cladonia*.

Teresa Iturriaga (Universidad Simon Bolivar, Venezuela) visited the Farlow in August to finish a project with **Rick Weinstein** and **Don Pfister** on the systematics of *Cookeina*.

Rick Weinstein left the Farlow in August to pursue a teaching position at the University of Tennessee, Knoxville. He will be greatly missed, both professionally and personally.

Don Pfister taught an ascomycete course this summer at the Humboldt Biological Station (formerly Eagle Hill). Several FOF members attended.

Anyone interested in forming a bryophyte study group is asked to contact **Scott LaGreca**, who attended **Norton Miller**'s class on "Mosses, Liverworts, and Sphagnum Mosses" this summer at Eagle Hill.

Margaret Soulman has been hired as a part-time Curatorial Aide to help integrate the New England Botanical Club's cryptogam collections (mostly mosses and lichens) with the general Farlow collections. She will assist **Anna Reid**, curator of the NEBC cryptogams.

FOF Exhibit

Lisa DeCesare deserves thanks for this year's FOF exhibit at the Cabot Science Library. "A Wreath to the Memory of Dr. Farlow:The Creation of *Icones Farlowianae* 1889-1930" will be on display from October 18 through December 1, 2000. The exhibit traces the long and complex journey that resulted in one of the finest references ever published on fungi native to the Northeast. An online version will also be available on the FOF website.