A Mycological Florilegium of the Phylogenetic Literature: *Looks Deceive*

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We saw an upsurge in the number of articles on big broad fungal phylogenies published in 2006 and 2007. A landmark was the completion of the first phase of the project to assemble the branches of the fungal tree of life (AFTOL). This involved researchers from many different universities who collaborated to give an overall picture of the origins and evolution of the fungi, based on sequences of 5-7 different genes and on morphological and ultrastructural characters.

Most of the findings of this huge project were published in *Mycologia* 98(6), which saw the light in April 2007; the 24 articles give a complete overview of the kingdom Fungi and show a renovated landscape. The new layout is especially evident in the gilled mushroom groups but everything from Chytrids to Zygomycetes and Ascomycetes gets its place and time. In-depth papers on different groups and overview papers on higher-level changes, estimates of the ages of the different branches are presented, and all papers are illustrated with photos of representative species. The work on the *Agaricales* – the "gilled" mushrooms – goes much farther than the two shockingly new publications in 2000 and 2002 (Moncalvo et al., 2000 and 2002) where we saw 117 clades instead of the familiar handful of families. With more genes and a wide sampling several well-supported groups are now apparent. Another set of articles just got published in the September 2007 issue of the British journal *Mycological Research*; here you can find several interesting papers on truffles and other Ascomycetes, but also on fruitbody shapes and especially on crusts.

Of course there are still many unresolved issues, and a lot of work has to be done to fill in the gaps and cracks of our knowledge. Some of that research is in progress and will be discussed in the second part of this overview.

As it is impossible to sum up all the new findings, I'll focus on a few aspects and groups: what are fungi and how did they originate; *Wallemia*; what happened to the *Tricholomataceae* and where do the club fungi fit in?

Featured Reports

Mycologia 98 (6). ("2006") 2007. A phylogeny for kingdom Fungi. Deep Hypha issue. edited by J.W. Spatafora, K.W. Hughes & M. Blackwell. 24 articles. This special issue of *Mycologia* can be ordered for $40 from Allen Press (1-800-627-0326).

Mycological Research 111 (9). 2007. New bottles for old wine. 9 articles.

James, T.Y. et 69 al., 2006. Reconstructing the early evolution of Fungi using a six-gene phylogeny. *Nature* 443: 818–22.

Matheny, P. B., J. A. Gossmann, T. K. A. Kumar & D. S. Hibbett, 2007. Resolving the phylogenetic position of the *Wallemiomycetes*: an enigmatic major lineage of *Basidiomycota*. *Canadian Journal of Botany* 84: 1794–1805.

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Origins and roots

Surprisingly enough, there was no clear idea about what groups are fungi and what ancestral fungi looked like before James et al. constructed the phylogenies published in *Nature*. All life forms started out in water and when they conquered the land many different groups and shapes arose. All those leafy flowering plants, for instance, derived from organisms that were just one cell big and swam through the water with little flagella. Fungal forebears also lived in the water, had spores with a flagellum and developed different ways of spore dispersal as soon as they came on land. These ranged from the complicated basidia and asci of the mushrooms and cup fungi to the specialized ways the endoparasitic microsporidia procreate. Unlike earlier ideas, the Chytridiomycetes (often in the news because they cause a disease in frogs and other amphibians), do not form a monophyletic group; this is an ancient group of fungi, that still has spores with a flagellum. Losing that flagellum has happened in several unrelated groups and at different times during the fungal past. The vast majority of fungi belong to the derived terrestrial groups of the Basidiomycetes and Ascomycetes.

Basidiomycetes

There are five main groups within the Basidiomycetes – the one we recognize as "mushrooms" (everything from gilled mushrooms to crusts, clubs, puffballs—now collectively called the *Agaricomycotina*), the smut fungi (*Ustilaginomycotina*), the rust fungi (*Pucciniomycotina*), the *Entorrhizomycetidae*, and the *Wallemiomycetes*. Never heard of *Wallemia* before? Do read Kathy Hodge's

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blog on the appearance one morning of a fungal blob in the maple syrup on her son's waffle; *Wallemia*! This is a genus with only three species that grow in low-water environments, such as salterns, dried fruits and nuts, and salted meat (and maple syrup). A sexual stage had never been found for these species, and before the present paper by Matheny et al., *Wallemia* was considered an ascomycete; now it is unequivocally shown that it fits in the Basidios, though where exactly is less clear.

White-spored and not a Lepiota, nor an Amanita

The family *Tricholomataceae* harbored all the species with white and light spores that did not have the good characters of *Lepiota* s.l. (lamellae free from stipe; spores dextrinoid), or *Amanita* and *Limacella* (lamella trama divergent). Waxcaps (*Hygrocybe* and *Hygrophorus*) were included in the *Tricholomataceae* by some authors. But there was not a unifying concept for the family and it was negatively defined, rather for what it was not, than for what it was. It was a typical example of a garbage bin family – everything that did not fit elsewhere was thrown into it.

There had been attempts to split it up into several smaller families, and some well defined units were split off, such as the *Termitomycetaceae*, the species that are cultivated by African and Asian termites. But an amorphous mass of species remained and the characters on which these splits were executed were often considered subjective.

Now, with objective character evaluation, the family has been divided in smaller units. While some members have moved far away from the original concept, some unexpected members have joined the new clubs.

To get a good picture, we take one step back and look at the *Agaricales* (most gilled mushrooms). This order is sister to the *Boletales* (boletes and relatives) and the *Atheliales*, and the three of them together are the closest relatives of *Russulales* (*Russula* and *Lactarius* and their relatives). The *Agaricales* as a whole is now subdivided into six groups (clades, in jargon), which are provisionally named, each after one genus: the Agaricoid clade, the Tricholomatoid clade, the Marasmioid clade, the Hygrophoroid clade, the Pluteoid clade, and the Plicutaropsidoid clade. Some clades contain several families; for example, the Pluteoid clade consists of *Pluteaceae, Amanitaceae, Pleurotaceae* and *Limnoperdaceae*.

Members of the old *Tricholomataceae* can now be found in the orders *Hymenochaetales*, *Boletales*, and all six clades of the *Agaricales:*

- *Tricholomataceae* which moved to the *Hymenochaetales* are all small moss inhabiting species which look like *Omphalina*: *Rickenella*, *Contumyces, Loreleia* (see also Redhead et al., 2002).
- The white-spored *Hygrophoropsis* was already in the bolete-related *Paxillus* family in Singer's treatments (1986), and that position has been confirmed.
- *Laccaria* forms with its truffle-like sister *Hydnangium* the *Hydnangiaceae* in the Agaricoid clade. *Cystoderma* also found its way into this clade, where most species have colored spores.
- The family *Tricholomataceae* in the Tricholomatoid clade is now restricted to *Tricholoma* and some members of *Clitocybe* and *Lepista*. Other members of this clade are the *Entolomataceae*, *Lyophyllaceae*, *Mycenaceae* and *Catathelasma*; the latter three harbor ex-*Tricholomataceae* members.
- The Marasmioid clade is made up of species with fruitbody shapes ranging from little cups (cyphelloid) to gilled mushrooms, but with some crusts and polypores thrown in as well. The purple smelly stereum-like crust *Chondrostereum purpureum*, and the juicy beefsteak fungus, *Fistulina hepatica*, find their home here, side by side with *Marasmius*.
- The Hygrophoroid clade is determined by the *Hygrophoraceae*, but *Pterulaceae / Typhulaceae* are its sister with *Xeromphalina*, *Typhula*, *Phyllotopsis*, and *Sarcomyxa (Panellus) serotina*.
- Oyster mushrooms and their relatives, the genera *Pleurotus*, *Hohenbuehelia* (both nematode trappers) plus *Resupinatus,* are in the *Pleurotaceae* in the Pluteoid clade.
- *Hygrotrama* (*Camarophyllopsis*), previously thought to be a relative of *Hygrocybe*, found its way into the Plicutaropsidoid clade with *Clavaria, Clavulinopsis* and of course *Plicutaropsis crispa*.
- The pink-spored *Macrocystidia*, the cucumber fungus, is on its own branch, separate from all six clades.

Fortunately not all families have undergone such drastic clipping: *Entolomataceae* are still intact with *Rhodocybe, Clitopilus* and *Entoloma* s.l., united by their unique spore architecture; *Amanitaceae* with *Amanita* and *Limacella* also survived the molecular age. The *Agaricaceae* on the other hand have been expanded greatly; the white-spored *Lepiotaceae* were there already on account of their morphology (Singer, 1986), but molecular work also put *Coprinus* s.str. and *Montagnea*, *Lycoperdaceae*, *Tulostomataceae,* and *Podaxis* within its pales. Now this family harbors more different spore colors—white, yellow, green, brown, blue, black, you name it—than any other mushroom family.

I find it fascinating to see these new arrangements of familiar species and try to look at them with fresh eyes searching for morphological characters they might have in common. For field guides and keys, artificial groups will continue to be used, but I trust that the real position of species will also get its place in popular books and Web sites.

Clubs

The story of the club fungi mirrors that of the *Tricholomataceae* and many other artificial groups: they are now scattered in families and orders with different evolutionary histories. *Clavaria*,

Clavulinopsis, *Ramariopsis*, *Pterula* and *Mucronella*, *Typhula* and *Macrotyphula* are in the *Agaricales* (but the first five in the *Clavariaceae* and the latter two in the *Typhulaceae*), *Clavariadelphus* is in the *Gomphales*, but the ectomycorrhizal *Clavulina* and the lichenized *Multiclavula* are in the *Cantharellales*. From these order names you can tell that pig's ears (*Gomphus*) and chanterelles (*Cantharellus*) are not particularly close either. The beautiful purple club fungus, *Clavaria purpurea*, does not follow the rest of the *Clavarias* into the *Agaricales* but goes with those small *Omphalina*-like agarics into the *Hymenochaetales*. The new genus *Alloclavaria* has been erected for this species. The nicely branching *Artomyces* (*Clavicorona*) *pyxidata* is a member of the *Russulales*, and a sister to *Lentinellus*; which brings us to *Ramaria* itself in the *Gomphales* with the aforementioned *Gomphus*.

Shape of the fruitbodies does not unify species, nor does life style. Truffles, crusts and puffballs all occur in many different groups. The shift to an ectomycorrhizal lifestyle from a saprotrophic or parasitic ancestor has happened multiple times throughout the *Agaricomycotina*. Unrelated *Pterula* and *Leucoagaricus/Leucocoprinus* species were taken in cultivation by attine ants, wheras all *Termitomyces* species are grown by termites. Crusts can be wood rotters or play a big role in the ectomycorrhizal community. Nothing is certain, but everything certainly fascinating.

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Letter to the Editor, continued from page 2

In the first part he takes to task the way we have been identifying and naming fungi, stating that it has been "ludicrous . . . largely unscientific . . . flimsy hypothesis . . . to arrange taxa on the basis of untheorized morphological findings."

Some of the above might possibly be true. BUT, it works for me in teaching basic and intermediate fungi courses, it works for me when I get an unknown in a "Poison Call," and it works for many others.

We all know that the initial division of Basidiomycetes into fungi with white and yellow spores, to pink, to various shades of brown or black spores is *completely artificial* but it helps us to begin to subdivide a tremendous number of macrofungi. You know the rest of the drill, e.g. gill attachment, presence or lack of veils, hairs, scales, pruina, etc. to microscopic characteristics all of which I have NOT assumed to give me an evolutionary history but all of which give me a fighting chance to ID an unknown mushroom. He notes that "taxonomic differences have been erected on the basis of whether the ring is 'persistent' or not, and on differences in spore lengths—without even a passing guess as to how these features might relate to natural selection . . . etc."

I recently was able to ID a poisonous *Paxillus* and differentiate it from a non-poisonous one on the basic of spore length. I was not concerned about "natural selection;" I was concerned if this was a toxic mushroom. And that is what I want to do. So, I don't care if it is unscientific or even ludicrous. It works. What doesn't work for me however, and for many other folks, is when someone comes to a foray table and picks up *Coprinus comatus,* and announces "No, this doesn't belong here; it should be over with the Lepiotas."

If he/she wants to give a lecture on the latest thinking of how fungi have evolved and what the latest DNA says who is now related to whom, then that would be interesting. And I go to such lectures when possible. But again, this does not help at the ID level. And until we all have little pocket DNA machines to scan over our fungi, I think the present ARTIFICIAL (non-scientific) system works.

Actually I think that Michael's Kuo's Web site is great and wonder if he really doesn't agree with me and was just trying to stir things up! The second part of his article gives good suggestions as to how we amateurs can help the science of fungi. I agree.

Respectfully,

Lawrence M. Leonard, Falmouth, Maine

[*The Kuo paper referred to above is posted on the FUNGI Web site in the archives. It was published in Vol. 17(1) of NAMA's journal* McIlvainea. *This was a very important article of benefit to mycologists, amateur and professional alike, and I urge everyone to read it. Michael Kuo is the creator of the tremendous MushroomExpert.com Web site. Laurie Leonard is a medical doctor, expert microscopist, and mycological educator.—Ed.*]