

A Mycological Florilegium: Literature of 2001–2005

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KEEPING TRACK of all the new developments that appear in the mycological literature is not easy these days. It demands time, access to journals, and attention to spot what is relevant. At least access has become easier. Now everybody with a computer and an internet connection can see the abstracts of most research papers for FREE! Many journals also put the full text of articles on line, though you may need to be a subscriber to read them. Finding articles of interest can still be a problem because mycologists publish in a wide array of journals. Important journals in English that specialize in mycology, especially those that publish systematic mycology, include *Mycologia*, a publication of the Mycological Society of America; *Mycological Research*, published by the British Mycological Society; *Mycotaxon*, *Mycological Progress* by the German Mycological Society, and *Mycoscience*, put out by the Mycological Society of Japan, all of which make abstracts freely available. *Mycotaxon* and *Mycological Progress* publish only a full paper version, but the other three do have the complete issues on line. However, new species and genera can appear in much more obscure places, such as *New Botany* of India which carried an article that I missed for seven years. Ecological and especially mycorrhizal research is published in a host of journals, from *Mycorrhiza* and *New Phytologist* to all kinds of ecological and forestry oriented journals. Phylogenetic articles find a place in new journals such as *Molecular Phylogenetics and Evolution*, *Molecular Biology and Evolution*, as well as *Systematic Biology* and the *American Journal of Botany*. Occasionally *Nature* or *Science*, the “big” generalist journals, carry mycological articles.

There is also a huge number of often small local mycological journals that can be seen only on paper. And these are the ones that are most likely to have keys to species, descriptions, and other basic information so invaluable for the person who simply wants to identify those mush-

rooms! The number of such journals in Europe in particular is very high and, of course, most are not in English. Often they carry high-quality mushroom pictures, and the articles reveal how advanced field mycology is conducted collaboratively by amateurs and professionals in these countries.

The French mycological society published in 2004 one big issue of its journal *Bulletin trimestriel de la Société mycologique de France* in homage to the life of Henri Romagnesi, who died in 1999 at the age of 87; it contains 36 papers in total, with 21 new taxa, mostly from Europe, but a few from this side of the Ocean. For American readers the paper by Petersen and Hughes describing a new *Xerula* species, *X. limonispora*, is of interest. This species with its relatively pale fruitbodies, has spores which have an apical apilla (hence the Latin name), and huge capitate pleurocystidia. It has been found in Tennessee and Arkansas. Another interesting character is the fact that the spores are rough when observed with a scanning electron microscope but smooth under the normal light microscope. Halling and Mata describe a new *Boletus* species from Costa Rica (growing with oak), and Courtecuisse and Fiard treat the *Cuphophyllus* (*Camarophyllus*, *Hygrocybe*) *pratensis* complex from the Lesser Antilles and describe a new species, *C. neopratenensis*.

The Danish Mycological Society celebrated its 100th anniversary in 2005 with many festivities and a special issue of its journal *Svampe*, “Svampe i Verden”—mushrooms in the world—with articles on hazelnut trees and their fungi, ectomycorrhizas, leafcutting ants and their fungi, dry rot and *Heterobasidion annosum*, nematode killing fungi, and much more. The latest regular issue of *Svampe*, (No. 52, 2005) features the mushroom dye queens of California: Miriam Rice and Dorothy Beebee! The pictures in the journal are of outstanding quality; that alone would be reason enough to become a member. The Danish is a

little tough, but the English summaries help a lot!

For the rest of this overview of recent literature I'll focus on the phylogenetic literature with articles treating the relationships between different groups of fungi, and I will pick a few other ones. Most abstracts can be found on line. This collection is based on my personal likes and dislikes, which are as idiosyncratic as anybody else's!

Agarics

Moncalvo, Vilgalys, Redhead, Johnson, James, Aime, Hofstetter, Verduin, Larsson, Baroni, Thorn, Jacobsson, Cléménçon, and Miller. 2002. One hundred and seventeen clades of Euagarics. *Molecular Phylogenetics and Evolution* 23:357–400.

This is a real who-is-whose-sister of gilled mushrooms and a must-read for everybody interested in mushrooms. Around 700 species of gilled mushrooms plus an additional 175 others have had their DNA examined for this big “family” research project. And many surprises does it hold. Only a few of the morphology-based families can still be recognized—Amanitaceae is one of them. Most of the families have been scattered, and the genera and species are in small clusters. Garbage-can families like Tricholomataceae and the Cortinariaceae definitely do not exist any more. Agaricaceae have been expanded and now include gasteroid groups (Lycoperdaceae, Tulostomataceae, *Podaxis*) and of course *Coprinus comatus* and its secotioid relative *Montagnea*. The Lepiotas were already in this family in the opinion of some authors, and they stay there on molecular grounds. One of the big surprises for me is that *Pluteus* and *Volvariella* are torn apart—further research will show whether this is real or just an artifact of the present data. The structure of their gill trama is so similar and different from anything else that it is hard to imagine that that structure has evolved twice in the history of the gilled mushrooms. In general, we see that agarics do not necessarily have to have gills, and also that gilled mushrooms are not necessarily agarics. Some *Omphalina* and *Rickenella* species belong to the hymenochaetoid group with *Trichaptum abietinum*. *Russula* and *Lactarius* are more remote relatives to the Agarics—dubbed here “euagarics”—than boletes.

The species sampled in this research came

mainly from temperate regions, and only one gene region was used, so there will be a lot more dust blown around before the ultimate word on the relationships of our fungi has been said.

Basidiomycetes

Larsson and Larsson. 2003. Phylogenetic relationships of russuloid basidiomycetes with emphasis on aphyllorphorean taxa. *Mycologia* 95:1037–65.

Binder, Hibbett, Larsson, Larsson, Langer, and Langer. 2005. The phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi (Homobasidiomycetes). *Systematics and Biodiversity* 3 (2):113–57.

Larsson, Larsson, and Kõljalg. 2004. High phylogenetic diversity among corticioid homobasidiomycetes. *Mycological Research* 108: 983–1002.

Bodensteiner, Binder, Moncalvo, Agerer, and Hibbett. 2004. Phylogenetic relationships of cyphelloid homobasidiomycetes. *Molecular Phylogenetics and Evolution* 33:501–15.

Hibbett and Binder. 2002. Evolution of complex fruiting-body morphologies in homobasidiomycetes. *Proceedings Royal Society, London B* 269 (1504):1963–69.

Hibbett. 2004. Trends in morphological evolution in Homobasidiomycetes inferred using maximum likelihood: a comparison of binary and multistate approaches. *Systematic Biology* 53:889–903.

Some papers focus on mushrooms with a certain shape, like crusts or the little cup-shaped cyphelloids. Others try to answer broad questions such as what is the general trend in the evolutionary history of the mushroom forming basidiomycetes; do we see that gilled mushrooms always evolve from crusts; are the puffballs an evolutionary dead end, or is the simple coral really at the base of all mushrooms, as once thought? Hibbett's 2004 paper delves into these big issues, using two methods to analyze the data. It does seem that if you have evolved into a puffball and have lost the ability to actively discharge your spores, you are stuck with that; there is no way back into a differ-

ent form. Also, there seems to be an active trend toward mushrooms with caps and stalks, but it is not yet possible to say anything about the shape of the ancestor of all mushrooms.

A different big question is what morphological characters unite species which do not look alike, but which form big monophyletic groups on the basis of their gene sequences?

For the russuloids (eu-russuloids) the story is the same as for the agarics—there is a wide range of forms, and shapes, so what does unite them? What do *Russula*, *Stereum*, *Hericium*, *Lentinellus*, *Echinodontium*, *Albatrellus*, and *Auriscalpium* have in common with the crust shaped *Gloeocystidiellum* species? Most share the spores with the ornamentation that stains with a iodine medium, but the most unifying factor is the presence of hyphae and cystidia with a content that stains with sulfovanillin (the so-called gloeoplerous hyphae). It is clear from all these studies, that things that look alike may not be closely related at all, and that the phylogenetic variation in groups that look alike is enormous.

Fungal Tree

Lutzoni, Kauff, Cox, McLaughlin, Celio, Dentinger, Padamsee, Hibbett, James, Baloch, Grube, Reeb, Hofstetter, Schoch, Arnold, Miadlikowska, Spatafora, Johnson, Hambleton, Crockett, Shoemaker, Sung, Lücking, Lumbsch, O'Donnell, Binder, Diederich, Ertz, Gueidan, Hansen, Harris, Hosaka, Lim, Matheny, Nishida, Pfister, Rogers, Rossman, Schmitt, Sipman, Stone, Sugiyama, Yahr, and Vilgalys. 2004. Assembling the fungal tree of life: progress, classification, and evolution of their subcellular traits. *American Journal of Botany* 91: 1446–80.

The biggest effort to get an overall picture of all fungi is the AFTOL project, in which AFTOL stands for Assembling the Fungal Tree of Life (<http://ocid.nacse.org/research/aftol/>). Its focus is on *all* fungi, not just macrofungi, and around 1100 representative species have been selected, for each of which seven gene regions will be sequenced. Besides the huge sequencing effort, morphological characters will also be used, as appropriate. A first progress report has been pub-

lished and highlights the areas where we still have very little knowledge.

Will all this molecular research change the way we key out mushrooms? No—it is still easiest to have one key for all earthstars, in the genera *Geastrum* and *Astraeus*; although the first is related to *Gomphus* and *Phallus*, and the second is a bolete relative. But it makes mycology more interesting when you know that *Pleurotus* and *Hohenbuebelia*, now shown to be closely related, are both nematode trappers, while *Resupinatus*, which looks like a *Hohenbuebelia*, is not a carnivore and belongs in a different group.

Crepidotaceae

Aime, Vilgalys, and Miller. 2005. The Crepidotaceae (Basidiomycota, Agaricales): Phylogeny and taxonomy of the genera and revision of the family based on molecular evidence. *American Journal of Botany* 92: 74–82.

Though *Crepidotus mollis*—the Jelly Crep or Flabby Crepidotus—is conspicuous on bark of living or dead trees, the genus does not receive a lot of attention from mycologists. Sure, they are small, and brown-spored, and definitely LBMs, but as they often grow in masses, they do stand for something! Fortunately, Cathy Aime has tackled this group and studied the genera of the Crepidotaceae: *Crepidotus*, *Tubaria*, *Simocybe* and *Melanomphalia*. She tested different compositions of the family and different alliances; and her data set does not support the inclusion of *Tubaria* and of *Melanomphalia* within the family. She finds that *Melanomphalia* groups with the white-spored genera *Omphalina*, while *Tubaria* huddles together with other brown-spored small mushrooms in the genera *Phaeomarasmium* and *Flammulaster*. *Crepidotus* and *Simocybe* stay together in a new, slimmed version of the family. The placement of *Melanomphalia* with white-spored species is another example that spore color is a less important factor than overall fruitbody morphology and developmental characters. The same is true for *Chlorophyllum*, which now includes both white-spored and green-spored species. I wonder whether the pigmentation of the *Melanomphalia* spores happens late in the development of those spores, just as it does for *Chl. molybdites*.

Inocybe/Inocybaceae

Matheny, P. B. 2005. Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*, Agaricales). *Molecular Phylogenetics and Evolution* 35:1–20.

Inocybe is one of those brown-spored genera that poses lots of difficulties when you try to name a collection. I always end up with the last name of the key; and as I try to deal with clearly different species, something is lacking. So every effort to bring some light into this darkness is appreciated! Brandon Matheny tackles the whole group and combines sequence data from two protein coding genes with those of LSU (a gene region which is generally used for phylogenetic analyses). He uses very elaborate and thorough methods to analyze the data. First of all his analysis shows that these genes really give good results in unraveling relationships, and his work has found followers working on other groups, e.g. *Cortinarius*. The genus is split into five clades, forming one monophyletic group for which a rank at family level is proposed. The biggest clade is formed by species formerly placed in subgenus *Inocybe*, with thick-walled cystidia on the sides and edge of the gills, and with either gibbous spores or smooth spores—this confirms the opinions of other authors that a division of the genus based on spore characters is artificial. The *Dulcamara* group forms its own clade *Mallocybe*, also an older idea, and then there are three other clades with a small number of species, e.g. the clade of species without pleurocystidia, such as *I. adaequata* and *I. calamistrata* (formerly subgenus *Inosperma*). Plans to recognize all the clades at genus level are underway.

Leccinum

Den Bakker, Gravendeel, and Kuyper. 2004. An ITS phylogeny of *Leccinum* and an analysis of the evolution of minisatellite-like sequences within ITS1. *Mycologia* 96:102–18.

Den Bakker, Zuccarello, Kuyper, and Noordeloos. 2004. Evolution and host specificity in the ectomycorrhizal genus *Leccinum*. *New Phytologist* 163:201–15.

Den Bakker and Noordeloos. 2005. A revision of European species of *Leccinum* Gray and notes on extralimital species. *Persoonia* 18:511–87.

Three papers (and a fourth to be published) deal with the notoriously difficult genus *Leccinum*. American readers will regret that the emphasis is on the European species, but Henk den Bakker lays a solid basis for further research. And, now he has left the Netherlands for Ithaca, NY! Many species have been described in the genus, based on color variations in the cap and the rough scales on the stipe, and on the changes in color when the fruitbodies are cut. The first paper sets out to get a good overview of the genus as a whole, using the markers which are used in other studies, viz. ITS1 and ITS 2. But ITS1 is no guide at all—this part of the genome is absolutely unsuitable for such analyses—making *Leccinum* stand out from the other boletes and agarics. ITS2 does help sort things out, and so does a protein coding gene which is used in a second set of analyses. Most species of *Leccinum* only grow with one host tree: *Leccinum scabrum* and its close relatives are only found with birch, and *L. manzanitae* only with madrone and manzanita. *Leccinum aurantiacum*, however, is not that discriminating, and is found with *Populus* (poplars, cottonwoods, aspens etc), birch, and oak and other Fagaceae. Its ancestor was probably more picky, but somewhere along the line it became less restrictive. The genus has undergone periods of rapid speciation during or just after a switch to a new host. Thus, as soon as birch was discovered as a host tree, the mushrooms went wild, and in different areas new species arose—there are now at least nine species growing specifically with birch. But here other factors may sort the species out; some species only occur on dry sandy soils, other in marshy peaty areas. Here, also isolation during ice ages might have played a role in the speciation process.

His third paper treats the genus *Leccinum* for Europe, and 16 species are recognized, this in stark contrast with the 35 treated by French authors Lannoy and Estades ten years ago. A thorough overview of the characters, a key, descriptions, figures and photos of all species are presented.

Hawaiian Inky Caps

Keirle, Hemmes, and Desjardin. 2004. Agaricales of the Hawaiian Islands. 8. Agaricaceae: *Coprinus* and *Podaxis*; Psathyrellaceae: *Coprinopsis*, *Coprinellus* and *Parasola*. *Fungal Diversity* 15:33–124.

No escape—even on the Hawaiian islands you now can identify those inky caps! A well-illustrated guide to all 29 species of coprinoids is provided by Matt Keirle and his co-authors. Add the newest volume of the Dutch “Flora agaricina neerlandica” that treats *Coprinus* (in the old wide sense), and the mainlanders too are thoroughly covered.

Agaricus

Geml, Geiser, and Royse. 2004. Molecular evolution of *Agaricus* species based on ITS and LSU rDNA sequences. *Mycological Progress* 3: 156–76.

The genus *Agaricus* is basking in attention from many mycologists, and its phylogeny is a magnet for research. This is one such phylogenetic paper, focusing on the representatives of the temperate subgenus *Agaricus*, but with special attention to the age of it. Depending on the calibration points, the time when the genus split off from its closest relatives varies from 15 to 73 million years ago. The authors also conclude that *Gyrophragmium dunalii* and *Longula texensis* are really just secotioid *Agaricus* species, and propose the name *Agaricus aridicola* for the former and *Agaricus texensis* for the latter. They confirm the position of *Endoptychum depressum*, which had already been included in the genus *Agaricus* as *A. inapertus*.

Sphaerobolus

Geml, Davis, and Geiser. 2005. Phylogenetic analyses reveal deeply divergent species lineages in the genus *Sphaerobolus* (Phallales: Basidiomycota). *Molecular Phylogenetics and Evolution* 35:313–22.

Geml, Davis, and Geiser. 2005. Systematics of the genus *Sphaerobolus* based on molecular

and morphological data, with the description of *Sphaerobolus ingoldii* sp. nov. *Mycologia* 97: 680–94.

The artillery fungus is one of the most fascinating fungi on earth: its mini basidiocarps, a few millimeters in diameter, are able to shoot off the cannonball with spores up to six meters away! Geml and co-authors give a nice overview of the natural history of this species and have done a thorough phylogenetic analysis of mainly eastern North American collections. Besides the familiar *Sph. stellatus*, *Sph. iowensis* is also a good species. The authors discover a third species, with a smaller gleba and bigger basidiospores, known from Georgia, Michigan, Ohio, Pennsylvania and Japan; they describe it as *Sph. ingoldii*. The three species are phylogenetically quite distinct, not just differing in a few base pairs here and there. Surprisingly, *Sph. iowensis* turns out to be more common than the better known *Sph. stellatus*.

Peziza and the Pezizaceae

Hansen, Laessøe, and Pfister. 2001. Phylogenetics of the Pezizaceae, with an emphasis on *Peziza*. *Mycologia* 93:958–90.

Hansen, Laessøe, and Pfister. 2002. Phylogenetic diversity in the core group of *Peziza* inferred from ITS sequences and morphology. *Mycological Research* 106:879–902.

Hansen, LoBuglio and Pfister. 2005. Evolutionary relationships of the cup-fungus genus *Peziza* and Pezizaceae inferred from multiple nuclear genes: RPB2, β -tubulin, and LSU rDNA. *Molecular Phylogenetics and Evolution* 36:1–23.

Three exemplary and thorough papers dealing with *Peziza* and the family it belongs to, combining molecular studies with the morphology of the species and genera—that sums it up. The first two have very nice and illustrative pictures of fruitbodies and spores to recommend them. The genus *Peziza* itself is spread over eight different branches within the family, presenting the authors with the options of recognizing just one big genus *Peziza* in the family, or splitting *Peziza* up into different genera, the solution which they prefer. Just as in the basidiomycetes, hypogeous and epigeous forms share common recent ances-

tors: the desert truffle *Terfezia* is sister to *Peziza ellipsospora* and *P. saniosa*. *Peziza* in its restricted form now accommodates species like *P. arvernensis*, *P. vesiculosa* and *P. fimetaria*, while many other species will have to get new genus names. Well-known names like *P. cerea* and *P. repanda* have disappeared—the first in the synonymy of *P. varia*, the second in the garbage bin of doubtful names.

Mitrula

Wang, Binder, and Hibbett. 2005. Life history and systematics of the aquatic discomycete *Mitrula* (Helotiales, Ascomycota) based on cultural, morphological, and molecular studies. *American Journal of Botany* 92:1565–74.

The enzymes produced by the basidiomycetes that handle terrestrial decay, such as the familiar polypores, need oxygen, and this is not available underwater. Accordingly, the leaf litter and wood that end up in streams and ponds are decomposed in a different way by ascomycetes. Among them is a fascinating group of fungi, the aquatic ascomycete genus *Mitrula*, which is the topic of Wang's research. Many ascomycetes are known from water, but mainly from their non-fruitbody forming stage. They are often referred to as Ingoldian fungi, in tribute to the English mycologist Ingold, who has studied them. Most of them have branched spores that float better in water than simple round spores. The genus *Mitrula* was different because only the ascus-forming stage was known. The funny little ascocarps, which stick out of the water like brightly colored match sticks, are a delight for the eye. The authors have now discovered the a-sexual spores of *M. elegans*, which are brown-walled, two-spored and ellipsoid, and do not seem particularly well suited to an aquatic environment. The genus *Mitrula* appears to be closely related to species in the Helotiales, such as *Vibrisea*, *Cudoniella*, and *Bisporella*, but the final word has not been written on this group. There are good morphological differences between the various species, but molecular differences are very small. As the two approaches are not completely congruent, it is not yet clear how many species there are in North America, nor how to recognize them.

Lichens

Wedin, Döring, and Gilenstam. 2004. Saprotrophy and lichenization as options for the same fungal species on different substrata: environmental plasticity and fungal lifestyles in the *Stictis*–*Conotrema* complex. *New Phytologist* 164:459–65.

Yuan, Xiao, and Taylor. 2005. Lichen-like symbiosis 600 million years ago. *Science* 308: 1017–20.

One thing we knew for certain about lichens: the fungal partner of the lichen symbiosis can not live its whole life cycle without a photosynthesizing slave providing sugars to the fungus. These enslaved, encapsulated algae and cyanobacteria (formerly known as blue algae) can live without the fungi, but the fungus had to find an algal or cyanobacterial partner, the photobiont. Now we have to rethink this certainty, as it has been recently shown that the same fungal species can exist both with and without photobionts and in each case the fungus forms fruitbodies and sexual spores. The fungus was known in both these lifestyles: the surprise is in their identification. *Stictis* species were the ones without a partner, growing on branches stripped of bark while *Conotrema* was the name for a lichenized species, growing on bark. Now, there can only be one name, and this is *Stictis*, since it is the older name. If a spore of the fungus lands on bare branches they will grow as a lonely fungus, as no algal cells are found in this habitat. If a spore lands on the bark of a tree it will find an algal partner and go on as a lichen. This strategy of optional lichenization has many advantages in fast changing ecosystems experiencing disturbance or succession.

The second paper shows lots of pictures of fossilized structures from marine environments in China, which could well be fungal hyphae and clusters of round cells grouped together. If these are really lichens, fungi did live in symbiosis with other organisms long before the colonization of land by plants. It is thought that the transition from a marine towards a terrestrial lifestyle for plants was made possible by the symbiosis with fungi. Now, that it has been shown that fungi were already trained in cooperative relationships, this is even more plausible.

Insects and Fungi

Munkacsi, Pan, Villesen, Mueller, Blackwell, and McLaughlin. 2004. Convergent coevolution in the domestication of coral mushrooms by fungus-growing ants. *Proceedings of the Royal Society, London B*. 271:1777–82.

Villesen, Mueller, Schultz, Adams and Bouck. 2004. Evolution of ant-cultivar specialization and cultivar switching in *Apterostigma* fungus-growing ants. *Evolution* 58:2252–65.

The leaf-cutting ants and all other members of the Attinae—the attine ants for short—grow *Leucocoprinus* and *Leucoagaricus* species as their sole food source. All Attinae? No, some members of the genus *Apterostigma*, Central and South American ants, have found another food source. Two papers describe how these ants cultivate fungi in the genus *Pterula*, small hanging *Clavaria*-like fruitbodies. Within this group, two sub-clades are cultivated, and the fungi in the ants' nests look totally different. The different ant species are specialized on one of the sub-clades, though within that group they may grow different species. How

in the first place the ants started to cultivate these *Pterulas* is a source of speculation, and how they recognized them in the second place is another question mark.

Aanen and Eggleton. 2005. Fungus-growing termites originated in African rain forest. *Current Biology* 15:851–55.

Termites which use fungi for their main food source do not occur in the new world, but the fruitbodies of these fungi in the genus *Termitomyces* are well-known as they are among the biggest on earth. The fungus growers are found in savannas and in tropical rain forests, but it is hypothesized in this paper that they originated in the African rain forests and conquered the savannas several times. Also, there were four independent waves of emigration into Asia and one into Madagascar. The savannas in themselves do not have such a good climate for fungus cultivation, but inside the termite mounds an environment with a constant temperature and a high humidity is maintained—a little piece of rain forest on the “prairie.”

