Courtesy M. G. Wood.

MYCOLEGIUM: New mushroom genera: Horn of plenty or deluge?

Making Sense of all the New Mushroom Names

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n 2014 and the first six months of 2015 alone, more than 20 new bolete genera were

proposed. Contrary to what

many people would expect, these genera are not restricted to some faraway exotic locale where the boletes have novel character combinations, no, these new genus names are for familiar species that occur in North America and Europe and that we have been calling by the name *"Boletus"* for a long time.

This creation of new genera is not restricted to the boletes. The numbers for the gilled mushroom species are comparable: we counted around 24 new genera published in that same time period, most of them white-spored, with six new genera for species we used to call *Clitocybe*, five new genera in the Lyophyllaceae, and three new ones in the *Psathyrella* family. However, there were only two new brown-spored genera. And the largest genus by far, *Cortinarius*, was not affected.

Most of these genera are for existing species, only a few, such as *Cercopemyces crocodilinus* from the Rocky Mountains (Baroni et al., 2014; and see the spring 2015 issue of FUNGI), are for newly discovered species.

Here we will try to explain what triggered this flood of new genera. We'll also have a critical look at what is necessary to make good, solid, acceptable genera. On that basis we can also look critically whether these new genera are, at least for the time being, warranted.

We give references to the original articles in which the research we cover here is described; many of those are freely accessible, so you can see for yourself how this type of science is done.

Definitions of some of the terms we use throughout this article are in Text box #1.

Text box #1 – Some definitions

- clade a monophyletic group consisting of a common ancestor and all its descendants.
- genus (plural: genera) a monophyletic group of species that have (preferably) morphological characters in common.
- monophyletic a genus is called monophyletic when all its members share a most recent common ancestor that is not shared by species outside that genus (the red and blue blocks in Fig. 1 represent monophyletic groups). A single species is monophyletic by definition.
- paraphyletic a genus is called paraphyletic, when only by including members of another genus or other genera, all its members share a common ancestor (the green block in Fig. 1 represents a paraphyletic genus).
- polyphyletic a genus is called polyphyletic as a more advanced case of paraphyly and the members of the genus are scattered over widely different clades (example: *Marasmius* with *M. androsaceus* falling inside *Gymnopus*, and *M. minutus* outside the family Marasmiaceae).
- sister group the closest relative of a clade or species in a phylogenetic tree (the red block in Fig. 1 is a sister group to the blue-green clade).
- taxon (plural: taxa) any taxonomic unit from forma to phylum.
- type species of a genus the species that is the name-bearing type of a genus (example: *Coprinus comatus* is the type species of the genus *Coprinus*; when *Coprinus* was split up, the name *Coprinus* stayed with *C. comatus*, and the other parts of the genus, got new names). The type species is not necessarily the most typical for the genus.

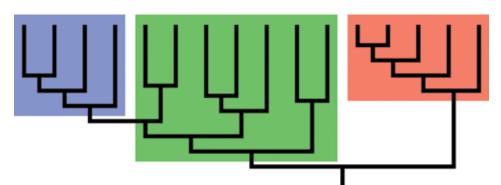


Figure 1. An example of a phylogenetic tree with the terminal branches each representing an individual species. The blue and the red parts of the tree represent monophyletic groups. The green part is not monophyletic, but paraphyletic, as the green and the blue together are monophyletic. The red clade is sister to the green/blue clade. (from Wikimedia)

Some historical background

Up to the mid 1990s mushroom genera were recognized and described based on morphological characters, with the underlying principle that what we recognized represented a natural system and that system was the result of evolution. These classifications were of course subjective and prone to a lot of debate. Different traditions reigned on the different continents: *Entoloma* in Europe included *Nolanea* and *Leptonia*, whereas in the USA these were three different genera, and *Hygrophorus* in North America included the colorful *Hygrocybe* species that were in their own genus in Europe.

Name changes happened, also in the past. An example is the turkey tail, now known as *Trametes versicolor*, which has resided in 12 different genera since its initial naming in 1753 (Linnaeus, 1753).

Alexander Smith was upset by the flood of new genera created by Singer who worked in the neotropics where the mushrooms did not fit the descriptions of the temperate genera. Smith (1968) thought that "When we have made a critical study from an adequate sample of a population, such as that of North America for the gill fungi, I believe that the generic concepts will be found to be rather self-evident."

Mushroom fruitbodies do not have a wealth of morphological characters, so they did not lend themselves very well to phylogenetic studies based on morphology as developed by Hennig (1950; 1965). There were simply no

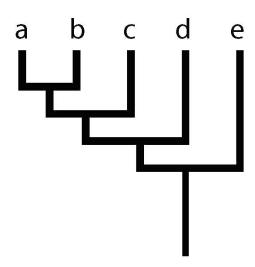


Figure 2. A phylogenetic tree with 5 terminal monophyletic taxa. This tree represents many different monophyletic genera: a; a and b together; a, b and c together; a, b, c, and d together, and all five together. A paraphyletic genus is formed by the d-e combination, or by c, d and e; the combination of a and e in one genus can be called polyphyletic. If a and b together are recognized as a genus, c, d, and e should each be considered a genus as well. characters that could be used to gauge the value of certain characters for genus definitions. What to do with those characters that were incongruent was a big problem. Was it more important that all species in a genus had amyloid spores than that they all were ectomycorrhizal or had an annulus? Those were unanswerable questions, though, of course; taxonomists would argue about these issues, but nobody could claim victory.

Molecular phylogenetics changes fungal systematics

With the advance of molecular methods to make many copies of pieces of DNA that could then be analyzed and sequenced, and the development of larger and faster computers that could deal with larger and more complicated data sets, mushroom systematics changed dramatically.

These methods made it possible to compare genetic markers (for instance pieces of spacer regions in between genes, and genes that code for the household chores in the cells, but not those that make the pigments) and we could formulate hypotheses for the evolution of these pieces of DNA. These hypotheses are in general presented as a phylogenetic tree, in which each terminal branch is a sample or a collection. The more different pieces of DNA that are used to make these trees, the more species and specimens are included, and the higher the statistical support for the branches on the tree is, the better this hypothesis will represent the true path of evolution. The tree might become a species tree instead of a gene tree. These trees are similar to the family trees one can build for their ancestors, though here the terminal branches represent an individual person.

These phylogenetic trees are used to determine what good species are, and also for the circumscription of genera. As indicated above, one needs to look carefully at the tree, and be aware of a few things:

 Which taxa are included in the tree? One can only draw conclusions about the taxa that are included in the study, not about those that are not there – it is like making a family tree without your twin brother who fled home at the age of 14 and has never been heard of again; from your family tree one could conclude that your cousin is your closest relative, though in reality it is your brother. So trees that are based exclusively on taxa of a certain area (e.g., the northern hemisphere), while the group itself has a much broader geographical distribution, as in the case of some bolete trees, are suspect.

2. Is your tree a gene tree, based on one piece of DNA only, or is it based on a critical examination of a number of different genes? And if it is based on one piece of DNA only, is that a piece that is known to be very variable and very helpful at the species level but not so much for genus recognition? The nrITS region (a spacer region that sits in between genes that do not show much variation among species) is very good at discriminating mushroom species (not all, but many; it is therefore used as the so-called bar code region. But while it is very good at species, that means there is a lot of variation among species, and it is much harder to use for species groups that are not so closely related. The nrITS region is not recommended as the sole marker for genus recognition. Unfortunately (or should we say of course) some mycologists still do base genera on trees derived from ITS data alone. A further advantage of making trees based on a number of (say 5-8)genes, is that it allows evaluation of alternative classifications in case the various genes provide contradictory information. If statistical support for the final tree is low, an attempt can be made to analyze the causes for that lack of congruence.

The first revolutionary results

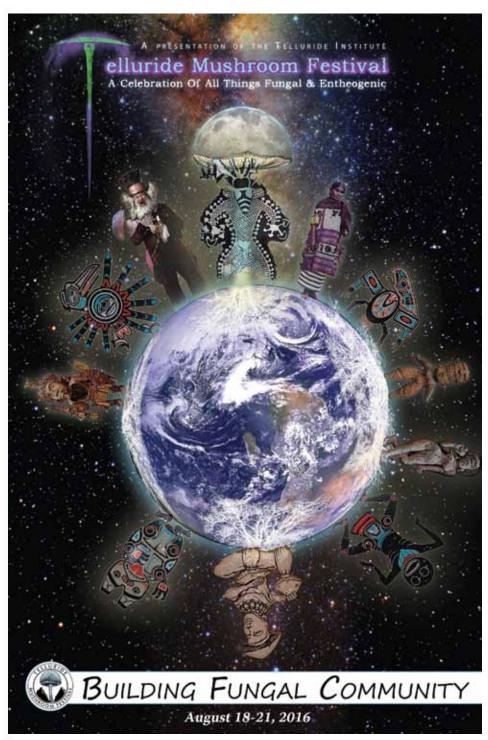
Coprinus, the inky cap genus, was one of the first genera to be analyzed with these new methods, and to everybody's surprise this genus turned out to be polyphyletic, with *Coprinus comatus* and its close allies closely related to *Lepiota*, and the rest of the genus not monophyletic, but clearly separating into three groups (Hopple and Vilgalys, 1999). These results were based on the analyses of one gene region only, and also the three new genera *Parasola*, *Coprinopsis*, and *Coprinellus* ended up

Text box #2 – Bolete genera described or names put to use since 2000 relevant for North America

Alessioporus – Gelardi et al., 2014 Baorangia – Wu et al., 2015 Borofutus – Hosen et al., 2013 Bothia – Halling et al., 2007 Butyriboletus – Arora and Frank, 2014 Caloboletus - Vizzini, 2014a Corneroboletus – Zeng et al., 2012 Crocinoboletus - Zeng et al., 2014 Cyanoboletus - Vizzini, 2014e Exsudoporus – Vizzini, 2014f Harrya – Halling et al., 2012a Hortiboletus – Vizzini, 2015 Hourangia – Zhu et al., 2015 *Imleria* – Vizzini, 2014b Imperator – Assyov et al., 2015 Lanmaoa – Wu et al., 2015 Neoboletus - Vizzini, 2014h Parvixerocomus – Wu et al., 2015 Pseudoaustroboletus - Li et al., 2014b Pseudoboletus – Šutara, 1991 Pulchroboletus - Gelardi et al., 2014 Retiboletus – Binder and Bresinsky, 2002 Rheubarbariboletus – Vizzini, 2015 Rubroboletus – Zhao et al., 2014 Rugiboletus - Wu et al., 2015 Suillellus – Murrill 1909; Vizzini, 2014g Sutorius – Halling et al., 2012b Veloporphyrellus – Li et al., 2014a Xerocomellus – Šutara, 2008 Zangia – Li et al., 2011

inside the genus *Psathyrella* making that genus paraphyletic [in other words this early study would not pass our bar!] (Padamsee et al., 2008). The *Coprinus* study really represented a landmark: it caused a storm of protest, and it took a long time to get used to these revolutionary results and ideas. Nowadays these placements and genera are all mainstream and accepted, but it took a while! *Coprinus comatus* has characters in common with *Lepiota*, but the spores with their almost black walls and the germ pore in the spore really make them stand out, and nobody had expected this (see also Redhead, 2001). The new genus *Parasola* (for *Coprinus plicatilis* etc.) is morphologically well defined, but *Psathyrella conopilus* has to be placed into it (Larsson and Örstadius, 2008). The other two are much vaguer and more diverse in their characters (Redhead et al., 2001). It took until this year, 2015, before three new genera were split off from *Psathyrella* (Örstadius et al., 2015) to make that genus monophyletic. *Psathyrella spadicea* is a sister to *Lacrymaria*, but does not share the ornamented spores with that genus, quite to the contrary it has pale smooth spores with a hardly visible germ pore, and cystidia with crystals on the top; now it is placed in the genus *Homophron* (Örstadius et al., 2015).

The second big discovery from these early studies was that many gasteroid and secotioid species really are closely related to and recently derived from gilled or pored mushrooms. This had been a bone of contention among



Text box #3 – Gilled mushroom genera described 2014–2015, family they belong to, evidence provided, and the reference

Albomagister – Tricholomataceae s.str. – multigene – Sánchez-Garcia et al., 2014 Atractosporocybe – position not clear yet – multigene – Alvarado et al., 2015 Bonomyces - for Clitocybe sinopica - no supporting evidence - Vizzini, 2014c Calocybella - Lyophyllaceae - LSU and ITS - Vizzini et al., 2015 Cercopemyces - close to Ripartitella and Cystodermella - multigene -Baroni et al., 2014 Ciboamyces - Physalacriaceae - LSU and ITS - Hao et al., 2014 Clitocella – Entolomataceae – multigene – Kluting et al., 2014 Corneriella – Tricholomataceae s.str. – multigene – Sánchez-Garcia et al., 2014 Crassisporium - Strophariaceae - multigene - Matheny et al., 2015 Cryptomarasmius – Physalacriaceae – LSU and ITS – Jenkinson et al., 2014 Homophron – Psathyrellaceae – multigene – Örstadius et al., 2015 Hygrophorocybe - for Clitocybe nivea - no supporting evidence - Vizzini, 2014d Kauffmania - Psathyrellaceae - multigene [name will probably to change] -Örstadius et al., 2015 Leucocybe – position not clear yet – multigene – Alvarado et al., 2015 Myochromella – Lyophyllaceae – multigene – Hofstetter et al., 2014 Pogonoloma - for Porpoloma spinulosum, position not clear yet - multigene -Sánchez-Garcia et al., 2014 Pseudolaccaria - position not clear yet - LSU and ITS - Lavorato et al., 2015 Pseudotricholoma – Tricholomataceae s.str. – multigene – Sánchez-Garcia et al., 2014 Rhizocybe - position not clear yet - multigene - Alvarado et al., 2015 Romagnesiella – Strophariaceae – multigene – Matheny et al., 2015 Sagaranella – Lyophyllaceae – multigene – Hofstetter et al., 2014 Sphagnurus (=Bryophyllum Vizzini) - Lyophyllaceae - no evidence provided -Redhead, 2014b Tephrocybella – Lyophyllaceae – ITS – Vizzini in Crous et al., 2015 Typhrasa – Psathyrellaceae – multigene – Örstadius et al., 2015

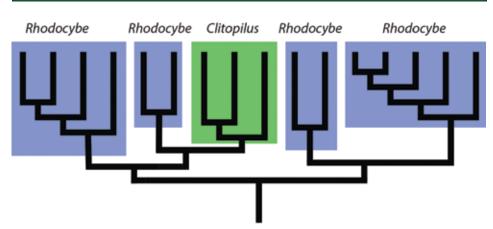


Figure 3. Schematic phylogenetic tree of *Clitopilus* and *Rhodocybe*, based on Co-David et al. (2009). *Clitopilus* is monophyletic, *Rhodocybe* is paraphyletic.

mycologists, who held strong opinions in which direction evolution had gone (were the puffballs and truffles primitive or advanced?). So, indeed, *Nivatogastrium nubigenum* is a *Pholiota* species (Redhead, 2014; Siegel et al., 2015), *Lycoperdon, Bovista*, and *Calvatia* are gasteroid Agaricaceae (Moncalvo et al. 2000 and 2002), *Gastroboletus* species have to be divided over several bolete genera (Nuhn et al., 2014), and *Gastrosuillus laricinus* is just a morphological variant of *Suillus grevillei* (Baura et al., 1992; Kretzer and Bruns, 1997). These are just a few examples that suggest how quickly (in evolutionary times) secotioid and gasteroid taxa can evolve.

Interpretation of phylogenetic trees

The genera of boletes and of gilled mushrooms that were described in the last year or so are listed in text boxes #2 and #3; there are many more new genera in the gilled mushrooms proposed this century – many more than we can analyze here in depth. There is hardly any group where there have not been new genera or new arrangements. But here, we'd like to focus on a few groups and show the approaches of different authors.

First up are the Entolomataceae and *Xerula*, followed by *Trametes*, and lastly we'll stop by the Tricholomataceae.

Entolomataceae

Pink spores that are box-shaped, have angles, bumps or ridges – those characterize the Entolomataceae. There are two main groups: species with spores with bumps or longitudinal ridges, and the species with more box-shaped angular spores.

There are two main issues to resolve in this family, having to do with the two different spore types that are present. We start with the bumpy and ridged spores.

Traditionally the species with the ridged spores (shaped like American footballs but a polygon in transverse view), are in the genus Clitopilus (the miller, sweetbread, Clitopilus prunulus is a good example), and the ones with the bumpy spores in *Rhodocybe*. Unfortunately these two groups that are so easy to recognize morphologically under the microscope, do not each form a monophyletic group; *Clitopilus* is monophyletic in phylogenies based on a set of quite different pieces of DNA, but *Clitopilus* is surrounded by Rhodocybe members (Fig. 3). For such a situation there are two solutions: either lump all together into one genus (in this case it would be called *Clitopilus*), or recognize the five different clades as separate genera (Clitopilus, Rhodocybe, Rhodophana, Clitopilopsis, and the newly named *Clitocella*). Both solutions have been proposed (Co-David et al., 2009 for the *Clitopilus* option; Kluting et al., 2014 for the five-genus option). We should also keep in mind that this group is relatively species poor in comparison to the other, much bigger clade in the family. Entoloma s.l.

Entoloma itself is the other component

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of the Entolomataceae; recognized as one huge genus in Europe by various authors (e.g., Noordeloos, 1992), but split up into smaller units (Nolanea, Leptonia, Pouzaromyces, Entoloma etc.) here in North America (e.g., Largent, 1994; Baroni et al., 2011). Again, the molecular-phylogenetic approach has shown that the smaller genera as proposed by the American authors are not all monophyletic; the conclusion drawn by the European authors is that Entoloma is best considered one big genus (Co-David et al., 2009). Here in North America the conclusion was that there should be more genera, so Entocybe was proposed for the basal group of Entoloma which has spores that are bumpy, but which are not as boxy as those in Entoloma proper, neither as irregularly bumpy as in Rhodocybe (Baroni et al., 2011).

The comparison of both sister groups raises a further question: should we treat them in comparable ways? That is, if we split *Clitopilus* into five genera, does that force us to split *Entoloma*; or alternatively, if we decide not to split *Entoloma*, does that force us to recognize a broadly circumscribed *Clitopilus*? Or can both decisions with regard to generic delimitation be considered separately?

Xerula and its relatives: what to do when morphology and molecules clearly tell different stories

We have an interesting problem here that resembles the situation around Rhodocybe and Psathyrella: a group of mushrooms that has in common very distinct morphological characters, but does not form a monophyletic group in phylogenetic trees based on two gene regions (ITS and LSU). We are talking about Xerula megalospora and her lookalikes. They definitely do not belong in *Xerula* as those species with the long setae on the cap and stipe form their own monophyletic group, well away from these species with the glutinous cap cuticles. But the beautiful porcelain-like Oudemansiella mucida from Europe, and the tropical species O. canarii fall in the middle of the X. megalospora group. Again, it is a matter of taste and choice how to solve such a problem. One group of researchers uses first morphological characters, and then the delimitations as presented in the phylogenetic trees,

Text box #4 – Criteria for solid work and genus recognition:

- 1. All genera that are recognized have to be monophyletic, not only the one that is the focus of the study, but also the group it is leaving and the group it ends up in. (A good example: when *Macrolepiota* was split into core *Macrolepiota* with *M. procera* as its type, and a second group containing *M. rachodes*, the latter was moved to *Chlorophyllum* that in itself was only monophyletic by including *Endoptychum agaricoides*; bad example: by splitting *Coprinus* up into 4 genera, 3 of them ended within *Psathyrella*, making that genus paraphyletic).
- 2. The phylogenetic tree has to be based on more than one gene.
- 3. The coverage of the phylogenetic tree has to be wide, in terms of species, and geographic distribution of the taxa, and should include type species of genera that are being included.
- 4. The branching of the phylogenetic trees has to be sufficient statistically supported (a measure of how realistic the pattern is). Weak support (or even absence of statistical support) indicates that alternative classifications cannot be rejected. And so the advice is: "*in dubiis abstine*," when in doubt refrain from proposing new genera.
- Phylogenetic methods often allow more than one formal classification with monophyletic groups. Therefore, the list of options should be discussed, and arguments for the final decision given. (A good example: the *Trametes* example).

resulting in small genera; some of these (new) genera are monophyletic, but *Hymenopellis*, the genus in which *X. megalospora* and *X. furfuracea* are placed, is paraphyletic (Petersen & Hughes, 2010). Other authors maintain fewer and larger, monophyletic genera that represent the ITS/LSU phylogenies (e.g., Hao et al., 2012; Qin et al., 2014a). *Oudemansiella* is in that case the name to use for *X. megalospora* and *X. furfuracea*. Here, it might be useful to make phylogenies based on a wider range of genes to solve these problems in a more satisfactory way.

We like to maintain that genera should pass the monophyly criterion (see also text box #4 for more criteria for solid work), and applaud the use of *Oudemansiella* for these species. Tests to evaluate the different scenarios of more or less inclusive genera can also be done, but in the mycological practice of the last years these are unfortunately hardly executed.

Turkey tails: a different approach?

Trametes, turkey tails and their relatives have also been studied by

several groups of scientists. There is a well-resolved phylogeny of the group based on five different gene regions, on which everybody agrees, but how the data are interpreted depends on the people. Justo and co-author (Justo and Hibbett, 2011; Justo, 2014) opted for a large genus Trametes, whereas Welti et al. (2012) proposed the option of small genera and then, of course, also had to make a new genus. Justo (2014) gives good insight into the process of reaching his conclusion of one genus as the ultimate and best solution! There is one silver lining to this cloud of difference: the two groups agreed on the position of Lenzites betulina: that species should be named Trametes betulina. The downside of the one-genus option is that the orange-red species that are so easily recognized as Pycnoporus, are now within Trametes.

These examples show that how the data are interpreted and where to draw genus borders is still very much subject to taste and human insight. That has not changed with the arrival of these new techniques and methods; these provide strict criteria for recognition of monophyletic groups but do not provide unambiguous answers for ranking of such groups. History and tradition still determine to some extent what is done with the data. Some of the current practices can therefore be better understood in the light of previous classifications. The ultrarapid and extensive splitting of the boletes is a good example of that phenomenon. We recognize, and have been recognizing, the genera Leccinum, Tylopilus, and Xerocomus, alongside Boletus. Now it is clear that Boletus species are spread out over the bolete tree around these other already named units; Boletus species do not form a monophyletic group (Nuhn et al., 2013; Wu et al., 2014). Hence, many new genera are characterized to accommodate the species formerly placed in Boletus (see text box #2 for the new bolete genera of 2014 and 2015). If we had not started splitting the boletes up into smaller units, who knows, we would still call all of them Boletus, and this avalanche of new names would not have happened. The name Boletus is now reserved for the type species of the genus, Boletus edulis, and its closest relatives. Many of the eastern North American species still have to be placed in these new genera, but Boletus bicolor has already moved to Baorangia, Sutorius accommodates Tylopilus eximius, and Harrya chromapes replaces Tylopilus chromapes. Most western species are already accommodated in the new genera.

Tricholomataceae: family matters

We cannot avoid talking about families as well. For several of the newly proposed genera we have indicated that the exact position is not yet known (text box #3), that has to do with the fact that those white-spored groups are still not very well sorted out, and this represents a wide open research field. There are quite a few different studies dealing with species that have white spores, decurrent gills, and very little else in terms of character. In fact, most of the other "characters" are negative characters (no cystidia, no differentiated pileus structure, no amyloid reactions, etc.). But all these studies use slightly different markers, and different species combinations, and the focus of most of these is on European species. Because of those slightly different approaches, it is hard to see how these different pieces of the puzzle fit together (Alvarado et al., 2015; Musumeci and Contu, 2010; Vizzini et al., 2012; Vizzini and Ercole, 2012).

One big surprise did turn up: the small *Collybia* species (*C. cirrhata*, *C. tuberosa*, and *C. cookei*) fall in the middle of *Clitocybe* – that would toll an end of the genus *Collybia*, as *Gymnopus*, *Rhodocollybia*, and *Dendrocollybia* had already left that genus. But in case you are indeed unhappily surprised by this merger: try to explain in words how you can recognize a large specimen of *Collybia cirrhata* from a small specimen of *Clitocybe candicans*. A microscope will not help you, as they are virtually identical in all microscopical characters.

The other development is the ultimate slimming of the family Tricholomataceae. In the past all species with light spores and lacking the distinctive characters of the Amanita family, the wax caps, or the parasol mushrooms, were thrown into the garbage can that represented that family. More than 90 genera were listed by Singer (1986) in his all-encompassing overview of the Agaricales. Now, eight are left (Sánchez-Garcia et al., 2014). But a good family home has not yet been found for all these remaining genera, and that is also applicable to those new genera that have been split off from Clitocybe et al. in recent years.

Again, as in *Trametes*, it might be a good idea to step back and to see whether perhaps bigger units do represent solid monophyletic groups, which can be named. In this case, one has to take many steps back, to the whole of what is called the Tricholomatoid clade by Matheny et al. (2007) in their big overview of the gilled mushrooms. Besides the slimmed version of the Tricholomataceae, the Lyophyllaceae, the Entolomataceae, the Marasmiaceae, Clitocybe and some of its split-offs, and other orphaned genera fall into this clade. Naming this big clade "Tricholomataceae" might be a good solution, but not one that everybody will happily and readily accept!

Conclusions

What can we make from all these changes? Should we rejoice, because the rise of new fungal genera is a long overdue process? Or should we become frustrated, because many of them are premature? It is currently so easy to download sequences from a public database and have new genera published without peer review – is that a good development? Our title reflects that there may well be difference of opinion to what extent these changes indicate scientific progress.

It is clear that recognizing genera is the work of humans, and as such there will be difference of opinion and insight. We strongly advise everybody active in the field adhere to our guidelines as outlined in text box #4, and not to make new genera without providing them with a family home. Taking a step back, and contemplating the merging of genera, instead of making new ones, is also our recommendation. Ask yourself the question: would it be best to have one large genus Boletus or do you want seven genera (Wu et al., 2014), or are you most satisfied with hundreds of genera, each with only a few species, which is the unavoidable outcome of the current splitting snowball (see text box #2)?

But, what is the average amateur mycologist to do with all the new names? Several, or possibly even many, names are definitely here to stay, and we have to learn them. Keeping track of all these changes is not so easy – there is a lot of literature! But, you are not on your own, there are many people who are following the newest developments, and who make name changes on popular web sites, such as MushroomObserver.org.

All these changes mean that our knowledge is also changing: we are gaining more and more insight in the relationships of our beloved mushrooms, and that is a development we only can applaud!

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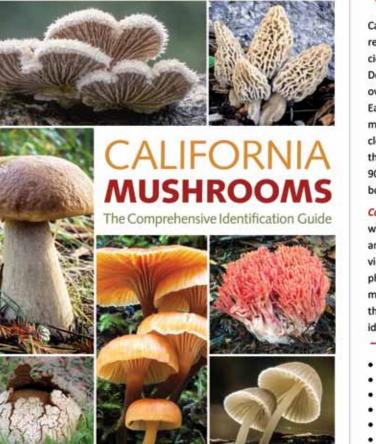
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