Not every milkcap is a Lactarius

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Abstract. – New insights, based on molecular analyses in the Russulaceae, learn us that the traditional two giant agaricoid genera Russula and Lactarius have to be considered in a new generic landscape. Multifurca Buyck & Hofstetter was already proposed as a new genus, grouping some former Russula- and Lactarius-species. Moreover, it has become clear that the remaining bulk of milkcaps actually consists of two disparate groups which both should be treated at the generic level. Since the proposal to conserve Lactarius with a conserved type has been accepted, most of the milkcaps will remain in Lactarius and 20 to 25% of them only will be recombined in Lactifluus. Lactarius was a well recognizable and large genus (with world-wide more than 600 accepted species, but the real number estimated to be at least 800 species). Within this traditional concept, many well recognizable subgroups, often considered as subgenera, are delimited. Most have a worldwide distribution (L. subg. Piperites, L. subg. Plinthogali), but some show a distinct geographical pattern (L. subg. Lactariopsis, L. subg. Lactifluus) or are even limited to one continent (L. subg. Edules in tropical Africa). Not all of the traditional subgenera appear to be supported by the molecular analyses. Other subgroups show to be new and well-supported subgenera (L. subg. Edules and L. subg. Gerardii). In this presentation an overview of the new genera of milkcaps and their respective subgenera is given, thus proposing a new and worldwide classification for the milkcaps. Though the majority of the species is agaricoid, it is clear that the evolution from gymnocarp to angiocarp fruiting bodies occurred several times within this group and that pleurotoid taxa are also included. Their position within the subgenera will be explained.

Résumé. – Tous les lactaires ne sont pas des Lactarius. De nouveaux éclairages, basés sur des analyses moléculaires dans les Russulaceae, nous apprennent que l’on doit considérer les deux genres géants et agaricoïdes traditionnels, Russula et Lactarius, dans un nouveau paysage générique. Multifurca Buyck & Hofstetter a déjà été proposé comme nouveau genre, pour rassembler quelques espèces classées jusque là dans les genres Russula et Lactarius. De plus, il est devenu clair que les lactaires restants sont en réalité constitués de deux groupes disparates qui devraient constituer deux genres distincts. Comme la proposition de conserver Lactarius avec un type conservé a été acceptée, la plupart des lactaires resteront dans le genre Lactarius et 20 à 25% d’entre eux seulement seront recombinés dans le genre Lactifluus. Lactarius était un genre vaste et bien reconnaissable (avec plus de 600 espèces acceptées dans le monde, mais un nombre estimé d’espèces d’au moins 800). Au sein de ce concept traditionnel, beaucoup de sous-groupes, bien reconnaissables et souvent considérés comme des sous-genres, ont été délimités. La plupart ont une distribution mondiale (L. subg. Piperites, L. subg. Plinthogali)

**Key words.** – *Lactarius*, *Lactifluus*, taxonomy, nomenclature.

**INTRODUCTION**

It is becoming a familiar fact that the insights gained in the current explosive molecular era are influencing and even turning upside down our traditional views on Basidiomycota. But in general, taxonomic implications are only put through with care and after a thorough search for morphological or ecological evidence and confirmation.

As for the Russulales, it is long accepted that the large agaricoid genera *Russula* Pers. and *Lactarius* Pers. are very different from other agaricoid mushrooms and form their own order. This was mainly based on the character of sphaerocytes present in the trama and the subsequent brittle context of the mushrooms. Their separate position was a confirmation of the fact that too much weight was traditionally given to the shape of the basidiocarps and the hymenophore.

In this light, it was also not so surprising that sequestrate or angiocarp representatives of the milking genera *Arcangeliella* Cavara and *Zelleromyces* Singer & A.H. Sm. and the non-milking *Cystangium* Singer & A.H. Sm., *Martellia* Mattir. and *Macowanites* Kalchbr. turn out to be included in the large and mainly agaricoid *Lactarius* and *Russula* respectively, though it has taken several years before this actually got taxonomically implemented and the gasteroid genera disappeared in synonymy (Eberhardt & Verbeken 2004, Nuytinck et al. 2004, Desjardin 2003).

The inclusion of hydnoid and corticioid genera in the Russulales did not come as a complete surprise since Donk (1971) and Oberwinkler (1977) already suggested links between taxa such as *Gloeocystidiellum* Donk, *Boidinia* Stalpers & Hjortstam, *Gloiothele* Bres. on one hand and typical Russulaceae on the other hand. Molecular data show a strong support for a russuloid clade with agaricoid, corticioid, resupinate, discoid, effused-reflexed, clavarioid, pileate and gasteroid taxa with smooth, poroid, hydnoid, lamellate or labyrinthoid hymenophores. To a certain extent, there is morphological support for this Russulales clade in the amyloid spores and the presence of gloeocystidia or a gloeoplereous hyphal system (Larsson & Larsson 2003, Miller et al. 2006).

But even in an era where we discover that widely accepted and long-known fungal genera and families are artificial, the idea of changing the concept of the two large agaricoid genera in this russuloid clade, is a larger shock to many mycologists than other changes in the Russulales have been.

**THE WELL-RECOGNIZABLE GENUS LACTARIUS**

*Lactarius* (raised by Persoon in 1797) and *Russula* (raised by Persoon one year earlier), are well-known agaricoid genera, that every mycologist and amateur-mycologist recognizes from the very beginning, in temperate regions at least.

*Lactarius* or milkcaps have the exuding latex becoming visible when fruiting bod-
ies are bruised or broken and are furthermore macroscopically distinguished from *Russula* by the so-called less bright colors, or at least less contrast between a pale stipe and brightly colored cap as often observed in *Russula*. But apart from this milk, it would not be so easy to recognize *Lactarius* as one group because the milkcaps show a giant variation when it comes to pileipellis structures (reflected in the macromorphological aspects: dry and velvety, smooth or scaly, viscid to extremely glutinous, hairy or not, zonate or not, ...), basidiocarp size (more than 30 cm diam. in some species, not even one cm in others), pigmentation...

The milk versus no-milk feature was often used as the distinction between *Lactarius* and the even larger genus *Russula*. It works fine in temperate regions, but is more problematic when one considers tropical representatives where the milk can be really scarce or lacking in some *Lactarius* species. The most reliable feature to distinguish between these genera is the presence versus absence of pseudocystidia, extremities of the lactifers that proceed in the hymenium (Buyck 1995, Verbeken 1997).

Milkcaps form ectomycorrhiza with many different trees, conifers as well as Angiosperms, some of the most important trees belonging to Salicaceae, Betulaceae, Fagaceae and gymnosperms in the temperate and cold regions, *Cistus* (Cistaceae) and *Pinus* in the Mediterranean region, Dipterocarpaceae, Fagaceae, Euphorbiaceae, Fabaceae, Myrtaceae in tropical and subtropical regions. Some species have a very broad host range; others are very host-specific. Due to these ectomycorrhizal associations with many wide-spread genera of trees, *Lactarius* is one of the dominant agaric genera in many ecosystems, from the boreal forests (Geml et al. 2009) to the temperate ones (Heilmann-Clausen et al. 1998, Basso 1999), but also in the subtropical woodlands of Africa (Verbeken & Buyck 2002, Riviere et al. 2007, Verbeken & Walleyn 2010, Tedersoo et al. 2010) and the extensive Dipterocarp forests in South-East Asia (Watling et al. 2002, Stubbe et al. 2007, 2008).

More than 500 species of milkcaps are actually known world-wide but we estimate the real number to be at least 650. In tropical Africa, all species are endemic. In other regions, such as North America versus Europe, many names are used in both continents, but so far no real conspecificity could be confirmed molecularly, except for collections of *L. controversus* (Nuytinck et al., in these proceedings) but this might be an introduction by humans.

**MULTIFURCA**

Multigene-based phylogenies of this group show that *Lactarius* and *Russula* are not two nicely defined and separate clades (Buyck et al. 2008). *Russula* appears to be monophyletic only if a small group of species is left out. This small group of species forms a clade where *Lactarius* and *Russula* are mixed. This clade was recently described as the new genus *Multifurca* Buyck & V. Hofstetter. Representatives are characterized by the furcations in the lamellae, dark yellowish lamellae and spore-prints, a strong zonation of the pileus and context and they do or do not have latex. The former *Russula* subsect. *Ochricompactae* Bills & O.K. Mill., but also the Asian *Russula zonaria* Buyck & Desjardin and the Mexican *Lactarius furcatus* Coker are included here.

**TWO CLADES OF MILKCAPS**

*Lactarius* falls apart in two clades, one larger clade and one smaller clade, and splitting the genus seems a better solution than lumping everything in a giant genus *Russula*.

Many synonyms are available to name and rename these milkcap-clades. The original type of *Lactarius* was *Lactarius piperatus* (L.: Fr.) Pers. Unfortunately *L. piperatus* fell in the distinctly smaller clade, which means that 20 to 25% of milkcaps stayed in *Lactarius* (in temperate regions only 10% !!) and 75 to 80% had to be recombined in *Lactariella* J. Schröt., which would have been the oldest available name for the larger clade since the former (and more used) synonyms *Lactifluus* (Pers.) Roussel and *Galorrheus* (Fr.: Fr.) Fr. are both typified by this same lectotype *L. piperatus*!
A proposal to conserve *Lactarius* with a conserved type was submitted for the International Committee of Nomenclature (Buyck et al. 2010) and arguments were given to indicate *L. torminosus* (Schaeff.: Fr.) Pers. as the type of *Lactarius*.

Since this proposal has been accepted (see *Taxon* 60 (1): 225 and 60 (4): 1212-1213), 75 to 80% of milkcaps remain in *Lactarius* and 20 to 25% have to be recombined in *Lactifluus* and thus significantly fewer nomenclatural changes will have to be conducted. An extra advantage is that, in the temperate regions, not even 10% of the milkcaps have to change name since the majority of this smaller clade are species which only occur in tropical Africa (about 65% of the names there will have to be recombined). Furthermore *Lactifluus* has been in more current use than e.g. *Lactariella*, and thus combinations have already been made (e.g. *Lactifluus volemus* (Fr.: Fr.) Kuntze, *Lactifluus piperatus* (L.: Fr.) Kuntze, *Lactifluus vellereus* (Fr.: Fr.) Kuntze, *Lactifluus pergamenus* (Sw.: Fr.) Kuntze). For our region, it means that only for *Lactarius glaucescens* Crossl., *Lactarius lutelus* Peck and *Lactarius oedematopus* (Scop.) Fr. a new combination has to be proposed.

The large clade: the proposed genus

*Lactarius sensu novo*

This clade consists of three large subgenera with their main distribution in the temperate zone: *L. subgenus Piperites* (Fr. ex J. Kickx f.) Kauffman, *L. subgenus Russularia* (Fr. ex Burl.) Kauffman and *L. subgenus Plinthogalus* (Burl.) Hesler & A.H. Sm.

The known angiocarpic representatives (from North America, Europe, tropical Africa, South-East Asia and Australia) all belong to this group and occur in the three subgenera.

*Lactarius subg. Piperites* is recognized by an ixocutis as pileipellis structure and thus typically has slimy to viscid or shiny caps, with or without a hairy margin, although species with a drier cap also occur. The caps are openly zonate and, as in the new genus *Multifurca*, we see that the zonation can also be present in the trama of the pileus. Scrobicules, on the cap or on the pileus, are often present. Latex color is variable in this subgenus but an important feature to recognize species or higher taxa: orange to reddish or wine-colored in the *L. sect. Deliciosi* (Fr.: Fr.) Redeuilh (though *L. porinus* Rol.-land has white milk, see Nuytinck & Verbeke 2007), changing lilac in *L. sect. Uvidi* (Konrad) Bon and *L. sect. Aspidei* (Burl.) Hesler & A.H. Sm., changing immediately yellow in *L. sect. Scrobiculati* Hesler & A.H. Sm. and white but drying greyish to greenish in many species. It is a dominant subgenus in temperate regions, but only represented by three species in tropical Africa (Verbeke & Walley, 2010).

*Lactarius subgenus Russularia* (Fr. ex Burl.) Kauffman is recognized by mainly orange to brick-red or brownish pigments, a dry to somewhat greasy cap (trichoderm or trichopalisade-like structures, often also with globose elements in it). The milk is usually white and unchanging, though changing yellow in some species, but not as variable and indicative as in the previous group. Just like *L. subg. Piperites*, this is a dominant subgenus in temperate regions but also well-represented in South-East Asia, and up to now completely absent in tropical Africa. There is no molecular support for the formerly recognized *L. subgenus Colorati* (Bataille) Bon. Its representatives are divided over *L. subg. Piperites* (e.g. *L. glyciosmus* (Fr.: Fr.) Fr.) and *L. subg. Russularia* (e.g. *L. helvus* (Fr.: Fr.) Fr.).

The smaller *L. subgenus Plinthogalus* (Burl.) Hesler & A.H. Sm. is well recognized by the dry, velvety and dull-colored caps (grey, brown, cream) with a palisade-like structure as pileipellis. The spores are among the most highly ornamented in the genus (often winged!) and the milk is turning pinkish in many European representatives and also stains the context as such, but shows more variation in North America (with lilac staining species too). Our discovery of many tropical taxa in this group strongly extends the limits of color changes in *L. subg. Plinthogalus*: from watery transparent to blood red and then black in tropical Africa (Pegler 1969, Verbeke 1996, Verbeke & Walley, 2010), yellow, greenish or even deep indigo blue in Malaysia (Stubbe et al. 2007).
The smaller clade: the proposed genus *Lactifluus*


The best known representative in *L. subg. Lactifluus* is *L. volemus* (Fr.: Fr.) Fr., a species originally described from Europe, but its name since then has been used in many other continents. Recent research (Van de Putte et al. 2010) shows that this is a complex of species, containing cryptic as well as pseudocryptic species. The subgenus is recognized by a palisade-structure in the pileipellis with or without typical thick-walled elements. Pleurocystidia, if present, are lamprocystidia and the spores are either reticulate and slightly winged or ornamented with more or less isolated warts. In tropical Africa, the diversity of this subgenus is extremely high. The variation in the group is large; this is also reflected in the spore ornamentation and in the color changes of latex and context. A brown color change is typical in the subgenus, but also reddish and even black changes occur. So far, 5 sections are recognized in this subgenus in tropical Africa, all together with 26 species (on a total of 97 species known for the continent, Verbeken & Walleyn 2010, Van de Putte et al. 2009).

*Lactarius* subg. *Lactariopsis* has recently been proposed by Stubbe et al. (2010) for a group of milkcaps that has traditionally been included in *L. subg. Plisthogalus* because they share the dull blackish, brownish and greyish colors, the velutinous aspect of the pileus, the lack of macrocystidia in the hymenium and a reticulate spore ornamentation. However, in *L. subg. Plisthogalus* spore print colors are never pure white but vary from cream to buff, while they are pure white in *L. Gerardii* Peck and its allies. In *L. subg. Gerardii* the subpellis of the pileipellis is a distinct layer of globose cells, while it is rather composed of strongly inflated hyphal elements in *L. subg. Plisthogalus*.

Both *L. sect. Edules* (which has to be recombined at subgeneric level) and *L. subg. Russulopsis* are only known from tropical Africa, where they form well-defined and well-represented groups (for separating characters see Verbeken & Walley 2010).
CONCLUSIONS

Rather than lumping all former Lactarius and Russula species in one giant genus Russula, it is preferable to accept, besides Russula and Multifurca, at least two new genera of milkcaps. Since our proposal to conserve Lactarius with a conserved type has been approved, the resulting genera will be Lactarius (with type species L. torminosus) and Lactifluus (with type species L. piperatus). It is hard to find synapomorphies for the two new clades, although some morphological generalities can be formulated:

- Thick-walled elements in the pileipellis and stipitipellis, as well as lamprocystidia, are general in the genus Lactifluus and very rarely observed in the genus Lactarius.
- A hymenophoral trama composed of sphaerocytes (as in the genus Russula) is common in the genus Lactifluus but hardly observed in Lactarius.
- Pleurotoid species are so far only known in the genus Lactifluus.
- Angiocarpic species are so far only known in the genus Lactarius and originated at least three times in this group, spread over three subgenera (Piperites, Russularia, Plinthogalus).

While the genus Lactarius sensu novo has its main distribution in the Northern hemisphere, the genus Lactifluus occurs mainly in the Southern hemisphere with a few very different representatives in the Northern part.

Genetically the two genera are very different: Lactarius is a large genus with a relatively low genetic diversity. We see many taxa where the morphological variation is high, but is not confirmed molecularly. While with the genus Lactifluus, we have a smaller group but with very high genetic diversity and subgroups in very different and distant clades, which even suggest that the genus will be falling apart in different genera once more taxa are involved in the analyses. Typical for this group are the species complexes such as L. volemus where the molecular variation is much higher than the morphological variation. It appears that in this paraphyletic group of milkcaps, all recognized by this striking character of exuding latex, we have two groups with a completely different phylogeographic history and different evolutionary rate.

REFERENCES


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