

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 world-wide 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 recombines 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*)

mais quelques-uns montrent une répartition géographique particulière (*L.* subg. *Lactariopsis*, *L.* subg. *Lactifluus*) ou sont même cantonnés à un seul continent (*L.* subg. *Edules* in tropical Africa). Les analyses moléculaires ne confirment pas tous les sous-genres traditionnels. D'autres sous-groupes sont apparus comme des sous-genres nouveaux et bien confirmés par le moléculaire (*L.* subg. *Edules* and *L.* subg. *Gerardii*). Dans cet article, un aperçu des nouveaux genres de lactaires et de leurs sous-genres respectifs est donné, proposant donc une nouvelle classification pour les lactaires du monde. Bien que la majorité des espèces soient agaricoïdes, il est clair que l'évolution de la fructification de la gymnocarpie à l'angiocarpie s'est produite plusieurs fois dans ce groupe et que des taxa pleurotoïdes sont également inclus. Leur position au sein des sous-genres sera expliquée.

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 hydroid 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, *Gloiothete* 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, hydroid, 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 gloeoplerous 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 & Walley 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. *Ochricompaetae* 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.) Rous-sel and *Galorrhheus* (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 luteolus* 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 often 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. porninsis* Rolland has white milk, see Nuytinck & Verbeken 2007), changing lilac in *L.* sect. *Uvidi* (Konrad Bon and *L.* sect. *Aspidei* (Burl.) Hesler & A.H. Sm., changing immediately yellow in *L.* subsect. *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 (Verbeken & 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 trichopalysade-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 palysade-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, Verbeken 1996, Verbeken & Walley 2010), yellow, greenish or even deep indigo blue in Malaysia (Stubbe et al. 2007).

The smaller clade: the proposed genus

Lactifluus

The clade is consisting of the following groups (names are provisional and refer to rankings in the traditional genus *Lactarius*): *Lactarius* subg. *Lactiflui* (Burl.) Hesler & A.H. Sm., *L.* subg. *Lactarius*, *L.* subg. *Lactariopsis* (Henn.) R. Heim, *L.* subg. *Gerardii* (A.H. Sm. & Hesler) Stubbe, *L.* sect. *Edules* Verbeken and *L.* subg. *Russulopsis* Verbeken.

All known pleurotoid representatives, from South-America, Asia and Tasmania, belong to this clade (*L. panuoides* Singer, *L. uyedae* Singer, *L. brunellus* S.L. Mill., Aime & T.W. Henkel, *L. multiceps* S.L. Mill., Aime & T.W. Henkel, *L. genevievae* Stubbe & Verbeken).

The best known representative in *L.* subg. *Lactiflui* 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 & Walley 2010, Van de Putte et al. 2009).

Lactarius subg. *Lactariopsis* also has its main distribution in tropical Africa, but has some well-known temperate representatives such as *L. vellereus* (Fr.: Fr.) Fr. and *L. bertillonii* (Neuhoff ex Z. Schaeff.) Bon. The pileipellis structure usually has hair-shaped, thick-walled elements in a palisade or trichopalisade, although quite some variation is observed. Typi-

cal for this group are the often extremely large and emergent pseudocystidia and, in tropical regions, the presence of a well-developed velum (Singer 1942, Verbeken 1998, Verbeken & Walley 2010). The temperate *L. bertillonii* and *L. vellereus* form a rather isolated clade in this group and the closest relatives of the African species are recorded in Papua New-Guinea and Thailand (Verbeken & Horak 1999, Le et al. 2007).

Lactarius subg. *Lactarius* is a small group with *L. piperatus* as the best known species. As *L. volemus*, *L. piperatus* is a name originally given to a European species but applied in many other continents. We assume that this is also a complex group of different species and are now re-searching *L. piperatus* and its allies. The group has a rather isolated position in the genus and also some particular characters: white and rather large fruiting bodies with extremely acrid context and/or latex, latex white and unchanging or drying green or yellow, pileipellis a layer of rounded cells with few pericline hyphae on top. The group occurs in North America, Europe and Asia.

Lactarius subg. *Gerardii* has recently been proposed by Stubbe et al. (2010) for a group of milkcaps that has traditionally been included in *L.* subg. *Plinthogalus* 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. *Plinthogalus* 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. *Plinthogalus*.

Both *L.* sect. *Edules* (which has to be re-combined 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

- Basso M.T. (1999) *Lactarius* Persoon. *Fungi Europaei* 7. Mykoflora, Alassio, 845 p.
- Buyck B. (1995) A global and integrated approach on the taxonomy of Russulales. *Russulales News* 3: 3-17.
- Buyck B., Hofstetter V., Eberhardt U., Verbeken A. & Kauff F. (2008) Walking the thin line between *Russula* and *Lactarius*: the dilemma of *Russula* sect. *Ochricompactae*. *Fungal Diversity* 28: 15-40.
- Buyck B., Hofstetter V., Verbeken A. & Walleyn R. (2010) Proposal to conserve *Lactarius* nom. cons. (Basidiomycota) with a conserved type. *Taxon* 59 (1): 295-296. [also published in *Mycotaxon* 111: 504-508]
- Desjardin D.E. (2003) A unique ballistosporic hypogeous sequestrate *Lactarius* from California. *Mycologia* 95 (1): 148-155.
- Donk M.A. (1971) Progress in the study of the classification of the higher Basidiomycetes. In: Petersen R.H. (ed.), *Evolution in the higher Basidiomycetes*. Knoxville, pp. 3-25.
- Eberhardt U. & Verbeken A. (2004) Sequestrate *Lactarius* species from tropical Africa: *L. angiocarpus* sp. nov. and *L. dolichocaulis* comb. nov. *Mycol. Res.* 108: 1042-1052.
- Geml J., Laursen G.A., Timling I., McFarland J.M., Booth M.G., Lennon N., Nusbaum C. & Taylor D.L. (2009) Molecular phylogenetic diversity assessment of arctic and boreal ectomycorrhizal *Lactarius* Pers. (Russulales; Basidiomycota) in Alaska, based on soil and sporocarp DNA. *Molec. Ecol.* 18 (10): 2213-2227.
- Heilmann-Clausen J., Verbeken A. & Vesterholt J. (1998) The genus *Lactarius*. *Fungi of Northern Europe* 2: 287 p.
- Larsson L. & Larsson K.-H. (2003) Phylogenetic relationships of russuloid basidiomycetes with emphasis on aphylophoralean taxa. *Mycologia* 95: 1037-1065.
- Le H.T., Verbeken A., Nuytinck J., Lumyong S. & Desjardin D. (2007) *Lactarius* in Northern Thailand, 3 – *Lactarius* subgenus *Lactariopsis*. *Mycotaxon* 102: 281-291.
- Miller S.L., Larsson E., Larsson K.H., Verbeken A.

- & Nuytinck J. (2006) Perspectives in the new Russulales. *Mycologia* **98**: 960-970.
- Nuytinck J. & Verbeken A. (2007) Species delimitation and phylogenetic relationships in *Lactarius* section *Deliciosi* in Europe. *Mycol. Res.* **111** (11): 1285-1297.
- Nuytinck J., Verbeken A., Delarue S. & Walleyn R. ("2003", publ. 2004) Systematics of European sequestrate lactarioid Russulaceae with spiny spore ornamentation. *Belg. J. Bot.* **136** (2): 145-153.
- Oberwinkler F. (1977) Das neue System der Basidiomyceten. In: Frey W., Hurka H., Oberwinkler F. (eds), Beiträge zur Biologie der neideren Pflanzen. Gustav Fischer Verlag, Stuttgart, New York: pp. 59-104.
- Pegler D.N. (1969) Studies on African Agaricales. II. *Kew Bull.* **23**: 219-249.
- Riviere T., Diedhiou A.G., Diabate M., Senthilarasu G., Natarajan K., Verbeken A., Buyck B., Dreyfus B., Bena G. & Ba A.M. (2007) Genetic diversity of ectomycorrhizal Basidiomycetes from African and Indian tropical rain forests. *Mycorrhiza* **17**: 415-428.
- Singer R. (1942) Das System der Agaricales. II. *Annl. mycol.* **40**: 1-132.
- Stubbe D., Nuytinck J. & Verbeken A. (2008) *Lactarius* subgenus *Plinthogali* of Malaysia. *Fungal Diversity* **32**: 125-156.
- Stubbe D., Nuytinck J. & Verbeken A. (2010) Critical assessment of the *Lactarius gerardii* species complex (Russulales). *Fungal Biol.* **114**: 271-283.
- Stubbe D., Verbeken A. & Watling R. (2007) Blue-staining species of *Lactarius* subgenus *Plinthogali* of Malaysia. *Belgian J. Bot.* **140** (2): 197-212.
- Tedersoo L., Nilsson R.H., Abarenkov K., Jairus T., Sadam A., Saar I., Bahram M., Bechem E., Chuyong G. & Koljalg U. (2010) 454 Pyrosequencing and Sanger sequencing of tropical mycorrhizal fungi provide similar results but reveal substantial methodological biases. *New Phytol.* **188**: 291-301.
- Van de Putte K., De Kesel A., Nuytinck J. & Verbeken A. (2009) A new *Lactarius* species from Togo with an isolated position. *Cryptog., Mycol.* **30** (1): 1-6.
- Van de Putte K., Nuytinck J., Stubbe D., Le H.T. & Verbeken A. (2010) *Lactarius volemus* sensu lato (Russulales) from northern Thailand: morphological and phylogenetic species concepts explored. *Fungal Diversity* **45**: 99-130.
- Verbeken A. (1996) Studies in tropical African *Lactarius* species. 3. *Lactarius melanogalus* and related species. *Persoonia* **16**: 209-223.
- Verbeken A. (1997) Biodiversity of the genus *Lactarius* Pers. in tropical Africa. Part 1, text, 342 p. Part 2, plates and maps, 296 & 29 p. PhD thesis, Ghent University.
- Verbeken A. (1998) Studies in tropical African *Lactarius* species, 6 – A synopsis of the subgenus *Lactariopsis* (Henn.) R. Heim emend. *Mycotaxon* **66**: 378-418.
- Verbeken A. & Buyck B. (2002) Diversity and ecology of tropical ectomycorrhizal fungi in Africa. In: Watling R., Frankland J.C., Ainsworth A.M., Isaac S. & Robinson C. (eds) Tropical Mycology, vol. 1 – Macromycetes: pp. 11-24.
- Verbeken A. & Horak E. (1999) *Lactarius* (Basidiomycota) in Papua New Guinea. 1. Species of tropical lowlands habitats. *Austral. Syst. Bot.* **12**: 767-779.
- Verbeken A. & Walleyn R. (2010) *Lactarius*. *Fungus Flora of Tropical Africa* **1**: 271 p. National Botanic Garden of Belgium, Meise.
- Watling R., Lee S.S. & Turnbull E. (2002) The occurrence and distribution of putative ectomycorrhizal Basidiomycetes in a regenerating South-East Asian rainforest. In: Watling R., Frankland J.C., Ainsworth A.M., Isaac S. & Robinson C. (eds) Tropical Mycology, vol. 1 – Macromycetes: pp 25-44.