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## A short story of nearly everything in *Lactifluus* (*Russulaceae*)

E. De Crop<sup>1\*</sup>, L. Delgat<sup>1,2</sup>, J. Nuytinck<sup>1,3</sup>, R.E. Halling<sup>4</sup>, A. Verbeken<sup>1</sup>

<sup>1</sup>Ghent University, Department of Biology, Research group Mycology, K. L. Ledeganckstraat 35, 9000 Ghent, Belgium

<sup>2</sup>National Botanic Garden of Belgium (BR), Research Department, Domein van Bouchout, 1860 Meise, Belgium

<sup>3</sup>Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands

<sup>4</sup>The New York Botanical Garden, Institute of Systematic Botany, Bronx, NY 10458 USA

\*Corresponding author: Eske.DeCrop@UGent.be

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**Abstract:** Fungi are a large and hyper-diverse group with major taxa present in every ecosystem on earth. However, compared to other eukaryotic organisms, their diversity is largely understudied. Since the rise of molecular techniques, new lineages are being discovered at an increasing rate, but many are not accurately characterised. Access to comprehensive and reliable taxonomic information of organisms is fundamental for research in different disciplines exploring a variety of questions. A globally dominant ectomycorrhizal (ECM) fungal family in terrestrial ecosystems is the *Russulaceae* (*Russulales*, *Basidiomycota*) family. Amongst the mainly agaricoid *Russulaceae* genera, the ectomycorrhizal genus *Lactifluus* was historically least studied due to its largely tropical distribution in many underexplored areas and the apparent occurrence of several species complexes. Due to increased studies in the tropics, with a focus on this genus, knowledge on *Lactifluus* grew. We demonstrate here that *Lactifluus* is now one of the best-known ECM genera. This paper aims to provide a thorough overview of the current knowledge of *Lactifluus*, with information on diversity, distribution, ecology, phylogeny, taxonomy, morphology, and ethnomycological uses of species in this genus. This is a result of our larger study, aimed at building a comprehensive and complete dataset or taxonomic framework for *Lactifluus*, based on molecular, morphological, biogeographical, and taxonomical data as a tool and reference for other researchers.

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## INTRODUCTION

### Fungal diversity and the need for a solid taxonomic framework

Fungi are one of the largest and most diverse groups of organisms on Earth. There are currently about 148 000 fungal species described (Cheek *et al.* 2020), but recent studies estimate that this is only a fraction of a total of 2.2 (6.5%)–3.8 (3.8 %) M fungal species (Hawksworth 2001, O’Brien *et al.* 2005, Schmit & Mueller 2007, Blackwell 2011, Hawksworth & Lücking 2017). Compared to flowering plants or vertebrates, where 80–90 % of estimated species numbers are described (Convention on Biological Diversity, CBD 2006, Pimm & Joppa 2015, Kew 2016), there is a major gap for fungi. The majority of fungi are undescribed; many are microscopic and cannot be cultured, many lineages have only been recovered with environmental sequencing, or they exist in remote and un- or underexplored areas. Likewise, even mushroom-forming lineages contain many undescribed taxa (Blackwell 2011).

One ecological guild with many mushroom-forming lineages is the ectomycorrhizal (ECM) fungi. Although various ECM fungi are well-studied, many species remain undiscovered or

undescribed. For example, a seven-year-long study of ECM fungi in the Guiana Shield (Guyana) led to the discovery of one new ECM genus (Sanchez-Garcia *et al.* 2016) and new taxon discovery rates were estimated to be around 60–70 % (Henkel *et al.* 2012). In tropical Africa, Verbeken & Buyck (2002) estimated the number of all undescribed ECM species to be double the number of described taxa.

This large gap between the estimated and the actual described number of fungal species became especially obvious since the development of next generation sequencing (NGS) tools, where one soil sample could reveal hundreds of potential new species (*e.g.* in Tedersoo *et al.* 2014). The use of these techniques results in a much faster molecular “species” discovery (operational taxonomical units, OTU’s) than the more traditional species discovery, based on a combination of morphology, molecular data and species delimitation techniques. Unfortunately, as most fungal groups are still underexplored, the majority of these OTU’s remain unidentified, especially at species level.

A solid taxonomic framework is needed by which the metagenomic sequences generated can be compared and linked to actual species. The existence of such a framework is rare, especially in tropical or underexplored areas, while when extant, it often only holds basic information. This has major

complications regarding the conclusions that can be drawn from such incomplete data. The compilation of detailed species descriptions, however, is a meticulous and time-consuming task, and a morphological description tied to a physical type specimen is needed at a minimum. This is not always easily available for fungi, for example for many microscopic fungi (Taylor *et al.* 2006, Hibbett 2016), or for species only known from environmental sequences.

The predominantly tropical ECM genus *Lactifluus* (*Russulaceae*) has been extensively studied during recent years, resulting in the availability of a solid phylogeny, combined with a revised taxonomy (De Crop *et al.* 2017). With this review, we want to contribute to the knowledge of this genus and supplement its taxonomic framework with detailed information on diversity, morphology, and ecology. We give an overview of all 224 described *Lactifluus* species, accompanied by information on their subgeneric classification and quality of those data. We discuss the distribution of *Lactifluus* species and their ecology, and we explore publicly available metabarcoding data and discuss their impact on our current knowledge of *Lactifluus*. We provide a thorough overview of macro- and microscopical features of *Lactifluus* species and discuss their use as renewable natural resources.

## Russulales

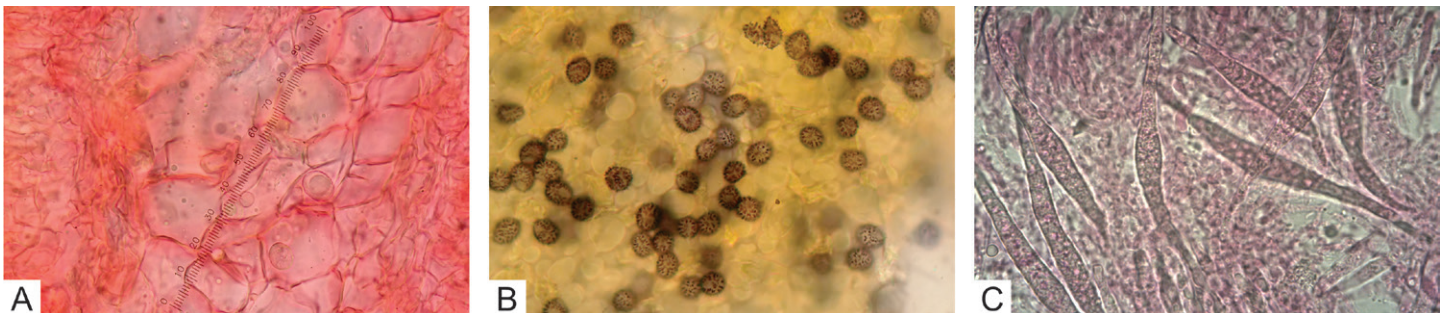
In 1796 and 1797, Persoon described the genera *Russula* and *Lactarius* as discrete genera of agaricoid fungi, differing primarily from other genera by their brittle context. *Russula* species have sporocarps with strikingly coloured caps and *Lactarius* species exude a milk-like solution (*latex*) when sporocarps are bruised (Persoon 1796, 1797). Due to their striking morphological characteristics, *Lactarius* and *Russula* were later classified in their own order, *Russulales*, within *Agaricomycetes* with pale-coloured spores (Kreisel 1969, Oberwinkler 1977). Morphologically, this classification was mainly supported by microscopical features such as sphaerocytes in the trama, responsible for the brittle context, amyloid spore ornamentation and a gloeoplerous hyphal system (*i.e.* hyphae with long cells that contain numerous oil droplets in the cytoplasm; Fig. 1). Combinations of these characters were also found in several taxa with other basidiocarp types and were included in this order (Romagnesi 1948, Donk 1971, Oberwinkler 1977). Next to the agaricoid *Russula* and *Lactarius*, *Russulales* further comprised coral fungi (*Artomyces*; Jülich 1981), poroid fungi (*Heterobasidion*), hydroid fungi (*Echinodontium*, and *Hericium*) and corticioid fungi (*Gloeocystidiellum*, *Boidinia*, and *Gloiothele*).

Over the last two decades, molecular phylogenetic research contributed to a revision of the *Russulales*. Molecular data showed strong support for a russuloid clade with corticioid, resupinate, discoid, clavarioid, pileate, effused-reflexed, and gasteroid taxa with smooth, poroid, hydroid, lamellate or labyrinthoid hymenophores (Fig. 2), but not all shared sphaerocytes and amyloid spore ornamentation (Hibbett *et al.* 1997, Hibbett & Binder 2002, Larsson & Larsson 2003, Larsson *et al.* 2004, Miller *et al.* 2006, Buyck *et al.* 2008). The *Russulales* order is morphologically supported by the presence of gloeocystidia or a gloeoplerous hyphal system (Larsson & Larsson 2003, Miller *et al.* 2006).

*Russula*, *Lactarius* and some pleurotoid and sequestrate genera form a discrete group within this clade and circumscribe the *Russulaceae* (Redhead & Norvell 1993, Miller *et al.* 2001, Larsson & Larsson 2003, Eberhardt & Verbeken 2004, Nuytinck *et al.* 2004).

## Russulaceae

Before 2000, *Russulaceae* classification was mainly based on morphological characters such as sporocarp type. Agaricoid species were placed in *Russula* and *Lactarius*. Pleurotoid species were placed in *Pleurogala*. Sequestrate species were classified as *Arcangeliella*, *Gastrolactarius*, *Zelleromyces*, *Cystangium*, *Elasmomyces*, *Gymnomyces*, *Martellia* and *Macowanites*. Veiled species were placed in the genus *Lactariopsis*. Generic concepts in the mushroom-forming *Russulaceae* changed when hypotheses were advanced that pleurotoid, sequestrate and veiled forms originated several times, both in *Lactarius* and *Russula*. Morphological and molecular studies of pleurotoid *Russulaceae* species (Verbeken 1998, Buyck & Horak 1999, Henkel *et al.* 2000), supported placement in either *Russula* or *Lactarius*. Hence, *Pleurogala* (Redhead & Norvell 1993) was abandoned. Likewise, sequestrate species originally allied to *Lactarius* (*Arcangeliella*, *Gastrolactarius* and *Zelleromyces*) and *Russula* (*Cystangium*, *Elasmomyces*, *Gymnomyces*, *Martellia* and *Macowanites*) were reclassified (Calonge & Martín 2000, Miller *et al.* 2001, Binder & Bresinsky 2002, Desjardin 2003, Nuytinck *et al.* 2003, Eberhardt & Verbeken 2004, Lebel & Tonkin 2007, Verbeken *et al.* 2014). Species with a velum occur both in *Lactarius* and *Russula*. This is in line with the standpoint of Verbeken (1998) and abandons the separate genus in which they were placed by other authors (Hennings 1902, Heim 1937, Redhead & Norvell 1993). From 2003 on, molecular analyses indicated that *Russulaceae* also contains several corticioid taxa from three genera: *Boidinia*,

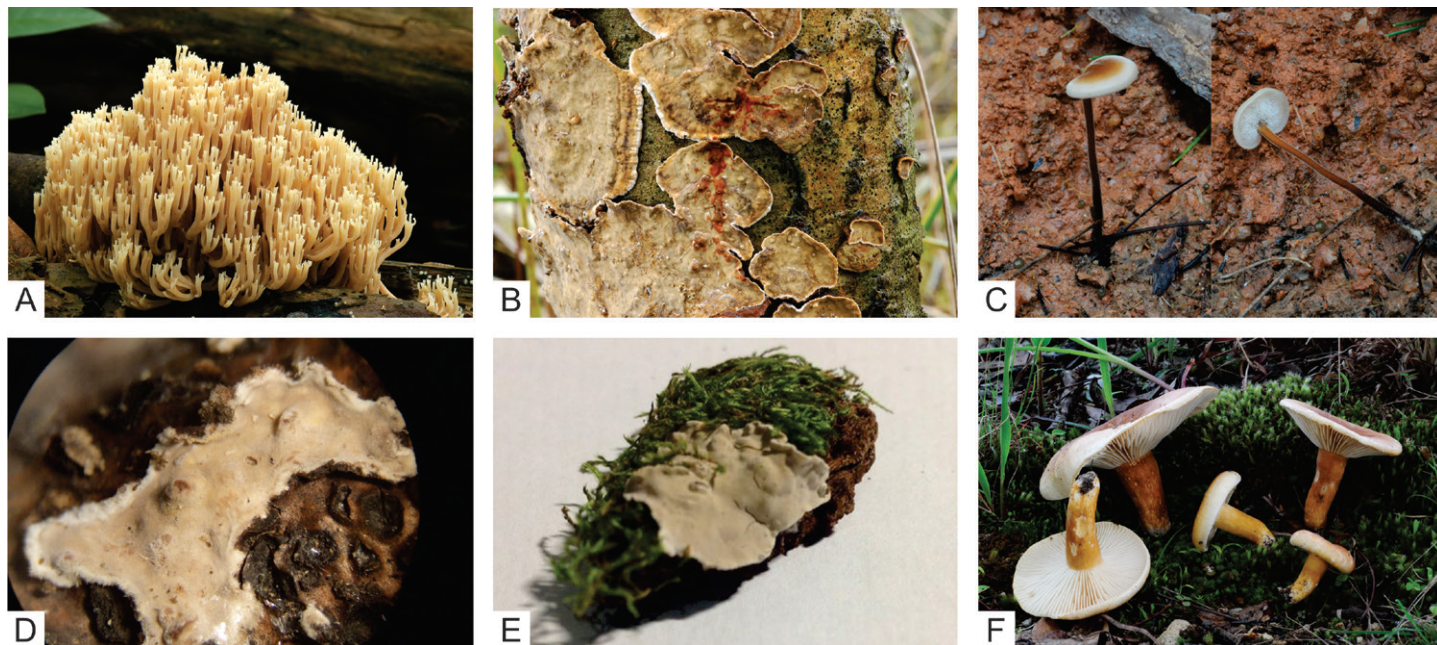


**Fig. 1.** A. Sphaerocytes within the trama of *Lactifluus* sp. (EDC 14-060). B. Amyloid spore ornamentation of *Lf. russulisporus* (REH 9398). C. Gloeocystidia in *Gloeocystidiellum porosum* [Photographs by E. De Crop (A, B) and N. Schoutteten (C)].

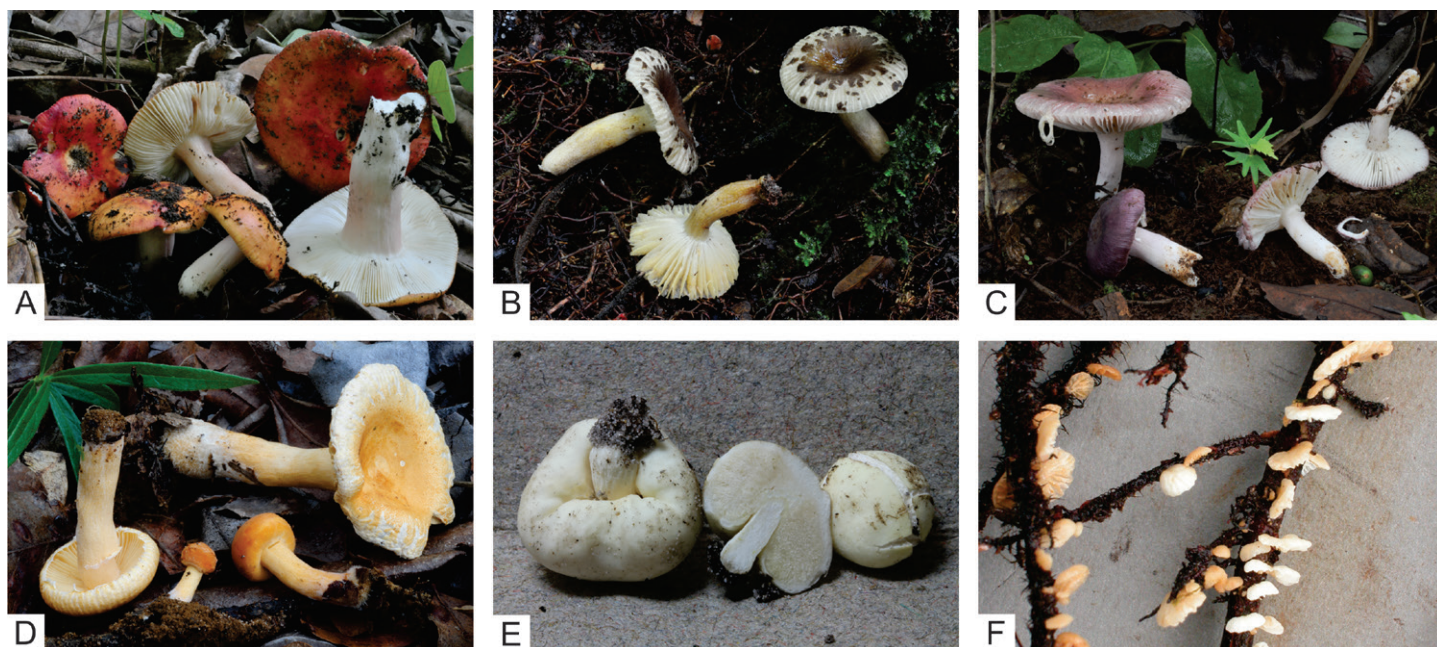
*Gloeopeniophorella* and *Pseudoxenasma* (Larsson & Larsson 2003, Miller *et al.* 2006).

Buyck *et al.* (2008) constructed a phylogeny of the agaricoid *Russulaceae* genera. They focused on more tropical taxa than previous studies. In some cases, tropical *Lactarius* and *Russula* species turned out to be indistinguishable from each other based on morphology. Their results showed that *Lactarius* and *Russula* were not two well-defined and separate clades. *Russula* appears to be monophyletic only if a small group of species is excluded. The genus *Russula sensu* Buyck *et al.* (2008) is the

largest *Russulaceae* genus, with more than 750–900 species described all over the world (Kirk *et al.* 2008, Buyck & Atri 2011, Looney *et al.* 2016). The majority of *Russula* species is agaricoid, but some are pleurotoid or sequestrate, and veiled species are also known (Fig. 3). All species lack latex production and lack pseudocystidia. They are characterised by a brittle context caused by sphaerocytes in the context and trama, and by the presence of bright pigments, especially in the cap (usually contrasting with a white or whitish stipe and gills that vary from white to yellow, depending on the colour of the spores).



**Fig. 2.** Different types of sporocarps and hymenophores within the *Russulales*. **A.** Clavarioid sporocarp of *Artomyces pyxidatus*. **B.** Effused-reflexed sporocarps with smooth hymenium of *Stereum rugosum*. **C.** Pileate sporocarp with hydroid hymenium of *Auriscalpium* sp. (EDC 14-511). **D.** Resupinate sporocarp with smooth hymenium of *Peniophora incarnata*. **E.** Discoid sporocarp with smooth hymenium of *Aleurodiscus disciforme*. **F.** Pileate sporocarp with lamellate hymenium of *Lactifluus urens* (EDC 12-032) [Photographs by R. Walley (A, B), E. De Crop (C, F) and N. Schoutteten (D, E)].



**Fig. 3.** Different *Russula* species. **A.** Agaricoid species *Russula* sp. (EDC 12-063). **B.** Agaricoid species *Russula* sp. (EDC 12-058). **C.** Annulate agaricoid species *Russula* sp. (EDC 14-381). **D.** Annulate agaricoid species *Russula* sp. (EDC 14-040). **E.** Secotoid species *Russula* sp. (former *Macowanites* sp.) (REH 9496). **F.** Pleurotoid species *R. campinensis* (TH 9252) [Photographs by E. De Crop (A–D), R. Halling (E) and T. Henkel (F)].

A small group of species excluded from the former *Russula* forms a clade together with some *Lactarius* species. This clade was described as the new genus *Multifurca* (Buyck et al. 2008). The former *Russula* subsect. *Ochricompactae*, the Asian species *Russula zonaria* and the American species *Lactarius furcatus* were included in this genus. *Multifurca* species are characterised by furcate lamellae, dark yellowish lamellae and spore-prints, a strong zonation of pileus and context (Fig. 4). Latex is only present in some *Multifurca* species and the presence of latex seems to be a variable character in this genus, even within one species. Only 11 *Multifurca* species are currently known (Buyck et al. 2008, Wang & Liu 2010, Lebel et al. 2013, Wang et al. 2018) from three biogeographic regions: Asia, Australasia and North/Central America.

The remainder of *Lactarius* was split in two different clades (Buyck et al. 2008). One large clade contained the majority of described milkcap species (about 75 % of those known) and one smaller clade with mainly tropical species. At that time, this smaller clade contained the type species of *Lactarius*: *Lactarius piperatus*. A proposal to conserve *Lactarius* (hereafter abbreviated as *L.*) with a conserved type species, *Lactarius torminosus* was accepted (Buyck et al. 2010, McNeill et al. 2011) and the name *Lactarius* has been retained for the larger

clade (Fig. 5). The subgenera *L.* subg. *Lactarius* (the former *L.* subg. *Piperites*), *L.* subg. *Russularia*, and *L.* subg. *Plinthogalus*, together with several undescribed tropical lineages that need to be described at subgenus level (Nuytinck et al. 2020), now constitute the larger milkcap genus *Lactarius sensu* Buyck et al. (2008), Buyck et al. (2010). Approximately 450 species are accepted in *Lactarius*, which occurs worldwide but has its main distribution in the temperate and boreal regions.

The smaller milkcap group, with approximately 200 described species, is named *Lactifluus* (hereafter abbreviated as *Lf.*) and is automatically typified by *Agaricus lactifluus*, currently known as *Lf. volemus* (Buyck et al. 2010). New combinations were made in a series of three papers for the different subgenera (Verbeken et al. 2011, Stubbe et al. 2012b, Verbeken et al. 2012).

The two milkcap genera, *Lactarius* and *Lactifluus*, are well-supported based on molecular inference, but no synapomorphic characteristics have been found to consistently separate both genera. The morphological distinction between the genera is thus far based on several trends:

*Characteristics of the pileus – Lactifluus* is generally characterised by the complete absence of zonate and viscoso to glutinous caps, while it contains many species with velvety caps, and even some with veiled caps. *Lactarius* however, contains



Fig. 4. Different *Multifurca* species. A. *M. zonaria* (FH 12-009). B. Detail on zonate context of *M. zonaria*. C. *M. pseudofurcata* (xp2-20120922-01) [Photographs by F. Hampe (A), A. Verbeken (B) and G. Jiayu (C)].



Fig. 5. Different *Lactarius* species. A. *L. torminosus* (JN 2011-087). B. *L. deliciosus* (JN 2003-055). C. *L. lacunarum*. D. *L. tenellus* (EDC 14-064). E. *L. chromospermus* (EDC 14-108). F. *L. stephensii* (EDC 14-575) [Photographs by J. Nuytinck (A, B), A. Verbeken (C) and E. De Crop (D–F)].

many species with zonate and viscose to glutinous caps (Verbeke & Nuytinck 2013). Veiled species are not known in *Lactarius*.

*Sporocarp characteristics* – pleurotoid milkcap species are so far only known in *Lactifluus* (Buyck *et al.* 2008, Verbeke & Nuytinck 2013), sequestrate species are most common in *Lactarius*, but were recently found to occur in *Lactifluus* too (Lebel *et al.* 2016).

*Hymenophoral trama* – the hymenophoral trama of *Lactifluus* species is mostly composed of sphaerocytes, which is also common in *Russula* (Verbeke & Nuytinck 2013). In contrast, these sphaerocytes are only rarely observed in *Lactarius* species, where the hymenophoral trama most often is composed of filamentous hyphae only.

*Thick-walled elements* – thick-walled elements in the pileipellis, stipitipellis and hymenophoral trama are common in the genus *Lactifluus*, while they are hardly observed in the genus *Lactarius* (Verbeke & Nuytinck 2013).

These features might be helpful when identifying milkcap species, but they are not exclusive. There are species, especially in the tropics, in which a molecular characterisation is needed to determine to which genus they belong.

## THE GENUS *LACTIFLUUS*

### Diversity and distribution

The milkcap genus *Lactifluus* is predominantly present in the tropics. Mainly due to this distribution, *Lactifluus* has long been understudied compared to its sister *Lactarius*. Before the start of our study of the genus *Lactifluus* at the end of 2010, the highest diversity of the genus was known from sub-Saharan Africa, with 60 species described (Verbeke & Walley 2010), and Asia, with 23 species described (Le *et al.* 2007, Stubbe *et al.* 2010, Van de Putte *et al.* 2010). However, the genus also appears to be well-represented in South America, as new species are being discovered since more South American habitats are being explored (Henkel *et al.* 2000, Miller *et al.* 2002, Smith *et al.* 2011, Sá *et al.* 2013, Sá & Wartchow 2013, Crous *et al.* 2017, Delgat *et al.* 2019, 2020, Duque Barbosa *et al.* 2020), and the majority of the proposed South American *Lactarius* species turns out to belong in *Lactifluus* (Pegler & Fiard 1979, Singer *et al.* 1983, Miller *et al.* 2002). Since 2010, 78 new *Lactifluus* species have been described: 34 from Asia (Stubbe *et al.* 2012a, Van de Putte *et al.* 2012, Wang *et al.* 2012, 2015, Morozova *et al.* 2013, Latha *et al.* 2016, Li *et al.* 2016, Uniyal *et al.* 2016, Zhang *et al.* 2016, Das *et al.* 2017, Hyde *et al.* 2017, Song *et al.* 2017, De Crop *et al.* 2018, Liu *et al.* 2018, Song *et al.* 2018, Bera & Das 2019, Dierickx *et al.* 2019a, b, Phookamsak *et al.* 2019), 16 from Africa (De Crop *et al.* 2012, Maba *et al.* 2014, 2015a, b, De Crop *et al.* 2016, 2019, Delgat *et al.* 2017, De Lange *et al.* 2018), 20 from the Neotropics (Miller *et al.* 2012, Montoya *et al.* 2012, Sá *et al.* 2013, Sá & Wartchow 2013, Wartchow *et al.* 2013, Crous *et al.* 2017, 2019, Delgat *et al.* 2019, 2020, Sá *et al.* 2019, Duque Barbosa *et al.* 2020, Silva *et al.* 2020), seven from Australasia (Stubbe *et al.* 2012a, Kropp 2016, Dierickx *et al.* 2019a, b, Crous *et al.* 2020a, b), and one species from Europe (Van de Putte *et al.* 2016). This brings the total number of described *Lactifluus* species to 226. However, recent phylogenetic studies suggest that there are more lineages that represent new species (De Crop *et al.* 2017; Delgat & De Crop unpubl.). De Crop (2016) performed a worldwide phylogeny of 1 306 *Lactifluus* ITS sequences on which species were delimited using the GMYC method (Pons *et al.*

2006). This resulted in 369 putative *Lactifluus* species. Based on this number of species and using a species accumulation curve, the total number of *Lactifluus* species was estimated to be around 530 species (De Crop 2016, He *et al.* 2019, Nuytinck *et al.* 2020). Although this is a rough estimate, it indicates that the majority of *Lactifluus* species is still undescribed. Many known species-level clades are not described yet because they lack detailed documentation, or they are singletons, and describing species is a laborious work.

So far, none of the *Lactifluus* species occurs with certainty on two or more continents (Table 1). Although, some species records used to suggest otherwise. For example, collections identified as the North American *Lf. luteolus* based on morphology were also found in Europe, Asia and Australia. All collections have typical cream-beige sporocarps, which exude white milk that quickly stains brownish. However, a recent molecular study of Dierickx *et al.* (2019b) showed that *Lf. luteolus* is a North American species. The records from other continents represent different species. Another example is the North American species *Lf. hygrophoroides* which was also reported from Asia. However, preliminary molecular results show the existence of multiple clades identified as *Lf. hygrophoroides*, each clade occurring on one continent, instead of one intercontinental species (De Crop, unpubl.). The recently described Australian species *Lf. austropiperatus* forms a strongly supported clade with a Thai specimen, however, the authors maintain the Australian material as distinct until further collections from Thailand can be examined and sequenced (Crous *et al.* 2020b). In all other known cases of possible intercontinental species, molecular inference rejected this possibility (Stubbe *et al.* 2010, Van de Putte *et al.* 2010, De Crop *et al.* 2014).

In *Russulaceae* in general, intercontinental conspecificity appears to be rare. In *Lactarius* it seems to be more common than in *Lactifluus*. For example, Nuytinck *et al.* (2007) reported *Lactarius deliciosus* to occur in Europe and China, Nuytinck *et al.* (2010) found *L. controversus* to be conspecific between Europe and North America, and Wisitrassameewong (2015) reported *L. badiusanguineus* to occur both in Europe and China. Some records of species occurring on two or more continents are due to the introduction of their host trees in a new continent. For example, *L. hepaticus* was introduced in Madagascar and South Africa, when European *Pinus* trees were introduced for cultivation (Verbeke & Walley 2010).

### Ecology

Species of the genus *Lactifluus* are found in subtropical and tropical regions and to a lesser extent in temperate areas, in a wide range of vegetation types, including tropical and subtropical rain forests, subtropical dry forests, monsoon forests, tree savannahs, Mediterranean woodlands, temperate broadleaf and coniferous forests and montane forests. Basidiocarps are commonly found on soil, but in tropical habitats with high humidity they are sporadically found on stems or epigeous roots of trees, such as *Lf. brunellus* on stems of *Dicymbe corymbosa* (Miller *et al.* 2002), *Lf. multiceps* and *Lf. raspei* on plant seedlings (Fig. 6).

*Lactifluus*, *Lactarius*, *Multifurca* and *Russula* species are ectomycorrhizal fungi, while the corticioid *Russulaceae* taxa are reported to be saprotrophic (Larsson & Larsson 2003, Miller *et al.* 2006, Tedersoo *et al.* 2010a). However, the latter is questioned by Miller *et al.* (2006), who suggest that these corticioid taxa might also be ectomycorrhizal symbionts.

**Table 1.** List of described *Lactifluus* species, together with the current authors, the original publication, and biogeographical region of origin. Biogeographic regions are based on biogeographic realms (<https://ecoregions2017.appspot.com/>), with three major differences: Western Palearctic (Western part of the Palearctic realm), Asia (Eastern part of the Palearctic realm combined with the Indo-Malay realm), and Australasia (Australasian realm combined with the Oceanian realm). See Supplementary data (Figure S1) for an overview of the biogeographical regions used. Varieties of species are not included in this list. See supplementary data (Table S1) for more information on the classification of the *Lactifluus* species.

Name	Current authors	Original publication	Biogeographical region
1 <i>Lf. acicularis</i>	(Van de Putte & Verbeken) Van de Putte	Van de Putte <i>et al.</i> (2010)	Asia
2 <i>Lf. acrisimus</i>	(Verbeken & Van Rooij) Nuytinck	Van Rooij <i>et al.</i> (2003)	Afrotropics
3 <i>Lf. adustus</i>	(Rick) Delgat <i>comb. nov.</i>	Rick (1938)	Neotropics
4 <i>Lf. albocinctus</i>	(Verbeken) Verbeken	Verbeken <i>et al.</i> (2000)	Afrotropics
5 <i>Lf. albomembranaceus</i>	De Wilde & Van de Putte	De Crop <i>et al.</i> (2016)	Afrotropics
6 <i>Lf. albopicri</i>	T. Lebel & L. Tegart	Crous <i>et al.</i> (2020b)	Australasia
7 <i>Lf. allardii</i>	(Coker) De Crop	Coker (1918)	Nearctic
8 <i>Lf. amazonensis</i>	(Singer) Silva-Filho & Wartchow	Singer <i>et al.</i> (1983)	Neotropics
9 <i>Lf. ambicystidiatus</i>	X.H. Wang	Wang <i>et al.</i> (2015)	Asia
10 <i>Lf. angustifolius</i>	(Hesler & A.H. Sm.) De Crop	Hesler & Smith (1979)	Nearctic
11 <i>Lf. angustus</i>	(R. Heim & Gooss.-Font.) Verbeken	Heim (1955)	Afrotropics
12 <i>Lf. annulatoangustifolius</i>	(Beeli) Buyck	Beeli (1936)	Afrotropics
13 <i>Lf. annulatolongisporus</i>	Maba	Maba <i>et al.</i> (2015a)	Afrotropics
14 <i>Lf. annulifer</i>	(Singer) Nuytinck	Singer <i>et al.</i> (1983)	Neotropics
15 <i>Lf. arcuatus</i>	(Murrill) Delgat	Murrill (1941)	Western Palearctic
16 <i>Lf. armeniacus</i>	De Crop & Verbeken	Li <i>et al.</i> (2016)	Asia
17 <i>Lf. arsenei</i>	(R. Heim) Verbeken	Heim (1938)	Afrotropics
18 <i>Lf. atrovelutinus</i>	(J.Z. Ying) X.H. Wang	Ying (1991)	Asia
19 <i>Lf. aurantiifolius</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
20 <i>Lf. aurantiorugosus</i>	Sá & Wartchow	Sá & Wartchow (2013)	Neotropics
21 <i>Lf. aurantiotinctus</i>	Kropp	Kropp (2016)	Australasia
22 <i>Lf. aureifolius</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
23 <i>Lf. auriculiformis</i>	Verbeken & Hampe	De Crop <i>et al.</i> (2018)	Asia
24 <i>Lf. austropiperatus</i>	T. Lebel & L. Tegart	Crous <i>et al.</i> (2020b)	Australasia
25 <i>Lf. austrovolemus</i>	(Hongo) Verbeken	Hongo (1973)	Australasia
26 <i>Lf. batistae</i>	Wartchow, J.L. Bezerra & M. Cavalc.	Wartchow <i>et al.</i> (2013)	Neotropics
27 <i>Lf. bertillonii</i>	(Neuhoff ex Z. Schaef.) Verbeken	Schaefer (1979)	Western Palearctic
28 <i>Lf. bhandaryi</i>	Verbeken & De Crop	De Crop <i>et al.</i> (2018)	Asia
29 <i>Lf. bicapillus</i>	Lescroart & De Crop	De Crop <i>et al.</i> (2019)	Afrotropics
30 <i>Lf. bicolor</i>	(Masse) Verbeken	Masse (1914)	Asia
31 <i>Lf. brachystegiae</i>	(Verbeken & C. Sharp) Verbeken	Verbeken <i>et al.</i> (2000)	Afrotropics
32 <i>Lf. brasiliensis</i>	(Singer) Silva-Filho & Wartchow	Singer <i>et al.</i> (1983)	Neotropics
33 <i>Lf. braunii</i>	(Rick) Silva-Filho & Wartchow	Rick (1930)	Neotropics
34 <i>Lf. brunellus</i>	(S.L. Mill., Aime & T.W. Henkel) De Crop	Miller <i>et al.</i> (2002)	Neotropics
35 <i>Lf. brunneocarpus</i>	Maba	Maba <i>et al.</i> (2015a)	Afrotropics
36 <i>Lf. brunneoviolascens</i>	(Bon) Verbeken	Bon (1971)	Western Palearctic
37 <i>Lf. brunnescens</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
38 <i>Lf. burkinabei</i>	Maba	Maba <i>et al.</i> (2015a)	Afrotropics
39 <i>Lf. caatingae</i>	Sá & Wartchow	Sá <i>et al.</i> (2019)	Neotropics
40 <i>Lf. caeruleitinctus</i>	(Murrill) Delgat	Murrill (1939)	Western Palearctic
41 <i>Lf. caliendrifer</i>	Froyen & De Crop	Dierickx <i>et al.</i> (2019)	Asia
42 <i>Lf. caperatus</i>	(R. Heim & Gooss.-Font.) Verbeken	Heim (1955)	Afrotropics
43 <i>Lf. caribaeus</i>	(Pegler) Verbeken	Pegler & Fiard (1979)	Neotropics
44 <i>Lf. carmineus</i>	(Verbeken & Walley) Verbeken	Verbeken <i>et al.</i> (2000)	Afrotropics
45 <i>Lf. catarinensis</i>	J. Duque, M.A. Neves & M. Jaegger	Duque Barbosa <i>et al.</i> (2020)	Neotropics

Table 1. (Continued).

Name	Current authors	Original publication	Biogeographical region
46 <i>Lf. ceraceus</i>	Delgat & M. Roy	Crous (2017)	Neotropics
47 <i>Lf. chamaeleontinus</i>	(R. Heim) Verbeken	Heim (1955)	Afrotropics
48 <i>Lf. chiapanensis</i>	(Montoya, Bandala-Muñoz & Guzmán) De Crop	Montoya <i>et al.</i> (1996)	Neotropics
49 <i>Lf. chrysocarpus</i>	E. S. Popov & O.V. Morozova	Morozova <i>et al.</i> (2013)	Asia
50 <i>Lf. claricolor</i>	(R. Heim) Verbeken	Heim (1938)	Afrotropics
51 <i>Lf. clarkeae</i>	(Cleland) Verbeken	Cleland (1927)	Australasia
52 <i>Lf. coccolobae</i>	(O. K. Miller & Lodge) Delgat	Miller <i>et al.</i> (2000)	Neotropics
53 <i>Lf. cocosmus</i>	(Van de Putte & De Kesel) Van de Putte	Van de Putte <i>et al.</i> (2009)	Afrotropics
54 <i>Lf. conchatulus</i>	(Stubbe & H.T. Le) Stubbe	Stubbe <i>et al.</i> (2012)	Asia
55 <i>Lf. coniculus</i>	Stubbe & Verbeken	Stubbe <i>et al.</i> (2012)	Asia
56 <i>Lf. corbula</i>	(R. Heim & Gooss.-Font.) Verbeken	Heim (1955)	Afrotropics
57 <i>Lf. corrugis</i>	(Peck) Kuntze	Peck (1879)	Nearctic
58 <i>Lf. crocatus</i>	Van de Putte & Verbeken	Van de Putte <i>et al.</i> (2010)	Asia
59 <i>Lf. cyanovirescens</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
60 <i>Lf. deceptivus</i>	(Peck) Kuntze	Peck (1885)	Nearctic
61 <i>Lf. denigricans</i>	(Verbeken & Karhula) Verbeken	Verbeken (1996b)	Afrotropics
62 <i>Lf. densifolius</i>	(Verbeken & Karhula) Verbeken	Verbeken (1996a)	Afrotropics
63 <i>Lf. dinghuensis</i>	Jianbin	Zhang <i>et al.</i> (2016)	Asia
64 <i>Lf. dissitus</i>	Van de Putte, K. Das & Verbeken	Van de Putte <i>et al.</i> (2012)	Asia
65 <i>Lf. distans</i>	(Peck) Kuntze	Peck (1873)	Nearctic
66 <i>Lf. distantifolius</i>	Van de Putte, Stubbe & Verbeken	Van de Putte <i>et al.</i> (2010)	Asia
67 <i>Lf. domingensis</i>	Delgat & Angelini	Delgat <i>et al.</i> (2019)	Neotropics
68 <i>Lf. dunensis</i>	Sá & Wartchow	Sá <i>et al.</i> (2013)	Neotropics
69 <i>Lf. dwaliensis</i>	(K. Das, J.R. Sharma & Verbeken) K. Das	Das <i>et al.</i> (2003)	Asia
70 <i>Lf. echinatus</i>	(Thiers) De Crop <i>comb. nov.</i>	Thiers (1957)	Nearctic
71 <i>Lf. edulis</i>	(Verbeken & Buyck) Buyck	Buyck (1994)	Afrotropics
72 <i>Lf. emergens</i>	(Verbeken) Verbeken	Verbeken <i>et al.</i> (2000)	Afrotropics
73 <i>Lf. epitheliosus</i>	(Buyck & Courtec.) Delgat <i>comb. nov.</i>	Courtecuisse & Buyck (1991)	Neotropics
74 <i>Lf. fazaensis</i>	Maba, Yorou & Guelly	Maba <i>et al.</i> (2014)	Afrotropics
75 <i>Lf. flammans</i>	(Verbeken) Verbeken	Verbeken (1995)	Afrotropics
76 <i>Lf. flavellus</i>	Maba & Guelly	Maba <i>et al.</i> (2015b)	Afrotropics
77 <i>Lf. flocktonae</i>	(Cleland & Cheel) Lebel	Cleland & Cheel (1919)	Australasia
78 <i>Lf. foetens</i>	(Verbeken) Verbeken	Van Rooij <i>et al.</i> (2003)	Afrotropics
79 <i>Lf. fuscomarginatus</i>	(Montoya, Bandala & Haug) Delgat	Montoya <i>et al.</i> (2012)	Neotropics
80 <i>Lf. genevieveae</i>	(Stubbe & Verbeken) Stubbe	Stubbe <i>et al.</i> (2012)	Australasia
81 <i>Lf. gerardiellus</i>	Wisitrassameewong & Verbeken	De Crop <i>et al.</i> (2018)	Asia
82 <i>Lf. gerardii</i>	(Peck) Kuntze	Peck (1874)	Nearctic
83 <i>Lf. glaucescens</i>	(Crossl.) Verbeken	Crossland (1900)	Western Palearctic
84 <i>Lf. goossensiae</i>	(Beeli) Verbeken	Beeli (1928)	Afrotropics
85 <i>Lf. guadeloupensis</i>	Delgat & Courtec.	Delgat <i>et al.</i> (2020)	Neotropics
86 <i>Lf. guanensis</i>	Delgat & Lodge	Crous <i>et al.</i> (2019)	Neotropics
87 <i>Lf. guellii</i>	Maba	Maba <i>et al.</i> (2015a)	Afrotropics
88 <i>Lf. gymnocarpoides</i>	(Verbeken) Verbeken	Verbeken (1995)	Afrotropics
89 <i>Lf. gymnocarpus</i>	(R. Heim ex Singer) Verbeken	Singer (1948)	Afrotropics
90 <i>Lf. hallingii</i>	Delgat & De Wilde	Delgat <i>et al.</i> (2019)	Neotropics
91 <i>Lf. heimii</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
92 <i>Lf. holophyllus</i>	H. Lee & Y.W. Lim	Hyde <i>et al.</i> (2017)	Asia
93 <i>Lf. hora</i>	Stubbe & Verbeken	Stubbe <i>et al.</i> (2012)	Asia

Table 1. (Continued).

Name	Current authors	Original publication	Biogeographical region
94 <i>Lf. hygrophoroides</i>	(Berk. & M.A. Curtis) Kuntze	Berkeley & Curtis (1859)	Nearctic
95 <i>Lf. igniculus</i>	O.V. Morozova & E.S. Popov	Morozova <i>et al.</i> (2013)	Asia
96 <i>Lf. ignifluus</i>	(Vrinda & C. K. Pradeep) De Crop <i>comb. nov.</i>	Vrinda <i>et al.</i> (2002)	Asia
97 <i>Lf. indicus</i>	K.N.A. Raj & Manim.	Latha <i>et al.</i> (2016)	Asia
98 <i>Lf. indovolemus</i>	I. Bera & K. Das	Bera & Das (2019)	Asia
99 <i>Lf. indusiatus</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
100 <i>Lf. inversus</i>	(Gooss.-Font. & R. Heim) Verbeken	Heim (1955)	Afrotropics
101 <i>Lf. kigomaensis</i>	De Crop & Verbeken	De Crop <i>et al.</i> (2012)	Afrotropics
102 <i>Lf. kivuensis</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
103 <i>Lf. lactiglaucus</i>	P. Leonard & Dearnaley	Crous <i>et al.</i> (2020a)	Australasia
104 <i>Lf. laevigatus</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
105 <i>Lf. lamprocystidiatus</i>	(Verbeken & E. Horak) Verbeken	Verbeken & Horak (2000)	Australasia
106 <i>Lf. latifolius</i>	(Gooss.-Font. & R. Heim) Verbeken	Heim (1955)	Afrotropics
107 <i>Lf. laeae</i>	Stubbe & Verbeken	Stubbe <i>et al.</i> (2012)	Asia
108 <i>Lf. leonardii</i>	Stubbe & Verbeken	Stubbe <i>et al.</i> (2012)	Australasia
109 <i>Lf. leoninus</i>	(Verbeken & E. Horak) Verbeken	Verbeken & Horak (1999)	Australasia
110 <i>Lf. leptomerus</i>	Van de Putte, K. Das & Verbeken	Van de Putte <i>et al.</i> (2012)	Asia
111 <i>Lf. lepus</i>	Delgat & Courtec.	Delgat <i>et al.</i> (2020)	Neotropics
112 <i>Lf. leucophaeus</i>	(Verbeken & E. Horak) Verbeken	Verbeken & Horak (1999)	Australasia
113 <i>Lf. limbatus</i>	Stubbe & Verbeken	Stubbe <i>et al.</i> (2012)	Asia
114 <i>Lf. longibasidius</i>	Maba & Verbeken	Maba <i>et al.</i> (2015b)	Afrotropics
115 <i>Lf. longipes</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
116 <i>Lf. longipilus</i>	Van de Putte, Le & Verbeken	Van de Putte <i>et al.</i> (2010)	Asia
117 <i>Lf. longisporus</i>	(Verbeken) Verbeken	Verbeken (1995)	Afrotropics
118 <i>Lf. longivelutinus</i>	(X.H. Wang & Verbeken) X.H. Wang	Wang & Verbeken (2006)	Asia
119 <i>Lf. lorenae</i>	Montoya, Caro, Ramos & Bandala	Montoya <i>et al.</i> (2019)	Neotropics
120 <i>Lf. luteolamellatus</i>	H. Lee & Y.W. Lim	Hyde <i>et al.</i> (2017)	Asia
121 <i>Lf. luteolus</i>	(Peck) Verbeken	Peck (1896)	Nearctic
122 <i>Lf. luteopus</i>	(Verbeken) Verbeken	Verbeken (1995)	Afrotropics
123 <i>Lf. madagascariensis</i>	(Verbeken & Buyck) Buyck	Buyck <i>et al.</i> (2007)	Afrotropics
124 <i>Lf. maenamensis</i>	K. Das, D. Chakr. & Buyck	Das <i>et al.</i> (2017)	Asia
125 <i>Lf. mamorensis</i>	(Rick) Silva-Filho & Wartchow	Singer <i>et al.</i> (1983)	Neotropics
126 <i>Lf. marielleae</i>	J. Duque & M.A. Neves	Duque Barbosa <i>et al.</i> (2020)	Neotropics
127 <i>Lf. marmoratus</i>	Delgat	Delgat <i>et al.</i> (2020)	Neotropics
128 <i>Lf. medusae</i>	(Verbeken) Verbeken	Verbeken (1995)	Afrotropics
129 <i>Lf. melleus</i>	Maba	Maba <i>et al.</i> (2015b)	Afrotropics
130 <i>Lf. membranaceus</i>	Maba	Maba <i>et al.</i> (2015a)	Afrotropics
131 <i>Lf. mexicanus</i>	Montoya, Caro, Bandala & Ramos	Montoya <i>et al.</i> (2019)	Neotropics
132 <i>Lf. midnapurensis</i>	S. Paloi & K. Acharya	Phookamsak <i>et al.</i> (2019)	Asia
133 <i>Lf. mordax</i>	(Thiers) Delgat	Thiers (1957)	Nearctic
134 <i>Lf. multiceps</i>	(S.L. Miller, Aime & TW Henkel) De Crop	Miller <i>et al.</i> (2002)	Neotropics
135 <i>Lf. murinipes</i>	(Pegler) De Crop	Pegler & Fiard (1979)	Neotropics
136 <i>Lf. nebulosus</i>	(Pegler) De Crop	Pegler & Fiard (1979)	Neotropics
137 <i>Lf. neotropicus</i>	(Singer) Nuytinck	Singer (1952)	Neotropics
138 <i>Lf. neuhoffii</i>	(Hesler & A.H. Sm.) De Crop	Hesler & Smith (1979)	Nearctic
139 <i>Lf. nodosicytidiosus</i>	(Verbeken & Buyck) Buyck	Buyck <i>et al.</i> (2007)	Afrotropics
140 <i>Lf. nonpiscis</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
141 <i>Lf. novoguineensis</i>	(Henn.) Verbeken	Hennings (1898)	Australasia



Table 1. (Continued).

Name	Current authors	Original publication	Biogeographical region
142 <i>Lf. ochrogalactus</i>	(Hashiya) X.H. Wang	Wang <i>et al.</i> (2006)	Asia
143 <i>Lf. oedematopus</i>	(Scop.) Kuntze	Scopoli (1772)	Western Palearctic
144 <i>Lf. olivescens</i>	(Verbeken & E. Horak) Verbeken	Verbeken & Horak (2000)	Australasia
145 <i>Lf. paleus</i>	(Verbeken & E. Horak) Verbeken	Verbeken & Horak (1999)	Australasia
146 <i>Lf. pallidilamellatus</i>	(Montoya & Bandala) Van de Putte	Montoya & Bandala (2004)	Neotropics
147 <i>Lf. pallidipes</i>	(Singer) Delgat <i>comb. nov.</i>	Singer <i>et al.</i> (1983)	Neotropics
148 <i>Lf. panuoides</i>	(Singer) De Crop	Singer (1952)	Neotropics
149 <i>Lf. parvigerardii</i>	X.H. Wang & D. Stubbe	Wang <i>et al.</i> (2012)	Asia
150 <i>Lf. paulensis</i>	(Singer) Delgat <i>comb. nov.</i>	Singer <i>et al.</i> (1983)	Neotropics
151 <i>Lf. pectinatus</i>	Maba & Yorou	Maba <i>et al.</i> (2015b)	Afrotropics
152 <i>Lf. pegleri</i>	(Pacioni & Lalli) Delgat	Lalli & Pacioni (1992)	Neotropics
153 <i>Lf. pelliculatus</i>	(Beeli) Buyck	Buyck (1989)	Afrotropics
154 <i>Lf. persicinus</i>	Delgat & De Crop	Delgat <i>et al.</i> (2017)	Afrotropics
155 <i>Lf. petersenii</i>	(Hesler & A.H. Sm.) Stubbe	Hesler & Smith (1979)	Nearctic
156 <i>Lf. phlebonemus</i>	(R. Heim & Gooss.-Font.) Verbeken	Heim (1955)	Afrotropics
157 <i>Lf. phlebophyllus</i>	(R. Heim) Buyck	Heim (1938)	Afrotropics
158 <i>Lf. pilosus</i>	(Verbeken, H.T. Le & Lumyong) Verbeken	Le <i>et al.</i> (2007)	Asia
159 <i>Lf. pinguis</i>	Van de Putte & Verbeken	Van de Putte <i>et al.</i> (2010)	Asia
160 <i>Lf. piperatus</i>	(L.: Fr.) Kuntze	Linnaeus (1753)	Western Palearctic
161 <i>Lf. pisciodorus</i>	(R. Heim) Verbeken	Heim (1938)	Afrotropics
162 <i>Lf. princeps</i>	(Berk.) Kuntze	Berkeley (1852)	Asia
163 <i>Lf. pruinatus</i>	(Verbeken & Buyck) Verbeken	Verbeken (1998)	Afrotropics
164 <i>Lf. pseudogymnocarpus</i>	(Verbeken) Verbeken	Verbeken (1995)	Afrotropics
165 <i>Lf. pseudohygrophoroides</i>	H. Lee & Y.W. Lim	Hyde <i>et al.</i> (2017)	Asia
166 <i>Lf. pseudoluteopus</i>	(X.H. Wang & Verbeken) X.H. Wang	Wang & Verbeken (2006)	Asia
167 <i>Lf. pseudotorminosus</i>	(R. Heim) Verbeken	Heim (1938)	Afrotropics
168 <i>Lf. pseudovolemus</i>	(R. Heim) Verbeken	Heim (1938)	Afrotropics
169 <i>Lf. puberulus</i>	(H.A. Wen & J.Z. Ying) Nuytinck	Wen & Ying (2005)	Asia
170 <i>Lf. pulchrellus</i>	Hampe & Wisitrassameewong	De Crop <i>et al.</i> (2018)	Asia
171 <i>Lf. pumilus</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
172 <i>Lf. putidus</i>	(Pegler) Verbeken	Pegler & Fiard (1979)	Neotropics
173 <i>Lf. rajendrae</i>	Uniyal & K. Das	Uniyal <i>et al.</i> (2016)	Asia
174 <i>Lf. ramipilosus</i>	Verbeken & De Crop	Li <i>et al.</i> (2016)	Asia
175 <i>Lf. raspei</i>	Verbeken & De Crop	De Crop <i>et al.</i> (2018)	Asia
176 <i>Lf. reticulatovenosus</i>	(Verbeken & E. Horak) Verbeken	Verbeken <i>et al.</i> (2001)	Asia
177 <i>Lf. robustus</i>	Y. Song, J.B. Zhang & L.H. Qiu	Song <i>et al.</i> (2017)	Asia
178 <i>Lf. roseolus</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
179 <i>Lf. roseophyllus</i>	(R. Heim) De Crop	Heim (1966)	Asia
180 <i>Lf. rubiginosus</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
181 <i>Lf. rubrobrunnescens</i>	(Verbeken, E. Horak & Desjardin) Verbeken	Verbeken <i>et al.</i> (2001)	Asia
182 <i>Lf. rubroviolascens</i>	(R. Heim) Verbeken	Heim (1938)	Afrotropics
183 <i>Lf. rufomarginatus</i>	(Verbeken & Van Rooij) De Crop	Van Rooij <i>et al.</i> (2003)	Afrotropics
184 <i>Lf. rugatus</i>	(Kühner & Romagn.) Verbeken	Kühner & Romagnesi (1953)	Western Palearctic
185 <i>Lf. rupestris</i>	(Wartchow) Silva-Filho & Wartchow	Wartchow <i>et al.</i> (2010)	Neotropics
186 <i>Lf. russula</i>	(Rick) Silva-Filho & Wartchow	Rick (1906)	Neotropics
187 <i>Lf. russulisporus</i>	Dierickx & De Crop	Dierickx <i>et al.</i> (2019)	Australasia
188 <i>Lf. ruvubuensis</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
189 <i>Lf. sainii</i>	Sharma & Atri	Liu <i>et al.</i> (2018)	Asia

Table 1. (Continued).

Name	Current authors	Original publication	Biogeographical region
190 <i>Lf. sepiaceus</i>	(McNabb) Stubbe	McNabb (1971)	Australasia
191 <i>Lf. sesemotani</i>	(Beeli) Buyck	Buyck (1989)	Afrotropics
192 <i>Lf. sinensis</i>	J.B. Zhang, Y. Song & L.H. Qiu	Song <i>et al.</i> (2018)	Asia
193 <i>Lf. subclarkeae</i>	(Grgur.) Verbeken	Grgurinovic (1997)	Australasia
194 <i>Lf. subgerardii</i>	(Hesler & A.H. Sm.) Stubbe	Hesler & Smith (1979)	Nearctic
195 <i>Lf. subiculatus</i>	S.L. Mill., Aime & T.W. Henkel	Miller <i>et al.</i> 2012	Neotropics
196 <i>Lf. subkigomaensis</i>	De Lange & De Crop	De Lange <i>et al.</i> (2018)	Afrotropics
197 <i>Lf. subpiperatus</i>	(Hongo) Verbeken	Hongo (1964)	Asia
198 <i>Lf. subpruinosis</i>	X.H. Wang	Wang <i>et al.</i> (2015)	Asia
199 <i>Lf. subreticulatus</i>	(Singer) Delgat <i>comb. nov.</i>	Singer <i>et al.</i> (1983)	Neotropics
200 <i>Lf. subtomentosus</i>	(Berk. & Ravenel) Kuntze	Berkeley & Curtis (1859)	Nearctic
201 <i>Lf. subvellerus</i>	(Peck) Nuytinck	Peck (1898)	Nearctic
202 <i>Lf. subvolemus</i>	Van de Putte & Verbeken	Van de Putte <i>et al.</i> (2016)	Western Palearctic
203 <i>Lf. sudanicus</i>	Maba, Yorou & Guelly	Maba <i>et al.</i> (2014)	Afrotropics
204 <i>Lf. tanzanicus</i>	(Karhula & Verbeken) Verbeken	Karhula <i>et al.</i> (1998)	Afrotropics
205 <i>Lf. tenuicytidiatus</i>	(X.H. Wang & Verbeken) X.H. Wang	Wang & Verbeken (2006)	Asia
206 <i>Lf. tropicosinicus</i>	X.H. Wang	Wang <i>et al.</i> (2015)	Asia
207 <i>Lf. uapacae</i>	(Verbeken & Stubbe) De Crop	Verbeken <i>et al.</i> (2008)	Afrotropics
208 <i>Lf. umbilicatus</i>	Silva-Filho, D.L. Komura & Wartchow	Silva <i>et al.</i> (2020)	Neotropics
209 <i>Lf. umbonatus</i>	K.P.D. Latha & Manim.	Latha <i>et al.</i> (2016)	Asia
210 <i>Lf. urens</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
211 <i>Lf. uyedae</i>	(Singer) Verbeken	Singer (1984)	Asia
212 <i>Lf. vellerus</i>	(Fr.) Kuntze	Fries (1838)	Western Palearctic
213 <i>Lf. velutissimus</i>	(Verbeken) Verbeken	Verbeken (1996a)	Afrotropics
214 <i>Lf. venezuelanus</i>	(Dennis) De Crop	Dennis (1970)	Neotropics
215 <i>Lf. venosellus</i>	Silva-Filho, Sá & Wartchow	Silva <i>et al.</i> (2020)	Neotropics
216 <i>Lf. venosus</i>	(Verbeken & E. Horak) Verbeken	Verbeken & Horak (2000)	Australasia
217 <i>Lf. veraecrucis</i>	(Singer) Verbeken	Singer (1973)	Neotropics
218 <i>Lf. versiformis</i>	Van de Putte, K. Das & Verbeken	Van de Putte <i>et al.</i> (2012)	Asia
219 <i>Lf. vitellinus</i>	Van de Putte & Verbeken	Van de Putte <i>et al.</i> (2010)	Asia
220 <i>Lf. volemoides</i>	(Karhula) Verbeken	Karhula <i>et al.</i> (1998)	Afrotropics
221 <i>Lf. volemus</i>	(Fr.: Fr.) Kuntze	Fries (1838)	Western Palearctic
222 <i>Lf. waltersii</i>	(Hesler & A.H. Sm.) De Crop	Hesler & Smith (1979)	Nearctic
223 <i>Lf. wangii</i>	(J.Z. Ying & H.A. Wen) De Crop <i>comb. nov.</i>	Ying & Wen (2005)	Asia
224 <i>Lf. wirrabara</i>	(Grgur.) Stubbe	Grgurinovic (1997)	Australasia
225 <i>Lf. xerampelinus</i>	(Karhula & Verbeken) Verbeken	Karhula <i>et al.</i> (1998)	Afrotropics
226 <i>Lf. zenkeri</i>	(Henn.) Verbeken	Singer (1942)	Afrotropics

Together with *Russula*, *Lactifluus* appears to be one of the most dominant ectomycorrhizal genera in the tropics (Tedersoo *et al.* 2010b, 2011). Host plants for *Lactifluus* are leguminous trees (*Fabaceae*), members of the *Dipterocarpaceae* and the *Fagaceae*, together with genera from several other families. European and North American *Lactifluus* species are mainly associated with trees of *Betulaceae* (e.g. *Betula*, *Carpinus*, *Corylus*), *Fagaceae* (e.g. *Castanea*, *Fagus*, *Quercus*), *Pinaceae* (e.g. *Abies*, *Picea*, *Pinus*), and *Cistaceae* (e.g. *Cistus*, *Halimium*) (Hesler & Smith 1979, Heilmann-Clausen *et al.* 1998, Comandini *et al.* 2006, Van de Putte 2012, Leonardi *et al.* 2016, Leonardi *et al.* 2020).

In Asia, *Lactifluus* species mainly occur with *Dipterocarpaceae* (e.g. *Dipterocarpus*, *Shorea*) and *Fagaceae* (e.g. *Castanopsis*, *Lithocarpus*) (Le 2007, Van de Putte 2012). In sub-Saharan Africa, *Lactifluus* species often grow with *Dipterocarpaceae* (e.g. *Monotes*), *Fabaceae* (e.g. *Afzelia*, *Berlinia*, *Brachystegia*, *Gilbertiodendron*, *Isobertinia*, *Julbernardia*), and *Phyllanthaceae* (e.g. *Uapaca*) (Verbeken & Walley 2010). In Central and South America, *Lactifluus* species grow with *Fabaceae* (e.g. *Dicymbe*), *Fagaceae* (e.g. *Quercus*), *Nyctaginaceae* (e.g. *Neea*, *Guapira*), and *Polygonaceae* (e.g. *Coccoloba*) (Tedersoo *et al.* 2010c). In Australasia, *Lactifluus* species are mainly associated



**Fig. 6.** *Lactifluus* species growing on trees or plant seedlings. **A.** Subiculum of *Lf. brunellus* on the stem of a tree. **B.** *Lf. multiceps* (TH 9807). **C.** *Lf. raspei* (EDC 14-517) [Photographs by T. Henkel (A), T. Elliot (B) and E. De Crop (C)].

with *Myrtaceae* (e.g. *Eucalyptus* and *Leptospermum*), and *Nothofagaceae* (e.g. *Nothofagus*) (McNabb 1971).

Present data suggest that especially generalists occur in *Lactifluus*, in contrast to *Lactarius* and *Russula* where many host specific species are known. It is hard to draw conclusions concerning hosts generalism or specialism in *Lactifluus*, as studies proving the mycorrhizal association are scarce, but for most *Lactifluus* species multiple host trees are suggested. *Lactifluus volemus*, for example, has a broad host range and is known to occur with hosts from both *Fagaceae* and *Pinaceae* (Van de Putte *et al.* 2016). The European *Lf. rugatus*, that was thought to grow solely with *Quercus*, is now also known to grow with *Cistus* in Mediterranean areas (Brotzu 1998, Comandini *et al.* 2006, Leonardi *et al.* 2016). The few species that appear to be host specific are so far only known from a few records, such as *Lf. madagascariensis* that is only known to occur with *Uapaca louvellii* in Madagascar (Buyck *et al.* 2007), *Lf. corbula* found both in the Democratic Republic of Congo and Cameroon in monodominant *Gilbertiodendron dewevrei* plots (Henkel, pers. comm.), or *Lf. coccolobae* which is only known from *Coccoloba uvifera* in the sand dunes of the Antilles (Miller *et al.* 2000).

For most *Lactifluus* species, the exact ECM connection generally remains undetermined. Ecological characteristics are not commonly recorded for every collection during field work, and it is hard to find out which tree a fungal species grows with in mixed forests. Common techniques to detect the host tree in mixed forests are labour-intensive and expensive, since ectomycorrhizal roots have to be excavated, both fungus and plant need to be sequenced, identified, and herbarium material needs to be collected [e.g. in the study of Osmundson *et al.* (2007)].

### Phylogeny and molecular diversity

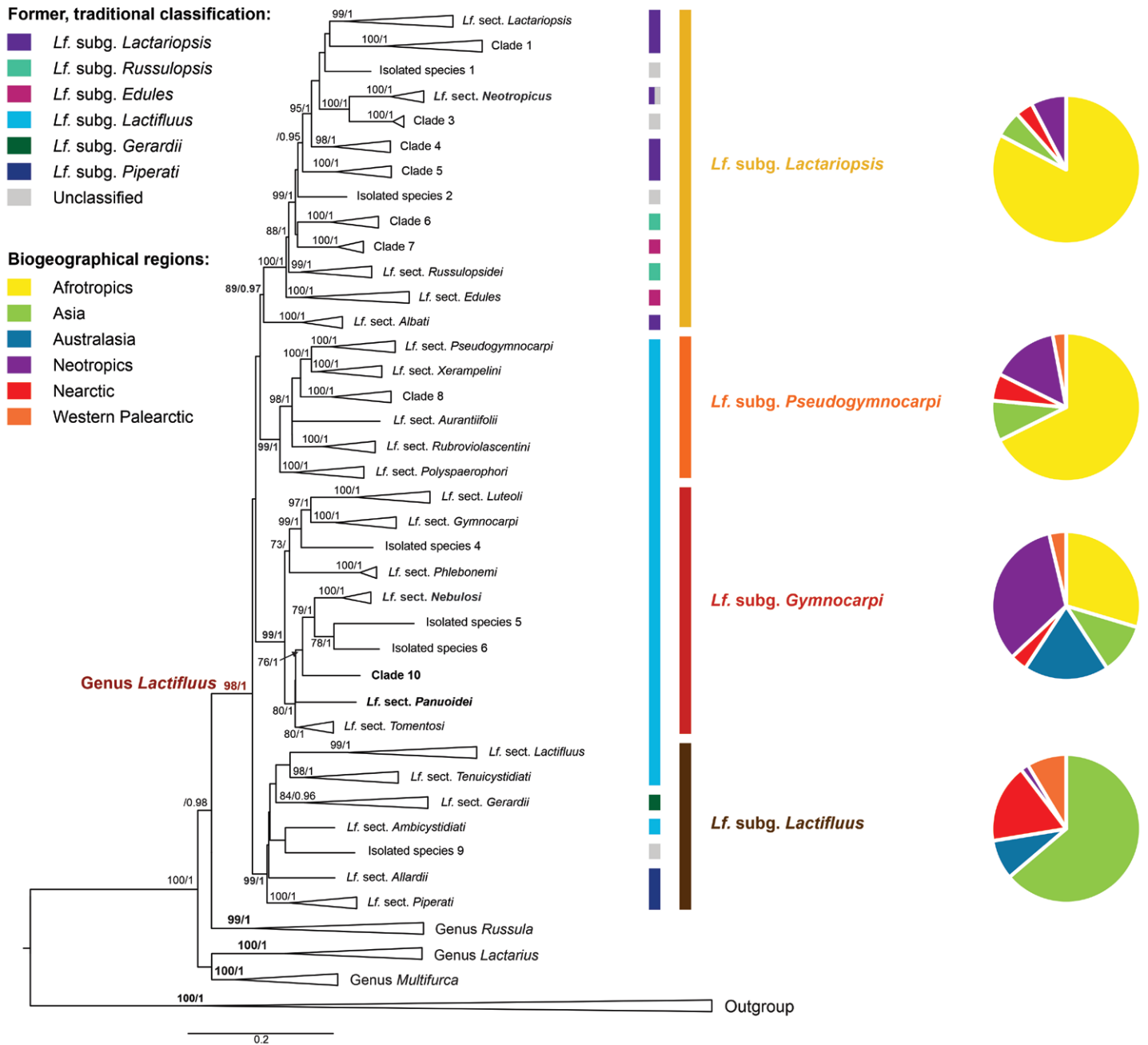
In 2017, De Crop *et al.* (2017) performed a global study of the genus *Lactifluus*, which resulted in a new infrageneric classification of the genus. Originally the genus was divided in 6 subgenera, 13 sections and three unclassified species, but De Crop *et al.* (2017) inferred that the genus could be divided into four subgenera: *Lf.* subg. *Gymnocarpi*, *Lf.* subg. *Lactariopsis*, *Lf.* subg. *Lactifluus*, and *Lf.* subg. *Pseudogymnocarpi* (Fig. 7). Each subgenus was further divided into four or more sections, together with undescribed clades and species on isolated positions.

The majority of species was combined into *Lactifluus* in a series of specific papers (Verbeken *et al.* 2011, 2012, Stubbe *et al.* 2012b), other species were combined in *Lactifluus* as part of larger studies (De Crop *et al.* 2017, Delgat *et al.* 2019, 2020), and the remaining species are combined here (see Taxonomy). Table

1 further gives an overview of the currently described species and the subgeneric classification of all *Lactifluus* species is given in Supplementary Table S1.

The occurrence of several species complexes and species on long and isolated branches reflects the large genetic diversity as was earlier described by Verbeken & Nuytinck (2013). Several species complexes have been intensively studied and have revealed an enormous diversity. In the complex around *Lf. volemus*, Van de Putte *et al.* (2010, 2012, 2016) applied phylogenetic species recognition and discovered about 45 different clades within this group. Some of them could be morphologically distinguished and were described as new species. Others remain cryptic since no morphological differences were found. Stubbe *et al.* (2010, 2012a) examined the group around *Lf. gerardii*. At the start of this study, only a handful of species were known, while at the end, more than 30 clades were discovered, of which about two-third are morphologically identifiable species. De Crop *et al.* (2014) studied the complex of *Lf.* sect. *Piperati*. They found 10–20 putative species worldwide, most of them morphological look-a-likes. Recently, Delgat *et al.* (2019) studied the complex of *Lf.* sect. *Albati* and reported 29 species, which had previously been identified as only a handful of species based on morphology. These four former species complexes contain species from a wide geographic range (Asia, Europe, Australasia, and North America), from the temperate regions to the tropics. However, no representatives in South America's eastern side of the Andes or sub-Saharan Africa are known. Apart from these four species complexes, several other species are assumed to be part of species complexes. These occur on a somewhat smaller scale (one continent). For example, within the African *Lf. gymnocarpoides*, *Lf. pumilus* and *Lf. longisporus* all have similar morphological characteristics and are hard to distinguish in the field. In the Neotropics, the species *Lf. annulifer* and *Lf. venezuelanus* are assumed to be part of a species complex (*L.* sect. *Neotropicus*). In Australasia, *Lf. clarkeae*, *Lf. flocktonae* and *Lf. subclarkeae* are morphologically rather similar and together with some undescribed clades, they presumably belong to a species complex (unpubl. res.).

Juxtaposed to the species complexes, several *Lactifluus* species occur on long branches and have isolated positions in the phylogenetic tree; these include *Lf. ambicystidiatus* from China (Wang *et al.* 2015), *Lf. aurantiifolius* from tropical Africa (Verbeken 1996a, Buyck *et al.* 2007), *Lf. cocosmus* from Togo (Van de Putte *et al.* 2009), *Lf. chrysocarpus* from Vietnam (Morozova *et al.* 2013), and *Lf. foetens* from Benin and Togo (Van Rooij *et al.* 2003, De Crop *et al.* 2016), and *Lf. russula* from Brazil (Delgat, unpubl. res.).



**Fig. 7.** Overview Maximum Likelihood tree of the genus *Lactifluus*, based on concatenated ITS, LSU, *RPB2* and *RPB1* sequence data, adapted from De Crop et al. (2017). The first column of colour bars represents the former, traditional classification. The second column represents the current classification. Pie charts represent the biogeographical regions in which species of each subgenus occur. Maximum Likelihood bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.95 are shown. Clade names in bold are names that changed since the publication of De Crop et al. (2017).

## Taxonomy

### New combinations

Eight species, originally described as *Lactarius*, need to be recombined in the genus *Lactifluus*.

***Lactifluus adustus*** (Rick) Delgat, **comb. nov.** MycoBank MB832778.  
*Basionym:* *Lactarius adustus* Rick, *Lilloa* **2**: 304. 1938.

***Lactifluus echinatus*** (Thiers) De Crop, **comb. nov.** MycoBank MB832779.  
*Basionym:* *Lactarius echinatus* Thiers, *Mycologia* **49**: 716. 1957.

***Lactifluus epitheliosus*** (Buyck & Courtec.) Delgat, **comb. nov.** MycoBank MB832780.  
*Basionym:* *Lactarius epitheliosus* Buyck & Courtec., *Mycologia Helvetica* **4**: 211. 1991.

***Lactifluus ignifluus*** (Vrinda & C. K. Pradeep) De Crop, **comb. nov.** MycoBank MB838409.  
*Basionym:* *Lactarius ignifluus* Vrinda & C. K. Pradeep, *Persoonia* **18**: 129. 2002.

***Lactifluus pallidipes*** (Singer) Delgat, **comb. nov.** MycoBank MB832781.  
*Basionym:* *Lactarius pallidipes* Singer, *Beih. Nova Hedwigia* **77**: 299. 1983.

*Lactifluus paulensis* (Singer) Delgat, **comb. nov.** MycoBank MB832782.

*Basionym:* *Lactarius paulensis* Singer, *Beih. Nova Hedwigia* **77**: 305. 1983.

*Lactifluus subreticulatus* (Singer) Delgat, **comb. nov.** MycoBank MB832783.

*Basionym:* *Lactarius subreticulatus* Singer, *Beih. Nova Hedwigia* **77**: 314. 1983.

*Lactifluus wangii* (J.Z. Ying & H.A. Wen) De Crop, **comb. nov.** MycoBank MB838408.

*Basionym:* *Lactarius wangii* J.Z. Ying & H.A. Wen, *Mycosystema* **24**: 156. 2005.

#### Excluded names

*Lactarius subpallidipes* appears to be a *Russula* species, for which a new combination is proposed.

*Russula subpallidipes* (Singer) Delgat, **comb. nov.** MycoBank MB832784.

*Basionym:* *Lactarius subpallidipes* Singer, *Beih. Nova Hedwigia* **77**: 298. 1983.

#### Uncertain species/genus status

From one species, *Lactarius steffenii*, the type material is apparently lost, and this makes it difficult to assess to which milkcap genus this Brazilian species belongs (Silva-Filho & Wartchow 2019).

#### Belowground diversity

*Lactifluus* species have been recovered from soil samples in several studies. In the recently published public database GlobalFungi (Vetrovsky *et al.* 2020, accessed on 28/07/2020) *Lactifluus* OTUs were found in 343 of the 20 009 sampled sites worldwide (in 498 samples when singletons, *i.e.* OTU abundance = 1, are included). On a global scale, the study of Tedersoo *et al.* (2014) have recovered *Lactifluus* OTU's from all continents. Other studies concentrate on a specific region within a country (*e.g.* Tian *et al.* 2017) or focus on a continent (*e.g.* Bissett *et al.* 2016).

Preliminary results (see supplementary Tables S2–S4) of the data (singletons excluded) suggest that these metabarcoding data recovered 18 possible new *Lactifluus* species. Only 23.8 % of the described species available in our dataset were recovered. If we consider both described species and species that are undescribed but known by our research group, only 16.6 % of the species were found. These low numbers are mainly due to an undersampling of the main distribution areas of *Lactifluus*, *i.e.* (sub)tropical Africa, Southeast Asia and South America, for which respectively only 22.7 %, 7.9 % and 6.8 % of the known species were found in soil samples. Furthermore, in order to find *Lactifluus*, samples need to be taken in proximity of ECM trees, which was mostly not the case.

Comparing the results between continents, different patterns emerge. Twenty-eight of the 240 sampled sites in **Africa** contained *Lactifluus* OTUs. Those 28 samples were taken in five regions in sub-Saharan Africa, all with a history of *Lactifluus* research. Those regions are largely covered by ECM vegetation. *Lactifluus* is one of the dominant ECM fungal groups present in those vegetation types and this is reflected in the results. In the 28 sampling sites, 22.7 % of the known and described African

species and ten possible new lineages were retrieved. These results suggest that with new regions explored, there might still be many new *Lactifluus* species to be found in sub-Saharan Africa.

The **Asian** samples were taken all over the continent, however, not always in ECM forest. Thus from the almost 3 000 sampled sites, *Lactifluus* was found in only 25 sampling sites. This includes 7.9 % of the known or described Asian species and three possible new lineages. This is only a fraction of the currently known Asian diversity.

Due to the BASE project (Bissett *et al.* 2016), the **Australasian region** is rather well sampled. Although *Lactifluus* OTUs were found in only 6 % of the sampled sites, 54.5 % of the known or described Australasian species were found. Ten known species were not retrieved in the soil samples and two more possible new lineages were found.

In absolute numbers, **Europe** is the best sampled region. However, samples were mainly taken for studies with a focus on specific regions, not covering the whole continent and not necessarily taken in proximity of ECM trees. This is reflected in the results for *Lactifluus*. Less than 1 % of the sampling sites contains *Lactifluus* OTUs, and of the nine known and described species, only four were retrieved. Due to the lack of sampling sites in Southern Europe, none of the more Mediterranean species was found. As the European *Lactifluus* species have been studied in great detail (Heilmann-Clausen *et al.* 1998, Basso 1999, De Crop *et al.* 2014, Leonardi *et al.* 2016, Van de Putte *et al.* 2016, Delgat *et al.* 2019, Dierickx *et al.* 2019b), we did not expect new lineages to emerge, which was indeed the case.

**North America** also contains a lot of sampled sites, however, again constricted to certain areas. *Lactifluus* OTUs were found in only 1.4 % of the samples, 27 % of the known species were retrieved in the soil samples, and two possible new lineages were found.

In **Central and South America**, ECM trees are mostly scattered throughout the forests, which makes it difficult to detect ECM fungi from soil samples. From the 33 sampling sites in which *Lactifluus* was found, the majority was taken in the forests of Western Guyana where monodominant forests of the ectomycorrhizal *Dicymbe corymbosa* occur and where *Russulaceae* have been the focus of a series of studies (Henkel *et al.* 2000, 2012, Miller *et al.* 2002, 2012). However, only 6.8 % of the known or described species was found, and those found were thus only species known to occur in those *Dicymbe* forests. Only one possible new lineage was found.

#### Macromorphology

Despite the existence of species complexes, in which morphological diversity is rather limited, the genus *Lactifluus* generally shows a large diversity of macromorphological characters (Fig. 8), which can often be used for species delimitation.

A striking first character is the **sporocarp type and size**. Currently, three different sporocarp types are known in *Lactifluus*: the agaricoid type (*i.e.* with cap, gills and centrally attached stipe, *e.g.* Fig. 8A), the pleurotoid type (*i.e.* with cap, gills and laterally attached stipe, *e.g.* Fig. 8L), and the sequestrate sporocarp type (Lebel *et al.* 2016). Sporocarps of *Lactifluus* species range from miniscule sporocarps, such as in *Lf. igniculus* (pileus 5–16 mm diam), to large basidiocarps, such as in *Lf. vellereus* (pileus 50–300 mm diam.). Most sporocarps grow directly on soil, but tiny

agaricoid and pleurotoid species may often grow on a subiculum (Fig. 6), which is an interwoven network of thick-walled hyphae from which sporocarps arise. This subiculum grows on saplings, roots, stems, soil or rocks, and can be intermixed with bryophyte growth and subtended by ectomycorrhizal rootlets. It can be small to very extensive, *e.g.* the subiculum of *Lf. multiceps* was recorded to stretch out over 15 m (Miller *et al.* 2002).

Within the *Russulaceae*, the genera *Lactifluus* and *Russula* are known to contain species with a **secondary velum**. In *Lactifluus*, this velum can be present as an annulus around the stipe or as velar remnants on the pileus edge (Fig. 9). The annulus is fibrous, membranous, thin to almost invisible and not mobile, unlike in some *Russula* species with a mobile annulus which often sticks to the growing cap (Fig. 3C). Species with a secondary velum, together with their closest relatives, are characterised by an involute pileus margin when young. This involute pileus margin can make contact with the stipitipellis and protects the developing lamellae (Heim 1937).

The **pileus** shape of *Lactifluus* species varies between applanate, planoconvex, concave, infundibuliform or deeply infundibuliform. Pileus colours range from white, yellow, orange, red to brownish colours. Pileus surfaces range from smooth caps to chamois-leather-like to velvety or woolly (Fig. 10). Some species, especially from *Lf. sect. Albati* are known for their woolly pileus surface and their local names often refer to this aspect (*e.g.* *Lactifluus vellereus* in Dutch: schaapje, in English: fleecy milkcap, in German: Wollige Milchling, Mildmilchender Wollschwamm or Samtiger Milchling, in Spanish: lactario aterciopelado). The pileus margin is often concentrically wrinkled near the edge and can be grooved or involute. The pileus edge is either entire, crenulate or eroded. **Stipe** colours and surface mainly resemble those of the pileus but are often slightly paler or less felted. The stipe is generally centrally attached and often tapering downwards or curved near the base.

**Lamellae** of *Lactifluus* species are mostly slightly paler than the pileus, except in some species, *e.g.* *Lf. aurantiifolius* with dark yellow-orange lamellae. Lamellae may be thin, almost paper-like, such as in *Lf. pelliculatus*; or thick and brittle, such as in *Lf. rubroviolascens*. They may be very broad, as in *Lf. sesemotani* or narrow, as in *Lf. inversus*. Some are distant, as in *Lf. distantifolius*, or very crowded, as in *Lf. phlebophyllus* (Fig. 11). The attachment to the stipe varies from adnate, adnate with a decurrent tooth to decurrent. Generally, the lamella edge is entire and concolourous with the rest of the lamellae. However in some species, like *Lf. bicolor*, the lamella edge is concolourous with the pileus or stipe. In almost all *Lactifluus* species, lamellulae (l) are present between the lamellae (L). These lamellulae often occur in a pattern: L–l–L or L–l<sub>s</sub>–l–l<sub>s</sub>–L, with l<sub>s</sub> the smallest lamellula. Various *Lactifluus* species have bifurcating lamellae, while others have venation patterns on their lamellae. Venation is either transvenose (when veins occur on the lamella surface) or intervenose (when veins occur between lamellae).

As indicated by their name, *Lactifluus* species, as *Lactarius* species, exude **latex** when bruised. Several latex features have been important in species delimitation in both genera. In *Lactifluus*, latex can be white, coloured, watery or whey-like and some species have latex changing colour (*e.g.* blue-green, brown or red-black) after contact with air (Fig. 12). In some species, the latex colours the lamellae and context after exposure to air. Species differ in latex abundance or taste. For instance, in *Lf. volemus* latex is very abundant and in *Lf. piperatus*, the latex is very acrid.

The **context** of *Lactifluus* species ranges from firm to stuffed, to partly hollow, chambered or hollow (Fig. 13). The context of most species is white or cream-coloured and in some species, the context changes colour after exposure to air. The context is mild or has a very acrid taste, such as in *Lf. acrisissimus* or *Lf. urens*. Some species smell like fish or seafood (*Lf. volemus*, *Lf. nonpiscis*), fruit (*Lf. edulis*, *Lf. aureifolius*), or coconut (*Lf. cocosmus*). Some of the typical odours that occur in the genus *Lactarius* are lacking here, for example the *Heteroptera*-odour of *L. quietus*, the odour of curry or camphor of *L. camphoratus*, or the fenugreek odour of *L. helvus*. The **spore print** of all *Lactifluus* species is white but cannot be used explicitly to delimit *Lactifluus* species.

## Micromorphology

The genus *Lactifluus* is known for the occurrence of thick-walled elements in many of its species. For terminology concerning these characters we follow Verbeke & Walley (2010).

### Structures of the pileipellis and stipitipellis

The structure of the pileipellis is an important character in this genus and is used to delimit species, sections or subgenera. As **pileipellis and stipitipellis** structures slightly change during their development (Verbeke & Walley 2010), pellis structures in this study were observed in mature specimens. Drawings were made using tissue taken halfway along the radius of the pileus or halfway up the stipe height.

For the description of the pellis structures, we follow Heilmann-Clausen *et al.* (1998) and Verbeke & Walley (2010). In *Lactifluus*, the pileipellis is regularly differentiated from the underlying trama and often consists of two layers, indicated as supra- and subpellis. The most important characters to look at are the presence of thick-walled elements, the presence of isodiametric cells and the orientation of the terminal elements.

Thick-walled elements are present in many *Lactifluus* species. They may occur as one consistent layer or as scattered hairs in a layer of thin-walled elements. Their presence is indicated with the prefix “lampro” in the name of that pileipellis structure, *e.g.* lampropalisade.

Many *Lactifluus* species are characterised by the presence of isodiametric cells, or sphaerocytes, in the subpellis, more rarely in the suprapellis. These are thin- or thick-walled and form one distinct layer or are mixed with cylindrical hyphae.

In case of a distinctly two-layered pileipellis, the suprapellis consists of terminal elements. These are either hair-like elements, hyphae or clavate elements. Their orientation is important in defining the different pellis structures.

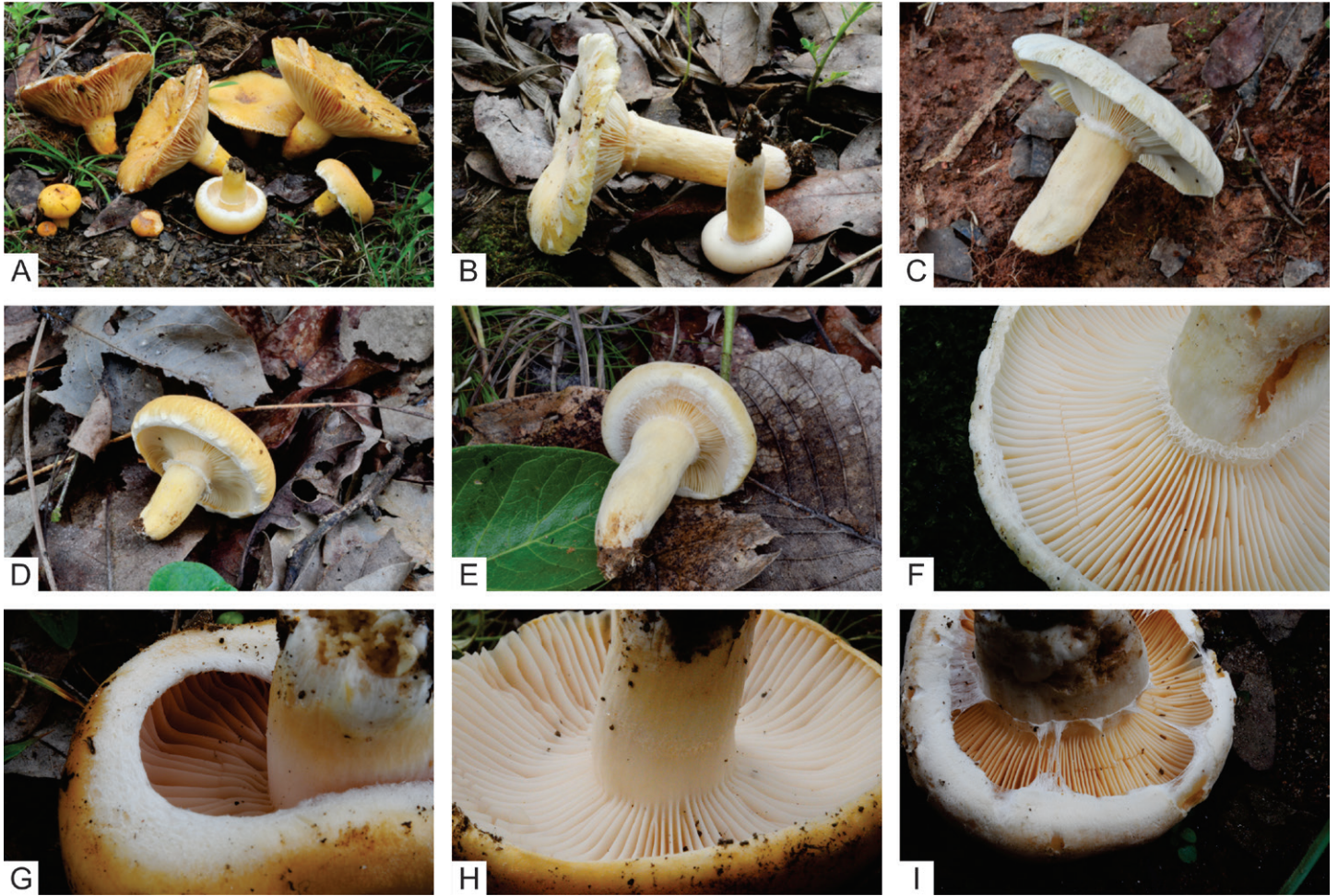
The combination of these characters leads to a differentiation between 14 pilei- and stipitipellis types (Fig. 14). Intermediate types sometimes occur.

### Pellis entirely composed of filamentous elements, without isodiametric cells

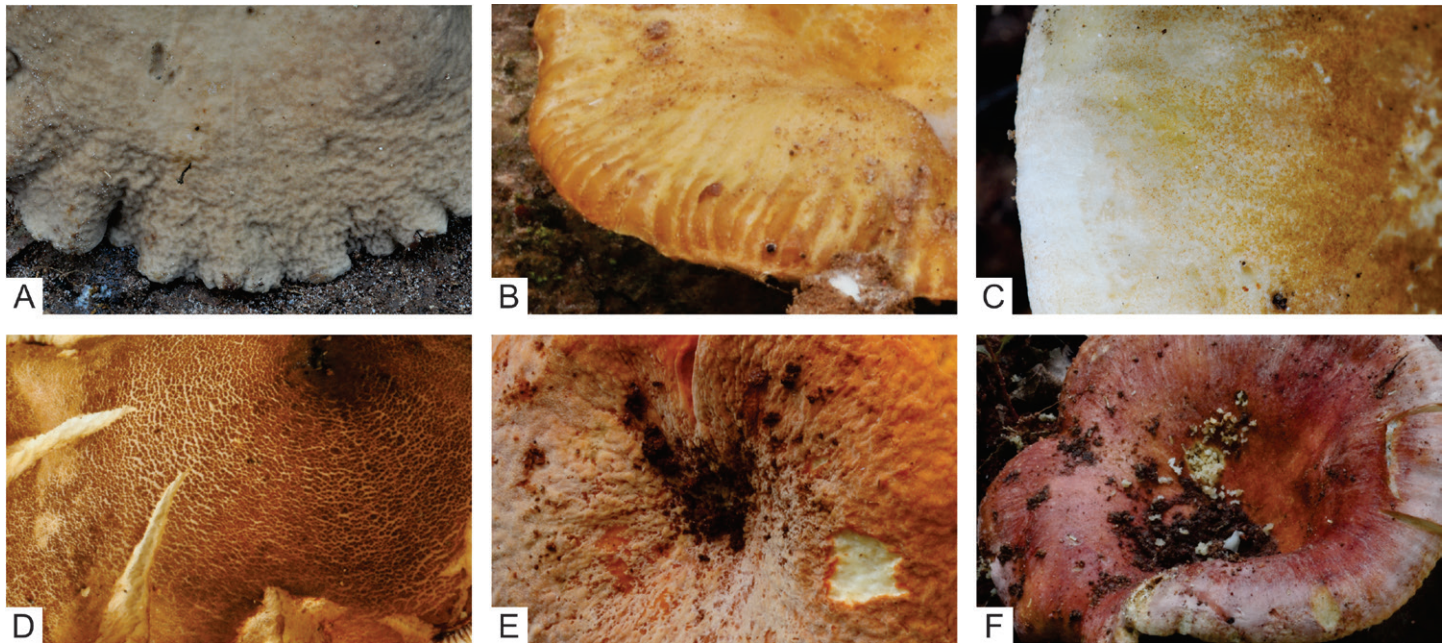
- *Cutis*: the suprapellis consists of hyaline, thin-walled hyphae, which lay parallel, pericline or are slightly intermixed. Differentiated terminal elements are mostly lacking, although in some species of *Lf. sect. Russulopsidei*, there are dermatocystidia present in this layer.
- *Irregular cutis*: the suprapellis consists of hyaline, thin-walled hyphae which are irregularly ordered.



**Fig. 8.** Overview of different types of *Lactifluus* sporocarps. ***Lf. subg. Gymnocarpi***: A. *Lf. nonpiscis* (EDC 14-056). B. *Lf. tanzanicus* (EDC 11-224). C. *Lf. gymnocarpus* (EDC 12-047). D. *Lf. albomembranaceus* (EDC 12-046). E. *Lf. cf. phlebonemus* (EDC 12-067). F. *Lf. panuoides*. G. *Lf. putidus* (LD 15-002). H. *Lf. clarkeae* (REH 9871). ***Lf. subg. Lactifluus***: I. *Lf. volemus*. J. *Lf. longipilus* (KVP 08-005). K. *Lf. atrovelutinus* (DS 06-003). L. *Lf. raspei* (EDC 14-517). M. *Lf. aff. piperatus* (DS 07-467). N. *Lf. roseophyllus* (JN 2011-076). O. *Lf. allardii* (C.C. 3.0). P. *Lf. aff. tenuicystidiatus* (DS 07-465). ***Lf. subg. Lactariopsis***: Q. *Lactifluus* sp. (EDC 11-068). R. *Lactifluus* sp. (EDC 14-091). S. *Lf. cyanovirescens* (EDC 11-021). T. *Lf. multiceps* (TH 9807). U. *Lf. longipes* (EDC 14-049). V. *Lactifluus* sp. (EDC 12-069). W. *Lf. roseolus* (EDC 14-228). X. *Lf. subvellereus* (AV 13-025). ***Lf. subg. Pseudogymnocarpi***: Y. *Lf. cf. gymnocarpoides* (EDC 14-106). Z. *Lf. medusae* (EDC 12-152). AA. *Lf. luteopus* (EDC 14-086). BB. *Lf. bicapillus* (EDC 12-176). CC. *Lf. rubiginosus* (EDC 11-067). DD. *Lf. armeniacus* (EDC-501). EE. *Lf. denigricans* (EDC 14-067). FF. *Lf. pegleri* (LD 15-014) [Photographs by E. De Crop (A–E,L,Q–S,U–W,Y–EE), T. Henkel (F), L. Delgat (G,FF), R. Halling (H), G. Boerio (I), K. Van de Putte (J), D. Stubbe (K,M,P), J. Nuytinck (N), D. Molter C.C. 3.0 (O), T. Elliot (T) and A. Verbeken (X)].

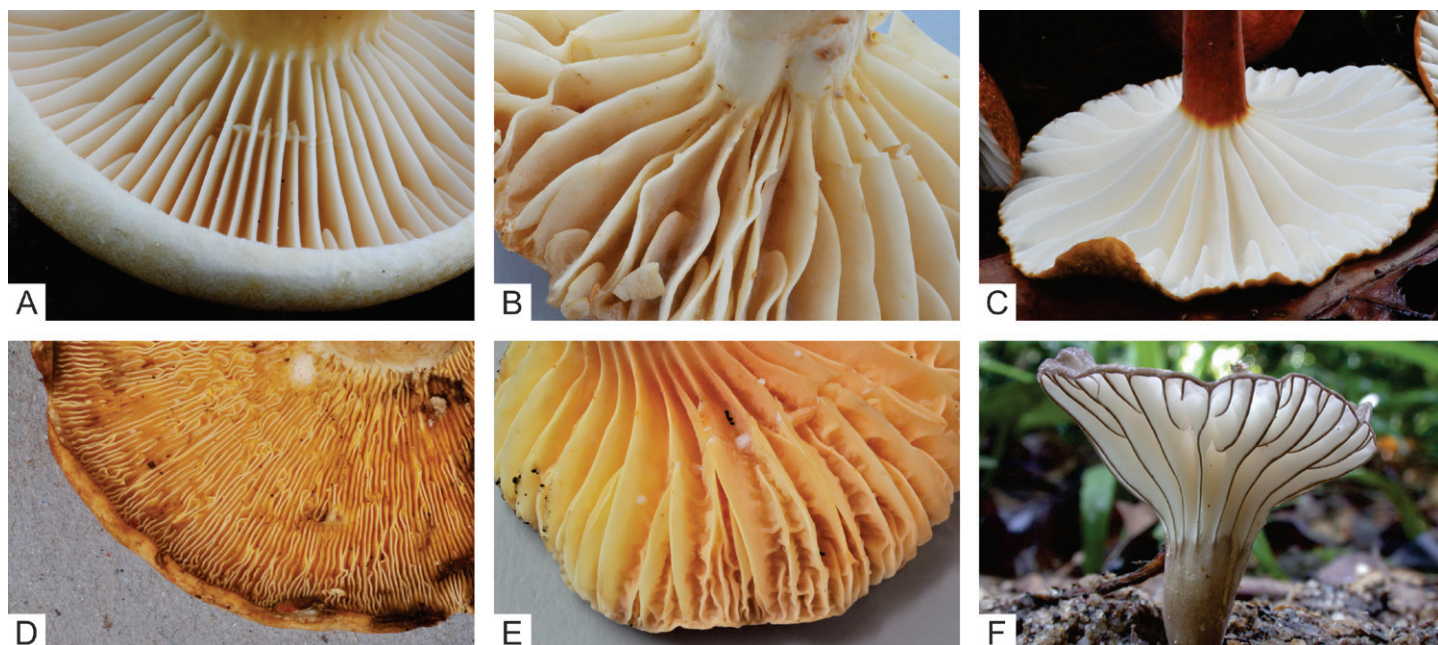


**Fig. 9.** Overview of different types of velum in unidentified *Lactifluus* spp. **A.** EDC 14-060. **B.** EDC 14-065. **C.** EDC 11-127. **D.** EDC 11-144. **E.** EDC 14-172. **F.** EDC 14-059. **G.** EDC 14-146. **H.** EDC 14-091. **I.** EDC 14-051. [Photographs by E. De Crop (A–D, F–I) and J. Nuytinck (E)].

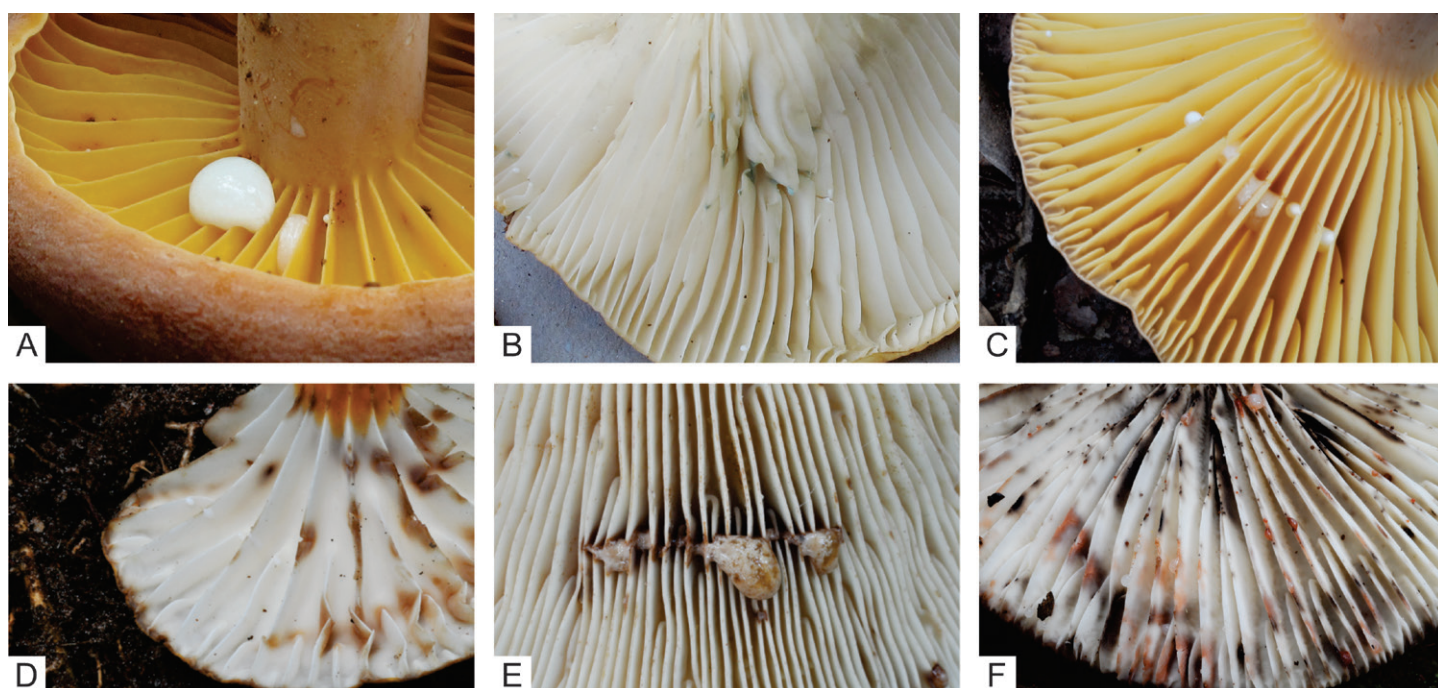


**Fig. 10.** Overview of different types of pileus surface in *Lactifluus*. **A.** Wrinkled and finely felty pileus of *Lf. brunnescens* (EDC 12-116). **B.** Sulcate pileus of *Lactifluus* sp. – *Lf.* sect. *Lactariopsis* (EDC 11-084). **C.** Finely squamulose pileus of *Lf. urens* (EDC 14-032). **D.** Pileus tomentose and cracked into small, felty flocks in *Lf. inversus* (EDC 12-070). **E.** Pruinoso pileus of *Lactifluus* sp. (EDC 14-153). **F.** Smooth and somewhat shiny pileus of *Lf. cyanovirescens* (EDC 11-021) (Photographs by E. De Crop).



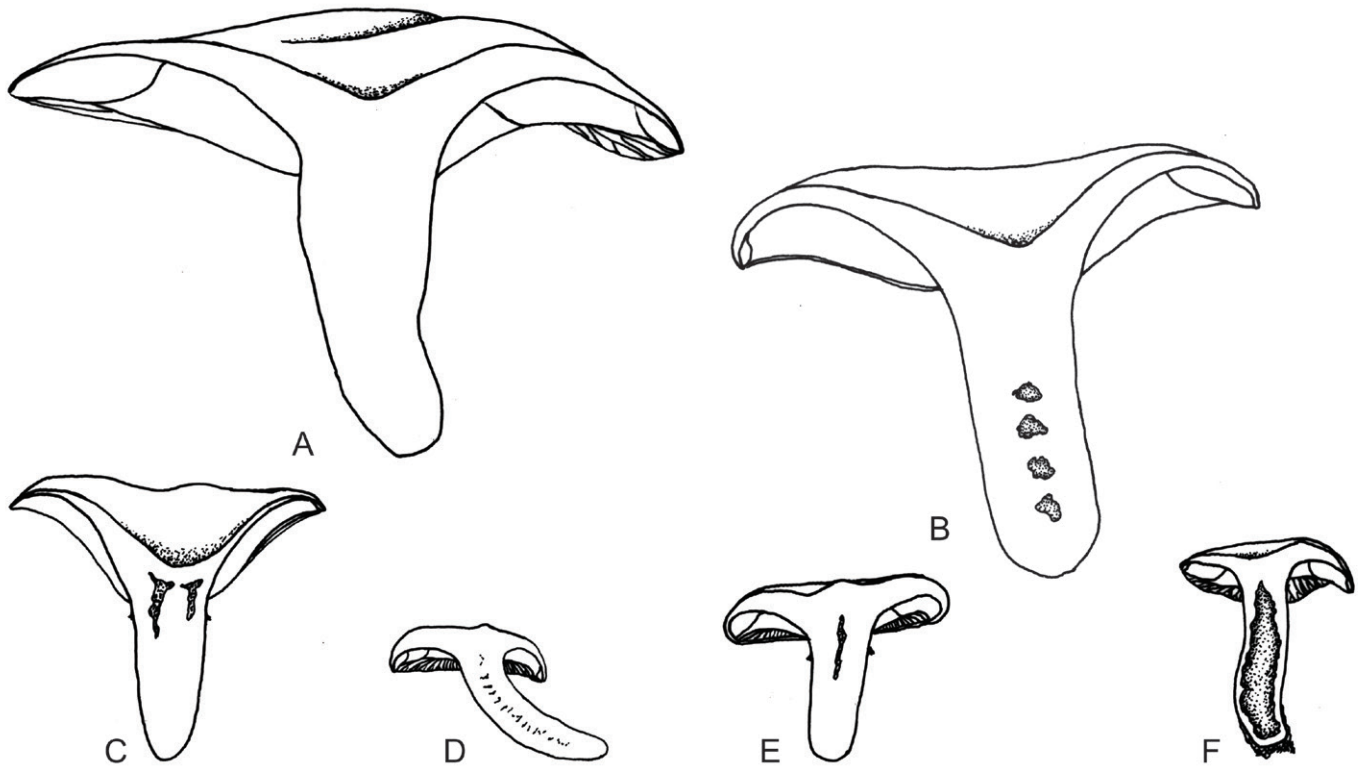


**Fig. 11.** Overview of different types of lamellae in *Lactifluus*. **A.** Thin and paper-like lamellae of *Lf. urens* (EDC 14-032). **B.** Thick and brittle lamellae in *Lf. aff. longisporus* (EDC 12-199). **C.** Distant and broad lamellae in *Lf. gymnocarpus* (EDC 12-055). **D.** Bifurcating narrow and crowded lamellae in *Lf. densifolius* (EDC 11-220). **E.** Lamellae with venation of *Lf. persicinus* (EDC 12-002). **F.** Lamellae with coloured edge in *Lf. bicolor* (DS 06-230) [Photographs by E. De Crop (A–E) and D. Stubbe (F)].



**Fig. 12.** Overview of different types of latex colourations in *Lactifluus*. **A.** Unchanging white latex in *Lactifluus* sp. (AV 11-089). **B.** White latex changing greenish in *Lf. cyanovirescens* (EDC 11-001). **C.** Unchanging watery white latex in *Lf. rubiginosus* (EDC 11-067). **D.** White latex that colours the lamellae brownish in *Lf. gymnocarpus* (EDC 12-103). **E.** Brown whey-like latex in *Lf. brunnescens* (EDC 12-116). **F.** Watery white latex changing red and later black in *Lf. rubroviolascens* (EDC 14-384) [Photographs by A. Verbeken (A) and E. De Crop (B–F)].

- *Ixocutis*: the suprapellis consists of hyaline, thin-walled hyphae which are embedded in a slime layer, which may be produced by hyphae secreting slime or by gelatinized hyphae walls.
- *Trichoderm*: the suprapellis consists of hyaline, thin-walled hyphae, of which the terminal elements are ascending and lay anticline. These hairs often form dense turfs.
- *Lamprotrichoderm*: the suprapellis consists of hyaline, thin-walled hyphae, of which the terminal elements are thick-walled, ascending and lay anticline.
- *Ixotrichoderm*: the suprapellis consists of hyaline, thin-walled hyphae, of which the terminal elements are ascending, lay anticline and are embedded in a slime layer, which may be produced by hyphae secreting slime or by gelatinized hyphae walls.



**Fig. 13.** Overview of different types of context in *Lactifluus*. **A.** Firm context in *Lf. urens* (EDC 14-032). **B.** Chambered context in *Lactifluus* sp. (EDC 14-061). **C.** Chambered context in *Lactifluus* sp. (EDC 14-046). **D.** Stuffed context in *Lactifluus* sp. (EDC 14-512). **E.** Partly hollow context in *Lactifluus* sp. (EDC 14-038). **F.** Hollow context in *Lf. nonpiscis* (EDC 14-056) [Scale bar = 1 cm. Line drawings by E. De Crop].

#### *Pellis with a distinct layer of isodiametric cells*

- *Hyphoepithelium*: the suprapellis consists of periclinal, hyaline and thin-walled hyphae, which lay on a cellular subpellis.
- *Palisade*: the suprapellis consists of anticlinal, thin-walled, elongated terminal elements, which lay on a cellular subpellis. The terminal elements are either hair-like or septate.
- *Lampropalisade*: the suprapellis consists of anticlinal, thick-walled, elongated terminal elements, which lay on a cellular subpellis.
- *Hymeniderm*: the suprapellis consists of anticlinal, thin-walled, short and clavate terminal elements, which lay on an often thin cellular subpellis.

#### *Pellis with isodiametric cells, but never forming a distinct layer*

- *Trichopalisade*: looks like a trichoderm in which some of the anticlinal hyphae are inflated or rounded, which gives it a palisade-like impression.
- *Lamprotrichopalisade*: as a trichopalisade, but with thick-walled terminal elements.
- *Mixed trichopalisade*: as a trichopalisade, in which some terminal elements are thick-walled.
- *Mixed trichopalisade with abundant thick-walled elements*: as a trichopalisade, in which the majority of terminal elements are thick-walled.

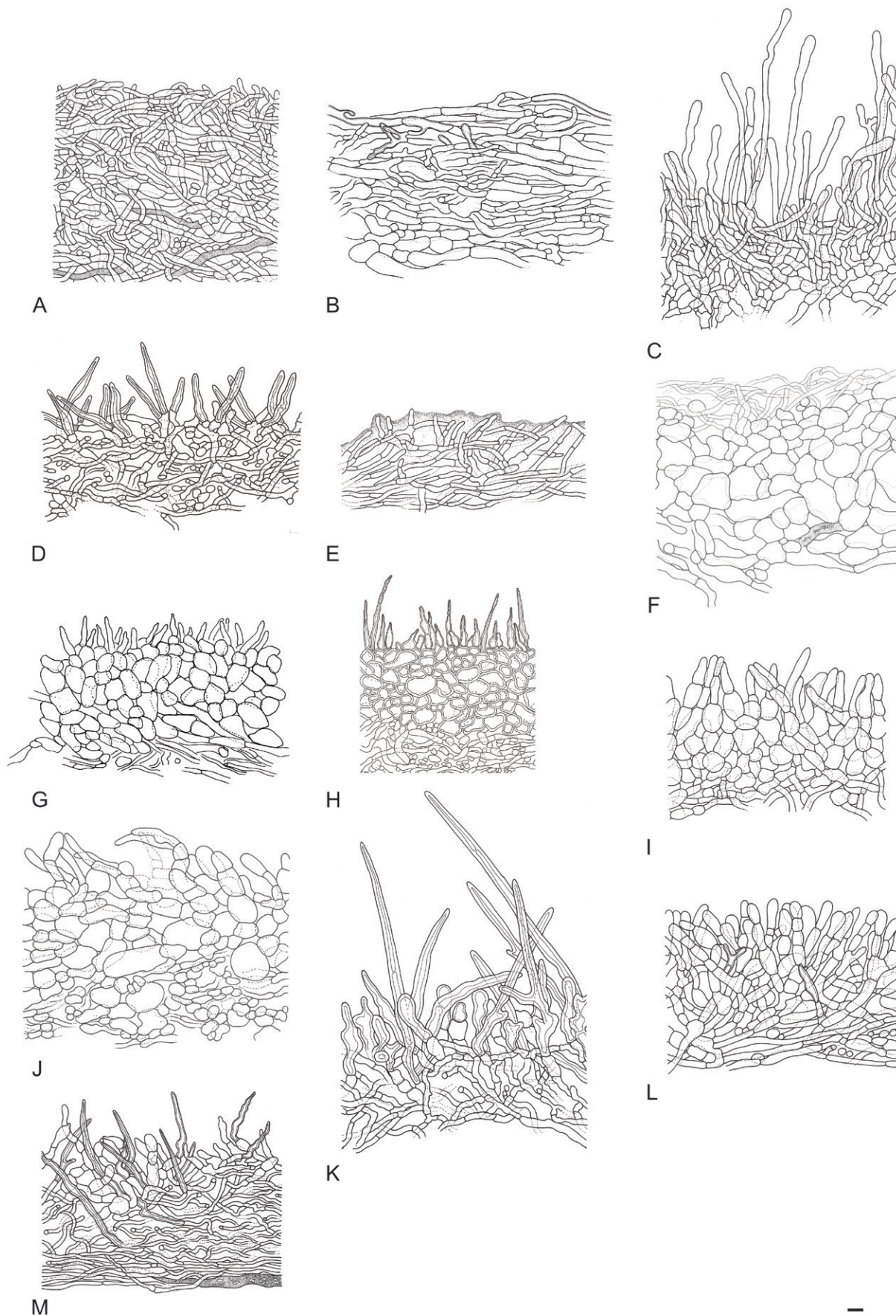
**Dermatocystidia** rarely occur in the genus *Lactifluus*. However, they are present in *Lf.* sect. *Russulopsidei* and *Lf.* sect. *Piperati*, in the upper layer of cutis-like structures or of a hyphoepithelium (Fig. 15).

#### *Hymenial elements*

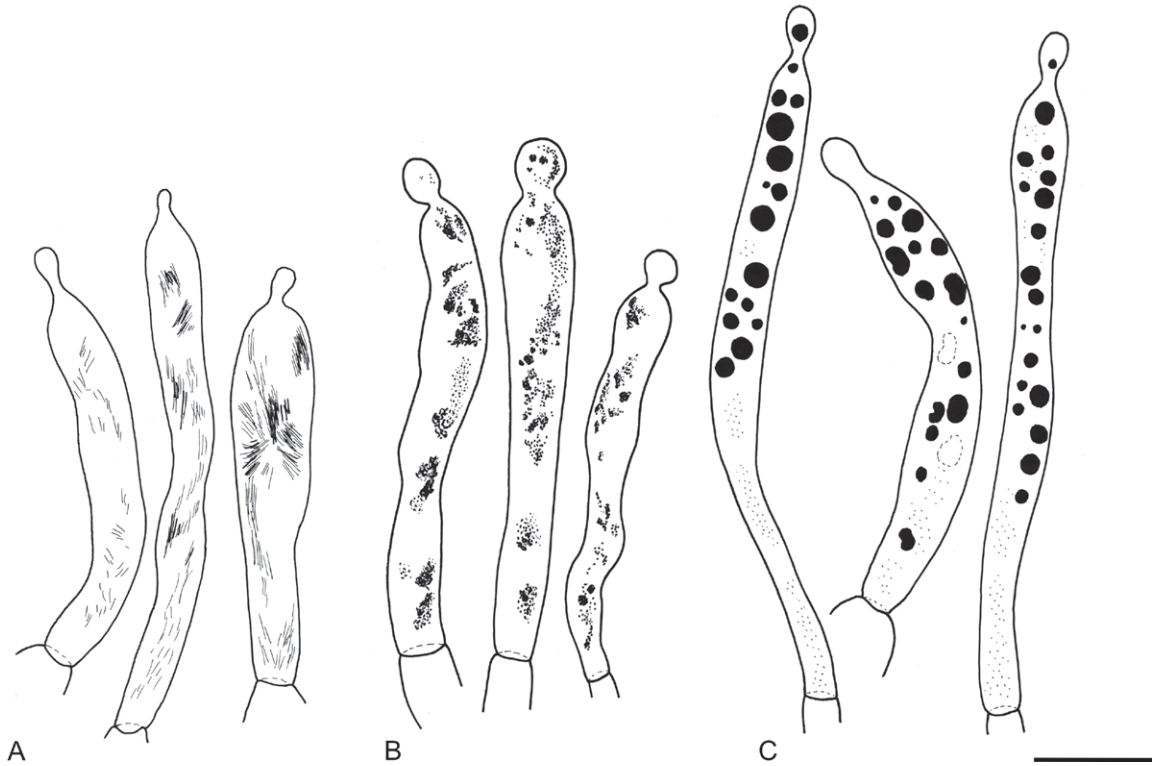
**Basidia and basidioles** only slightly differ between closely related species (Fig. 16). Some species have long and slender basidia, such as *Lf. albomembranaceus*, while others have small and almost clavate basidia, such as *Lactifluus* sp. (EDC 14-061; Fig. 16B). Sterigmata can be short, or long and slender. Most basidia have four sterigmata and form four spores. However, several *Lactifluus* species also have two- or one-spored basidia, such as *Lf. bicapillus* (EDC 12-071; Fig. 16D). Basidia are measured excluding sterigmata and their width is measured at the broadest place.

The genus *Lactifluus* displays different cystidium types. **Pseudocystidia**, which also occur in *Lactarius* and some *Multifurca* species, have no septum and are the extremities of lactiferous hyphae (Fig. 17). Their content therefore resembles the content of lactiferous hyphae, which is refringent, dense, oleiferic or needle-like to granular (Verbeken & Walley 2010). In *Lactifluus*, their abundance and form may vary considerably. In many species of *Lf.* subg. *Pseudogymnocarpi* they are scarce, while in many species of *Lf.* sect. *Lactariopsis* they are conspicuous and abundant. Pseudocystidia are slender or broad and in some species strongly emergent. Their top is rounded, tapering, moniliform or even forked. Depending on their position on the lamellae, they are called pleuropseudocystidia, when located at the lamella side, or cheilopseudocystidia, when located at the lamella edge.

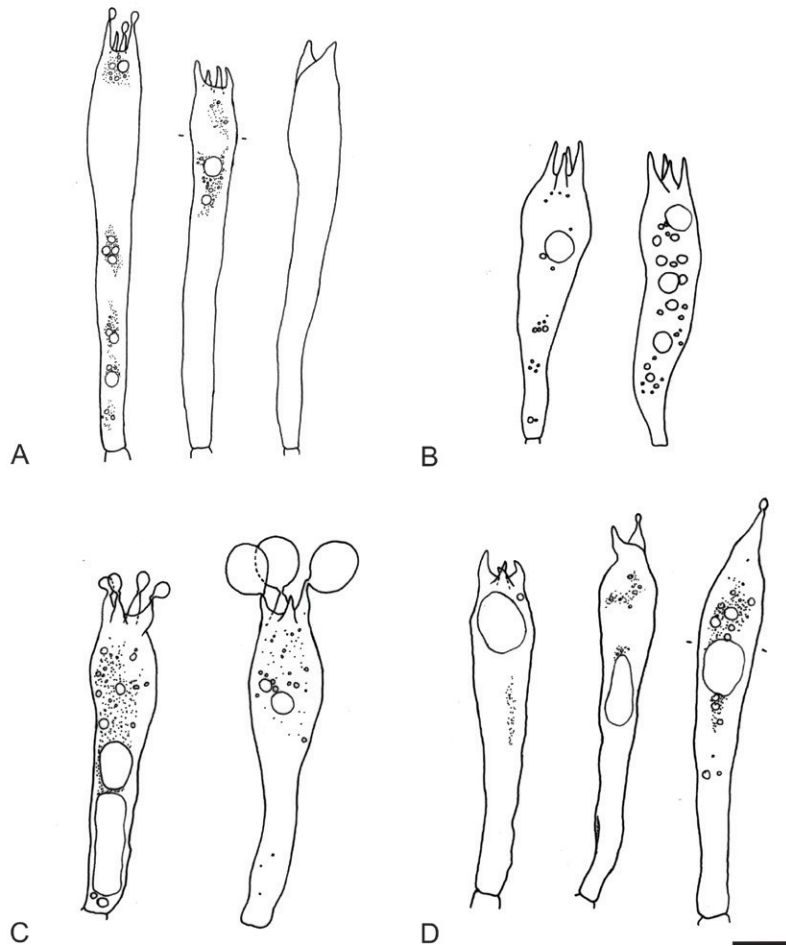
**True pleurocystidia and cheilocystidia** also occur. Three different types of true cystidia are known in *Lactifluus* species (Fig. 18). *Lamprocystidia*: thick-walled cystidia, which are often very large, frequently emergent to strongly emergent and sometimes septate. Some of the largest lamprocystidia emerge from within



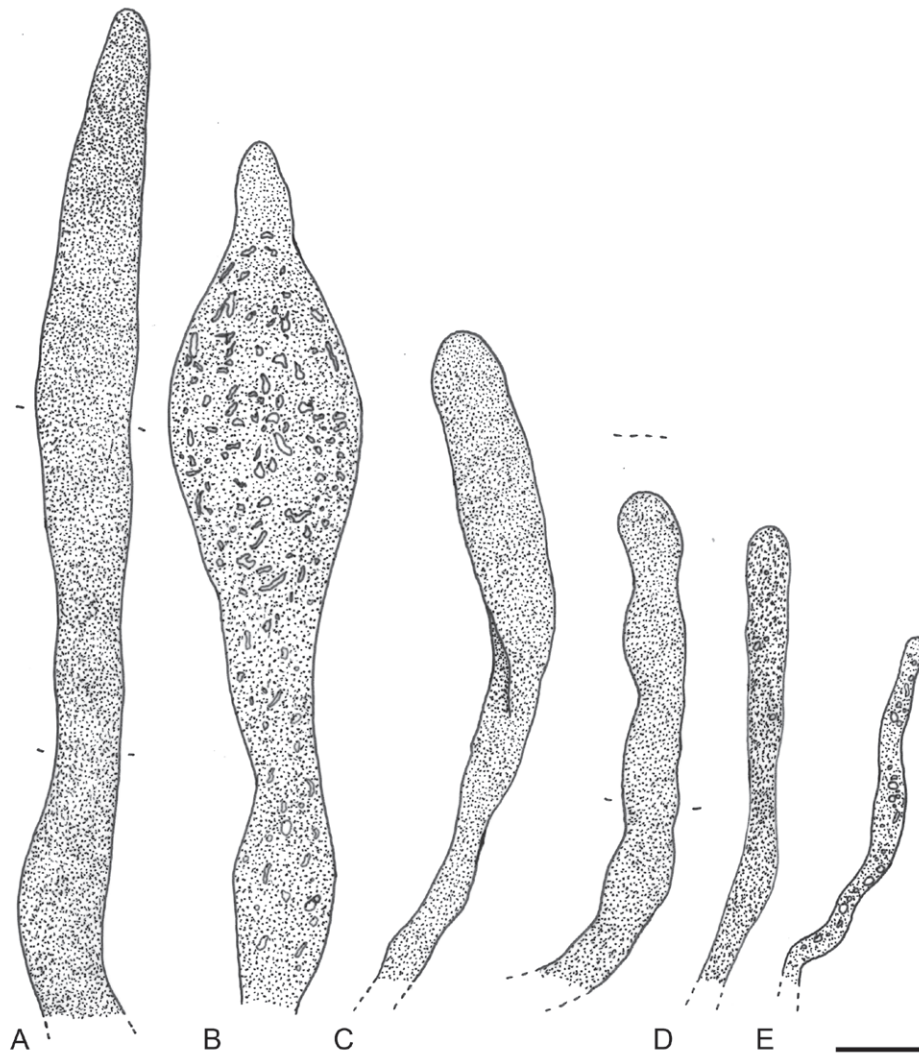
**Fig. 14.** Overview of different pileipellis types found in the genus *Lactifluus*. **A.** Cutis in *Lf. urens* (JR 6002). **B.** Irregular cutis in *Lf. hallingii* (FH 18-077). **C.** Trichoderm in *Lf. aurantiifolius* (AV 94-063). **D.** Lamprotrichoderm in *Lf. pruinatus* (BB 3248). **E.** Ixotrichoderm in *Lf. rufomarginatus* (ADK 3011). **F.** Hyphoepithelium in *Lf. piperatus* (HP 8475). **G.** Palisade in *Lf. atrovelutinus* (DS 06-003). **H.** Lampropalisade in *Lf. oedematopus* (RW 1228). **I.** Hymeniderm in *Lf. roseolus* (AV 94-064). **J.** Trichopalisade in *Lf. xerampelinus* (TS 1116). **K.** Lamprotrichopalisade in *Lf. heimii* (AV 94-465). **L.** Mixed trichopalisade in *Lf. indusiatus* (AV 94-122). **M.** Mixed trichopalisade abundant thick-walled elements in *Lf. sesemotani* (GF 143). [Scale bar = 10  $\mu$ m. Line drawings by A. Verbeke (A, C–F, I–M), L. Delgat (B), D. Stubbe (G) and K. Van de Putte (H)]. Adapted from fig. 1 from De Crop *et al.* (2017).



**Fig. 15.** Overview of different types of dermatocystidia found in the genus *Lactifluus*. **A.** *Lf. ruvubuensis* (AV 94-617). **B.** *Lf. longipes* (BB 1345). **C.** *Lf. claricolor* (R. Heim J18bis) [Scale bar = 10 µm. Line drawings by A. Verbeken (A–C)].



**Fig. 16.** Overview of different basidium types found in the genus *Lactifluus*. **A.** Long and slender basidia in *Lf. albomembranaceus* (EDC 12-046). **B.** Short and clavate basidia in *Lactifluus* sp. (EDC 14-061). **C.** Four-spored basidia in *Lf. heimii* (EDC 11-082). **D.** One-, two- and four-spored basidia in *Lf. bicapillus* (EDC 12-071) [Scale bar = 10 µm. Line drawings by E. De Crop].



**Fig. 17.** Overview of different pseudocystidium types found in the genus *Lactifluus*. **A.** Broad and emergent pseudocystidium in *Lactifluus* sp. (EDC 12-040). **B.** Very broad pseudocystidium in *Lactifluus* sp. (EDC 12-030). **C.** Not emergent pseudocystidia in *Lf. cyanovirescens* (FN 05-631). **D.** Narrow pseudocystidium in *Lactifluus* sp. (JN 2011-071). **E.** Very narrow pseudocystidium in *Lf. cf. phlebonemus* (EDC 12-067) [Scale bar = 10  $\mu\text{m}$ . Line drawings by E. De Crop (A–C, E) and S. De Wilde (D)].

the hymenophoral trama, such as in species of *Lf.* sect. *Lactifluus*. **Macrocystidia:** thin-walled cystidia with a specific content, which is oil-like, needle-like or granular. Their top is rounded, tapering or moniliform.

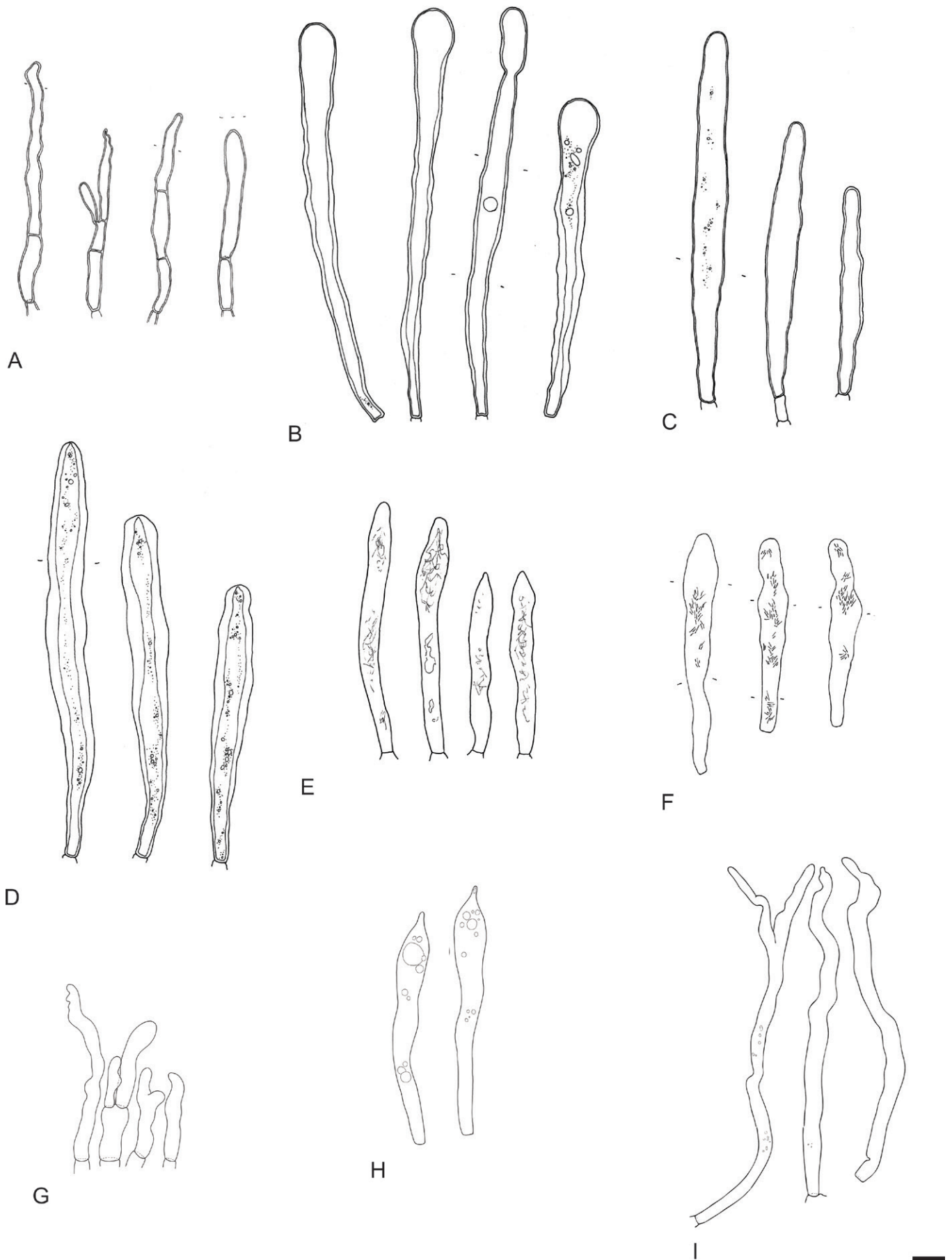
**Leptocystidia:** thin-walled cystidia, without a remarkable content, but with a deviating shape. They are rather rare in *Lactifluus*.

Next to different types of cystidia, some *Lactifluus* species have **sterile elements** in their hymenium (Fig. 19). These cells are septate, thin-walled, with no remarkable content and no deviating shape. They are cylindrical and usually ending blunt. Dierickx *et al.* (2019b) dismiss the idea that these cells represent basidioles or cystidia. They are known to occur in a handful of species (Delgat *et al.* 2017, De Crop *et al.* 2019, Dierickx *et al.* 2019b), but due to their unremarkable shape and content, they might be overlooked and thus more common than currently known.

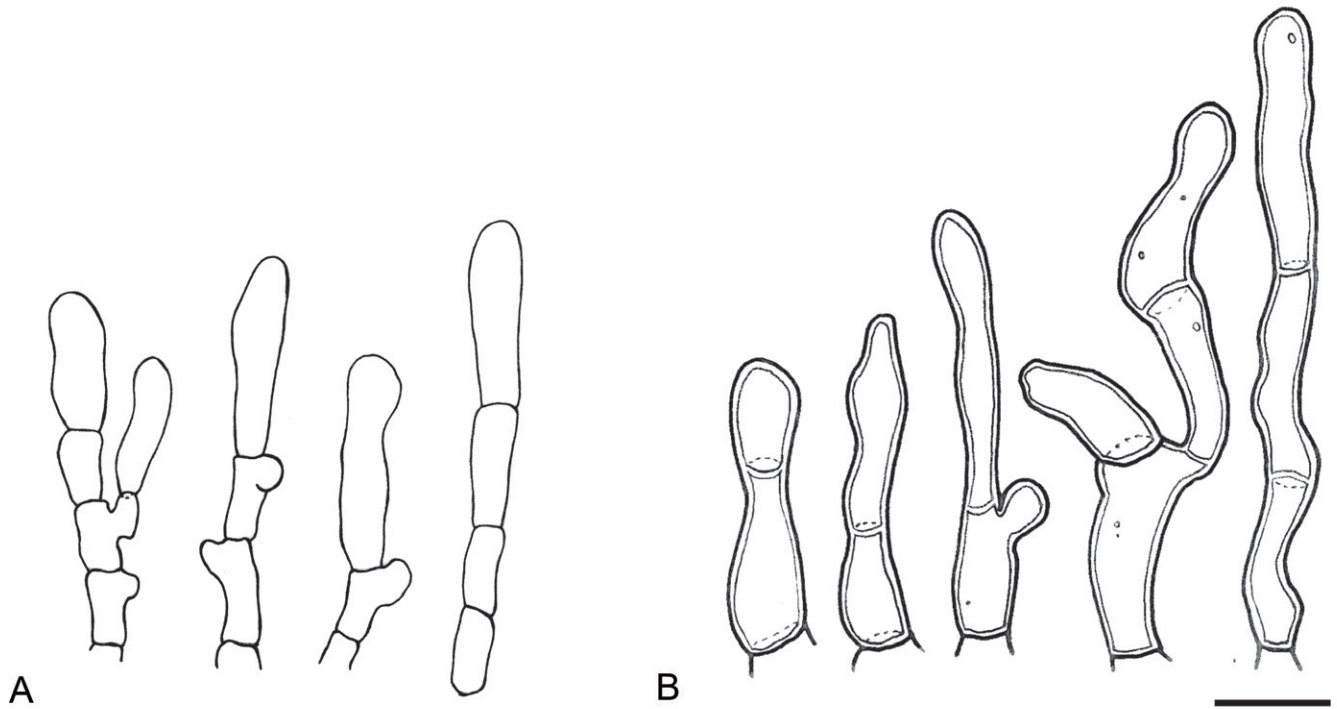
The **lamella edge** may contain different elements, such as pseudocystidia, true cystidia, basidioles, basidia, sterile elements or marginal cells. Cheilopseudocystidia, true cystidia and other elements that are present at the lamella edge are often smaller than those on the lamella sides. In several *Lactifluus* species,

the lamella edge is sterile and entirely composed of sterile **marginal cells** (Fig. 20). These marginal cells are either thin- or thick-walled, hyaline, with a clavate, fusiform to irregular shape (Verbeken & Walley 2010).

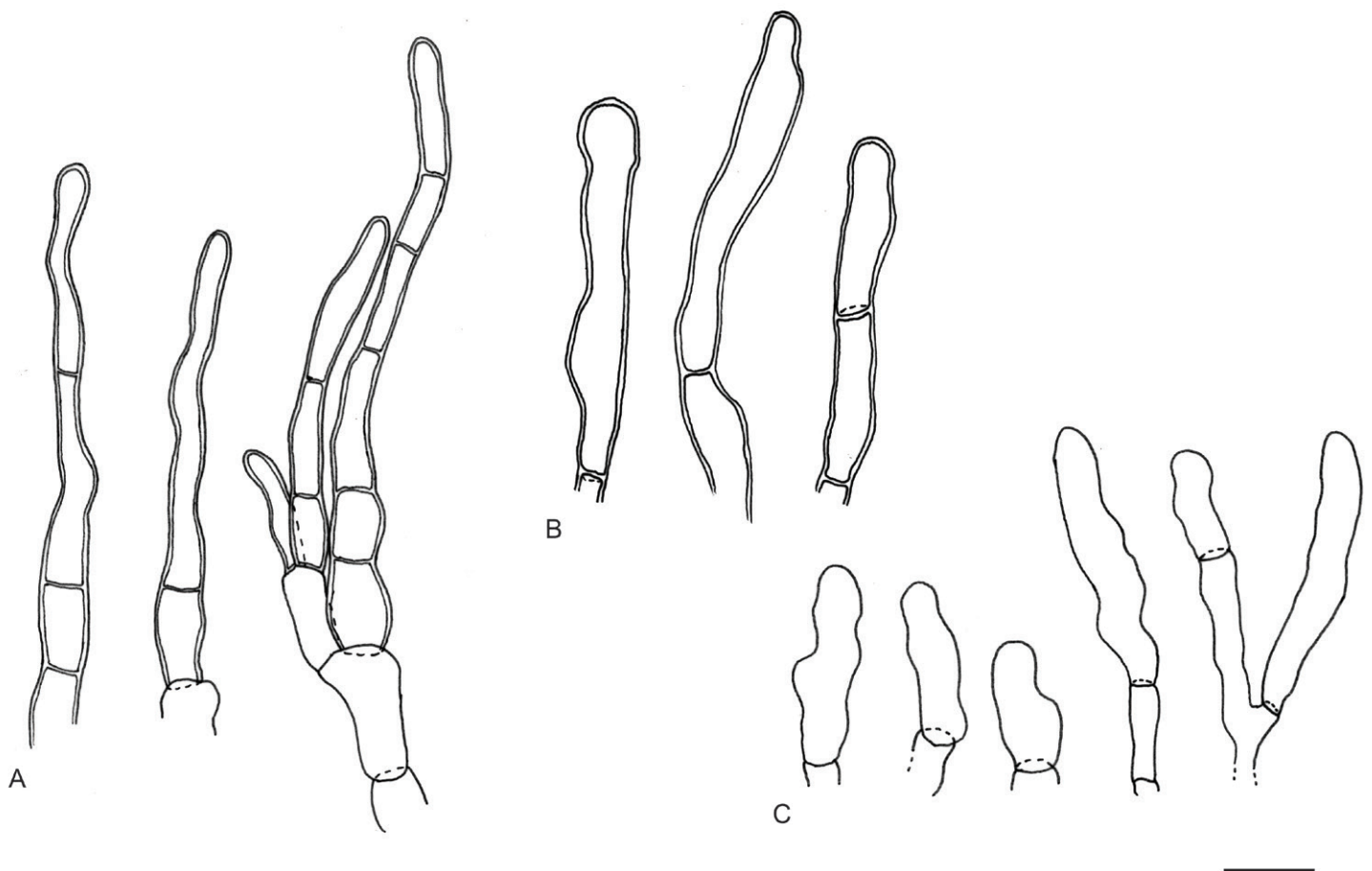
*Russulaceae* species, together with many species of other *Russulales* families, are characterised by **basidiospores** with an amyloid spore ornamentation (Fig. 21). In *Lactifluus*, the spore ornamentation patterns are important in delimiting species or sections, and range from isolated warts and warts connected with fine connective lines, to a complete reticulum. Spore ornamentation can be very low (<0.1  $\mu\text{m}$  in *Lf. indusiatus*) to rather high (ridges up to 2.3  $\mu\text{m}$  in *Lf. longipilus*). The plage (smooth area just above the apiculus) is either inamyloid, centrally amyloid, distantly amyloid or completely amyloid. The length and width of *Lactifluus* spores are measured in side view, excluding ornamentation. Most *Lactifluus* spore dimensions fit the following range 6.1–13.4  $\times$  4.8–11.1  $\mu\text{m}$ . *Lactifluus carmineus* has the longest spores (11.0–13.4  $\mu\text{m}$  long), while *Lf. conchatulus* has the shortest spores (6.1–7.8  $\mu\text{m}$  long). *Lactifluus subvolemus* has the broadest spores (7.3–11.1  $\mu\text{m}$  broad), while *Lf. foetens* has the narrowest spores (4.8–6.5  $\mu\text{m}$  broad). The overall spore shape is determined by the length : width-ratio (quotient or



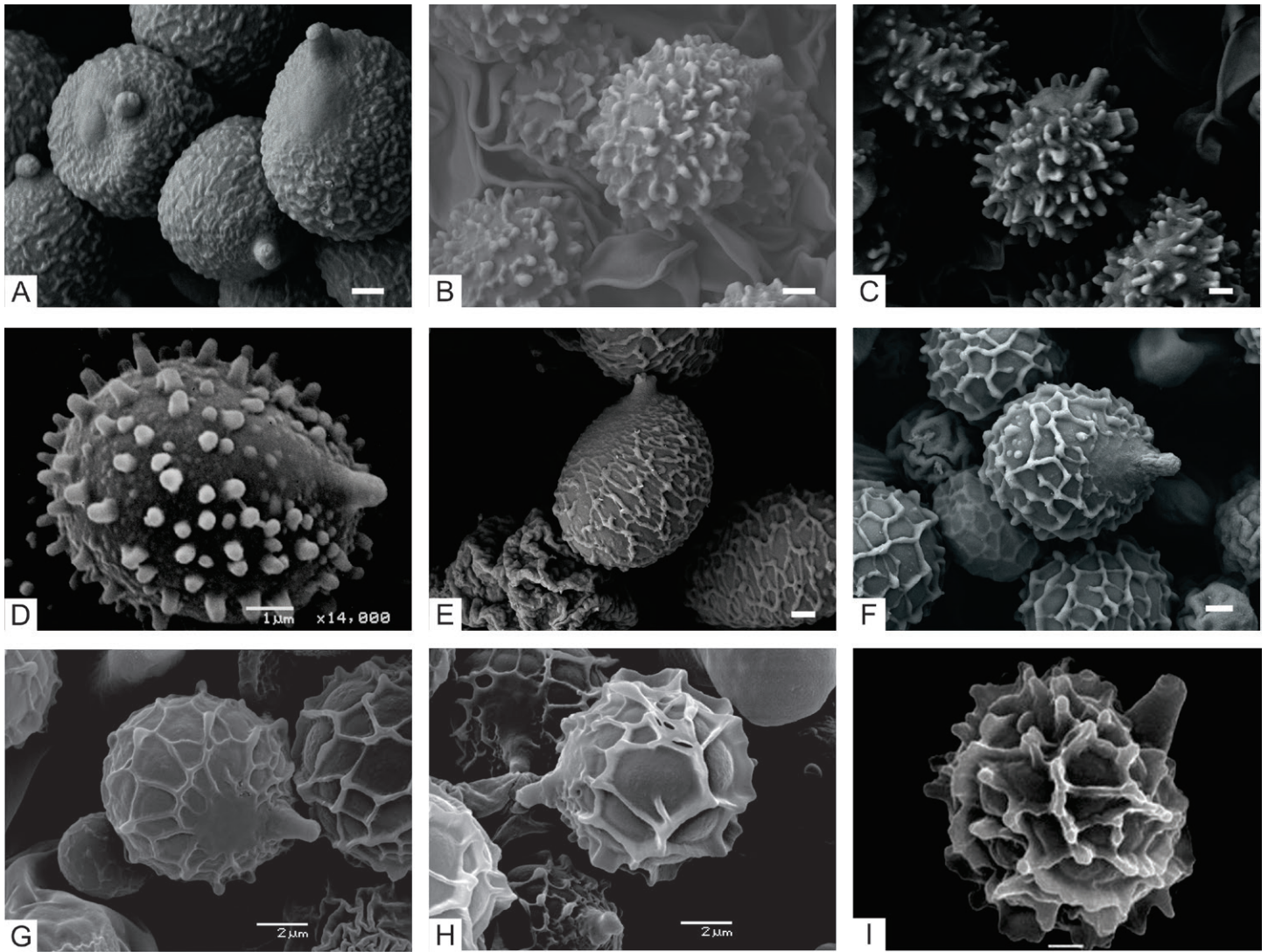
**Fig. 18.** Overview of different true cystidium types found in the genus *Lactifluus*. **A–D** Lamprocystidia. **A.** In *Lf. armeniacus* (EDC 14-501). **B.** In *Lf. kigomaensis* (AV 11-006). **C.** In *Lf. cf. pumilus* (EDC 12-066). **D.** In *Lf. cf. volemus* (REH 9320). **E–F** Macrocytistidia. **E.** In *Lf. hallingii* (REH 7993). **F.** In *Lf. roseophyllus* (JN 2011-076). **G–I** Leptocystidia. **G.** In *Lf. ruvubuensis* (AV 94-599). **H.** In *Lf. indusiatus* (AV 94-122). **I.** In *Lf. densifolius* (BB 3601) [Scale bar = 10  $\mu$ m. Line drawings by E. De Crop (A–D, F), L. Delgat (E) and A. Verbeken (G–I)]. Adapted from fig. 2 from De Crop et al. (2017).



**Fig. 19.** Overview of different types of sterile elements found in the genus *Lactifluus*. **A.** Thin-walled, cylindrical, and septate sterile elements, sometimes with clamp-like bulges under the septum, of *Lf. bicapillus* (EDC 12-169, adapted from De Crop *et al.* 2019). **B.** Cylindrical, septate, and slightly thick-walled sterile elements of the hymenium in *Lf. persicinus* (EDC 14-376, EDC 14-371 and EDC 14-380, adapted from Delgat *et al.* 2017). [Scale bar = 10  $\mu$ m].



**Fig. 20.** Overview of different marginal cell types found in the genus *Lactifluus*. **A.** *Lf. russulisporus* (REH 9398). **B.** *Lf. armeniacus* (EDC 14-501). **C.** *Lf. cf. phlebonemus* (EDC 12-067) [Scale bar = 10  $\mu$ m. Line drawings by E. De Crop (A–C)].



**Fig. 21.** SEM pictures of different basidiospore types found in the genus *Lactifluus*. **A.** Very low ornamentation in *Lf. ramipilosus* (EDC 14-503). **B.** Ornamentation of warts connected by fine connective lines in *Lf. albomembranaceus* (EDC 12-046). **C.** Ornamentation of high warts connected by fine connective lines in *Lf. caliendrifera* (KW 378). **D.** Rounded warts in *Lf. angustus* (MGF 713). **E.** Low ornamentation forming an almost complete reticulum in *Lactifluus* sp. (AV 11-029). **F.** Ornamentation forming an almost complete reticulum in *Lf. armeniacus* (EDC 14-501). **G.** Reticulated ornamentation in *Lf. volemus* (KVP 08-045). **H.** Reticulated ornamentation with moderately high ridges in *Lf. oedematopus* (RW 1228). **I.** Reticulated ornamentation with high ridges and warts in *Lf. aff. gerardii* (LTH 270) (Scale bar = 1  $\mu$ m).

Q-value): globose spores are defined by a Q-value ranging from 1.00–1.05, subglobose spores by Q between 1.06–1.12, ellipsoid spores by Q between 1.13–1.39 and elongate spores by Q >1.39 (Verbeken & Walley 2010). The spore shape in *Lactifluus* species ranges between subglobose to ellipsoid (average Q between 1.10–1.37), only a few species have globose spores, such as in some *Lf. oedematopus* collections (Q = 1) or elongate spores, such as in some *Lf. longisporus* collections (Q = 1.6).

**Hymenophoral trama** in *Lactifluus* typically consists of isodiametric sphaerocytes (globose cells), sometimes in combination with hyphae, and rarely only hyphae (Fig. 22). In between the trama, **lactiferous hyphae** are found. They have a refringent, dense, oleiferic, or needle-like to granular content and are rather broad (4–16  $\mu$ m). In some species they are abundant, while scarce in others.

#### *Characteristics of the ectomycorrhizas*

The ectomycorrhizas of only very few *Lactifluus* species have been studied until now: *Lf. piperatus* (Beenken 2004), *Lf. rugatus*

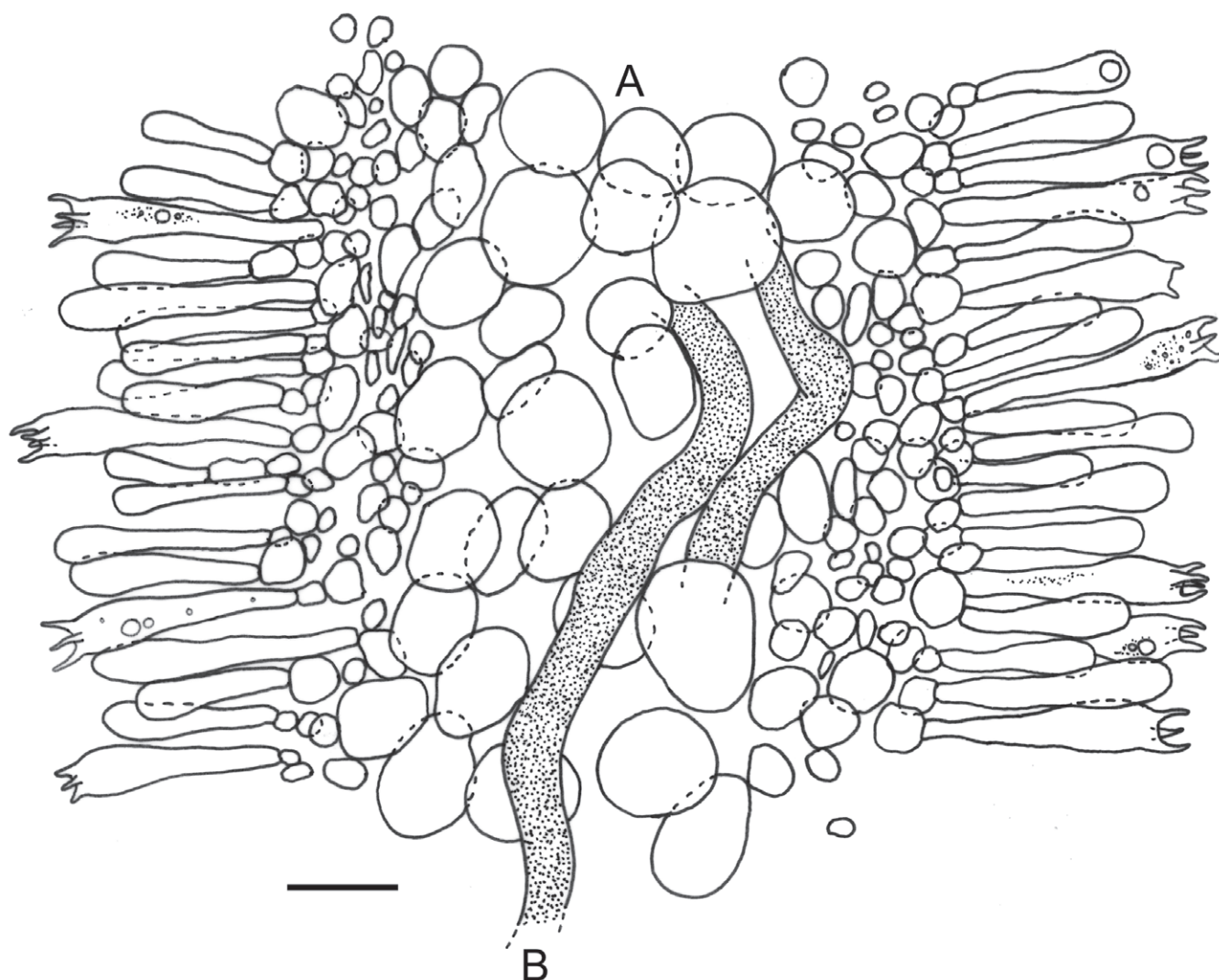
(Leonardi *et al.* 2016), *Lf. vellereus* (Grebenc *et al.* 2009) and *Lf. aff. volemus* (Kumar & Atri 2016). Leonardi *et al.* (2016) concluded that there are no significant ECM features shared by those four species, which reflects their relatively far phylogenetic distance (from three different subgenera).

The different mantle layers can be plectenchymatous to pseudoparenchymatous. The outer mantle layer may contain cystidia (*L. rugatus*), extramatrical hyphae (*L. piperatus* and *L. aff. volemus*) or a hyphal net (*L. vellereus*). Lactifers may be present in the inner mantle layer (*L. vellereus* and *L. aff. volemus*). Rhizomorphs are sometimes present (*L. piperatus* and *L. vellereus*). See Leonardi *et al.* (2016) for a more detailed description of ECM characteristics.

#### **Ethnomycological uses**

Wild edible mushrooms, often ectomycorrhizal fungi, are one of the more important renewable natural resources in many regions worldwide. Milkcap species are easily recognised and often





**Fig. 22.** Section through the hymenium in *Lactifluus* sp. (EDC 14-060). **A.** Cellular trama. **B.** Lactiferous hyphae (Scale bar = 25  $\mu$ m. Line drawing by E. De Crop).

fruit in large numbers, which makes them popular at markets. Depending on the culture, different species are consumed and prepared in a variety of ways. Species of the genus *Lactifluus* are consumed in large parts of Africa, Asia, Europe, Central and North America (Nuytinck *et al.* 2020).

In many sub-Saharan **African** countries, mushrooms are of great importance to the local people. Large parts of these countries are covered by Sudanian or Miombo woodlands, by a woodland-savannah mosaic intermingled with riparian forests, or by rainforests; and all those vegetation types are characterised by the occurrence of a variety of ECM trees. In regions with woodland or riparian forests, fungi fruit in large numbers at the beginning of the rain season, which is the traditional hunger period (Rammeloo & Walley 1993, Smith & Allen 2004). Mushrooms are eaten fresh, dried or cooked (Fig. 23). Milkcap species, especially the sharp-tasting species, are often parboiled, and the boiling water is thrown away (Härkönen *et al.* 2003). Mushrooms are commonly sold on markets and along roadsides, particularly by women and children (Härkönen *et al.* 2003, Mittermeier *et al.* 2003, Williams *et al.* 2008).

Some *Lactifluus* species are eaten over their whole range of distribution, such as *Lf. densifolius*, *Lf. edulis*, *Lf. gymnocarpoides*, *Lf. gymnocarpus*, or *Lf. rubroviolascens*. Others are only eaten locally, such as *Lf. albomembranaceus*, *Lf. brunnescens*, *Lf. longipes*, and *Lf. persicinus* in Cameroon (Njouonkou *et al.* 2016);

*Lf. heimii*, *Lf. luteopus*, and *Lf. xerampelinus* in Tanzania (Härkönen *et al.* 2003); *Lf. brunnescens* and *Lf. longisporus* in Haut-Katanga (DRC; De Kesel *et al.* 2017); *Lf. flammans* in Benin (De Kesel *et al.* 2002, Yorou *et al.* 2014); *Lf. rubiginosus* in Zambia (Härkönen *et al.* 2015); or *Lf. brachystegiae* in Zimbabwe (Sharp 2011, 2014).

*Lactifluus* species are traditionally appreciated in many **European, Asian, North and Central American** countries. In particular, *Lf. volemus* and its sister species from *Lf.* sect. *Lactifluus* are eaten in many countries over their entire range of distribution (Russell 2006, Wang & Yang 2006, Garibay-Orijel *et al.* 2007, Le 2007, Liu *et al.* 2009, Lincoff 2010, Van de Putte 2012, Nuytinck *et al.* 2020). These species often have large sporocarps which are easy to identify, even by non-experts, and they can locally fruit in large numbers (Van de Putte 2012). Species of *Lf.* sect. *Pseudogymnocarpi* (e.g. *Lf. rugatus* or *Lf. hygrophoroides*) are also popular and eaten in almost every country where these often brightly coloured species with large sporocarps occur (Marchand 1980, Bessette *et al.* 1997, Foiera *et al.* 1998, Roody 2003, Miller & Miller 2006, Bessette 2007). Species of *Lf.* sect. *Albati* and *Lf.* sect. *Piperati* have white, large and firm sporocarps with an acrid taste. These are only eaten in certain regions, often after removing the acrid taste by parboiling or preservation with salt (Montoya & Bandala 1996, Heilmann-Clausen *et al.* 1998), but in other regions they are considered poisonous (Bessette 2007). Other species are only



**Fig. 23.** Edible *Lactifluus* species in Africa. **A.** Our local guide with a basket full of *Lactifluus* species (Foumban, Cameroon). **B.** Cooked *Lactifluus* species for sale on the market (Foumban, Cameroon). **C.** *Lactifluus* species for sale on the market (Kigoma, Tanzania). **D.** A variety of *Lactifluus* species collected for consumption (Kigoma, Tanzania). **E.** Cooked *Lactifluus* species (Foumban, Cameroon) [Photographs by A.L. Njouonkou (B) and E. De Crop (A, C–E)].

eaten locally, such as species from *Lf.* sect. *Luteoli*, *Lf.* sect. *Gerardii* or *Lf.* sect. *Tenuicystidiati* (Roody 2003, Bessette 2007, Nuytinck *et al.* 2020).

To our knowledge, few *Lactifluus* species are only occasionally eaten in **Australasia** (e.g. *Lf.* aff. *piperatus* and *Lf.* *wirrabara*, pers. comm. T. Lebel), and some are considered being poisonous (e.g. *Lf.* aff. *piperatus*; Grgurinovic 1997). We currently have no records of consumed *Lactifluus* species in northeastern **South America** (T. Henkel, pers. comm.).

### Bioactive secondary metabolites

*Lactifluus* species are known to contain bioactive secondary metabolites in their sporocarps. Several *Lactifluus* species are reported to have anti-mutagen properties, such as *Lactifluus volemus* (Wasser 2002, Dai *et al.* 2009, Van de Putte 2012) or *Lf. vellereus* (Mlinaric *et al.* 2004). In China, *Lf. cf. vellereus* contains a highly functionalized lactarane sesquiterpene, velleratretraol, which shows weak anti-HIV activity (Luo *et al.* 2009). Some *Lactifluus* species appear effective as antioxidant agent due to their bioactive compounds, such as the Asian representatives of *Lf. cf. volemus* and *Lf. cf. piperatus* (Ferreira *et al.* 2009, Ozen *et al.* 2011, Abdullah *et al.* 2012, Van de Putte 2012, Joshi *et al.* 2013) and the European *Lf. rugatus* (Sevindik 2020), *Lf. vellereus* and *Lf. bertillonii* (Heleno *et al.* 2012). *Lactifluus piperatus* is reported to have possibilities as a biosorbent and can be used to remove cadmium (Cd II) and zinc (Zn II) ions from wastewater (Nagy *et al.* 2014a, b). In Turkey, *Lf. vellereus* and *Lf. rugatus* are used as food and as traditional medicine and respectively Dogan *et al.* (2013) and Sevindik (2020) showed that they indeed have antimicrobial properties.

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**Conflict of interest:** The authors declare that there is no conflict of interest.

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**Figure S1.** Overview map of the biogeographical regions used for Table 1. Biogeographic regions are based on biogeographic realms (<https://ecoregions2017.appspot.com/>), with three major differences: Western Palearctic (Western part of the Palearctic realm), Asia (Eastern part of the Palearctic realm combined with the Indo-Malay realm), and Australasia (Australasian realm combined with the Oceanian realm). The Palearctic realm was spilt into Western Palearctic and Eastern Palearctic, Eastern Palearctic and the Indo-Malay realm form together the Asia region, and the Australasian realm is combined with the Oceania realm to form the Australasian region.

**Table S1.** List of described *Lactifluus* species, together with the year of description, taxonomical classification (subgenus, section), the indication of how this taxonomical position was defined, the source(s) of this classification, and notes.

**Table S2.** Extra information on the preliminary study of metabarcoding data of the genus *Lactifluus*, retrieved from the GlobalFungi website.

**Table S3.** Overview of the results of the preliminary study of metabarcoding data of the genus *Lactifluus*, retrieved from the GlobalFungi website. Due to the generally shorter length and lower quality of environmental sequence data, the numbers in the table are to be considered an estimate.

**Table S4.** List of the putative new species found in the environmental sequences. References of studies cited are given in S3.