Chapter 9
Recent Insights in the Phylogeny, Species Diversity, and Culinary Uses of Milkcap Genera *Lactarius* and *Lactifluus*

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9.1 Introduction

Milkcaps belong to the Russulales, one of the larger orders within the Agaricomycotina with an estimated diversity of approximately 4000 species (Miller et al. 2006). The order represents a remarkable diversity in basidiocarp (fruiting body) morphologies including corticioid, polyporoid, coralloid, discoid, hydnoid, agaricoid, pleurotoid, and gasteroid species. Equally diverse are the life strategies, with white rot saprotrophic, ectomycorrhizal (EM), parasitic, endophytic, and entomosymbiotic species. From all families within the Russulales, the Russulaceae has the highest species richness and is most diverse both in fruiting body morphologies and life strategies. Apart from the Albatrellaceae, it is the only family in the Russulales in which an EM symbiosis has evolved (Hibbett et al. 2014). The family originally encompassed only the genera *Lactarius* Pers. and *Russula* Pers., characterized by the agaricoid habit and the presence of large isodiametric cells called sphaerocytes (Miller et al. 2006). But with the molecular revolution in taxonomy, our concept of Russulaceae has fundamentally changed, and the family now includes species previously classified in Corticiaceae (Larsson and Larsson 2003),

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Elasmomycetaceae (Miller et al. 2001; Buyck et al. 2008; Nuytinck et al. 2003; Desjardin 2003), and some pleurotoid and annulate taxa (Miller et al. 2001; De Crop et al. 2017).

Perhaps the most striking insight is the abandoning of the strict *Lactarius* (with milk and pseudocystidia) - *Russula* (without milk or pseudocystidia) bifurcation (Buyck et al. 2008). This traditional partition was largely based on European species and does not hold when including species from the tropics (Verbeken and Nuytinck 2013). Nowadays, four agaricoid[1] genera are distinguished. The traditional genus *Russula* is quasi monophyletic, only a small clade: *Russula* subsect. *Ochricompactae* Bills and O.K. Mill. was left out and is now forming, together with the former species *Lactarius furcatus* Coker and *Lactarius stenophyllus* Berk., the new genus *Multifurca* Buyck and V. Hofst. (Buyck et al. 2008; Wang et al. 2018). *Multifurca* can be recognized by the orange spore print, forking gills, and a characteristic zonation of the context (Buyck et al. 2008). Latex can be present or absent. *Multifurca* is by far the less diverse of the four agaricoid genera, with only twelve described species (Wang et al. 2018; Verbeken et al. 2018).

Lactarius in a traditional sense consisted of two reciprocal monophyletic clades: a smaller clade including the type species for the genus *Lactarius* (*Lactarius piperatus* (L.: Fr.) Pers.) and a clade containing the majority of the known *Lactarius* species (Buyck et al. 2008). Because of the quantitative difference in species richness, it was proposed to conserve the name *Lactarius* for the largest clade with type species *Lactarius torminosus* (Schaeff.: Fr.) Pers., and to change the smaller clade into the genus *Lactifluus* (Pers.) Roussel (a former taxonomic synonym of *Lactarius* with type species *Lactifluus volemus* (Fr.) Kuntze) (Buyck et al. 2010). The proposal was accepted (Barrie 2011).

There are no true synapomorphies characterizing each of the two milkcap genera. In general, *Lactifluus* shows the tendency to have a hymenophoral trama composed of sphaerocytes and often possesses thick-walled elements in the stipiti- or pileipellis or lamprocystidia in the hymenium, while most *Lactarius* species lack these features (Verbeken and Nuytinck 2013). *Lactifluus* is also generally characterized by the complete absence of zonate and viscid to glutinous caps, while it contains many species with veiled and velvety caps. In *Lactarius* many, but not all species, have zonate and sticky to slimy caps (Verbeken and Nuytinck 2013). Pleurotoid milkcaps are so far only known in *Lactifluus* (Buyck et al. 2008; Verbeken and Nuytinck 2013), while gasteroid and secotioid species are only known within *Lactarius*. Besides these morphological trends, the genera also differ in distribution, with *Lactarius* mainly distributed in the Northern hemisphere, while *Lactifluus* has its main range in the tropics. These trends might be helpful when identifying milkcap species, but they are not exclusive. There are species, especially in the tropics, in which a DNA marker is needed to determine which genus they belong to (De Crop 2016).

[1] These genera are almost entirely agaricoid (pileate-stipitate with lamellae), but *Russula* and *Lactarius* include some angiocarpic representatives, and *Lactifluus* includes species with a pleurotoid morphology.

This contribution highlights our most recent insights in the phylogenic relationships and evolutionary history of the milkcap genera. We also summarize knowledge on the edibility of some well-known milkcap taxa.

9.2 *Lactarius*

The most comprehensive molecular phylogenies of *Lactarius* s.s. that have up to now been published comprise only a fraction of the ±420 species that have been described. Buyck et al. (2008) included 12 species and classified them within the three traditionally recognized subgenera: *L.*[2] subg. *Plinthogalus* (Burl.) Hesler and A.H. Sm., *L.* subg. *Russularia* (Fr. ex Burl.) Kauffman, and *L.* subg. *Piperites* (Fr. ex J. Kickx f.) Kauffman. Since the type species of the genus changed to *L. torminosus*, we should now use the name *L.* subg. *Lactarius* for the latter taxon. Eberhardt and Verbeken (2004) and Geml et al. (2009) included more species in their studies, but still placed all of them in the same three traditional subgenera. Verbeken et al. (2014) showed in their phylogeny that several tropical *Lactarius* species form a diverging grade to the recognized subgenera. Figure 9.1 gives insight in our current understanding at subgenus level of the phylogeny of *Lactarius.* Several new tropical lineages need to be described at subgenus level.

Other studies have focused on subgenera or sections in *Lactarius* in more detail. Much work has been done on *L.* sect. *Deliciosi* (Fr.) Redeuilh, Verbeken, and Walleyn. Nuytinck et al. (2007) and Nuytinck and Verbeken (2007) included all up to then described species in a two-locus worldwide phylogeny and concluded that intercontinental overlap is much smaller than previously assumed. Several new species have since been described and illustrate that our knowledge of the genus in North America and Asia still has gaps (Nuytinck and Ammirati 2014; Wang et al. 2015b; Wang 2016; Nuytinck et al. 2017).

Wisitrassameewong et al. (2014a, b, 2015, 2016) explored the diversity of *L.* subg. *Russularia* focusing mainly on Southeast Asia. They revealed 23 new species and explored the historical biogeography of the subgenus. The European taxa of *L.* subg. *Plinthogalus* and American varieties of *L. lignyotus* Fr. were re-evaluated in Stubbe and Verbeken (2012). Some tropical species of the same subgenus were explored in Stubbe et al. (2008) and Verbeken et al. (2008).

The diversity in Europe is rather well understood, although an ongoing study reveals cryptic diversity in some species (Nuytinck et al., unpublished results). To better understand the worldwide diversity and evolution of *Lactarius*, we need to focus our attention on the following four questions: (1) Where did the genus originate and can we revise our Eurocentric view on the classification of the genus by including more tropical taxa? (2) What are the important drivers of diversification in *Lactarius*? (3) We understand the distribution of circum-arctic *Lactarius* species but

[2] We use *L.* as the abbreviation of *Lactarius* and *Lf.* to abbreviate *Lactifluus*.

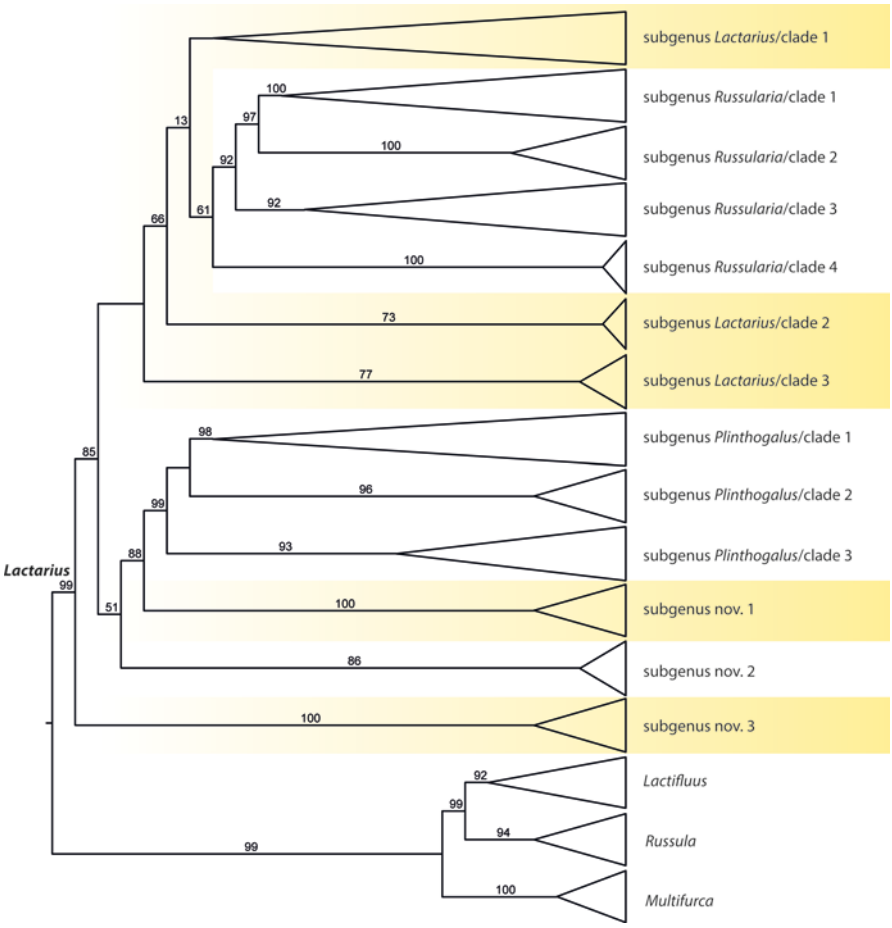

Fig. 9.1 Phylogenetic overview of the genus *Lactarius*, based on an unpublished Maximum Likelihood analysis of a dataset of four markers (ITS, LSU, *rpb1*, *rpb2*)

which boreal and temperate taxa have an intercontinental distribution? How and when did they migrate and what is the role of their EM partner therein? and (4) Can our understanding of the delimitation of and relationships between the many sections and subsections in *L.* subg. *Lactarius* be improved? The delimitation of *L.* subg. *Russularia* from *L.* subg. *Lactarius* is not straightforward (Fig. 9.1). Morphology and phylogeny are in many instances in conflict. A well-resolved phylogeny based on a balanced worldwide sampling will allow to estimate divergence times for the origin and diversification of *Lactarius* and reconstruct the geographical history of the genus. More sampling in North America and in the tropics deserves special attention.

9.3 *Lactifluus*

Lactifluus appears to be one of the dominant EM genera in the tropics (Tedersoo et al. 2010, 2011), yet until recently a robust phylogenetic framework and classification for the genus was lacking. De Crop et al. (2017) assembled a multi-gene dataset representing 80% of the described *Lactifluus* species diversity and 30% of the type specimens. This multi-gene phylogeny was combined with a morphological study, focusing on five important characteristics (basidiocarp type, presence of a secondary velum, color reaction of the latex/context, pileipellis type and presence of true cystidia). The results show that *Lactifluus* can be subdivided in four well-supported subgenera (Fig. 9.2). Two of the traditional, morphology-based subgenera were retained but amended (*Lf.* subg. *Lactariopsis* (Henn.) Verbeken and *Lf.* subg. *Lactifluus*), and two new subgenera were proposed (*Lf.* subg. *Gymnocarpi* (R. Heim ex Verbeken) De Crop and *Lf.* subg. *Pseudogymnocarpi* (Verbeken) De Crop). Within these subgenera, many sections could be delimited. Some of them were confirmed in their traditional delimitation, others were either amended or synonymized. At least ten additional clades were revealed that could represent new sections (Fig. 9.2).

The majority of *Lactifluus* species remains undescribed. There are currently 191 named *Lactifluus* species, 25 of which are not present in any DNA sequence database. In the ITS dataset De Crop (2016) assembled, she delimited 371 species, many thus were labelled as *Lactifluus* sp. Using a species accumulation curve, she estimated that there might be approximately 530 (95% Confidence Interval: 461–601) *Lactifluus* species on earth (Fig. 9.3).

Considering this large amount of unknown species, it is not surprising that new lineages are still discovered, an example of which was published in Wang et al. (2015a). This study, based on 28 samples from southern China, revealed three new lineages of *Lactifluus*. Two of these lineages were described as new sections, *Lf.* sect. *Ambicystidiati* X.H. Wang and *Lf.* sect. *Tenuicystidiati* X.H. Wang and Verbeken. From a morphological point of view, *Lf. ambicystidiatus* X.H. Wang is a striking new species, with both lamprocystidia and macrocystidia in the hymenium, a unique combination within the Russulaceae. Furthermore, only remnants of lactiferous hyphae are present in *Lf. ambicystidiatus*, suggesting that the ability to form a lactiferous system has been lost in this lineage (Wang et al. 2015a).

A striking observation is the occurrence of several large, cryptic or semi-cryptic species complexes in *Lactifluus*. Stubbe et al. (2010, 2012) examined the lineage of *Lf. gerardii* (Peck) Kuntze. At the start of this study, only a handful of species were known; in the end more than 30 phylogenetic species were discovered. Based on the current data, merely two-thirds are morphologically identifiable species. In the complex around *Lf. volemus*, Van de Putte et al. (2010, 2012, 2016) applied phylogenetic species recognition and discovered about 45 different clades. Some of them could be morphologically distinguished and were described as new species. Others remain cryptic; i.e., no morphological differences were found up to now. *Lactifluus piperatus* is also part of a species complex, estimated to contain over 30 clades, the

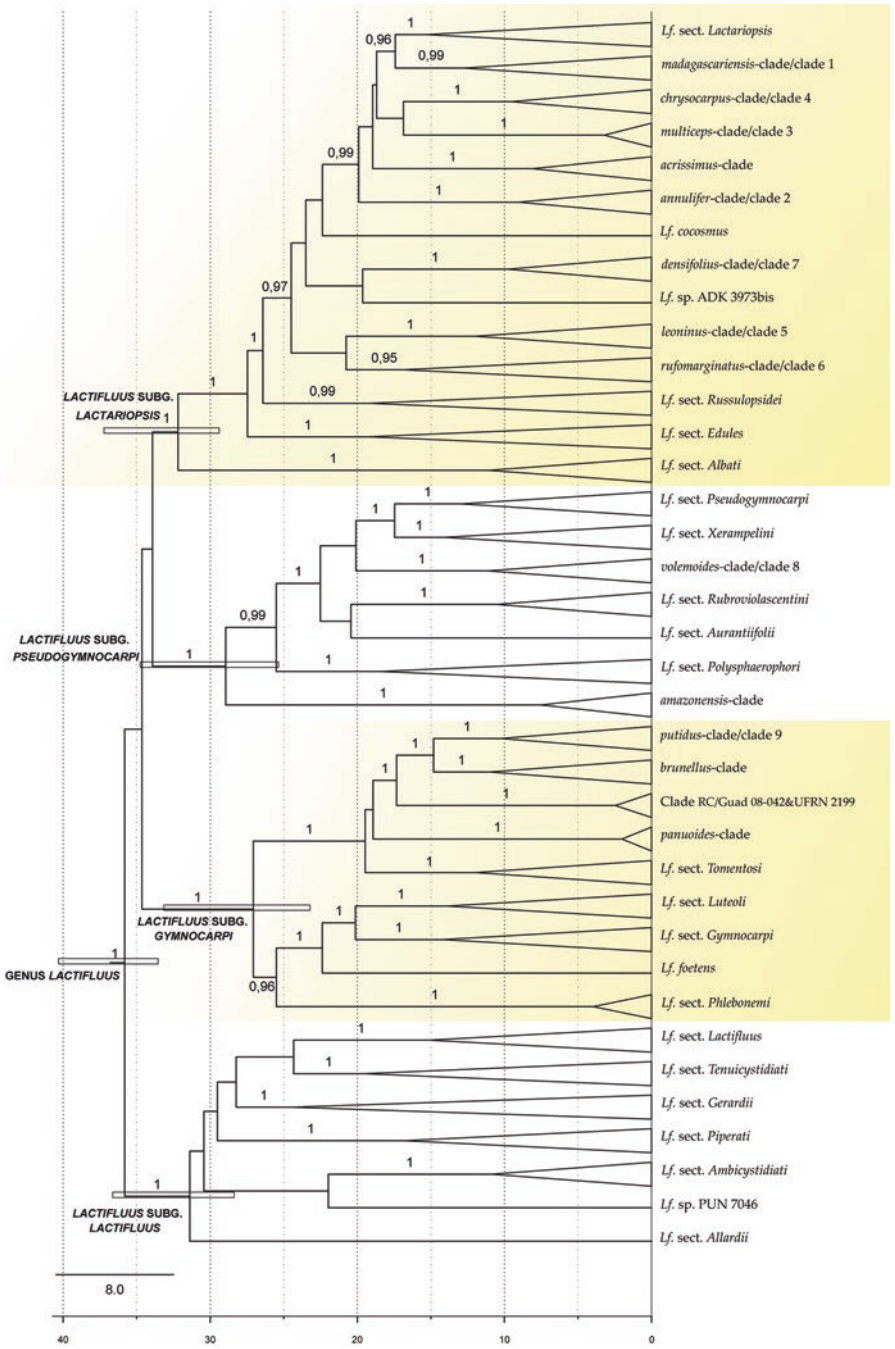

Fig. 9.2 Phylogenetic overview of the genus *Lactifluus*, inferred from a dated BEAST phylogeny presented in De Crop (2016). Time scale = million years. Undescribed clades are named after one representative inside that clade and received consecutive clade numbers

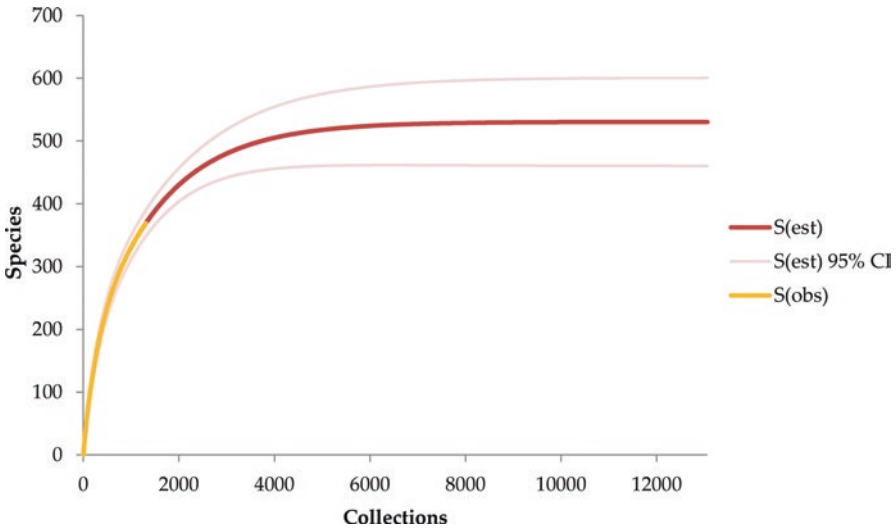

Fig. 9.3 Species accumulation curve of observed (obs) and estimated (est) species richness (S) of the genus *Lactifluus*. Species richness was estimated by extrapolation of the rarefaction curve, with 95% confidence interval (pink lines)

majority being undescribed (De Crop et al. 2014; De Crop 2016). Apart from these species complexes, several other species are assumed to be part of species complexes (De Crop 2016; Wang et al. 2015a). For example, the African *Lf. gymnocarpoides* (Verbeken) Verbeken, *Lf. pumilus* (Verbeken) Verbeken, and *Lf. longisporus* (Verbeken) Verbeken all have similar morphological characteristics and are hard to distinguish in the field. In the temperate regions, *Lf. vellereus* (Fr.) Kuntze and *Lf. bertillonii* (Neuhoff ex Z. Schaef.) Verbeken are also assumed to be part of a species complex.

9.4 Culinary Uses

In many parts of the world, mushrooms are of great importance as seasonal food source. Which species are consumed and the way they are prepared differ according to cultural habits. Russulaceae species are eaten in many parts of Africa, Asia, Europe, and Central and North America. Milkcaps can hardly be confused with deadly poisonous mushrooms because of their latex, and they often fruit in large numbers, which makes them popular at markets. The only studied species that is potentially harmful is *Lactarius necator* (Bull.: Fr.) Pers. It is reported to contain the mutagen necatorin (=7-hydroxycoumaro(5,6-c)cinnoline, von Wright and Suortti (1983); Suortti (1984)). Necatorin has been shown to be comparable to aflatoxin B1 in the strength of its mutagenic activity. Boiling reduces the concentration of this compound, but does not effectively eliminate it (Suortti 1984). Probably due to the

acrid taste, most western European authorities classify this mushroom as inedible or poor. However, it has popularly been used (after pickling or parboiling) as a spice in mushroom dishes in northern and eastern Europe and Siberia.

Several European countries have a strong tradition in collecting wild edible fungi, and milkcaps are often very popular. Due to cultural differences, the same species can be considered a delicacy in northern Europe and an indigestible poisonous terror in the south (e.g., *L. torminosus* and *L. necator*; Basso 1999). As the name of the section and its most popular species give away, many species in *Lactarius* sect. *Deliciosi* are edible and delicious. In fact, all species are probably edible, but some are very inferior in taste (e.g., *L. salmonicolor*; Heim and Leclair 1950). Much depends however on the way of preparation; in several regions, a mix of any *Lactarius* sect. *Deliciosi* species is collected or sold (e.g., in Slovakia and Barcelona, own observations). The culinary properties of these orange milkcaps are especially appreciated in southern Europe (e.g., in Catalunya, but also in the rest of Spain and southern France, and on a smaller scale in Greece and Italy), eastern Europe, and Russia. People from Catalunya seem to prefer the taste of *L. sanguifluus* and even more the taste of *L. vinosus*. *Lactarius vinosus* is said to be most tasteful when greenish stains have developed on the pileus by the first frosts. In Catalunya, these species are commercially the second most important, after the *Tuber* P. Micheli ex F.H. Wigg. species. *Lactarius deliciosus* must have been popular since long in the Mediterranean region. A fresco from Herculaneum, a city that was buried during the same series of eruptions that destroyed Pompeii in the year 79, accurately depicts several basidiocarps of *L. deliciosus* together with pheasants (Ainsworth 1976). *Lactarius deliciosus* and relatives are being sold freshly or canned and are eaten roasted, prepared in a dish or in a cold salad. Eating *L. deliciosus* (and perhaps other species with orange latex) may cause the urine to be blood red, while this is not the case for red-milked species such as *L. sanguifluus* (Heim and Leclair 1950; Marchand 1971; Sterner and Anke 1995). This is by no means harmful. In a Russian study, the protein content of *L. deliciosus* was determined (Stankyavichene and Urbonas 1988). Nineteen amino acids, including all essential ones, were found, and these mushrooms were recommended as valuable food. The lipid content of *L. deliciosus* was shown to be only 1.02% (Ondrušek and Proštenik 1978). *Lactarius deliciosus* and relatives have also been used in several studies focusing on the concentrations of trace elements such as Cd, Co, Cu, Fe, Hg, Mn, Ni, Pb, and Zn in edible mushrooms (Falandysz et al. 2002; Isiloglu et al. 2001). For example, *Lactarius sanguifluus* was shown to accumulate easily several of these metals (a.o. Cd, Mn, Pb, and Zn), especially when growing close to a road (Isiloglu et al. 2001).

Some European *Lactifluus* species are edible and consumed in several countries. *Lactifluus volemus*, *Lf. oedematopus*, and *Lf. subvolemus*, for example, are popular species as they produce many large fruiting bodies that are easily identified and have an excellent taste (Van de Putte 2012). A recent Turkish report discusses two cases of acute pancreatitis caused by the consumption of *Lf. subvolemus* however (Karahan et al. 2016). The European large and white species, *Lf. vellereus*, *Lf. bertillonii* (Neuhoff ex Z. Schaef.) Verbeken, *Lf. piperatus*, and *Lf. glaucescens* (Crossl.) Verbeken, have an acrid taste and are only eaten in some regions, where they are

Fig. 9.4 Edible *Lactifluus* species on African markets: (**a**) cooked *Lactifluus* species for sale on Foumban market (Cameroon); (**b**) a local guide with a basket full of *Lactifluus* species (Foumban, Cameroon); (**c**) *Lactifluus* species for sale on Kigoma market (Tanzania); (**d**) *Lf. rubroviolascens* collected for consumption (Foumban, Cameroon); (**e**) cooked *Lactifluus* species (Foumban, Cameroon) (Photographs by E. De Crop)

parboiled or preserved with salt before consumption to remove the acrid taste (Heilmann-Clausen et al. 1998).

In African countries with woodlands and riparian forests, fungi, and especially EM fungi appear in great numbers at the beginning of the rain season. Mainly women and children go out in the forests to collect edible species, which are then sold at the local markets and along roadsides, either fresh, dried, or boiled (Fig. 9.4). Many *Lactarius*, *Lactifluus*, *Russula*, *Amanita* Pers., *Cantharellus* Juss., and *Termitomyces* R. Heim species are considered edible mushrooms (Härkönen et al. 2003). Milkcap species often found at the market are *Lf.* cf. *rubroviolascens* (R. Heim) Verbeken, *Lf. denigricans* (Verbeken and Karhula) Verbeken, *Lf. gymnocarpus* (R. Heim ex Singer) Verbeken, *Lf. albomembranaceus* De Wilde and Van de Putte, *Lf. densifolius* (Verbeken and Karhula) Verbeken, *Lf. edulis* (Verbeken and Buyck) Buyck, *Lf. gymnocarpoides*, *Lf. volemoides* (Karhula) Verbeken, *Lf. xerampelinus* (Karhula and Verbeken) Verbeken, and *L. kabansus* Pegler and Piearce (Rammeloo and Walleyn 1993; Verbeken and Walleyn 1999; De Kesel et al. 2002; Härkönen et al. 2003; Kinge et al. 2011; Sharp 2011, 2014).

Milkcap species are among the favorite edible mushrooms for local mushroom pickers in North America, and among them are several *Lactifluus* species. In Pennsylvania, for example, some locals go on "milkie mushroom" hunting trips, especially to collect milkcaps (Russell 2006). *Lactifluus* cf. *volemus*, *Lf. corrugis* (Peck) Kuntze and *Lf. hygrophoroides* (Berk and Curtis) Kuntze are the most famous ones, with *Lf.* cf. *volemus* recurrently being reported as the best and most flavorful milkcap (Peck 1885; Metzler and Metzler 1992; Roody 2003; Russell 2006; Lincoff 2010; Van de Putte 2012). Some authors also mention *Lactifluus gerardii* and *Lf. luteolus* (Peck) Verbeken as edible (Roody 2003; Bessette 2007), while only a minority likes to eat the milkcaps with peppery latex, such as *Lf.* cf. *piperatus*, *Lf.*

cf. *glaucescens*, *Lf. deceptivus* (Peck) Kuntze, *Lf. subvellereus* (Peck) Nuytinck, and *Lf. subgerardii* (Hesler and Sm.) Stubbe. Some authors even report some of these peppery tasting species as being poisonous (Bessette 2007). For other species, such as *Lf. allardii*, the edibility is unknown (Bessette 2007). Also famous is a *Hypomyces* (Fr.) Tul. and C. Tul. species (*H. lactifluorum* (Schwein.) Tul. and C. Tul.) that parasitises milkcaps and *Russula* species, turning them into "lobster mushrooms." The infected basidiocarps that show a red "crust" on the outside (the *H. lactifluorum* subiculum) and are white inside are considered a delicacy. Members of *L.* subg. *Russularia* are not often consumed, possibly due to their inferior taste, their fragile texture and small size. Additionally, the odor is rather unpleasant in some species (bug-like). A notable exception is the "candy caps," e.g., *L. rubidus* (Hesler and Sm.) Methven and *L. rufulus* Peck, which have a delightful sweetish and strong fragrance and are used to flavor desserts and cookies, but also smoked meats.

In Central America the tradition of eating wild fungi was already present centuries ago, in cultures like the Aztec and the Mayans. Today, the tradition persists in Mexico and Guatemala. Several milkcap species, like *L. indigo*, *L.* cf. *deliciosus*, *L.* cf. *salmonicolor*, *Lf. Deceptivus*, and *Lf.* cf. *volemus* are known to be sold on local and regional markets and to be collected for self-consumption (Kong Luz 1995; Montoya and Bandala 1996; Montoya et al. 1996; Comandini et al. 2012; Van de Putte 2012). Lobster fungus is also very popular in this area. However, south of these countries, in South America and the rest of Central America, the custom of eating wild fungi appears to be mostly absent (Boa 2004). To our knowledge no Russulaceae species are being consumed there, even though edible species do occur.

In Asia, members of *Lf.* sect. *Lactifluus* are known to be collected and eaten by local people of China, Japan, and Thailand (Wang et al. 2004; Le 2007; Lincoff 2010; Van de Putte et al. 2012). For example, in China, Yunnan province harbors the biggest number of ethnic minorities and most diverse habitats, and might be the place with the highest diversity of commercialized milkcaps in the country. Milkcaps are one of the most popular fungal groups collected, commercialized, and consumed by the local people there. These milkcaps are often sold freshly in summer (June to October), but dried products are also seen in supermarkets. Local people fry them with green chili. Wang (2000) reported 13 species of milkcaps from the local markets in Yunnan, accounting for 6.7% of the total number of commercialized fungi in the province (Wang and Liu 2002). The most common species among them are *L. deliciosus*, *L. hatsudake* Tanaka, and several species of *Lactifluus*, e.g., *Lf.* cf. *volemus*, *Lf.* cf. *hygrophoroides*, *Lf. echinatus* (basionym: *L. echinatus* Thiers), and *Lf.* cf. *gerardii*. These *Lactifluus* species turn out to be species complexes in molecular phylogenies (Stubbe et al. 2010; Van de Putte 2012; Van de Putte et al. 2016; Wang et al. 2015a). Therefore, the real number of commercialized milkcaps is even higher. Later, Wang et al. (2004) added *Lf.* cf. *rugatus* and the peppery *Lf.* cf. *piperatus* to the list of commercialized milkcaps in Yunnan. The Yunnan *Lactifluus rugatus* turned out to be a new species *L. tenuicystidiatus* X.H. Wang and A. Verbeken described by Wang and Verbeken (2006). The most recent molecular phylogeny shows that it represents a species complex including at least four species (Wang

et al. 2015a) with an additional edible species related to it, *Lf. subpruinosus* X.H. Wang. In central and eastern China, one of the most famous edible mushrooms is *L. vividus* X.H. Wang, Nuytinck, and Verbeken. This mushroom, which is called "pine mushroom," has passed under the names *L. deliciosus*, *L. akahatsu*, and *L. salmonicolor* in Chinese literature for many years and has only recently been formally named (Wang et al. 2015b). A paper published in 2019 investigates the chemical composition, antioxidant, and antihyperglycemic activities of *L. vividus*, but wrongly identifies the species as *L. deliciosus* (Xu et al. 2019). The study concludes that it is a valuable wild mushroom with high protein, carbohydrate, and dietary fiber contents, while low in fat and calorie, extensive unsaturated fatty acids contents, with negligible health risks about harmful metal elements (Xu et al. 2019). In total, the collected and consumed milkcaps of *L.* sect. *Deliciosi* in subtropical parts of China include at least five species: *L. akahatsu* Tanaka, *L. deliciosus*, *L. hatsudake*, *L. vividus*, and *L. subindigo*. Very recently Wang (2016) found that some dealers transport subalpine *L. pseudohatsudake* X.H. Wang and *L. hengduanensis* X.H. Wang to markets in central Yunnan and sell them using the same local names for *L. hatsudake* and *L. deliciosus*. In western Sichuan, where spruces grow, *L. deterrimus* is one of the most commonly collected edible mushrooms (our observation). Although this species also grows in northwestern China (Gansu and Qinghai Provinces), local people do not collect it. The same situation occurs with *L. deliciosus* in northeastern China (Inner Mongolia): it fruits luxuriantly in *Pinus sylvestris* var. *mongolica* forests, but is not touched by local people (our observation). They do not recognize it as an edible mushroom. Apparently people in different regions in China have different traditions to recognize milkcaps as culinary material or not.

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